Fungal Diversity
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An online resource for marine fungi

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Abstract
Index Fungorum, Species Fungorum and MycoBank are the key fungal nomenclature and taxonomic databases that can be sourced to find taxonomic details concerning fungi, while DNA sequence data can be sourced from the NCBI, EBI and UNITE databases. Nomenclature and ecological data on freshwater fungi can be accessed on http://fungi.life.illinois.edu/, while http://www.marinespecies.org/provides a comprehensive list of names of marine organisms, including information on their synonymy. Previous websites however have little information on marine fungi and their ecology, beside articles that deal with marine fungi, especially those published in the nineteenth and early twentieth centuries may not be accessible to those working in third world countries. To address this problem, a new website www.marinefungi.org was set up and is introduced in this paper. This website provides a search facility to genera of marine fungi, full species descriptions, key to species and illustrations, an up to date classification of all recorded marine fungi which includes all fungal groups (Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Mucoromycota and fungus-like organisms e.g. Thraustochytriales), and listing recent publications. Currently, 1257 species are listed in the marine fungi website (www.marinefungi.org), in 539 genera, 74 orders, 168 families, 20 classes and five phyla, with new taxa continuing to be described. The website has curators with specialist mycological expertise who help to provide update data on the classification of marine fungi. This article also reviews knowledge of marine fungi covering a wide range of topics: their higher classification, ecology and world distribution, role in energy transfer in the oceans, origin and new chemical structures. An updated classification of marine fungi is also included. We would like to invite all mycologists to contribute to this innovative website.

Keywords Fungal classification · marine fungi website · High-throughput sequencing techniques · Fungal diversity · Origin of marine fungi

Introduction

Marine fungi have been studied since the first record of the species *Sphaeria posidoniae* (= *Halotthia posidoniae*) on the rhizome of the sea grass *Posidonia oceanica* in Algeria by Durieu and Montagne (in Montagne 1856), but as yet there has been no webpage to accommodate all of the information on these organisms. This review introduces the website, www.marinefungi.org which has been developed to provide an up-to-date compendium on marine fungi.

There have been various definitions as to what a marine fungus is, the generally quoted one is by Kohlmeyer and Kohlmeyer (1979): "obligate marine fungi are those that grow and sporulate exclusively in a marine or estuarine habitat". Jones et al. (2015) broadened this as they were of the opinion it was too narrow and they included marine derived fungi, as many are taxa isolated during bioprospecting for new secondary metabolites (Fenical and Jensen 1993; Fenical et al. 1998). Marine derived fungi are

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generally asexual morphs, isolated from a wide range of substrates, dominating off shore habitats (e.g. deep sea) and are a good source of natural products. Various studies around the globe recognise these as a core group of fungi that are repeateadly isolated from various substrata in marine habitats. The definition used in the present article is that of Pang et al. (2016b) who reviewed the use of the terms "marine fungi' and 'marine-derived fungi'. They proposed the following definition for a marine fungus 'any fungus that is recovered repeatedly from marine habitats, because: (1) it is able to grow and/or sporulate (on substrata) in marine environments; (2) it forms symbiotic relationships with other marine organisms; or (3) it is shown to adapt and evolve at the genetic level or be metabolically active in marine environments.

A recurring question that has often been posed is "how many marine fungi are there?" (Jones 2011b). It has been estimated that there are at least 1.5 million fungal species on earth (Hawksworth 1991), while Blackwell (2011) puts the figure as 5.1 million. Recently, Hawksworth and Lucking (2017) have reviewed data on fungal diversity based on new evidence on plant/fungus ratios, environmental sequences studies and indicate the figure 1.5 million was conservative. They suggest that the figure should be in the range 2.2 to 3.8 million. However, only 120,000 to 143,273 fungi have been described so far (Hawksworth and Lücking 2017; Wijayawardene et al. 2017b; Index Fungorum 2018), most of which are terrestrial. Many authors stress that marine fungi are poorly studied in comparison to the number of other marine microorganisms (Jones and Richards 2011; Raghukumar 2017). The documentation of circa 1200 species in 72 years of marine mycological studies is great compared with some 120,000 terrestrial fungi that were described over 200 years of study (Kirk et al. 2008). Tisthammer et al. (2016) also opine that very little is known about the global distribution and diversity of marine fungi, while Drake et al. (2017) predict that much of the fungal diversity occurs in anaerobic deep sediments. These include "the dark fungi", detected by next generation sequencing (NGS) techniques and which have never been observed in culture. Hassett et al. (2019), in exploring marine fungal diversity, discovered that only half of the known marine fungal species have a publicly available DNA locus, and hypothesized that this is likely to hinder accurate high-throughput sequencing taxonomic classification as the discipline advances. Greater effort is required to sequence all known marine fungi to enable the identification of unculturable and cryptic taxa.

All agree that fungi play a pivotal role in the marine ecosystem in the recycling of recalcitrant substrata, essential to marine food webs (Hyde and Jones 1988; O'Rorke et al. 2013), that they play a vital role as symbionts of marine and mangrove plants (Hyde and Lee 1998; Yarden 2014), are a source of various vitamins and sterols, and new bioactive compounds (Kagami et al. 2007; Ebel 2012; Raghukumar 2017). Many of these topics will be considered in greater detail later in this article. Marine fungi are an ecological assemblage that includes all classes of fungi from the zoosporic chytrids, ascomycetes (the largest group) and basidiomycetes (Kohlmeyer and Kohlmeyer 1979; Hyde et al. 1998; Pang and Jones 2012; Jones et al. 2015; Pang et al. 2016b; Raghukumar 2017). Various techniques are required to study such a diverse group of fungi and this has led to a polarization of views on the numbers of marine fungi (Vrijmoed 2000; Overy et al. 2019; also see below).

To establish an understanding of the marine occurring mycota, a wide range of techniques has been used for their documentation; collection of substrates at selected locations (Pang et al. 2016a; Overy et al. 2019), removal of discs of wood from marine pilings (Petersen and Koch 1997), exposure of timber test blocks/panels (Meyers and Reynolds 1960; Byrne and Jones 1974) and other materials (Jones and Le Campion-Alsumard 1970), pre-inoculation of fungi into wood blocks before their exposure in the sea (Panebianco et al. 2002), isolation of fungi directly from water or sediments (Damare and Raghukumar 2008) and analysis of traces in sections of rocks and other solid geological substrates from marine environments (Drake et al. 2017). Recently developed molecular techniques, such as high-throughput sequencing, have been developed to identify species in environmental samples (Hongsanan et al. 2018). No single method can give a total remit of the worldwide distribution of marine fungi or of the interactions between taxa. Panebianco et al. (2002) have shown that interactions between fungi can affect the sequence of fungi colonising wood in the sea. For example, four marine fungi (*Ceriosporopsis halima, Corollospora maritima, Halosphaeriopsis mediosetigera*, *Marinospora calyptrata* were inoculated into balsa test blocks and submerged in the sea for 2, 6, 9 and 15 months and their colonization by native marine fungi recorded. Control balsa test blocks were similarly submerged and were colonized by a succession of marine fungi. However, the pre-inoculated *C. maritima* and *H. mediosetigera* blocks were not colonized by native marine fungi until they had been in the sea for 6 and 9 months, respectively. In other words, the preincoluated test blocks suppressed the development of native species.

Various estimates of the number of marine fungi have been made: Jones and Mitchell (1996) put the figure at 1500, but these included many species that were inadequately described, or facultative species or synonyms of existing taxa. K. Schaumann (personal communication) estimated there are some 6000 marine fungi, but this figure included taxa isolated from Arctic ice. Schmit and Shearer (2003, 2004) listed some 600 mangrove taxa, but this figure also included facultative marine fungi and those growing on the aerial parts of mangrove trees. Jones et al. (2009) reported 530 marine taxa in 321 genera, which included 424 Ascomycota (251 genera), 94 asexual morphs (61 genera), and 12 Basidiomycota (9 genera). Currently, 1257 species are listed in the marine fungi website (www.marinefungi.org), in 539 genera, 74 orders, 168 families, 20 classes and five phyla, with new taxa continuing to be described. The above is an underestimate as the list includes only fully identified fungi, as many taxa are identified only to genus or even a higher-level taxonomical rank (Supaphon et al. 2017) while "the dark fungi" remain unaccounted.

Sequence data has enabled a more natural classification of the fungi to be developed (Hyde et al. 2013; Jones et al. 2015; Maharachchikumbura et al. 2016; Abdel-Wahab et al. 2017). The great leap in marine fungal numbers between 2009 and 2019 is accounted for by the inclusion of zoosporic fungi, marine yeasts, marine derived fungi and a broader interpretation in defining what constitutes a marine fungus (Jones et al. 2015; Pang et al. 2016b). Early estimates included only obligate marine fungi as defined by Kohlmeyer and Kohlmeyer (1979) which many marine mycologists considered too restrictive.

Jones (2011b) estimated that the number of marine fungi may be 10,000 to 12,500 species based on the substrates and geographical locations to be sampled. Topics suggested for indepth study include: 1. Unidentified species on a range of substrates; 2. Marine derived fungi isolated from soils, sand, and water; 3. Planktonic fungi; 4. Deep-sea fungi; 5. Endobiota of marine algae; 6. Uncultured fungi; and 7. Cryptic species. Kis-Papo (2005) reviewed the number of marine fungi and based on the assumption that only circa 5% of all fungi have been described, she predicted there are 10,000 marine fungi. All this data is based on direct microscopical observations which limits knowledge of unculturable taxa and the characterization and identification of cryptic species (O'Brien et al. 2005). This topic is considered in greater detail below.

Because of the limitations of microscopical studies mentioned above, other avenues have to be explored to determine total marine fungal biodiversity. Richards et al. (2012, 2015) identified 36 distinct and novel marine lineages, the majority (24) of which branched with the chytrids. Such studies vary widely in the diversity they document. Richards et al. (2012) concluded that fungi are present in low diversity and in low abundance in many marine environments, especially in the upper water column. However, such methods have their limitations in that they identify groups of organisms, and at most to generic level or species groups (Pang and Jones 2017).

Xu et al. (2017) in a culture-dependent and high-throughput sequencing study at a deep-sea hydrothermal vent site located at the Mid-Atlantic Ridge of the South Atlantic Ocean showed that the fungal community was dominated by members of the Ascomycota and the Basidiomycota. Several new phylotypes (28 of 65 fungal OTUs and 2 of 19 culturable fungal phylotypes) were identified to species level. Some phylotypes showed 100% similarity to taxa already reported from the marine environment: e.g. *Cladosporium sphaerospermum, Stachybotrys chartarum.* In that study, no sequences of the Chytridiomycota and the Mucoromycota were detected (Xu et al. 2017). Poli et al. (2018) identified 36 basidiomycete species that belong to six classes from various marine substrates from Mediterranean Sea using multi gene phylogenetic analyses. Xu et al. (2018) in a culture-dependent and high-throughput sequencing study of deep-sea sediments of a hydrothermal vent system in the Southwest Indian Ridge identified 14 fungal taxa, including 11 Ascomycota taxa (7 genera) and 3 Basidiomycota taxa (2 genera) based on internal transcribed spacers (ITS1, ITS2 and 5.8S) of rDNA. The Ascomycota dominated, accounting for 96.96% of the fungal community in the deep-sea hydrothermal area, while 36 OTUs belonged to unknown fungi.

So, have these techniques greatly expanded our knowledge of marine fungi and their distribution? *Malassezia*-like organisms have been recorded as true marine residents in environmental sequences recovered from habitats and locations, from polar regions to deep-sea vents (Edgcomb et al. 2011; Orsi et al. 2013; Amend 2014). *Malassezia* species are generally associated with skin diseases, such as dandruff and eczema and are generally difficult to culture axenically (Theelen et al. 2018). Amend (2014) therefore queried but accepted they were also true marine fungi. Bass et al. (2007), in a study on fungal diversity in deep-sea sediments of the Central Indian Basin at ~ 5000 m depth, concluded that most sequences clustered with known sequences of existing taxa with only seven divergent taxa. They noted the occurrence of Exobasidiomycetes and Cystobasidiomycetes for the first time from the deep-sea. Orsi et al. (2013), employing 18S rDNA amplicon pyrosequencing technique of deep-sea sediment samples, noted that many of the fungi detected were of known taxonomical groups but included many taxa not observed by isolation/microscopical examination of marine substrates. Massana et al. (2015) noted the prevalence of Chytridiomycota in seawater, the group accounting for 60% of the diversity of the rDNA sequences sampled in six near-shore sites in Europe, and in Arctic and sub-Artic coastal sites. Many others reported that the Chytridiomycota were the most common fungal group in marine habitats (Mohamed and Martiny 2011; Guo et al. 2015; Richards et al. 2015; Comeau et al. 2016; Hassett and Grading 2016; Hassett et al. 2017; Picard 2017). This differs from the observations of Tisthammer et al. (2016) working on marine water and sediments, in that chytrids were relatively rare in their study. It is surprising that chytrids are so common in these studies as numerically Jones et al. (2015) only list 21 species in 13 genera. Comeau et al. (2016) note that the Ascomycota, Cryptomycota and Basidiomycota contribute only moderate-to-minor diversity in their studies, while Tisthammer et al. (2016) regarded the Ascomycota and Basidiomycota the most abundant phyla in their sampling of marine water and sediments, with the three most abundant classes in their samples Pezizomycetes, Agaricomycetes and Eurotiomycetes. Poli et al. (2018) investigated the marine mycobiota mainly in the Mediterranean Sea, confirming the scarcity of Basidiomycota. At the subclass/ordinal level *Pezizales,* Hymenomycetidae and *Eurotiales* were the three most abundant. Of the marine Dikarya operational taxonomic units (OTU) clusters reported by Richards et al. (2015), most of the Ascomycota and Basidiomycota were yeasts and no sequences matched those of the marine taxa listed by Jones et al. (2015). Examination of fungi present in seawater by filtration technique developed by Iqbal and Webster (1973) for freshwater fungi, yielded few taxa (Fazzani and Jones 1977; unpublished data). However, sampling foam along the seashore yielded a variety of species trapped in the air bubbles of foam: *Corollospora* species dominate with many other species, *Lindra marinera, Asteromyces cruciatus, Nia vibrissa, Paradendryphiella arenaria* and *Torpedospora radiata* (Kohlmeyer and Kohlmeyer 1979; Tokura et al. 1982; Nakagiri 1989).

Of the 1257 taxa listed in the marine fungi website, none have been recorded at a single location. These fungi have been reported from a wide variety of substrates, habitats and geographical locations, are pelagic in the open ocean, occur as endobiotes or parasites of marine plants or were recovered from the deep sea. A further question with respect to the OTUs recovered from deep sea sediments and seawater is whether they are biologically functioning in that environment or present as dormant spores? So, in high-throughput sequencing studies are we expecting too much as most fungi require specific substrates to grow on.

The main purpose of this paper is to introduce the website marinefungi.org, to promote further study of marine fungi and document their worldwide distribution. We also present updated information on the numbers of marine fungi, their taxonomic groupings, recent techniques for studying their occurrence and distribution, suggest where further diversity might be encountered, their role in marine habitats and discuss the origin of marine fungi.

Fungal websites

The internet has become a major source for obtaining information worldwide. Over the last decades, fungal research has extended its horizon yielding a vast amount of data leading to the development of many websites dealing with different aspects of mycology. An integrated database, such as GenBank, provides us with a one stop solution where we can find DNA, protein, and articles. Similarly, there are some other websites which deal with specific mycological topics, and a selection is listed here:

http://www.mycobank.org/.
http://www.indexfungorum.org/.
http://www.theyeasts.org.
http://fungalgenera.org/.
http://www.marinespecies.org/.
http://www.mycology.net/index.html.
http://www.mykoweb.com/index.html.
https://www.gbif.org/.
http://www.sp2000.org/.
http://mycology.cornell.edu/funinfo.html.
https://www.nature.com/omics/index.html.
https://www.sanger.ac.uk/resources/downloads/fungi/.
http://www.fgsc.net/.
http://www.facesoffungi.org/.
https://www.genome.jp/.
http://www.lias.net/.
http://www.fungi.com/.

Very few of these websites specifically deal with marine fungi, while others are not open access portals such as Marine Lit (http://pubs.rsc.org/marinlit/, got to May 2017) and Dictionary of Natural Products (http://dnp.

chemnetbase.com/faces/chemical/ChemicalSearch.xhtml). The site 'omics tools' can be utilized as a beginning stage to get to required databases (https://omictools.com/) and can be a stepping stone in combining mass spectra data for comprehensive networking studies. The database (http://fungalgenera.org/) provides a classification and notes on all genera of fungi, including marine fungi (Wijayawardene et al. 2017b). However, all databases cited above are biased towards terrestrial fungi and there is currently no database exclusively for marine fungi. The database (http://fungi.life.illinois.edu/) is exclusively devoted to freshwater Ascomycota and provides general information, recorded reports of freshwater species, and offers an illustrated profile of selected fungi (Shearer and Raja 2007).

Another database is the Indian marine fungal database (www.fungifromindia.com/), which lists 233 strains of marine fungi found in India and is linked to MycoBank. The World Register of Marine Species (WoRMS) (www.marinespecies.org) plans to give a definitive and extensive documentation of names of all marine life forms. A further developed database "Faces of Fungi" (www.facesoffungi.org/) provides data of fungi and fungi-like life forms and includes fungal profiles, data on isolate status, chemistry, connections to sequences and culture collections, morphological and phylogenetic data, data of ecological and human significance (Jayasiri et al. 2015). Unfortunately, this database is still scantily populated, again with a predisposition towards terrestrial fungi.

Keeping the above in mind, we are launching an exclusive marine web portal "www.marinefungi.org". This web portal will allow readers to access the classification of all known marine and marine derived fungi, detailed descriptions with illustrations, and their worldwide distribution. These details will be updated on a regular basis as data becomes available. The site also documents recently published papers on marine fungi.

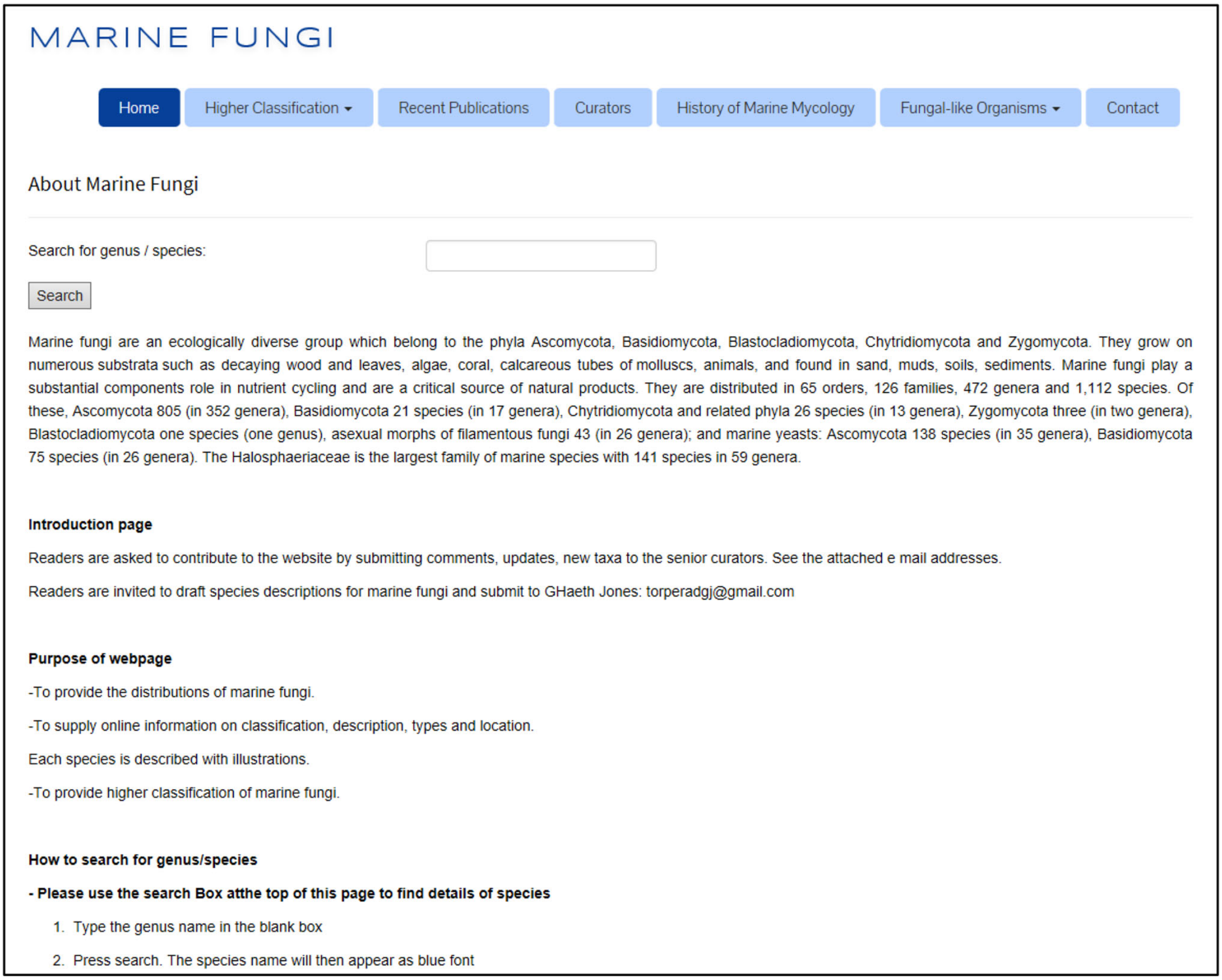
Need for a marine fungi website

Databases have a role in bringing together data scattered in a range of journals and this is particularly so for marine fungi where publications appear in journals in mycology, microbiology, marine biology, biofouling, botany, drug discovery and marine biomedicine and those on environmental issues. This is because marine fungi are an ecological assemblage and studies cover a broad spectrum of activities: taxonomy, molecular phylogeny, biochemistry, ecology, including biodegradation of recalcitrant compounds and their role in the food web in marine environments. Therefore, the primary objective of this website is to bring all this information together in a comprehensive database.

The purpose of the marine fungi webpage is to (1) provide data on the distribution of marine fungi, (2) supply online information on classification, species description, specimen types and distribution, with each species described with illustrations where possible and (3) provide a higher classification of all documented marine fungi. It also includes a list of recent publications and a history of marine mycology. In the last three decades, sequence-based phylogenetic studies have revolutionised the systematics of fungi, leading to a more natural classification of fungi. However, it has also caused a taxonomic revolution to a number of fungal groups which were classified traditionally based on morphology. This also applies to many marine fungi and this website can provide up-to-date information for their classification.

Operation of the marine fungi website

The website marinefungi.org includes a number of functions:



MARINE FUNGI

Home | Higher Classification ▾ | Recent Publications | Curators | History of Marine Mycology | Fungal-like Organisms ▾ | Contact

About Marine Fungi

Search for genus / species:

Search

Marine fungi are an ecologically diverse group which belong to the phyla Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota and Zygomycota. They grow on numerous substrata such as decaying wood and leaves, algae, coral, calcareous tubes of molluscs, animals, and found in sand, muds, soils, sediments. Marine fungi play a substantial components role in nutrient cycling and are a critical source of natural products. They are distributed in 65 orders, 126 families, 472 genera and 1,112 species. Of these, Ascomycota 805 (in 352 genera), Basidiomycota 21 species (in 17 genera), Chytridiomycota and related phyla 26 species (in 13 genera), Zygomycota three (in two genera), Blastocladiomycota one species (one genus), asexual morphs of filamentous fungi 43 (in 26 genera); and marine yeasts: Ascomycota 138 species (in 35 genera), Basidiomycota 75 species (in 26 genera). The Halosphaeriaceae is the largest family of marine species with 141 species in 59 genera.

Introduction page

Readers are asked to contribute to the website by submitting comments, updates, new taxa to the senior curators. See the attached e mail addresses.

Readers are invited to draft species descriptions for marine fungi and submit to GHaeth Jones: torperadgj@gmail.com

Purpose of webpage

-To provide the distributions of marine fungi.

-To supply online information on classification, description, types and location.

Each species is described with illustrations.

-To provide higher classification of marine fungi.

How to search for genus/species

- Please use the search Box atthe top of this page to find details of species

1. Type the genus name in the blank box
2. Press search. The species name will then appear as blue font

Home:

This provides a general introduction to the website, how to search for particular species and lists all the species currently described in the database. Descriptions can be accessed by typing in the generic name which brings up the species name(s) associated with that genus and clicking one of these leads to a detailed account of its classification, description and illustration. A key is provided for a genus with more than one marine species. This list is updated as curators submit detailed descriptions of marine fungi.

Genus	Species	Author
Corollospora	*maritima*	Werderm., Notizblatt des Königl. bot. Gartens u. Museum zu Berlin 8: 248 (1922)

Class	Order	Family
Sordariomycetes, Subclass Hypocreomycetidae	*Microascales*	*Halosphaeriaceae*

Synonymy:

Description

Corollospora Werderm., Notizbl. Bot. Gart. Berlin-Dahlem 8: 248 (1922)

Higher classification:
This is the central part of the website as it taxonomically lists all currently known marine fungi. This is updated on a regular basis and indicates species for which sequence data is available. The higher classification of the fungi follows currently accepted schemes (Wijayawardene et al. 2017b, 2018).

The classification is divided into seven parts and commences with an index to the major higher taxa and orders. The reader is directed to parts that list species under those higher order headings, for example part 1 is devoted to the Chytridiomycota, part 2 to the Basidiomycota and some orders of the Ascomycota while part 7 details marine yeasts belonging to both Ascomycota and Basidiomycota. In all cases individual species are listed under their families, orders and higher order taxa. For example:

CHYTRIDIOMYCOTA

1. *CHYTRIDIALES* Cohn, Jber Schles Ges Vaterl Kultur 57: 279 (1879), emend. MozleyStandridge et al., Mycol. Res. 113: 502 (2009)

Chytridiaceae Nowak., Akad Umiejetnosci Krakowie Wydzíat mat Przyród: 174: 191 (1878), emend. Vélez et al., Mycologia 103: 123 (2011)

Chytridium A. Braun, Betrach. Erschein. Verjüng. Natur.: 198 (1851)

1. *Ch. codicola* Zeller, Publ. Puget Sound Biol. Sta. Univ. Wash. 2: 121 (1918)

Recent publications:
This section provides all recently published papers on marine fungi abstracted from a wide range of mycological journals, currently mostly taxonomical.

Curators:
The database is serviced by specialists in marine mycology and is headed by Professor Gareth Jones aided by post-graduate students Vinit Kumar and Mark Galabon, who are responsible for updating the website. Others that contribute are listed along with their expertise and experience of working with marine fungi.

History of marine mycology:
This is planned in two sections, the origin of the International Marine Mycology Symposium (IMMS) which is held approximately every two years (completed) and a personal account of the history of marine mycology (work in progress).

Fungal-like organisms:
This is an early draft listing marine fungal-like organisms e.g. taxa in the Oomycota, once regarded as fungi. A curator is required to update the information and run this section of the website.

Contact:
This website handles a large amount of information and it is prone to minor errors. You can leave a message here reporting these so that we can revise the content of the website. Any suggestions/comments are also welcomed. Alternatively, you can send your comments to the e-mail torperadgj@gmail.com.

Review of current information on marine fungi

Traditional surveys of marine fungi

Marine fungi have been traditionally studied by collection, incubation, and examination of a range of substrates, each yielding its own characteristic group of fungi (Vrijmoed 2000; Sarma and Hyde 2001). Fungi are identified microscopically and illustrated with line drawings or photographs. Most studies have attempted their isolation and growth in culture, although this has not always been successful as in early studies e.g. *Orcadia ascophylli* (Sutherland 1915c), or more recently collected species, e.g. the wood inhabiting cleistothecial ascomycetes *Biflua physasca* and *Marisolaris ansata* (Koch and Jones 1989). Many marine fungi have been studied at the ultrastructure level in order to elicit morphological features that can be used in their classification, namely scanning and transmission electron micrographs of ascospores appendages (Johnson et al. 1984, 1987). Jones et al. (1983a) studied the fine structure of ascospores in *Corollospora* species and erected two new genera to accommodate two *Corollospora* species that did not group in the genus, namely: *Kohlmeyeriella* and *Nereiospora* and restored a third species to its original generic name *Arenariomyces*. Studies of the polar-unfurling appendages of *Halosarpheia* species also led to the characterization of similar genera, *Cucullosporella* and *Tirispora* (Alias et al. 2001; Jones et al.

1994). Each substrate generally tends to support different fungal species which may also differ according to the geographical location of the initial collection site: cold water species (Pugh and Jones 1986), tropical taxa (Jones and Pang 2012), or deep-water species (Dupont et al. 2009; Dupont and Schwabe 2016; Raghukumar 2017). Different substrates have also resulted in the adoption of various techniques for their study: observational, isolation and culture.

Observational studies

Driftwood, intertidal and trapped wood, timber sea defences, mangrove wood, leaves, seeds, fruits, decayed sea grasses, and algae are collected from the intertidal and sublittoral zones and returned to the laboratory for study. Samples are placed in clean plastic bags and examined with a dissecting microscope for marine fungi upon return to the laboratory, incubated in sterile humid plastic boxes and examined periodically for up to 2 months (Vrijmoed 2000; Abdel-Wahab et al. 2010).

Isolation studies

Marine fungi from seawater, sediments, deep-sea, and endobiotes have traditionally been discovered by the isolation of sporulating structures or plating out of subsamples of a substrate. A wide range of techniques have been used to isolate, grow on and obtain fruiting bodies of marine fungi (Vrijmoed 2000; Overy et al. 2019).

Lignicolous fungi

This group has been the most studied group of marine fungi, initially occurring on driftwood, trapped wood and test blocks/panels submerged in the sea (Meyers and Reynolds 1958; Byrne and Jones 1974; Panebianco 1994; Garzoli et al. 2015). Pilot studies were from temperate and cold-water locations (Hughes and Chamut 1971; Pugh and Jones 1986; Rama et al. 2014). Subsequently, a wealth of fungi has been reported from mangrove wood (Kohlmeyer 1968a; Abdel-Wahab et al. 2014, 2019; Devadatha et al. 2018a, b). Bugni and Ireland (2004) estimated that 10% of all known marine fungi were lignicolous species, which is a gross underestimate. Raghukumar (2017) stated that 190 marine fungi were recorded from driftwood and test panels exposed in the sea and about 300 species from decomposing mangrove wood.

Algicolous marine fungi

Algal samples are collected in sterile containers to prevent contamination and maintained cool as the thalli can quickly begin to decompose. Thalli need to be washed under running tap water to remove sediments and incubated in sterile containers. The first marine fungus from an alga was *Blodgettia bornetii* found in the filamentous green alga *Cladophora caespitosa* on the coasts of France and North America (Montagne 1856; Wright 1881). Kohlmeyer and Kohlmeyer (1979) listed 60 fungi from algal hosts that included 32 pathogenic on marine algae (31 ascomycetes and one asexual fungus) and 18 saprobic fungi (8 ascomycetes and 10 asexual fungi). Most recent accounts of algicolous fungi have been by Jones et al. (2012) and Raghukumar (2017). Algicolous marine fungi belong to Ascomycota, Basidiomycota, Chytridiomycota, Labyrinthulomycota and fungal-like taxa classified in Straminopiles. Basidiomycetes on algae include *Mycaurola dilseae* (initially described as an ascomycete) that infects *Dilsea carnosa* (Binder et al. 2006), and several marine yeasts e.g. *Leucosporidium scottii* occurred abundantly on brown seaweeds (Phaeophyta) particularly in the cooler months in southern British Columbia (Summerbell 1983). Bugni and Ireland (2004) suggested that circa 9% of marine fungi were isolated from marine algae. Zuccaro and Mitchell (2005) list 79 fungi from the brown alga *Fucus serratus*, while Jones (2011b) and Jones et al. (2012) consider this an underestimate with a potential for far greater diversity. Many of the taxa isolated from seaweeds are identified to genus level and these are generally marine-derived fungi. The application of sequence data has enabled better identification of fungi isolated from algae as the studies of Gnavi et al. (2017) and Garzoli et al. (2018) have shown for taxa isolated from the green seaweed *Flabellia petiolata* and the brown seaweed *Padina pavonica*.

Deep sea marine fungi

Deep sea environment is an extreme habitat that has the following characteristics: dark, high hydrostatic pressure, low temperature (except hydrothermal vents) low oxygen level, and low nutrient availability. The International Geophysical Year 1958 initiated studies of deep waters, with the German programme focusing on marine mycology, with two cruises of the fishery research ship "Anton Dohrn" to Greenland, Iceland and Ireland (Höhnk 1959). Baiting bottom samples with pollen (*Pinus montana*), seeds, and cellophane recovered "Phycomycetes" and asexual morphs at depths of 3425 m (Höhnk 1961). Roth et al. (1964) isolated fungi from water samples collected from the surface to 4500 m deep from Atlantic Ocean. Kohlmeyer (1968b, 1977) described the first fungi from the deep sea and Kohlmeyer and Kohlmeyer (1979) listed five marine fungi recovered from the deep sea: *Abyssomyces hydrozoicus*, *Bathyascus vermisporus*, *Oceanitis scuticella*, *Allescheriella bathygena*, *Periconia abyssa*. *Abyssomyces hydrozoicus* was described from chitin of a hydrozoan at a depth of 613 m deep while the other species grew on wood. Gaertner (1982) reported the presence of thraustochytrids from depths up to 3900 m in Atlantic waters.

During the last two decades, several studies have been carried out to document fungi from deep sea environments from all major oceans using both culture-based and metagenomic methods and have resulted in the recognition of deep-sea fungal communities (Damare and Raghukumar 2008; Raghukumar et al. 2010; Nagahama and Nagano 2012; Zhang et al. 2013a, b; Ruff et al. 2013; Takishita 2015). Raghukumar and Damare (2008) listed 38 fungal taxa from various substrata (chitin of Hydrozoa, calcareous shells, sediments, water and wood) collected from depths that ranged between 600 m in Atlantic Ocean to 10,500 m in Mariana Trench. Burgaud et al. (2009) obtained 97 fungal isolates (62 filamentous and 35 yeasts) from 210 hydrothermal samples. In a metagenomic study, Nagahama et al. (2011) obtained 35 phylotypes from methane cold-seep sites at 1080 m depth in Sagami Bay, Japan. Of the 35 phylotypes, 12 were early diverging fungi while the remaining 23 phylotypes belonged to Dikarya. Nagahama et al. (2006, 2008) also isolated a number of new yeasts from such environments e.g. *Rhodotorula pacifica* and *Dipodascus tetrasporeus* from deep sea sediments. Deep sea fungi showed abilities to produce antimicrobial compounds (Zhang et al. 2013), secondary metabolites (Li et al. 2007) and antifouling chemical structures (Zhang et al. 2014).

Fungi in sea water and sediment

Marine sediments cover two-thirds of the earth's surface and represent a huge reservoir of microbes. Sparrow (1937) in a pioneer study explored fungi from mud samples collected offshore at the Woods Hole Oceanographic Institute, Massachusetts. He collected samples from depths ranging between 18 and 1127 m deep. Isolated fungi were similar to those found in terrestrial habitats with *Penicillium* species in abundance, while species of the genera *Aspergillus, Cephalosporium, Trichoderma, Chaetomium, Alternaria, Cladosporium* and *Rhizopus* were less abundant. Species of obligate marine fungi, *Lulworthia* and *Ceriosporopsis,* were also isolated from marine sediments (Johnson and Sparrow 1961). Höhnk (1952, 1955, 1956) conducted several studies on fungi in beach sand, eulittoral sediments, and brackish muds, where he isolated several fungal-like taxa (Straminopiles) belonging to the genera: *Pythiomorpha, Pythiogeton, Pythium* and *Saprolegnia*. Similar experiments resulted in the isolation of hundreds of fungal isolates that mostly resemble those isolated from terrestrial habitats (Höhnk 1956,1959; Apinis and Chesters 1964; Roth et al. 1964; Meyers et al. 1967; Schaumann 1974; Moustafa 1975; Abdel-Fattah et al. 1977; Damare et al. 2006). A wide range of habitats have been investigated including salt marshes (Pugh 1962), sand (Nicot 1958; Steele 1967), mangrove soils (Swart 1963) and oil spills (Bovio et al. 2016), leading to the discovery of new taxa: *Dendryphiella arenaria* (= *Paradendryphiella arenaria*; Nicot 1958) and *Penicillium dimorphosporium* (Swart 1970). Previous studies incubated sediment or water samples with baits or isolated fungi using plating method, but such methods cannot determine whether the fungi were active in degradation of organic matter present in sediments or water samples or present as dormant spores.

Fungi in sea foams

A unique group of fungi is found trapped in sea foam and attached to sand grains. Kohlmeyer (1966) identified twelve marine fungi namely: *Alternaria* sp., *Arenariomyces trifurcatus, Corollospora lacera, C. maritima* (most common), *C. ramulosa, Paradendryphiella arenaria, Leptosphaeria australiensis, Lignincola laevis, Nereiospora comata, Halobyssothecium* (= *Passeriniella*) *obiones, Pestalotia* sp., and *Pleospora pelagica* from foam samples collected from sandy beaches of North Carolina, Canary Islands and Georgia, USA. Extensive sampling of foam samples has been carried out by Tokura et al. (1982) and Nakagiri (1989).

Marine-derived fungi

Marine-derived fungi as defined by Pang et al. (2016b) have been found on drift- and intertidal wood, sediments, seawater, marine animals (especially sponges and nematodes), deep sea, saprobes and endobiotes of mangroves, salt marshes plants and seaweeds (Janson et al. 2005). Hundreds of species and isolates have been accumulated in the literature and a considerable number of the isolated fungi have been screened for natural products and proven to yield new secondary metabolites.

Marine-derived fungi are mostly asexual morphs of ascomycetes and common genera are: *Aspergillus, Cladosporium, Fusarium, Gliocladium, Microsphaeriopsis, Paecilomyces, Penicillium, Phoma, Phomopsis, Trichoderma* and *Ulocladium* (Bugni and Ireland 2004). Marine derived fungi have been isolated from a variety of sources: 617 fungal isolates from coral reefs (Morrison-Gardiner 2002), 1000 isolates from sediments (Pivikin et al. 1999), 800 as endobiotes of mangroves (Pang et al. 2008) and 1743 as endobiotes and saprobes of mangroves and seaweeds (Schulz and Boyle 2005; Schulz et al. 2008). Many of these strains did not sporulate, while others could only be identified to genus. Marine derived fungi have also been isolated from anoxic environments. Jebaraj et al. (2010) analysed fungal diversity in samples from the oxygen minimum zone (OMZ) of the Arabian Sea and obtained 26 cultures that could be assigned to the Basidiomycota, predominantly Pucciniomycotina (five cultures) and Pezizomycotina of Ascomycota (21 cultures). Araujo and Hagler (2011) documented yeasts found in sediments in 8 Brazilian mangroves, *Kluyveromyves aestuarii* was absent at one site with heavy plastic bag pollution.

In the last update of the classification of marine fungi (Jones et al. 2015), 214 species of marine-derived fungi have been considered true marine fungi because they have been isolated from marine hosts or substrates more than once and their identity confirmed by molecular data. They included: 3 basidiomycetes, 210 ascomycetes and one mucoromycete. Specious genera represented by 5 species or more were: *Aspergillus* (35 species), *Penicillium* (29), *Arthrobotrys* (17), *Trichoderma* (9), *Cladosporium* (7), *Talaromyces* (7), *Acremonium* (6), *Fusarium* (5), *Manacrosporium* (5) and *Phoma* (5).

Sponges are a good source of marine-derived fungi. Höller et al. (2000) isolated 681 fungal isolates referred to the Ascomycota (13 genera), Mucoromycota (2) and asexual fungi (37) from 16 species of sponges collected from temperate, subtropical, and tropical regions. Members of the following genera *Acremonium, Arthrinium, Coniothyrium, Fusarium, Mucor, Penicillium, Phoma, Trichoderma*, and *Verticillium* were frequently isolated from sponges, however, dominant genera are different from one host or location to another (Jones 2011a). Morrison-Gardiner (2002) isolated 208 fungal isolates from 70 sponge samples collected from Australian coral reefs with *Alternaria, Aspergillus, Cladosporium, Fusarium*, and *Penicillium* as the dominant genera. Bovio et al. (2018) described two new species: *Thelebolus balaustiformis* and *T. spongiae* from three Atlantic sponges, and reported great fungal diversity. Each sponge hosted a specific fungal community with more than half of the associated fungi being exclusive of each invertebrate.

Endolithic fungi

Endolithic fungi are considered a special category of rock transforming microorganisms and defined as those which are capable of boring into solid inorganic substrates. They include many species of Ascomycota, Basidiomycota, Mucoromycota and Chytridiomycota, but only a few of these species, such as *Aspergillus sydowii*, have been properly identified (Gleason et al. 2017a, b). The endolithic environment includes the pore spaces in shells and skeletons of living animals or of those buried in the sediments, in rocks and in the pores between mineral grains and is ubiquitous in all marine ecosystems (Golubic et al. 2005). Hyphae of endolithic fungi can penetrate calcium carbonate, silica and other inorganic solid substrates formed by living organisms and by geological processes (Kohlmeyer 1969b). Endolithic fungi cause significant bioerosion of many geological substrates over time and are involved in diseases of a number of commercially and ecologically important host animals in marine ecosystems, such as corals and bivalve molluscs (Golubic et al. 2005; Gadd 2007; Gleason et al. 2017a, b). Endolithic fungi include *Aspergillus sydowii* and *Penicillium avellaneum* in coral skeletons (Kendrick et al. 1982; Gleason et al. 2017a, b) and *Fusarium solani* reported from turtle egg shells (Sarmiento-Ramirez et al. 2016).

Environmental sequencing surveys: high-throughput sequencing techniques

High-throughput sequencing techniques have augmented our capacity to assess microbial eukaryotic diversity and related functions in microbial ecology (Peršoh 2015; Jayawardena et al. 2018; Xu et al. 2018). The use of molecular tools for identification of chytrid sequences originating from environmental DNA by reference to sequence databases (Hibbett et al. 2016) can overcome many limitations of traditional microscopic and culturing approaches. In this context, two key considerations are (i) there does not appear to be a universal genetic marker able to discriminate among distant taxa, and simultaneously provide adequate resolution to identify organisms at the species level (Hongsanan et al. 2018), and (ii) the current representation of Chytridiomycota, and especially parasitic chytrids, in sequence databanks is limited (Frenken et al. 2017). Although ITS rDNA regions are often used to examine species and strain-level fungal diversity, Vu et al. (2018) employed sequences of two nuclear ribosomal genetic markers, the Internal Transcribed Spacer and 5.8S gene (ITS) and the D1/D2 domain of the 26S Large Subunit (LSU), to generate DNA barcode data for ca. 100,000 fungal strains (Summerbell et al. 2007; Schoch et al. 2012; Jayawardena et al. 2018). However, 18S rDNA sequences give greater clarity in many fungal analyses (Freeman et al. 2009; Naff et al. 2013; Panzer et al. 2015; Tisthammer et al. 2016; Hassett and Gradinger 2016; Xu et al. 2016a, b; Hongsanan et al. 2018). Furthermore, it was shown the moderately-sized ($\sim$ 440 bp) V4 amplicons are able to resolve fungal sequences to at least the genus level, confirmed by manual BLASTn of taxonomic identifications (Comeau et al. 2016).

To extend the ecological coverage of chytrids, Comeau et al. (2016) conducted an in-depth analysis of fungal sequences within their collection of V4 18S rDNA pyrosequences originating from 319 individual marine (including sea-ice) libraries generated within diverse projects studying Arctic and temperate biomes in the past decade. In this study, almost all sample types were dominated by marine Chytridiomycota-like sequences, followed by moderate to minor contributions of Ascomycota, Cryptomycota and Basidiomycota. The species and/or strain richness was found to be high, with many novel sequences and high niche separation.

The high dominance of chytrids in Arctic sea-ice (93%) agrees with a recent 18S V2–V3 Alaskan study showing 70–95% chytrids among fungal sequences from land-fast ice and underlying marine sediments, identifying Mesochytriales, Chytridiales, Rhizophydiales and the Lobulomycetale*s* as the closest related taxonomic orders in their BLAST queries and phylogenetic estimates of the five most abundant operational taxonomic units (OTUs) from each month in ice and sediment (Hassett and Gradinger 2016).

In contrast, a recent meta-analysis by Tisthammer et al. (2016) focused on marine water and sediments and found that Dikarya were dominant and chytrids were relatively rare. However, their study was based upon only 56 samples from 33 sites, identified less than half the number of fungal sequences as the Comeau et al. (2016) study, and had a limited coverage of polar regions. They also targeted the small ~ 65 bp V9 variable region of the 18S rRNA gene and, consequently, greater than 50% of their 10,793 sequences remained unidentified. The V4 analysis with a larger dataset over a broad range of aquatic environments, with emphasis on planktonic and sea-ice systems, implies that chytrids may be more abundant than previously suspected and that aquatic fungi deserve renewed attention for their role in algal succession and carbon cycling.

One of the major constraints for the taxonomy of Chytridiomycota is a general lack of sequence data, especially parasitic species (or those described as such). A survey of key databases for fungal taxonomic assignment reveals that Chytridiomycota represent between 0.1 and 4% of the fungal sequences, while the number of parasitic species may be fewer than a few dozen. The use of culture independent molecular methods, e.g. single cell/colony/spore PCR (Ishida et al. 2015), as well as sequencing of bulk phytoplankton samples, will likely improve the representation of chytrids in future sequence databases (Frenken et al. 2017).

Clearly high-throughput sequencing and next generation sequencing techniques bode well for the characterization of marine fungal communities and the determination of their role in deep water habitats (Xu et al. 2016a, b, 2018; Hassett et al. 2019).

Classification of marine fungi

Marine fungi, as with all fungi, have traditionally been classified based on morphological features (Inui et al. 1965), however this does not lead to a natural scheme. Johnson and Sparrow (1961), in a detailed treatise of marine fungi, classified fungi in oceans and estuaries into four classes, i.e. 'Phycomycetes', 'Fungi Imperfecti' (asexual morphs), 'Ascomycetes' (Ascomycota) and 'Basidiomycetes' (Basidiomycota). It is now known that 'Phycomycetes' and 'Fungi Imperfecti' are not natural groups; 'Phycomycetes' included both fungi and fungus-like organisms (Adl et al. 2012), while 'Fungi Imperfecti' are asexual morphs of the Ascomycota and the Basidiomycota. Johnson and Sparrow (1961) provided a higher-level classification of the marine 'Ascomycetes' based on characteristics of spores (shape and septation). Such phenotypic classifications are highly subjective, and do not say much on the evolutionary significance of these characters. For example, Barr (1983) considered that trabeculate pseudoparaphyses to be important at the ordinal level in the classification of the *Melanommatales,* yet Liew et al. (2000) showed that they were not phylogenetically distinguishable from cellular pseudoparaphyses. Such classifications have over the past 30 years been replaced with those based on SSU and LSU rDNA sequence data, which has enabled construction of the evolutionary relationships of fungi and identification of morphological characters that are of evolutionary importance (Wijayawardene et al. 2017, b). Molecular based studies have also highlighted the polyphyletic nature of many genera e.g. *Halosarpheia* (Pang et al. 2003), *Ceriosporopsis,* and *Remispora* (Sakayaroj et al. 2011). Consequently, Jones et al. (2009, 2015) provided updated classifications of marine fungi based on results from recent phylogenetic studies. Phylogenetic analysis of SSU and LSU rDNA also enabled linking of asexual morphs with their sexual states (Shenoy et al. 2006; Abdel-Wahab et al. 2010; Seifert et al. 2011; Abdel-Wahab and Bahkali 2012). Thus, this has revolutionised the taxonomic placements of asexual fungi as demonstrated for the marine asexual genera *Hydea, Matsusporium, Molesporium, Moromyces*, and *Orbimyces* in the Lulworthiaceae, Lulworthiales, genera with no known sexual morphs (Abdel-Wahab et al. 2010). More recent studies have included the sequencing of a wider range of genes e.g. LSU, SSU, TEF1α, RPB2 and β-tubulin (Wanasinghe et al. 2017). Marine yeasts were included in the most recent classification treatise of marine fungi (Jones et al. 2015) and can be classified based on sequencing of the D1/D2 domain of the 28S rDNA. Morphological characters can still be useful for higher-level taxa. The classification in this paper follows Liu et al. (2015a, b, c), Wang et al.

(2015, b) and Wijayawardene et al. (2017a, b) with some updates.

Identification of species and genera based on sequence data has also been questioned especially when dealing with cryptic species. For yeasts, taxa are generally based on the sequence of the D1/D2 domain of the LSU rRNA gene and the nucleotide differences between closely related species. Kurtzman and Ribnett (1998), in a phylogenetic analysis of 26S D1/D2 nucleotide sequences, demonstrated that 12 substitutions (2%) to 20 substitutions (3.3%) differentiated between two closely related *Candida* species. Jeewon and Hyde (2016) have addressed the issue of the identification and demarcation of taxa and made a number (15) of recommendations, the key elements being: (1). Phylogenetic relationships of a novel taxon should include a comparison of at least ITS based phylogeny with a minimum of 4–5 closely related/similar taxa of the same genus, where available; (2). Regions of the ITS sequence (including 5.8S) analysed should be of a minimum 450 base pairs with $< 1\%$ position ambiguities and 3). For practical purposes, a minimum of $> 1.5\%$ nucleotide differences in the ITS regions may be indicative of a new species (for fast evolving introns of protein coding genes, a higher percentage in nucleotide differences is warranted).

Higher classification

The transition from a morphology-based to a phylogeny-based classification has advanced our knowledge on the phylogenetic diversity of fungi (Wijayawardene et al. 2017a, b) and more recently evolution (Hongsanan et al. 2017; Hyde et al. 2017; Liu et al. 2017a, b). From four phyla of fungi described in Alexopoulos et al. (1996), 18 are recognised by Tedersoo et al. (2018), of which at least 6 phyla have marine representatives (Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Glomeromycota, Mucoromycota) in the Kingdom Fungi based on molecular phylogenomic analyses of genome data and expressed sequence tags (Hyde et al. 2018; Tedersoo et al. 2018). In a more recent metabarcoding proteome analysis using whole-genomic information, Cryptomycota was also found to be related to the Kingdom Fungi (Choi and Kim 2017), but the phylogenetic positions of Neocallimastigomycota and Microsporidia were not stable from one study to another.

The major advance in the classification of the fungi was by Hibbett et al. (2007) which set a framework for studies into their taxonomy and lead to major taxonomical changes over the next 10 years. Currently, the arrangement of genera, families, orders and subclasses is progressing towards a natural classification (Wijayawardene et al. 2017a, b). These are notable for taxa at the class level Dothideomycetes (Hyde et al. 2013, Ariyawansa et al. 2014, Wijayawardene et al. 2014, 2018), Sordariomycetes (Maharachchikumbura et al. 2015, 2016), Agaricostilbomycetes, Atractiellomycetes, Classiculomycetes, Cystobasidiomycetes, Microbotryomycetes, Mixiomycetes, Pucciniomycetes Spiculogloeomycetes, Tremellomycetes, and Tritirachiomycetes (Liu et al. 2015a, b, c; Wang et al. 2015a, b; Zhao et al. 2018) and the subclasses Diaporthomycetidae (Senanayake et al. 2016, 2017, 2018), Savoryellomycetidae (Hongsanan et al. 2018), Lulworthiomycetidae (Dayarathne et al. 2018), Pleosporomycetidae (Schoch et al. 2006) and Xylariomycetidae (Senanayake et al. 2015).

For marine fungi, Johnson and Sparrow (1961) classified all zoosporic fungi and fungus-like organisms into 'Phycomycetes' and filamentous fungi mainly into 'Fungi Imperfecti' (Sphaeropsidales, Melanoconiales, Moniliales and 'Ascomycetes' (Plectomycetes, Pyrenomycetes, and Discomycetes). 'Ascomycetes' was further divided into Scolecosporae, Amerosporae, Didymosporae, Phragmosporae and Dictyosporae based on spore morphology. Increased efforts have been made in recent years for the collection of a number of marine fungi with unknown/problematic taxonomic positions and phylogenetic studies have since resolved their higher-level classification. For example, *Manglicola guatamalensis* was originally classified in the *Pleosporaceae*, *Venturiaceae* (Kohlmeyer and Kohlmeyer 1971) or *Hypsostromataceae* (Huhndorf 1994). A phylogenetic analysis of the 18S and 28S rDNA revealed the species was related to the *Jahnulales*, an order previously known for the freshwater genus *Jahnula* (Pang et al. 2002). Recently, Jones et al. (2015) reorganised the classification of the known marine fungi (filamentous, zoosporic and yeasts) into Ascomycota, Basidiomycota, Blastocladiomycota Chytridiomycota and Mucoromycota. For the major marine groups, the Ascomycota was subdivided into six classes (Dothideomycetes, Eurotiomycetes, Leotiomycetes, Lichinomycetes, Orbiliomycetes, and Sordariomycetes) with 943 species while the Basidiomycota was referred to three classes (Agaricomycetes, Exobasidiomycetes, and Ustilaginomycetes) with a total of 96 species (www.marinefungi.org). The most recent classification of marine fungi is found in "List of marine fungi logged in the marine fungi website" and "Marine yeasts Ascomycota and Basidiomycota" in the Appendix section

Ascomycota

Jones et al. (2015) listed a total of 943 marine Ascomycota (805 filamentous fungi in 352 genera), yeasts 138 species (in 35 genera), a huge leap from 424 species in Jones et al. (2009). This difference was mainly due to the inclusion of a number of fungi which occur both in the terrestrial and marine environments, such as *Aspergillus* spp., *Penicillium* spp. often listed as marine derived fungi, and yeasts.

Major lineages of marine Ascomycota include the orders Microascales (the Halosphaeriaceae), Pleosporales, Eurotiales and Saccharomycetales, among which the latter two orders constitute taxa mainly associated with seawater, sand/sediment, plant substrates and animals (Jones et al. 2015). Marine fungi in the order Pleosporales mostly belong to some well-known terrestrial genera, such as *Didymella*, *Leptosphaeria, Massarina* and *Phaeosphaeria*, while others are genera known only from marine habitats and with few species, suggesting marine Dothideomycetes may have evolved recently in the sea (Vijaykrishna et al. 2006; Jones et al. 2015; Liu et al. 2017a, b). This view is supported by the fact that many marine occurring Dothideomycetes maintain an active mechanism of spore dispersal, especially those occurring in mangrove environments (Suetrong et al. 2009), and Vijaykrishna et al. (2006) provide molecular clock evidence that marine Dothideomycetes evolved from terrestrial species.

A different character scenario is observed in the marine Sordariomycetes that also evolved from terrestrial ancestors (Vijaykrishna et al. 2006). An example is the family *Halosphaeriaceae* which was inferred to have evolved from a terrestrial environment (Spatafora et al. 1998) and is predominantly marine with 166 species occurring in 63 genera (Jones et al. 2015, 2017), many being monophyletic. Taxa in *Halosphaeriaceae* generally have deliquescing asci and diverse spore/spore appendage morphology and ontogeny, adaptations to dispersal/finding growth substrates in the marine environment (Jones 1994, 1995). Another order with exclusively marine taxa is the *Lulworthiales* (Kohlmeyer et al. 2000). Species of this order generally have filiform (filamentous) ascospores with many species found obligately on macroalgae or corals (Kohlmeyer et al. 2000, Campbell et al. 2005). Savoryellales, an order of aquatic fungi, was established to include *Savoryella, Ascotaiwania* and *Ascothailandia* (= *Canalisporium*) but only a few *Savoryella* species are marine (Abdel-Wahab and Jones 2000; Boonyuen et al. 2011). Other marine Sordariomycetes are either monotypic genera or belong to known terrestrial genera.

Molecular data has yielded many new lineages of marine fungi. Marine *Saccardoella* species were examined phylogenetically based on 18S, 28S rRNA and tef1 genes and found to be unrelated to the Sordariomycetes but formed a monophyletic clade close to the Dothideomycetes (Pang et al. 2013). A new genus, *Dyfrolomyces*, was introduced to accommodate the marine *Saccardoella* species and a new species *D. tiomanensis* in a new family *Dyfrolomycetaceae* (Pang et al. 2013) and a new order *Dyfrolomycetales* (Hyde et al. 2013). Jones et al. (2015) introduced the new order *Torpedosporales* (Hypocreomycetidae) with three new marine families: *Juncigenaceae, Etheirophoraceae* and, *Torpedosporaceae*, all with marine genera based on a combined analysis of the 18S and 28S rDNA genes. The terrestrial asexual morph genus *Falcocladium* formed the fourth family, *Falcocladiaceae* (Jones et al. 2014), and was not previously assigned to any family or order (Crous et al. 1994; Somrithipol et al. 2007). Thus, the study of marine fungi at the molecular level helped in broadening our ability to classify taxa from other habitats. *Tirisporella beccariana*, a species commonly found on fronds/rhizomes of the brackish water palm *Nypa fruticans*, was found to represent a new lineage with *Thailandiomyces bisetulosis* in the Diaporthales, based on a phylogenetic analysis of the 18S and 28S rDNA (Suetrong et al. 2015). A new family, *Tirisporallaceae*, was established to accommodate these two genera (Suetrong et al. 2015), and a third genus *Bacusphaeria* was subsequently included (Abdel-Wahab et al. 2017). *Lanspora*, an exclusively marine genus previously thought to have close phylogenetic relationship with the *Ophiostomatales*, was recently placed in the new order *Phomatosporales* based on analyses of the 18S, 28S and internal transcribed spacer regions of the rDNA (Senanayake et al. 2016) (www.marinefungi.org).

Basidiomycota As reported earlier, basidiomycetes are the least represented taxonomical group in marine ecosystems (Kohlmeyer and Kohlmeyer 1979; Pang et al. 2011; Jones and Fell 2012; Sakayaroj et al. 2012; Hattori et al. 2014; Poli et al. 2018). Jones et al. (2015) listed 21 filamentous marine basidiomycetes in 17 genera with 75 marine basidiomycete yeasts in 26 genera. These figures changed little 4 years later: 22 (17) and 80 (39) filamentous and basidiomycete yeasts, respectively. The greater number of yeast genera is due to a major phylogenetic revision of basidiomycetous yeasts by Liu et al. (2015a, b, c) and Wang et al. (2015a, b). These revisions resulted in the introduction of many new genera and families which also applied to marine yeasts, e.g. *Saitozyma, Solicoccozyma, Symmetrospora* and *Vishniacozyma* (Liu et al. 2015a, b; Wang et al. 2015a, b, c).

Generally, basidiomes of marine Basidiomycota are small, rarely greater than 5 mm in diameter and this has been attributed to the prevailing conditions in marine habitats with strong wave action (Jones 1982, 1988; Binder and Hibbett 2001). However, basidiomycetes with larger basidiomes, such as *Grammothele fuligo, Hyphoderma sambuci,* and *Schizophyllum commune,* have been reported from the petioles of brackish water palm *Nypa fruticans* (Loilong et al. 2012). A study of butt rot attack of the mangrove tree *Xylocarpus granatum* identified three new species of the genus *Fulvifomes* (*Hymenochaetaceae, Hymenochaetales*): *Fulvifomes halophilus, F. siamensis, F.*

Fig. 1 Stem/butt rot of *Xylocarpus granatum* trees with multi-branching and hollow trunks

xylocarpicola as the causative agents. *Fulvifomes* species have woody bracket basidiocarps with tubes, round pores, circa 4–6 mm diameter (Hattori et al. 2014). These *Fulvifomes* species cause extensive decay of the *Xylocarpus granatum* trees (Sakayaroj et al. 2012) (Fig. 1) and like other basidiomycetes possess lignolytic enzymes causing brown rot decay (Pointing et al. 1998, 1999; Bucher et al. 2004). While new marine Ascomycota are continuing to be described, few new basidiomycetes have been documented (www.marinefungi.org).

Blastocladiomycota and Chytridiomycota Jones et al. (2015) list few marine chytrids (27 species in 13 genera) and this is considered to be an underestimate bearing in mind sequence data from marine sediments, the deep sea and seawater (Hassett et al. 2017). In high throughput sequencing studies, representatives of the Chytridiomycota accounted for more than 60% of the rDNA sequences sampled in six near-shore sites around Europe (Massana et al. 2015; Richards et al. 2015). In Arctic and sub-Arctic coastal habitats, Chytrids have been described as the most abundant fungal group (Comeau et al. 2016; Hassett and Gradinger 2016; Hassett et al. 2017). Given the relatively high abundance of chytrid sequences recovered from the marine environment in comparison with recent descriptions of infections of marine diatoms by such parasites, there has been only full taxonomical descriptions for three marine representatives namely *Rhizophydium littoreum*, *Thalassochytrium gracilariopsis* and *Chytridium polysiphoniae* (= *Algochytrops polysiphoniae*) (Gleason et al. 2011; Ohtsuka et al. 2016).

Recent taxonomic studies on chytrids based on molecular phylogenies and zoospore ultrastructure were mainly conducted using isolates of saprobic chytrids (Letcher et al. 2008; Simmons 2011; Seto et al. 2017) which can be cultured on alternative substrates (e.g. pine pollen) instead of the far more complicated method of co-culturing host and parasites. Although there are a large number of described species of parasitic chytrids (Jones et al. 2015), only a few parasitic chytrid species have been sequenced and their phylogenetic positions clarified (Küpper et al. 2006; Karpov et al. 2010, 2014; Vélez et al. 2011; Lepelletier et al. 2014; Letcher et al. 2015; Seto et al. 2017).

There appears to be no new chytrids described since the list published by Jones et al. (2015), however, the advent of sequence data has enabled better resolution of their taxonomy. Three species previously classified in *Phlyctochytrium* and *Rhizophydium* have now been assigned to new genera: *Halomyces* (*H. littoreus* = *Rhizophydium littoreum*), *Paludomyces* (*P. mangrovei* = *Phlyctochytrium mangrovei*) and *Ulkenomyces* (*U. aestuarii* = *Phlyctochytrium aestuarii*) (Letcher et al. 2015). These three genera are assigned to a new family *Halomycetaceae* in *Rhizophydiales* (Letcher et al. 2015). The taxonomic assignment of *Chytridium polysiphoniae* has been in doubt for many years (Jones et al. 2015) and Doweld (2014) introduced a new genus *Algochytrops* to accommodate *A. polysiphoniae*. Many marine *Rhizophydium* species require isolation and sequencing to determine their taxonomic assignment (www.marinefungi.org).

Asexual filamentous marine fungi The first three asexual marine fungi were described from marine algae (Wright 1881; Cooke 1888). Sutherland (1916b) in a major article described eight asexual fungi that are saprobic on decaying fronds of the brown alga *Laminaria* growing along the coasts of Dorset and Orkney and other sites in UK. The new fungi were: *Alternaria maritima, Diplodina laminariae, Epicoccum maritimum, Fusidium maritimum, Monosporium maritimum, Paradendryphiella salina* (= *Cercospora salina*), *Sporotrichum maritimum,* and *Macrosporium laminarianum*. He carefully assigned them to their respective genera so that seven of them still carry their original names.

Barghoorn and Linder (1944) described two new genera and seven new species of asexual marine fungi namely: *Botryophialophora marina, Dictyosporium pelagicum, Diplodia orae-maris, Helicoma maritimum* (synonymized with *Zalerion maritima*), *Orbimyces spectabilis, Phialophorophoma litoralis,* and *Zalerion maritima.* Nilsson (1957) described *Dinemasporium marinum* from driftwood in Denmark. Moore and Meyers (1959) described the basidiomycete genus, *Nia*, as an asexual fungus. Meyers and Moore (1960) also described three new genera and one new species namely: *Cirrenalia macrocephala, Cremasteria cymatilis* (a rejected species), *Halosphaeriopsis mediosetigera* (= *Trichocladium achrasporum*) and *Humicola alopallonella* (= *Trichocladium alopallonella*). Johnson and Sparrow (1961) listed 26 species in 24 genera of asexual marine fungi. Kohlmeyer and Kohlmeyer (1979) listed 53 asexual marine fungi in 40 genera and that number increased to 60 species (40 genera) in the illustrated key to the filamentous higher marine fungi published by Kohlmeyer and Volkmann-Kohlmeyer (1991).

Jones et al. (2009) in the updated classification of marine fungi listed 94 asexual fungi in 61 genera. Abdel-Wahab et al. (2010) in a major publication revised the phylogeny of the genera *Cirrenalia* and *Cumulospora* based on SSU and LSU rDNA and erected eight new genera, four new species and made six new combinations. Abdel-Wahab and Bahkali (2012) reviewed asexual filamentous marine fungi and listed 117 asexual marine fungi in 82 genera. Of the 116 listed species, 59 were sequenced for one or more genes and their sequences are present in GenBank. Forty sexual/asexual connections have been established based on morphology, and 31 of those connections are supported by molecular data. The listed 117 fungi belong to Dothideomycetes (33 species), Eurotiomycetes (1), Leotiomycetes (3), Orbiliomycetes (15), Sordariomycetes (46), Pezizomycotina *incertae sedis* (18) and one species, *Allescheriella bathygena*, belongs to Basidiomycota. In the last update of the classification of marine fungi, Jones et al. (2015) listed 300 marine asexual filamentous taxa in 91 genera. They included the marine-derived fungi that are repeatedly isolated from marine hosts or substrates and identified to species level. The 300 species belong to Dothideomycetes (63 species), Eurotiomycetes (93), Leotiomycetes (7), Orbiliomycetes (24) and Sordariomycetes (72). The sexual morphs of the remaining species are unknown. Genera represented by 5 species or more are: *Acremonium* (13 species), *Arthrobotrys* (13), *Aspergillus* (47), *Cladosporium* (7), *Curvularia* (5), *Penicillium* (39), *Periconia* (5), *Phoma* (11), *Stachybotrys* (6), *Stemphylium* (5) and *Trichoderma* (12).

Several asexual fungi have been transferred to their sexual morph genera with the application of the International Code of Nomenclature for algae, fungi, and plants (ICN; McNeill et al. 2012). Two or more names for different morphs of the same species are no longer allowed (one fungus = one name). Examples are species of the genera *Halosigmoidea, Sigmoidea, Varicosporina* that have been transferred to *Corollospora*; *Moheitospora* to *Juncigena* and *Glomerulispora* to *Torpedospora* (Réblová et al. 2016). The marine fungi website (www.marinefungi.org) presently lists only 17 asexual morphs as there is no sequence data available to link them to their sexual morph: e.g. *Asteromyces cruciatus, Pycnodallia dupla* and *Sporidesmium salinum*. Many of these were described before molecular data was used and they need to be recollected and sequenced to determine their taxonomic placement. Furthermore, type material is no longer available or in poor condition, e.g. the marine fungi described by Barghoorn and Linder (1944). Other asexual morph taxa mentioned above are listed under their sexual morphs as sequence data is available for them.

Marine yeasts Jones et al. (2015) listed 213 marine yeasts in 61 genera, including taxa in the Basidiomycota and Ascomycota. Currently we list 220 species in 74 genera with representatives in 9 classes, 15 orders and 28 families. Thus, the number of marine yeasts has not increased dramatically over the past 4 years, but sequence data has fundamentally changed their taxonomic assignment. Liu et al. (2015a, b, c) and Wang et al. (2015a, b) have undertaken a major revision of the classification of basidiomycetous yeasts, especially the Agaricomycotina, Tremellomycetes, Pucciniomycotina and Ustilaginomycotina, previously based on physiological and biochemical characteristics, resulting in many genera being polyphyletic. This revision was based on the analysis of sequences of seven genes: three rRNA genes, namely the small subunit of the ribosomal DNA (rDNA), D1/D2 domains of the large subunit rDNA, and the internal transcribed spacer regions (ITS 1 and 2) of rDNA including 5.8S rDNA; and four protein-coding genes, namely the two subunits of the RNA polymerase II (RPB1 and RPB2), the translation elongation factor 1-α (TEF1) and the mitochondrial gene cytochrome b (CYTB). This study has seen the introduction of a number of new families: *Bulleribasidiaceae*, Malasseziaceae [classes = Tremellomycetes and Malasseziomycetes respectively], *Mrakiaceae, Piskurozymaceae, Sakakuchiaceae*, *Symmetrosporaceae*, and *Trimorphomycetaceae* (all Basidiomycota) and all with representative marine yeasts. New genera containing marine yeasts are *Bandonia, Cutaneotrichosporon, Hasegawazyma, Pseudohyphozyma, Saitozyma* [= reinstated], *Solicoccozyma, Sampaiozyma, Symmetrospora, Tausonia* [= reinstated], and *Vishniacozyma.* It would appear that such a revision of ascomycetous yeasts, i.e., Saccharomycotina, is warranted to address their phylogeny based on modern concepts. (www.marinefungi.org).

Ecological groups of marine fungi

Many marine fungi have been documented as the result of ecological studies, e.g. endobiotes, salt marsh and mangrove fungi (Jones and Pang 2012).

Marine fungal endobiotes

Endophytic fungi are defined as fungi that colonize host plant tissues without causing any obvious symptoms of disease (Schulz and Boyle 2005). They have been isolated from a wide range of plant hosts, including temperate conifers (Arnold 2007; Higgins et al. 2007), tropical trees and plants (Oses et al. 2008; Tao et al. 2008), lichens (Li et al. 2007a, b), terrestrial grasses (Sánchez Márquez et al. 2008). Marine fungi can also be isolated from a wide range of animals and plants, especially marine associated plants from salt marshes, mangroves, seagrass species and marine algae (Zuccaro et al. 2003, 2008; Raghukumar 2008; Sakayaroj et al. 2010, 2012; Suryanarayanan et al. 2010; Buatong et al. 2012; Jones et al. 2012; Supaphon et al. 2013, 2014, 2017; Hong et al. 2015; Doilom et al. 2017).

Researchers have been attracted to study fungal endobiotes due to their potential importance in ecology, which includes an array of benefits to their hosts, such as tolerance to heavy metals, increased drought resistance, reduced herbivory, defence against pathogens, enhanced growth and competitive ability (Saikkonen et al. 1998). Additionally, endophytic fungi, especially marine endobiotes, have currently been recognized as the most promising sources of novel natural products for their bioprospecting in medicine, agriculture and industry (Debbab et al. 2013; Wang et al. 2013; Pang et al. 2016a). In the last decade, secondary metabolites and, novel chemical structures, and a diverse array of compounds from marine and mangrove endophytic fungi have been discovered (Debbab et al. 2013; Wang et al. 2013; Pang et al. 2016a).

Most of the research of marine fungal endobiotes has been made in exploring their occurrence, diversity and species richness. A review by Sakayaroj et al. (2012) documented 52 species of mangrove plant hosts, marine associated plants, salt-affected land plants, seagrasses, as well as seaweeds, that have been investigated for the presence of endophytic fungi. Most of the early studies focused on the abundance and presence of fungi based on morphological identification. The use of rDNA sequence data has been helpful in comparing sequence divergence and taxonomic identities within phylogenetically referenced databases of recognized species (Arnold 2007). Recently, there have been several studies undertaken using rDNA sequences, especially the ribosomal rDNA regions, to identify the phylogenetic diversity of endophytic fungi from various marine and mangrove plant hosts (Alva et al. 2002; Sakayaroj et al. 2010; Xing et al. 2010; Xing and Guo 2011; Sakayaroj et al. 2012; Li et al. 2016; Supaphon et al. 2017).

So far circa 63 marine and mangrove plant species from 24 families have been investigated for fungal endobiotes (Sakayaroj et al. 2012; Mata and Cebrián 2013; Panno et al. 2013; Shoemaker and Wyllie-Echeverria 2013; Gnavi et al. 2014; Venkatachalam et al. 2015a, b; Li et al. 2016; Vohník et al. 2016; Supaphon et al. 2017; Doilom et al. 2017). One of the largest mangrove plant family *Rhizophoraceae* (*Bruguiera cylindrica, B. gymnorrhiza, B. parviflora, B. sexangula var. rhynchopetala, Rhizophora apiculata, R. mucronata, R. stylosa*) harbours a high diversity of endophytic fungi. Up to 2700 fungal strains have been documented from these hosts (Sakayaroj et al. 2012). Another large family of mangrove plants *Sonneratiaceae* (*Sonneratia alba, S. apetala, S. caseolaris, S. griffithii, S. hainanensis, S. ovata, S. paracaseolaris*) also constitutes as many as 637 endophytic fungi (Sakayaroj et al. 2012).

The number of studies of endophytic fungi from sea grasses have dramatically increased over the past few years. The occurrence and phylogenetic diversity of fungal endobiotes associated with the four major seagrass families (*Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Zosteraceae*) have been undertaken. The families *Hydrocharitaceae* and *Posidoniaceae* harbour the greatest number of fungi isolated, namely 258 and 286 strains, respectively. While the families *Cymodoceaceae* and *Zosteraceae,* yielded 141 and 119 strains, respectively (Mata and Cebrián 2013; Panno et al. 2013; Shoemaker and Wyllie-Echeverria 2013; Supaphon et al. 2013; Gnavi et al. 2014; Supaphon et al. 2014; Kirichuk and Pivkin 2015; Torta et al. 2015; Venkatachalam et al. 2015a, b; Subramaniyan et al. 2016; Vohník et al. 2016; Supaphon et al. 2017).

Fungi from marine algae and endomycobiota in seaweeds have been reviewed by Jones et al. (2012) and Suryanarayanan (2012). Fungi on algal hosts consist of saprobic, parasitic, endophytic, lichens and mycophycobionts (Kohlmeyer and Kohlmeyer 1979). Since seaweeds cover large areas of the sea floor and oceans, they can be expected to yield a wide variety of fungi (Jones 2011b). Endophytic fungi from marine macroalgae have been identified as a potential source of biologically active natural products and enzymes (Flewelling et al. 2013; Sarasan et al. 2017). Based on the present literature survey by Sarasan et al. (2017), the maximum proportion of bioactive compounds produced are from fungi isolated from brown algae, followed by red and green algae.

The identification of marine fungal endobiotes revealed a highly diverse taxonomic community. Most belong to the Ascomycota, and are dominated by the major classes: Dothideomycetes, Sordariomycetes, Eurotiomycetes and Leotiomycetes (Sakayaroj et al. 2012; Supaphon et al. 2017). Most endophytic fungi isolated are asexual morphs and are typical terrestrial lineages including the orders *Capnodiales*, *Eurotiales*, *Hypocreales*, *Pleosporales*, *Trichosphaeriales* and *Xylariales* (Sakayaroj et al. 2012; Supaphon et al. 2017). The predominant genera found as marine endobiotes from a wide range of hosts include *Acremonium, Aspergillus, Cladosporium, Fusarium, Penicillium, Pestalotiopsis, Phomopsis* and *Phyllosticta*. They have been mostly shown to dominate in terrestrial habitats from a wide range of hosts as well as in other marine sources, i.e. sediments, corals, sponges, sea fans (Zalar et al. 2007; Li and Wang 2009). Only a few reports documented the fungal endobiotes that are truly marine lineages. For example, *Corollospora angusta, C. intermedia, Dendryphiella salina* (= *Paradendryphiella salina*), *Emericellopsis minima, Lindra obtusa* and *Sigmoidea marina* (= *Corollospora marina*) have been observed as endobiotes of marine seaweeds (Zuccaro et al. 2003, 2004, 2008). Among these *Acremonium fuci* and *Corollospora* (= *Halosigmoidea* = *Sigmoidea*) *marina* were reported as new species. Moreover, *Corollospora angusta* was the dominant species described from the brown seaweed, *Sargassum* sp. (Hong et al. 2015). Mata and Cebrián (2013) and Torta et al. (2015) also reported a few marine species: *Trichocladium alopallonellum*, *Halenospora varia*, *Paradendryphiella arenaria, Lindra thalassiae* as endobiotes of the seagrasses *Halodule wrightii* and *Thalassia testudinum*, while *Lulwoana* sp. was found in the roots of *Posidonia oceanica*. Similarly, sequences of unidentified lulworthialean and aigialean species were also detected in roots of *P. oceanica* (Vohník et al. 2016).

In many cases, the endobiotes could be identified only at the ordinal or genus level, due to the use of only morphological identification as well as the lack of reference DNA sequences in the GenBank database for comparison. In three publications on mangrove fungal endobiotes an average of 87% were identified at genus level, while only of 41% were identified at species level (Xing et al. 2010; Xing and Guo 2011; Li et al. 2016). For sea grass endobiotes, an average of 77% of isolates were identified at generic level, while only 34% isolates were identified at species level. In addition, for seaweeds an average of 91% were identified at genus level, while only 32% isolates identified to species level (Table 1). Sakayaroj et al. (2010) and Supaphon et al. (2017) reported several unidentified hypocrealean and pleosporalean taxa from sea grass species that potentially may represent new taxa. This agrees with Gnavi et al. (2014) in which several potential new species belonging in the order Pleosporales were isolated from *Posidonia oceanica*. Additionally, Vohník et al. (2016) described a new monotypic lineage of pleosporalean species within the *Aigialaceae* associated with *P. oceanica* roots (www.marinefungi.org).

For a meaningful evaluation of their diversity in the marine environment, identification of endophyte isolates to ordinal or genus level is not sufficient. A greater effort is required to generate sequence data to support their precise identification, i.e. sequencing of their protein-encoding genes and multigene sequence analysis. Moreover, the culture-independent approaches, including the genome-based techniques using metagenomics, next-generation genome sequencing and phylogenomics approaches, will help to evaluate the diversity of fungal communities and the discovery of novel genes and metabolites.

The importance of culturomics is not disputed in this article, and this technique has been used to study the diversity of marine fungi. However, the fungal diversity resulted from isolation does not necessary represent true marine fungi, especially at the marine/terrestrial interface. NGS also suffers from the same pitfalls but this technique offers detection of minor populations, active populations and interactions between different microorganisms, the mentioned advantages of culturomics.

Marine pathogens

Most marine fungi are saprobes occurring on various substrates, while some form symbiotic associations with algae and some are pathogens of a wide range of organisms (Bauch 1936; Sparks and Hibbits 1979; Hatai 2012). Table 2 lists some examples of marine fungi that are regarded as parasites on various hosts, including seaweeds, salt marsh plants, mangrove plants, rhizomes of *Posidonia oceanica* and marine animals.

Table 1 Numbers of marine fungal endobiotes that can be fully identified to genus and species level

Substratum	Number of isolates fully identified to genus level	Number of isolates fully identified to species level	References
Mangrove plants			
	39/39 (100%)	17/39 (43.5%)	Xing et al. (2010)
	27/38 (71%)	12/38 (32%)	Xing and Guo (2011)
	33[#]/36[*] (91.7%)	17/36 (47.2%)	Li et al. (2016)
	Average = 87%	Average = 41%	
Seagrasses			
	14/16 (87.5%)	5/16 (31.2%)	Mata and Cebrián (2013)
	69/88 (78.4%)	58/88 (66%)	Panno et al. (2013)
	31/34 (91.2%)	7/38 (18.4%)	Shoemaker and Wyllie-Echeverria (2013)
	14/21 (66.7%)	5/21 (23.8%)	Gnavi et al. (2014)
	26/42 (62%)	4/42 (9.5%)	Sakayaroj et al. (2010)
	35/47 (74.5%)	15/47 (32%)	Supaphon et al. (2014)
	28/29 (96.6%)	27/29 (93.1%)	Kirichuk and Pivkin (2015)
	40/44 (91%)	10/44 (2.3%)	Venkatachalam et al. (2015a)
	25/32 (78.1%)	3/32 (9.4%)	Venkatachalam et al. (2015b)
	15/42 (35.7%)	25/42 (59.5%)	Subrmaniyan et al. (2016)
	68/81 (84%)	23/81 (28.4%)	Supaphon et al. (2017)
	Average = 77%	Average = 34%	
Marine seaweeds			
	30/31 (96.8%)	7/31 (22.6%)	Zuccaro et al. (2003)
	41/42 (97.6%)	15/42 (35.7%)	Zuccaro et al. (2008)
	56/72 (77.8%)	7/72 (9.7%)	Suryanarayanan et al. (2010)
	44/50 (88%)	30/50 (60%)	Hong et al. (2015)
	68/73 (93.2%)	25/73 (34.2%)	Venkatachalam et al. (2015a)
	Average = 91%	Average = 32%	

[#]Identified genus/species,* total species

Seaweed pathogens

Seaweeds represent the second largest source of marine fungi (Bugni and Ireland 2004; Schulz et al. 2008; Loque et al. 2010; Suryanarayanan et al. 2010; Godinho et al. 2013; see text on seaweed fungi above). Seaweed-associated fungi mostly include parasites, saprobes, or asymptomatic fungi (Bugni and Ireland 2004; Zuccaro et al. 2008; Loque et al. 2010; Suryanarayanan et al. 2010; Jones et al. 2012). The best documented seaweed parasites are *Spathulospora* species on the red alga *Ballia* (Kohlmeyer and Kohlmeyer 1979). The thallus of *Spathulospora* is crustose surrounding the algal host cells, bearing sterile and fertile hairs and trichogynes, the mycelium penetrating the host cell. Sometimes a single ascoma is born externally on a cell, the infecting mycelium confined to one algal cell. Of the six *Spathulospora* spp., three occur in the Pacific Ocean.

Phycomelaina laminaria is a member of the Sordariomycetes and parasitic on the kelps, *Laminaria* species and *Alaria esculenta*, forming black spots on the stems. New collections, isolation and sequencing is required to resolve the taxonomic position of *Phycomelaina* within the Sordariomycetes. Another genus found exclusively as parasites of algae is *Haloguignardia* (Lulworthiales) with five species (Kohlmeyer and Kohlmeyer 1979). Host taxa include the brown seaweeds *Cystoseira, Halidrys*, and *Sargassum* spp. Similarly, *Pontogenia* (Koralionastales) species (8 species) are all algal parasites occurring on a wide spectrum of hosts *Castagnea chordariaeformis*, *Halopteris scoparia*, *Padina durvillaei* (Phaeophyta), *Codium* spp. and *Valoniopsis pachynema* (Chlorophyta). The six *Chadefaudia* species (*Halosphaeriaceae*) are also known pathogens of various marine algae, but are not as host-specific as the other fungi mentioned above (Kohlmeyer and Kohlmeyer 1979). A well-documented pathogenic taxon is *Mycaureola dilsea* (*Physalacriaceae*,

Table 2 Pathogenic marine fungi and their hosts

Taxa	Host
Algochytrops polysiphoniae[b]	*Pylaiella littoralis*
Anthostomella sp.[r]	*Rhizophora mangle*
Atkinsiella panulirata[h]	Spiny lobster
Cercospora sp.[o]	*Rhizophora* spp.
Chadefaudia balliae[a]	*Ballia callitricha*
Chadefaudia gymnogongri[l]	*Curdiea*, *Gigartina*, *Gymnogongrus*, *Laurencia*, *Microcladia*, *Ptilonia* spp.
Chadefaudia marina[l]	*Rhodymenia palmata*
Chadefaudia polyporolithi[l]	*Polyporplithon* spp.
Cytospora rhizophorae[j]	*Rhizophora mangle*
Cytospora lumnitzericola[p]	*Lumnitzera racemosa*
Cytospora thailandica[p]	*Xylocarpus moluccensis*
Cytospora xylocarpi[p]	*Xylocarpus granatum*
Didymella fucicola[l]	*Fucus spiralis*, *F. vesiculosus*, *Pelvetia canaliculata*
Didymella gloiopeltidia[l]	*Gloiopeltis furcata*
Didymella magnei[l]	*Rhodymwnia palmata*
Didymosphaeria danica[l]	*Chondrus crispus*
Exophiala spp.[g]	Pathogens of fish
Fulvifomes halophilus[s]	*Xylocarpus granatum*
F. siamensis[s]	*Xylocarpus granatum*
F. xylocarpicola[s]	
Flamingomyces ruppiae[a]	*Ruppia marina*
Haliphthoros milfordensis[e]	Juvenile stages of lobster
Haloguignardia decidue[l]	*Sargassum daemelii*, *Sargassum* sp.
Haloguignardia irritans[l]	*Cystoseira osmundaceaI*, *Halidrys dioica*
Haloguignardia oceanica[l]	*Sargassum fluitans*, *S. natans*
Haloguignardia tumefaciens[l]	*Sargassum* spp.
Halotthia posidoniae[n]	*Posidonia oceanica*, *Cymodoce nodosum*
Koorchaloma galateae[m]	*Juncus roemerianus*
Labyrinthuloides haliotidis[b]	Juvenile abalone
Lagenidium callinectes[f]	Larvae of mangrove crab
Leptosphaeria avicenniae[l]	*Avicennia* spp.
Lindra thalassiae[l]	*Sargassum* sp. (also in turtle grass, *Thalassia testudinum*)
Lulworthia fucicola[l]	*Fucus versiculosus*
Lulworthia kniepii[l]	*Lithophyllum*, *Porplithon*, *Pseudolithophyllum* spp.
Massarina cystophorae[l]	*Cystoseira osmundacea*, *C. subfarcinata*
Mycosphaerella ascophyhlii	*Ascophyllum nodoasum*, *Pelvetia canaliculata*
Mycaureola dilsea[q]	*Dilsea carnosa*
Ochroconis humicola[g]	Fish
Orcadia ascophylli[l]	*Ascophyllum*, *Fucus*, *Pelvetia* spp.
Parvulago marina[a]	*Eleocharis parvula* (Urocystidales)
Pestalotiopsis juncestris[n]	*Juncus roemerianus*
Phycomelaina laminariae[l]	*Laminaria* spp., *Alaria esculenta*
Plectosporium oratosquillae[d]	Mantis shrimp
Pontogeneia calospora[k,l]	*Castagnea chordariaeformia*
Pontogeneia codiicola[l]	*Codium fragile, C. simulans*
Pontogeneia cubensis[l]	*Halopteria scoparia*
Pontogeneia enormia[l]	*Halopteria scoparia*
Pontogeneia padinae[l]	*Padina durvillaei*

Table 2 (continued)

Taxa	Host
Pontogeneia valiniopsidis[l]	*Valoniopsis pachynema*
Pontoporeia biturbinata[i]	*Posidonia oceanica*, *Cymodoce nodosum*
Pseudocercospora avicenniae[t]	*Avicennia marina*
Spathulospora adelpha[l]	*Ballia callitricha*
Spathulospora antarctica[l]	*Ballia callitricha*
Spathulospora calva[l]	*Ballia callitricha*
Spathulospora lanata[l]	*Ballia hirsute*, *B. scoparia*
Spathulospora phycophila[l]	*Ballia callitricha*, *B. scoparia*
Tetranacriella papillata[n]	*Juncus roemerianus*
Thalassoascus tregoubovii[l]	*Aglaozonia*, *Cystoseira*, *Zanardinia* spp.
Trailia ascophylli[l]	*Ascophyllum nodosum*, *Fucus* sp.
Trichomaris invadens[u]	Tanner crab
Scytalidium sp.[g]	Fish
Sphaeceloma cecidii[l]	*Cystoseira*, *Halidrys*, *Sargassum* spp.

[a]Bauer et al. (2007); [b]Bower (1987); [c]Doweld (2014); [d]Duc et al. (2010); [e]Fisher et al. (1975); [f]Hatai et al. (2000); [g]Hatai (2012); [h]Kitancharoen et al. (1994); [i]Kohlmeyer (1963a); [j]Kohlmeyer (1969c); [k]Kohlmeyer (1975); [l]Kohlmeyer and Kohlmeyer (1979); [m]Kohlmeyer and Volkmann-Kohlmeyer (2002); [n]Kohlmeyer and Volkmann-Kohlmeyer (2001a); [o]McMillan (1984); [p]Norphanphoun et al. (2018); [q]Porter and Farnham (1986); [r]Stevens (1920); [s]Sakayaroj et al. (2012); [t]Shivas et al. (2009); [u]Sparks (1982)

Basidiomycota) on the red seaweed *Dilsea carnosa* (Porter and Farnham 1986; Stanley 1992; Binder et al. 2006). Originally described as an ascomycete, but later studies confirmed it as a basidiomycete which can be found sporulating on *Dilsea* in September to October in temperate climates (Stanley 1992; Jones et al. 2012). Recent studies of pathogenic marine fungi on algae are few apart and are mainly taxonomic observations with only some being supported by sequence data (Inderbitzin et al. 2004; Binder et al. 2006; Gueidan et al. 2009; Pérez-Ortega et al. 2010; Taxopeus et al. 2011).

Zoosporic fungi and fungal-like organisms also cause disease symptoms on marine algae, especially phytoplankton (Raghukumar 1987; Küpper and Müller 1999; Gleason et al. 2012; Doweld 2014; Scholz et al. 2014b; Gutiérrez et al. 2016; also see section above on Blastocladiomycota and Chytridiomycota). One species frequently identified as parasitic on a broad spectrum of red algae is *Algochytrops polysiphoniae* (= *Chytridium polysiphoniae*) (Küpper and Müller 1999; Gleason et al. 2012; Doweld 2014).

Pathogens of salt marsh plants

Salt marshes represent coastal marine ecosystems that occur mainly in temperate and high-latitude estuaries (Allen and Pye 1992; Simas et al. 2001), low hydrodynamic and periodic tidal flooding conditions (Simas et al. 2001). A number of aquatic plants, such as *Spartina* spp., *Juncus roemerianus*, *Phragmites australis* and sea grass species of *Halodule, Thalassia* and *Zostera*, grow in such environments, and are the main sources of organic matter for fungi (Teal 1962; Christian et al. 1990; Newell et al. 1996; Van Ryckegem et al. 2006; Al-Nasrawi and Hughes 2012). Labyrinthulomycetes are reported to cause wasting diseases of *Zostera marina* and *Halodule writghtii* sea grasses with heavy losses (Sullivan et al. 2013). Two pathogenic basidiomycetes on maritime angiosperms are *Flamingomyces ruppiae* on *Ruppia marina*, and *Parvulago marina* on *Eleocharis parvula* (Urocystidales) (Bauer et al. 2007). Although a wide range of saprobic fungi occur on salt marsh plants such as *Spartina* spp., *Juncus roemerianus, Phragmites australis*, the parasitic fungi are known only from aerial shoots (Kohlmeyer and Volkmann-Kohlmeyer 2002). Kohlmeyer and Volkmann-Kohlmeyer (2001c) described 43 new species belonging to 14 new genera from the needle rush *Juncus roemerianus*, and all are saprobes of senescent standing culms and leaves.

The sea grasses *Posidonia oceanica* and *Cymodocea nodosum* support a number of ascomycetes that grow on their living rhizomes: *Halotthia posidoniae* and *Pontoporeia biturbinata* (Kohlmeyer 1963b). Generally, they are found commonly on washed up rhizomes along the Mediterranean coast (Cuomo et al. 1985; Suetrong et al. 2009; Zhang et al. 2013a, b; Jones et al. 2015). Further studies are required to determine the relationship between these ascomycetes and their hosts.

Mangrove plants

Many fungal pathogens of aerial parts of mangrove trees are documented, but few are known from submerged parts (Shivas et al. 2009; Norphanphoun et al. 2018). Butt rot of roots and lower parts of the mangrove tree *Xylocarpus granatum* have been shown to be caused by *Fulvifomes* species and is widespread in Thai mangroves (Sakayaroj et al. 2010; Hattori et al. 2014) (Fig. 1).

On animal hosts

Marine fungi also cause diseases of marine animals and plants, but this is a topic requiring greater investigation (Kohlmeyer and Volkmann-Kohlmeyer 2003; Gachon et al. 2010; Gleason et al. 2011; Jones 2011a). Crustacean species, fish and shell fish are the most frequently cited hosts for pathogenic marine fungi (Hatai et al. 2000; Hatai 2012). The substrates of animal origin consist of cellulose, chitin, keratin, and calcium carbonate with an organic matrix (Kohlmeyer and Kohlmeyer 1979; Alderman and Jones 1967; Jones 2011a). This is a well-researched topic because of the economic impact on commercial marine aquaculture facilities. Studies on zoosporic fungal-like parasites have been documented in a series of papers by Gleason et al. (2017a, b) and Collier et al. (2017), while Scholz et al. (2017a, b) consider the chytrid infection prevalence of marine diatoms. Le Campion-Alsumard et al. (1995) showed fungal hyphae in coral skeletons and soft coral tissue, while Porter and Lingle (1992) found thraustochytrids bore into mollusc shells. Marine fungi invade mollusc shells as endoliths (Golubic et al. 2005) and as pathogens causing shell disease (Alderman and Jones 1971). *Ostracoblabe implexa* was implicated in the debilitating disease of oysters in the UK (Alderman and Jones 1971). A number of fungi belonging to the genera *Alternaria, Aspergillus, Cladosporium, Fusarium, Phoma,* and species *Aureobasidium pullulans, Hormonema dematioides,* and *Phialophora bubakii*, have been isolated from corals along the coast of Bay of Bengal and the Arabian Sea (Raghukumar 2017), some of which have been implicated in coral diseases. Some of these form a constant association with living corals, pervading deep in coral skeletons. Black mat syndrome of the carapace of the tanner crab (*Chionoecetes bairdi*) has been attributed to *Paraphoma fimeti* (= *Phoma fimeti*) for a long time. Sparks and Hibbits (1979) investigated the invasive disease and reported that the fungus was probably fatal and significantly affected the crab population in Kodiak area of Alaska. The bleaching of corals and the role of fungi in colonizing such substrates warrants greater investigation.

Common fungi and fungal-like organisms that are pathogens of various cultured fish and shellfish are *Haliphthoros milfordensis* juvenile stages of lobster (Fisher et al. 1975), *Trichomaris invadens* in tanner crab (Sparks 1982), *Labyrinthuloides haliotidis* of juvenile abalone (Bower 1987, 2000), *Atkinsiella panulirata* from spiny lobster (Kitancharoen et al. 1994), *Lagenidium callinectes* in larvae of mangrove crab (Hatai et al. 2000) and *Plectosporium oratosquillae* in mantis shrimp (Duc et al. 2010), to name but a few. Pathogens of fish include *Ochroconis humicola*, *Exophiala* spp., and *Scytalidium* sp. (Hatai 2012).

Fungi on diatoms

Chytrid infections of marine microalgae and cyanobacteria, and diatoms, have only been considered in recent years (Scholz et al. 2014a, b, 2016a, b; Gutiérrez et al. 2016). In particular, marine planktonic diatoms such as *Pseudo-nitzschia pungens* (Hanic et al. 2009), *Chaetoceros, Thalassiosira* (Scholz 2015; Gutiérrez et al. 2016; Scholz et al. 2016a, b) and *Cylindrotheca closterium* (Elbrächter and Schnepf 1998; Scholz et al. 2014a, 2016a, b) as well as species of the genera *Skeletonema* (Gutiérrez et al. 2016), *Rhizosolenia, Bellerochea*, and *Leptocylindrus* (e.g. Scholz 2015) were identified as common host species for chytrids. Even in the marine microphytobenthos infections by chytrids were recently recorded, mainly affecting epipelic taxa of the order *Naviculales* (*Diploneis bombus, Navicula digitoradiata* and *Achnanthales* (*Ach. brevipes*), *Thalassiophysales* (*Amphora ovalis*) and *Fragilariales* (*Fragilaria striatula*) amongst others (Scholz 2015; Scholz et al. 2014a, 2016a). Therefore, the potential for the discovery and documentation of further marine chytrids in other hosts is high and may provide a better estimate of their numbers in the marine environment. Of the marine chytrid parasites of dinoflagellates identified so far, only one, *Dinomyces arenysensis*, is parasitic on the dinoflagellate *Alexandrium minutum* (Lepelletier et al. 2014). In the ocean, even though the presence of these parasitic fungi on planktonic and microphytobenthic diatoms has been reported (Elbrächter and Schnepf 1998; Hanic et al. 2009; Scholz et al. 2014a, b, 2016a, b), their impacts on marine diatom communities and in the food-web remain unclear (Wang and Johnson 2009; Gleason et al. 2011).

Chytrids are often considered to be highly host-specific parasites (Kagami et al. 2007). Our current knowledge of host range and chytrid specificity is greatly biased by the fact that morphological identification often does not provide enough resolution to identify chytrids (and sometimes also hosts) at the species level (Frenken et al. 2017). Cross-infection assays under laboratory conditions often expose an even more complex picture, with some chytrids infecting specific host strains only (e.g. Scholz et al. 2017a) and others are capable of infecting different species, and within single host species both susceptible and resistant strains occur as well (e.g. Lepelletier et al. 2014; Scholz et al. 2017a, b). In addition, laboratory test series with marine host-diatom and chytrid isolates indicated the potential of the diatoms to defend themselves against the infection by chytrid zoospores (Scholz et al. 2017a) as well as demonstrated a direct link between environmental stressors and host-susceptibility (Scholz et al. 2017b).

Distribution of marine fungi

Although marine fungi are worldwide in distribution certain taxa may be restricted geographically to the tropics, subtropics, temperate or polar waters (Hughes 1974, 1986; Hyde 1986; Hyde and Jones 1988; Schmit and Shearer 2003) (Fig. 2). Tropical marine fungi are known from the Atlantic, Indian and Pacific Oceans, from a wide range of substrates, with mangrove habitats supporting the greatest diversity (Schmit and Shearer 2003; Alias and Jones 2010; Pang et al. 2011). However, there is little overlap in fungal species from tropical (Fig. 2b) and temperate (Fig. 2a) regions (Jones and Pang 2012).

Substantial information is available on the distribution of mangrove fungi with Schmit and Shearer (2003) listing 625 species, but this also included terrestrial species. Currently, some 500 fungi are known from mangrove habitats on 69 mangrove plants, sediments and seawater, with data from 80 countries. Schmit and Shearer (2003) indicate that the mangrove fungi in the Atlantic Ocean (12–47: mean 25.6) are fewer in number in comparison to those from the Indian (12–64: mean 42.9) and Pacific (17–95: mean 44) Oceans (Schmidt and Shearer 2003; Jones and Abdel-Wahab 2005). It had been suggested that this is because the mangrove trees diversity is lower in the Atlantic Ocean than in the Indian and Pacific Oceans. Mangrove tree species in the Atlantic Ocean are few and are often mangrove fringe communities, often *Avicennia* species. For example, only three tree species are present in the Florida locations studied by Jones and Puglisi (2006). In contrast, only one mangrove tree species is found in Red Sea mangroves, when extensive collections were made (Abdel-Wahab 2005; Abdel-Wahab et al. 2014).

The greatest fungal diversity is in the Pacific Ocean and this reflects the intensity of study at these locations (Alias and Jones 2010; Pang et al. 2011). Kohlmeyer and Volkmann-Kohlmeyer (1989) opined that fungal diversity was dependent on the maturity of the mangrove trees, the nature of the host tissue, size of the mangrove forest and damage to the trees and the frequency of sampling (Jones 2000).

Many tropical fungi are unique to mangrove substrates (Table 3) or host-specific to the brackish water palm *Nypa fruticans,* e.g. *Aniptodera nypae, A. intermedia, Anthostomella nypae, Fasciatispora nypae, Helicascus nypae, Lignincola nypae, Linocarpon appendiculatum, Oxydothis nypae, Tirisporella beccariana,* and *Helicorhoidion nypicola*, to list but a few (Loilong et al. 2012).

Whether we can integrate observational documentation with high-throughput sequencing detection requires greater collaboration and selection of sampling locations. In broad terms there is a general agreement in the diversity to be found; Ascomycota is the dominant taxonomic group, while the Basidiomycota and chytrids are rare taxa (www.marinefungi.org). Both approaches detect fungi not documented by the other, therefore give a greater insight into the fungal diversity of the oceans.

Role of marine fungi in the web of the oceans

Energy fixed by primary photosynthetic producers in the oceans is channelled to various trophic levels to sustain biodiversity and ecosystem functioning. Microorganisms play a key role in regulating this energy flow (Fig. 3).

Marine fungi are one of the major components in marine food webs and occur as saprobes, endobiotes, parasites and mutualists. Figure 4 schematically represents such fungal activities in the marine ecosystem. Firstly, as saprobes they transform the detritus or organic matter that originated from plants, algae and animals into valuable nutrients for consumers. Such turnover of organic matter gears up energy flow to the higher trophic levels. Ageing improves the nutrient composition and digestibility of mangrove leaves, compared to freshly fallen ones with fungi contributing to this feed improvement (Raghukumar 2005).

By virtue of their ecological activities, marine fungi have the potential to play a major role in regulation of energy flow in marine ecosystems (Fig. 5). Fungi associated with living and dead organisms play various roles in energy transfer. Indeed, there is now sufficient evidence to show that fungi can affect energy flow in the oceans in many ways. A few representative examples from a vast amount of literature available are given in Table 4.

Symbionts

Mutualistic fungi ensure that the organisms they are associated with achieve optimal productivity in terms of energy. A highly diverse group of fungi distributed in various genera and orders, mostly found in terrestrial habitats, live as endobiotes in macrophytes and macroalgae and as symbionts in lichens (Gueidan et al. 2009; Sakayaroj et al. 2012, Table 4). However, their quantitative importance has been inadequately studied. Jones (2011b) is of the opinion that 6000 species of endobiotes of marine plants, seaweeds, and marine animals may occur.

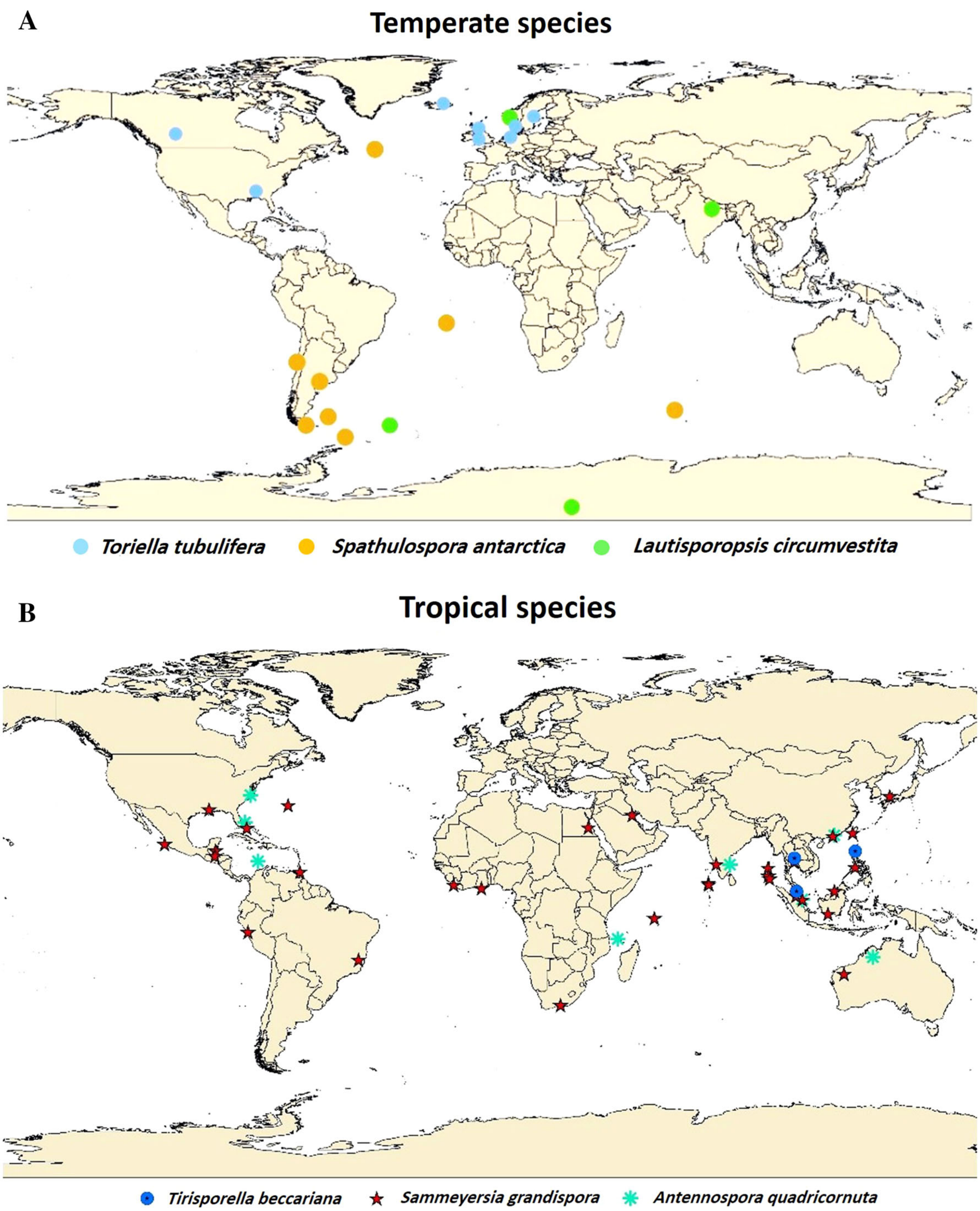


Fig. 2 World distribution of marine fungi: **a** temperate species. **b** Tropical species. **c** Cosmopolitan species

Parasites

As parasites of primary producers, fungi can cause leaching of dissolved organic matter (DOM) and decimation of populations of microalgae. This can seriously affect production of grazers, which constitute secondary production. Numerous examples of parasites in macroalgae and phytoplankton are now known (Raghukumar 2017; see section on pathogenic marine fungi). The importance of chytrids in phytoplankton, particularly in cold waters is now gradually coming to light (Hassett and Gradinger 2016; Gutierrez et al. 2016; Comeau et al. 2016).

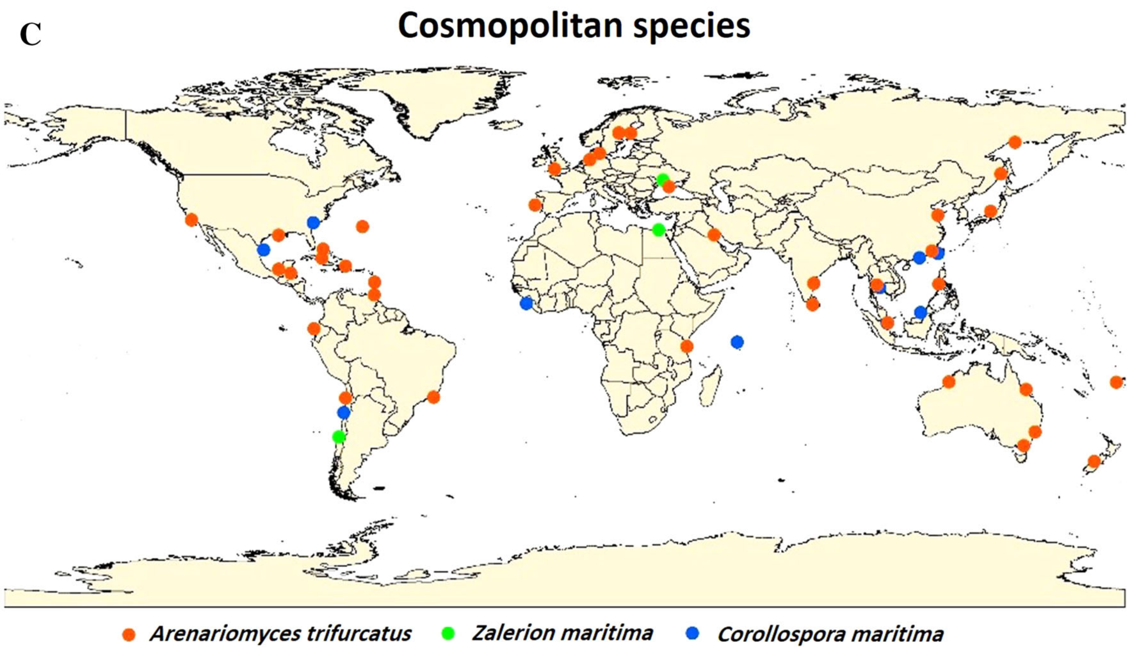


Fig. 2 continued

Table 3 Core mangrove fungi

Ascomycota:	*Savoryella lignicola* E.B.G. Jones et R.A. Eaton
Antennospora quadricornuta (Cribb et J.W. Cribb)	*Massarina velatospora* K.D. Hyde et Borse
Aigialus grandis Kohlm. et S. Schatz	*Verruculina enalia* (Kohlm.) Kohlm. et Volkm.-Kohlm.
Dactylospora haliotrepha (Kohlm. et E. Kohlm.) Hafellner	Asexual morphs:
Halorosellinia oceanica (S. Schatz) Whalley, E.B.G. Jones, K.D. Hyde et Læssøe,	*Bactrodesmium linderi* J.L. Crane et Shearer) M.E. Palm et E.L. Stewart
Kallichroma tethys (Kohlm. et E. Kohlm.) Kohlm. et Volkm.-Kohlm	*Hydea pygmea* (Kohlm.) K.L. Pang et E.B.G. Jones
Leptosphaeria australiensis (Cribb et J.W. Cribb) G.C. Hughes	*Periconia prolifica* Anastasiou (= *Okeanomyces cucullatus* (Kohlm.) K.L. Pang et E.B.G. Jones)
Natantispora retorquens (Shearer et J.L. Crane) J. Campb., J.L. Anderson et Shearer	Basidiomycota:
Neptunella longirostris (Cribb et J.W. Cribb) K.L. Pang et E.B.G. Jones	*Calathella mangrovei* E.B.G. Jones et Agerer
Saagaromyces ratnagiriensis (S.D. Patil et Borse) K.L. Pang et E.B.G. Jones	*Halocyphina villosa* Kohlm. et E. Kohlm.
Sammeyersia grandispora (Meyers) S.Y. Guo, E.B.G. Jones et K.L. Pang	

Saprobic fungi in detritus

Colonization of primary producers upon their death, caused either by parasites or natural means, is another aspect of energy flow. Saprobic growth of fungi in detritus is believed to improve their nutritional value and sustains the growth of detritivores. Some of the best evidence for the role of fungi in this process comes from detritus produced by coastal macrophytes, such as mangrove leaves and wood, salt marsh grasses and macroalgae (Table 4; Lee et al. 2017; Raghukumar 2017). A large part of dead *Spartina* is converted into fungal biomass (Newell and Porter 2000). Fungal biomass is also an important component of mangrove leaf detritus (Newell and Fell 1992). An energy budget study on mangroves from the mangrove estuary in north Brazil by Koch and Wolff (2002) has

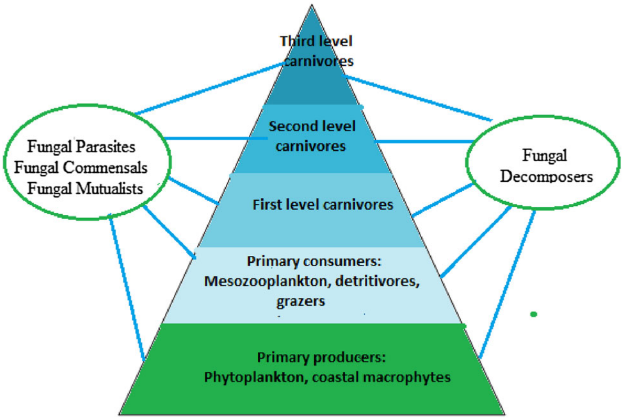


Fig. 3 Interactions of fungi with organisms in the marine trophic pyramid

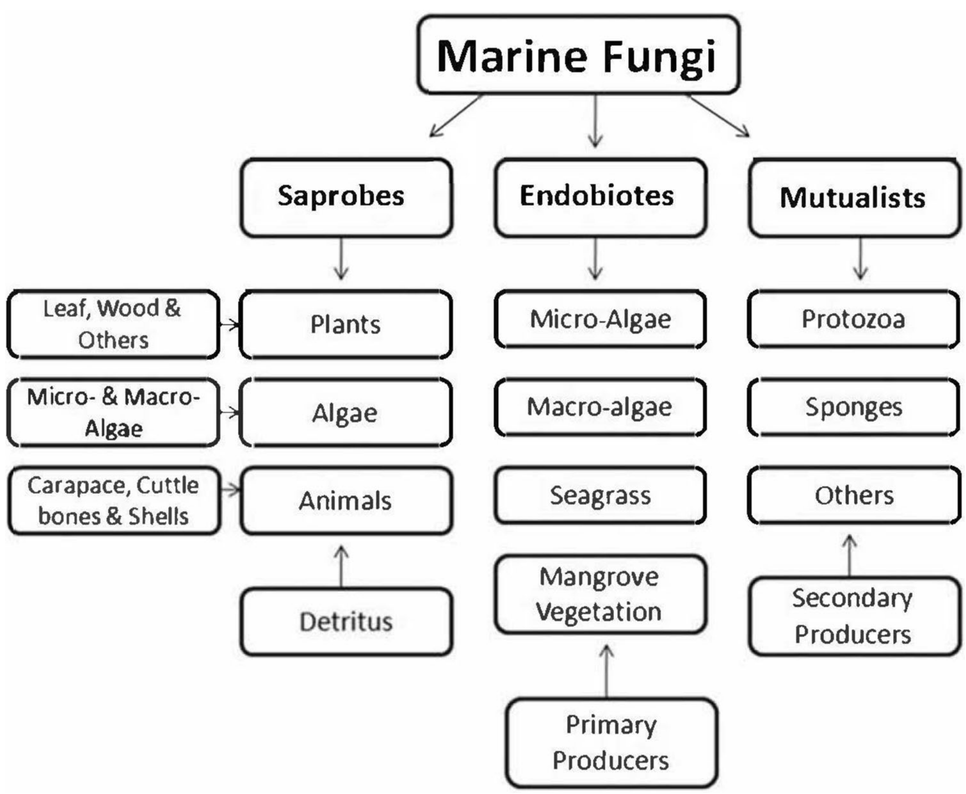
shown that the total leaf litter fall amounts to 13,700 kJ m^{-2} $year^{-1}$, corresponding to approximately 685 g of dry weight production m^{-2} $year^{-1}$. Nearly 75% of this is consumed by the crab *Ucides cordatus*. Ageing improves the nutrient composition and digestibility of mangrove leaves, compared to freshly fallen ones with fungi contributing to this feed improvement (Nordhansl and Wolff 2007). Enzymatic degradation improves digestibility and supplies essential nutrients to animal feeders. Release of DOM by the saprobic activities of fungi is important in channelling energy, as shown in the next section.

Saprobic fungi in DOM

Both living and dead marine macrophytes leach substantial amounts of dissolved organic matter (DOM) into surrounding waters, which is then converted to varying extents into microbial biomass. Conversion of DOM to microbial particulate organic matter (POM) makes energy available to detritivores and supports trophic levels of upper echelons. DOM likely supports the considerable numbers of yeasts in the water column (Fell 1967, 2012). However, their biomass and involvement in energy transfer is still inadequately known and deserves attention. Better studied are the biomass of Basidiomycota, Ascomycota and Labyrinthulomycetes in the oceanic water column. All these groups are now well known to rival bacteria in biomass (Gutiérrez et al. 2011, 2016; Raghukumar 2017).

Marine snow, formed by aggregation of dead phytoplankton and their exudates, dead zooplankton, empty larvacean carcases, pteropod feeding webs, and faecal pellets of marine invertebrates are important substrates for bacteria and fungi. The importance of fungi in colonizing marine aggregates, a long-neglected aspect, is now gaining further attention. At least two studies have shown that fungi are capable of densely colonizing marine snow and

Fig. 4 Schematic processes of interaction of organic matter and fungi in marine ecosystem



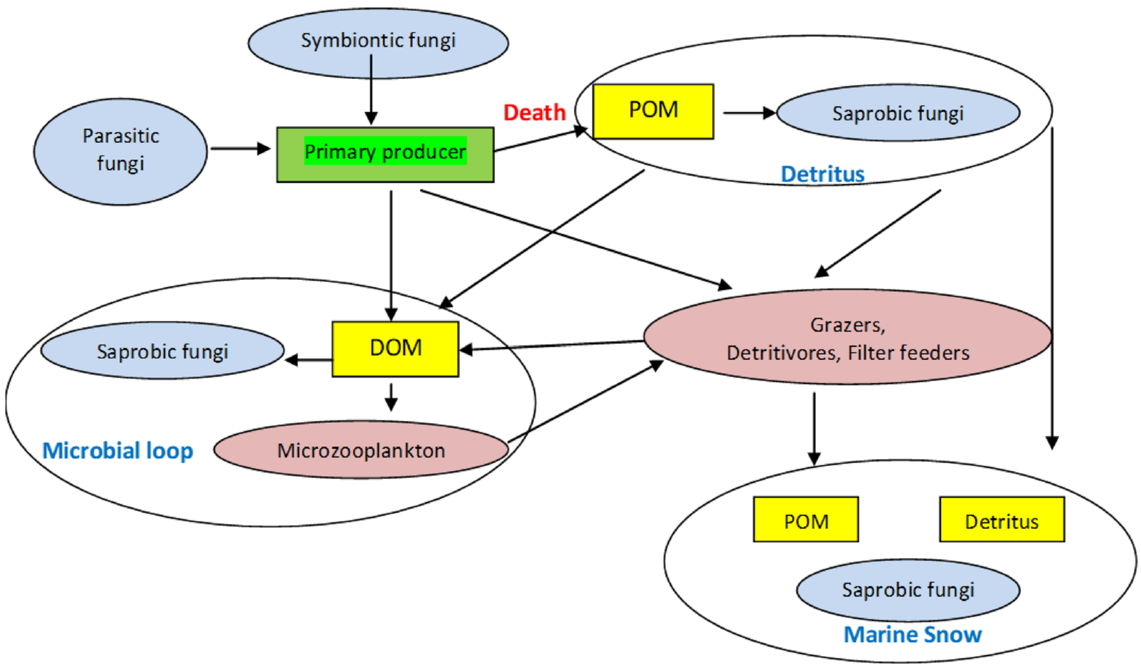


Fig. 5 Various mechanisms by which fungi influence energy transfer in the marine ecosystem

attaining biomass levels equal to that of bacteria (Gutiérrez et al. 2011; Wang et al. 2014a, b). The importance of Labyrinthulomycetes in colonization of marine snow is now well-established (Bai et al. 2018).

Fungi might be important in sinking of marine aggregates, the biological pump that transports organic matter to the deep-sea. Marine aggregates that sink to deeper waters from the surface harbour fungi. Using hybridization signals from CARD-FISH technique, Bochdansky et al. (2017) have recently shown that fungi and Labyrinthulomycetes accounted for ∼ 1/5 each of all eukaryotic microbes on particles obtained from bathypelagic marine snow at depths of 1000 to 3900 m in North Atlantic and Arctic waters. Biomass of Labyrinthulomycetes was approximately equal to that of prokaryote biomass, while the combined biomasses of fungi and Labyrinthulomycetes exceeded that of prokaryotes. Bochdansky et al. (2017) opine that 'eukaryotic microbes can no longer be considered sideshows to ecosystem processes of the deep sea'.

Fungi in animal nutrition

Fungi can mediate energy transfer to the trophic levels of grazers and detritivores through their growth in marine detritus. Salt marsh periwinkles can ingest 7% of naturally decayed leaves of the salt marsh grass per day and are capable of digesting 51% of the consumed detritus. Almost their entire nitrogen comes from fungi (Newell and Bärlocher 1993; Bärlocher and Newell 1994). Similar studies for mangrove and macroalgal detritus, and also for the oceanic water column are required. Very often, the biomass or saprobic abilities of marine fungi may not be commensurate with their importance in terms of energy transfer to other animals. For instance, Kohlmeyer et al. (1995) found that the actual decomposition of wood by marine fungi is minimal compared with that of teredinid borers in mangrove wood, because fungi are restricted to the outer layers of the wood due to high oxygen requirements. However, fungi, along with bacteria, are essential as 'preconditioners' of the wood surface and enable teredinid larvae to settle and penetrate the substrate (Lee et al. 2017).

It is now evident that fungi can contribute to substantial amounts of organic carbon at various levels of energy transfer in the oceans. A comprehensive study linking fungal biomass and productivity with various levels of primary and secondary production in the ocean pelagic is now needed to clarify their role in energy transfer mechanisms in the oceans. Such a study can draw inspiration of similar studies that have been carried out extensively in the *Spartina alterniflora* salt marsh grass ecosystem (Fell et al. 1984).

For a holistic understanding of the role of fungi in energy transfer, their productivity and biomass at every stage of energy transfer should be comprehensively studied. Gessner and Chauvet (1993) and Newell (2001) have provided methods to study fungal productivity based on ergosterol synthesis.

Table 4 Representative examples of fungi and fungal-like organisms to show their role in various energy flow mechanisms

Energy flow mechanism	Examples	Potential role of fungi	References
Through parasitic infection of primary producers	Diatoms *Skeletonema, Thalassiosira* and *Chaetoceros*	Chytrid sporangia contributed up to 4.2 mg C L^{-1}; zoospores contributed up to 10.1 mg C^{-L}	Gutiérrez et al. (2016)
	Diatom *Pseudo-nitzschia pungens*	Up to 15.9% of the bloom *comprising* 15 × 10^6 cells per litre of potential production infected by a chytrid and oomycete	Bates et al. (1998), Hanic et al. (2009), and Scholz (2015)
	Diatom *Coscinodiscus* sp.	Up to 500 cells L^{-1}, with up to 51% cells infected by *Lagenisma coscinodiscii*	Wetsteyn and Peperzak (1991)
	Filamentous brown alga *Pylaiella littoralis*	70% of the population can be infected by Oomycetes and chytrids	Marano et al. (2012)
Through biomass build up in detritus	Leaf detritus of *Rhizophora mangle* leaves from Florida Bay	0.17% of the dry weight biomass comprises fungi; roughly 121 dry kg of fungi in leaf detritus, presuming a conservative 712 dry kg/ha of leaves	https://www.fws.gov/verobeach/msrppdfs/mangroves.pd Newell and Fell (1992)
	Detritus of *Spartina alterniflora*	190 kg of fungi per hectare of salt marsh grass *Spartina*	Newell and Porter (2000)
Through utilisation of DOM and POM	Oceanic waters across the Pacific Warm Pool from Hawaii to Australia	DNA quantity of Basidiomycota was occasionally 20 to 100% that of bacteria	Wang et al. (2014a, b)
	Upwelling waters of the The Humboldt Current System in the South Pacific	Mycelial fungi contribute up to 40 µg C L^{-1}, often rivalling that of bacteria	Gutiérrez et al. (2011)
	Coastal and oceanic water column	Yeasts abundant and likely play an important role in DOM utilisation	Fell (2012)
	Subtropical coastal waters of China	Thraustochytrid biomass ranged from 5.27 to 36.20 *µ*g carbon L^{-1}, ofen equalling that of and bacterioplankton that ranged and 3.38 to 28.65 µg carbon L^{-1}	Liu et al. (2017a, b)
Through growth on marine snow	Arabian Sea	Labyrinthulomycetes contribute up to 27.0 µg C and 1.51 µg N L^{-1}	Raghukumar (2017)
	1000 to 3900 m in North Atlantic and Arctic waters	Combined biomasses of yeasts, mycelia fungi and Labyrinthulomycetes exceeded that of prokaryotes	Bochdansky et al. (2017)
As food for grazers and detritivores	Salt marsh grass, *Spartina alterniflora* along east coast of USA	Almost the entire nitrogen in standing, decomposed detritus may be present in the form of fungi and is ingested by the shredder gastropod *Littoraria irrorata* (salt marsh periwinkle)	Newell and Bärlocher (1993) and Bärlocher and Newell (1994)
	Calanus sinicus during winter in Tosa Bay of Japan	A maximum of up to 8% of the sequence compositions in the gut comprised *Aplanochytrium kerguelense*	Hirai et al. (2018)

Origin of marine fungi. When did they migrate to the sea?

It is postulated that the majority of life forms evolved in the sea, but this is unclear as far as fungi are concerned (Minic 2009). Fungi are presumed to have evolved in the Late Proterozoic (900-570 million years ago (MYA)) (Remy et al. 1994, 1995; Taylor et al. 1992, 1994, 1995, 1997, 2004). However, according to protein clock analyses by Heckman et al. (2001), fungi emerged in oceans approximately 1 billion years ago during the Proterozoic era of the Precambrian with deep branches such as the Chytridiomycota (Le Calvez et al. 2009). It is thus possible that the emergence and initial diversification of fungi occurred in the marine environment (Le Calvez et al. 2009). The earliest possible date when fungi became adapted to freshwater habitation is estimated at 390 MYA (Vijaykrishna et al. 2006). In contrast to this, most of the fungi described from the deep sea have relations to species reported in the terrestrial environment. This indicates that their recent arrival in marine environments might have occurred by either wind or terrestrial runoff (Raghukumar et al. 2010). Alker et al. (2001) and Zuccaro et al. (2004) have also isolated “so called terrestrial fungi” from marine habitats and suggested that they may have evolved to live in marine habitats. Most fungal structures have been poorly preserved as fossils. Fungal hyphae have very few unique morphological features and this makes it difficult to establish much of the fossil record for fungi (Berbee and Taylor 1993, 2010; Samarakoon et al. 2016). Marine fungi can be either mycetaen fungi or straminipilan organisms; hence, it is worth to consider the evolutionary origin of the two groups when considering the origin of marine fungi (Raghukumar 2017).

The Kingdom Fungi comprises the phyla Chytridiomycota, Neocallimastigomycota, Blastocladiomycota, Glomeromycota, Ascomycota, Mucoromycota and Basidiomycota and the subphyla Kickexellomycotina, Zoopagomycotina Entomophthoromycotina, Mucoromycotina (*incertae sedis*), which are osmoheterotrophic (Hibbett et al. 2007). Data indicates that the Kingdom Mycetae and the Kingdom Metazoa shared a common ancestor (Baldauf 2003; Adl et al. 2012). The Kingdom Mycetae and its closest relatives, the aphelids, the cryptomycota, and the microsporidia, which are collectively called Holomycota (Lara et al. 2010), are most closely related to nucleariids, a group of single-celled opisthokont amoeboid protists. It represents the basal, earliest diverging branches of Mycetae (Jones et al. 2011; Gleason et al. 2012; James et al. 2013; Karpov et al. 2014). Mycetaean fungi probably evolved from a phagotrophic life style around 760 MYA–1.06 BYA (Gingras et al. 2011; Beraldi-Campesi 2013). Sparrow (1960) and Karling (1977) suggested that early fungi may have moved onto "land" by first living in slime of microbes, with mats of streptophyte algae in soil near fresh-water habitats at the edges of rivers or ponds, the current habitat of *Rozella*, the Chytridiomycota, and Blastocladiomycota. It is believed that fungi with flagellated cells (Chytridiomycota) are the sister group of the remaining phyla of non-flagellated fungi (Mucoromycota, Glomeromycota, Ascomycota and Basidiomycota), indicating a single loss of the flagellum coincident with a shift to land (James et al. 2006). Molecular studies of chytrids are mostly of taxa from freshwater or terrestrial origin (James et al. 2006). There is no thorough evidence yet to show that ancestral chytrids were marine (James et al. 2006). However, recently, Bass et al. (2007) have recovered novel lineages of chytrids from environmental DNA from marine ecosystems and further studies should be conducted to find their phylogenetic relationships with other chytrids.

Did bitunicate and unitunicate ascomycetes make the transition to the marine environment about the same time or at different geological times? It is reported that different lineages of ascomycetes and basidiomycetes made independent transitions from terrestrial and freshwater to the marine ecosystem (Spatafora et al. 1998; Vijaykrishna et al. 2006; Jones et al. 2009, 2015; Pang 2012; Chang et al. 2015). Ascomycota were believed to have evolved from marine red algae (Sachs 1874; Bessey 1950; Chang et al. 2015). *Spathulospora* was considered to be the earliest, ancient fungus related to Laboulbeniomycetes and to represent the hypothetical ancestor of the ascomycetes (Kohlmeyer 1973a, b). This "Floridean hypothesis" is no longer accepted (Kohlmeyer and Kohlmeyer 1979; Kohlmeyer 1986; Vijaykrishna et al. 2006; Jones et al. 2009) as parasitism is usually considered reductive in evolution because it simplifies the nutritional apparatus of organisms (Demoulin 1974). Beimforde et al. (2014) and Pérez-Ortega et al. (2016) reported that ascomycetes diverged from basidiomycetes between 512 and 588 MYA ago, with a median value of 533 MYA, which is consistent with other recent studies (Lücking et al. 2009; Berbee and Taylor 2010; Oberwinkler 2012; Hibbett et al. 2014; Hyde et al. 2017). The occurrence of marine ascomycetes as sister clades to terrestrial or freshwater taxa and the number of ascomycete genera containing both terrestrial and freshwater species, along with marine taxa provide evidence for the migration of ascomycetes from land to the marine environment (Vijaykrishna et al. 2006). It also indicates that transition to the marine environment occurred many times and was not a one-off occurrence. Many terrestrial and freshwater genera have marine members, i.e., *Mycosphaerella, Passeriniella, Lophiostoma, Massarina, Trematosphaeria, Phaeosphaeria, Leptosphaeria*, and *Savoryella* species (Pinruan et al. 2002, 2007; Vijaykrishna et al. 2006; Jones et al. 2009; Suetrong et al. 2015; Sakayaroj et al. 2011). Sakayaroj et al. (2011) documented that bitunicate and unitunicate ascomycetes may have followed different evolutionary pathways, the former preferably adapting to mangrove environments and the unitunicate forms to oceanic conditions. The transition may have brought about morphological diversity and changes in response to environmental conditions (Spatafora et al. 1998; Vijaykrishna et al. 2006).

Recent studies with molecular clock analyses provide divergence time estimates of different marine lineages. The crown node and the stem node age should be taken into consideration when reviewing evidence from the molecular clock. The crown node age is affected by the model selection, species number used in the analysis and number of base pair differences between species (Gueidan et al. 2011; Prieto and Wedin 2013; Beimforde et al. 2014; Pérez-Ortega et al. 2016; Samarakoon et al. 2016; Zhao et al. 2016; Hongsanan et al. 2017; Hyde et al. 2017; Zhao et al. 2016, 2018). In addition, the use of a single fossil for the calibration leads to unpredictable results (Hug and Roger 2007). However, Hug and Roger (2007) suggested that the taxon sampling of the data set is less important for the age estimation.

The Sordariomycetes diverged circa 290–380 MYA (Middle Devonian to Late Carboniferous), while

Samarakoon et al. (2019), Beimforde et al. (2014) and Pérez-Ortega et al. (2016) place the crown group as in the Permian (308, 256, 260 MYA, respectively). The subclasses Lulworthiomycetidae, Hypocreomycetidae, Savoryellomycetidae and Xylariomycetidae evolved during the Early Mesozoic (250–290 MYA), while Sordariomycetidae and Diaporthomycetidae originated in the Middle Mesozoic (145–200 MYA) (Hyde et al. 2017; Hongsanan et al. 2017; Dayarathne et al. 2018). Many lineages of marine fungi: *Koralionastetales*, *Lulworthiales* and *Torpedosporales*, comprise only marine taxa (Jones et al. 2015). The orders *Koralionastetales* and *Lulworthiales* co-evolved with a divergent age of 289 MYA (Hongsanan et al. 2017) which represents the most basal group.

Thirty-five genera (of 58) of the *Halosphaeriaceae* are monotypic and found only in the marine environment e.g. *Kitesporella, Moana*, and *Ocostaspora* (Jones et al. 2015). *Halosphaeriaceae* species are well-adapted to an aquatic existence with early deliquescing asci and passive release of the ascospores, many of which have ascospore appendages that may aide dispersal and attachment (Jones 1994). The status of the Microascales (including the *Halosphaeriaceae*) and the marine order Torpedosporales is supported with a divergence time of 170–240 MYA (Hongsanan et al. 2017). Vijaykrishna et al. (2006) showed that *Halosphaeriaceae* evolved around 100 MYA and this has been confirmed by Dayarathne et al. (2018) e.g. 45–130 MYA. The vast diversity of *Halosphaeriaceae* suggests a recently evolved group with rapid speciation in response to a new environment. For example, circa 25 *Corollospora* species that are all marine oceanic species. Spatafora et al. (1998), and Campbell et al. (2003) provided data that the *Halosphaeriales* are secondary marine ascomycetes, derived from terrestrial ancestors. When considering the divergence of freshwater representatives, the *Halosphaeriaceae* are therefore secondary aquatic ascomycetes (Vijaykrishna et al. 2006). The divergent time for the marine *Tirisporellales* is put as 115 MYA with the order closely related to the *Pseudovalsaceae* in the phylogenetic tree (Hongsanan et al. 2017). Another order with marine, freshwater and terrestrial species is the Savoryellales with a stem age of 140 MYA (Hongsanan et al. 2017; Hyde et al. 2017). Within the Xylariomycetidae, the family *Oxydothiaceae* has a number of marine/mangrove species and appear to have a more recent divergent time of 115 MYA. No data is available for other marine lineages in the Sordariomycetes. When considering the available divergence time estimates, *Koralionastetales* and *Lulworthiales* might be the earliest marine lineages among marine ascomycetes.

Bitunicate, marine ascomycetes belonging to the class Dothideomycetes have evolved several times from terrestrial counterparts with many distinct lineages (Suetrong et al. 2009). Phylogenetic analyses of four nuclear genes, namely, the large and small subunits of the nuclear ribosomal RNA, transcription elongation factor 1-alpha, and the second largest RNA polymerase II subunit, established that the ecological group of marine bitunicate ascomycetes has representatives in the orders *Capnodiales*, *Hysteriales*, *Jahnulales*, *Mytilinidiales*, and *Pleosporales* (Jones et al. 2009, 2015; Suetrong et al. 2009). Eighteen out of 28 clades of Dothideomycetes have marine representatives, indicating that different lineages of these fungi colonized the sea independently (Liu et al. 2017a, b). The most common among these were the families *Aigialaceae, Morosphaeriaceae, Trematosphaeriaceae*, and *Halojulellaceae*. Divergence times (crown age) for most orders of Dothideomycetes (20 out of 32, or 63%) are between 100 and 220 MYA, while divergence for most families (39 out of 55, or 71%) are between 20 and 100 MYA (Liu et al. 2017a, b).

Marine ascomycetous and basidiomycetous yeasts are fewer in number than their terrestrial counterparts and colonize a wide range of substrates: sea-grasses, seaweeds, free floating in the sea, sediments, and deep-sea coral (Am-In et al. 2008; Fell et al. 2011; Fell 2012). Divergence times for yeasts such as species of *Rhodotorula, Wallemia, Malassezia* and *Ustilago,* range from 250 to 500 MYA, all containing species known from the marine environment (Tedersoo et al. 2018). When they migrated/adapted to the marine milieu remains to be determined (Tables 5, 6).

Marine filamentous basidiomycetes occur on mangrove wood or timbers submerged, trapped or floating in the sea (boats, piling, sea defences), seaweeds, and maritime plants (Jones and Fell 2012; Sakayaroj et al. 2012). One of the changes that resulted from the migration from terrestrial to marine aquatic habitats is the reduction in the size of the basidiocarp, e.g. as in *Halocyphina villosa* and *Nia vibrissa* (Binder and Hibbett 2001). The other is the production of appendaged basidiospores, as in *Nia vibrissa* and *Digitatispora* species (Binder et al. 2006; Jones and Choeyklin 2008). Transformations leading to the evolution of these basidiomycetes probably involved a shift from terrestrial to periodically immersed to fully submerged substrates, loss of ballistospory, and evolution of appendaged spores and an enclosed fruiting body (Binder and Hibbett 2001). However, most of these studies have been conducted with mostly terrestrial representatives rather than those of marine origin, hence, a thorough analysis with all the marine representative fungal taxa is recommended.

Table 5 Divergent times for selected marine Sordariomycetes (after Samarakoon et al. 2016; Hongsanan et al. 2017; Hyde et al. 2017, Dayarathne et al. 2018)

Class/order/family	Divergent time (crown age, MYA)	Divergent time (stem age, MYA)
Sordariomycetes	320	340 (290–380)
Halosphaeriaceae	50–130	170–240
Lulworthiales	100–125	290
Koralionastetales	200	290
Torpedosporales	170–240	165 (130–250)
Tirisporellales	110	190 (130–250)
Savoryellales	115	140 (130–250)

Table 6 Divergent times for selected marine Dothideomycetes (After Liu et al. 2017a, b)

Family	Divergent time (crown age, MYA)	Divergent time (stem age, MYA)
Acrocalymmaceae	25 (8–45)	115 (70–155)
Aigialaceae	25 (8–45)	115 (70–155
Halojulellaceae	20 (6–35)	150 (110–185)
Halottiaceae	55 (20–109)	185 (135–135)
Pleosporaceae	50 (25–70)	90 (65–120)
Morosphaeriaceae	95 (65–130)	145 (110–180)
Salsuginaceae	2 (0–2)	165 (85–180)
Testudinaceae	95 (55–140)	150 (100–200)
Trematosphaeriaceae	65 (35–90)	90 (60–120)

Prospecting for novel chemical structures

Endobiotes of marine plants and seaweeds have been a rich source of novel natural products for bioprospecting in medicine, agriculture and industry (Saikkonen et al. 1998; Debbab et al. 2013; Wang et al. 2013; Pang et al. 2016a).

Marine fungi gained great interest for their natural product productivity and structural diversity. Researchers have found the same marine fungal species recovered from different locations are able to produce different metabolite profiles but the rate of re-isolation has recently increased. Until 2002, there were 272 newly discovered marine fungal natural products. This number has increased reaching 1120 by the end of 2010, roughly 100 new compounds being discovered on a yearly basis. During 2011 till 2013, the numbers of the new reported marine fungal compounds increased to around 250–300 per year. After 2013, the number of the new compounds increased dramatically to between 420 and 490 in 2014 till 2016, and peaked to a record 540 by the end of 2017 (Fig. 6). This statistical data indicated that the total number of newly discovered marine fungal natural products is approximately 4000 by the end of 2017 and it is increasing again in 2018.

In terms of chemical diversity, marine fungi have a proven track of producing metabolites belonging to diverse structural classes of compounds, mainly polyketides, prenylated polyketides, meroterpenoids, terpenoids, peptides including diketopiperazines, alkaloids and other nitrogen-containing metabolites, and few other classes (Rateb and Ebel 2011). This vast diversity is hard to find in nature if compared with other marine organisms, marine bacteria, or plants. To date, the global marine pharmaceutical pipeline consists of seven approved pharmaceuticals, four of which are anticancer drugs. Currently there are about 21 marine natural products or natural product-derived compounds in Phase I to Phase III clinical trials, mainly in the area of cancer therapy (Marcel et al. 2016).

Despite the large number of new marine fungal-derived metabolites with promising pharmacological activities, only the broad-spectrum antibiotic cephalosporin C can be tracked back as a marine fungal-derived drug which was discovered from the fungus *Acremonium chrysogenum* collected from the Sardinian coast (Abraham 1979). Another important marine fungal molecule is the diketopiperazine halimide **[1]** which was initially discovered by Fenical's group in the 1990s as a tubulin depolymerising agent (Fenical et al. 1998). This molecule served as a lead structure for the closely related synthetic analogue plinabulin (NPI-2358, **[2]**), Beyond Spring Pharmaceuticals' lead asset, which is currently in late-stage phase III clinical development for the prevention of chemotherapy-induced neutropenia (CIN) and as an anticancer therapy in non-small cell lung cancer (NSCLC) (https://clinicaltrials.gov/ct2/results?term=plinabulin&pg=1, https://www.beyondspringpharma.com/en/pipeline/plinabulin/). The minor input of fungi from marine habitats as a source of new drug leads is likely attributed to the fact that the chemical investigation of these micro-organisms for bioactive metabolites production was almost neglected till the end of the 1980s. Only 15 secondary metabolites were reported from marine-derived fungi until 1992 (Bugni and Ireland 2004). Herein we highlight a few biologically potent fungal secondary metabolites derived from marine habitats. In the following sections, a few examples of the recently discovered marine fungal natural products that exhibited strong or potent anti-infective or anticancer activities will be discussed.

Antiviral marine fungal natural products

Chemical investigation of the marine-derived fungus *Eurotium rubrum* led to the isolation of the prenylated indole diketopiperazine alkaloid neoechinulin B **[3]** which displayed a strong inhibitory effect against the H1N1 virus

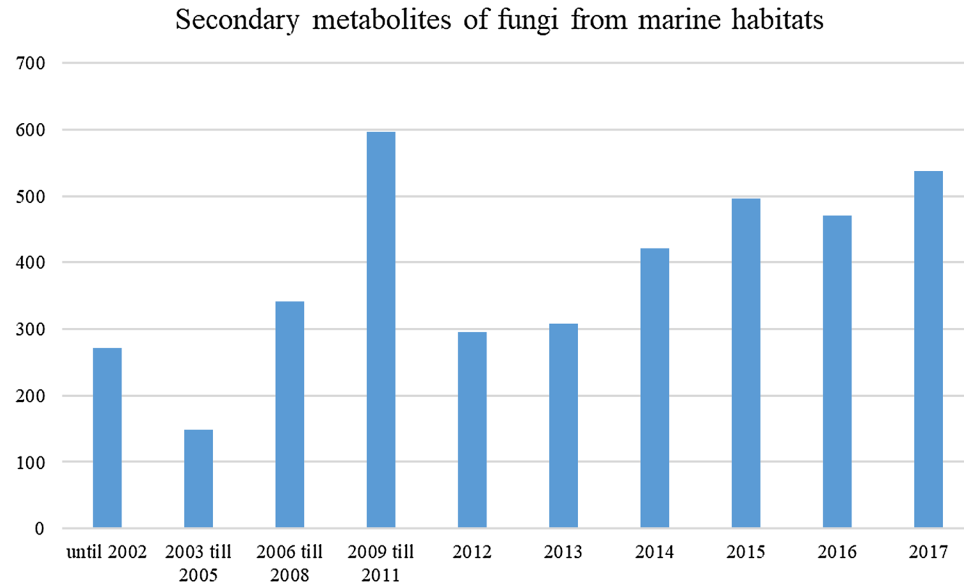
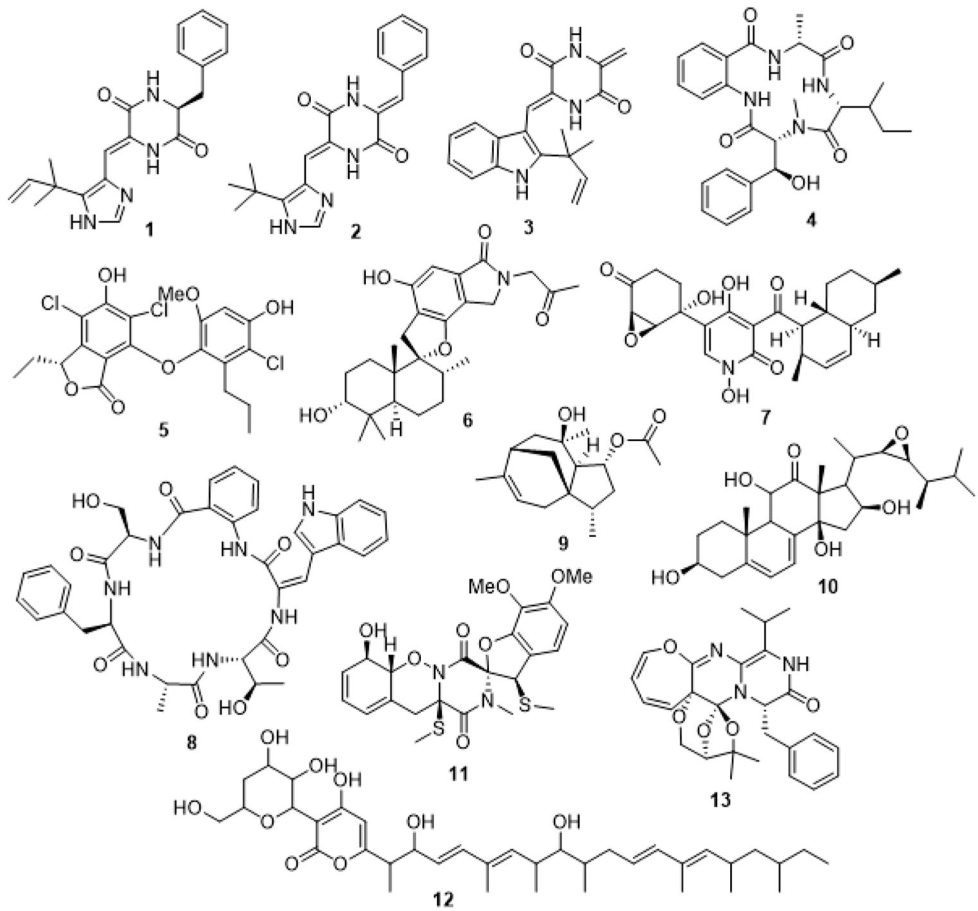


Fig. 6 Secondary metabolites of fungi from marine habitats

in infected Madin Darby Kidney (MDCK) cells, and also inhibited a panel of amantadine, oseltamivir and ribavirin resistant influenza clinical isolates. The absence of cytotoxic effect in addition to the broad spectrum of action against drug-resistant viral clinical isolates together with the diminished induction of drug resistance indicated the potential use of neoechinulin B to treat clinically resistant viral infections (Chen et al. 2015). The cyclic tetrapeptide asperterrestide A **[4]** isolated from the gorgonian coral-derived fungus *Aspergillus terreus* SCSGAF0162 contains a rare 3-OH-N-CH_3-Phe residue and exhibited an inhibitory effect against the M2-resistant influenza strain A/WSN/33 H1N1 replication in MDCK cells. It also exhibited cytotoxic effect on the human leukemic monocyte lymphoma U937 and acute lymphoblastic leukaemia MOLT-4 cell lines (He et al. 2013). Spiromastilactone D **[5]** isolated from a deep-sea derived fungus *Spiromastix* sp. was another potent inhibitor to a panel of amantadine and oseltamivir-resistant influenza virus strains (Niu et al. 2016). The phenylspirodrimane stachybotrin D **[6]** isolated from the marine sponge-associated fungus *Stachybotrys chartarum* MXH-X73 inhibited HIV-1 replication through the inhibition of reverse transcriptase without showing any cytotoxicity. Additionally, its assessment indicated similar inhibitory effects on HIV-1 replication of wild and several NNRTI-resistant HIV-1 strains (Ma et al. 2013).

Antifungal marine fungal natural products

Chemical investigation of the marine-derived fungus *Stagonosporopsis cucurbitacearum* led to the isolation of a 4-hydroxy-2-pyridone alkaloid didymellamide A **[7]** which exhibited good antifungal activity against azole-resistant and sensitive *Candida albicans, C. glabrata*, and *Cryptococcus neoformans* (Haga et al. 2009). Sclerotide B **[8]** is a novel cyclic hexapeptide isolated from the marine-derived halotolerant *Aspergillus sclerotiorum* PT06-1 in a nutrient-limited hypersaline medium. It showed strong antifungal activity against *C. albicans* (Zheng et al. 2009)]. The sesquiterpene penicibilaene B **[9]** was isolated from *Penicillium bilaiae* MA-267 derived from the rhizospheric soil of a mangrove plant. It exhibited selective activity against the plant pathogenic fungus *Colletotrichum gloeosporioides* (Meng et al. 2014). The ergosteroid (22*R*,23*S*)-epoxy-3b,11a,14b,16b-tetrahydroxyergosta-5,7-dien-12-one **[10]** isolated from the halotolerant fungus *Aspergillus flocculosus* PT05-1 obtained from a marine sediment in Fujian Province of China and exhibited good antifungal activity against *Candida albicans* (Zheng et al. 2013). Chemical investigation of the sponge-derived fungus *Penicillium adametzioides* AS-53 led to the isolation of the dithiodiketopiperazine derivative peniciadametizine A **[11]** which exhibited selective antifungal activity against the plant pathogenic fungus *Aspergillus brassicae* (Liu et al. 2015a). YM-202204 **[12]** is an antifungal antibiotic isolated from the culture broth of the sponge-derived fungus *Phoma* sp. Q60596 which showed strong inhibitory effect of the growth of *Cryptococcus neoformans* and *Saccharomyces cerevisiae* (Nagai et al. 2002). The alkaloid varioxepine A **[13]** isolated from the marine algal-derived endophytic fungus *Paecilomyces variotii*, characterized by a structurally unprecedented condensed 3,6,8-trioxabicyclo[3.2.1]octane motif and exhibited potent inhibitory activity against the plant-pathogenic fungus *Fusarium graminearum* (Zhang et al. 2014).

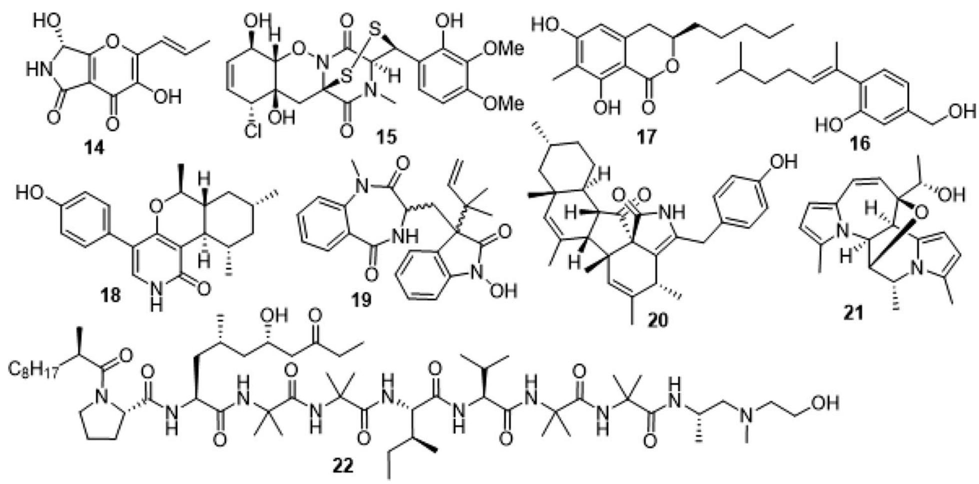


[1] Number in bracket refers in the text to the compound listed above.

Antibacterial marine fungal natural products

Chemical investigation of the marine mangrove plant-derived *Penicillium brocae* MA-231 led to the isolation of polyoxygenated dihydropyrano[2,3-c]pyrrole-4,5-dione derivative, pyranonigrin A **[14]** which possess strong antimicrobial activity against a panel of Gram positive and negative bacterial pathogens (Meng et al. 2015). Chemical investigation of the marine sponge-derived fungus *Penicillium adametzioides* AS-53 resulted in the isolation of the bisthiodiketopiperazine derivative adametizine A **[15]** which exhibited good inhibitory activity against *Staphylococcus aureus, Aeromonas hydrophilia, Vibrio* spp., *V. harveyi* and *V. parahaemolyticus* (Liu et al. 2015b). Aspergillusene A **[16]** is a sesquiterpenoid isolated from the sponge-associated fungus *Aspergillus sydowii* ZSDS1-F6 and displayed antimicrobial activities against *Klebsiella pneumonia* and *Aeromonas hydrophila* (Wang et al. 2014). The dihydroisocoumarin derivative penicisimpin A **[17]** isolated from the marine mangrove plant-derived fungus *Penicillium simplicissimum* MA-332 and exhibited strong activity against *Escherichia coli, P. aeruginosa, Vibrio parahaemolyticus*, and *V. harveyi* (Xu et al. 2016a, b). The pyridone trichodin A **[18]** was isolated from the marine fungus *Trichoderma* sp. strain MR106 and possessed moderate antibiotic activities against the Gram-positive *B. subtilis, S. epidermidis*, and methicillin-resistant *S. aureus* (MRSA) (Wu et al. 2014). Chromatographic analysis of the marine sponge-derived fungus *Aspergillus* sp. yielded unusual tryptophan-derived alkaloid, 3-((1-hydroxy-3-(2-methylbut-3-en-2-yl)-2-oxoindolin-3-yl)methyl)-1-methyl-3,4-dihydrobenzo[e][1,4]diazepine-2,5-dione **[19]** which selectively inhibited a panel of *Vibrio* species (Zhou et al. 2014). Diaporthalasin **[20],** a pentacyclic cytochalasin isolated from the marine-derived fungus Diaporthaceae sp. PSU-SP2/4 and displayed significant antibacterial activity against both *S. aureus* and MRSA (Khamthong et al. 2014). Chromatographic fractionation of the EtOAc extract from the culture of the white croaker (*Genyonemus lineatus*)-derived *Curvularia* sp. IFB-Z10 gave a dinitrogenated alkaloid curvulamine **[21]** which exhibited strong antibacterial against a panel of patients-derived pathogens (Han et al. 2014). The aminolipopeptide trichoderin A **[22]** isolated from the marine sponge-derived *Trichoderma* sp. exhibited potent anti-mycobacterial activity against *M. smegmatis, M. bovis* BCG, and *Mycobacterium tuberculosis* H37Rv under standard aerobic growth conditions as well as dormancy-inducing hypoxic conditions (Pruksakorn et al. 2010).

in vitro cytotoxicity against a panel of human cancer cell lines (Chen et al. 2016). Chemical investigation of the marine-derived fungus *Aspergillus ochraceus* Jcma1F17 led to the isolation of 6β,9α-dihydroxy-14-p-nitrobenzoylcinnamolide **[26]**, a metabolite that belongs to the rare nitrobenzoyl sesquiterpenoid class. It displayed significant

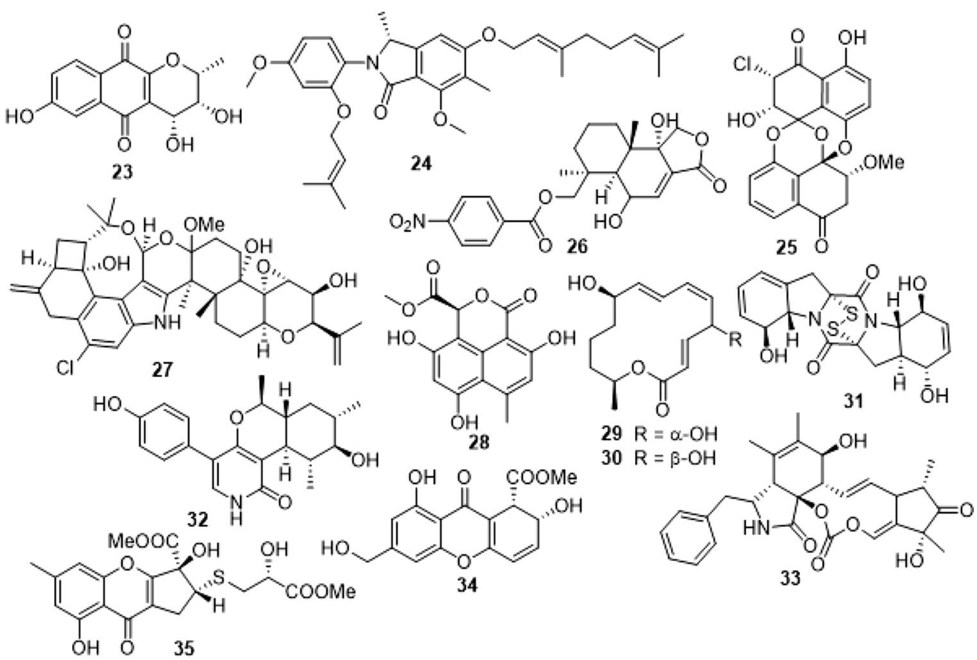


A study by Soowannayan et al. (2019) demonstrated that the cell-free culture broths of Thai obligate marine fungi inhibited the growth and biofilm formation of *Vibrio* species. The most potent marine fungal strain identified as *Oceanitis cincinnatula* showed that it can protect shrimp against acute hepatopancreatic necrosis disease (AHPND). The results suggested that this obligate marine fungus may contain a substance(s) that did not inhibit the growth of pathogenic *Vibrio* bacteria and could potentially be used as shrimp feed supplement to protect shrimp against AHPND, possibly by inhibiting biofilm formation in the shrimp stomach.

Anticancer marine fungal natural products

Bio-guided isolation of the deep-sea derived fungus *Acaromyces ingoldii* FS121 led to the isolation of a new naphtha-[2,3-*b*]pyrandione analogue acaromycin A **[23]** which exhibited potent in vitro growth inhibitory activities against four tumour cell lines (MCF-7, NCI-H460, SF-268 and HepG-2) comparable to the positive control cisplatin (Gao et al. 2016b). Chemical investigation of the bioactive extract of the marine sponge-derived fungus *Stachylidium* sp. led to the isolation of phthalimidine derivative mariline A1 **[24]** which was a potent inhibitor of human leukocyte elastase (Almeida et al. 2012). Chloropreussomerin A **[25]** obtained from the mangrove plant-derived endophyte *Lasiodiplodia theobromae* ZJ-HQ1 was the first chlorinated metabolite in the preussomerins family and showed potent cytotoxicity against 10 cancer cell lines (Fang et al. 2014). Genome mining of the fungus *Mucor irregularis* QEN-189 isolated from fresh inner tissue of a marine mangrove plant resulted in the discovery of 20 structurally diverse complex indole-diterpenes compounds. Among them, rhizovarin B **[27]**, showed good activity against the human A-549 and HL-60 cancer cell lines (Gao et al. 2016a). A novel oxaphenalenone, penicimutalidine **[28],** was isolated from the diethyl sulfate mutagenesis of the marine-derived *Penicillium purpurogenum* G59. Its inhibitory effects were stronger than that of the positive control 5-FU (5-Fuorouracil) on the same HL-60 cancer cells (Li et al. 2016). Pestalotioprolides E and F **[29&30]**, are 14-membered macrolides isolated from the mangrove-derived endophytic fungus *Pestalotiopsis microspora*. Both compounds showed significant cytotoxicity against the murine lymphoma cell line L5178Y while compound **[29]** showed potent activity against the human ovarian cancer cell line A2780 (Liu et al. 2016). The diketopiperazine brocazine G **[31]** was characterized from the mangrove-derived *Penicillium brocae* MA-231. It exhibited potent cytotoxicity against both sensitive and cisplatin-resistant human ovarian cancer cells A2780 and A2780, respectively, and showed significantly stronger effect than that of the positive control cisplatin on both cell lines (Meng et al. 2016). Chemical analysis of a marine-derived fungus *Chaunopycnis* sp. (CMB-MF028) yielded the pyridinone derivative chaunolidone A **[32]** which was a selective and potent inhibitor of human non-small cell lung carcinoma cells (NCI-H460)

(Shang et al. 2015). Cytochalasin K **[33]** isolated from the marine sponge-derived fungus *Arthrinium arundinis* ZSDS1-F3 exhibited strong cytotoxicity against a panel of human cancer cell lines (Wang et al. 2015). The chromone engyodontiumone H **[34]** was isolated from the deep-sea-derived fungus *Engyodontium album* DFFSCS021 and showed significant selective cytotoxicity against the human histiocytic lymphoma U937 cell line (Yao et al. 2014). Chromosulfine **[35]** is a novel cyclopentachromone sulphide isolated from a neomycin-resistant mutant of the marine-derived fungus *Penicillium purpurogenum* G59 and could not be traced in the original strain. It showed good cytotoxic effect against a panel of cancer cell lines (Yi et al. 2016).



Marine fungi are extremely versatile as studies on their pharmaceutical applications have been demonstrated above, and also their role in the decomposition of materials in the sea and the food web of the oceans (Sridhar 2012). However, they play a vital role in other biological fields, such as bioremediation, production of biosurfactants for different uses, industrial enzymes, pigments and dyes (Velmurugan and Lee 2012; Pang et al. 2016a). Their potential for industrial application has only recently been addressed (Jones et al. 2015) or as Carter and Berman (2016) opine "Has industry missed the boat". While marine Labyrinthulomycetes have been studied as a source of omega-3-polyunsaturated fatty acids and potential use in fish food (Jaritkhuan et al. 1998; Pang et al. 2016a, b). The use of filamentous fungi and yeasts as animal feed has largely gone unexplored. Currently the worlds concern over plastic in our seas and oceans has attracted much media attention. Do marine fungi have the potential in its breakdown! Mycelial adhesion by marine fungi to surfaces has been demonstrated by Hyde et al. (1986) while a number have been shown to colonise and degrade polyurethane panels exposed off the French coast (Jones and Le Campion-Alsumard 1970).

Conclusion

Marine mycology can be considered to have come of age with over 150 years documenting the occurrence and distribution of marine fungi (Desmazieres 1849; Meyers 1996; Jones 2011a). Although Sutherland (1915a, b, c, 1916a, b) made a significant contribution to marine fungi on seaweeds, it was the paper by Barghoorn and Linder (1944) that probably influenced the development and study of this ecological group of fungi. The period 1960–1990 was the most intense time for the description of marine fungi, especially those found on mangrove substrates (Kohlmeyer 1966; Hyde and Jones 1988). Documentation of marine fungi has grown steadily from 100 species (circa 1960) to 1181 (2015) and new taxa continue to be introduced (1255 in 2018) (Jones et al. 2015; www.marinefungi.org). Over the past century techniques for their study has changed dramatically especially the introduction of sequencing methods and the application of high-throughput sequencing and next generation sequencing techniques. These have enabled a more natural classification of marine fungi and the discovery of taxa whose morphology has yet to be established. Progress has been made in determining their ecological role in a number of habitats, their physiological requirements, and interactions in the colonization of substrates in the sea. Marine fungi have yielded an array of interesting secondary metabolies, some in advance stage of clearance. Some taxonomical groups require more intense study especially the Chytridiomycota and their role in the colonization of planktonic organisms. It is hoped that greater interaction between their study by traditional means and by high through put sequencing can be established to enable a better understanding of the global diversity of marine fungi.

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Appendix

List of marine fungi logged in the marine fungi website

Taxa with the prefix * are asexual morphs whose sexual stage is unknown; # indicates molecular data available for these fungi.
Taxa in underline text are new taxa in press.
Phylum: **BASIDIOMYCOTA**
Subphylum: **Ustilaginomycotina**
Class: **Ustilaginomycetes** R. Bauer, Oberw. & Vnky, Can. J. Bot. 75: 1311 (1997)
Subclass: **Ustilaginomycetidae** Jlich, Bibliotheca Mycologica 85: 54 (1981)
1. UROCYSTIDALES R. Bauer & Oberw., Can. J. Bot. 75 (8): 1311 (1997)
Urocystidaceae Begerow, R. Bauer & Oberw., Can. J. Bot. 75(12): 2052 (1998)
Flamingomyces R. Bauer, M. Lutz, Piątek, Vánky & Oberw., Mycol. Res. 111(10): 1202 (2007)
1. #*F. ruppiae* (Feldmann) R. Bauer, M. Lutz, Pitek, Vnky & Oberw., Mycol. Res. 111(10): 1203 (2007)
2. USTILAGINALES G. Winter, Rab Kryptog-Flora, Pilze - Schizomyceten, Saccharomyceten und Basidiomyceten 1(1): 73 (1880)
Ustilaginaceae Tul. & C. Tul., Annls Sci. Nat., Bot., sr. 3 7: 14 (1847)
Parvulago R. Bauer, M. Lutz, Piątek, Vnky & Oberw., Mycol. Res. 111(10): 1203 (2007)
1. #*P. marina* (Durieu) R. Bauer, M. Lutz, Piątek, Vnky & Oberw., Mycol. Res. 111(10): 1203 (2007)

Class: **Exobasidiomycetes** Begerow, M. Stoll, R. Bauer, Mycologia 98(6): 908 (2006)
Subclass: **Exobasidiomycetidae** Jlich, Bibliotheca Mycologica 85: 55 (1981)

1. EXOBASIDIALES Henn. (1900) Graphiolaceae Clem. & Shear, The genera of Fungi: 156 (1931)
Family *incertae sedis*
Graphiola Poit., Ann Sci Nat (Paris) 3: 473 (1824)
1. *G. cylindrica* Kobayasi, Nagaoa 1: 36 (1952)

Exobasidiomycetidae ***incertae sedis***
Tilletiopsis Derx, Bull Jardin Bot Buitenzorg 17: 471 (1948)
1. #*T. albescens* Gokhale, Nova Hedwigia 23: 801 (1972)
Subphylum: **Pucciniomycotina**
Class: **Tritirachiomycetes** ***incertae sedis***
1. TRITIRACHIALES Aime & Schell, Mycologia 103 (6): 1339 (2011)
Tritirachiaceae Locq., Mycol Gén Struct (Paris): 208 (1984)
Tritirachium Limber, Mycologia 32: 26 (1940)
1. *T. candoliense* Cathrine Sumathi Manohar, Teun Boekhout & Thorsten Stoeck, Fung Biol 118(2): 143 (2014) (marine sediments, Manohar et al. 2014)
Subphylum: **Agaricomycotina**
Class: **Agaricomycetes** Doweld, Prosyllabus Tracheophytorum, Tentamen systematis plantarum vascularium (Tracheophyta): LXXVII (2001)
Subclass: **Agaricomycetidae** Parmasto, Windahlia 16: 16 (1986)
1. AGARICALES Underw., Moulds, mildews and mushrooms: 97 (1899)
Niaceae Jülich, Bibliotheca Mycologica 85: 381 (1981)
Calathella D.A. Reid, Persoonia 3: 122 (1964)
1. #*C. mangrovei* E.B.G. Jones & Agerer, Bot. Mar. 35: 259 (1992)
Halocyphina Kohlm. & E. Kohlm., Nova Hedwigia 9: 100 (1965)
1. #*H. villosa* Kohlm. & E. Kohlm., Nova Hedwigia 9: 100 (1965)
Nia R.T. Moore & Meyers, Mycologia 51(6): 874 (1961)
1. *N. epidermoidea* M.A. Rosell & Descals, Mycol. Res. 97(1): 68 (1993)
2. *N. globospora* Barata & Basilio, Mycol. Res. 101(6): 687 (1997)

3. *#N. vibrissa* R.T. Moore & Meyers, Mycologia 51(6): 874 (1961)

2. **CANTHARELLALES** Gum., Vergl. Morph. Biol. Pilze (Leipzig): 495 (1926)
Botryobasidiaceae (Parmasto) Jlich, Biblthca Mycol. 85: 357 (1981)
**Allescheriella* Henn., Hedwigia 36: 244 (1897)
1. *A. bathygena* Kohlm., Revue Mycol., Paris 41(2): 199 (1977)
Physalacriaceae Corner, Beihefte zur Nova Hedwigia 33: 10 (1970)
Physalacria Peck, Bull. Torrey Bot. Club 9: 2 (1882)
1. *#P. maipoensis* Inderb. & Desjardin, Mycologia 91(4): 666 (1999)
Mycaureola Maire & Chemin, C R Sanc. Acad. Sci., Paris 175: 321 (1922)
1. *#M. dilseae* Maire & Chemin., C R Sanc. Acad. Sci., Paris 175: 321 (1922)
Schizophyllaceae Qul, Fl. Mycol. France: 365 (1888)
Henningsomyces Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483 (1898)
1. *H. candidus* cf (Pers.) Kuntze, Revis. gen. pl. (Leipzig) 3(2): 483 (1898)
Schizophyllum Fr., [as 'Schizophyllus'], Observ. Mycol. 1: 103 (1815)
1. *#S. commune* Fr., Syst. Mycol. 1: 330 (1821)

3. **POLYPORALES** Gum., Vergl Morphol Pilze: 503 (1926)
Meruliaceae Rea, British Basidiomycertae: A handbook to the larger British fungi: 620 (1922)
Hyphoderma Wallr., Fl. Crypt. Germ. 2: 576 (1833)
1. *H. sambuci* (Pers.) Jlich, Persoonia 8(1): 80 (1974)
Polyporaceae Corda, Icon Fung hucusques cognitoru 3: 49 (1839)
Grammothele Berk. & M.A. Curtis, J. Linn. Soc. Bot. 10: 327 (1869)
1. *G. fuligo* (Berk. & Broome) Ryvarden, Trans. Br. Mycol. Soc. 73: 15 (1979)
Cerrena Gray, A natural arrangement of British plants 1: 649 (1821)
1. *C. unicolor* (Bull.) Murrill, J Mycol. 9(2): 91 (1903)

4. **HYMENCHAETALES** Oberw., Beitrge zur Biologie der niederen Pflanzen: 89 (1977)
Hymenochaetaceae Donk, Bull. bot. Gdns Buitenz. 17(4): 474 (1948)
Fulvifomes Murrill, North Polyp (5): 49 (1914)
1. *#F. halophilus* T. Hatt., Sakay. & E.B.G. Jones, Mycoscience 55: 347 (2014)
2. *#F. siamensis* T. Hatt., Sakay. & E.B.G. Jones, Mycoscience 55: 346 (2014)
3. *#F. xylocarpicola* T. Hatt., Sakay. & E.B.G. Jones (2014), Mycoscience 55: 345 (2014)
Agaricomycetes *incertae sedis*
1. **RUSSULALES** Kreisel ex P.M. Kirk, P.F. Cannon & J.C. David, Ainsworth & Bisby's Dictionary of the Fungi, Edn 9 (Wallingford): xi (2001)

***Digitatispora* clade**
Digitatispora Doguet, C. r. hebd. Sanc. Acad. Sci., Paris 254(25): 4338 (1962)
1. *D. lignicola* E.B.G. Jones, Mycotaxon 27: 155 (1986)
2. *#D. marina* Doguet, C. r. hebd. Sanc. Acad. Sci., Paris 254(25): 4338 (1962)
Peniophoraceae Lotsy, Vortr. Bot. Stammesgesch. 1: 687, 689 (1907)
Haloaleurodiscus N. Maek., Suhara & K. Kinjo, Mycol. Res. 109(7): 826 (2005)
1. *#H. mangrovei* N. Maek., Suhara & K. Kinjo, Mycol. Res. 109(7): 827 (2005)

Phylum: **ASCOMYCOTA**
Subphylum: **Pezizomycotina**
Class: **Dothideomycetes** E. Erikss. & Winka, Myconet 1: 5 (1997)
Subclass: **Dothideomycetidae** P.M. Kirk, P.F. Cannon, J.C. David & Stalpers ex C.L. Schoch, Spatafora, Crous & Shoemaker, Mycologia 98 (6): 1045 (2007)
1. **CAPNODIALES** Woron., Annales Mycologici 23: 177 (1925)
Cladosporiaceae Chalm. & R.G. Archibald, The Yearbook of Tropical Medicine and Hygiene 1: 25 (1915)
**Cladosporium* Link, MagGesell Naturf Freunde Berlin 7: 37 (1816)
1. #*C. cladosporioides* (Fresen.) G.A. de Vries, Contrib. Knowledge of the Genus Cladosporium Link ex Fries: 57 (1952)
2. *C. herbarum* (Pers.) Link, in Willdenow, Mag. Gesell. Naturf. Freunde, Berlin 8: 37 (1816)
3. *C. macrocarpum* Preuss, Deutschlands Flora, Abt. III. Die Pilze Deutschlands 6-25/26: 27, t. 14 (1848)
4. *#C. oxysporum* Berk. & M.A. Curtis, Bot. J. Linn. Soc. 10: 362 (1869)
5. *C. pseudocladosporioides* Bensch, Crous & U. Braun, Studies in Mycology 67: 71 (2010)
6. *C. psoraleae* M.B. Ellis, Mycol Pap 131: 16 (1972)
7. *#C. sphaerospermum* Penz., Michelia 2(8): 473 (1882)
8. *#C. tenuissimum* Cooke, Grevillea 6(40): 140 (1878)
9. *#C. uredinicola* Speg., Anal. Mus. Nac. Hist. Nat. B. Aires 23: 122 (1912)

Mycosphaerellaceae Lindau, in Engler & Prantl, Nat. Pflanzenfam. Teil. 1 (Leipzig) 1: 421 (1897)
Davidiella Crous & U. Braun, Mycol. Progr. 2 (1): 8 (2003)
1. #*D. tassiana* (De Not.) Crous & U. Braun, in Braun, Crous, Dugan & de Hoog, Mycol. Progr. 2(1): 8 (2003)
Mycosphaerella Johanson, fvers. K. Svensk. Vetensk.-Akad. Frhandl. 41: 163 (1884)
1. *M. punctiformis* (Pers.) Starbäck, Bihang till Kungliga svenska Vetenskaps-Akademiens Handlingar 15 (2): 9 (1889)
2. *M. salicorniae* (Rabenh.) Lindau, Hilfsb Sammeln Ascomyc. 2: 103 (1903)
3. *M. staticicola* (Pat.) Dias, Mem. Soc. Brot.: 21 (1970)
4. *M. suaedae-australis* Hansf., Proc Linn Soc New South Wales 79(3–4): 122 (1954)
5. *M. tassiana* (De Not.) Johanson, Öfvers. K. Vetensk. Akad. Förh. 41 (9): 167 (1884)
Pseudocercosporella Deighton, Mycological Papers 133: 38 (1973)
1. *P. fraxini* (Ellis & Kellerm.) U. Braun, Nova Hedwigia 58 (1–2): 212 (1994)
****Ramichloridium*** Stahel ex de Hoog, Stud. Mycol. 15: 59 (1977)
1. *#R. apiculatum* (J.H. Mill., Giddens & A.A. Foster) de Hoog, Stud. Mycol. 15: 69 (1977)
Septoria Sacc., Sylloge Fungorum 3: 474 (1884)
1. *S. arundinacea Sacc., Michelia 1 (2): 195 (1878) Capnodiales, Mycosphaerellaceae,*
2. *S. ascophylli* Melnik & J.E. Petrov, Novosti Sistematiki Nizshikh Rastenii 3: 211 (1966)
Sphaerulina Sacc., Michelia 1(4): 399 (1878)
1. *S. albispiculata* Tubaki, Publs. Setomar. Biol. Lab. 15(5): 366 (1967)
2. *S. orae-maris* Linder, Farlowia 1(3): 413 (1944)
Pharcidia Krb., Parerga Lichenol. 5: 469 (1865)
1. *P. balani* (G. Winter) Bausch, Publ. Stn. Zool. Napoli 15: 379 ((1936)
2. *P. laminariicola* Kohlm., Bot. Mar. 16: 209 (1973)
3. *P. rhachiana* Kohlm., Bot. Mar. 16: 210 (1973)
****Rhabdospora*** (Durieu & Mont. ex Sacc.) Sacc., Syll. Fung. 3: 578 (1884)
1. *R. avicenniae* Kohlm. & E. Kohlm., Mycologia 63(4): 851 (1971) 269 (2006)
Capnodiales *incertae sedis*
Stigmidium Trevis., Conspect. Verruc.: 17 (1860)
1. *S. ascophylli* (Cotton) Aptroot, CBS Diversity Ser. (Utrecht) 5: 41 (2006)
2. *S. apophlaeae* (Kohlm.) Aptroot, CBS Diversity Ser. (Utrecht) 5: 36 (2006)
Teratosphaeriaceae Crous & U. Braun, Studies in Mycology 58: 8 (2007)
Acrodontium de Hoog, Studies in Mycology 1: 23 (1972)
1. *A. hydnicola* (Peck) de Hoog, Studies in Mycology 1: 31 (1972)
2. *A. salmoneum* de Hoog, Studies in Mycology 1: 29 (1972)

2. **DOTHIDEALES** Lindau, Natrl Pflanzenfam.: 373 (1897)
Dothideaceae Chevall., Fl. gn. env. Paris 1: 446 (1826)
Scirrhia Nitschke ex Fuckel, Jb Nassau Ver Naturk 23-24: 220 (1870)
1. *S. annulata* Kohlm., Volkm.-Kohlm. & O.E. Erikss., Can. J. Bot. 74(11): 1835 (1996)
Dothioraceae Theiss. & P. Syd., Annales Mycologici 15 (6): 444 (1918)
Aureobasidium Viala & G. Boyer, Revue Gn Bot 3: 371 (1891)
1. *A. pullulans* (de Bary & Lwenthal) G. Arnaud, Annals d'cole Nat d'Agric. de Montpellier, Sr 2 16(1–4): 39 (1918) [1917]

3. **BOTRYOSPHAERIALES** C.L. Schoch, Crous & Shoemaker, Mycologia 98(6): 1050 (2007)
Botryosphaeriaceae Theiss. & Syd., Annls Mycol 16:16 (1918)
Amarenomyces O.E. Erikss., Opera Bot. 60: 124 (1981)
1. *A. ammophilae* (Lasch) O.E. Erikss., Opera Bot. 60: 124 (1981)
****Diplodia*** Fr., in Montagne, Annls. Sci. Nat. Bot. 1: 302 (1834)
1. *D. orae-maris* Linder, Farlowia 1(3): 403 (1944)
2. *D. thalassia* N.J. Artemczuk, Mikol. Fitopatol.: 95 (1980)
****Lasiodiplodia*** Ellis & Everh., Bot. Gazette Crawfordsville 21: 92 (1896)
1. *#L. theobromae* (Pat.) Griffon & Maubl., Bull. Soc. Mycol. Fr. 25: 57 (1909)
Phyllostictaceae Fr. [as 'Phyllostictei'], Summa veg. Scand. (Stockholm) 2: 420 (1849)
****Phyllosticta*** Pers., Trait sur les Champignons Comestibles: 147 (1818)
1. *Ph. spartinae* Brunaud, J. Hist. Nat. Bordeaux sud-ouest: 4 (1888)

4. **MICROTHYRIALES** G. Arnaud, Annal. Sci. Nat. Paris: 847 (1925)
Microthyriaceae Sacc., Syll. Fung. 2: 658 (1883)
Ellisiodothis Theiss., Annls. Mycol. 12(1): 73 (1914)
1. *E. inquinans* (Ellis & Everh.) Theiss., Annls Mycol 12(1): 73 (1914)

Subclass: **Pleosporomycetidae** C.L. Schoch, Spatafora, Crous & Shoemaker, Mycologia 98 (6): 1048 (2007)
1. PLEOSPORALES Luttr. ex M.E. Barr, Prodromus to class Loculoascomycetes: 67 (1987)

Ascocylindricaceae Abdel-Wahab, Bahkali, E.B.G. Jones, Ariyawansa & K.D. Hyde, Fungal Divers. 75: 19 (2015)
Ascocylindrica Abdel-Wahab, Bahkali & E.B.G. Jones, Fungal Divers. 75: 45 (2015)
1. #*A. marina* Abdel-Wahab, Bahkali & E.B.G. Jones, Fungal Divers. 75: 20 (2015)
Aigialaceae Suetrong, Sakay., E.B.G. Jones Kohlm., Volkm.-Kohlm. & C.L. Scoch, Stud. Mycol. 64: 166 (2009)
Aigialus Kohlm. & Schatz, Trans. Br. Mycol. Soc. 85: 699 (1985)
1. #*A. grandis* Kohlm. & S. Schatz, Trans. Br. Mycol. Soc. 85(4): 699 (1986)
2. #*A. mangrovis* Borse, Trans. Br. Mycol. Soc. 88: 424 (1987)
3. #*A. parvus* S. Schatz & Kohlm., Trans. Br. Mycol. Soc. 85(4): 704 (1986)
4. #*A. rhizophorae* Borse, Trans. Br. Mycol. Soc. 88: 425 (1987)
5. *A. striatispora* K.D. Hyde, Mycol. Res. 96: 1044 (1992)
Ascocratera Kohlm., Can. J. Bot. 64: 3036 (1986)
1. #*A. manglicola* Kohlm., Can. J. Bot. 64: 3036 (1986)
Rimora Kohlm., Volkm.-Kohlm., Suetrong, Sakay., E.B.G. Jones, Stud. Mycol. 64: 166 (2009)
1. #*R. mangrovei* (Kohlm. & Vittal) Kohlm., Volkm.-Kohlm., Suetrong, Sakay. & E.B.G. Jones, Stud. Mycol. 64: 166 (2009)
Amniculicolaceae Y. Zhang ter, C.L. Schoch, J. Fourn., Crous & K.D. Hyde, Stud. Mycol. 64: 95 (2009)
Neomassariosphaeria Y. Zhang, J. Fourn. & K.D. Hyde, Stud. Mycol. 64: 96 (2009)
1. #*N. typhicola* (P. Karst.) Y. Zhang, J. Fourn. & K.D. Hyde, Stud. Mycol. 64: 96 (2009)
Astrosphaeriellaceae Phook. & K.D. Hyde, Fungal Diversity 74: 161 (2015)
Astrosphaeriella Syd. & P. Syd., Annls. Mycol. 11: 260 (1913)
1. *A. asiana* (K.D. Hyde) Aptroot & K.D. Hyde, Nova Hedwigia 70(1–2): 145 (2000)
2. *A. mangrovei* (Kohlm. & Vittal) Aptroot & K.D. Hyde, Nova Hedwigia 70(1–2): 154 (2000)
3. *A. nypae* K.D. Hyde, J. Linn. Soc. Bot. 110(2): 96 (1992)
****Pithomyces*** Berk. & Broome, Bot. J. Linn. Soc. 14: 100 (1873)
1. #*P. atro-olivaceus* (Cooke & Harkn.) M.B. Ellis, Mycol. Pap. 76: 8 (1960)
Biatriosporaceae K.D. Hyde, Fungal Divers. 63: 50 (2013)
Biatriospora K.D. Hyde & Borse, Mycotaxon 26: 263 (1986)
1. #*B. marina* K.D. Hyde & Borse, Mycotaxon 26: 264 (1986)
Caryosporaceae Huang Zhang, K.D. Hyde & Ariyaw., Fungal Diversity 75: 54 (2015)
Caryospora De Not., Micromyc. Ital. Novi: 7 (1855)
1. *C. australiensis* Abdel-Wahab & E.B.G. Jones, Mycoscience 41(4): 379 (2000)
Coniothyriaceae W.B. Cooke, Revta Biol. Lisb. 12: 289 (1983)
****Coniothyrium*** Corda, Icon. Fung. hucusque cognitorum 4: 38 (1840)
1. *C. cerealis* E. Mll., in Zogg, Phytopath. Z. 18: 11 (1951)
2. *C. obiones* Jaap, Schr. Naturw. Ver. Schles.-Holst. 14(1): 29 (1907)
Cucurbitariaceae G. Winter, Rabenhorst's Kryptogamen-Flora, Pilze - Ascomyceten 1(2): 308 (1885)
Neocucurbitaria Wanas., E.B.G. Jones & K.D. Hyde, Mycosphere 8 (4): 408 (2017)
1. #*N. aquatica* Valenz.-Lopez, Crous, Stchigel, Guarro & J.F. Cano, Studies in Mycology 90: 45 (2017)
Cyclothyriellaceae Jaklitsch & Voglmayr, Studies in Mycology 85: 39 (2016)
Massariosphaeria (E. Mll.) Crivelli, ber die heterogene Ascomyceten gattung Pleospora Rabh.: 141 (1983)
1. *M. erucacea* Kohlm., Volkm.-Kohlm. & O.E. Erikss., Can. J. Bot. 74(11): 1835 (1996)
2. *M. phaeospora* (E. Müll.) Crivelli, Über die heterogene Ascomycetengattung Pleospora Rabh.: 141 (1983)
3. *M. scirpina* (G. Winter) Leuchtm., Sydowia 37: 174 (1984)
Quintaria Kohlm. & Volkm.-Kohlm., Bot. Mar. 34: 34 (1991)
1. #*Q. lignatilis* (Kohlm.) Kohlm. & Volkm.-Kohlm., Bot. Mar. 34: 35 (1991)
Dictyosporiaceae Boonmee & K.D. Hyde, Fungal Diversity 80: 462 (2016)
Dictyosporium Corda, Beiträge zur gesammten Natur- und Heilwissenschaften: 87 (1836)
1. #*D. oblongum* (Fuckel) S. Hughes, Canadian Journal of Botany 36 (6): 762 (1958)
2. *D. pelagicum* (Linder) G.C. Hughes ex T.W. Johnson & F.K. Sparrow, 1961. Fungi in Oceans and Estuaries, Cramer, p. 391.
Jalapriya D'souza, H.Y. Su, Z. Luo & K.D. Hyde, Fungal Diversity 80: 476 (2016)
1. #*J. inflata* (Matsush.) D'souza, H.Y. Su, Z. Luo & K.D. Hyde, Fungal Diversity 80: 478 (2016)
2. #*J. toruloides* (Corda) D'souza, H.Y. Su, Z. Luo & K.D. Hyde, Fungal Diversity 80: 478 (2016)
Didymosphaeriaceae Munk, Dansk Bot. Ark. 15(2): 128 (1953)
Deniquelata Ariyawansa & K.D. Hyde, Phytotaxa 105 (1): 15 (2013)
1.#*D. vittalii* Devadatha, V.V Sarma, E.B.G Jones, Mycosphere 9 (3): 570 (2018)
https://doi.org/10.5943/mycosphere/9/3/8
Didymocrea Kowalski, Mycologia 57(3): 405 (1965)
1. #*D. sadasivanii* (T.K.R. Reddy) Kowalski, Mycologia 57(3): 405 (1965

Didymosphaeria Fuckel, Jahrb. Nassau. Ver. Naturkd. 35: 140 (1870)
1. *D. lignomaris* Strongman & J.D. Mill., Proc. Nova Scotian Inst. Sci. 35(3–4): 102 (1986)
Paraconiothyrium Verkley, Studies in Mycology 50 (2): 327 (2004)
1. *P. fuckelii* (Sacc.) Verkley & Gruyter, Studies in Mycology 75: 25 (2012)
Pseudopithomyces Ariyaw. & K.D. Hyde, Fungal Diversity 75: 64 (2015)
1. #P. maydicus (Sacc.) J.F. Li, Ariyaw. & K.D. Hyde, Fungal Diversity 75: 69 (2015)
Tremateia Kohlm., Volkm.-Kohlm. & O.E. Erikss., Bot. Mar. 38(2): 165 (1995)
1. *#T. halophila* Kohlm., Volkm.-Kohlm. & O.E. Erikss., Bot. Mar. 38(2): 166 (1995)
Didymellaceae Gruyter, Aveskamp & Verkley, Mycol. Res. 113(4): 516 (2009)
Ascochyta Lib., Pl Crypt: 8 (1830)
1. *A. salicorniae* Magnus, in Jaap, Schr. Naturw. Ver. Schles.-Holst. 12: 30 (1902)
Boeremia Aveskamp, Gruyter & Verkley, Stud Mycol 65: 36 (2010)
1. *B. exigua* (Desm.) Aveskamp, Gruyter & Verkley, Stud Mycol 65: 37 (2010)
Didymella Sacc., Michelia 2 (6): 57 (1880)
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1. *H. stellatacula* (P.W. Kirk ex Marvanov & Sv. Nilsson) Marvanov, Trans. Br. Mycol. Soc. 75(2): 224 (1980)
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****Mycoenterolobium*** Goos, Mycologia 62(1): 172 (1970)
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****Phragmospathula*** Subram. & N.G. Nair, Anton. van Leeuw. 32(4): 384 (1966)
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1. *P. nypae* K.D. Hyde & B. Sutton, Mycol. Res. 96(3): 211 (1992)
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1. *P. dupla* Kohlm. & Volkm.-Kohlm., Mycol. Res. 105(4): 500 (2001)
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5. *T. nypae* K.D. Hyde & Goh, in Hyde, Goh, Lu & Alias, Mycol. Res. 103(11): 1420 (1999)
****Cytoplacosphaeria*** Petr., Annls Mycol. 17(2–6): 79 (1919)
1. *C. rimosa* Petr., Annls Mycol. 17(2/6): 79 (1919)
****Phialophorophoma*** Linder, Farlowia 1(3): 402 (1944)
1. *P. litoralis* Linder, Farlowia 1: 403 (1944)
****Phragmostilbe*** Subram., Mycopath. Mycol. Appl. 10(4): 351 (1959)
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Zygosporium Mont., Annales des Sciences Naturelles Botanique 17: 152 (1842)
1. *Z. masonii* S. Hughes, Mycol. Pap. 44: 15 (1951)

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Absidia Tiegh., Annales des Sciences Naturelles Botanique 4 (4): 350 (1878)
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Mucor Fresen., Beitrge zur Mykologie 1: 7 (1850)
1. *M. hiemalis* Wehmer, Annales Mycologici 1(1): 39 (1903)
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Rhizopus Ehrenb., Nova Acta Academiae Caesareae Leopoldino-CarolinaeGermanicae Naturae Curiosorum 10: 198 (1820
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2. *Rh. stolonifer* (Ehrenb.) Vuill., Revue Mycol., Toulouse 24: 54 (1902)

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Chytridiaceae Nowak., Akad Umiejetnosci Krakowie Wydzíat mat Przyród: 174: 191 (1878), emend. Vélez et al., Mycologia 103: 123 (2011)
Chytridium A. Braun, Betrach. Erschein. Verjüng. Natur.: 198 (1851)
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Catenochytridium Berdan, Am. J. Bot. 26(7): 460 (1939)
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Algochytrops Doweld, Index Fungorum, 123: 1 (2014)
1. #*Al. polysiphoniae* (Cohn) Doweld, Index Fungorum, 123: 1 (2014)

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1. #*D. arenysensis* S.A. Karpov & L. Guillou, Protist 165(2): 230–244 (2014)
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Fungi *incertae sedis*

Olpidiaceae J. Schröt., Krypt.-Fl. Schlesien: 180 (1886)

Olpidium (A. Braun) J. Schröt., Krypt.-Fl- Schlesien 31(2): 180 (1886)

1. *O. rostriferum* Ivimey Cook, Trans. Sapporo Nat. Hist. Soc. 13(2–3): 80 (1934)

? Valid taxon

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1. *C. consuens* K.N. Deckenb., Flora (Regensburg) 92: 265 (1903)

Phylum: **BLASTOCLADIOMYCOTA**
BLASTOCLADIOMYCETES

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Catenariaceae Couch, Mycologia 37: 187 (1945)

Catenaria Sorokin, Revue Mycol. Toulouse 11: 139 (1889)

1. *C. anguillulae* Sorokin, Annls Sci. Nat., Bot., sér. 6: 67 (1876)

Marine yeasts Ascomycota and Basidiomycota

Updated 31 December 2018

All species listed have been reported from marine habitats, even if they are facultative!

Phylum: **BASIDIOMYCOTA**

Subphyllum: **Agaricomycotina**

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Trimorphomycetaceae X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, Studies in Mycology 81: 133 (2015)
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2. *V. dimennae* (Fell & Phaff) X.Z. Liu, F.Y. Bai, M. Groenew. & Boekhout, Studies in Mycology 81: 124 (2015)
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