Review

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Recent progress in marine mycological research in different countries, and prospects for future developments worldwide

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Abstract: Early research on marine fungi was mostly descriptive, with an emphasis on their diversity and taxonomy, especially of those collected at rocky shores on seaweeds and driftwood. Subsequently, further substrata (e.g. salt marsh grasses, marine animals, seagrasses, sea foam, seawater, sediment) and habitats (coral reefs, deep-sea, hydrothermal vents, mangroves, sandy beaches, salt marshes) were explored for marine fungi. In parallel, research areas have broadened from micro-morphology to ultrastructure, ecophysiology, molecular phylogenetics,

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biogeography, biodeterioration, biodegradation, bioprospecting, genomics, proteomics, transcriptomics and metabolomics. Although marine fungi only constitute a small fraction of the global mycota, new species of marine fungi continue to be described from new hosts/substrata of unexplored locations/habitats, and novel bioactive metabolites have been discovered in the last two decades, warranting a greater collaborative research effort. Marine fungi of Africa, the Americas and Australasia are underexplored, while marine Chytridiomycota and allied taxa, fungi associated with marine animals, the functional roles of fungi in the sea, and the impacts of climate change on marine fungi are some of the topics needing more attention. In this article, currently active marine mycologists from different countries have written on the history and current state of marine fungal research in individual countries highlighting their strength in the subject, and this represents a first step towards a collaborative inter- and transdisciplinary research strategy.

Keywords: Ascomycota; Basidiomycota; ecology; ecosystem; fungal community

1 Introduction

Since our last update on the number of marine fungi (Jones et al. 2019), 641 species in 231 genera have been added, bringing the current total to 1898 species (Calabon et al. this issue). Although this number constitutes only a little over 1 % of the global diversity of fungi (Phukhamsakda et al. 2022), it represents the hard work of a consortium of mycologists over the last 150 years to look for this fascinating group of fungi with unique morphology in different marine habitats/niches and substrata all around the world (Jones et al. 2015).

Barghoorn and Linder (1944) studied marine fungi of Massachusetts, and this study triggered a significant interest in the fungal group, especially in America and Europe (Denmark, UK). Marine mangrove fungi have attracted much interest since the study by Cribb and Cribb (1955). Subsequently, a wealth of new species has been described from mangrove habitats in tropical and subtropical countries, such as Hong Kong (Pang et al. 2016), Thailand (Jones et al. 2006), Taiwan (Pang et al. 2011b), and Malaysia (Alias and Jones 2010; Lee et al. 2012). In recent years, new researchers have documented the marine fungi of Portugal (Azevedo et al. 2010; Barata 2002), Norway (Pang et al. 2011a; Rämä et al. 2014a,b) and Italy (Panno et al. 2013).

Early research on marine fungi was mostly descriptive, with an emphasis on their diversity and taxonomy (e.g. Barghoorn and Linder 1944; Jones 1962, 1968; Kohlmeyer and Kohlmeyer 1964, 1971). Ultrastructure (both scanning and transmission electron microscopy) of ascospores and ascospore appendages was used extensively to delineate species of marine fungi, especially those in the Halosphaeriaceae with diverse ascospore appendage morphology (summarized in Jones 1995). Spatafora and Blackwell (1994) were the first to use a sequence of a marine fungus in the Halophaeriaceae (*Halosphaeriopsis mediosetigera*) in a phylogenetic study and found it grouped with the Microascales. Sequence data, either from the ribosomal RNA gene cluster or protein genes, have significantly improved the classification of marine fungi (Jones et al. 2009, 2015, 2019). With the advancement of high throughput sequencing, environmental DNA from various substrata in the ocean has revealed a high diversity of marine fungi, in particular, the vast diversity of marine Chytridiomycota and allied taxa (Abdel-Wahab et al. 2021a; Comeau et al. 2016).

This article is a community effort to report the history and current state of research in marine mycology by experts of their respective countries. Active marine mycologists are studying different topics of mycology in Africa (Egypt), Asia (China, Hong Kong, India, Malaysia, Philippines, Saudi Arabia, Taiwan, Thailand), the Americas (Canada, Mexico, United States), Europe (France, Germany, Italy, Norway, Portugal, Sweden, United Kingdom) and Australasia (Australia), from ecology, systematics and biotechnology of marine fungi in habitats from the coasts to the deep-sea. Many of the countries listed in this section also hosted the 15 meetings of the International Marine Mycology Symposium (IMMS: see www.marinefungi.com). Similarly, other organisations have included marine fungi in their research programmes and meetings, for example, the Organisation for Economic Co-operation and Development (OECD) working groups on the biodeterioration of materials in marine environment (Furtado and Jones 1980; Jones 1971; Jones et al. 1972).

This article is a first step to encourage discussion on topics related to marine mycology and to promote international collaborations, knowing the research strength/ interest of each laboratory. Collaborative grants such as Biodiversa+ (https://www.biodiversa.eu/) are available every year for international marine mycologists to apply. This review gives an account of past and current research in marine mycology, highlighting key mycologists and major research findings, provides a comprehensive reference list of published papers, and offers ideas on future research topics in marine mycology.

2 Africa

2.1 Egypt (M.A. Abdel-Wahab)

The pioneer Egyptian marine mycologist Anwar Abdel Aleem (University of Alexandria, Egypt) studied marine fungi from various parts of the world: UK (Aleem 1950a), France (Aleem 1950b,c, 1952a,b), Sweden (Aleem 1952c, 1953), Russia (Aleem 1962), Romania (Aleem 1974, 1975), Saudi Arabia (1978) and Sierra Leone (Aleem 1980a; Aleem and Malibari 1981). Aleem (1980b) reported the first marine stramenopile, *Pythium marinum*, infesting *Porphyra leucosticta* in the Mediterranean Sea, Egypt. Subsequently, Scott Schatz (Institute of Marine Sciences, University of North Carolina) described *Adomia avicenniae* from pneumatophores of *Avicennia marina* from both Australia and Egypt (Schatz 1985).

Mohamed A. Abdel-Wahab started his MSc in 1993 studying marine fungi colonizing different substrata at three mangrove sites along the Red Sea coast in Egypt. He recorded 50 marine fungi (47 sexual and asexual ascomycetes, one basidiomycete and two straminopiles) from decaying driftwood, intertidal wood of *Avicennia marina*, decaying seaweeds and sediment samples. All recorded fungi are new for Egypt and the research work resulted in the following publications: Abdel-Wahab (2005) and El-Sharouny et al. (1998, 1999). Abdel-Wahab (2000), during his PhD study, recorded 26 species from 432 samples collected from three mangrove sites: Abu-Mingar, Safaga and Sharm El-Sheikh. He exposed test blocks of *Bruguiera parviflora*, *Kandelia candel* and *Sonneratia alba* at Safaga mangroves at three tidal levels and this yielded 11 species. During his PhD study, three new species were described (Abdel-Wahab et al. 2001a,b).

Abdel-Aziz (2004) studied diversity of aquatic fungi from seven water bodies in Egypt, that ranged between freshwater (River Nile) and the salinity of the open ocean (Qaroun Lake). She recorded 184 species from the seven study sites, of which 150 were new records for Egypt. Abdel-Wahab (2005) examined diversity of marine fungi on intertidal decayed wood of *Avicennia marina* and on decayed prop roots of *Rhizophora mucronata* at six mangrove stands along the Red Sea coast in Egypt; 39 species were recorded in his study, of which 19 were new records. Abdel-Wahab et al. (2009) described two new *Corollospora* species, *C. anglusa* and *C. portsaidica*, which were isolated from the coast of the Mediterranean Sea, Egypt. Abdel-Aziz (2010) identified 31 species (19 ascomycetes and 12 asexual fungi) with 21 new records from 100 driftwood samples collected from two sandy beaches at the Mediterranean Sea. *Corollospora maritima* was the most common fungus found during her study. Abdel-Wahab et al. (2010) described three new asexual genera and species: *Halazoon* (*H. melhae*), *Moleospora* (*M. maritima*) and *Moheitospora* (*M. fruticosae*, later transferred to *Juncigena* as *J. fruticosae*; Réblová et al. 2016) from the Mediterranean Sea coast of Egypt.

Abdel-Aziz (2008) studied the diversity of aquatic fungi in Lake Manzala (brackish lake). Sixty taxa with 19 new records for Egypt, including 26 ascomycetes and 34 asexual ascomycetes, were recorded from 300 samples collected from three sites of Manzala Lake. El-Sharouny et al. (2009) studied the fungal diversity of brackish and saline lakes in Egypt; 97 species (40 ascomycetes, 55 asexual fungi and 2 basidiomycetes) with 70 new records for Egypt were identified from 764 fungal collections recorded in 545 samples from Lakes Edku, Marriott, Burullus and Qaroun. Nour El-Din (2022) recorded 70 marine fungi (35 ascomycetes, 33 asexual fungi and two basidiomycetes) from 2400 decaying submerged herbaceous and wood samples that were collected from Qaroun Lake. Seven recorded fungi were novel to science, of which *Qarounispora grandiappendiculata* was formally described (Nour El-Din et al. 2022). Recently, Bakhit and Abdel-Wahab (2022) described the new genus and species, *Safagamyces marinus* from decaying stems of *Phragmites australis* collected at Safag mangrove, Egypt.

3 Americas

3.1 Canada (S.J. Adams and A.K. Walker)

Marine mycology in Canada began in the late 1960s with studies of intertidal lignicolous fungi from Newfoundland (1968) and British Columbia (1969) by Gilbert C. Hughes of the University of British Columbia, who further studied the geographical distribution of marine fungi (Hughes 1974, 1975). In the following decades, most marine mycology in Canada was conducted on the Atlantic coast by both Canadian and American mycologists. The students of Darryl W. Grund (Acadia University, in Nova Scotia) studied lignicolous marine fungi from marine inundated wood along the coastline (Neish 1970) and in the saltmarshes of the Minas Basin (Boland and Grund 1979). J. David Miller and Norman J. Whitney (University of New Brunswick) then completed a series of papers investigating marine fungal diversity in seawater, macroalgae, marine sediments and salt marsh grasses throughout the Bay of Fundy and the coast of Prince Edward Island. Growth characteristics and metabolites of several marine fungi were described, the new species *Didymosphaeria lignomaris* was characterized (Miller and

Savard 1989; Miller and Whitney 1981a,b,c, 1983; Miller et al. 1984; Strongman et al. 1985) and thraustochytrids were documented from seawater (Miller and Whitney 1981d). Felix Bärlocher (Mount Allison University, New Brunswick) further investigated the fungal diversity of *Spartina alterniflora* and the impacts of these fungi and the snail *Littoria saxatalis* on smooth cordgrass growth and decomposition (Bärlocher and Moulton 1999; Bärlocher et al. 1989; Mansfield and Bärlocher 1993; Samiaji and Bärlocher 1996). Trussell and Jones (1970) investigated the role of marine fungi in the decomposition of wood in the sea.

Since the early 2010s, growing interest in the chemical compounds produced by fungi adapted to the North Atlantic and Arctic Oceans led to increased research on natural product discovery. David Overy and Russell Kerr (University of Prince Edward Island), Alyssa Grunwald (Atlantic Veterinary College), and Andrew Flewelling, Christopher Gray and John Johnson (University of New Brunswick) led the isolation of marine fungi from seafoam, marine sediments and macroalgae, and description of antimicrobial and other chemical compounds (Flewelling et al. 2013; Grunwald et al. 2016, 2017; Morehouse et al. 2020; Overy et al. 2014, 2019). Recent advances in sequencing and bioinformatic techniques allowed detection of novel chytrid lineages from marine environments led by Andre Comeau, Dalhousie University (Comeau et al. 2016).

The new marine fungus *Lulworthia fundyense* was recently described from marine inundated wood (Taylor et al. 2022). Allison Walker and her students at Acadia University also characterized *Spartina* rhizosphere fungi, including arbuscular mycorrhizae in Nova Scotia salt marshes (d'Entremont et al. 2021), fungi and microarthropods in *Spartina* decomposition (Malloch et al. 2022), littoral zone lichens (Vail and Walker 2021) and algicolous fungi (Cooper and Walker 2022) from the Bay of Fundy. Currently, over 300 species of marine fungi are known from Atlantic Canada.

3.2 Mexico (M.C. González)

Despite nearly 60 years of study, much of the diversity of marine fungi in Mexico still remains to be discovered. The first exploration was by Jan Kohlmeyer (1966), when he collected several species of marine fungi from mangroves located in the State of Veracruz on the Gulf of Mexico coast. The publication of that expedition in 1966 established the beginning of marine mycology in Mexico. In collaboration with Erika Kohlmeyer and Brigitte Volkmann-Kohlmeyer, Jan Kohlmeyer undertook several expeditions in the period 1971–1993, registering several species of Mexican marine fungi from coastal habitats, mainly mangroves and sandy beaches. Interestingly, during these explorations the Kohlmeyers noted that the marine coasts of Mexico harbor a high and unregistered diversity of fungi. A decade later, Kevin Hyde described a new manglicolous genus (*Falciformispora*), and two new species: *F. lignatilis* and *Trematosphaeria lineolatispora* in the State of Colima on the Pacific Ocean coast (Hyde 1992a).

In the early 1990s, Maria C. Gonzalez was enrolled in the Graduate Biology Sciences Program under the tuition of Teofilo Herrera and Jan Kohlmeyer to study the biodiversity of arenicolus marine fungi on sandy beaches of Mexico. Her research deals mainly with the exploration and taxonomy of culturable marine fungi from sandy beaches, mangroves, and associated fungi on coral reefs. A few graduate students successfully completed their studies under her tuition, including: Patricia Velez (sandy beach marine fungi, and population genetics of *Corollospora*), María Cristina Medina Ortiz (diversity of coral reef associated fungi) and Carlos Alpuche González (diversity of mangrove marine fungi). Velez continued her studies with the exploration of diversity (sandy beaches, deep-sea, oxygen minimum zones, and hydrothermal vents), molecular ecology, bioremediation, and genetics of *Corollospora*. At present, marine mycology at the Institute of Biology continues as the first successfully developed research program in Mexico.

González et al. (2001) listed a total of 62 species (in 41 genera) of marine fungi in Mexico, including 47 ascomycetes (in 29 genera), one basidiomycete and 14 asexual fungi (in 11 genera). Velez et al. (2013, 2015) added two new records of marine fungi, *Arenariomyces majusculus* and *Ceriosporopsis capillacea*. Recently, an updated checklist of the marine fungi of Mexico was published (Portillo-Lopez and Gonzalez-Martinez 2021).

3.3 United States of America (S.J. Adams and A.K. Walker)

'Marine fungi: their taxonomy and biology' (Barghoorn and Linder 1944) was a seminal work on marine mycology in the United States. T.W. Johnson completed work during the 1950s–60s on marine lignicolous fungi, ascomycetes and hyphomycetes found on wood and *Spartina* (e.g. Johnson 1958). In 1961, he co-authored the comprehensive book 'Fungi in oceans and estuaries' with F.K. Sparrow who had discovered thraustochytrids in 1934. S.P. Meyers and E.S. Reynolds were responsible for additional effort on marine lignicolous fungi (Meyers and Reynolds 1957, 1959). Meyers (1974) then characterized species associated with seagrasses and saltmarsh grasses. D. Ahearn, F.J. Roth and J.W. Fell completed pioneering work on marine yeasts isolated from marine sediments, water, seagrass and invertebrates (Fell et al. 1960; Roth Jr. et al. 1962). R.V. Gessner completed extensive taxonomic characterization of fungi associated with cordgrass (*Spartina*) from salt marshes along the Atlantic coast of the US and Canada (Gessner 1976, 1977; Gessner and Goos 1973; Gessner and Kohlmeyer 1976). Carol Shearer, a leading authority on aquatic ascomycetes, began her career researching the distribution and taxonomy of lignicolous ascomycetes of the Chesapeake Bay (Shearer and Crane 1971), and proceeded to document a wide range of marine fungi. Steve Newell later completed long-term studies on the role of marine fungi in the decomposition of saltmarsh grass, using ergosterol as a proxy for fungal biomass (Newell 1993; Newell et al. 1987). Joey Spatafora's phylogenetic studies refined our understanding of marine fungal evolution, resulting in the removal of the genera *Lindra* and *Lulworthia* from the Halosphaeriaceae (Kohlmeyer et al. 2000; Spatafora et al. 1998). Jinx Campbell worked on phylogenetic studies on multiple orders of marine fungi (Campbell 2005; Campbell et al. 2003, 2005, 2009; Walker and Campbell 2010).

Jan Kohlmeyer, with a research career spanning more than 70 years, was a giant of North American marine mycology. The Kohlmeyers (including Erika Kohlmeyer and Brigitte Volkmann-Kohlmeyer) described 149 species, 50 genera, four families and four new orders of marine fungi, in 158 papers and four books. Their collections are preserved at the New York Botanical Garden. 'Marine mycology: the higher fungi' (Kohlmeyer and Kohlmeyer 1979) was one of the first comprehensive publications to combine literature, monograph genera and species and remains an indispensable reference.

An international marine fungi workshop held at the Marine Biological Laboratory (Woods Hole, MA) led to the publication of 'Fungi in the marine environment: open questions and unsolved problems', providing a new focus for global marine mycological research (Amend et al. 2019). Identification of genes responsible for biomass degradation and fungal assimilation of nitrogen was undertaken to better understand the role of fungi and the oceanic 'mycoloop', re-assessing fungal biogeographical processes, revision of their taxonomy and improving protocols for isolating marine fungi as well as highlighting further research topics. Current American marine mycological research features global collaborations led by Anthony Amend (Hawaii) on patterns of biogeography, community phylogenetics and fungal biodiversity (Gladfelter et al. 2019; Tisthammer et al. 2016; Wainwright et al. 2017); Brandon Hassett on Arctic marine fungal communities; their spatial distribution, ecological roles and functional genetics (Hassett et al. 2017, 2019; Rämä et al. 2017), Cassie Ettinger (California) on *Zostera marina* – associated fungi (Ettinger and Eisen 2020; Ettinger et al. 2021) and Amy Gladfelter (UNC) on marine fungal cell division using time-lapse imagery (Gladfelter et al. 2019; Mitchison-Field and Gladfelter 2021; Mitchison-Field et al. 2019).

4 Asia

4.1 China (J. Jin and E.B.G. Jones)

Although China has a long coastline and many renowned mycologists, few have ventured to examine its marine fungal diversity. The first reports are those of Lilian Vrijmoed who collected marine fungi on Hainan Island (Vrijmoed et al. 1996). Liu et al. (2010) documented the phylogenetic diversity of culturable fungi associated with two marine sponges: *Haliclona simulans* and *Gelliodes carnosa,* also collected at Hainan Island.

Jin et al. (2004a,b) presented preliminary data on marine fungi from wood substrata collected at various locations along the coast of the Yellow Sea and extended knowledge of their occurrence in China. Jin et al. (2005) reported on the collection of *Dryosphaera navigans* and *Torpedospora radiata* from the Yellow Sea, both new records for China. There then followed a series of papers documenting marine fungi of China (Diao et al. 2009; Du and Jin 2010; Qiao and Jin 2011; Sun et al. 2008a,b; Yang et al. 2009a,b). Jin and Huang (2009) reported on the collection of *Monosporascus cannonballus* in the marine environment for the first time. In total some 142 species in 74 genera were reported on driftwood and intertidal wood collected from the Bohai Sea and the Yellow Sea, China, of which 8 genera and 36 species were regarded as new records for China.

Moving on a decade, studies involved molecular techniques in documenting marine fungi in the deep sea and resulted in a number of publications from the Institute of Oceanography, Xiamen, and collaborating institutions. Xu et al. (2014, 2016) reported on the fungal diversity of deep-sea sediments of the Pacific Ocean as assessed by comparison of ITS, 18S and 28S ribosomal DNA regions. Further studies documented deep-sea fungi associated with chimney and sulfide samples from a South Mid-Atlantic Ridge hydrothermal site (Xu et al. 2017); those on deep-sea sediments of a hydrothermal vent system in the Southwest Indian Ridge (Xu et al. 2018) and fungi in the deep-sea hadal sediments of the Yap Trench (Xu et al. 2019).

In the early 2000s, a collaborative research programme was established between Prof. Yong-Cheng Lin and his colleagues at Sun Yat Sen (Zhongshan) University, Guangzhou with Prof. Lilian Vrijmoed at the City University of Hong

Kong. This resulted in the discovery of many novel compounds such as: N-cinnamoylcyclopeptide (Lin et al. 2001a), xyloketals (Lin et al. 2001b), gamma-lactone, eutypoid-A (Lin et al. 2002a), 1-(2,6-dihydroxyphenyl), isocoumarins from the mangrove endophytic fungus #2533 (Lin et al. 2001c), eniatin G from the mangrove fungus *Halosarpheia* sp. (#732) from the South China Sea (Lin et al. 2002b) and butanone (Huang et al. 2005), along with many others.

Many other centers are investigating marine fungi in China including: College of Marine Life Sciences, Ocean University of China, Qingdao; College of Food Science and Technology, Guangdong Ocean University; the State Key Laboratory of Mycology, Institute of Microbiology, Beijing; Department of Biology, Shaoxing University, Shaoxing; Shenzhen Key Laboratory of Microbial Genetic Engineering, Shenzhen University (Han et al. 2022; Wang et al. 2016, 2017; Wu et al. 2023; Zhang et al. 2021; Zhou et al. 2016).

Zhang and colleagues (Shi et al. 2021) have sequenced whole genomes of seven fungi (*Westerdykella dispersa, Trichoderma lixii, Aspergillus tubingensis, Penicillium brefeldianum, Neoroussoella solani, Talaromyces fuscoviridis, Arthrinium marii*) isolated from rhizospheres of two mangrove plants (*Acanthus ilicifolius* and *Kandelia obovata*) from East Harbour National Nature Reserve (Hainan, China). They were able to identify gene clusters for carbohydrate active enzymes and secondary metabolite biosynthesis.

4.2 Hong Kong (K.L. Pang and E.B.G. Jones)

Marine mycology in Hong Kong was initiated by Prof. Peter Thrower and Lilian Vrijmoed studying for the PhD degree which was awarded in 1983 (Vrijmoed 1983). This led to British Council exchanges and the first joint publications on marine fungi (Vrijmoed and Jones 1993). In 1996, Gareth Jones joined the City University of Hong Kong as the Royal Society Kan Tong Po Visiting Professorship and thus the establishment of a strong research group. During this period, City University of Hong Kong hosted the 7th International Marine Mycology Symposium in 1999. It was one of the largest meetings of this group (see www.marinefungi.com). Studies included potential development of thraustochytrids as a source of polyunsaturated fatty acids (PUFAs), mangrove fungal ecological studies and taxonomic studies, wood decay by marine fungi and early studies of fungi on bamboo. A few graduate students successfully completed their studies: Eduardo Leaño (ecology of *Halophytophthora* species in mangrove), Rex Sadaba (mangrove fungal ecology), Keith Fan (thraustochytrids in Hong Kong mangroves and their potential use for PUFAs production), Wen Luo (wood-degrading enzymes of marine fungi), Ka-Lai Pang (molecular phylogeny of the Halosphaeriaceae). Steve Pointing joined the group as a research fellow and Mohamed Abdel-Wahab undertook much of his field work in Hong Kong for his PhD. After the retirement of Lilian Vrijmoed, research on marine fungi has been discontinued.

In November 1992, Kevin Hyde was appointed to a tenured Associate Professorship at the Department of Ecology and Biodiversity, University of Hong Kong, and continued with his contributions to marine mycology. Studies included the taxonomy of mangrove fungi, with a number of graduate students/post-doctoral researchers: Sally Fryar (brackish water in Brunei and Philippines), Vivienne Bucher (wood decay of marine fungi), V.V. Sarma (marine fungi in *Spartina* and mangroves), A.D. Poonyth (taxonomy of marine fungi in Mauritian mangroves), M.V. Ranghoo (phylogeny of aquatic fungi), M.O.K. Poon (intertidal mangrove fungi) and studies by T.K. Goh (taxonomy of mangrove asexual fungi). Steve Pointing also joined University of Hong Kong to carry on his studies on the lignocellulose-degrading marine fungi. With Kevin's move to Thailand in 2007, studies on marine fungi at the University of Hong Kong ceased.

Pang et al. (2016) listed a total of 141 species (in 96 genera) of marine fungi in Hong Kong, including 125 ascomycetes (in 83 genera), 3 basidiomycetes (in 3 genera) and 13 asexual fungi (in 10 genera).

4.3 India (B. Devadatha and V.V. Sarma)

In India, marine fungal studies were carried out on various substrata such as algae, animals, driftwood, intertidal wood, sea grasses, sea foam, mangrove wood, sediments and water. Early research was descriptive: *Antennospora quadricornuta* on small fishing boats at the coasts of Kerala and Chennai (Becker and Kohlmeyer 1958), *Paraliomyces lentiferus* (new genus and species) on wooden fishing boats from Chennai (Kohlmeyer 1959), and *Corollospora pulchella* from the Kerala coast (Kohlmeyer et al. 1967), while Jones (1968) recorded five marine fungi from test blocks of wood immersed near the shores of Mumbai and Kochi coasts. Nair (1970) was the first Indian scientist to investigate marine fungi on intertidal wood from the Kerala coast. Raghukumar (1973) was the first Indian researcher to examine marine fungi on intertidal decomposing mangrove wood from the Tamil Nadu coast and reported 18 species of Ascomycota.

Seshagiri Raghukumar completed his PhD on marine fungi from Tamil Nadu coast in 1973 at Madras University under the supervision of C.V. Subramanian. He later studied the ecology and taxonomy of thraustochytrids with Alwin Gaertner. Later at the CSIR National Institute of

Oceanography, Goa, India, he began with detailed studies on the role of fungi in the marine detrital food web (Raghukumar 2005) and the seasonal dynamics of thraustochytids of the Arabian Sea. Raghukumar made significant contributions to the ecology of these stramenopilan fungi (Raghukumar 2002; Raghukumar and Damare 2011) and, in particular, he developed a novel epifluorescence technique to detect and quantify thraustochytrids in seawater and marine samples (Raghukumar and Schaumann 1973). His students who graduated in marine fungal studies include Varada Damare (ecology and molecular characterization of thraustochytrids and aplanochytrids from oceanic water column; Damare and Raghukumar 2006), Veena Sathe (ecological investigations on fungi associated with detritus from marine macrophytes) and Ruchi Jain (polyunsaturated fatty acids and extracellular polymeric substances from thraustochytrid protists).

Chandralata Raghukumar graduated with a PhD in Plant Pathology from Madras University in 1975 and subsequently worked at the Institute for Marine Research, Bremerhaven, Germany for five years, where she began to work on fungal diseases of algae with Alwin Gaertner. Later at the CSIR-National Institute of Oceanography, Goa, India, she undertook studies on fungal diseases of marine algae along the coast of Goa, describing numerous algal diseases not reported till then (Raghukumar 1986). Raghukumar et al. (1992) isolated several higher marine fungi and thraustochytrids from surface-sterilized macroalgae. She was a pioneer in studying fungi in deep-sea marine sediments. Together with her students, she carried out various research studies on diversity and biology of deep-sea fungi from the Central Indian Ocean Basin (CIOB) at a depth of 5000 m; Damare et al. (2006) and Singh et al. (2012) isolated a number of fungi, the majority of which belonged to the genera *Aspergillus*, *Penicillium*, and *Cladosporium*. Another important area of her research was on the role of fungi in the oxygen minimum zone of the Arabian Sea, where Manohar and Raghukumar (2013) reported marine fungal diversity and anaerobic denitrification of fungi from coastal marine sediments of Goa. She also pioneered the study of fungi in hard corals of the Lakshadweep islands, along with J. Ravindran (Raghukumar and Ravindran 2012).

B.D. Borse and colleagues studied marine fungi of mangroves extensively and described many new species: *Didymella avicenniae* and *Halosarpheia ratnagiriensis* (now *Saagaromyces ratnagiriensis*) (Patil and Borse 1983), *Aigialus mangrovis*, *A. rhizophorae* and *Pleospora avicenniae* (now *Halojulella avicenniae*) (Borse 1984, 1985, 1987), *Acrocordiopsis patilii* (new genus) (Borse and Hyde 1989), *Biatriospora marina* (new genus) and *Massarina velataspora* (now *Morosphaeria velataspora*) (Hyde and Borse 1986a, 1986b). Borse et al. (2013) listed 207 marine fungi recorded along the coastal states and islands of India.

B.P.R. Vittal from University of Madras, Chennai and his students M. Ravikumar and V.V. Sarma also investigated marine mangrove fungi of India focusing on frequency of occurrence, host specificity, substrate recurrence, vertical distribution and seasonality (Sarma and Vittal 1998–1999, 2000, 2001, 2002; Sarma et al. 2001; Vittal and Sarma 2006), and introduced the new species *Lophiostoma mangrovei* (now *Rimora mangrovei*) (Kohlmeyer and Vittal 1986) and *Bathyascus mangrovei* (Ravikumar and Vittal 1991). Sarma and Vittal (2004) proposed a dichotomous key to 88 marine fungi recorded from mangroves of Godavari and Krishna deltas, east coast of India and developed an interactive CD-ROM for mangrove fungi, which included 85 mangrove fungi from Indian and Hong Kong mangroves (Sarma et al. 2000).

In 2009, V.V. Sarma acquired a faculty position at Pondicherry University, India where he is now conducting research in the field of fungal biotechnology. His student B. Devadatha studied the biodiversity, morpho-molecular characterization of marine fungi in India and their anti-quorum sensing potential. This resulted in five novel genera, namely *Halocryptosphaeria*, *Pseudoastrosphaeirellopsis*, *Raghukumaria*, *Thyridariella* and *Vittaliana*, and 25 new marine fungal species (Devadatha et al. 2017, 2018, 2019, 2021a; Dayarathne et al. 2020a).

K.R. Sridhar completed his doctorate in Biosciences from Mangalore University. He made significant contributions to the fields of freshwater, mangrove, and marine mycology in India (Sridhar and Kaveriappa 1988, 1991). Ananda and Sridhar (2002) documented 10 ascomycetes and one basidiomycete on intertidal mangrove wood, and studied endophytic fungi in roots of mangrove plants from Udyavara mangroves (Ananda and Sridhar 2002). Prasannarai et al. (2000) described a new species *Corollospora indica* on intertidal wood, and Maria and Sridhar (2002) introduced *Passeriniella mangrovei* on *Rhizophora mucronata* from Karnataka mangroves. Maria et al. (2005) investigated the antimicrobial and enzymatic activities of endophytic fungi isolated from *Acanthus ilicifolius* and *Acrostichum aureum* from Nethravathi mangroves. Further studies on fungal diversity on decaying intertidal wood were conducted by Maria and Sridhar (2003) and Ghate and Sridhar (2015).

Suryanarayanan and Kumaresan (2000), Kumaresen and Suryanarayanan (2002), Suryanarayanan (2012a,b) and Venkatachalam et al. (2015) documented the endophytes of various mangrove plants, sea sponges, sea grasses and marine macroalgae of southwest coast of India. Suryanarayanan et al. (2010) assessed the ability of endophytes to produce antialgal, antifungal, antibacterial, antiinsect, and antioxidant compounds.

Raveendran and and Manimohan (2007) published a book entitled 'Marine fungi of Kerala', which covers 80 marine fungal species from the Kerala coast. Khan and Manimohan (2011) listed 23 marine fungi associated with driftwood from coastal sites in Kerala State and the Lakshadweep Islands of India.

Nambiar and Raveendran (2009) examined the marine mycoflora across several coastal locations in Andhra Pradesh, Kerala, and Tamil Nadu, while Nambiar and Raveendran (2010) and Nambiar and Raveendran (2015) focused on the frequency and abundance of fungi on arenicolous marine and animal substrata, respectively.

Samir Damare joined as a Scientist at the CSIR National Institute of Oceanography, Goa, India in 2009, and he currently works on diversity of deep-sea fungi and their biotechnological potential. Fungal growth in a simulated deep-sea environment was investigated using a proteomic technique by Krishnaswamy (2019).

The highest number of mangrove fungi, 339, has been documented in India in studies compiled by Devadatha et al. (2021b). A total of seven novel genera and 44 species were described along the coasts of India. At present, the Department of Biotechnology, Pondicherry University and the National Institute of Oceanography in Goa, India are the only two institutions actively involved in marine fungal research. Marine fungal research, however, needs greater resources, including dedicated research facilities and personnel. Marine fungi are an integral part of India's bioresources, and the country's extensive coastline provides ample opportunities for exploration.

4.4 Malaysia (E.B.G. Jones)

Marine fungi, especially those on mangrove substrata, have been extensively studied in Malaysia, resulting in the compilation of a monograph on Malaysian mangrove fungi (Alias and Jones 2009). Jones and Tan (1987) initiated the study of manglicolous marine fungi in Malaysia listing 32 species collected at Gelang Patah mangrove, Johor, while Jones and Kuthubutheen (1989) recorded 82 species from Morib, Kuala Selangor, Port Dickson and Sementa mangroves. Alias et al. (1995) listed 100 species of marine fungi (82 ascomycetes, 15 asexual fungi and three basidiomycetes) collected from three mangrove stands in Kuala Selangor, Morib and Port Dickson, while Alias and Jones (2000a,b) recorded 53 species of fungi associated with *Rhizophora apiculata* from Morib mangrove. Currently, 390 marine mangrove fungi are recorded from Malaysia (Alias et al. 2010).

Investigations of marine fungi in Malaysia fall under several headings: systematics, generally supported by molecular data (*Acrocordiopsis sphaerica*, Alias et al. 1999; *Calathella mangrovei*, Jones and Agerer 1992; *Corollospora besarispora*, Sundari et al. 1996a; *Fasciatispora lignicola*, Alias et al. 1994; *Phomatospora nypae*, Hyde 1993b; *Pyrenographa xylographoides*, Alias et al. 1996; *Tirisporella beccariana*, Jones et al. 1996, and others); surveys of different substrata and locations (Alias and Jones 2009; Alias et al. 2010; Hyde 1993b; Hyde and Alias 2000; Jones and Alias 1996; Jones and Kuthubutheen 1989; Jones and Tan 1987; Kuthubutheen 1981; Pang et al. 2010b; Sundari et al. 1995, 1996a,b; Yanna et al. 2001; Zainuddin et al. 2008), production of antimicrobial compounds (Zainuddin et al. 2008, 2010), ultrastructure studies (TEM, SEM) (Alias et al. 2001; Yusoff et al. 1994a,b,c, 1995), and experimental studies (Alias and Jones 2010; Sundari and Vikineswary 2002).

Several monographs have been published: 'Marine fungi from mangroves of Malaysia' by Alias and Jones (2009), 'Checklist of fungi of Malaysia' (Lee et al. 2012, includes marine fungi), 'Malaysian fungal diversity' (Jones et al. 2007, includes marine fungi).

4.5 Philippines (E.B.G. Jones and M. Calabon)

Many published studies explore the marine fungi in the Philippines, the earliest by Kohlmeyer (1968) based on his single collection from Subic Bay of *Antennospora quadricornuta* observed from test panels of *Dipterocarpus* sp. and *Pseudotsuya* sp.

Flor Uyenco was the guiding light for marine mycology in the Philippines and was the course leader of the innovative idea from UNESCO to provide funding for a six-week workshop on mangrove fungi at the University of the Philippines, Diliman campus, which supported one scientist from each Asian country, with lecturing staff that included C.V. Subramanian, Gareth Jones, and the publication of the presented papers (Agate et al. 1988). A number of the students went on to work in the subject (W.F. Leong, Singapore; J. Torres, Philippines; A. Chalermongse and T. Boonthavikoon, Thailand).

Using sugarcane bagasse and rice straw as baits, Gacutan and Uyenco (1983) isolated *Antennospora quadricornuta*, *Clavariopsis bulbosa*, *Halocyphina villosa*, *Nia vibrissa*, *Torpedospora radiata*, *Verruculina enalia* and *Lulworthia* sp. in the Province of Aklan. Jones et al. (1988) recorded 31 manglicolous fungi (30 Ascomycota, 1 Basidomycota) from Pagbilao mangrove, Quezon. Most are Sordariomycetes (16 species), followed by Dothideomycetes (12 species), Eurotiomycetes (*Sclerococcum haliotrephum*), and Leotiomycetes (*Halenospora varia*). Jones et al. (1996) introduced a novel genus *Tirisporella* typified by *Tirisporella beccariana* isolated from both the rachis of *Nypa fruticans* in Pampanga Province and the petioles in Quezon Province. Alias et al. (1999) studied marine fungi from mangrove driftwood and decayed wood attached to their host in three different sites (Boracay, Taklong, Pagbilao), and recorded 51 taxa including a novel species *Acrocordiopsis sphaerica*. In Siargao Island, Besitulo et al. (2010) identified 66 taxa with 46 new records for the Philippines. For the past decade, most researchers have focused on terrestrial fungi and there is still a large knowledge gap on the diversity of marine fungi in the Philippines. Other contributions to marine mycology in the country have been by: Thomas Edison Dela Cruz on antimicrobial, antioxidant activities and decoloration of dyes by marine fungi from mangrove material and seaweeds (Torres et al. 2012); Resurreccion B. Sadaba on marine fungal communities in bunker C oil-impacted sites off southern Guimaras, Philippines (Sadaba and Sarinas 2010).

4.6 Saudi Arabia (M.A. Abdel-Wahab and A.H. Bahkali)

The first report of marine fungi from Saudi Arabia was by Aleem (1978) who reported two species: *Corollospora pulchella* and *Okeanomyces cucullatus* from driftwood samples collected along the Red Sea coast. Bokhary et al. (1992) recorded 37 fungal species from sea water and sea foam samples collected from the Arabian Gulf, of which 7 species were marine: *Paradendryphiella salina*, *Nereiospora comata*, *Dictyosporium pelagicum*, *Ophiobolus australiensis*, *Papulaspora halima*, *Pontogeneia calospora* and *Okeanomyces cucullatus*. Mohamed A. Abdel-Wahab joined King Saud University in 2011 where he carried out taxonomic and ecological studies on marine fungi and recently on thraustochytrids from mangroves along the coast of the Red Sea and the Arabian Gulf in Saudi Arabia. He supervised two master students (Mohamed S. Hodhod and Mohamed O. Al-Hebshi). Gareth Jones joined King Saud University in 2013 where he collaborated with Ali H. Bahkali through the Distinguished Scientist Fellowship Program (DSFP) and this collaboration is ongoing. These collaborative studies have resulted in several ecological, physiological and taxonomic studies with the introduction of 12 new species, four new genera and one new family (Abdel-Wahab et al. 2014, 2016, 2017, 2018, 2019a,b, 2020, 2021a,b,c, 2022; Ariyawansa et al. 2015; Hodhod et al. 2012; Hyde et al. 2016; Li et al. 2016; Liu et al. 2015).

Hodhod et al. (2012) conducted the first study of marine fungi from mangroves in Saudi Arabia. He collected decayed mangrove wood and leaf samples of *Avicennia marina* from two mangrove sites at Yanbu city in Saudi Arabia. He recorded 36 fungi (19 from decaying intertidal wood and 17 from decaying submerged leaves) of which 21 marine fungi (including 18 from wood and 3 from leaves) were new for Saudi Arabia. The recorded fungi included 7 new species, of which *Amarenographium solium* was published (Hodhod et al. 2012).

Abdel-Wahab et al. (2014) recorded 37 marine fungi from 457 samples of driftwood and intertidal decayed wood of *Avicennia marina* collected from three sites along the Red Sea coast of Saudi Arabia. Most of the recorded fungi (31) were new records for Saudi Arabia. That study further documented marine fungi from the tropical mangroves at Al-Leith city along the coast of the Red Sea, Saudi Arabia. Al-Hebshi (2015) studied marine fungi from mangroves in the Arabian Gulf, Saudi Arabia for the first time. He recorded 19 species (11 ascomycetes and 8 asexual ascomycetes) from 60 samples of dead wood of *Avicennia marina* and driftwood that were collected from Tarut Island mangroves, Saudi Arabia. Of these 19 species, 14 were new records for Saudi Arabia and 9 were new to science, of which *Halocryptovalsa avicenniae* was formally described (Abdel-Wahab et al. 2017; Dayarathne et al. 2020b).

Abdel-Wahab et al. (2021a) conducted high-throughput amplicon sequencing study of the mycobiome associated with leaves of the seagrass *Halophila stipulacea* collected from a mangrove site in Saudi Arabia. They sequenced the first 300 bp of the 28S rDNA amplicon using Illumina MiSeq (bTEFAP). Fungi represented between 1.1 % and 5.8 % of the total reads in the five samples. A total of 18,279 reads (representing 1.96 % of the total reads) were recorded from the five samples representing 296 molecular species (operational taxonomic units, OTUs) that belong to 13 fungal phyla. At the phylum level, Basidiomycota dominated the community (37.2–51.6 %) in three of the five samples, while Neocallimastigomycota (37.5 %) and Mucoromycota (42.1 %) dominated the community in the fourth and the fifth samples, respectively.

4.7 Taiwan (K.L. Pang)

Early research on marine fungi/fungus-like organisms in Taiwan was on *Halophytophthora*, thraustochytrids and chytrids. Volz et al. (1976) isolated a number of species of the Thraustochytriaceae in coastal habitats of Taiwan, in conjunction with a few marine true chytrids, *Chytridium chaetophilum*, *Diplochytridium citriforme*, *Rhizophydium sphaerotheca* (Chytridiomycota) and *Olpidium pendulum*

(Olpidiomycota). *Chytridium lagenaria*, *Rhizophydium keratinophilum*, *Globomyces pollinis-pini* and *Paludomyces mangrovei* were also documented from marine habitats of Taiwan (Chen 2020). Ho and Jong (1990) established the genus *Halophytophthora* and described *H. kandeliae* (now in *Phytopythium*) (Ho et al. 1991) and *H. elongata* (now in *Salisapilia*) from fallen mangrove leaves in Taiwan (Ho et al. 2003). Sung-Yuan Hsieh (Bioresource Collection and Research Center, Hsinchu, Taiwan) obtained his PhD from the University of Portsmouth, UK on ultrastructure of marine fungi, especially arenicolous species (Hsieh et al. 2007). He documented 9 arenicolous marine fungi from Taiwan, including *Arenariomyces* spp., *Carbosphaerella leptosphaerioides* and *Corollospora* spp. (Hsieh 2002). In the same year, Hsieh et al. (2002) published a monograph of marine fungi from Taiwan and illustrated 59 species, predominantly Ascomycota. Research on marine fungi has been mainly undertaken by Ka-Lai Pang and his main collaborators Sung-Yuan Hsieh and Gareth Jones (King Saud University). In Taiwan, 107 species of Ascomycota, Basidiomycota and asexual fungi were recorded from coastal habitats (mangroves, sandy beaches, rocky shores) of Taiwan (Pang and Jheng 2012a), including many new species such as *Kitesporella keelungensis* (Pang and Jheng 2012a), *Sedecimiella taiwanensis* (Pang et al. 2010a), *Pileomyces formosanus* (Pang and Jheng 2012b) and *Sclerococcum vrijmoediae* (Pang et al. 2014). Pang et al. (2011b) published a monograph on the marine mangrove fungi of Taiwan, with full descriptions and illustrations. Currently, his research topics include the morphological and molecular diversity of marine fungi in coastal environments of Taiwan, and the ecology of fungi in a marine shallow-water hydrothermal vent at Kueishan Island, Taiwan.

4.8 Thailand (Mark S. Calabon and E.B. Gareth Jones)

The first report of a marine fungus from Thailand was by Kohlmeyer (1984) who reported 15 species from the Chonburi area. Koch (1986) listed 16 species with two new marine fungi *Arenariomyces parvulus* and *Corollospora cinnamomea*. Hyde (1989), Hyde and Jones (1992), and Hyde et al. (1990) collected mangrove fungi from the Ranong and Phang Nga Provinces, and driftwood along shores at Phuket, and introduced the fungi: *Astrosphaeriella mangrovei*, *Bathyascus grandisporus*, and *Hypophloeda rhizospora*. Sakayaroj et al. (2004) listed 147 marine fungi from Thailand including three Basidiomycota, 117 Ascomycota and 26 asexual morphs. Research on marine fungi continued thereafter at BIOTEC (National Centre for Genetic Engineering and Biotechnology), Pathum Thani; Burapha University, Chonburi; and Mae Fah Luang University, Chiang Rai, Thailand, resulting in extensive additions to the marine mycology literature (see selected literature: Calabon et al. 2021; Dayarathne et al. 2017; Hattori et al. 2014; Hyde and Nakagiri 1989; Hyde et al. 1993; Jarikhuan 2002; Jones et al. 2017; Loilong et al. 2012; Pang et al. 2013; Pilantanapak et al. 2005; Suetrong et al. 2015, 2017; Supaphon et al. 2017; Unagul et al. 2017; Wijesinghe et al. 2023; Zhang et al. 2019). All these refer to the documentation of new taxa. Marine yeasts have been studied at Kasetsart University, Bangkok by Am-in et al. (2008) and Limtong et al. (2010) with many new taxa described from mangroves in Thailand. Another intensively researched topic in Thailand is secondary metabolite production from marine fungi at two centers: BIOTEC, Bangkok and Prince of Songkla University, Songkhla (selected literature: Chinworungsee et al. 2001; Isaka et al. 2002, 2010; Phongpaichit et al. 2006; Rukachaisirikul et al. 2009, 2011; Trisuwan et al. 2009, 2011).

5 Australasia

5.1 Australia (S.C. Fryar)

The first record of a marine fungus in Australia was by Johnson and McNeil (1941) who recorded an unidentified ascomycete in hardwood immersed in seawater in Sydney. Cribb and Herbert (1954) reported three species of fungi parasitizing marine algae in Tasmania (*Haloguignardia tumefaciens* [as *Guignardia tumefaciens*], *Massarina cystophorae* [as *Otthiella cystophorae*], *Chadefaudia gymnogongri*), the first two were new species.

Cribb and Cribb then went on to document 20 more marine fungi between 1955 and 1969 (Cribb and Cribb 1955, 1956, 1960, 1969), leading to the description of 10 new species. They were among the first in the world to study mangrove fungi. Following this, Jan Kohlmeyer and Brigitte Volkmann-Kohlmeyer expanded our knowledge of marine fungi in Australia, mostly with collections in Queensland (Kohlmeyer 1972, 1973a, 1984, 1986; Kohlmeyer and Volkmann-Kohlmeyer 1987, 1989, 1991).

During the 1990s, Kevin Hyde added to the records (Hyde 1990, 1992b,c, 1995; Hyde and Nakagiri 1991), describing a number of new taxa including *Tunicatispora australiensis* (Hyde 1990), *Cryptovalsa halosarceicola* (Hyde 1993a), *Eutypa bathurstensis* (Hyde and Rappaz 1993), and *Eutypella naqsii* (Hyde 1995). Most of these studies were focused on fungi on mangrove wood and driftwood in Queensland, with some work also in New South Wales and Victoria. Abdel-Wahab and Jones (2000) reported three new species from driftwood collected from a sand dune at Mornington Peninsula Nature Park, Victoria, Australia: *Caryospora australiensis*, *Platystomum scabridisporum* and *Savoryella melanospora*.

A recent survey of fungi on mangrove wood in South Australia listed 43 marine fungal species (Fryar et al. 2020). Only one species, *Corollospora maritima*, had previously been found in South Australia and 11 had not previously been recorded in Australia. Also, in South Australia a new genus *Annabella*, was introduced from intertidal mangrove wood with one species *Annabella australiensis* (Fryar et al. 2019).

Currently, there are 132 marine fungi recorded for Australia (https://freshwaterandmarinefungiaustralia.com/). Most of these records are from mangrove wood or pneumatophores. Although a range of other substrata have been investigated, such as live corals (Kendrick et al. 1982), macroalgae (Cribb and Cribb 1969), sand grains (Kohlmeyer and Volkmann-Kohlmeyer 1991), samphire (Hyde 1993a), and animal pathogens (Langdon and McDonald 1987; Norton et al. 1994), these records are rare. McCarthy (1991, 1994, 2001, 2008) reported a number of *Verrucaria* marine lichens from Australia, including the new species: *V. alborimosa*, *V. coralliensis*, *V. meridionalis*, *V. australiensis*, *V. sessilis*, and *V. subdiscretia*. Other species recorded from Australia include: *Verrucaria mucosa*, *V. serpuloides*, *V. microsporoides*, *V. halizoa*, *V. aucklandica*, *V. prominula*, *V. striatula*, *V. subdiscreta*, *V. fusconigrescens* and *V. maura* (McCarthy and Kantvilas 2015).

To understand the ecology of marine fungi in Australia, their role and importance in marine habitats, there needs to be significantly more investment in baseline data. Most records of marine fungi in Australia are single records. We have little idea of the distribution of most species or the stability of their populations. These organisms are likely to be under significant threat from human activity and we currently have no way of knowing their conservation status.

Australia has more than 34,000 km of coastline, many offshore islands, more than 1000 estuaries and hundreds of inland saltwater lakes. In other parts of the world seagrasses (Poli et al. 2022), deep-sea hydrothermal vents (Pang et al. 2019), microscopic invertebrates (Holt et al. 2022), sediments (Zhang et al. 2021) have been found to support high fungal diversity. In Australia, the vast majority of these habitats and substrata have not yet been explored for marine fungi.

6 Europe

6.1 France (G. Burgaud, L. Meslet-Cladière, M. Mehiri, J. Dupont, S. Prado and C. Roullier)

Marine mycology in France started with the description of the first marine fungus, *Leptosphaeria typharum* (current name *Juncaceicola typharum*) by Jean Baptiste Henri Joseph Desmazières (Desmazières 1849). Early marine mycology in France consisted of sporadic descriptions of marine fungal species by (i) the Crouan brothers in their "Florule du Finistère" which can be translated as the "Flora of the extreme west of Brittany" (Crouan and Crouan 1867), (ii) Feldmann (1957) describing the ascomycetous parasite *Chadefaudia marina* on the marine alga *Palmaria palmata*, and (iii) Doguet (1962) describing the basidiomycete *Digitatispora marina* on submerged wood in seawater. A total of 14 ascomycetous (*Leptosphaeria typharum*, *Sphaeria posidoniae*, *Camarosporium roumeguerei*, *Thalassoascus tregoubovii*, *Chadefaudia marina*, *Asteromyces cruciatus*, *Diplocladiella scalaroides*, *Didymella magnei*, *Xylomyces rhizophorae*, *Nais inornata*, *Ceriosporopsis capillacea*, *Haloguignardia cystoseirae*, *Corollospora armoricana*, *Acremonium neocaledoniae*) and three basidiomycetous (*Mycaureola dilseae*, *Digitatispora marina*, *Flamingomyces ruppiae*) taxa were described from France and French territories (French Guiana, Guadeloupe, Martinique, Mayotte, Réunion, French Polynesia, New Caledonia, etc.) during the period spanning 1849 to 2008. It should be noted that this list of 17 species is not exhaustive as it was obtained by cross-referencing the marinefungi.org and indexfungorum.org databases and some information was missing for certain taxa.

This limited number of studies describing the marine fungal diversity in France and French territories indirectly highlights the unexplored reservoir of biodiversity in the very different and contrasted habitats spread in this vast and expanded country. For example, mangroves, lagoons, coral reefs of French overseas departments and territories, unique habitats of French Austral Lands and Seas, exploration of deep-sea and deep subseafloor habitats, etc. Marine mycology in France is currently conducted mainly by four laboratories using complementary approaches and thus working together on many research projects related to marine fungi.

(i) ISOMer ("Institut des Substances et Organismes de la Mer"): Studies on marine fungi in Nantes began in the late 1990s at the instigation of Yves François Pouchus, who first hypothesized that fungi might explain some atypical episodes of seafood toxicity. Several samples in shellfish farming areas were then collected and allowed to build a collection of more than 1000 marine fungal strains from the Atlantic coast (Sallenave-Namont et al. 2000). These were then first investigated for mycotoxin production (Grovel et al. 2003; Landreau et al. 2002; Ruiz et al. 2007; Vansteelandt et al. 2012). Many families of compounds could then be identified from these fungal strains and led to more recent research, which aims at understanding their role in nature such as for communication or defense. The team has then gained expertise in mass spectrometry metabolomics and associated bioinformatics to decipher the impact of abiotic and biotic stresses on metabolite production from marine fungi. Media enriched with environmental samples (extracts from mussels, shrimps and sponges) as well as co-cultures (fungi-fungi, fungi-bacteria, fungi-microalgae) have been developed and are now used on a regular basis for all sorts of studies (Berry et al. 2023; Bertrand et al. 2017; Fernand et al. 2017; Hoang et al. 2018; Kerzaon et al. 2009; Roullier et al. 2016; Vansteelandt et al. 2013). In addition, the potential of marine fungi and fungal metabolites for biocontrol and drug discovery, particularly in the fight against cancer and infectious diseases, is also investigated (Dias et al. 2015; van Bohemen et al. 2021). Recent developments also include the assessment of marine fungal enzymes (more specifically vanadium-haloperoxidases) as new tools for biocatalysis and green chemistry (Cochereau et al. unpublished). Following an initial workshop in July 2014 in Prince Edward Island in Canada, the team hosted in Nantes the first international conference on Marine Fungal Natural Products (MaFNaP) in July 2015. It was a joint meeting with the 14th International Marine and Freshwater Mycology Symposium and was the first event of this type uniting both ecologists and chemists.

(ii) The LUBEM, a research laboratory of the "Université de Brest, (UBO)", began studying marine fungi in the early 2000s at the initiative of Georges Barbier, who hypothesized that fungi may occur in deep-sea habitats and more precisely in deep-sea hydrothermal vents. Having confirmed this hypothesis by highlighting fungal communities in such extreme habitats using culture-dependent and culture-independent methods with the help of several PhD students (Burgaud et al. 2009, 2010, 2011; Le Calvez et al. 2009), the research theme has then evolved towards the analysis of other habitats, either extreme, such as deep subsurface sediments (Ciobanu et al. 2014; Rédou et al. 2014), or non-extreme, such as coastal waters (Li et al. 2019; Wang et al. 2021). The team has acquired expertise in uncovering the diversity, activity and ecological roles of marine fungi by using a combination of approaches, i.e., metabarcoding, (meta)genomics, (meta) transcriptomics, metabolomics and high-throughput culturing technique. Recently, the LUBEM has implemented screening strategies to uncover the biotechnological potential of the hundreds of marine fungal isolates generated in the frame of numerous research projects and preserved in the UBO Culture Collection (https://nouveau.univ-brest.fr/ubocc/fr). These recent developments include the assessment of marine fungal enzymes involved in depolymerization of plastics (Burgaud et al. 2022; Philippe et al. 2023), degradation of hydrocarbons (Maamar et al. 2020), or more specifically vanadium-haloperoxidases as new tools for biocatalysis and green chemistry (Cochereau et al. 2022).

(iii) The Marine Natural Products (MNP) team, led by Mohamed Mehiri, is a strong component of the Institute of Chemistry of Nice (ICN, UMR 7272 CNRS). Located at Université Côte d'Azur (UCA), the MNP team has a long tradition in the study of marine organisms, including marine fungi (Bovio et al. 2019a,b; Elsebai et al. 2018; Keeler et al. 2021; Marchese et al. 2020; Quémener et al. 2021). The research activity of the Natural Products group focuses on high value-added molecules isolated from diverse marine (micro)organisms with the aim to isolate and identify new bioactive compounds using the analytical facilities of the UCA (nHPLC, 2 NMR, HPLC-MS, MS L&H resolution) and an established network of collaborations, notably for screening. As leader of the MNP team, Mehiri has great experience in isolation, structural elucidation, synthesis and valorization of high value-added molecules.

(iv) National Museum of Natural History (MNHN) has always had considerable expertise in mycology. The Museum's collection of fungal strains currently contains more than 6,000 strains (including 350 types) corresponding to 1,425 different species (https://www.mnhn.fr/en/fungal-strain-collection). The collection is particularly focused on terrestrial ascomycetes and zygomycetes, but contains some specimens from marine and aquatic environments (Dupont et al. 2009; Samadi et al. 2010). Research on marine fungi has increased in recent years with the collaboration between the Chemistry of Fungal and Bacterial Natural Products (CPNFB) team of the Unit Molecules of Communication and Adaptation of Microorganisms (UMR 7245 MCAM) and the MNHN collection. Indeed, the CPNFB team is developing integrative and multi-omics approaches, from the "gene to the molecule", to decipher the molecular interactions between microbiota (bacteria and fungi) and macroalgae. In this context, endophytes and epiphytes associated with kelps (Fucales and Laminariales) were analyzed using cultivable and non-cultivable approaches along with the chemical characterization of their metabolites. These studies highlighted the key role of the chemical mediation in fungi-microbiota, fungi-pathogen and fungi-host interactions (Tourneroche et al. 2020; Vallet et al. 2018, 2020). These works have also generated a collection of marine fungal strains (>500) along with a library of fungal crude extracts that are exploited in the frame of various national, European and international research projects for their biosynthetic potential, ecological role and potential uses (Dezaire et al. 2020). Today, marine mycology is a key theme of CPNFB projects and its study should open new avenues on the ecological role of fungi in the marine holobiont.

6.2 Germany (T. Rämä and M. Reich)

Germany has long traditions in the studies of marine fungi and several of the pioneering researchers in the field were German. The studies made during the 20th century focused on the taxonomy, geographical and vertical distribution within the sublittoral-tidal zone and physiology of marine fungi, whereas current research focuses on molecular biosystematics, the roles and importance of marine fungi in biogeochemical processes and natural products discovery.

In 1922, Erich Werdermann, the curator of the mycological collections in Berlin-Dahlem, described perhaps the most iconic marine fungus *Corollospora maritima* (Werdermann 1922). Willy Höhnk at the Institut für Meeresforschung in Bremerhaven studied the occurrence and taxonomy of marine fungi (Höhnk 1955). Through these studies he became convinced of the distinct nature of fungi in saline waters that legitimized the existence of marine mycology as an independent research field, and initiated the first International Marine (and later Freshwater) Mycology Symposium (IMMS) in Bremerhaven in 1966. Karsten Schaumann continued research on marine fungi in Bremerhaven with special interest in their growth and enzyme production. He isolated fungi from German and foreign waters, from the subtropics to the polar regions, thereby establishing the KMPB (Kulturensammlung Mariner Pilze Bremerhaven) collection (Schaumann 1968).

Other studies at the Institut für Meeresforschung include marine and mangrove chytrids (Ulken 1970, 1972) and quantitative estimation of thraustochytrids in sea water and their taxonomy (Gaertner 1980, 1982). Zuccaro et al. (2008) investigated marine fungi associated with the brown seaweed *Fucus serratus* and their identification. Physiological studies of marine fungi, their reproduction and tolerance of hydrostatic pressure were conducted by Molitoris and his research team at Regensburg University (Lorenz and Molitoris 1997).

At the same time, Ingeborg Schmidt conducted an extensive study on marine fungi along the German Baltic coast (Schmidt 1974). The renowned Jan Kohlmeyer started his career in Germany, with biodeterioration studies of fungi in marine wood at the Bundesanstalt für Materialprüfung in Berlin-Dahlem, but continued his career, which resulted in the description of hundreds of new taxa (Kohlmeyer and Kohlmeyer 1979) and later Kohlmeyer and Volkmann-Kohlmeyer (2001), as professor at the University of North Carolina, USA.

Currently active German marine mycologists include Marlis Reich (University of Bremen) who is developing molecular toolkits for the taxonomic classification and detection of marine fungi in environmental samples (Priest et al. 2021) and studies of marine fungal diversity (Yang et al. 2021). Additionally, she is interested in the carbon turnover of marine fungi, and recently isolated hundreds of marine fungi to establish model organisms.

Hans Peter Grossart in Stechlin has been working on the biological aspects of the aquatic carbon cycle since his PhD in Constance, initially with a main focus in bacteria, but increasingly also fungi. Even though most of his work is carried out in freshwater systems, many of his results and concepts are equally valid for marine systems, such as the concept of mycoflux, mycoloop, and fungal shunt that describe the ecological roles fungi play in aquatic carbon turnover and food chains (Grossart et al. 2019; Klawonn et al. 2021). A former doctoral student of Grossart, Christian Wurzbacher (Technical University of Munich), investigates unknown fungi in aquatic biofilms, and established Oxford Nanopore Sequencing for aquatic fungi (Wurzbacher et al. 2018).

Noteworthy is also William Orsi (Ludwig Maximilian University of Munich) who works on the effects of benthic microbial diversity on biogeochemical processes. Using omics and stable-isotope probing techniques, he defined a specialized role of fungi in carbohydrate recycling in the seafloor, distinct from Bacteria and Archaea (Orsi et al. 2018), and showed that marine fungi can assimilate similar amounts of carbon as bacteria (Orsi et al. 2022).

Johann F. Imhoff, former professor for Marine Microbiology at the "Institut für Meereskunde" in Kiel (now GEOMAR), sustainably established the discovery of natural products of marine microbes in science and politics in Germany. In 2000s, he took over the KMPB collection, was able to draw from it a large spectrum of new secondary metabolites for various applications demonstrating the great potential of culture collections for natural product mining (Imhoff 2016). Imhoff retired in 2014 and was succeeded by Deniz Tasdemir. Tasdemir has been increasingly successful in using co-cultivation to isolate new secondary metabolites from marine fungi through interaction-dependent activation (Oppong-Danquah et al. 2018). Antje Labes (Flensburg University of Applied Sciences), a former colleague of Imhoff and Tasdemir, focused in her newest research in mycoremediation using marine fungi. She has accommodated a large part of the KMPB collection with about 16,000 previously unused isolates (pers. comm.) at the Flensburg strain collection of marine fungi.

Frank Kempken (Christian Albrechts University in Kiel) has been working since 2001, focusing on plant and terrestrial fungi. In recent years, however, he is using his expertise to obtain information about biosynthetic gene clusters from genome sequences of marine fungi and thus deduce potential biotechnological applications (Kumar et al. 2018).

The number of marine fungi documented in Germany has not been summarized in recent decades. However, it can be estimated that there are about 20,000 marine fungal isolates in existing culture collections. Molecular work in German marine waters predicts several thousand species (Banos et al. 2020).

6.3 Italy (E.B.G. Jones)

In the early 1980s the seeds of marine mycology research were initiated by Vincenzo Cuomo who was working at Ciba Geigy at their plant in Torre Annunziata, as the company was interested in seeking new bioactive compounds from marine fungi. Cuomo was registered for his PhD at the University of Portsmouth and published a number of papers about marine fungi on the seagrasses *Posidonia oceanica* and *Cymodoce nodosa* (Cuomo et al. 1985, 1988) and on marine algae (Cuomo et al. 1983). In a joint paper (Jones et al. 1983) he described spore appendage development in the lignicolous marine pyrenomycetes *Marinokulati chaetosa* and *Halosarpheia trullifera*. These early studies lead to the discovery of new secondary metabolites by Francesco Pietra and his group (University of Trento), especially dendryphiellin A, the first fungal trinor-eremophilane isolated from the marine fungus *Paradendryphiella salina* (Guerriero et al. 1988). Subsequently, other eremophilanes were elucidated by this group (Guerriero et al. 1989). Also at this time, marine fungi were studied at the University of Messina, where Sofia Grasso was working on her PhD documenting fungi found in the local harbors (Bruni et al. 1982; Grasso et al. 1985, 1990). C. Panebianco, undertook her PhD at Messina, with practical work at the University of Portsmouth on the physiology of marine fungi (Panebianco 1990) and experimental work on the sequential colonization of wood in the sea (Panebianco et al. 2002).

During this period, Montemartini Corte (1975, 1979) also contributed to our knowledge on the marine fungi of Italy with particular interest in the decay of wood in the marine environment. Italy also took part in an international co-operative research programme (OECD) into the biodeterioration of wood in the sea, leading to a number of publications (Jones et al. 1972, 1976). Jones (2010) published a list of marine fungi reported from Italian seas documenting 42 species, as part of a checklist of the flora and fauna.

The next generation of marine mycologists came from the University of Turin where their work focused on marine fungi colonizing or endophytic on the seagrass *Posidonia oceanica,* but their first account documented asexual morphs best described as marine derived (Panno et al. 2013). These studies continued with observations of marine fungi on algae (Garzoli et al. 2014, 2018; Gnavi et al. 2017; Poli et al. 2020), *Posidonia oceanica* (Gnavi et al. 2014), woody substrata (Garzoli et al. 2015), oil spills (Bovio et al. 2017), and marine sponges (Bovio et al. 2019b). Many new fungal taxa were described from *P. oceanica*: the new genus *Elbamycella* with *E. rosea* as the type species (Juncigenaceae, Torpedosporales; Poli et al. 2019), *Corollospora mediterranea* (Halosphaeriaceae; Poli et al. 2021a,b) and *Paralulworthia* (Lulworthiaceae, Lulworthiales; Poli et al. 2019, 2022). These contributions are summarised in their recent publication (Poli et al. 2022) covering fungi on seagrasses, seaweeds and plant debris.

6.4 Norway (T. Rämä)

Marine mycology is a young field of science in Norway. In the 19th and 20th centuries, a few marine fungal observations were made by mostly foreign mycologists during short visits to the country or based on exported material (summarized in Rämä et al. 2014a,b). These studies focused on studying wood substrata and seaweeds, but also fungi pathogenic in aquaculture and resulted in species described as new for science (e.g., Kohlmeyer 1973b; Pang et al. 2008, 2009; Pedersen and Langvad 1989), giving first indications that the Norwegian coastline is rich in fungal life. Systematic studies on Norwegian marine fungi were started by Teppo Rämä during his PhD studies in 2010–2014 that was initiated by Geir Mathiassen and Ove E. Eriksson from Umeå, Sweden. Eriksson had collected marine fungi in Norway and suggested Rämä to start studying these. Rämä´s thesis focused on studying the diversity and ecology of wood-inhabiting fungi in the North of the country, whereas marine fungal research has expanded to other research avenues in recent years. However, the geographical focus has been in Northern and Arctic waters, since marine mycologists have been based at UiT (The Arctic University of Norway, Tromsø at 71°N).

Norwegian research on marine fungi was strengthened by Brandon Hassett who moved to Tromsø from Alaska, USA in 2017. Hassett stayed in Norway for some years and his postdoctoral research focused on the ecology of Arctic marine fungi, especially chytridiomycetes, and other protists. Other persons involved in marine fungal research in Norway include Ole Christian Hagestad who defended his PhD thesis on bioprospecting of Arctic marine fungi in April 2021. Hagestad´s thesis involved culturing work and genome sequencing of promising fungal isolates to reveal their biosynthetic potential to produce new and interesting secondary metabolites. Rämä´s work as a postdoc and associate professor has continued characterizing the species diversity and expanding the culture collection of Arctic marine fungi while contributing with fungal isolates to the biodiscovery work done in the research group Marbio and Centre for New Antibacterial Strategies at UiT.

The main research trends in Norwegian research on marine fungi have been in biosystematics, ecology and bioprospecting for antibacterial secondary metabolites using both traditional microscopy, culturing and bioassay, as well as -omics methods. The work has contributed to increased knowledge of the ecological importance of marine fungi and characterization of the new biological and chemical diversity of fungi in Arctic waters.

Rämä et al. (2014a,b) provide a list of 61 species of marine fungi (60 ascomycetes and one basidiomycete) documented in Norway. DNA-based methods have revealed a much greater diversity but with uncertainties related to the molecular identification of fungi. Recent morphological work and the Norwegian marine fungi project (2022–2025) funded by the Norwegian Biodiversity Information Centre has already revealed several new species for Norway that is likely to bring the number of morphologically identified Norwegian species of marine fungi into the hundreds.

6.5 Portugal (E. Azevedo, M.F. Caeiro, A. Alves and M. Barata)

Marine mycology in Portugal started in 1992 with the PhD work of Margarida Barata at the University of Lisbon (FCUL). The study involved the salt marshes of three rivers (Tejo, Sado and Mira) located on the west coast of Portugal and was the first report of marine fungi associated with *Spartina maritima* plants. This study contributed to knowledge of the vertical distribution of marine fungi in intertidal environments, as well as the recognition of the succession pattern of the marine fungi associated with *S. maritima* baits, placed for this purpose in the marsh of Mira River. Gareth Jones played a key role as a scientific consultant in this doctoral work, since he visited Portugal in 1993 and introduced the baiting method, essential for the detection of marine fungi on selected substrata. He helped to confirm the identification of a new basidiomycete associated with baits permanently submerged in waters of the Mira River, *Nia globispora* (Barata et al. 1997). The work resulted in the publication of a book chapter (Barata 2002) and two scientific articles (Barata 2006; Barata et al. 1997).

Margarida Barata was the supervisor of one MSc and two PhD theses. The MSc thesis of Dulce Figueira targeted the marine fungi associated with drifting substrata (wood and plant stems) collected in the intertidal zone of two beaches (Rosário and Guincho) located in the Sintra-Cascais area (Figueira and Barata 2007).

Egídia Azevedo obtained a PhD degree in 2012, mainly addressing the occurrence, diversity, and similarity of marine mycota detected in *Fagus sylvatica* and *Pinus pinaster* baits submerged for a 1-year period in two marinas (Cascais and Sesimbra; Azevedo et al. 2010, 2011). This PhD project also included an inventory of the marine fungal communities associated with five categories of drift substrata (driftwood, *Arundo donax*, *Phragmites australis*, *Spartina maritima*, and other plant stems) randomly collected at four sandy beaches (Vagueira, Meco, Cascais and Vila Nova de Mil Fontes), leading to the proposal of a new sampling methodology to assess the representative marine mycota on drift substrata (Azevedo et al. 2012). This project was also the starting point, under the supervision of Maria F. Caeiro (FCUL), for the application of molecular techniques for fungal identification, the first publication addressing the molecular identification of isolates of asexual morphs not morphologically identified to species level (Azevedo et al. 2011). This approach, based on rRNA gene sequences, was also applied to establish phylogenetic relationships among isolates belonging to the genus *Lulworthia*, and the new taxon *Lulworthia atlantica* (Azevedo et al. 2017). Later, phylogenetic analysis associated with the estimation of pairwise distances was applied to evaluate the *Nia vibrissa* species complex (Azevedo et al. 2018).

The PhD of Maria da Luz Calado concluded in 2016 and focused on *Spartina maritima* plants collected in two salt marshes: Ria de Aveiro (west north coast) and Castro Marim, Ria Formosa (south coast). This study provided an inventory of the filamentous higher marine fungi associated with this host plant, giving a better understanding of the ecology and functional roles of those fungi in the early stages of decomposition of *S. maritima*, also contributing to the evaluation of the effects of seasonality and environmental parameters on fungal communities (Calado et al. 2015). The molecular approach allowed either confirmation of fungi previously identified by morphological characteristics, or identification of additional fungal species only detected by this methodology (Calado et al. 2019).

After her graduation, Calado et al. (2021) screened the endophytic fungi associated with the seaweed *Halophteris* *scoparia* for secondary metabolites with potential dermo-cosmetic applications. In 2021, Pedro Correia successfully completed his MSc thesis under the supervision of Egídia Azevedo and Maria F. Caeiro. This work aimed to characterize and evaluate the diversity of the *Corollospora maritima sensu lato* found in Portugal, and was extended to the molecular relationships between the species of the genus *Corollospora*, with published molecular data.

Sridhar et al. (2012), while visiting Portugal, carried out a survey on seven sandy beaches on the north and central regions of west Portugal, with collections of driftwood and seaweeds, to study the occurrence, diversity and similarity of the marine fungi detected in these substrata and environments. By using direct observation of fungal morphology, Margarida Barata's team and Sridhar et al. (2012) identified a total of 98 species of marine fungi (62 Ascomycota, five Basidiomycota and 31 asexual ascomycetes).

Artur Alves group at CESAM and the University of Aveiro started working on fungi from marine environments in 2017. Since then, one PhD (Micael Gonçalves) and two MSc (Alberto Abreu, Tânia Vicente) are complete, and two PhD projects are ongoing. The overall aim of these studies is to unravel the diversity and biotechnological potential of fungi from marine environments. Strains were isolated from seawater, algae, saltmarsh plants, driftwood, submerged wood baits and sponges. Through morphological and molecular characterization (including multilocus phylogenies), more than 240 species were identified. This led to the description of 18 novel species, from 12 different genera, including some strictly marine, such as *Zalerion pseudomaritima* (Gonçalves et al. 2021a). A new genus, *Neptunomyces*, isolated from marine algae, was also described (Gonçalves et al. 2019).

Gonçalves et al. (2021b) screened a collection of fungal isolates (marine-derived and strictly marine) for their ability to produce diverse extracellular enzymatic activities. Mycelial and medium extracts were also screened for antimicrobial, antioxidant, and cytotoxic activities. The genome and metabolome of *Emericellopsis cladophorae*, a new species from marine algae (Gonçalves et al. 2020), were analysed to gain knowledge on the biology and ecology of this fungus, and marine fungi in general, and to determine the biosynthetic potential of the species (Gonçalves et al. 2022).

6.6 Sweden (S. Tibell and L. Tibell)

Carl A. Agardh, in his *Syn. Alg. Scand.* (Agardh 1817), included *Lichina,* with the marine lichen and generic type *Lichina pygmaea.* Elias Fries described many species, but none of them marine, although *Patellaria atrata*, type of *Patellaria,* was sanctioned in his *Systema* 2 (Fries 1822). Fries also described *Vibrissea*, which includes *V. nypicola*, a marine species. Although systematic mycology in Sweden, as built on the founding works of Elias Fries, remained strong in the 19th and 20th centuries, interest in marine fungi remained scant and fragmentary. Johanson (1884) described *Mycosphaerella* which later was to include numerous species (e.g. the marine *Mycophycias ascophylli*). The next note on a marine fungus did not appear until Starbäck (1896) reported *Lizonia halophila* as *Sphaerulina halophila*.

Juel (1901) described *Pyrrhosorus* in the Labyrinthulales – at that time considered a fungus. An early 20th century report was provided by Cotton (1909), when describing *Mycosphaerella ascophylli* (now *Stigmidium ascophylli*) in Sweden (west coast). Nannfeldt, in his influential 'Studien' (1932), described *Laetinaevia,* and subsequently *Orbilia marina* was transferred to this genus (Kirk and Spooner 1984), so as to eventually end up in *Calycina* (*Calycina marina*). In his 1957 thesis, Lennart Holm reported *Leptosphaeria littoralis* and combined it into *Phaeosphaeria*. Similarly, Nils Lundquist described *Tripterospora latipes* (Lundquist 1969), the basionym for *Zopfiella latipes*. Rolf Santesson, an eminent lichenologist, had many-faceted interests and collected marine fungi on the Swedish west coast in the 1950s, collections that still remain mostly unrevised and kept in Uppsala.

A pioneering, but neglected work, is the thesis by Erneholm (1972, in Swedish), where the author presented the methodology for studying and cultivating marine fungi. The investigations were focused on marine fungi occurring on algae from the Swedish West Coast and Kenya. The thesis also included discussions of the ecology of marine fungi and generally aimed to introduce marine mycology in Sweden. It remained unpublished, however, and the results were overlooked, although to some extent referred to by Henningsson (1974). Erneholm reported 12 'deuteromycete' species from Sweden.

Niels Fries, professor of physiological botany in Uppsala, initiated another line of research insofar that he concentrated on the physiology of marine fungi. Fries recruited PhD students for their study, Ulla Gustafsson being one of them (Fries 1965; Gustafsson and Fries 1956; Pedersen and Fries 1977). In the first of these papers, 10 marine ascomycetes were cultivated from material collected by Santesson. In a subsequent study, Fries (1979) described the physiology of an 'algal endophyte', viz. *Stigmidium ascophylli*. In another paper Fries and Thorén-Tolling (1978) reported on the endosymbiotic relationship between *Stigmidium ascophylli* and its host and identified the endophytic mycelium by antibody techniques. Here the term 'endosymbiotic' was used for a relationship involving a marine fungus for the first time. The material used by Fries and his students was mainly obtained from wooden panels submersed at Kristineberg (now the Sven Lovén Centre, Sweden) collected by Santesson and the material identified by him. Henningsson, another pupil of Nils Fries, initially studied wood degradation and the physiology of marine fungi (Henningsson 1976a,b) and her thesis also included a first census of marine fungi of Sweden (Henningsson 1974) focusing on lignicolous species. The material was partly obtained from three different areas with different salinities along the Swedish coasts, including the Baltic, and 34 species were recorded. Birgitta Norkrans, yet another researcher who under Niels Fries' leadership devoted herself to marine fungi and particularly their physiology, examined the physiological requirements of marine yeasts. Norkrans published on marine yeasts (Lundström-Eriksson and Norkrans 1968) and also described a new species, *Candida suecica*. Sven Nilsson in his thesis (Nilsson 1964) treated freshwater aquatic fungi of Sweden and in a later paper (Nilsson 1971) described *Clavatospora*, a genus later to accommodate *C. bulbosa*, the anamorph of *Corollospora pulchella*. In his thesis, Ove Eriksson (1981) described *Amarenomyces* based on *A. ammophilae* and also later continued to study marine/shoreline fungi (Eriksson 1964, 1973, 1982; Kohlmeyer et al. 1995a,b,c, 1996, 1997, 1998). He meticulously included them in his checklist of non-lichenized ascomycetes of Sweden (2014), which also incorporated numbers from Fungi exsiccate suecici as published in Thunbergia volumes (Fasc. 26, 75). In addition, he referred to several of the Santesson collections of marine fungi. The precursor of the 2014 list (Eriksson 1992) also contained information on marine fungi.

The international upsurge of interest in marine fungi during the late 20th century also impacted on Sweden, and a semi-popular review paper was published by Tibell (2016). Here, seven species previously unknown from Sweden were presented, two of them new to science (based on Santesson's collection). This was part of a pilot-project funded by the Swedish Taxonomy Initiative in 2016. A crucial aspect of finding new material was a 'kick-off' meeting and joint fieldwork with E.B. Gareth Jones from the UK, and Ka-Lai Pang from Taiwan in June 2017 at the Sven Lovén Centre. The first outcome of the project 2018–2020 (financed by 'ArtDatabanken') was a compilation of previous records with substantial updates (Tibell et al. 2019) offering a census of Swedish species now amounting to 74, roughly doubling the number of species previously known from the country. The project was much indebted to the mentorship offered by Gareth Jones and Ka-Lai Pang, who both also joined in fieldwork on the Swedish east coast in 2019. Another contribution followed, including the description of a new species from Sweden, *Coniochaeta marina* (Jones et al. 2020). A review of the marine fungi of the Baltic (Tibell et al. 2020) enumerated 77 species, where historical records were supplemented by the results of joint fieldwork in 2019. Thirteen species were reported new to Sweden. Further material collecting, axenic culturing and DNA sequence production followed until the project was discontinued due to lack of funding.

6.7 United Kingdom (E.B. Gareth Jones)

Marine fungi have been extensively studied in the UK with observations from England, Ireland, Scotland and Wales. Sutherland (1915, 1916) undertook the first serious studies of marine fungi on various substrata, introducing the new genus *Lulworthia* on the brown alga *Fucus* and a number of new species: *Cercospora salina,* (=*Paradendryphiella salina*), and the doubtful species: *Ophiobolus laminariae, Pleospora laminariana, P. pelvetiae, Rosellinia laminariana* and *Stigmatea pelvetiae*. This was followed by the introduction of new taxa by Wilson (1954, 1956): *Ceriosporopsis cambrensis, Halophiolobus purpurea* (=*Lulworthia purpurea*), *Halophiolobus rufus* (=*Lulworthia rufus*) and the new genus *Lindra* (type species *L. inflata*). Studies by other British mycologists include: E.B. Gareth Jones, with circa 30 graduate students in marine mycology (systematics, wood decay, ultrastructure, ecology, physiology, phylogenetic studies, drug discovery); D.H. Jennings and his students (fungal physiology); D.J. Alderman (oyster diseases, thraustochytrids); R.A. Eaton (wood decay); S.T. Moss (ultrastructure of Ascomycota and *Thraustochytrium* species, Trichomycetes); G.J.F. Pugh (fungi in marine sediments, Antarctic marine fungi); L.V. Evans (fungal symbioses in marine algae); P. Curran (ecology and systematics marine fungi); and J.L. Polglase (mycotic infections of marine animals). The culture collection of marine fungi at the University of Portsmouth, comprising over 7,000 strains, including type strains, was lost through neglect on the departure of E.B.G. Jones.

Key events: hosting two meetings of IMMS; edited volume by S.T. Moss 'The Biology of marine fungi' and checklists of marine fungi (Jones et al. 2009, 2015, 2019). Current research on marine fungi in the UK continues at the Plymouth laboratory of the Marine Biological Association U.K. with a major government project on plastic in the marine environment (Cunliffe 2023).

7 Conclusions

Currently active marine mycologists have written briefly on the history and current state of marine fungal research of 20 different countries, highlighting their research interests and strengths. This is in the hope that such a paper will stimulate international and transdisciplinary research collaborations in marine mycology. What are the topics that marine mycologists will tackle in the forthcoming decades?

(1) Few genomes of marine fungi have been sequenced and this has to be a priority area for the future (*Amylocarpus encephaloides*, *Calycina marina*, *Corollospora maritima*, and others). These will be important as a source of biosynthetic data that will provide information on the metabolic diversity of marine fungi, multilocus information for phylogenetic characterisation, a better resolution of their taxonomy, and comparative data on the evolution of individual genes (Galagan et al. 2005; Hagestad et al. 2021).
(2) With the recent signing of a global diversity agreement for the conservation of the oceans, it is timely that marine mycologists play a greater role in the promotion of conservation, and examine the risk of extinction of marine fungi in response to climate change.
(3) Future research should include a greater effort to determine the hidden diversity of basal lineages (e.g. Aphelidiomycota, Chytridiomycota, Rozellomycota), especially in global locations for which there are currently little data, including Africa, South America and Australasia (Jones 2011).
(4) Greater effort is required to confront the pollution of the oceans by plastics and to educate the public about the fragility of the marine ecosystem. Many studies are in progress to determine the role of marine fungi in the breakdown of plastics, and also to evaluate how this information can be applied in the marine mileu (Cunliffe 2023; Ekanayake et al. 2022).

Research funding opportunities, for example Biodiversa, are available for international consortia to apply to, and these may bring marine mycologists together to tackle these topics. Workshops/conferences (in-person/virtual) may serve as platforms for communication between marine mycologists, especially the new wave of young marine mycologists. For example, the International Marine and Freshwater Mycology Symposium has been held every 2–4 years since 1966, and was last held in 2019 in Xiamen, China. A special issue was published in *Botanica Marina* summarizing the contributions in this meeting (Pang et al. 2020), and the current article, as well as this new special issue, aims to encourage a more focused effort, bringing together scientists with different backgrounds in marine mycology.

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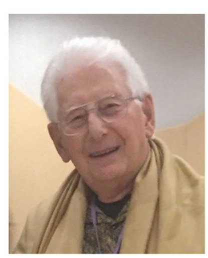

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