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Freshwater fungal biology

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Abstract

Research into freshwater fungi has generated a wealth of information over the past decades with various published articles, i.e., reviews, books, and monographs. With the advancement of methodologies used in freshwater fungal research, and numerous mycologists working on this ecological group, our knowledge progress and understanding of freshwater fungi, including novel discoveries and new insights in the ecology of freshwater fungi, has advanced. With this enormous progress, it is timely that an updated account of freshwater fungi be compiled in one volume. Thus, this account is published to give a comprehensive overview of the different facets of freshwater fungal biology. It includes an updated classification scheme based on the latest taxonomic and phylogenetic analysis of freshwater fungal taxa, including their evolutionary history. The biology, diversity, and geographical distribution of higher and basal freshwater fungi are also discussed in the entries. A section on dispersal and adaptation of filamentous freshwater fungi is included in the present work. The ecological importance and role of fungi in the breakdown of wood in freshwater habitats, including their physiology, are discussed in detail. The biotechnological potential of freshwater fungi as producers of bioactive metabolites are reviewed, with methodologies in antimicrobial drug discovery. The present volume also provides an overview of different high throughput sequencing (HTS) platforms for freshwater fungal research highlighting their advantages and challenges, including recent studies of HTS in identification and quantification of fungal communities in freshwater habitats. The present volume also identifies the knowledge gaps and direction of future research in freshwater fungi.

Keywords – Aquatic mycology – biology of microfungi – ecosystem functions – fungal classification – fungal ecology – taxonomy – systematics

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Introduction

Freshwater fungi are morphologically, phylogenetically, and ecologically a diverse group. For species to be considered freshwater fungus, the life cycle, whole or part, must rely on free freshwater or submerged substrates from lentic and lotic ecosystems, including artificial reservoirs and extreme habitats (Thomas 1996, Jones et al. 2014a, Calabon et al. 2020a). Fungi from freshwater habitats were reported as early as mid-19th century (Russell 1856, Saccardo 1880, de Wildeman 1893, 1894, 1895) and fungal communities were documented with various studies on their ecology, biology, biodiversity, and taxonomy (Tsui & Hyde 2003, Krauss et al. 2011, Jones et al. 2014a, El-Elimat et al. 2021). In early research on freshwater fungi, identification relied mainly on morphology, and in the case of yeasts, biochemical, fermentation, and assimilation tests. Molecular data were later incorporated in taxonomic studies of freshwater fungi with early works of Ranghoo (1998), Ranghoo et al. (1999), Nikolcheva & Bärlocher (2002), and Vijaykrishna et al. (2006). Following barcoding of nuclear ribosomal regions (ITS, LSU, SSU), protein-coding genes were added for a better resolution of the phylogenetic tree and resolving the evolutionary relationships of closely related taxa (Luo et al. 2019, Bao et al. 2020, Hongsanan et al. 2020a, b, Hyde et al. 2020c, 2021, Dong et al. 2020b). These resulted in a well-defined classification scheme that is unceasingly changing as continuous exploration of various freshwater habitats in tropical and temperate countries lead to discovery of novel taxa and recollection of taxa wherein phylogenetic placement is unclear (Wijayawardene et al. 2020, 2022). Despite all the published information, our knowledge of freshwater fungi is limited and research on the ecology of this group is a neglected field. Almost 20 and 8 years after the publications of Tsui & Hyde (2003) and Jones et al. (2014a), we review the recent information of freshwater fungi regarding their updated taxonomic classification, numbers, ecological roles and functions, evolution, and adaptation to changing environmental conditions.

The information on freshwater fungi has been compiled through reviews and books. Ingold (1975) published an illustrated a guide to aquatic and water-borne hyphomycetes to encourage mycologists at that time to study freshwater fungi, not only on taxonomic works but also their role in freshwater habitats. A year later, Jones (1976), in his book *Recent Advances in Aquatic Mycology*, brough together information on freshwater and marine fungi, and reviewed relevant work over the past 12 years. Bärlocher (1992c) provided a discussion on aquatic hyphomycetes and their roles in nature. Almost a decade later, the first book *Freshwater Mycology* was published that dealt with the ecology and biology of freshwater fungi, including methodology for physiological and biodiversity studies (Tsui & Hyde 2003). Cai et al. (2006a) reviewed and compiled descriptions of 100 freshwater fungal genera with comprehensive description, photographic plates, and notes.

Jones et al. (2014a), in the book, *Freshwater Fungi and Fungal-like Organisms*, reviewed the recent information on molecular data and classification of freshwater fungi and fungus-like taxa, with biodiversity and ecological reviews of the group. Several reviews of freshwater fungi (Bärlocher 1992a, b, Goh & Hyde 1996a, Shearer et al. 2007, Sridhar 2009, Wurzbacher et al. 2010, Chauvet et al. 2016, Gulis et al. 2019, El-Elimat et al. 2021), and keys and monographs (Gulis et al. 2005, Luo et al. 2019, Dong et al. 2020b) dealing with certain taxonomic and ecological groups have also been published. In addition to the published literature, the online databases, www.freshwaterfungi.org and http://fungi.life.illinois.edu/, have compiled all the scattered data on taxonomic classification of freshwater fungi (Shearer & Raja 2013, Calabon et al. 2020a).

Classification and biodiversity of freshwater fungi

Calabon et al. (2022) provided the latest classification of freshwater fungi and listed 3,870 species reported from different substrates and geographical locations (Table 1). Among these, 2,968 species (in 1,018 genera) belong to Ascomycota, 333 species (in 97 genera) to Chytridiomycota, 221 species (in 105 genera) to Rozellomycota, and 218 species (in 100 genera) to Basidiomycota. Other phyla with less than 50 species include Blastocladiomycota, Monoblepharomycota, Mucoromycota, Aphelidiomycota, Entomophthoromycota, Mortierellomycota, Olpidiomycota, Zoopagomycota, and Sanchytriomycota. Most freshwater taxa belong to Sordariomycetes (823 species, 298 genera) and Dothideomycetes (677 species, 229 genera). Pleosporales and Laboulbeniaceae are the largest freshwater fungal order (391 species) and family (185 species), respectively. Calabon et al. (2022) provides a list of freshwater fungal basal clades belonging to 11 phyla and 692 species (in 246 genera).

The freshwater fungal numbers in Calabon et al. (2022), 3,870 species, is within the estimated range of Jones et al. (2014a) which suggested 3,069–4,145. The estimated number accounts for 0.26% of the conservative estimates of fungal species (Hawksworth 2001), and around 3–4% of the extant fungal species (Kirk et al. 2008, Hyde et al. 2020b, c, Wijayawardene et al. 2020). Although the list of Calabon et al. (2022) is not exhaustive and does not reflect the overall diversity of freshwater fungi, the provided number gives an idea of species composition, distribution, and habitat type to better understand their biology, biodiversity, and ecology.

Table 1 Classification and estimated number of freshwater fungi.

Taxa	**Number of genera/species**	
	Jones et al. (2014a)	**Calabon et al. (2022)**
Ascomycota		
Arthoniomycetes	3/7	8/12
Candelariomycetes	–	2/4
Coniocybomycetes	–	1/4
Dothideomycetes	31/86	229/677
Eurotiomycetes	27/158	49/276
Laboulbeniomycetes	1/1	25/259
Lecanoromycetes	52/75	93/185
Leotiomycetes	19/28	82/260
Lichinomycetes	16/43	12/24
Orbiliomycetes	–	10/19
Pezizomycetes	9/9	9/13
Saccharomycetes	–	57/158
Sordariomycetes	61/142	298/823
Ascomycota *incertae sedis*	3/7	141/252
Pezizomycotina *incertae sedis*	–	2/2
Basidiomycota		
Agaricomycetes	10/14	20/28
Agaricostilbomycetes	–	1/1

Table 1 Continued.

Taxa	Number of genera/species	
	Jones et al. (2014a)	**Calabon et al. (2022)**
Atractiellomycetes	1/1	1/1
Bartheletiomycetes	–	3/5
Classiculomycetes	2/2	2/2
Cystobasidiomycetes	2/6	7/14
Exobasidiomycetes	11/13	7/7
Microbotryomycetes	7/26	14/43
Moniliellomycetes	–	1/1
Tremellomycetes	12/41	28/81
Ustilaginomycetes	2/9	11/30
Agaricomycotina *incertae sedis*	–	1/1
Basidiomycota genera *incertae sedis*	11/13	4/4
Aphelidiomycota		
Aphelidiomycetes	–	3/15
Blastocladiomycota		
Blastocladiomycetes	–	10/47
Chytridiomycota		
Chytridiomycetes	97/946	52/181
Cladochytriomycetes	–	7/47
Lobulomycetes	–	3/3
Mesochytriomycetes	–	2/2
Polychytriomycetes	–	5/8
Rhizophlyctidomycetes	–	2/4
Rhizophydiomycetes	–	19/72
Spizellomycetes	–	1/1
Synchytriomycetes	–	3/8
Chytridiomycota genera *incertae sedis*	–	2/3
Entomophthoromycota		
Entomophthoromycetes	–	4/6
Kickxellomycota		
Asellariomycetes	3/7	–
Harpellomycetes	44/176–212	–
Monoblepharomycota		
Hyaloraphidiomycetes	–	1/1
Monoblepharidomycetes	6/50	5/28
Sanchytriomycetes	–	2/2
Mortierellomycota		
Mortierellomycetes	–	3/5
Mucoromycota		
Endogonomycetes	–	1/1
Mucoromycetes	–	9/18
Olpidiomycota		
Olpidiomycetes	–	1/4
Rozellomycota		
Microsporidea	–	105/221
Rozellomycota genera *incertae sedis*	–	3/20
Zoopagomycota		
Zoopagomycetes	–	2/3

Freshwater Ascomycota

Since 1856, the number of novel taxa discovered from freshwater habitats has an increasing trend with no sign of reaching a plateau (Fig. 1). It has the highest number of discoveries in the past decade (2010–2019), wherein about 433 species have been discovered from 2010–2019 [data

extrapolated from Calabon et al. (2022), Figs 2, 3]. Most are Sordariomycetes represented by 489 freshwater species followed by Dothideomycetes (409 species), Laboulbeniomycetes (259 species), Ascomycota *incertae sedis* (174 species), Leotiomycetes (133 species), and Eurotiomycetes (77) species. The increase in the number of novel taxa discovered over the last years has occurred because of continuous explorations of freshwater habitats in Asia. In fact, 169 and 129 novel species were documented from 2015–2020 in China and Thailand, respectively (Bao et al. 2021, Calabon et al. 2021a). Furthermore, there are more mycologists trained and presently working in various research and training institutions in Asia focusing on taxonomy and phylogeny of freshwater fungi. The published works of Luo et al. (2019) and Dong et al. (2020b) on freshwater Sordariomycetes and Dothideomycetes, respectively, paved the way to the documentation of these classes, and escalation of their species numbers.

Most studies on freshwater Ascomycota have focused on observation of unidentified submerged decaying plant substrates (Hyde & Goh 1999, Ho et al. 2001, Tsui et al. 2003, Sivichai & Boonyene 2004, Hyde et al. 2016a, Lu et al. 2018b). There are reports also of freshwater fungal associates of specific hosts/habitats [e.g., peat swamp palms *Eleiodoxa conferta, Licuala longicalycata, Metroxylon sagu* (Pinruan et al. 2007, 2014), grasses *Phragmites, Typha, Scirpus, Carex, Eriophorum* (Webster & Lucas 1961, Pugh & Mulder 1971, Apinis et al. 1972a, b, Cavaliere 1975, Magnes & Hafellner 1991), and wood (e.g., *Alnus glutinosa*, *Calophyllum brasiliense*, *Fagus sylvatica*, *Pinus roxburghii*, *Shorea obtusa*, *S. roxburghii*, *Wrightia tomentosa*, *Xylia xylocarpa*, *Zollingeria dongnaiensis*), shrubs (*Beluba, Salix*), and bushes (Roldan et al. 1992, Czeczuga et al. 2005, Baschien et al. 2013, Fiuza et al. 2019)]. Wood test blocks (e.g., *Dipterocarpus alatus*, *Erythrophleum teysmannii*, *Xylia dolabriformis*) were also used to determine species composition of freshwater fungi (Sivichai et al. 2000, 2002, Sivichai & Boonyene 2004, Boonyuen et al. 2012). Other freshwater substrates include water (Yamaguchi et al. 2007, Biedunkiewicz & Baranowska 2011, Raposeiro et al. 2018), wood in water cooling towers (Eaton & Jones 1971a,b), glacial melt waters (Libkind et al. 2003, 2014, de García et al. 2007), foam (Dixon 1959, Ingold 1967, Descals & Webster 1983, Bärlocher 1987, Harrington 1997, Descals et al. 1998, Hosoya et al. 2019), rocks (Aptroot & Seaward 2003, Orange 2009, 2013, Shivarov et al. 2017), stemflow and throughfall of tree canopies (Gonczol & Revay 2004, Karamchand & Sridhar 2008, Ghate & Sridhar 2015), wastewaters and polluted freshwater habitats (Spencer et al. 1970, Woollett & Hedrick 1970, Sláviková & Vadkertiová 1995, Sridhar et al. 2000, Raghu et al. 2001, Luo et al. 2004, Pires et al. 2017)

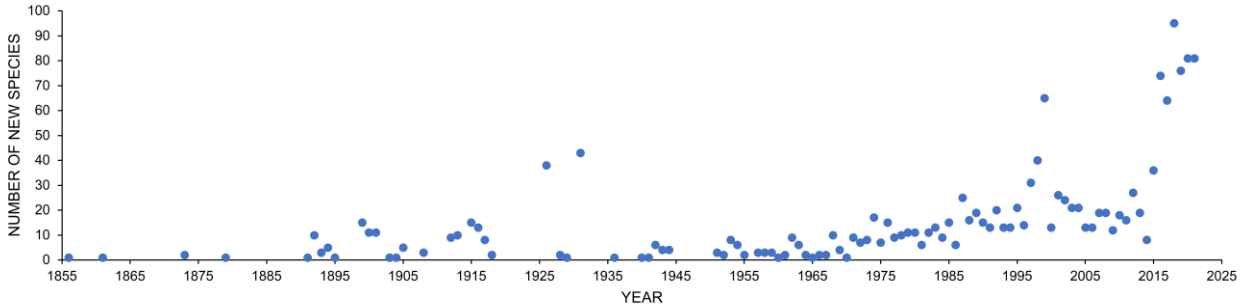


Figure 1 – Number of new species discovered from freshwater habitats from 1856–2021.

Freshwater Basidiomycota

Calabon et al. (2022) listed and provided the latest number of freshwater Basidiomycota to be around 218 species (in 100 genera, 43 families, 26 order, 11 classes). Fifty-six of these are unique basidiomycetous taxa observed from freshwater habitats. Most of the taxa were under Agaricomycetes (21 species), followed by Ustilaginomycetes (10 species), Microbotryomycetes (8 species), and Tremellomycetes (6 species) (Fig. 4) (Calabon et al. 2022). Almost 75% of these basidiomycetous species are yeasts.

Filamentous Basidiomycota in freshwater habitats have mostly been documented in woody and herbaceous substrates (Escobar et al. 1976, Desjardin et al. 1995, Hyde & Goh 1998, Yamaguchi et al. 2009), foam (Nawawi et al. 1977, Marvanová & Barlocher 1998, Marvanová & Bärlocher 2000), and sediments (Frank et al. 2010). Agaricomycetes (27 taxa) have mostly been observed from streams and rivers, followed by Ustilaginomycetes (10 *Doassansiopsis* species) and Bartheletiomycetes (5 species) (Calabon et al. 2022). Few taxa were recorded from Exobasidiomycetes (*Burrillia narasimhanii*, *Pseudodermatosorus alismatis-oligococci*, *Rhamphospora nymphaeae*), Microbotryomycetes (*Camptobasidium hydrophilum*, asexual morph = *Crucella subtilis*), Atractiellomycetes (*Helicogloea angustispora*), Classiculomycetes (*Classicula fluitans*, *Jaculispora submersa*), and Tremellomycetes (*Xenolachne flagellifera*), see Jones et al. (2014b) and Calabon et al. (2022).

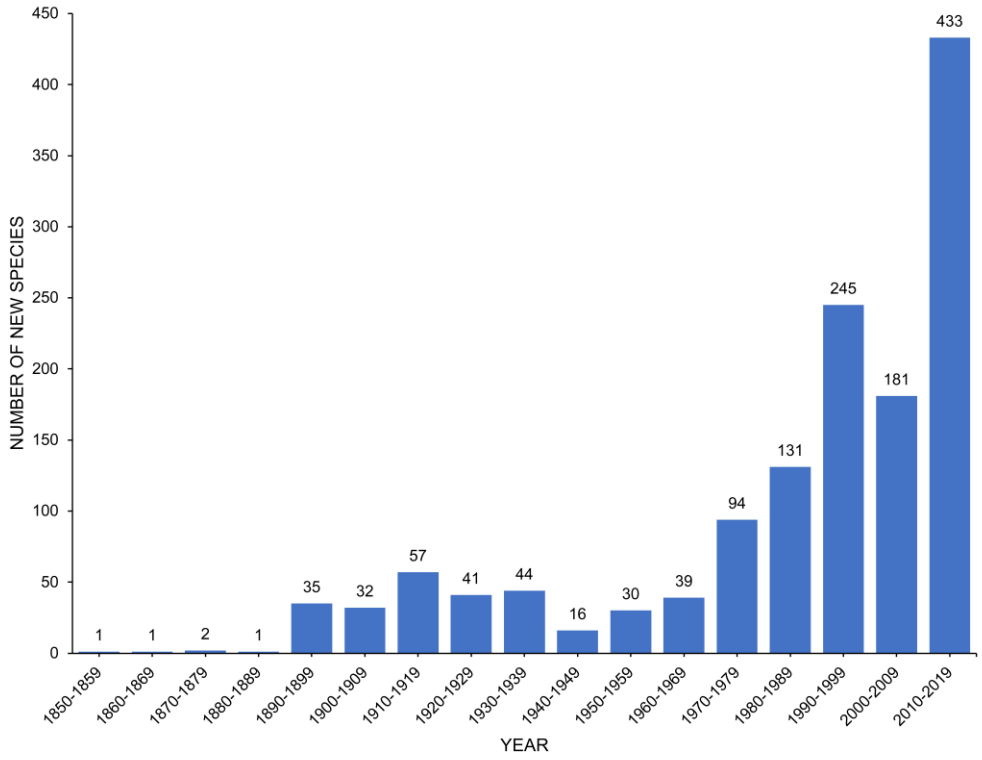
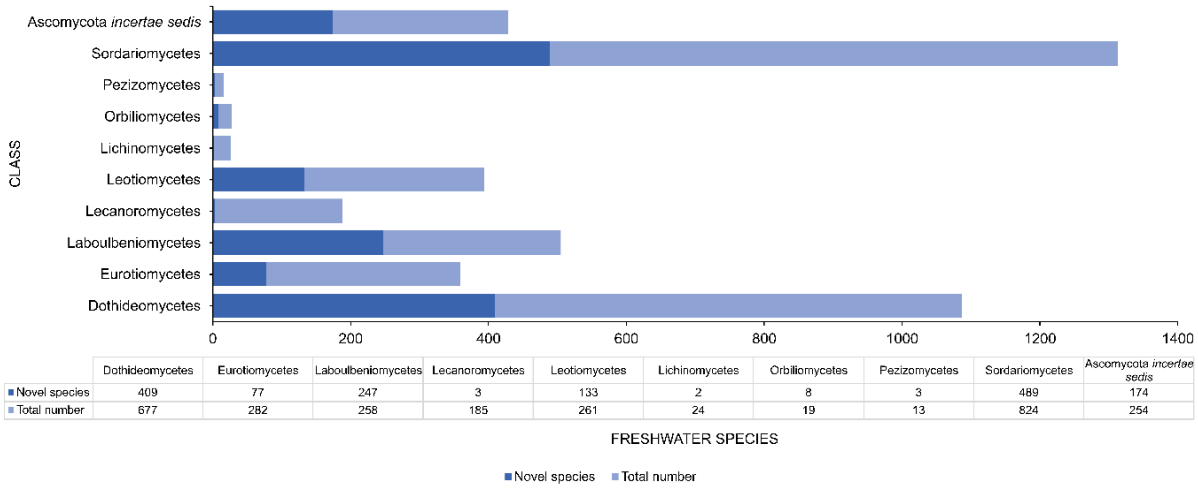


Figure 2 – Decadal data in the number of novel fungi from freshwater habitats.



	Dothideomycetes	Eurotiomycetes	Laboulbeniomycetes	Lecanoromycetes	Leotiomycetes	Lichinomycetes	Orbiliomycetes	Pezizomycetes	Sordariomycetes	Ascomycota *incertae sedis*
Novel species	409	77	247	3	133	2	8	3	489	174
Total number	677	282	258	185	261	24	19	13	824	254

Figure 3 – Number of freshwater fungal species under Ascomycota.

Freshwater basidiomycetous yeasts have also been reported also on a variety of substrates (e.g., water, aquatic plants and animals, sediment) in a wide range of aquatic environments (e.g., polluted and unpolluted rivers, streams, artificial and natural lakes, wastewater, drinking and tap water, acidic water, glacial meltwater) (Spencer et al. 1970, Libkind et al. 2003, 2009, 2014, Yamaguchi et al. 2009, Morais et al. 2010, 2020, Brandão et al. 2011). Calabon et al (2022) listed 162 yeasts. Tremellomycetes constitutes 81 species (in 28 genera), followed by Microbotryomycetes (43 species, 14 genera), Ustilaginomycetes (20 species, 11 genera), Cystobasidiomycetes (14 species, 7 genera), Exobasidiomycetes (7 species, 7 genera), Agaricostilbomycetes (*Sterigmatomyces elviae*), and Moniliellomycetes (*Moniliella spathulata*).

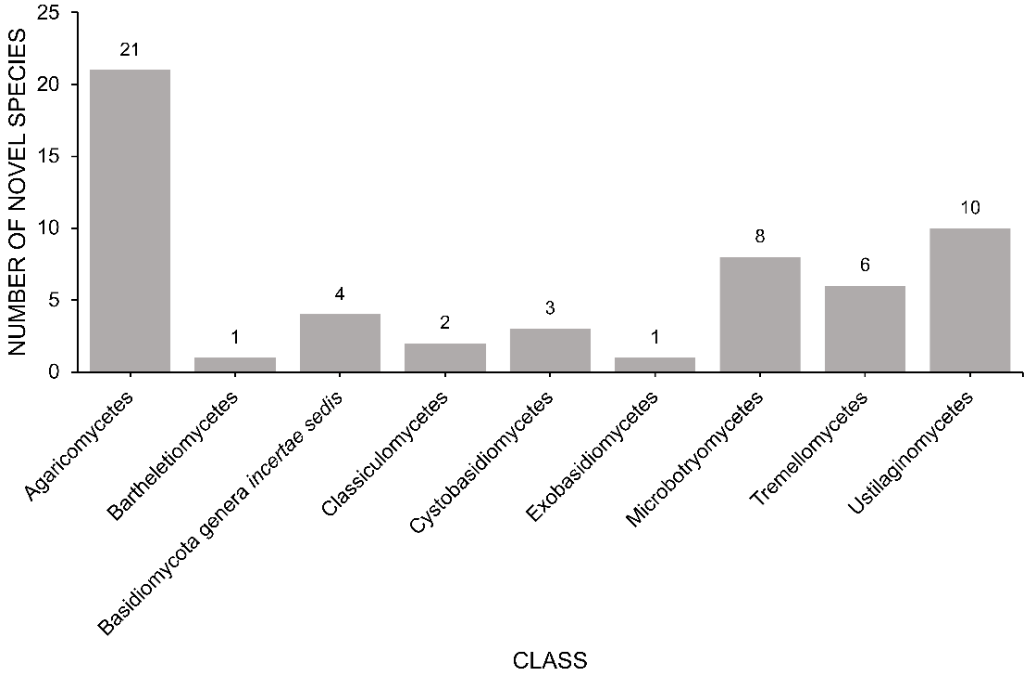


Figure 4 – Novel Basidiomycota taxa from freshwater habitats.

Freshwater fungal basal clades

The basal lineages of fungi found in freshwater habitats were distributed in 11 phyla with 684 species (Calabon et al. 2022). Chytridiomycota, distinguished by a posterior whiplash uniflagellate zoospores, constitutes the largest phylum (333 species), followed by Rozellomycota (221 species), Blastocladiomycota (47 species), Monoblepharomycota (29 species). Few taxa were recorded under Mucoromycota (19 species), Aphelidiomycota (15 species), Entomophthoromycota (six species), Mortierellomycota (five species), Olpidiomycota (four species), Zoopagomycota (three species), and Sanchytriomycota (two species). Most of the basal taxa are parasites or saprobes of freshwater phytoplankton, zooplankton, plants, fungi, and other invertebrates (Sparrow 1960, Gleason et al. 2008, Hurdeal et al. 2021).

Ecology and biodiversity of freshwater fungi

Fungi from freshwater habitats can be saprobes, mutualists, or parasites and have also been isolated as endophytes (Bärlocher 1992c, Wong et al. 1998, Ibelings et al. 2004, Bärlocher 2007, Tsui et al. 2016). Saprobic taxa are key decomposers of a wide range of organic substrates, mostly woody, leaf litter, and herbaceous debris. Freshwater ascomycetes and basidiomycetes are mostly responsible for the degradation of woody debris (Shearer & Von Bodman 1983, Boonyuen et al. 2014), while hyphomycetes mainly break down leaf litter and herbaceous materials (Bärlocher & Kendrick 1974, Gessner & Van Ryckegem 2003, Tsui et al. 2016). Freshwater fungi have mutualistic relationships (Søndergaard & Laegaard 1977, Bärlocher 2007, Kohout et al. 2012) with

economically and ecologically important aquatic plants and animals. For instance, freshwater trichomycetes are endosymbionts attached to the inner gut lining of the host (i.e., insects, crustaceans, and millepedes) extracting nutrients from the food particles passing through the host's digestive system (Lichtwardt et al. 2003, 2014). Lichens are good example also wherein a fungus has a symbiotic association with photosynthetically active algae or cyanobacteria (Thüs et al. 2014). Aquatic plants and animals are susceptible also to fungal parasites (Ibelings et al. 2003, Gleason et al. 2014, Glockling et al. 2014). A large and interesting ascomycetous order, Laboulbeniales, is obligate ectoparasitic on atrthopods, mainly insects. These endophytic, parasitic, or competitive fungi in general, produce secondary metabolites with an array of biological activities that enhance their functions contributing to the survival of the species in freshwater ecosystems.

The different molecular methods employed in fungal studies wherein from single or multi-locus phylogenetic analysis for introduction of novel taxa or reassessment of certain groups, additional analyses like ancestral state reconstruction methods and evolutionary analysis using divergence time estimates, were incorporated. These revolutionized our knowledge on the origin, early history, and evolutionary relationships of freshwater fungi (Vijaykrishna et al. 2006, Luo et al. 2019, Calabon et al. 2020a, Dong et al. 2020b, Hyde et al. 2021). Ecological studies of freshwater fungal communities using high-throughput sequencing (HTS) have advanced the field. HTS are useful in determining the individual microbiome structure in freshwater ecosystems, and even a community-wide analyses of fungal diversity, and interaction with the environment and other organisms including forces that influence and shape these communities (Debroas et al. 2017, Lepère et al. 2019). A vast diversity of Chytridiomycota-like sequences was uncovered in freshwater habitats using HTS methods by Comeau et al. (2016).

Freshwater fungal communities are susceptible to various environmental changes and human disturbances. Studies show that climate change can alter the structure of freshwater fungal communities (e.g., species composition, abundance) in the future (Bärlocher et al. 2008, Dang et al. 2009, Větrovský et al. 2019). Anthropogenic disturbances (e.g., heavy metal loads, nutrient enrichment, nanoparticles, xenobiotic concentrations) in freshwater habitats may also affect aquatic fungal diversity and activity, and ecosystem functioning as a whole (Krauss et al. 2003a, Ferreira et al. 2014).

Molecular Phylogeny of Freshwater Ascomycetes

Introduction

Fungi found in freshwater habitats can be classified into several morphological and ecological groups: freshwater ascomycetes, freshwater hyphomycetes (i.e., Ingoldian fungi, aero-aquatic hyphomycetes or asexual ascomycetes, terrestrial-aquatic hyphomycetes, submerged-aquatic hyphomycetes), freshwater basidiomycetes, coelomycetes, zygomycetes, microsporidia, and zoosporic fungi (Goh & Hyde 1996a, Shearer et al. 2007, Tsui et al. 2016, Schuster et al. 2022). Freshwater fungi are distributed in thirteen phyla: Aphelidiomycota, Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Entomophthoromycota, Monoblepharomycota, Mortierellomycota, Mucoromycota, Olpidiomycota, Rozellomycota, Sanchytriomycota, and Zoopagomycota, with Ascomycota being the most speciose (Calabon et al. 2022).

In contrast to a taxonomic group that represents freshwater fungi as distinct lineages, freshwater fungi constitute a phylogenetically varied Ascomycota group that may be conceived of as an ecological group. Freshwater ascomycetes have been found in freshwater lentic (ponds, pools, lakes, peat swamps) and lotic (creeks, streams, brooks, rivers) habitats and complete part or all of their lifecycle within the freshwater environment (Shearer 1993, Wong et al. 1998, Tsui & Hyde 2003, Jones et al. 2014a). They also include sexual (teleomorphs) and asexual morphs (anamorphs) of ascomycetes that grow on submerged wood and leaves (Cai et al. 2006b, Vijaykrishna et al. 2006). Freshwater fungi can also be found in artificial aquatic habitats in urban locations such as, gutters, sewage, water-cooling towers, water pipes, and wastewater treatment plants (Jones & Eaton

1969, Hosagoudar & Udaiyan 1993, Kane et al. 2002, Ghate & Sridhar 2018, Grossart et al. 2019), as well as in ecologically extreme conditions, including, varied static and water movement, pressure, temperature, nutrients, and salinity (Nakatsu & Hutchinson 1988, López-Archilla et al. 2001, Gadanho & Sampaio 2006, Gadanho et al. 2006, Vishniac 2006, Branda et al. 2010, Buzzini et al. 2012, Libkind et al. 2004, 2014).

The study of fungi in freshwater habitats began in the 1880s. Pioneer mycologists were drawn to the tetraradiate, sigmoid, and branching conidia because they were unusual. *Heliscus lugdunensis* was initially reported as a hyphomycete species from freshwater by Saccardo (1880). De Wildeman (1893, 1894, 1895) discovered four new fungal species on various substrates in ponds, ditches, and marshy areas, making a significant addition to aquatic hyphomycete research. When Ingold (1942) discovered and introduced species from a typical freshwater habitat, growing on submerged decaying leaves in well-aerated waters, he made a significant breakthrough. Later, Ingold discovered the structure and details of 16 freshwater fungal species, ten of which were new (Ingold 1942, 1953). However, it took almost 50 years after De Wildeman to observe the first aquatic ascomycete where the sexual state was known, *Aquanectria penicillioides* (= *Flagellospora penicillioides*) (Ranzoni 1956).

Ingold (Ingold 1951, 1954, 1955) noted the profusion of freshwater ascomycetes on reed swamp plant stalks in the 1950s, with many of the ascospores having well developed appendages, such as, *Ceriospora caudaesuis* and *Loramyces macrospora*. Following Ingold's first study, many extensive investigations were published (Ranzoni 1953, Tubaki 1957, Petersen 1963, Ingestad & Nilsson 1964, Jones & Eaton 1969, Eaton & Jones 1970, Webster & Descals 1981, Descals et al. 1981, Dudka 1985, Goh & Hyde 1996a, Chan et al. 2000, Pinruan et al. 2004a, b, Pinnoi et al. 2006). Numerous studies on sexual and asexual ascomycetes have been published from all over the world (Tubaki et al. 1983, Hyde 1992a, Sridhar et al. 1992, Chang et al. 1998, Sivichai et al. 1998, 2011, Suh et al. 1999, Wong et al. 1999b, Hyde & Wong 2000, Tsui et al. 2001a, c, Tsui & Hyde 2003, Pinruan et al. 2004b, Shearer et al. 2004, 2007, 2014, Zhang et al. 2011, Liu et al. 2015b). Whereas Ingold emphasized the prevalence of ascomycetes in temperate freshwater habitats (Ingold 1951, 1955), Hyde emphasized their presence in tropical locales such as Australia (Hyde 1992b), Taiwan (Chang et al. 1998), the Philippines (Hyde & Wong 2000, Cai et al. 2003), and Hong Kong (Tsui et al. 2001b, c, Dong et al. 2020b). Apart from that, Neubert et al. (2006) conducted a genetic assessment of the phanerogam *Phragmites australis'* fungal diversity and discovered 350 different operational taxonomic units (OTU). Many of the fungi were yet to be identified (Luo et al. 2004, Šlapeta et al. 2005, Hyde et al. 2020b). In recent years, several new species, genera, families, and orders of freshwater ascomycetes have been discovered (Zhang et al. 2017, Li et al. 2017, Bao et al. 2018, 2021, Luo et al. 2019, Calabon et al. 2020b, 2021a, b, Dong et al. 2020b, 2021a, b). Shearer et al. (2014), Luo et al. (2019), Dong et al. (2020b), and Calabon et al. (2022) are the most recent notable papers on freshwater ascomycetes.

Currently, there are 2,968 freshwater fungal species in Ascomycota, in 1,108 genera. Most studies on freshwater ascomycetes have been morphological, with sequencing data utilized to aid in the resolution of phylogenetic relationships. The earliest use of sequence data to resolve the taxonomy of a freshwater ascomycetes was in the early 2000's (Inderbitzin et al. 2001, Pang et al. 2002, Shearer et al. 2009). Freshwater ascomycetes are distributed in 13 classes: Arthoniomycetes, Candelariomycetes, Coniocybomycetes, Dothideomycetes, Eurotiomycetes, Laboulbeniomycetes, Lecanoromycetes, Leotiomycetes, Lichinomycetes, Orbiliomycetes, Pezizomycetes, Saccharomycetes, and Sordariomycetes. Sordariomycetes is the largest of the thirteen fungal classes (823 species, 28%), whereas Dothideomycetes account for 23% (677 species) (Calabon et al. 2022).

The use of molecular sequence data has substantially enhanced the present classification system of the Kingdom of Fungi (Hibbett et al. 2007, Maharachchikumbura et al. 2015, Spatafora et al. 2017). Shearer et al. (2014) presented a phylogenetic tree of Dothideomycetes based on molecular data and provided the phylogenetic placement of freshwater taxa. Four orders, i.e., Pleosporales, Jahnulales, Natipusillales, Tubeufiales, constitutes the major freshwater

Dothideomycetes. Cai et al. (2014) used LSU sequence data to provide the phylogenetic placements of freshwater Sordariomycetes which includes three subclasses: Sordariomycetidae, Hypocreomycecetidae, and Xylariomycetidae, with 11 orders (Calosphaeriales, Coniochaetales, Diaporthales, Hypocreales, Magnaporthales, Microascales, Phyllachorales, Savoryellales, Sordariales, Trichosphaeriales, Xylariales). Luo et al. (2019) undertook a comprehensive classification of freshwater sordariomycetous taxa, by a multi-locus phylogenetic tree, which are distributed in five subclasses *viz.* Diaporthomycetidae, Hypocreomycetidae, (no freshwater taxa) Savoryellomycetidae, Sordariomycetidae and Xylariomycetidae. Dong et al. (2020b) outlined the genera of freshwater Dothideomycetes with comprehensive notes on taxa, and multi-locus phylogenetic analysis for freshwater Dothideomycetes. Six orders, 43 families and 145 genera of Dothideomycetes include freshwater taxa.

The use of DNA data has substantially expanded taxonomic research on freshwater fungi, resulting in a rapid increase in fungal numbers (Zhang et al. 2017, Bao et al. 2019, 2020, Calabon et al. 2021a) and recommendations to follow when introducing new species have been published by Chethana et al. (2021) for fungi in general, Maharachchikumbura et al. (2021) for Sordariomycetes and Pem et al. (2021) for Dothideomycetes. Dong et al. (2020b) also opined, that huge numbers of fungi have yet to be reported in underexplored areas. Freshwater Sordariomycetes and Dothideomycetes are well-studied with molecular data, while other classes of freshwater ascomycetes are poorly studied, most of them were identified solely based on morphology, and if coupled with phylogenetic analysis, only a single locus is available.

Herein, we review freshwater fungi in the main classes: Eurotiomycetes, Dothideomycetes, Sordariomycetes, and conclude by considering other Ascomycota classes.

Freshwater Dothideomycetes

Dothideomycetes, are an intriguing ascomycetous class due to their incredible diversity of lifestyles, habitats, and spores, as well as studies of their ecological, evolutionary, biological, and taxonomic status (Suetrong et al. 2009, Hyde et al. 2013, Haridas et al. 2020, Hongsanan et al. 2020a, b, Saxena et al. 2021). It has become clear that Dothideomycetes is a single entity in Ascomycota based on a divergence time and multi-locus phylogenetic study (Liu et al. 2017). With more and more DNA sampling, Dothideomycetes was revealed to have evolved several lineages with distinctive genetic variations to adapt to freshwater environments (Inderbitzin et al. 2001, Shearer et al. 2009, Raja et al. 2012, 2015). In the past decade, many novel freshwater species have been established in Dothideomycetes (Pang et al. 2002, Ferrer et al. 2011, Raja et al. 2011, 2013b, Zhang et al. 2014a, Hyde et al. 2020a, b) and some higher taxa were also proposed (Fig. 5). Natipusillales is the only order in Dothideomycetes with fusiform or clavate ascospores having complex gelatinous sheaths and appendages (Hyde et al. 2013). Minutisphaeraceae (Minutisphaerales) and Wicklowiaceae (Pleosporales) are another two distinct lineages with all species from freshwater habitats (Dong et al. 2020b). Nevertheless, most freshwater species are distributed throughout families of Pleosporales (the largest order) and Tubeufiales, and with affinities to marine and terrestrial fungi (Lu et al. 2018b, Dong et al. 2020b, Calabon et al. 2022). To better understand the fungal diversity of this class and its systematics, Dong et al. (2020b) reviewed all freshwater Dothideomycetous species including their worldwide distribution, taxonomic problems, phylogenetic relationships, and possible morphological traits adapted to freshwater environments.

Molecular phylogeny of freshwater Dothideomycetes

The first major molecular phylogeny of freshwater Dothideomycetes was initially investigated by Shearer et al. (2009). The results indicated that all freshwater taxa clustered in Pleosporomycetidae as opposed to Dothideomycetidae. Four clades were revealed comprising only freshwater taxa, with the Jahnulales clade as the largest of these, followed by Lindgomycetaceae, Amniculicolaceae and Lentitheciaceae. However, further molecular studies showed that this

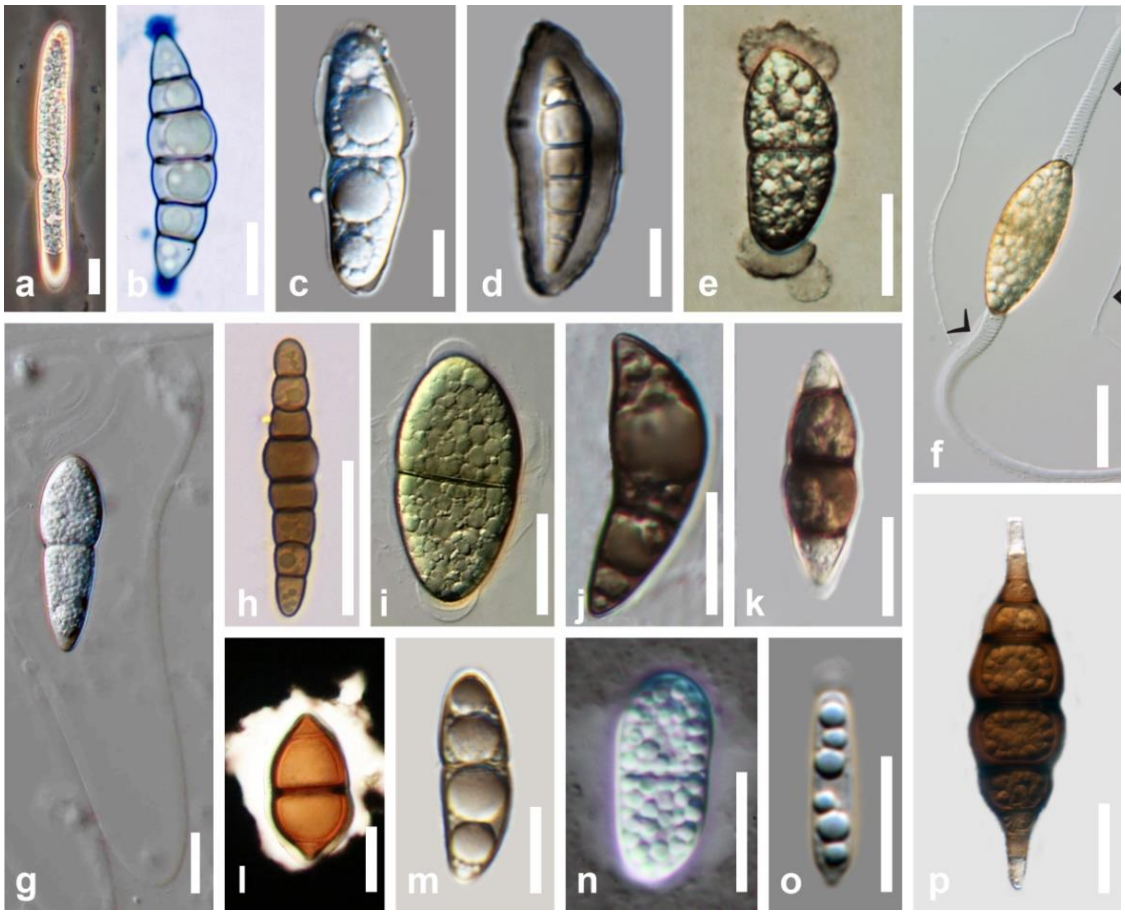


Figure 5 – Freshwater Dothideomycetes. a *Setoseptoria magniarundinacea* (culture of KT 1174 = CBS 139702). b *Neotrematosphaeria biappendiculata* (KT 1124, holotype, in black-blue ink). c *Wicklowia phuketensis* (MFLU 20–0143). d *Aquastroma magniostiolatum* (MFLU 22–0121, in Indian Ink). e *Ascagilis submersa* (MFLU 18–1527, holotype). f *Jahnula appendiculata* (PE0010). g *Aliquandostipite khaoyaiensis* (MFLU 21-0125. h *Aquimassariosphaeria kunmingensis* (HKAS 102148, holotype). i *Pseudojahnula potamophila* (F111). j *Mamillisphaeria dimorphospora* (BRIP 22967a). k *Byssothecium circinans* (G-K 18367). l *Caryospora aquatica* (MFLU 18–1202). m *Neohelicascus elaterascus* (MC0430–1). n *Clohesyomyces aquaticus* (MFLU 11–1112). o *Acrocalymma aquatica* MFLU 22–0114. p *Pseudoxylomyces elegans* MFLU 20–0554. Scale bars: a–p = 10 µm

ecological group was not monophyletic as some of these evolved together with terrestrial and marine fungi (Raja et al. 2013a, Zhang et al. 2014b, Ariyawansa et al. 2015, Fournier et al. 2015, Luo et al. 2016a, Huang et al. 2018). More recently, multi-locus phylogeny of Dothideomycetes showed freshwater taxa were scattered in most pleosporalean families with many in Tubeufiaceae, Tubeufiales (Dong et al. 2020b) (Fig. 6). There are 46 genera exclusively found in freshwater habitats, with 14 freshwater species reported in *Lindgomyces* (Lindgomycetaceae, Pleosporales), 11 in *Jahnula* (Aliquandostipitaceae, Jahnulales) and eight in *Neohelicascus* (Morosphaeriaceae, Pleosporales) (Dong et al. 2020b, Calabon et al. 2022). Based on a multi-locus phylogeny and morphology, a taxonomic revision of *Helicascus* resulted in the transfer of some species to *Aquihelicascus* and *Neohelicascus,* but marine species, including the type species, were retained in the genus (Dong et al. 2020b).

Pang et al. (2002) introduced Jahnulales in Dothideomycetes with two families Aliquandostipitaceae and Manglicolaceae, which contain approximately 80 species (Wijayawardene et al. 2020). Aliquandostipitacea was introduced by Inderbitzin et al. (2001) and typified with *Aliquandostipite.* The family has undergone significance changes with further research resulting in nine genera: *Aliquandostipite*, *Ascagilis*, *Brachiosphaera*, *Jahnula*,

Megalohypha, *Neojahnula*, *Pseudojahnula*, *Speiropsis*, and *Xylomyces* (Suetrong et al. 2011, Dong et al. 2020b, Wijayawardene et al. 2020).

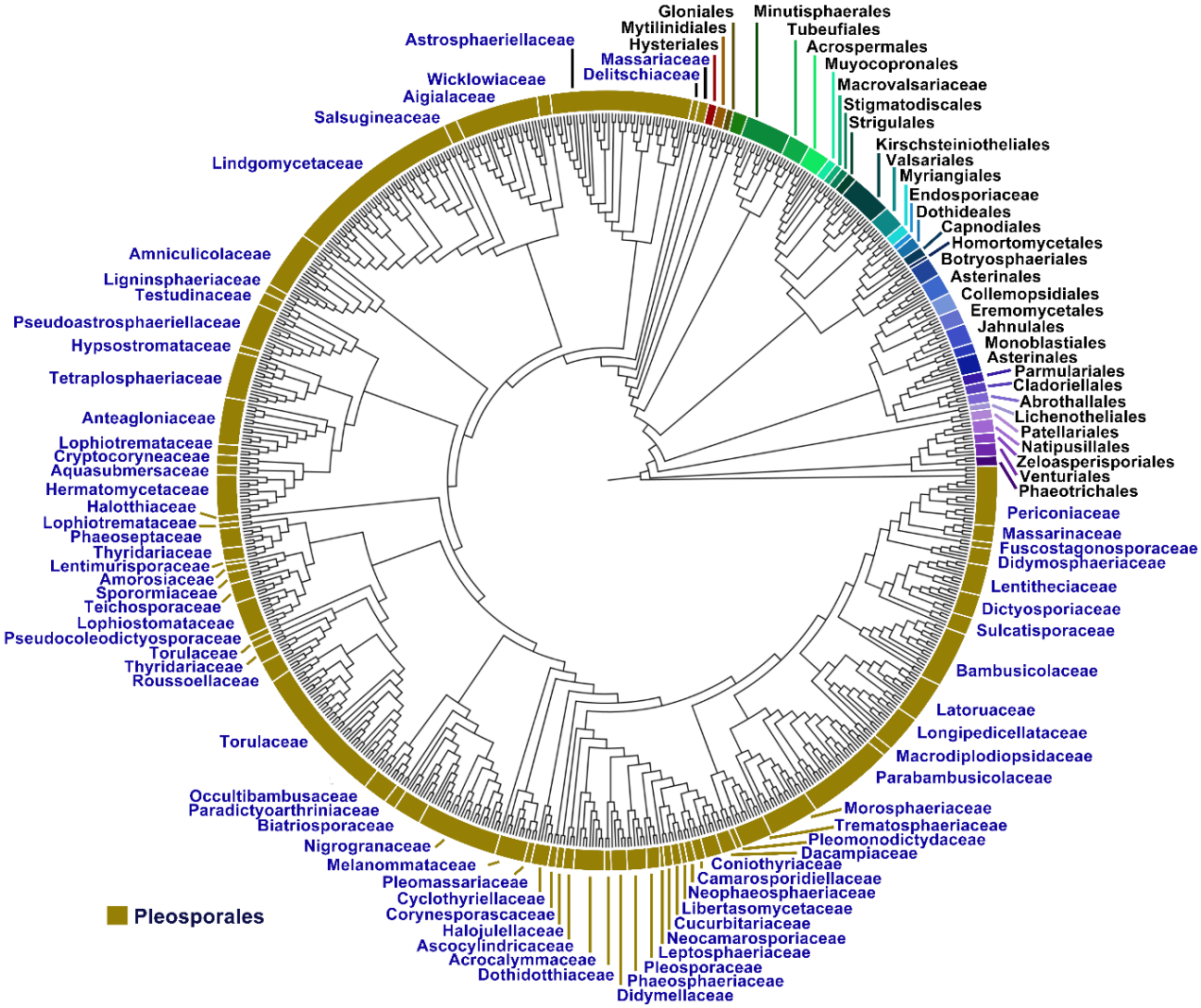


Figure 6 – Radial phylogenetic circular tree representation of freshwater Dothideomycetes.

Distribution and discussion of freshwater Dothideomycetes (Based on molecular data)

The distribution of freshwater Dothideomycetes is an eternal and unresolved topic as distribution patterns are still largely based on the locations of researchers and this limits discussion. Dothideomycetes is one of the largest classes in the phylum Ascomycota and it is also shown to be highly adapted to freshwater environments (Dong et al. 2020b) as compared to Eurotiomycetes (Liu et al. 2015b, Dong et al. 2018, 2020a, Wang et al. 2019). Therefore, freshwater Dothideomycetes are distributed all over the world where suitable freshwater environments occur for fungal growth. Freshwater dothideomycetous species have been extensively studied in some countries ranging from temperate to tropical regions, such as Australia (Hyde 1995, Hyde & Wong 1999), Japan (Tanaka et al. 2009, 2015), China (Hong Kong, Guangxi, Guizhou, Yunnan) (Tsui et al. 1999, Ho et al. 2000, Su et al. 2016, Lu et al. 2018b), Thailand (Luo et al. 2016c, Zhang et al. 2016) and USA (Raja et al. 2010, 2015). Dong et al. (2020b) concluded that freshwater Dothideomycetes are distributed in 35 countries, with China having the most species, followed by Thailand. Mycologists are questioning if global warming will affect fungal distribution (Hyde et al. 2016a) with studies undertaken by Luo et al. (2019) and Dong et al. (2020b). However, because of the limited number of studies, it is still untenable to speculate how climate change will exactly affect the distribution of freshwater fungi, but they are very likely to be sensitive to environmental change and global

warming (Hyde et al. 2016a). Based on the current data, many species occur worldwide, e.g., *Aliquandostipite crystallinus*, *Aquihelicascus thalassioideus*, *Jahnula aquatica* and *Lindgomyces ingoldianus* (Dong et al. 2020b). It is still puzzling to understand the subtle connection between these cosmopolitan species and freshwater ecology. Another challenge is that researchers are facing a problem dealing with the fungal taxa discovered earlier because DNA sequence data was not available, therefore the identification and geographical distribution must be treated with caution. The worldwide distribution of freshwater Dothideomycetes, with or without molecular data, are listed in Dong et al. (2020b).

Freshwater Sordariomycetes

Sordariomycetes is the second largest class of Ascomycota, after Dothideomycetes (Hyde et al. 2020c). Research on Sordariomycetes started from the early morphological studies of Barr (1983, 1987, 1990) and Eriksson & Hawksworth (1986, 1993) to the incorporation of molecular data by Lumbsch & Huhndorf (2007, 2010), Maharachchikumbura et al. (2015, 2016), and Hongsanan et al. (2017). The recent classification of Sordariomycetes is continuously updated and recently compiled by Hyde et al. (2020c), with seven subclasses distributed in 45 orders and 167 families, as outlined by Wijayawardene et al. (2020). Sordariomycetous taxa are mainly characterized by non-lichenized, perithecial ascomata and inoperculate unitunicate or non-fissitunicate asci (Maharachchikumbura et al. 2016, Hyde et al. 2020c). Members of Sordariomycetes have a cosmopolitan distribution and are mostly observed from terrestrial habitats. In aquatic habitats, Sordariomycetes are mostly saprobic on submerged decaying wood (Luo et al. 2019, Calabon et al. 2022) (Fig. 7).

From the discovery of *Lunulospora curvula* by Ingold (1942) in submerged decaying leaves of *Alnus glutinosa* and *Salix*, to the recent outline and monograph of freshwater Sordariomycetes by Luo et al. (2019), knowledge on the classification of freshwater Sordariomycetes has improved significantly. Annulatascaceous, distoseptisporaceous, pleurotheciaceous, and halosphaeriaceous species are the most typical and common freshwater Sordariomycetes on submerged wood (Luo et al. 2019, Calabon et al. 2022).

Molecular phylogeny of freshwater Sordariomycetes

The first major phylogenetic analysis of freshwater Sordariomycetes was by Cai et al. (2014) and based on LSU sequence data, represented in three subclasses (Sordariomycetidae, Hypocreomycecetidae, Xylariomycetidae) and 13 orders. The phylogenetic analysis of Cai et al. (2014) resulted in a phylogenetically polyphyletic Annulatascaceae with members distributed in five clades. Later, Maharachchikumbura et al. (2015) introduced Annulatascales to accommodate the family Annulatascaceae and referred to the Diaporthomycetidae. The most comprehensive phylogenetic study of combined LSU, SSU, RPB2 and TEF1α sequence data of freshwater Sordariomycetes was conducted by Luo et al. (2019) wherein 356 freshwater fungal strains were included in the study, with 129 fresh isolates. The 854 strains clustered in six Sordariomycetes subclasses, Diaporthomycetidae, Hypocreomycetidae, Lulworthiomycetidae, Savoryellomycetidae, Sordariomycetidae, and Xylariomycetidae (Lumbsch & Huhndorf 2010, Maharachchikumbura et al. 2015, Hongsanan et al. 2017). Freshwater Sordariomycetes is well-distributed in 47 clades under 30 orders. Hypocreales contains the greatest number of genera (19 genera), followed by Chaetosphaeriales (16 genera), Sordariales (13 genera), and Annulatascales (10 genera) (Fig. 8). Hyde et al. (2021) studied the evolution of freshwater Diaporthomycetidae with a divergence time of 238 MYA, with the introduction of novel taxa (orders: Barbatosphaeriales, Cancellidiales, Ceratolentales, Conlariales, Rhamphoriales; families: Aquapteridosporaceae, Cancellidiaceae, Ceratolentaceae, Bullimycetaceae, Phialemoniopsaceae, Pseudostanjehughesiaceae; species: *Cancellidium atrobrunneum, C. cinereum, C. griseonigrum*.). Lately, newly introduced taxa are supported with molecular data, and it gives a better understanding of the phylogeny and evolution of freshwater Sordariomycetes. Unfortunately, the placements of many freshwater Sordariomycetes remains unresolved and there are taxa without living cultures thus sequence data are unavailable.

Distribution and discussion of freshwater Sordariomycetes (Based on molecular data)

Like freshwater Dothideomycetes, the distribution of freshwater Sordariomycetes is still dependent on the locations of the laboratories wherein researchers are active in doing fungal explorations on this group. There are taxa frequently isolated in tropical and temperate regions like, *Annulatascus velatisporus* (Hyde 1992b, Hyde et al. 1998, Wong et al. 1999a, Ho et al. 2001, Tsui et al. 2003, Hu et al. 2010, Sudheep & Sridhar 2011, Dayarathne et al. 2016); *Ophioceras commune* (Shearer et al. 1999, Tsui et al. 2001c, 2003, Raja et al. 2009, Abdel-Aziz 2016); *Aquanectria penicillioides* (Duarte et al. 2012, Ghate & Sridhar 2015, Lombard et al. 2015, Mun et al. 2016, Luo et al. 2019); *Neonectria lugdunensis* (Gulis & Suberkropp 2003, Baschien et al. 2006, 2008, Cornut et al. 2014, Raposeiro et al. 2018, Pietryczuk et al. 2018); *Clavatospora longibrachiata* (Gulis & Suberkropp 2003, Menéndez et al. 2012, Cornut et al. 2014, Raposeiro et al. 2018, Pietryczuk et al. 2018)*;* and *Lunulospora curvula* (Schoenlein-Crusius et al. 2009, Duarte et al. 2012, Cornut et al. 2014, Pietryczuk et al. 2018, Raposeiro et al. 2018). Some genera are speciose with various novel taxa introduced from Thailand and China: *Pleurotheciella*, *Canalisporium*, *Chaetosphaeria*, *Tainosphaeria*; see Luo et al. (2019) and Calabon et al. (2022) for species and distribution. Though most of the present taxonomic studies incorporate molecular data in the introduction of taxa, there are still taxa with uncertain placements due to lack of living cultures and type sequences. Furthermore, most of the geographical data of freshwater Sordariomycetes are mainly based on biodiversity studies using morphology and it is worth noting to take cautions when dealing with distributions of freshwater fungi.

Freshwater Eurotiomycetes

Eurotiomycetes is a morphologically diverse group of ascomycetes. The class was established by Eriksson & Winka (1997) and presently consists of five subclasses: Chaetothyriomycetidae, Coryneliomycetidae, Cryptocaliciomycetidae, Eurotiomycetidae, Mycocaliciomycetidae, and Sclerococcomycetidae (Geiser et al. 2006, Hibbett et al. 2007, Wood et al. 2016, Réblová et al. 2017, Prieto et al. 2021). The microcolonies of Eurotiomycetes formed under natural conditions are morphologically similar leading to difficulty in accurately distinguishing species from one another The incorporation of molecular techniques in fungal taxonomy makes the classification of fungi more objective, accurate, and comprehensive, and significantly improves our understanding of the phylogeny and evolution of freshwater Eurotiomycetes (Wood et al. 2016, Réblová et al. 2017, Luo et al. 2019, Wijayawardene et al. 2020; Dong et al. 2020a, Prieto et al. 2021). The new taxa published in recent years are supported by molecular data which enables a better understanding of phylogenetic relationship of Eurotiomycetes. Based on the phylogenetic analysis of molecular data, the specific taxonomic status of some taxa of Eurotiomycetes has been clarified (Wood et al. 2016, Réblová et al. 2017, Prieto et al. 2021). Wijayawardene et al. (2020) provides an outline of the classification of the Fungi and fungus-like taxa and accepted 3,994 published species in the Eurotiomycetes.

Compared with the classes Dothideomycetes and Sordariomycetes, the number of freshwater Eurotiomycetes species was small (217 species), accounting for only 5.4% of the total number (Fig. 9). But these species still play an important role in freshwater environments as saprophytes on submerged wood, decaying leaves, branches, and plant debris in lakes and streams (Liu et al. 2015b, Dong et al. 2018, Liu et al. 2018, Wang et al. 2019). Eurotiomycetes are also known growing on inundated rocks and pebbles (e.g., *Verrucaria* spp.) and isolated from sediments and freshwater (e.g., drinking water, groundwater, tap water) (Iwatsu et al. 1991, de Hoog et al. 2011, Crous et al. 2013, Calabon et al. 2022). Some groups are parasitic on or in the body of aquatic animals, causing disease or death of the animals e.g., *Aspergillus* and *Penicillium* infecting organs of ornamental and aquacultures fishes (Iqbal et al. 2012, Chauhan et al. 2014, Chauhan & Bankhede 2013). In addition, some freshwater Eurotiomycetes species are also potential producers of biologically active substances (Yamazaki et al. 2016, Rotinsulu et al. 2017, Abdel-Wahab et al. 2018, Steenwyk et al. 2020), and they play important roles in basic research, industry, and public health.

Herein, we used the ITS, LSU, and β-tubulin (tub2) sequence data available from Eurotiomycetes in freshwater and other environments to construct a phylogenetic tree (Fig. 10). The phylogenetic position and distribution of freshwater Eurotiomycetes species in the main orders and families are summarized.

Figure 7 – Freshwater Sordariomycetes. a, b *Lepteutypa aquatica* (MFLU 15–0077). c, d *Fluminicola thailandensis* (MFLU 15–0085). e, f *Tainosphaeria obclavata* (MFLU 18–1455). g *Distoseptispora cangshanensis* (MFLU 18-0474). h *Acrodictys liputii* (MFLU 21–0034). i, j *Aquapteridospora fusiformis* (MFLU 18–1601). k, l *Pseudodactylaria aquatica* (MFLU 21–0037). m, n *Sporoschisma longicatenatum* (MFLU 21–0033). o, p *Sporoschisma chiangraiense* (MFLU 21–0036). q, r *Neospadicoides thailandica* (MFLU 21–0032). s, t *Chloridium gonytrichii* (MFLU 21–0026). u *Sporidesmium nujiangense* (HKAS 115795). v *Cancellidium atrobrunneum* (MFLU 20–0429). Scale bars: a, i, m, q, s, t, v = 50 µm, b = 5 µm, c = 40 µm, d, f, j, l = 10 µm, e = 30 µm, g = 60 µm, h, k, n, p, r, s, u, = 20 µm, o = 100 µm.

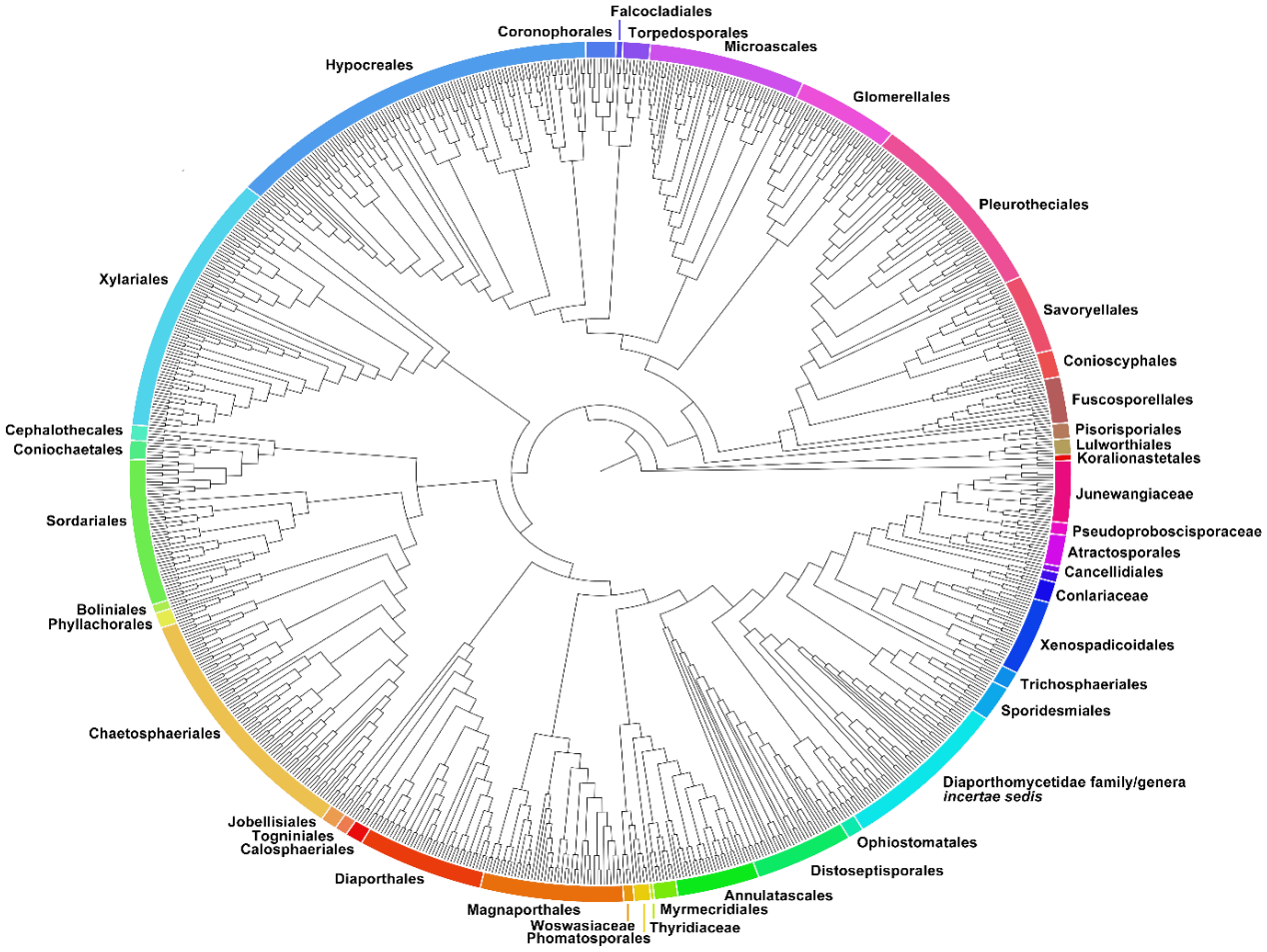


Figure 8 – Radial phylogenetic circular tree representation of freshwater Sordariomycetes.

Discussion of Eurotiomycetes

Herein, we constructed a phylogenetic tree using the available molecular sequences of most of the currently known freshwater Eurotiomycetes species (Fig. 10). Our analysis shows that freshwater Eurotiomycetes are dispersed in three subclasses, Chaetothyriomycetidae, Eurotiomycetidae and Sclerococcomycetidae. The main orders include Chaetothyriales, Eurotiales and Verrucariales, and a small number are distributed in Sclerococcales. Although many species have molecular sequence data, the specific taxonomic status of some species is still unclear. For example, in our phylogenetic tree, the two species of *Anthopsis*, *A. catenata* (CBS 492.81), *A. deltoidea* (CBS 263.77) was placed in Chaetothyriomycetidae and Sclerococcomycetidae, respectively, and with good support.

Chaetothyriales

Chaetothyriales is a diverse group, is renowned for containing so-called black yeasts and their filamentous relatives, among which are numerous opportunistic agents of disease in humans and cold-blooded vertebrates (Quan et al. 2020), including saprobes, pathogens, lichenized taxa, and epilithic fungi (Gueidan et al. 2008, Chomnunti et al. 2012a, b, Réblová et al. 2013, Hubka et al. 2014). Currently, five families are accepted in this order, *viz*. Chaetothyriaceae, Cyphellophoraceae, Epibryaceae, Herpotrichiellaceae, and Trichomeriaceae (Réblová et al. 2013, Gueidan et al. 2014, Chomnunti et al. 2012a, Barr 1976, 1987, Wijayawardene et al. 2020). Most of the freshwater species are found in the Herpotrichiellaceae.

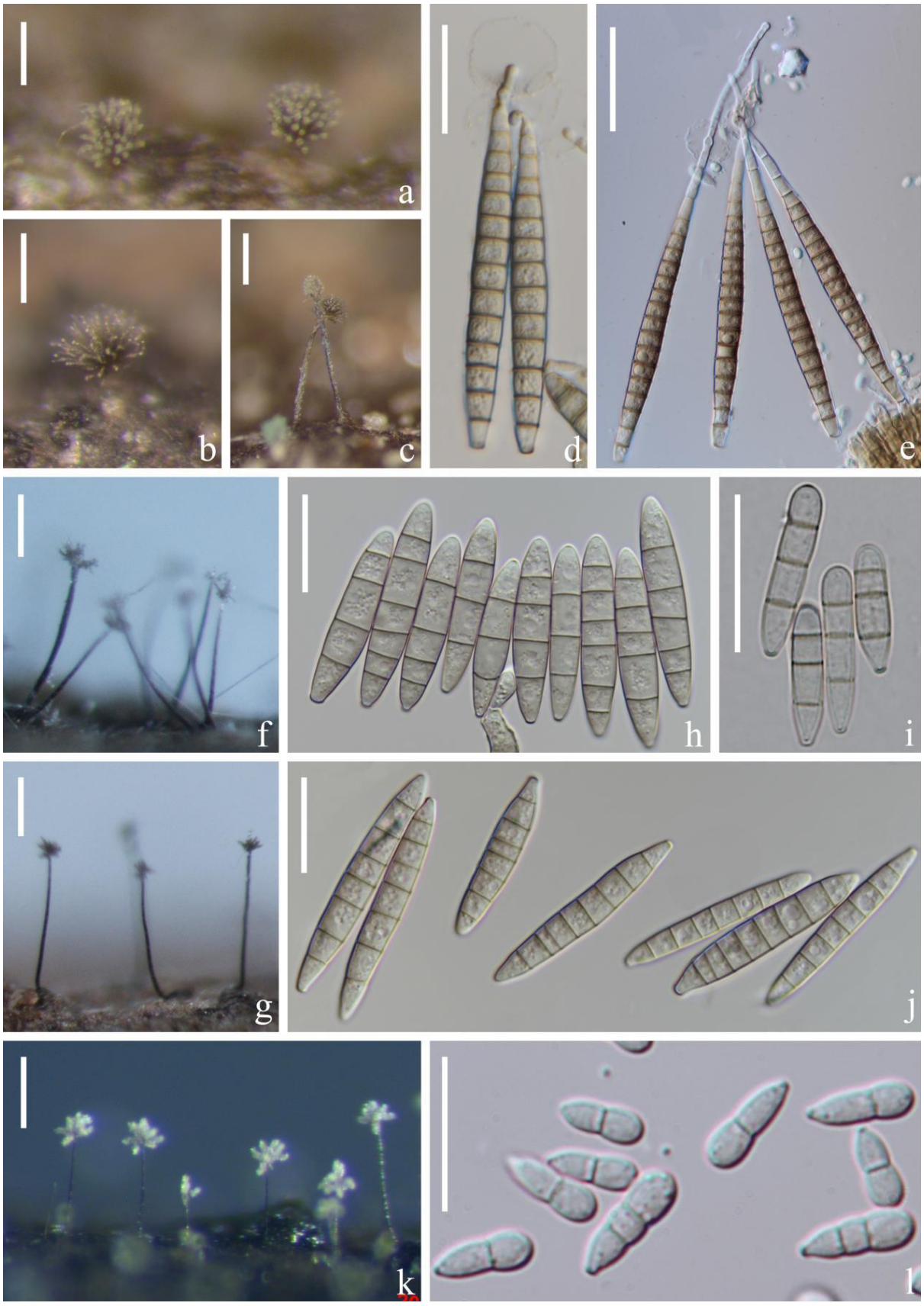


Figure 9 – Freshwater *Eurotiomycetes* spp. a–c Colonies of *Pseudobactrodesmium* spp. on natural substrates. d, e Conidia with sheath of *Pseudobactrodesmium* spp. f, g Colonies of *Minimelanolocus* spp. on natural substrates. h–j Conidia of *Minimelanolocus* spp. k Colonies of *Thysanorea papuana* on natural substrates. l Conidia of *Thysanorea papuana*. Scale bars: a, k = 150 µm, b, f, g = 100 µm, a = 50 µm, d, e, h–j = 20 µm, l = 10 µm.

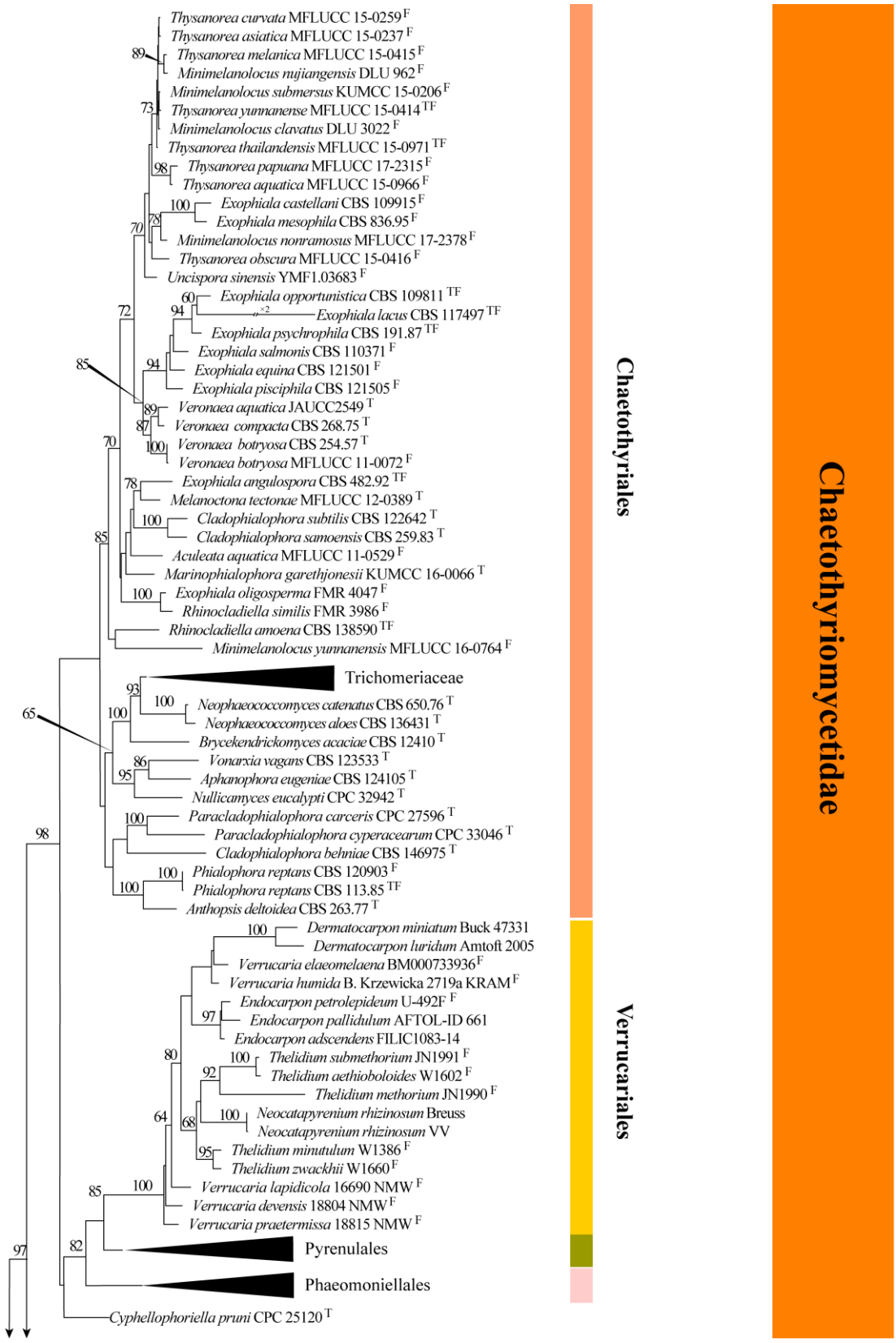


Figure 10 – Multi-gene phylogeny analysis was performed using the maximum likelihood analysis method, and the online tool RAxML-HPC2 on XSEDE (8.2.12) under the CIPRES website was used for analysis. All parameters in the analysis were set by default. The type species are indicated with "T" after the strain/specimen number, the species found in freshwater are indicated by "F" after the strain/specimen number. *Lectera nordwiniana* (CNUFC HRS5-3 and CNUFC HRS5-3-1) as the outgroup.

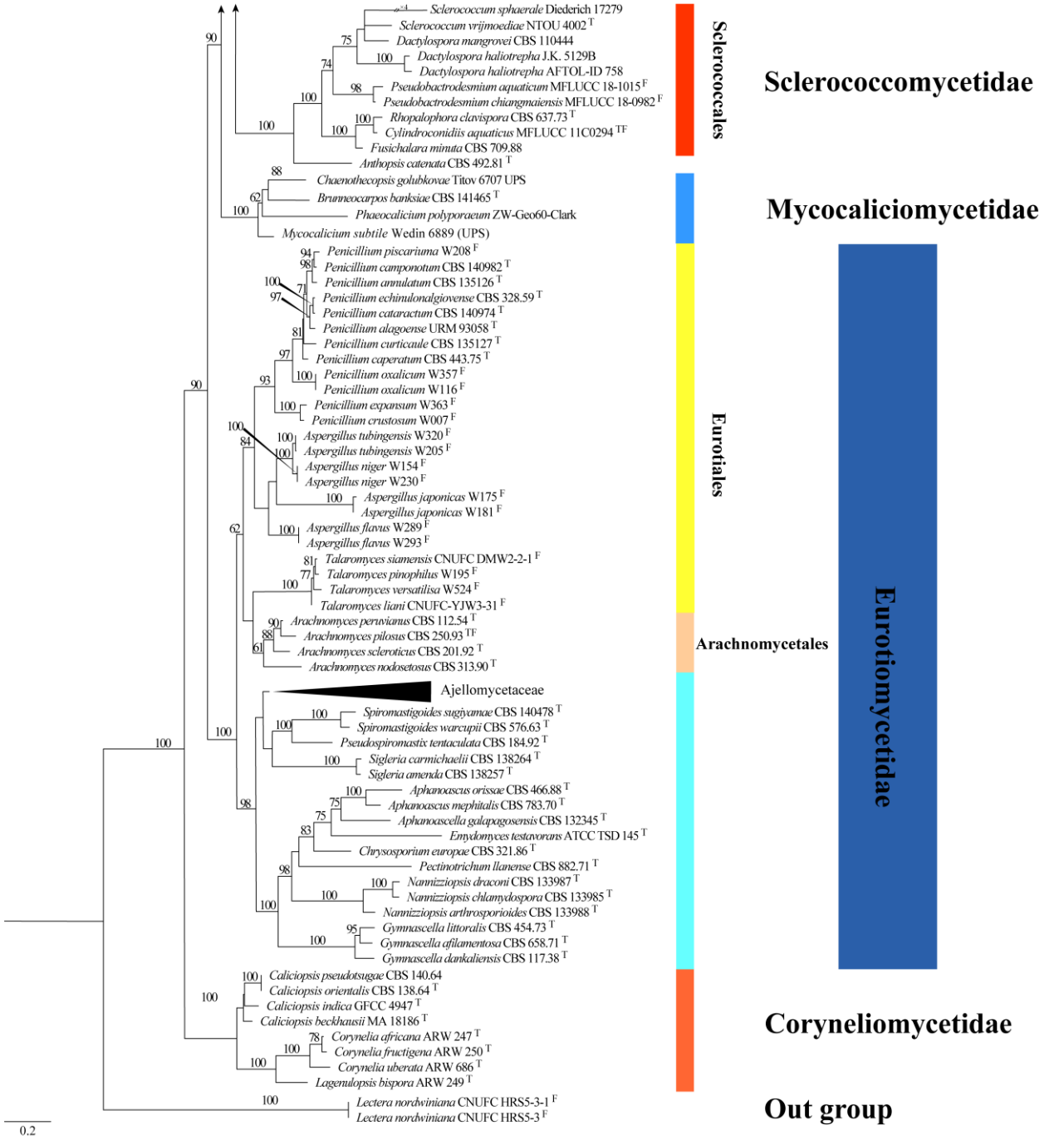


Figure 10 – Continued.

Herpotrichiellaceae is the best-known family in the order Chaetothyriales, which has been well supported by molecular data, as most of the known species were described from cultures (Quan et al. 2020). Herpotrichiellaceae comprise morphologically diverse dematiaceous fungi that include some saprophytic and pathogenic taxa isolated from humans and animals (Haase et al. 1999, de Hoog et al. 2000, Liu et al. 2015b, Wang et al. 2019, Dong et al. 2018). The freshwater species in this family are mainly distributed in the genera *Exophiala*, *Minimelanolocus* and *Thysanorea*, isolated from submerged woody substrates and water bodies (Liu et al. 2015b, Fiuza et al. 2017, Dong et al. 2018, Wang et al. 2019, Wan et al. 2021).

Verrucariales

The order Verrucariales is dominated by lichenized ascomycetes, most members have the typical thallus morphologies, including crustose, squamulose, foliose and rarely subfruticose thalli

(Muggia et al. 2017). Verrucariales species are widely distributed, from marine to freshwater to terrestrial habitats, from wet intertidal stones to submerged stones and wood in streams to dry rocks and tree trunks (Brodo et al. 1997, Harada & Wang 2004, Sanders et al. 2004, Orange et al. 2009, 2012, 2013, Thüs et al. 2015, Lucban et al. 2019). Freshwater Verrucariales is mainly distributed in the genera *Thelidium* and *Verrucaria*. Since the early classification, species of Verrucariales has been reported based on morphological characteristics, the phylogenetic relationships between members are unclear. For this reason, many researchers use molecular sequence data obtained from cultures to study the diversity of Verrucariales and the phylogenetic relationship of individual members (Muggia et al. 2010, Gueidan et al. 2007).

Verrucariaceae is a group of mainly lichenized ascomycetes from widely diverse habitats. Species classified within Verrucariaceae grow mainly on rocks, either epilithically or endolithically within the superficial layer of the rock (Gueidan et al. 2007). They are can also colonize other types of substrates in dry environments: soils (Breuss 1996), wood or bark (Orange 1989, Breuss 1998), mosses (Dőbbeler 1997); in aquatic habitats: boulders located in rivers (Keller 2000, Thüs 2002), or marine intertidal and supralittoral zones of rocky shores (Harada & Wang 2004, Sanders et al. 2004). Currently, 50 species of Verrucariaceae have been reported in freshwater environments, mainly growing on rocky surfaces in freshwater streams and rivers (McCarthy 1995, Harada & Wang 2008, Harada 2012, Orange 2013, Krzewicka et al. 2017).

Eurotiales

Eurotiales is a relatively large order of Eurotiomycetidae, which is widely distributed in the world. Its members are found in various environments: soil, food, drinking water and human and animal organisms (Yu et al. 2005, Hedayati et al. 2007, Engelhart et al. 2009, do Nascimento Barbosa et al. 2016, Pangging et al. 2019, Samson et al. 2010, 2019), and have a positive and negative impact on human activities. Aspergillaceae and Trichocomaceae are the two larger families in the order Eurotiales, containing 15 and 8 genera, respectively (Wijayawardene et al. 2020). Freshwater Eurotiales species include the genera *Aspergillus*, *Penicillium*, and *Trichoderma* (Aspergillaceae and Trichocomaceae), and are mainly reported in the sediments and water bodies of lakes, rivers, and ponds (Gupta & Kushwaha 2012, Heo et al. 2019, Pangging et al. 2019, Piontelli et al. 2019, Mun et al. 2020). Many Eurotiales reported in freshwater environments are also often reported from terrestrial habitats. Therefore, some scholars believe these to be runoff from terrestrial habitats and not true freshwater fungi. For example, *Aspergillus*, *Penicillium*, and *Trichoderma* species reported in freshwater environments are not considered true aquatic species (Daniel et al. 2007, Lind et al. 2017, Nielsen et al. 2017). It is because they are everywhere, being washed into streams or lakes from terrestrial habitats. Therefore, it is challenging to determine if all Eurotiales species isolated from freshwater are truly active in this environment.

Sclerococcales

Réblová et al. (2017) introduced Sclerococcomycetidae, Sclerococcales, and Sclerococcaceae, based on five loci (nucSSU, ITS, nucLSU, mitSSU, rpb1 and rpb2) phylogeny. The latest revision of the classification of lichenicolous fungi by Diederich et al. (2018) synonymized Sclerococcaceae as Dactylosporaceae since *Sclerococcum* and *Dactylospora* represent a monophyletic group based on a two-locus (nuLSU and mtSSU) phylogeny. *Sclerococcum* (1821) predates *Dactylospora* (1855) so the former was set as the type genus.

The order Sclerococcales currently contains one family and five genera, including some lichenicolous, marine, and lignicolous species. Freshwater Sclerococcales species are rare: *Pseudobactrodesmium* and *Cylindroconidiis*, with a total of four species, *C. aquaticus*, *P. aquaticum*, *P. chiangmaiensis*, and *P. stilboideum* (Yu et al. 2018, Dong et al. 2020a, Boonmee et al. 2021).

Leotiomycetes

The class Leotiomycetes was introduced by Eriksson & Winka (1997) and is often referred as

the “inoperculate discomycetes”, because the traditional concept of Leotiomycetes only includes apothecial ascomycetes with inoperculate, unitunicate asci that open by apical perforation or pore to release their ascospores (Nannfeldt 1932, Korf 1973, Pfister & Kimbrough 2001). In recent years, more molecular sequences have been used for classification of their taxonomy, and some previous groups have been removed to establish a more natural system (Baral et al. 2015). Freshwater Leotiomycetes mostly grow on submerged or floating substrates such as scums, spume, cryptogamic plants, herbaceous and woody substrates (Ingold 1954, 1974, Magnes & Hafellner 1991, Tsui et al. 2000, Wong & Hyde 2001, Baschien et al. 2013) in various lotic and lentic freshwater environments, like ponds, rainfall, melting ice, lakes, springs, swamps, rivers, and water distribution system (Ingold 1954, Shearer & Crane 1986, Czeczuga & Orłowska 1999, Luo et al. 2004, Czeczuga et al. 2007, Grabińska-Loniewska et al. 2007, Raja et al. 2008, Funck et al. 2015). Previous discoveries of new taxa and sexual morph association of freshwater Leotiomycetes were solely based on morphological and culture observation (Ingold 1942, Beaton & Weste 1977, Shearer 1993, Webster 1993, Webster et al. 1995). In recent years, advances in sequencing technology have introduced deeper morpho-phylogenetic insights on novel species and holomorph revelation of freshwater Leotiomycetes (Belliveau & Bärlocher 2005, Campbell et al. 2006, 2009, Baschien et al. 2013, Duarte et al. 2015, Sri-indrasutdhi et al. 2015, Baudy et al. 2019). Currently, Leotiomycetes includes 14 orders and 52 families (Wijayawardene et al. 2020). Members of freshwater Leotiomycetes are mainly distributed in Helotiales (188) and Leotiomycetes families *incertae sedis* (54 species), and a few species are distributed in Thelebolales (8 species), Rhytismatales (4 species), and Lauriomycetales (3 species) (Calabon et al. 2022).

Lichinomycetes

Freshwater Lichinomycetes is a group of lichen-forming fungi, and little is known about their occurrence in freshwater habitats (Jørgensen et al. 2007). These species form gelatinous lichen-like symbioses with cyanobacteria, relatively small and grow on rocks and soil in moist or dry but temporarily wet localities (Egea & Rowe 1988, Gilbert 1996, Thüs et al. 2014, Kantvilas 2018, Gumboski et al. 2019). Currently, Lichinomycetes contains one order and three families, and the members found in freshwater environments are distributed in the families Lichinaceae (22 species) and Peltulaceae (3 species) (Wijayawardene et al. 2020, Calabon et al. 2022).

Orbiliomycetes

The class Orbiliomycetes comprises a large group of inoperculate discomycetes previously included in Helotiales. Based on morphological and molecular phylogenetic data, Orbiliaceae was raised to Orbiliomycetes, and currently contains only a single order, a single family, and 12 genera (Eriksson et al. 2003, Wijayawardene et al. 2020). Members of freshwater Orbiliomycetes mostly grow on submerged decaying wood, leaves, and spores in foam in freshwater streams, rivers, and swamps (Ingold 1944, Marvanová & Marvan 1969, Karamchand 2009, da Silva & Gusmão 2015, Fiuza et al. 2019). Currently, 14 species in ten genera, *viz*. *Arthrobotrys*, *Hyalorbilia*, *Dactylella*, *Dicranidion*, *Helicoon*, *Monacrosporium*, *Orbilia*, *Orbiliella*, *Trinacrium*, *Vermispora*, are found in freshwater environments (Calabon et al. 2022).

Pezizomycetes

The class of Pezizomycetes is commonly known as cup-fungi or operculate discomycetes and is one of the earliest diverging lineages of Pezizomycotina along with Orbiliomycetes (Spatafora et al. 2006, Schoch et al. 2009). Pezizomycetes taxa are characterized by asci that usually open by rupturing to form a terminal or eccentric lid or operculum, although some hypogeous and cleistothecial forms lack an operculum (Lumbsch et al. 2005, Hansen & Pfister 2006), and they occur on a variety of substrates, including soil, wood, dung (Abbott & Currah 1997, Kirk et al. 2008, Cheraghian 2016, Ekanayaka et al. 2016, 2017). Pezizomycetes are rarely reported from freshwater habitats. Jones et al. (2014a) recorded eight species from freshwater. Currently, 13

species in four families (Ascobolaceae, Pezizaceae, Pyronemataceae, Rhizinaceae) from freshwater habitats, all of which are found on woody substrates (Calabon et al. 2022).

Saccharomycetes

Saccharomycetes is a monophyletic lineage, comprise more than 1,200 species of yeasts (Wijayawardene et al. 2020). Saccharomycetes yeasts are found in nearly all regions of the world, including hot deserts, polar areas, in freshwater, in salt water, and in the atmosphere (Kurtzman et al. 2015). Their growth is mainly saprotrophic, often in association with plants, animals, but some members are important pathogens of humans (Mortimer & Polsinelli 1999, Vega & Black 2005, Martins et al. 2014, Erdogan & Rao 2015, Kurtzman et al. 2015). Freshwater Saccharomycetes species can grow on various substrates (water bodies, mud, sediments, and stones) in various freshwater environments (i.e., wetlands, lakes, ponds, canals, polluted water, tapwater) and some species are also isolated on the surface of animal bodies (Sláviková & Vadkertiová 1995, Khan et al. 2002, de García et al. 2007, Morais et al. 2010, 2020, Fell et al. 2011, Biedunkiewicz et al. 2013, Moubasher et al. 2018). Based on morphological and analytical phylogenetic analysis, 14 families of one order, Saccharomycetales, were accepted in Saccharomycetes (Wijayawardene et al. 2020). Some 150 Saccharomycetes species have been reported from freshwater habitats, and are mostly distributed in 11 families, with 50 reported from Saccharomycetales genera *incertae sedis* (Calabon et al. 2022).

Conclusion

From the reviews of Cai et al. (2014) and Shearer et al. (2014) to the recent class-level phylogenetic analysis of Luo et al. (2019) and Dong et al. (2020b), our understanding of the classification and interrelationships of freshwater ascomycetes has increased significantly. Freshwater fungal taxonomists recently introduced novel taxa with cultures and sequence data, and integrated protein-coding loci in the phylogenies, leading towards a natural classification of freshwater fungi. However, gaps remain in the molecular phylogeny of freshwater ascomycetes mainly to the lack in availability of living cultures and molecular data, leading to uncertain taxonomic placements and unknown evolutionary relationships, see Calabon et al. (2022) for list of freshwater fungal taxa in the Ascomycota *incertae sedis*. Further exploration of freshwater habitats with comprehensive sampling of various substrates, herbarium material observations, and generation of nuclear and protein-coding sequence data will help in the further delineation of freshwater ascomycetes and better resolution of their phylogenetic relationship.

Biology of Freshwater Basal Fungi

Introduction

Early branching fungi (basal fungi) are classified in several phyla including Aphelidiomycota, Blastocladiomycota, Chytridiomycota, Monoblepharomycota, Mucoromycota, and Rozellomycota (Hibbett et al. 2007, Tedersoo et al. 2018, Adl et al. 2019, Naranjo-Ortiz & Gabaldón 2019, James et al. 2020, Voigt et al. 2021). They consist of two major lineages namely the zoosporic and zygosporic fungi (Hibbett et al. 2007, Voigt et al. 2021). Zoosporic fungi refer to basal lineages that produce motile spores called zoospores, while the spores of zygosporic fungi are non-motile (O'Donnell et al. 2001, Powell & Letcher 2014a, Longcore & Simmons 2020, Voigt et al. 2021). Basal fungi have been primarily discovered from freshwater, terrestrial, and marine ecosystems (Abdel-Wahab et al. 2014, Longcore & Simmons 2020). The ecological roles of fungi in the freshwater environment are pivotal and diverse, aiding in the overall function of that habitat. Freshwater fungal species complete at least one part of their life cycle in freshwater, distribute propagules in or above water, or use any resource of predominantly aquatic or semi-aquatic nature as substratum (Tsui et al. 2016, Calabon et al. 2020a). Examples of freshwater habitats are streams, ditches, canals, lakes, peats, and swamps (Tsui et al. 2016).

Among basal fungal lineages, zoosporic taxa, especially Chytridiomycota, are the most common in freshwater ecosystems. The currently reported diversity of zygosporic fungi (e.g., Mucoromycota and Mortierellomycota) in freshwater is significantly lower in terms of described species or sequences generated from high throughput sequencing (Lepère et al. 2019). The roles of basal fungi in freshwater ecology have been largely overlooked. Saprobic freshwater fungi assist in the breakdown of allochthonous organic material, like leaves and twigs, which results in the provision of 99% of total energy input in surface water (Ittner et al. 2018). Parasitic zoosporic species infect numerous phytoplankton groups (diatoms, green algae, cyanobacteria, and dinoflagellates) and invertebrates (opisthokonts), and they regulate the population density of their hosts (Kagami et al. 2012, Ishida et al. 2015). Planktonic fungi are also indicators of water quality (Ishida et al. 2015, Chen et al. 2018). The parasitic chytrid fungi, namely *Batrachochytrium dendrobatidis* and *B. salamandrivorans*, have devastating effects on amphibians (Martel et al. 2013, Van Rooij et al. 2015). Batrachochytrids have caused mass declines and the near extinction of several species of amphibians (Fisher & Garner 2020). *Catenaria*, *Coelomomyces* and *Olpidium* are common parasites of freshwater and terrestrial invertebrates worldwide (Whisler 1985, Barron 2004). Most invertebrates that come into contact with freshwater at any stage of their life cycle, whether as larvae or adults, can be parasitized by zoosporic fungi (Gleason et al. 2010a). Given the importance of these groups of fungi, more studies on their diversity, and ecological significance in freshwater habitats are needed.

This entry focuses on the biology of freshwater basal fungi. It aims to provide a brief overview on the various aspects of basal fungi in freshwater habitats. However, it is not intended to cover all aspects within this discipline or provide a full literary review.

Taxonomic classification of basal fungi

Fungi colonizing freshwater habitats are scattered across various phyla including the early branching fungal groups. The taxonomic classification of early diverging lineages of fungi has been revised in the last few years (James et al. 2006a, b, 2020, Hibbett et al. 2007, Spatafora et al. 2016, Choi & Kim 2017, Tedersoo et al. 2018, Naranjo-Ortiz & Gabaldón 2019). Previously, all zoosporic lineages were placed in the phylum Chytridiomycota, while zygosporic ones comprised the now invalid phylum "Zygomycota" (Barr 2001, James et al. 2006b, Hibbett et al. 2007, James et al. 2020). The advent and increased resolution of molecular tools has allowed the circumscription of monophyletic groups, such as Blastocladiomycota, Chytridiomycota, and Neocallimastigomycota. These groups are well supported not only by molecular evidence, but also cellular ultrastructure such as the structure of the mitotic apparatus (James et al. 2006a, b, Hibbett et al. 2007, Powell & Letcher 2014a, Longcore & Simmons 2020). The artificial phylum Zygomycota was broken down to several phyla such as Mucoromycota, and Mortierellomycota (James et al. 2006b, Hibbett et al. 2007, Spatafora et al. 2016). The classification of Zygomycota was traditionally based on morphological characteristics, but molecular biology has revolutionized the taxonomic classification of this group (Hibbett et al. 2007, Spatafora et al. 2016). Zygosporic taxa have been grouped into new phyla, classes, orders, and families (Voigt et al. 2021). In freshwater, members of Aphelidiomycota, Blastocladiomycota, Chytridiomycota, Entomophthoromycota, Monoblepharomycota, Mortierellomycota, Mucoromycota, Olpidiomycota, and Zoopagomycota have been found. Table 2 lists the genera that have been found in freshwater habitats.

Chytridiomycota is the most species-rich zoosporic phylum (Blaalid & Khomich 2021). Members of this phylum (or in some classification schemes, the class Chytridiomycetes) are commonly referred to as chytrids or chytrid fungi (Powell & Letcher 2014a, Fisher & Garner 2020). Tedersoo et al. (2018a) proposed nine classes and ten orders, Naranjo-Ortiz & Gabaldón (2019) accepted three classes and seven orders, and James et al. (2020) accepted 14 orders. Visualization and proper identification of chytrids is difficult due to their small size and lack of distinct morphological characters. Due to these reasons, chytrids are often misidentified as protists (Blaalid & Khomich 2021). The zoospores (zoosporangiospores) of chytrids swim with a

characteristic abrupt hopping and darting pattern assisted by a single posteriorly directed whiplash flagellum (Powell & Letcher 2014a, Longcore & Simmons 2020). The motile spores are unwalled but have a carbohydrate coat that protects them against desiccation (Longcore & Simmons 2020). Chytrids, and zoosporic fungi in general, were referred to as aquatic fungi, however these have also been reported in terrestrial habitats (Powell 2017a). To date, very few basal taxa have been isolated from marine habitats (Abdel-Wahab et al. 2014, Jones et al. 2019, Hassett et al. 2020b). High throughput sequencing (HTS) studies have shown a high diversity of some zoosporic lineages including chytrids in oceanic networks (Abdel-Wahab et al. 2014, Comeau et al. 2016). However, their diversity in marine habitats is poorly understood despite their predicted ecological significance and function. The various distinct methodologies that are required to isolate zoosporic organisms as opposed to those conventionally used for filamentous fungi, poses a constraint for their study. In environmental surveys, chytrid sequences are seemingly difficult to amplify possibly due to primer bias, which might partly explain their underreporting (Grossart et al. 2019, Blaalid & Khomich 2021). These issues highlight that the taxonomy and systematics of these fungi is far from resolved.

Rozellomycota (also known as Cryptomycota) and Aphelidiomycota consist of endoparasitic taxa placing at a basal position in the fungal tree of life. Both form the Opisthosporidia with ongoing debates on whether they are indeed fungi (Karpov et al. 2014b, Tedersoo et al. 2018, Wijayawardene et al. 2018, 2020, Adl et al. 2019, Naranjo-Ortiz & Gabaldón 2019, James et al. 2020). Aphelids and rozellids have several similarities. Both are endoparasites that feed by phagocytosis (Letcher & Powell 2019). Aphelids parasitize various green algae and diatoms and currently comprise a single class, order, and family with four genera (Letcher & Powell 2019, Wijayawardene et al. 2020). Rozellomycota species are endoparasites of oomycetes and opisthokonts, such as chytrids, Bryozoa, fish and invertebrates, such as *Daphnia* species, and amphipods. This group (including Microsporidia) accounts for 105 genera, 221 species in four orders and 21 families of freshwater taxa, thus a significant group of basal fungi (Calabon et al. 2022). All described species can produce a chitinous cell wall, yet they grow as naked protoplasts inside their host. They vary greatly in morphology where some species are fungus-like (*Rozella*) and infect their host during their motile stage (flagellated), while others lack flagella and infection occurs from spores through a polar filament (Weiss 2001, Franzen 2004, Corsaro et al. 2014, Quandt et al. 2017). Data on the distribution of these members comes mostly from environmental surveys. Most aphelids and rozellids have been isolated or described from freshwater habitats such as streams, ditches, and lakes (Calabon et al. 2022). High throughput sequencing has also unveiled a plethora of diversity from freshwater ecosystems (Rojas-Jimenez et al. 2017).

Microsporidia comprises a distinct lineage of unicellular eukaryotes, which groups as sister to, or within Rozellomycota (Tedersoo et al. 2018, Naranjo-Ortiz & Gabaldón 2019, James et al. 2020, Wijayawardene et al. 2020). Microsporidia are obligate intracellular eukaryotic parasites that use the polar tube, a unique invasion apparatus, to infect hosts (Weiss 2001, Franzen 2004). These organisms inhabit many ecosystems including freshwater. They infect both vertebrates and invertebrates and have been reported from a broad range of hosts from protists to mammals, including humans, to arthropods (Desportes et al. 1985, Call et al. 1998, Meissner et al. 2012, Han et al. 2020). In freshwater, microsporidia infect fish, crustaceans, amphipods, Bryozoa and other fauna (Jones et al. 2019, Drozdova et al. 2020, Liu et al. 2020, Weng et al. 2022). The intracellular lifestyle of microsporidia has led to compact genomes, highly reduced mitochondria, which are referred to as mitosomes, and presence of many types of transporters that enhance uptake of compounds from the host (Tsaousis et al. 2008, Williams et al. 2008, Nakjang et al. 2013, Bass et al. 2018, Park & Poulin 2021).

Zygosporic fungi are considered as the basal terrestrial lineages that most likely evolved from flagellate, aquatic ancestors (Hibbett et al. 2007, Hoffmann et al. 2011). Currently, scarce data are available on the distribution of these fungi in aquatic habitats. Only few species from the phyla Entomophthoromycota, Monoblepharomycota, Mortierellomycota, Mucoromycota, and Zoopagomycota have been found in freshwater. This could be due to several factors such as low

number of studies targeting these fungi, difficulty in isolating them and primer bias during HTS. Alternatively, it is possible that freshwater might not be the ideal habitat for these fungi. Among the zygosporic fungi, Mucoromycota seems to be more prevalent in freshwater than other zygosporic taxa.

Diversity of basal fungi in freshwater ecosystems

Freshwater accounts for less than 1% of the Earth's surface and comprises 2.5% of all water on the planet. Fungal taxa in freshwater habitats are important components of microbial communities of water columns and sediments in both lentic and lotic systems (Sutcliffe et al. 2018). Zoosporic fungi, especially chytrids, are the most speciose representatives in aquatic ecosystems (Gleason et al. 2017). The worldwide distribution of zygosporic fungi in freshwater habitats is comparatively poorly documented. The study of freshwater zoosporic fungi dates to 1960s, but studies on their diversity, quantitative abundance and especially their interaction with other microorganisms are scarce (Gleason et al. 2017, Grossart et al. 2019).

High throughput sequencing studies have revealed a high biodiversity and predominance of unexplored zoosporic taxa in freshwater habitats. In ice-covered lakes of Antarctica, Rozellomycota and Chytridiomycota are the most abundant fungal phyla (Comeau et al. 2016). In the temperate Lake Tahoe, in the United States and freshwater Arctic habitats, Chytridiomycota-like sequences seemingly representing novel lineages dominated the fungal diversity (Comeau et al. 2016, Gleason et al. 2017). Pelagic zones of lakes also have high diversity of undescribed zoosporic fungi (Lefèvre et al. 2010). However, morphological studies involving light microscopy have revealed the opposite (Sime-Ngando et al. 2011). Furthermore, not all environmental surveys of freshwater habitats show a dominance of zoosporic fungi, several indicate that Dikarya is the predominant group (Shearer et al. 2007, Lepère et al. 2019). For example, in a study of 25 lakes and four rivers, Dikarya fungi (Ascomycota and Basidiomycota) represented the most OTU-rich groups (Lepère et al. 2019). Nonetheless, even though Dikarya were the most abundant, basal groups such as Rozellomycota and Chytridiomycota were also found. The results of these studies indicate the presence of undocumented diversity of these fungi in various habitats.

An increasing number of freshwater zygosporic species are being described with several being novel taxa. Previously, known species from freshwater habitats included members of *Erynia* and *Acaulopage*, which are parasites of aquatic insects (Goh & Hyde 1996a). The distribution and diversity studies on these taxa have now expanded. Aquatic zygosporic species include *Aquamortierella*, *Mortierella*, *Gryganskiella*, *Endogone*, *Gilbertella*, *Cunninghamella*, *Absidia*, *Gongronella*, *Rhizomucor*, *Actinomucor* and *Mucor* (Table 2) (Schell et al. 2011, Nguyen & Lee 2016, Nguyen et al. 2017a, b, 2019, Moubasher et al. 2018, Crous et al. 2020, Vandepol et al. 2020).

Ecology of freshwater basal fungi

Basal fungi contribute to various processes in freshwater habitats, but only scant studies exist. They are mainly involved in water purification and recycling of organic matter that is used by other organisms (such as invertebrates) (Voronin 2008). Furthermore, basal fungi aid in mineralization of organic matter, and regulation of insect population abundance. In freshwater ecosystems, these fungi have various life modes such as parasites or saprobes. Saprobic freshwater basal fungi survive on dead organic matter found in waterbodies. Zoosporic fungi are usually isolated by means of baits, such as snake skin, cellophane, exoskeleton of shrimp, and pollen. Examples of freshwater saprobes are *Homolaphlyctis polyrhiza*, and *Synchytrium microbalum* (Longcore et al. 2012, 2016). Parasites depend on their hosts for food, such as *Collimyces mutans* and *Staurastromyces oculus*, and parasitize *Microglena coccifera* and *Staurastrum* sp. (Van den Wyngaert et al. 2017, Seto & Degawa 2018a). Being heterotrophs, these fungi consume live organic matter, but they primarily process dead organic matter hence are involved in the formation of the structural-functional organization of aquatic biocenoses (Voronin 2008). Basal fungi are ecological competitors, can tolerate stress and are ruderals (Dix & Webster 1995). These fungi

thrive in environments that have a continuous supply of substrates/nutrients and with optimal conditions, such as temperature (Sparrow 1960). They have commonly been isolated from terrestrial environments such as soil and sometimes their diversity is picked up in hydrothermal vents (Le Calvez et al. 2009). Basal fungi can survive harsh habitats due to the production of resistant structures, such as zoospore cysts and resistant sporangia. Depending on the environment, these fungi use optimal strategies to occupy several ecological niches (Gleason et al. 2010a, b, 2012).

Parasites of freshwater phytoplankton

Recently, there has been a surge of research in phytoplankton parasitism by zoosporic fungi. Chytrids and aphelids comprise common parasites of phytoplankton (Kagami et al. 2007, Sime-Ngando et al. 2011, Lepère et al. 2019, Song et al. 2021). Studies on chytrids parasitizing algae have been the main focus, while aphelids research is still lagging. Phytoplankton is responsible for a large proportion of primary production and crucial for the survival of food webs (Winder & Schindler 2004). Due to the importance of phytoplankton in aquatic ecosystems, the ecological roles of both groups of fungal parasites are of interest (Jephcott et al. 2017). The increased encroachment of freshwater habitats and surrounding environment may lead to disturbances in the relationship and dynamics between organisms. For instance, invasive species may move afield into a new ecosystem rapidly and disturb the delicate balance between a host and its parasite. Hence, an understanding of host parasite relationships is crucial to recognize ecosystems under stress (Jephcott et al. 2017). In this context, basal freshwater fungal parasites may be used as such indicators.

In freshwater ecosystems, where phytoplankton and zooplankton abound, fungal parasitism has an important role (Voronin 2008). Fungal parasitism affects and controls the population density of planktonic species and influences competitive interactions between hosts and other species. Selective parasitism is a decisive factor in the seasonal succession and food web relationships (Canter & Lund 1951). For example, fungal parasitism of one algal species favorably affects the development of other phytoplankters; when parasites infect one algal species, its resources may become available to other phytoplankton species thereby increasing their population density (Paterson 1960).

Chytrid parasitism has been documented in several species of diatoms, dinoflagellates and cyanobacteria in various habitats. Chytrids are involved in nutrient cycling and comprise vital components of the mycoloop. The mycoloop is defined as a process that alters carbon flow in aquatic habitats. Specifically, chytrids infect inedible phytoplankton, such as *Asterionella*, or cyanobacteria that are poorly edible to other organisms, use the nutrients of their host to grow and produce zoospores that have high content of fatty acids and sterol (Voigt et al. 2021). When zooplankton (e.g., *Daphnia*) grazes on the nutrient-rich zoospores, carbon that would have otherwise been inaccessible is recycled (Kagami et al. 2007).

The extent of host-specificity of chytrids has not been fully explored to date. Chytrids are usually considered as highly host specific parasites, however this is only speculative. Chytrids with narrow and broader host ranges have been reported (Gromov et al. 1999). Parasites can be facultative or obligate. Among chytrids, facultative parasitism has been observed in *Dinochytrium kinnereticum*. This fungus is parasitic on weakened cells of the dinoflagellate *Peridinium gatunense*, but is also saprobic on pollen. In this type of parasitism, the parasite can infect and reproduce on the living host but is also able to exploit other nutrient sources or hosts (Leshem et al. 2016). One example of obligate parasitism among chytrids is *Rhizophydium planktonicum*, which parasitizes the diatom *Asterionella formosa* (Canter & Jaworski 1978).

Infection by chytrids encompasses several phases (Frenken et al. 2017). The initial attraction of zoospores to the host is most likely mediated by chemotaxis. Upon encounter, the zoospores encyst, retract their flagellum, produce a cell wall, and a germ tube, which is used to penetrate the host cell. However, depending on the host, chytrids use a different feature of the host cell to invade (Powell 1994, Gromov et al. 1999).

Table 2 Classification of freshwater basal fungi.

Phylum	Class	Order	Family	Genus	References
Aphelidiomycota	Aphelidiomycetes	Aphelidiales	Aphelidiaceae	*Amoeboaphelidium*	Letcher et al. (2015b), Letcher & Powell (2019)
				Aphelidium	Gromov & Mamkaeva (1975), Tcvetkova et al. (2019)
				Paraphelidium	Karpov et al. (2017b, c)
Blastocladiomycota	Blastocladiomycetes	Blastocladiales	Blastocladiaceae	*Allomyces*	Sparrow (1964), Ali & Abdel-Raheem (2003), Powell (2017a)
				Blastocladia	Dasgupta & John (1988a), El-Hissy et al. (1996), Steciow & Marano (2006)
				Blastocladiopsis	Hsiao (1969), Waterhouse (1942), Czeczuga et al. (1990)
			Catenariaceae	*Catenophlyctis*	Karling (1968b)
				Nematoceromyces	Martin (1978)
			Paraphysodermataceae	*Paraphysoderma*	James et al. (2012)
		Catenomycetales	Catenomycetaceae	*Catenomyces*	Hanson (1944b)
			Coelomomycetaceae	*Coelomomyces*	Porter et al. (2011)
				Coelomycidium	Weiser (1984)
				Microallomyces	Emerson & Robertson (1974)
Chytridiomycota	Chytridiomycetes	Chytridiales	Asterophlyctaceae	*Asterophlyctis*	Letcher et al. (2018)
				Wheelerophlyctis	Letcher et al. (2018)
			Chytridiaceae	*Chytridium*	Nowakowski (1876), Rooney & McKnight (1972), Dasgupta & John (1988b)
				Dendrochytridium	Powell & Letcher (2014b)
				Dinochytrium	Leshem et al. (2016), Hassett et al. (2020a)
				Irineochytrium	Dogma (1969)
				Polyphlyctis	Letcher & Powell (2018)
				Zopfochytrium	Powell et al. (2018)
			Chytriomycetaceae	*Avachytrium*	Vélez et al. (2013)
				Chytriomyces	Karling (1945), Willoughby & Townley (1961), Letcher & Powell (2002), Davis et al. (2019)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Entophlyctis	Sparrow (1943), Haskins (1946), Karling (1968a), Dasgupta & John (1988b), Shin et al. (2001)
				Fayochytriomyces	Davis et al. (2015)
				Obelidium	Karling (1967), Blackwell et al. (2012)
				Odontochytrium	Vélez et al. (2013)
				Pendulichytrium	Seto & Degawa (2018b)
				Physocladia	Davis et al. (2019)
				Podochytrium	Sparrow (1951), Willoughby & Townley (1961)
				Rhizidium	Karling (1944), Dayal & Kirin (1981)
				Rhizoclosmatium	Paterson (1967), Davis et al. (2019)
				Siphonaria	Karling (1967), Dogma (1976)
			Phlyctochytriaceae	*Phlyctochytrium*	Ajello (1945), Johnson (1969)
			Phlyctorhizaceae	*Phlyctorhiza*	Hanson (1946)
			Pseudorhizidiaceae	*Pseudorhizidium*	Davis et al. (2019)
			Scherffeliomycetaceae	*Scherffeliomyces*	Sparrow (1938)
		Zygorhizidiales	Zygorhizidiaceae	*Zygorhizidium*	Canter (1963), Seto et al. (2020)
		Zygophlyctidales	Zygophlyctidaceae	*Zygophlyctis*	Paterson (1958), Seto et al. (2020)
				Delfinachytrium	Vélez et al. (2013)
		Polyphagales	Polyphagaceae	*Polyphagus*	Bartsch (1945), Johns (1964), Doweld (2014)
			Sparrowiaceae	*Sparrowia*	Papa & Cruz-Papa (2020)
			Chytridiomycetes genera *incertae sedis*	*Bertramia*	Weiser & McCauley (1974)
				Blyttiomyces	Sparrow & Barr (1955), Dasgupta & John (1988b), Blackwell et al. (2011)
				Canteria	Karling (1971)
				Dangeardia	Canter (1946), Geitler (1963), Batko (1970)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Dangeardiana	Johns (1956), Valkanov (1964)
				Dictyomorpha	Mullins (1961), Sarkar & Dayal (1988)
				Ichthyochytrium	Korting (1983)
				Loborhiza	Hanson (1944a)
				Macrochytrium	Crasemann (1954)
				Mitochytridium	Dangeard (1911), Hassan (1982)
				Mucophilus	Červinka et al. (1974)
				Perolpidium	Canter (1949b)
				Pseudopileum	Canter (1963)
				Rhizosiphon	Canter & Lund (1968), Gleason et al. (2014)
				Rhopalophlyctis	Karling (1945), Davis et al. (2019)
				Saccomyces	Demchenko (2019)
				Septosperma	Seymour (1971), Dogma (1974)
				Sorokinocystis	Saccardo (1888)
				Sporophlyctidium	Sparrow (1978)
				Sporophlyctis	Sparrow (1960)
				Truittella	Karling (1949)
				Volvorax	Van den Wyngaert et al. (2018)
				Zygochytrium	Sorokin (1874)
	Cladochytriomycetes	Cladochytriales	Catenochytridiaceae	*Catenochytridium*	Willoughby & Townley (1961)
			Cladochytriaceae	*Cladochytrium*	Czeczuga et al. (2005)
			Endochytriaceae	*Diplophlyctis*	Willoughby & Townley (1961), Dogma (1976)
				Endochytrium	Karling (1941)
			Nowakowskiellaceae	*Nowakowskiella*	Jerônimo et al. (2019)
			Septochytriaceae	*Septochytrium*	Karling (1942), Johanson (1943)
	Lobulomycetes	Lobulomycetales	Lobulomycetaceae	*Algomyces*	Van den Wyngaert et al. (2018)
				Clydaea	Simmons et al. (2009)
				Lobulomyces	Simmons et al. (2009), Davis et al. (2018)
	Mesochytriomycetes	Gromochytriales	Gromochytriaceae	*Gromochytrium*	Karpov et al. (2014a)
		Mesochytriales	Mesochytriaceae	*Mesochytrium*	Gromov et al. (2000)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
	Polychytriomycetes	Polychytriales	Arkayaceae	*Arkaya*	Longcore & Simmons (2012)
			Polychytriaceae	*Karlingiomyces*	Blackwell et al. (2004)
				Lacustromyces	Longcore (1993)
				Neokarlingia	Longcore & Simmons (2012)
				Polychytrium	Ajello (1945)
	Rhizophydiomycetes	Rhizophydiales	Alphamycetaceae	*Alphamyces*	Canter (1961), Letcher et al. (2012), Davis et al. (2018)
				Betamyces	Letcher et al. (2012)
			Angulomycetaceae	*Angulomyces*	Letcher et al. (2008b)
			Aquamycetaceae	*Aquamyces*	Letcher et al. (2008b)
			Collimycetaceae	*Collimyces*	Seto & Degawa (2018a)
			Coralloidiomycetaceae	*Coralloidiomyces*	Letcher et al. (2008a)
			Globomycetaceae	*Globomyces*	Sparrow (1952), Letcher et al. (2008b)
				Urceomyces	Letcher et al. (2008b)
			Gorgonomycetaceae	*Gorgonomyces*	Letcher et al. (2008b)
			Halomycetaceae	*Halomyces*	Letcher et al. (2015a)
				Paranamyces	Letcher et al. (2015a)
				Ulkenomyces	Letcher et al. (2015a)
			Kappamycetaceae	*Kappamyces*	Letcher & Powell (2005)
			Pateramycetaceae	*Pateramyces*	Letcher et al. (2008b)
			Protrudomycetaceae	*Protrudomyces*	Letcher et al. (2008b)
			Rhizophydiaceae	*Rhizophydium*	Dayal & Kirin (1981), Dasgupta & John (1988b), Gromov et al. (1999), Davis et al. (2018, 2019)
			Staurastromycetaceae	*Staurastromyces*	Van den Wyngaert et al. (2017)
				Homolaphlyctis	Longcore et al. (2012)
			Terramycetaceae	*Boothiomyces*	Davis et al. (2016), Jerônimo & Pires-Zottarelli (2020)
	Rhizophlyctidomycetes	Rhizophlyctidales	Borealophlyctidaceae	*Borealophlyctis*	Davis et al. (2016)
			Rhizophlyctidaceae	*Rhizophlyctis*	Sparrow (1952), Willoughby & Townley (1961), Dasgupta & John (1988b)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
	Spizellomycetes	Spizellomycetales	Spizellomycetaceae	*Karlingia*	Hassan (1983), Czeczuga et al. (1990)
				Spizellomyces	Wakefield et al. (2010)
	Synchytriomycetes	Synchytriales	Synchytriaceae	*Endodesmidium*	Canter (1949b)
				Synchytrium	Canter (1949b), Longcore et al. (2016)
				Micromyces	Roberts (1953), Davis et al. (2019)
	Chytridiomycota genera *incertae sedis*			*Achlyella*	Czeczuga & Muszynska (2001)
				Achlyogeton	Czeczuga & Muszyńska (1993)
Entomophthoromycota	Entomophthoromycetes	Entomophthorales	Ancylistaceae	*Ancylistes*	Davis et al. (2019)
				Conidiobolus	Sparrow (1952)
			Entomophthoraceae	*Erynia*	Sridhar & Kaveriappa (1992), Voglmayr (1996)
				Zoophthora	Davis et al. (2019)
Monoblepharomycota	Hyaloraphidiomycetes	Hyaloraphidiales	Hyaloraphidiaceae	*Hyaloraphidium*	Ustinova et al. (2000)
	Monoblepharidomycetes	Monoblepharidales	Gonapodyaceae	*Gonapodya*	Thaxter (1895), Waterhouse (1942)
			Harpochytriaceae	*Harpochytrium*	Jane (1946), Schumacher & Whitford (1961)
			Monoblepharidaceae	*Monoblepharis*	Lagerheim (1900), Perrott (1957), Sparrow (1960)
			Oedogoniomycetaceae	*Oedogoniomyces*	Kobayasi & Ôkubo (1954)
			Telasphaerulaceae	*Telasphaerula*	Karpov et al. (2017a)
	Sanchytriomycetes	Sanchytriales	Sanchytriaceae	*Amoeboradix*	Karpov et al. (2018)
				Sanchytrium	Karpov et al. (2017a)
Mortierellomycota	Mortierellomycetes	Mortierellales	Mortierellaceae	*Aquamortierella*	Vandepol et al. (2020)
				Gryganskiella	Vandepol et al. (2020)
				Mortierella	Hyde et al. (2016b), Nguyen & Lee (2016), Nguyen et al. (2019)
Mucoromycota	Endogonomycetes	Endogonales	Endogonaceae	*Endogone*	Sparrow (1952)
	Mucoromycetes	Mucorales	Choanephoraceae	*Gilbertella*	Lee et al. (2018)
			Cunninghamellaceae	*Absidia*	Moubasher et al. (2018)
				Cunninghamella	Nguyen et al. (2017a)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Gongronella	Crous et al. (2020)
			Lichtheimiaceae	*Rhizomucor*	Schell et al. (2011)
			Mucoraceae	*Actinomucor*	Nguyen et al. (2017b)
				Mucor	Nguyen et al. (2020), Magray et al. (2020)
			Rhizopodaceae	*Rhizopus*	Gonçalves et al. (2006)
			Syncephalastraceae	*Syncephalastrum*	El-Morsy et al. (2013)
Olpidiomycota	Olpidiomycetes	Olpidiales	Olpidiaceae	*Olpidium*	Canter (1949a), Sparrow (1957), Czeczuga et al. (1990)
Zoopagomycota	Zoopagomycetes	Zoopagales	Zoopagaceae	*Acaulopage*	Voglmayr (1996)
				Zoophagus	Karling (1966), Davis et al. (2019)
Rozellomycota	Microsporidea	Amblyosporida	Amblyosporidae	*Amblyospora*	Andreadis et al. (2012, 2018)
				Becnelia	Tonka & Weiser (2000)
				Crepidulospora	Simakova et al. (2004)
				Culicospora	Weiser & Prasertphon (1982)
				Culicosporella	Hazard et al. (1984)
				Dimeiospora	Simakova et al. (2003)
				Hyalinocysta	Andreadis & Vossbrinck (2002)
				Intrapredatorus	Chen et al. (1998)
				Novothelohania	Andreadis et al. (2012)
				Parathelohania	Andreadis et al. (2012)
				Trichoctosporea	Andreadis et al. (2012)
				Tricornia	Pell & Canning (1992)
			Caudosporidae	*Binucleospora*	Bronnvall & Larsson (1995)
				Caudospora	Vávra & Undeen (1981)
				Flabelliforma	Bronnvall & Larsson (2001)
				Neoflabelliforma	Morris & Freeman (2010)
				Scipionospora	Bylén & Larsson (1996)
			Gurleyidae	*Agglomerata*	Sokolova et al. (2016), Weng et al. (2020)
				Binucleata	Larsson & Voronin (2000)
				Conglomerata	Vávra et al. (2018)
				Episeptum	Hyliš et al. (2007)
				Gurleya	Friedrich et al. (1996)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Lanatospora	Vávra et al. (2016b)
				Larssonia	Vidtmann (1993)
				Marssoniella	Vávra et al. (2005)
				Norlevinea	Vávra (1984)
				Paraepiseptum	Hyliš et al. (2007)
				Pseudoberwaldia	Vávra et al. (2019)
				Senoma	Simakova et al. (2005)
				Zelenkaia	Hyliš et al. (2013)
			Amblyosporida genera *incertae sedis*	*Alfvenia*	Sokolova et al. (2016)
				Takaokaspora	Andreadis et al. (2013)
				Trichotuzetia	Vávra et al. (1997)
		Glugeida	Glugeidae	*Alloglugea*	Paperna & Lainson (1995)
				Amazonspora	Azevedo & Matos (2003)
				Cambaraspora	Bojko et al. (2020b)
				Glugea	Ward et al. (2005), Minter (2019)
				Loma	Casal et al. (2009)
				Pseudoloma	Ramsay et al. (2010)
			Spragueidae	*Apotaspora*	Sokolova & Overstreet (2018)
				Microgemma	Ralphs & Matthews (1986)
				Potaspora	Ding et al. (2016)
				Pseudokabatana	Liu et al. (2019)
			Thelohaniidae	*Cucumispora*	Bojko et al. (2015)
				Napamichum	Larsson (1990a)
				Nudispora	Larsson (1990b)
				Thelohania	Pretto et al. (2018)
			Unikaryonidae	*Dictyocoela*	Terry et al. (2004)
				Unikaryon	Voronin (1977, 1999)
			Glugeida genus *incertae sedis*	*Triwangia*	Wang et al. (2013a)
		Neopereziida	Berwaldiidae	*Berwaldia*	Simakova et al. (2018)
				Fibrillanosema	Galbreath Slothouber et al. (2004)
			Neopereziidae	*Bacillidium*	Morris et al. (2005b)
				Bryonosema	Canning et al. (2002)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Neoperezia	Issi et al. (2012)
				Pseudonosema	Canning et al. (2002)
				Schroedera	Morris & Adams (2002), Morris et al. (2005a)
				Trichonosema	Desser et al. (2004)
			Neopereziida genera *incertae sedis*	*Janacekia*	Weng et al. (2021)
				Systenostrema	Sokolova et al. (2006)
		Nosematida	Enterocytozoonidae	*Paranucleospora*	Nylund et al. (2010)
			Mrazekiidae	*Helmichia*	Tokarev et al. (2012)
				Jirovecia	Liu et al. (2020)
				Mrazekia	Larsson et al. (1993)
			Nosematidae	*Nosema*	Terry et al. (2004)
				Vairimorpha	Pretto et al. (2018)
			Ordosporidae	*Ordospora*	Larsson et al. (1997)
			Nosematida genera *incertae sedis*	*Anisofilariata*	Tokarev et al. (2010b)
				Crispospora	Tokarev et al. (2010a)
				Enterocytospora	Jiang et al. (2020)
				Glugoides	Larsson et al. (1996)
		Microsporidea families *incertae sedis*	Cougourdellidae	*Cougourdella*	Larsson (1989)
			Duboscqiidae	*Duboscqia*	Larsson & Yan (1988)
				Tardivesicula	Larsson & Bylén (1992)
				Trichoduboscqia	Batson (1982)
			Fibrillasporidae	*Fibrillaspora*	Simakova et al. (2018)
			Golbergiidae	*Krishtalia*	Kilochitskii (1997)
			Microfilidae	*Microfilum*	Matos & Azevedo (2004)
			Neonosemoidiidae	*Neonosemoides*	Faye et al. (1991)
			Pleistophoridae	*Heterosporis*	Phelps et al. (2015), Tomamichel et al. (2018)
				Ovipleistophora	Lovy & Friend (2017), Bojko et al. (2020a)

Table 2 Continued.

Phylum	Class	Order	Family	Genus	References
				Pleistophora	Casal et al. (2016)
			Toxoglugeidae	*Toxospora*	Voronin (1993)
			Tuzetiidae	*Pankovaia*	Simakova et al. (2009)
				Paratuzetia	Poddubnaya et al. (2006)
				Tuzetia	Voronin (1986)
			Microsporidea genera *insertae sedis*	*Baculea*	Loubes & Akbarieh (1978)
				Caullerya	Wolinska et al. (2004)
				Evlachovaia	Issi (1986)
				Globulispora	Vávra et al. (2016a)
				Gurleyides	Voronin (1986)
				Hamiltosporidium	Haag et al. (2011)
				Holobispora	Voronin (1986)
				Kabataia	Casal et al. (2010)
				Kabatana	Lom et al. (2001)
				Microsporidium	Jones et al. (2017, 2020)
				Myosporidium	Jones et al. (2020)
				Stempellia	Voronin (1996)
			Rozellomycota genera *incertae sedis*	*Mitosporidium*	Haag et al. (2014)
				Paramicrosporidium	Corsaro et al. (2014)
				Rozella	Canter (1969)
	Rozellomycota orders *incertae sedis*	Chytridiopsida	Chytridiopsidae	*Chytridiopsis*	Larsson (1993)

Chytrids that infect diatoms enter the host cell through the girdle region of the frustule using a germ tube. Infection in other algal hosts is via the mucilage surrounding the host or directly through the cell wall if a mucilage layer is absent (Frenken et al. 2017). Rhizoids are produced, which expand through the host cell to enable nutrient gathering. Chytrid parasites use the host resources to mature and produce zoospores, which are released to the environment (Canter 1950, Canter & Lund 1951).

All aphelids described to date are obligate parasitoids (biotrophs) and can only be cultured with their hosts (Held 1981, Gleason et al. 2012, Letcher & Powell 2019). Aphelids appear to be very common parasitoids in many aquatic ecosystems, for example the genera *Aphelidium* and *Amoeboaphelidium* (Schweikert & Schnepf 1996, Letcher et al. 2013, Ilicic & Grossart 2022). Green algae and diatoms are common hosts of aphelids (Gleason et al. 2014, Jephcott et al. 2017). For example, several species of *Aphelidium* and *Amoeboaphelidium* infect unicellular freshwater green algae (Jephcott et al. 2017). Frequently, aphelid infection is observed in chlorococcous algae and *Tribonema gayanum* and hence these hosts are commonly used to maintain gross cultures of these parasites. Host specificity of aphelids has been previously investigated (Gromov & Mamkaeva 1968a, b, Letcher et al. 2017). Most often these host-parasite relationships are genus specific (Karpov et al. 2014b). However, scarce data is available to fully comprehend the extent of host-specificity of these organisms and to understand how aphelids detect and differentiate between host cells (Höger et al. 2021).

The life cycles of *Aphelidium*, *Amoeboaphelidium* and *Pseudaphelidium* are to some degree comparable to each other (Letcher et al. 2013, Karpov et al. 2017b, Hurdeal et al. 2021, Ilicic & Grossart 2022). The life cycle of aphelids is complex with different stages such as cyst, trophont, plasmodium and zoospore stage (Karpov et al. 2014a, Letcher & Powell 2019). Briefly, the parasitoid zoospore attaches to the host, encysts, and sheds the flagellum. The cyst germinates, producing an infection tube through which it penetrates the host cell. A vacuole is produced within the cyst, which enlarges and eventually pushes the cyst contents into the host cell (Karpov et al. 2017c). The parasitoid undergoes an intracellular phagotrophic amoebic life stage during which it engulfs the cytoplasmic contents of the host and transports the nutrients into a central digestive vacuole. As the parasitoid grows, it forms an endobiotic plasmodium that consumes the cytoplasm of the host cell. The plasmodium then divides into uninucleate cells (zoospores) (Letcher & Powell 2019). Once the uniflagellate zoospores mature, they are released from the empty host cell through the hole previously made by the infection tube. The cycle starts again, with the new zoospores infecting other host cells (Letcher et al. 2013, Karpov et al. 2014a).

The endobiotic nature of aphelids may decrease the likelihood of observing them in culture-based studies (Jephcott et al. 2017). The plasmodial stage is the most common phase observed in culture due to its longevity and consists of a large vacuole containing the residual body of this stage (Karpov et al. 2014a). Hence, studies on the ecological roles of the different life stages might provide more insight on their importance in freshwater habitats.

Adaptations of basal fungi to aquatic habitats

Zoosporic fungi produce and propagate motile spores that require free water for dispersal (Longcore & Simmons 2020). Presence of water is necessary, even for the culture and baiting of zoosporic fungi from substrates such as soil (Gleason et al. 2012). Fungal zoospores are usually uniflagellated (Sparrow 1960, Gleason & Lilje 2009). Some genera, especially parasites of algae, invertebrates and fungi produce amoeboid zoospores with pseudopodia (Gleason & Lilje 2009). The role of pseudopodia is speculative and needs to be further investigated. A proposed role is that they might be assisting in spore movement over solid surfaces of the hosts. For short dispersal of the zoospores, two mechanisms for active movement are known: flagellar and amoeboid. Flagellar movement is best suited and common in larger volumes of water, while amoeboid movement is best adapted for wet surfaces. For long range dispersal in water, zoospores may also use passive mechanisms. Structures, such as the zoospore cyst, mature and/or resistant sporangium, and the entire thallus function as asexual propagules. In freshwater habitats, these are carried horizontally by currents and vertically in water columns (Gleason et al. 2008, Gleason & Lilje 2009).

Zoospores use chemotaxis to scour fresh substrates (Gleason et al. 2017). They are attracted to specific sugar and amino acid exudates released as photosynthetic by-products by the host or substrate. These spores swim for minutes to hours (or even days in rare cases) seeking new substrates and encyst when favorable conditions are met (Powell & Letcher 2014a). The zoospore relies exclusively on endogenous reserves, primarily lipids, and glycogen for energy (Powell &

Letcher 2014b). Once spores find a suitable substrate, they adhere to it and encyst. During encystment, depending on the group of zoosporic fungi, the zoospores retract the flagellum or shed it prior to assuming a spherical shape. Zoospores can then adhere firmly to the surface of the substrates upon contact to encyst (Sparrow 1960). This behavior is of ecological significance for both saprobic and parasitic taxa as this establishes a permanent contact between the fungus and its potential food source. Zoospores become adhesive only during the initial stages of encystment before a cyst wall is made and the adhesiveness only lasts for 30–60s (Tsui et al. 2016). The timing of the adhesive phase coincides with the change from motile to sessile form, which is ecologically beneficial to the fungus. Once the cell wall forms and the cyst matures the adhesive properties are lost. Then, the cyst germinates, followed by penetration and colonization of the substrate (Tsui et al. 2016).

Microsporidian species are mostly unable to grow or divide outside of their host cells (Keeling 2009). They can only survive without their hosts as environmentally resistant, chitin-containing spores, which also comprise their infective stage (Wadi & Reinke 2020). The intimate relationship of microsporidia with their hosts, has led to a heavy dependence on the host for resources. Hence, microsporidia have undergone extensive genomic reduction (Corradi 2015, Wadi & Reinke 2020). The invasion apparatus of microsporidia is distinct from other intracellular eukaryotic pathogens. During infection and upon spore germination, the polar tube pierces the host cell. The parasite cytoplasm is delivered inside the host cytoplasm through the polar tube. The parasite then proliferates and eventually produces spores (Keeling 2009, Wadi & Reinke 2020).

Abiotic and biotic factors affecting basal lineages of fungi

Spatial distribution, and seasonal fluctuations affect the community structure of zoosporic fungi (Nascimento et al. 2011). Freshwater habitats are subject to variations in physical conditions. The pH, temperature, concentration of soluble metals and salinity may fluctuate and have repercussions on the freshwater microbial communities (Gleason et al. 2017). Temperature is an important factor that affects the fungal community. Research based on saprobic isolates from soil indicates the maximum temperature at which most of these zoosporic species grew was 30 °C. While some grew at 35 °C, 37 °C, few at 40 °C, none survived at 45 °C or over (Gleason et al. 2017). *Blastocladia* species grew well in temperatures varying from 11 °C to 14 °C and the maximum temperature at which they produce zoospores varied between 5 °C and 7 °C (Sparrow 1968). *Batrachochytrium dendrobatidis*, an important pathogenic chytrid, usually grows between 4–25 °C and does not survive long exposures at high temperatures (Powell 2017b). Some basal taxa can tolerate a wide range of temperatures. Examples are the parasites *Rhizophydium planktonicum* and *Rhizosiphon anabaenae* (Canter & Lund 1948, Paterson 1960).

Oxygen content in water is an integral part of freshwater habitats and dictates the survival of basal fungi in those environments. It regulates the abundance of zoosporic fungi at differing depths of the aquatic habitat by affecting their growth, distribution, and development (Voronin 2008). Dissolved oxygen content has been correlated with parasitism by *Rhizosiphon anabaenae* (Paterson 1960). Specifically, the parasite maximum occurred when the oxygen content was around 6.4–8.0 ppm indicating that these values were optimal for growth, development, and reproduction of the parasite in that study. However, whether infection rate is indeed affected by these values of oxygen content remains undetermined. The amount of dissolved oxygen content in water depends on factors such as the temperature of the water and concentration of salts. Temperature is inversely proportional to the quantity of dissolved oxygen in water; high temperature decreases the solubility of water oxygen content. Some basal fungal lineages grow at high oxygen content, while others grow at low concentration (Lund 1934, Paterson 1960, Sparrow 1968, Voronin 2008). Zoospores are usually concentrated in the oxygen rich water layers and the number of spores positively correlates with the water oxygen content (Lund 1934, Paterson 1960). Among zygosporic fungi, *Mucor* species may have higher resistance to the lack of oxygen than other freshwater fungal species (Collins & Willoughby 1962).

Acid rainfall, runoff, and fertilizers cause pH fluctuations in aquatic ecosystems. Some species grow in acidic water, some at neutral-alkaline, and others in alkaline waters. Most fungi grow at a pH between 4.0 and 9.0. Species diversity of zoosporic fungi decreases at acidotrophic conditions (Sparrow 1968). However, some species have been found in environments of extreme pH (Starkey & Waksman 1943). Zoosporic fungi have been found in bogs with pH as low as 3.6 (Mullen et al. 2000, Gleason et al. 2010a). In a fungal-based molecular survey of the acidic Rio Tinto River in Spain (pH: 2.0), sequences corresponding to chytrids were recovered (Zettler et al. 2002). Several species of chytrids, including *Rhizophlyctis rosea*, have been cultured in a broad pH range (Gleason et al. 2010a). In the case of zoosporic fungi, the dispersal stage might be the most affected by variation in the environment as the zoospores are unwalled.

The concentration of dissolved organic matter (DOM) strongly influences zoosporic fungi. An increase in DOM, increased the number of fungal species if the temperature and salt concentration were relatively low. Nonetheless, a significant increase in DOM with varying pollution decreased species diversity and occurrence, both of which could potentially lead to extinction (Harvey 1952, Tan & Lim 1984). Toxic metals have both beneficial and detrimental effects on basal fungi especially on the zoospores. The type of toxic metal and the life stage of the organism dictates the effects. Presence of some of these metals can promote encystment and germination of the zoospores (Gleason et al. 2017). For example, low levels of copper, lead and zinc have a stimulatory effect on zoospore release (Henderson et al. 2015). The effects of abiotic factors on fungal parasitism are still scarce and largely unknown. Canter & Lund (1948) noticed that all but one epidemic by *Rhizophydium* on *Asterionella* occurred when the concentrations of dissolved nitrate, silica and phosphate were high or rising. These epidemics were also noted to happen when the concentration of inorganic matter was low. This study was based on Esthwaite Water, and the south and north basins of Lake Windermere. The correlation of abiotic factors such as available silica in water, duration and intensity of light to degree of parasitism is difficult (Lund 1934, Canter & Lund 1951, 1953). Some researchers have speculated on the effects of factors such as light in parasitism. Bruning (1991) investigated the effects of light and phosphorus limitation on the parasite *Rhizophydium*. The effects of these two variables on the growth of the parasite in the study were comparable. Phosphorus limitations, as well as light limitation, reduced zoospore production, and slightly delayed the development of the sporangia. Ultimately, they could reduce epidemic threshold to a certain degree.

Biotic factors significantly affect growth and proliferation of basal fungi. A high diversity of *Rhizophydium* and *Nowakowskiella* was observed in the mesotrophic Lake Bourget in eastern France, when green algae and diatoms were abundant (Lepère et al. 2008). Moreover, a decline of rotifer population was linked to the Olpidiomycota species *Olpidium gregarium* in the Rio Grande Reservoir, São Bernardo do Campo, São Paulo State, Brazil (Meirinho et al. 2013). Studies have also shown a positive correlation between either total chlorophyll concentration or proportions of diatom sequences and zoosporic fungi, which may indicate the likelihood to parasitize algae (Gleason et al. 2017).

The Trichomycetes, an Aquatic Group of Arthropod-Gut Endosymbionts

Introduction and overview of the group

The Trichomycetes were once a fungal Class within the Zygomycota (Lichtwardt 1986), but actually the trichomycetes (with lower t, to indicate that this is not a natural, monophyletic clade) are recognized as a polyphyletic group of fungal and protozoan microorganisms sharing the ecological characteristic of living as obligate symbionts associated with diverse arthropod groups (Lichtwardt et al. 2001a). Most trichomycetes are endosymbionts, living attached to the inner gut lining of their hosts and extract nutrients from the food particles passing through the digestive system. Only one known genus contains ectosymbiont species (*Amoebidium* spp) living on the host's chitinous exoskeleton (Lichtwardt et al. 2001a). Most trichomycetes are aquatic, associated with immature stages of insects in freshwater and crustaceans in freshwater and marine ecosystems,

but some species have terrestrial hosts such as collembolans, coleoptera, miriapoda and isopoda (Lichtwardt et al. 2001a).

This ecological group includes three fungal orders: Harpellales, Orphellales and Asellariales, placed within the Zoopagomycota, subphylum Kickxellomycotina (Hibbett et al. 2007, Tretter et al. 2014, Spatafora et al. 2016, White et al. 2018), which are the subject of the present entry. On the other hand, the Eccrinales and Amoebidiales ("protistan trichomycetes") are now placed within the protist class Mesomycetozoea (= Ichthyosporea), Order Eccrinida (Cafaro 2005), but were once classified as fungi due to their thallial and spore structure and their ecology. This is the historical and practical reason why mycologists studying aquatic arthropod gut endobionts (trichomycetologists) also study this group of protists. In fact, species of *Paramoebidium* (Amoebidiales) are frequently found sharing the insect host hindgut with their fungal counterparts (Harpellales and Orphellales), while the Asellariales and Eccrinales are mostly associated with non-insect hosts such as Crustacea and Diplopoda, with a few Eccrinid species found in terrestrial beetles (Coleoptera).

The ecology of Trichomycetes

Ecologically, the trichomycetes may have a role in the integrity of the system since they take part in the macroinvertebrates' biology. As often, unexpected changes in inland water systems are due to the alterations in the complex connections among macroinvertebrates and associated trophic webs (Goedkoop & Johnson 1996, Lodge et al. 1998, Stockley et al. 1998), the study of arthropod-associated microorganisms becomes interesting indeed. It is now known that aquatic macroinvertebrates harbor a wide diversity of gut endosymbionts serving different functions, some of which are not yet well understood, especially regarding fungi. The existence of gut bacteria has long been recognized in freshwater and marine environments (Sochard et al. 1979, Gowing & Silver 1983, Sinsabaugh et al. 1985, Harris 1993). The metabolic activity of these microorganisms provides essential amino acids and vitamins (Fong & Mann 1980) and enhances the digestibility of plant food by providing enzymes such as cellulases into the gut of their host (Sochard et al. 1979). Although the bacterial microbiome is generally well recognized, fungal gut associates are less familiar, but they are not rare, even in the gut of aquatic arthropods, as demonstrated by the ubiquitous and common presence of trichomycetes (Lichtwardt et al. 2001a, Valle 2006, 2007). Most species of trichomycetes are regarded as commensalistic (Lichtwardt et al. 2001a), although some may be mutualistic by providing vitamins (Horn & Lichtwardt 1981) and parasitic relations have been documented in a few cases (Sweeney 1981a, b). However, there is much more to learn about this particular fungal-arthropod symbiosis.

The reproductive spores of trichomycetes enter the digestive system of their hosts by direct consumption with their food. Thus, the nutritional behavior of the host is very important (if not determinant) for the success of the symbiosis (Valle & de Figueroa 2015). The currently known species of trichomycetes are associated with mandibulate arthropods that feed on various decaying or living non-animal organisms, or are omnivorous, but are presumably never associated with obligate predaceous or parasitic hosts (Lichtwardt et al. 2001a). Most of the species of trichomycetes are associated predominantly with shredder, collector, or scraper hosts, which only occasionally may ingest some animal tissues, but do not behave as true predators (Valle & de Figueroa 2015).

After being ingested, the germinating spore anchors at particular zones of the gut lining, according to specific preferences (Lichtwardt et al. 2001a) After attachment, the thallus undergoes fast development, growing to form branched or unbranched filamentous or sac-like thalli that will ultimately sporulate, producing asexual or, when conditions are adequate, sexual spores that will reach the external environment through elimination of food waste. Most species of trichomycetes spend all their growth and nutritional stages within the gut, taking nutrients from food particles transiting through the lumen (Misra & Horn 2001, Lichtwardt et al. 2001a). Apparently, trichomycetes do not affect the normal host nutritional activity or requirements, since most of the nutrients required by the arthropod host, have already been absorbed in the foregut and midgut,

before reaching the hindgut, where most species of trichomycetes are found, using complex or undigested nutrients (Misra & Horn 2001).

The life cycle of the trichomycetes, both the vegetative and especially the reproductive stages, are coordinated with the growth cycle of the host, so that all the thallial and sporic development of the endosymbiont are adapted and chronologically adjusted to occur within the intermolt period of the arthropod (Lichtwardt et al. 2001a), as we will explain later.

The degree of host-fungus specificity when establishing the symbiosis is variable. While some trichomycetes show a wide range of potential hosts, others live specifically only in certain groups, supporting the theory of a tight host-fungal coevolution (Misra & Horn 2001, White et al. 2001, Valle & Santamaria 2005). It is among the species of Eccrinales and Asellariales that we find a higher degree of specificity. The genera *Orchesellaria* and *Asellaria* can be clearly separated only on the basis of the host, the former being found in Collembola (insects), and the latter in isopod Crustaceans. Within Harpellales, we find all the extremes, from *Smittium* species, that can live in larvae of chironomids, simulids and culicids (e.g., *S. culisetae*, now *Zancudomyces culisetae* (Lichtwardt et al. 2001a), to others showing specific associations with a single genus of insects [e.g., *Tectimyces robustus* (Valle & Santamaria 2002)].

Geographical distribution of trichomycetes

The trichomycetes have a broad world-wide distribution, being present wherever their hosts thrive, in both continental and island habitats, from the tropics to the arctic, and may range from the deep sea (Eccrinales associated with marine crustaceans) to high mountains (Lichtwardt et al. 2001a). Lichtwardt (2012) suggested that the wide geographic distribution and primitive nature of trichomycete hosts indicates that the group represents an ancient symbiosis. This hypothesis is strengthened by the fact that some members of the Harpellales occur on hosts whose ancestors are believed to have evolved perhaps 250 million years ago (mya), in the early Triassic period (Grimaldi & Engel 2005). There are many countries and habitats that have not yet been fully investigated, and thus, several new species of trichomycetes are expected to be discovered in the future from unexplored regions and hosts.

The Harpellales

Main characteristics of Harpellales

Harpellales are the most diverse and species-rich of the trichomycetes, with about 250 described species (Valle & Stoianova 2020) distributed worldwide. They reside anchored to the chitinous inner gut lining of larval and nymphal stages of insects and more rarely freshwater isopods (Lichtwardt et al. 2001a).

The thalli of Harpellales are septate and can be either branched or unbranched. Branches, when present, usually appear at the apical area of elongated thallial cells, just below each septum. Different branching patterns can be observed, sometimes having a relative taxonomic importance (Valle 2004) (Fig. 11).

The anchoring element or holdfast of Harpellales can be cellular (holdfast cell) or, more commonly, an acellular secretion (Lichtwardt 1986) (Fig. 12). A combination of both is possible and, in any case, we find great morphological diversity in the holdfast structure. The thallus may be erect, and then fixed by a basal holdfast, or prostrate, laying on the inner gut membrane. In this case, the thallial cells that contact directly with the gut, often develop secondary pit-like or peg-like fixation structures (Fig. 12a), or secreted holdfast material, to ensure a secure adhesion to the gut lining (Valle 2004). Several species found attached to the peritrophic matrix in dipteran hosts penetrate the lining and form a “foot-like” holdfast, or they can adhere by a drop of secreted material (Lichtwardt 1986) (Fig. 12m).

Harpellid species are characterized by their asexual undeciduous monosporic sporangiospores, named trichospores. The trichospores originate from generative cells arranged in series on fertile branches (Lichtwardt et al. 2001a). The number of trichospores and arrangement on

a fertile branch can be important in classification (Fig. 13). Trichospores usually have one or more appendages, which facilitate its adhesion to the substrate outside the gut, reducing dispersal by water drift (Lichtwardt et al. 2001a, Valle 2004). There are no appendages in the genera *Bactromyces, Carouxella, Caudomyces, Gauthieromyces, Klastostachys, Tectimyces, Zygopolaris* and *Zygopolaropsis* (Lichtwardt 2004, Valle 2004). Trichospores can also bear a collar at the basal end, which are cellular remnants of the generative cell where it was attached, or they can be collarless (Lichtwardt et al. 2001a) (Figs 12, 13).

The cell wall of trichospores is formed by two well-differentiated layers. The outermost one is continuous with the wall of the generative cell, more specifically from the neck or collar, from which the trichospore expands through a holoblastic process (Lichtwardt et al. 2001a). The inner wall encompasses the sporoplasm (or spore content, which corresponds to a sporangiospore). Once the trichospore is released, the typical kickxellid septum, with the central cap, will remain in its basal portion (Horn 1989a, b, c). During germination, after ingestion by a suitable host, the sporangiospore wall separates from the sporangium (or merosporangium) wall and slides through it until it is released into the gut lumen (Moss and Lichtwardt 1976, Horn 1989a, 2001). Only some species in two genera do not follow this process: *Spartiella* (Valle 2004) (Fig. 13g) and *Orphella* (within Orphellales) (Valle 2004), since they release the sporangial content into the environment, not necessarily after consumption of the trichospore by the host. *Carouxella* is also peculiar in that it has an unbranched thallus with disarticulating generative cells bearing trichospores (Manier & Lichtwardt 1968).

Some species of Harpellales also reproduce asexually by means of propagules, vegetative structures that detach from the thallus and germinate endogenously within the same gut, to rapidly increase the colonization. This is characteristic of the mayfly associated genera *Graminella* (Léger & Gauthier 1937, Manier 1962, Lichtwardt & Moss 1981, Valle 2004) and *Gauthieromyces* (Lichtwardt & Williams 1983, Valle et al. 2008, Strongman & Wang 2015, Barón & Valle 2018) which produce these propagules from the basal cell. On the other hand, the genus *Ejectosporus*, associated with plecoptera, produces non-deciduous vegetative spores at the upper section of the thallus that also extrude their contents endogenously (Strongman 2005, 2007)

The sexual reproduction of Harpellales is by means of the zygospores in zygosporangia (Fig. 13h, i), which are usually biconial or more rarely conical (in *Carouxella, Lancisporomyces, Plecopteromyces* and *Zygopolaris*), thick-walled resistant sporangia containing the zygote. The shape of these unique zygospores may be an adaptation for a rapid circulation and germination within the host gut and, like trichospores, these can also have one or more appendages (Lichtwardt et al. 2001a). The thick wall found in most zygospores may also serve a protective function allowing these spores to survive a period of time in the system outside a host. The zygospores grow on a specialized cell called a zygosporophore (Fig 13h, arrow). Zygospore formation often occurs near the end of a molting cycle in the host (Lichtwardt et al. 2001a), to ensure fungal survival and propagation after ecdysis (Valle 2010), and it is believed that the molting hormone of the host, or ecdysone, stimulates the sexual process in endosymbiont fungi (Lichtwardt et al. 2001a). The effect of ecdysone on an endosymbiont life cycle has been studied in the mosquito *Adedes aegypti* infected with the fungus *Coelomomyces stegomyiae* (Lucarotti 1992).

Harpellales can reproduce homothallically (Fig. 13h) or heterothallically. In heterothallic species, the zygospores arise from the middle of a conjugating tube between conjugants, or in a branch next to it; more rarely they may grow on a distant branch (Valle 2004). In homothallic species, particular cells accompanying the zygospore may be present, as in the case of *Genistellospora homothallica* or *Tectimyces robustus* (Valle 2010). The morphometric characteristics of the reproductive structures (trichospores and zygospores) plus accompanying cells and appendages are of great taxonomic importance, together with thallial features such as branching pattern, generative cell disposition, basal cell structure, holdfast and other anchoring elements, general disposition, and host identity (Lichtwardt et al. 2001a, Lichtwardt 2004, Valle 2004).

Figure 11 – Different examples of fertile branches and trichospores of Harpellales and Orphellales. a *Stachylina prolifica:* In the unbranched Harpellales, the generative cells develop basipetally and the trichospores show a uniseriate disposition. b Trichospore bearing a minute collar and one appendage in *Stachylina prolifica.* c *Tectimyces* produces thin and long generative cells with latero-apical trichospores. d *Smittium* species have a branched thallus with fertile branches bearing trichospores. Some species show sporic dimorphism such as this *Smittium heterosporum*. e Loose trichospore of *Smittium* showing a single appendage and a collar on its base. f Disposition of trichospores on the fertile cap in *Orphella coronata*. g Generative cells with trichospores in *Stipella vigilans.* h Trichospores of *S. vigilans* with 3-6 petaloid appendages. i Fertile branches with distal series of generative cells and small trichospores in *Graminella bulbosa*. j *Legeriomyces ramosus* produces dense branching and bottle-like trichospores in series. k Loose trichospores of *L. ramosus* with two filiform appendages. l *Genistellospora homothallica* has fertile branches with rather long generative cells producing apical or lateral trichospores. From (Valle 2004).

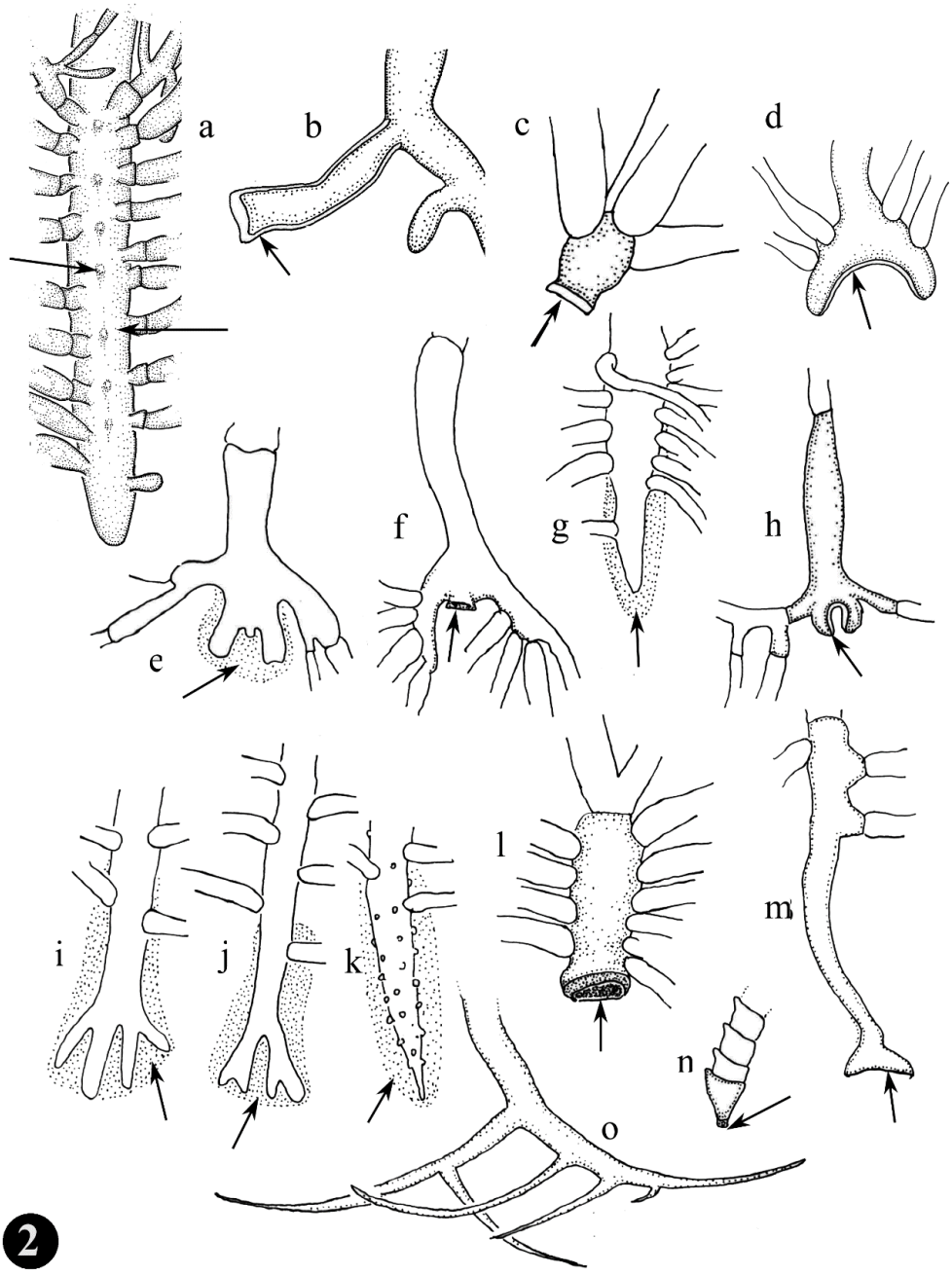


Figure 12 – Different morphologies of basal cells and holdfast in Harpellales and Orphellales. a Main axis of the prostrate thallus of *Lancisporomyces vernalis*, with peg-like subsidiary holdfast structures (arrows) along the cell in contact with the gut lining. b Basal cell covered with adhesive holdfast material (arrow) in *Smittium hecatei*. c Basal cell with a discoid holdfast structure (arrow) in *Smittium heterosporum*. d Horse-shoe shaped basal cell with a thin layer of holdfast material (arrow), in *Furculomyces boomerangus*. e Lobulate basal cell with amorphous holdfast material (arrow) in *Orphella haysii*. f Bifurcated basal cell with a central discoid holdfast (arrow) and subsidiary branching arising from the two lobes in *Orphella helicospora*. g Attenuating basal cell with amorphous adherent holdfast material (arrow) in *Orphella catalaunica*. h Bilobe basal cell with a lining of holdfast material (arrow) in *Spartiella barbata.* i–j Lobulate basal cell with amorphous holdfast substance (arrow) in *Stipella* sp. k Attenuated and verrucose basal cell with amorphous substance in *Stipella* sp. l Discoidal holdfast (arrow) in *Genistellospora homothallica*. m Basal cell with a thin holdfast layer (arrow) in a young thallus of *Tectimyces leptophlebiidarum*. n Minute holdfast (arrow) in *Stachylina* sp. o Rhizoid-like basal cell in *Tectimyces leptophlebiidarum.* From Valle (2004).

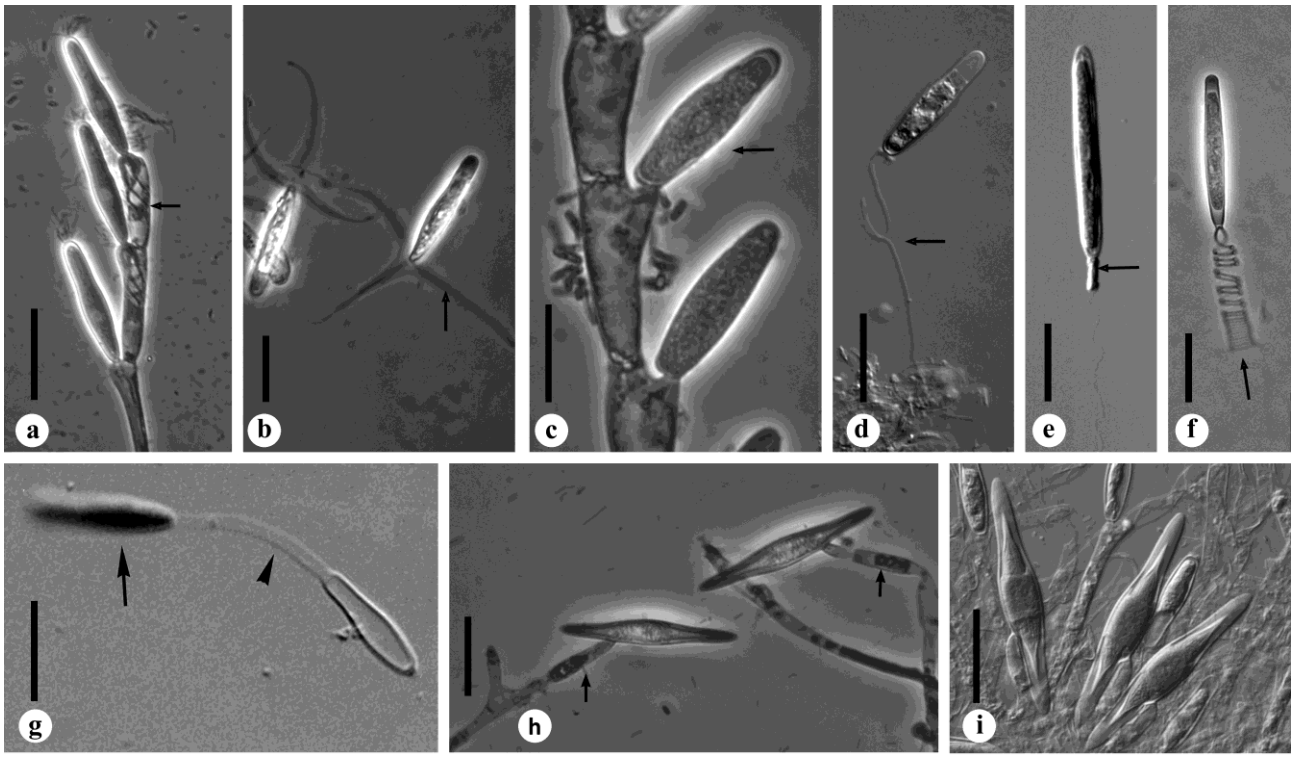


Figure 13 – Trichospores and zygospores from various Harpellales. a *Legeriosimilis cebennensis* from Heptageniidae nymphs (Ephemeroptera), trichospores on generative cells, note the appendages inside the generative cells (arrow). b *L. cebennensis*, loose trichospores with three petaloid appendages (arrow). c *Harpellomyces aputinus* from Thaumaleiidae larva (Diptera), fertile branches with trichospores (arrow). d *Legeriomyces ramosus* from Baetidae nymphs (Ephemeroptera). e *Smittium megazygosporum* from Chironomidae larvae (Diptera). f *Lancisporomyces vernalis* from Nemouridae (Plecoptera), loose trichospore with two helicoidal appendages. g *Spartiella barbata* from Baetidae nymph, loose trichospore extruding the inner spore (arrow). h *Tectimyces leptophlebiidarum* from Leptophlebiidae nymph (Ephemeroptera), two zygospores on the zygosporophores (arrows). i *Legeriomyces ramosus*, various zygospores. Scale bar: a, b, d–f = 25 µm, c = 10 µm, g–i = 25 µm.

Ecology and symbiotic relationships

Harpellales are usually associated with immature larval and nymphal aquatic stages of non-predaceous insects including different Nematocera dipteran families (Blepharidae, Chironomidae, Culicidae, Simuliidae, Dixidae, Psychodidae, Stratiomyiidae, Thaumaleidae and Tipulidae); Ephemeroptera nymphs (Baetidae, Caenidae, Ephemerellidae, Heptageniidae, Leptophlebiidae, Leptohyphidae and Siphlonuridae); Plecoptera nymphs (Capniidae, Gripopterygidae, Leuctridae, Nemouridae and Taeniopterygidae) and Trichoptera nymphs (Glossosomatidae, Leptoceridae and Limnephilidae). Only one species has been reported from a beetle (Coleoptera), in the gut of a Scirtidae larva (Lichtwardt et al. 1999), and one species also from an aquatic isopod (White 1999).

The arthropod gut is an intriguing ecosystem with a rich and diverse microbiota (Wang et al. 2014). The relationship that harpellid gut endobionts establish with their hosts is not well understood, and are usually regarded as commensals, like most other trichomycetes (Lichtwardt et al. 2001a). However, there is evidence pointing to the existence of a more dynamic interaction, ranging from commensalism to mutualism (or also from commensalism to parasitism), so that a range of different possibilities may arise as a consequence of the host-environment context and the identity of interacting symbionts (Lichtwardt et al. 2001a, McCreadie et al. 2005, Nelder et al. 2006). In Harpellales, specifically in species of *Smittium*¸ the ability to mutualistically provide specific vitamins to the host has been documented (Horn 1989a), as well as the capacity of some species to behave parasitically by perforating the gut, infecting the ovarian cells, and replacing the

eggs with cysts in Simuliidae (Moss & Descals 1986, Labeyrie et al. 1996, White et al. 2006). They may even be lethal to their dipteran hosts such as the well-studied *Smittium morbosum* in mosquito larvae (Sweeney 1981a, Williams 2001, White et al. 2006).

Recently, a genome-scale study has provided new evidence to understand some genetic cues about the relationship established between arthropods and gut fungi (Wang et al. 2018). The study has revealed important genetic differences between Harpellales behaving as commensals and those behaving as parasites. The commensal gut fungi establish the symbiotic association by means of adhesion protein anchors that target the host digestive system, while the genome of entomopathogenic fungi present higher numbers of genes coding for transmembrane helices, signal peptides and pathogen-host interaction (PHI) proteins (Wang et al. 2018). The authors also indicate that pathogenic gut fungi may have functional gene domains aimed to inactivate the inflammatory system of infected hosts and suppress further host defense mechanisms to avoid the programmed response due to fungal colonization (Wang et al. 2018). Further studies will help to better understand the ecology of these fascinating organisms from a molecular and physiological perspective.

Distribution and evolution of Harpellales

Several species of Harpellales are cosmopolitan, but the arthropod species that host them usually have a narrower distribution: a single species of Harpellales can be found in very distant geographic regions, within the gut of different host species or genera, or even within endemic species (Williams & Lichtwardt 1993, Valle & Santamaria 2005). The chronological data accumulated over a century of studies on trichomycetes, provided the basis for a theory that place the origin of the symbiotic relationship at the time when most primitive groups of arthropods were spreading and diversifying, the same primitive hosts that are currently hosts for Harpellales, including the previously listed Plecoptera, Ephemeroptera and Nematoceran dipterans (Lichtwardt et al. 2001a, Valle 2004). This happened about 250–200 million years ago when the land surface formed the super-continent Pangea (Illies 1965, Noonan 1988). Because the dispersal capacity of these arthropods was greatly reduced, especially that of Plecoptera (Hynes 1976, 1988, Stewart and Stark 1988, Zwick 2000), and wind dispersal is possibly negligible (Gressitt 1958), it is considered that tectonic drift was the main driver of inter-continental dispersive events affecting ancient arthropods, together with their already established endosymbionts (Lichtwardt 1986). The diversification of arthropods, resulting from the disappearance of the land bridges between continents during the Eocene (Brown & Gibson 1983) was apparently faster than the diversification of certain genera of Harpellales, which have remained morphologically unaffected, sheltered inside hosts that have undergone adaptive radiation (Valle 2004). Examples of this are *Smittium mucronatum*, from France (Manier & Mathiez 1965) and from the USA (Lichtwardt & Williams 1999); *Bojamyces repens*, from the USA, in *Leptophlebia intermedia* (Longcore 1989) and also from Spain, in *Habroleptoides confusa* (Valle & Santamaria 2005); or *Legeriomyces rarus* from Australia, in the endemic genus *Tasmanocoenis* (Williams & Lichtwardt 1993) and also from Spain, in the European genus *Caenis* (Valle & Santamaria 2005), among other taxa of disjunct distribution (Valle 2004).

Life cycle and adaptations to an endobiotic lifestyle

The arthropod hosts of Harpellales undergo a molting cycle that likely impacts their fungal gut partners. During ecdysis, the ectodermic exoskeleton will be shed and replaced by a new one, including the chitinous hindgut lining where fungal symbionts are attached (Lichtwardt et al. 2001a). Especially those endobionts associated with insect dipteran larvae undergoing short developmental cycles, like branched Harpellales (traditionally included in the Legeriomycetaceae) and Amoebidiales living in the hindgut, which are adapted to stressful conditions and have evolved towards a fast and compressed growth cycle. Under optimal controlled conditions, a larva of *Aedes aegypti* (Diptera, Culicidae) needs about 23–30 hours to reach the first molting period (Christophers 1960, Lichtwardt 1996). Correspondingly, it has been demonstrated that

Zancudomyces (*Smittium*) *culisetae* can grow and sporulate in about 22 hours (Williams & Lichtwardt 1972). For the unbranched Harpellales living in the midgut of dipteran larva and traditionally placed within the family Harpellaceae which is not phylogenetically justified (White 2006, Tretter et al. 2013, 2014), the situation is quite different. The chitinous midgut peritrophic matrix is of endodermic origin, and thus, endosymbionts attached to it are not directly affected by the molting cycle of the host. However, they are subjected to another temporal challenge which may also be quite stressful, if not more: the peritrophic matrix has a continuous growth from the front toward the hindgut, where it is then expelled with the spent food particles (Lichtwardt et al. 2001a). In this short time, the trichospores must be ingested, and if the correct host is detected, the extrusion process of the inner sporangiospore will proceed. A mucilaginous holdfast is then excreted which secures the thallus initial to the gut lining of the host (Lichtwardt et al. 2001a, Tretter et al. 2013). The thallus develops, and ultimately, at maturity, it sporulates producing asexual trichospores or sexual zygospores, as described before. (Fig. 14). Unsurprisingly, given this short time for growth and sporulation there are many fewer species in the Harpellaceae with described zygospores (Lichtwardt et al. 2001a).

Harpellales generally cannot develop outside the host, but zygospores are shed together with the chitinous molt into the surrounding aquatic environment, acting as resistant dispores. In fact, zygospore formation is associated with the molting cycle of the host to ensure fungal survival and propagation after ecdysis (Lichtwardt et al. 2001a, Valle 2010). Within Harpellales living in the hindgut, the peculiar *Bojamyces transfuga* has the ability to develop outside the host (Valle & Santamaria 2004). In this study the authors provided SEM images of the interior of the shed abdominal exoskeleton, showing *B. transfuga* expanding outside of the shed hindgut lumen into the surrounding abdominal cavity, indicating active hyphal growth after ecdysis, occupying the whole interior of the shed exoskeleton with long branched filaments of elongated cells. In fact, the hyphal density was higher outside than inside the hindgut. *Bojamyces transfuga* also produced both trichospores and zygospores in the shed exoskeleton. This growth and sporulation outside instead of inside the living host is not typical of other Harpellales (Valle & Santamaria 2004). This represents the only known case among Harpellales where the cycle of the hindgut-associated endosymbiont is longer than the molting cycle of the host, so that the sporulation culminates exclusively outside the living host digestive system, and only very young trichospores are observable within the host (Valle & Santamaria 2004).

In most cases, the fixation element of Harpellales does not pierce the intestinal membrane (Fig. 12), i.e., there is no tissue invasion, except in a few species of the genus *Smittium*, such as *S. heterosporum* (Valle & Santamaria 2004), *S. morbosum* (Dubitskii 1978, Sweeney 1981a, b), *S. longisporum* (Williams et al. 1982) and *S. perforatum* (Williams & Lichtwardt 1987, Lichtwardt et al. 1997). Among these cases, only *S. morbosum* is pathogenic to the host, invading tissues of the Malpighian tubules the hemocoel, or the pyloric chamber where it is fixed (Dubitskii 1978, Sweeney 1981a, López Lastra 1990). In this particular case we would speak of parasitism. Experiments reported by Sweeney (1981a, b) showed a mortality rate between 50-95% of infected *Anopheles hilli* larvae. Other cases have been discovered in which the presence of the trichomycete may adversely affect the development of the host, or its reproductive capacity, such as *Harpella melusinae* and *Genistellospora homothallica*, in which the participation of adults in the dispersal and colonization of new environments was discovered by means of fungal cysts formed in the ovaries of adult females. These infested ovaries do not affect egg laying behavior in the adult in the aquatic environment but cystospores deposited infest new host populations if ingested (Moss & Descals 1986).

Diversity and most representative species of Harpellales

Among the most common, cosmopolitan, and species-rich genera of Harpellales, we find the branched *Smittium* (Figs 11d, 12c, d, 13e) and the unbranched *Stachylina* (Fig. 11a), mostly associated with Simuliidae, Chironomidae and Culicidae. Many species in *Smittium* can be cultured and numerous studies focusing on different aspects of their biology, taxonomy and phylogeny have

been published on members of this genus living in the hindgut of their hosts (see Lichtwardt et al. 2001a, b). *Stachylina* is also a speciose genus, with 43 described species, most of them associated with Chironomidae midges, more rarely with Thaumaleidae, Blephariciдae and Psychodidae (Williams & Lichtwardt 1984, Lichtwardt & Williams 1990, Sato & Degawa 2018). *Genistellospora* (branched) (Fig. 11l) and *Harpella* (unbranched) are not as diverse as *Smittium* or *Stachylina* but are also common, cosmopolitan genera inhabiting the hindgut and midgut, respectively, of Simuliidae larva. Among the more common genera associated with Plecoptera we find *Lancisporomyces* (Figs 12a, 13f) *Genistelloides* and *Ejectosporus* and among frequent symbionts of Ephemeroptera we find *Legeriomyces* (Fig. 13d) and, although not as common and widespread, *Glotzia* and *Graminella*, among others (see Lichtwardt et al. 2001a). Other hosts not as well studied but also house endosymbionts, are Trichoptera (caddisflies), including a species of *Smittium* and one of *Legeriomyces* (Strongman & White 2019).

The Orphellales

Main characteristics of Orphellales

Recently, the order Orphellales was separated from Harpellales, characterized by the very peculiar, plecopteran-associated genus *Orphella*, which has many unique characteristics, especially in its sexual spores that make this genus exceptional within the Kickxellomycotina (White et al. 2018). Although the order was only recently erected, the concept that the Orphellales were different from the Harpellales was raised many years ago (White et al. 2003, Valle 2004, Valle & Santamaria 2005, Tretter et al. 2013, 2014).

Orphella was described from France by Léger and Gauthier (1931), with the type species *O. coronata* originally placed within the Harpellales (Cl. Trichomycetes). Morphologically, *Orphella* species are remarkable due to the disposition of fertile elements; the peculiar spore-accompanying cells called the dispersion unit, and the structure of the thallus with a characteristic arborescent branching (Léger & Gauthier 1931, Lichtwardt et al. 2001a, Valle 2004, Valle & Santamaria 2005, White et al. 2018) (Figs 15, 16), resembling somewhat that of other genera in the Kickxellales and also the unusual harpellid genus *Pteromaktron* (Whisler 1963, Moss & Young 1978, William & Strongman 2012, 2013).

Morphological characteristics of Orphellales

Thallial and sporic characteristics of the genus *Orphella* were described by Léger and Gauthier (1931). However, new elements were discovered later and incorporated into the terminology, especially regarding spores and accompanying cells. The presence of the so called "dispersion unit", used to describe the trichospore plus accompanying cells that detach together for dispersion purposes, was described originally in *Orphella haysii* (Williams & Lichtwardt 1987) and is characteristic of the genus. The nature of this dispersion unit was then revised (Santamaria & Girbal 1998, Valle & Santamaria 2005). The set of 4– (or 3) cells in the trichospore dispersion unit (Figs 17, 18) are now routinely incorporated in the description of new species, as these are considered of important ontogenic and taxonomic significance (Valle & Santamaria 2005, White et al. 2018). Trichospores are straight (e.g., *O. catalaunica*) (Fig. 16e), allantoid (e.g., *O. haysii, O hiemalis*) (Fig. 16d) or helicoidal (e.g., *O. pseudoavalonensis*) (Fig. 16a, b) and sometimes the spore head protrudes from the gut out of the anus before detaching from the thallus for dispersion from an infested host (Valle 2004, White et al. 2018).

The most distinctive elements of Orphellales are, undoubtedly, the sexual spores (zygospores) and their accompanying cells (Valle & Santamaria 2005) (Figs 16g, f, 17), which are absolutely different from all other known Zoopagomycota and also from related Harpellales (Valle & Santamaria 2005, White et al. 2018). The zygospores also form a dispersion unit, being slightly different from the trichospore dispersion unit. There are other cells associated with the development of zygospores which are not detached with the dispersion unit; these cells are key for a clear identification of zygospores in those species where both trichospores and zygospores have a similar

morphology (Fig. 17) (Valle & Santamaria 2005). Zygospores are typically helicoidal (as in *O. avalonensis*) or semi-helicoidal (as in *O. catalaunica*) (White et al. 2018) (Fig. 16g, f).

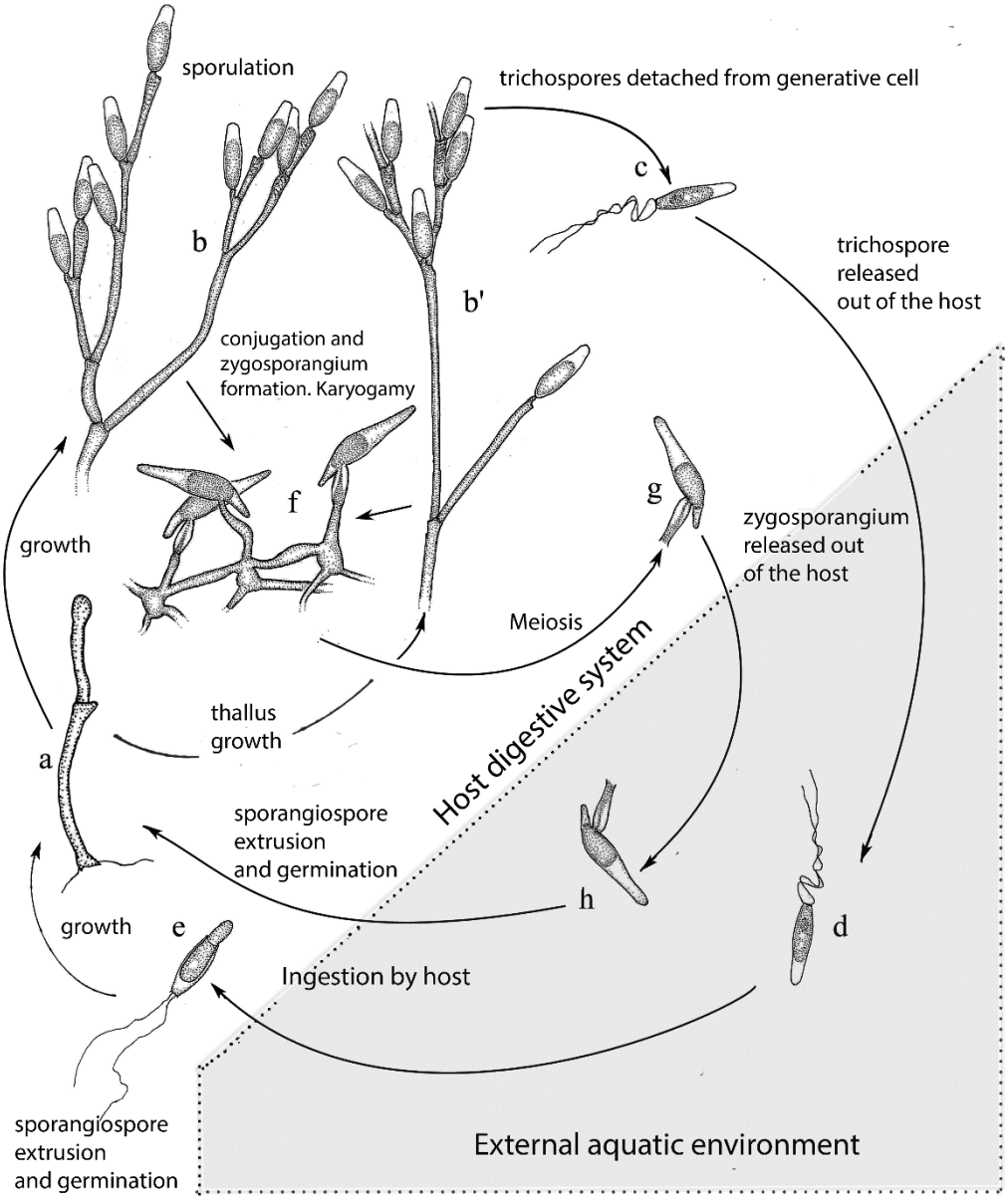


Figure 14 – Harpellales life cycle (e.g., *Legeriomyces* sp.). a Young thallus growing attached to the hindgut lining. b Mature thallus with fertile branches and trichospores. b another mature thallus, sexually compatible with b. c Released trichospore circulating towards the anus to be expelled outside the host. d Trichospore in the aquatic environment, the sticky appendages will attach the spore in the host environment. e The trichospore is ingested by the appropriate host; the inner spore is extruded and anchored to the gut lining by adhesive holdfast material. f Two heterothallic thalli conjugate by means of conjugation tubes (hyphae), resulting in the formation of zygosporangia. g A zygosproangium is released and circulates outside the host to the external aquatic environment (h), where it may be ingested by the host and then germinates inside the gut. The Orphellales show the same cycle, but different morphologies. From Valle (2004).

Most species of Harpellales have biconical zygospores that can be assigned to one of three types (Type I-III), or turbinate/conical (Type IV), as described by Moss et al. (1975). These hydrodynamic shapes seem to be perfect for the ingestion and circulation within the host digestive

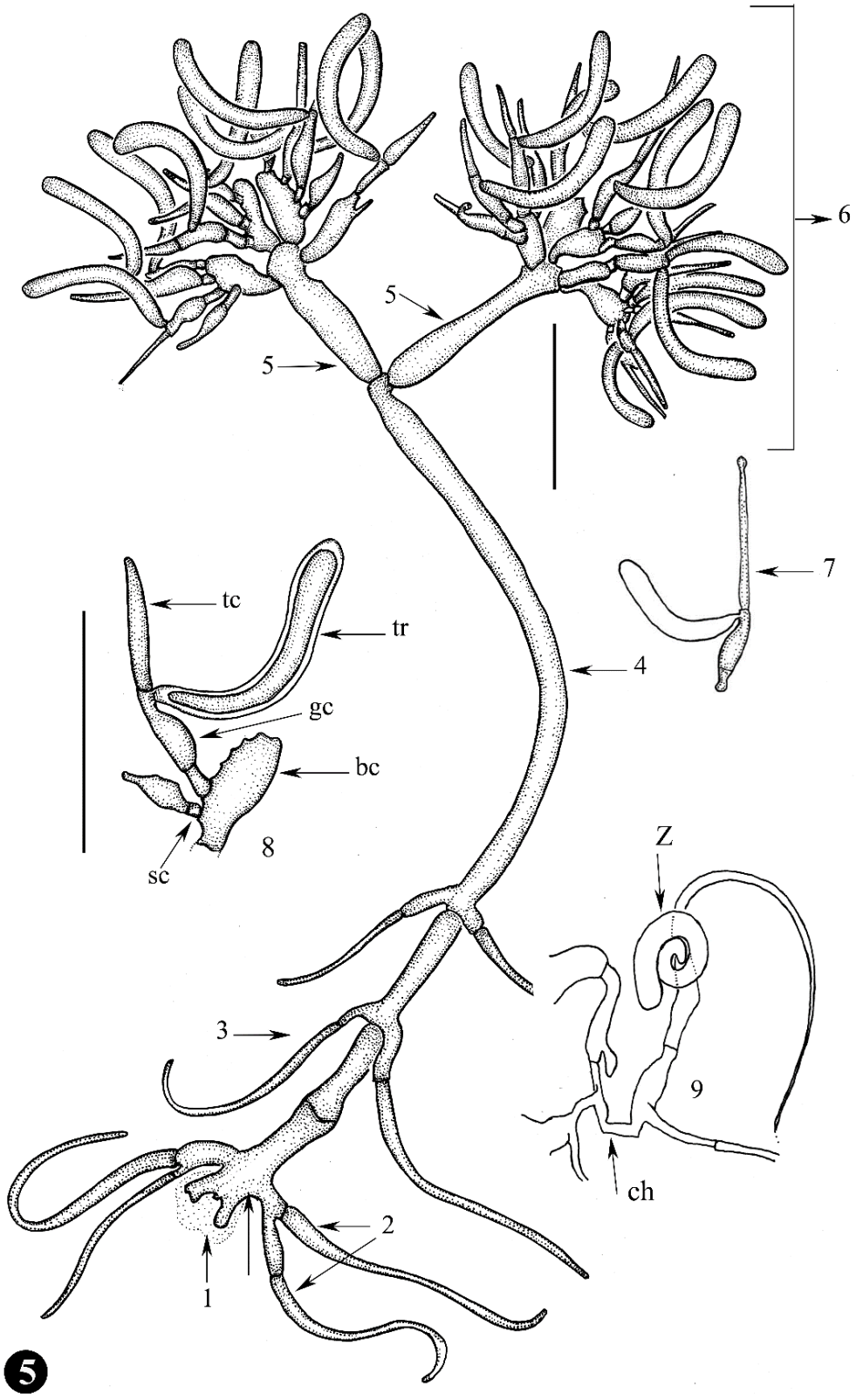


Figure 15 – *Orphella coronata* from Nemouridae (Plecoptera). 1 Basal cell with amorphous holdfast material. 2 Basal cell branches. 3 Subsidiary cells (branches) in the main axis. 4 Main axis (2-3 elongated cells). 5 Branches bearing the fertile caps. 6 Fertile caps with trichospores and accompanying cells. 7 Trichospore dispersion unit. 8 Detail of the fertile cap with bc: basal cell of the fertile cap. gc: *generative cell. tr: trichospore. tc: terminal cell, sp: support cell. 9 Detail of conjugation process and zygospore formation, z: zygospore; ch: conjugating hyphae. Scale bar = 50 µm. From Valle (2004).

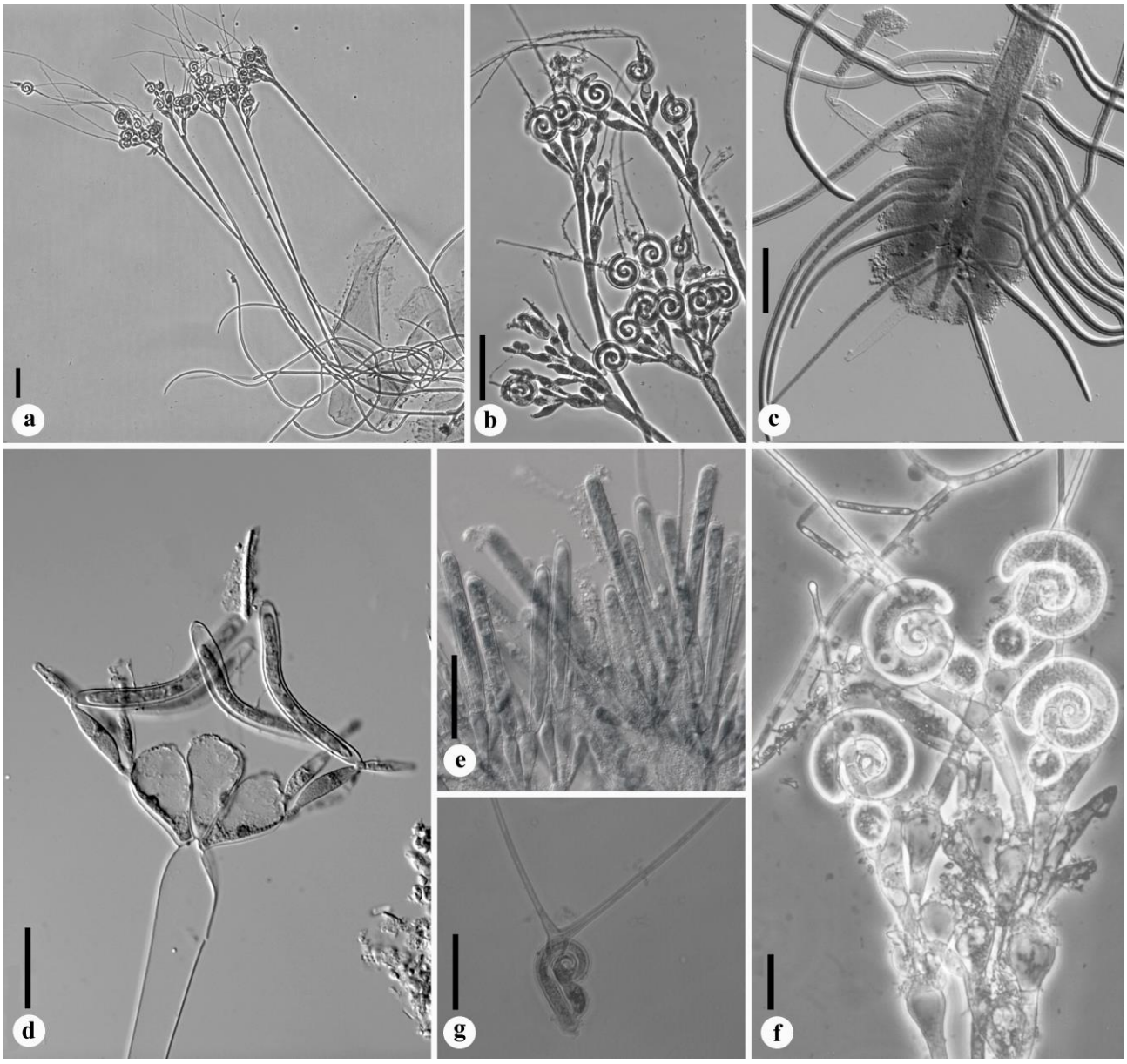


Figure 16 – *Orphella* diversity. a, b *O. pseudoavalonensis* from Leuctridae (Plecoptera), thallus overview (a) and detail of the fertile cap with helicoid trichospores (b). c *O. cataloochensis* from Leuctridae, basal cell with lateral branches. d *O. pseudohiemalis* from Leuctridae, fertile cap with allantoid trichospores. e *O. catalaunica* from Leuctridae, fertile cap with straight trichospores and accompanying cells. f O. *pseudoavalonensis*, fertile cap with zygospores and accompanying cells. g *O. catalaunica*, loose zygospore with accompanying cells, including two long terminal cells. Scale bar: a = 50 µm, b–d, g = 20 µm, e, f = 25 µm.

system and may be involved in the process of rapid extrusion and attachment of the sporangiospore (Lichtwardt et al. 2001a). So, the coiled shape of *Orphella* species is odd, taking into consideration the putative advantage of biconical hydrodynamic structures. We could think about some possible advantages of coiled spores, and maybe the most evident would be the optimization of space, since a long sporangiospore linear length may be achieved within an overall smaller container, so that after attachment, the germling has more overall cytoplasmic mass to provide a better chance of survival and rapid completion of the growth and reproductive cycle, very much constricted by the intermolt periods of the host (White et al. 2018).

White et al. (2003) provided the first genetic evidence of the phylogenetic relationship between *Orphella* and members of the Kickxellales, even more than *Orphella* is related to other

genera in the Order Harpellales. In fact, *Orphella* has long been recognized for its unusual morphological characteristics (Lichtwardt 1986) and was considered one of the most derived genera within the Harpellales (Valle 2004, Valle & Santamaria 2005, White et al. 2006, 2018, Tretter et al. 2014) before the creation of a new order. Valle and Santamaria (2005) first recognized and described the presence of helicoidal or partially helicoidal zygospores in several European *Orphella* species. Zygospores were initially misidentified as unusually large trichospores, due to their similarity in appearance to the asexual spores (Williams & Lichtwardt 1987, Lichtwardt et al. 2001b). However, zygospore-associated cells (Fig. 17) and conjugation in homothallic species of *Orphella* were consistent and similar with those of homothallically formed zygospores in some species of Harpellales, such as *Genistellospora homothallica*. This evidence was the key to recognizing the zygosporic nature of those unusually large spores (Valle 2004, Valle & Santamaria 2005, White et al. 2018).

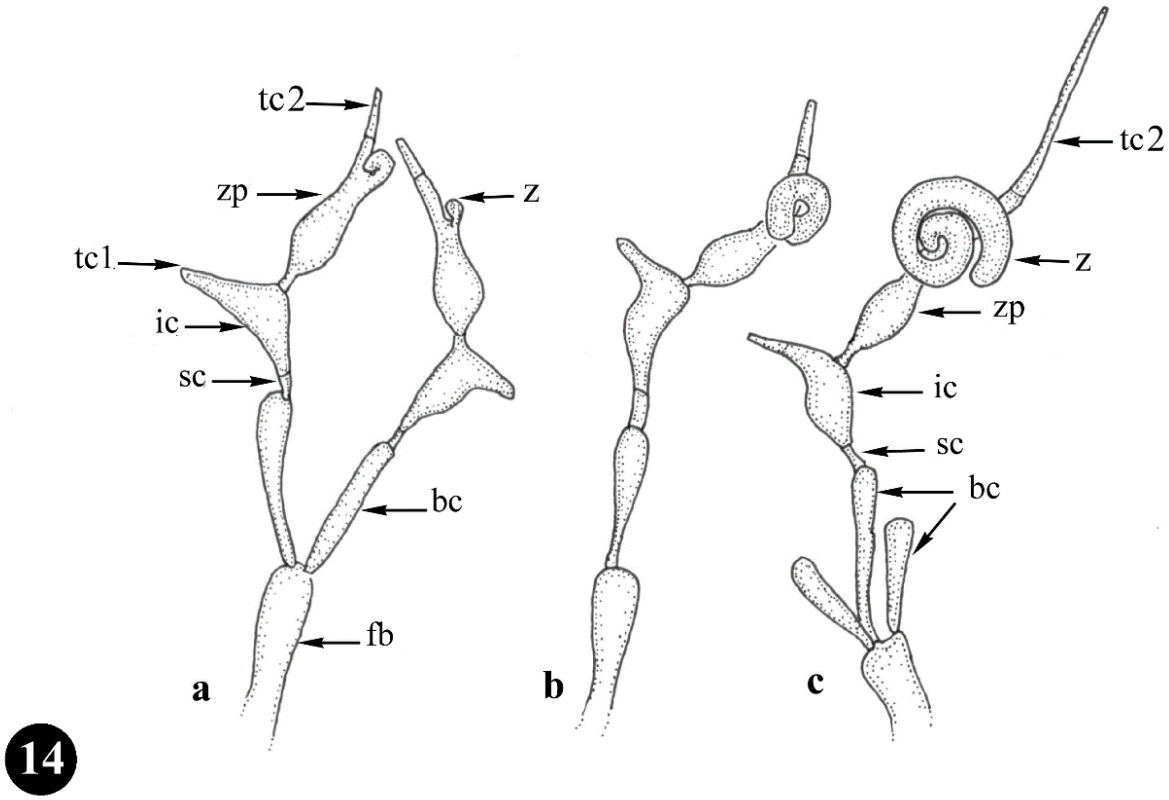


Figure 17 – Zygospore development in *Orphella coronata.* From a (youngest) to c (mature), three development stages. The following cells are indicated: tc2 = terminal cell 2; zp = zygosporophpore; tc1 = terminal cell 1; ic = intermediate cell; sc = supporting cell; Z = zygospore; bc = basal cell of the fertile cap; fb = fertile branch. From Valle (2004).

Ecology, life cycle, and distribution

There are 15 species of *Orphella*, all associated with non-predaceous stonefly (Plecoptera) nymphs in the Northern Hemisphere. Species of *Orphella* are associated with Plecoptera nymphs in the Orders Capnidae, Leuctridae, Nemouridae and more rarely, Taeniopterygidae. Their life cycle and relationship with the host is the same as is known for Harpellales, as far as we know. The most noticeable characteristic of the spores and related cells in the dispersion unit is the presence of a long terminal cell, both in the sexual and asexual spores (Fig. 16a, b, g). This terminal cell is thin and can be very long, surpassing 200 µm in length, when most spores measure about 20–50 µm. The terminal cell, with a sticky consistency, has the same function as the appendages of spores in Harpellales, i.e., reduce the effect of water flow and downstream drift (Valle 2004, Valle &

Santamaria 2005, White et al. 2018). The function of appendages, or the terminal cell in *Orphella* species, is important indeed to assure the colonization of new hosts, as each species of insect host has a very particular ecology in the water system, occupying a specific habitat and niche that may not be found downstream (Merritt & Cummins 1996), where most spores would drift without these sticky structures.

Species of *Orphella* attach to the inner lining of the hindgut of their immature stonefly hosts. Thallial growth can be profuse, and it is not uncommon to observe the distal section of *Orphella* thalli with spore-bearing branches protruding through the anus out of the host, therefore they grow at the interface of their internal and external environments (Lichtwardt et al. 2001a, White et al. 2018). This phenomenon is not exclusive to Orphellales and is observed in genera of the Harpellales (*Genistellospora*, *Pteromaktron* and *Zygopolaris*) as well (White et al. 2018, Valle & Stoianova 2020).

Geographically, species of the genus *Orphella* provide a good example of coevolution with their plecopteran hosts, and their distribution, both being known only from the Northern Hemisphere. *Orphella* species reflect a vicariant origin linked to continental drift and subsequent species diversification, so that we find different clusters identifiable as sister species in a Nearctic–Palearctic disjunction (White et al. 2018).

The Asellariales

Overview of the group

The Asellariales is an order of understudied endosymbiotic fungi phylogenetically related to the more diverse Harpellales, both assigned to the subphyl. Kickxellomycotina (Hibbett et al. 2007, Tretter et al. 2014). The Asellariales comprise only 15 species within three genera: *Orchesellaria* (associated with springtails, Collembola), *Asellaria*, and *Baltomyces* (both associated with Isopoda). Among these, *Baltomyces styrax* has an uncertain position (Cafaro 1999) and a particular thallial morphology. In fact, all three genera differ in morphology and general habit, and it is possible that the order is not a natural assemblage, especially regarding *Baltomyces* (Tretter et al. 2014).

Thallial structures and reproductive spores

Asellaria and *Orchesellaria* have branched thalli and a differentiated basal cell which is of taxonomic importance (Lichtwardt et al. 2001a). In fact, *Asellaria* species are identified primarily by holdfast characteristics (Lichtwardt & Moss 1984, Valle 2006, Valle & Cafaro 2008), while thallial and sporic features may complement the information for classification (Fig. 17). These two genera produce arthrospore-like cells produced by fragmentation of the branches (Fig. 17). According to Lichtwardt et al. (2001a), the arthrospores may be the equivalent of generative cells in Harpellales, since they develop a kind of an outgrowth that somewhat resembles the trichospores of Harpellales, although the complete development of these structures has not been observed. Terminal or intercalary spherical chlamydospores can be formed in some species as resistant asexual structures (Lichtwardt et al. 2001a).

Baltomyces has a particularly unusual basal cell compared to other Asellariales, this having a prostrate position, lying on the gut lining and with multiple septa within it. The asexual spores are also particular in that they are released through a tear in the wall of the generative cell (Cafaro 1999, Oman & White 2012).

Asellaria and *Orchesellaria* reproduce asexually by means of uninucleated arthrospores, which are passed out the anus to the external environment to colonize new hosts. More rarely, the arthrospores germinate within the same gut to recolonize in situ (Lichtwardt et al. 2001a). However, in most Asellariales, the arthrospores only germinate after having been ingested by another individual host, rapidly developing a holdfast to attach to the hindgut lining and growing into mature spore-bearing thalli (Poisson 1932, Manier 1958, 1964, 1979). *Asellaria* is the most representative of the order, with 9 described species, all of them being obligate commensals of

marine, freshwater, or terrestrial isopods (Lichtwardt 1986). *Orchesellaria* includes four described species living in the hindgut of springtails (Collembola), many of them living near aquatic environments (e.g., stream banks and pools).

Sexual reproduction by means of conjugation tubes was observed in *Asellaria jatibonicua*, followed by the formation of spherical, thick-walled zygospores, similar to those of Kickxellales (Valle & Cafaro 2008). Scalariform conjugations between thalli of *Asellaria ligiae* were also reported in freshwater *Ligia* isopods from Hawaii (Lichtwardt 1973). Other indications of sexuality were observed by Lichtwardt & White (Valle & Cafaro 2008) in different species of *Asellaria*. Species of the genus *Orchesellaria* can produce spherical chlamydospores (Lichtwardt & Moss 1984) in the springtail host. These chlamydospores may resemble the zygospores of *Asellaria*, but are thick-walled asexual, resistant spores that do not have associated conjugation, which precedes genetic interchange between sexually reproducing thalli (Valle & Cafaro 2008). In Asellariales, as well as in Harpellales, the zygospores may be formed at some distance from the conjugation tubes, this being possible because of the existence of the characteristic kickxellid septum with a central plugged pore that allows nuclear migration (Saikawa 1989, Saikawa et al. 1997).

The exact process involving the nuclei of cells during zygospore formation in Harpellales and Asellariales is not well understood. Nonetheless TEM images suggest that meiosis in Harpellales occurs after an early plasmogamy and karyogamy between conjugant cells, just before zygospore formation (Moss & Lichtwardt 1977). This process in the zygospore ensures fast germination and growth after being consumed by the host (Moss & Lichtwardt 1977, Lichtwardt et al. 2001a). Within Asellariales the process has not been investigated, due to the rarity of sexual structures in this order.

Phylogenetic studies on Trichomycetes

The orders Asellariales, Harpellales, and Orphellales are placed within the Kickxellomycotina in the Phylum Zoopagomycota, together with the Orders Dimargaritales and Kickxellales (Hibbett et al. 2007, Tretter et al. 2013, 2014, White et al. 2018). Various studies have dealt with the phylogenetic relationships, diversification, and life history within and among the different orders of Kickxellomycotina and related evolutionary basal groups of fungi (O'Donnell et al. 1998, Tanabe et al. 2000, Gottlieb & Lichtwardt 2001, James et al. 2006a, White 2006, White et al. 2006, Tretter et al. 2013, 2014, Wang et al. 2013b) so now we have quite a clear vision of the evolution of the whole group. According to Tretter et al. (2014) the Kickxellomycotina, closely related to the Zoopagomycotina, is a monophyletic, consistent group including the mentioned orders (but not

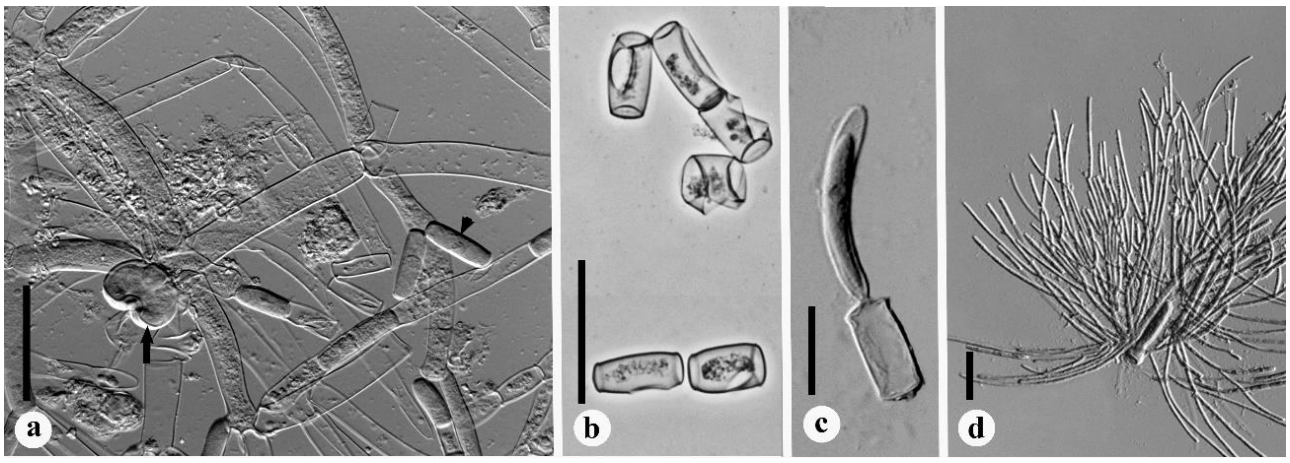


Figure 18 – Asellariales. a *Asellaria ligiae*. Basal cell (arrow) and some loose arthrospores (arrowhead). b Free arthrospores, empty of content because of lateral rupture of the sporangiospore wall. c Germination of an arthrospore, producing an elongated structure; note the resemblance with a generative cell and its trichospore (in Harpellales). d *Asellarria saezi*, thallus overview. Scale bar: a, b, d = = 50 µm, c = 25 µm.

Orphellales), plus four other clades represented by the genera; *Barbatospora* (actually included within Harpellales), *Ramicandelaber* and *Spiromyces* (at present, both within the Kickxellales) and *Orphella*, previously embedded in Harpellales and now placed within Orphellales (White et al. 2018). The results supported the evolutionary significance of the shared feature among all Kickxellomycotina: the kickxellid lenticular septal pore with the electron-dense plug (Tretter et al. 2014).

The orders Harpellales and Asellariales appear to be sister groups, as well as the Orphellales and the Kickxellales (Tretter et al. 2013, 2014, White et al. 2018). On the other hand, *Pteromaktron*, morphologically resembling *Orphella*, is closely related with the harpellid genus *Zancudomyces*, and any resemblance with *Orphella* is perhaps only due to convergent morphologies in a similar environment (Tretter et al. 2014). Within the Harpellales, Wang et al. (2013b) revealed that *Smittium*, the largest genus in the order, seemed not to be monophyletic, and according to molecular analysis it separated into several well supported clades.

Regarding the Asellariales, only *Asellaria ligiae* auth has been successfully sequenced, and thus the position and evolutionary relationships with the other genera *Baltomyces* and *Orchesellaria* is still a mystery to resolve.

Freshwater Laboulbeniales

The Laboulbeniales are a large group of Ascomycota currently including about 2,100 species. Together with the much smaller orders of the Herpomycetales and Pyxidiophorales, and a few taxa of uncertain position, they are members of the class Laboulbeniomycetes. As a direct result of their peculiar morphology and distinctive development, their taxonomic position has been debated over the past one and a half centuries, with hypotheses linking members of the class to other fungal phyla, to red algae, and even to Animalia (two species have even been described as parasitic worms). The position of these fungi among the Ascomycota as a sister group of the Sordariomycetes has only recently been ascertained by molecular analyses (Weir & Blackwell 2001, Blackwell et al. 2020). Detailed information on the various theories that have occurred over time are found in the latter of these two papers.

Because they are obligate ectoparasites on arthropods, the species that we consider as "freshwater" Laboulbeniales are those occurring on aquatic arthropods which, in our case, are all insects of the orders Coleoptera (beetles) and Hemiptera (true bugs). The first problem is that it is practically impossible to establish with certainty which of the thousands of insects reported as host of the Laboulbeniales is aquatic or not. Therefore, we have chosen the families of insects that are reported as aquatic in an entomological paper that deals specifically with this topic (Jäch 1998). Even so, within the families that are usually considered as "chiefly aquatic", there are insects that spend most of their life outside the freshwater environment. Based on these choices, the fungi listed in our table are "about" 258 and represent 12% of the currently accepted species of Laboulbeniales (Table 3). These 258 species are unequally distributed in 24 genera, of which 20 include only aquatic species, while the other 4 are mainly composed of parasites occurring on host-insects that live in other ecosystems. The most speciose one among the genera listed in Table 3 is the genus *Chitonomyces* (Fig. 20), which includes 87 species (Kong et al. 2022). These numbers are provisional because several species of Laboulbeniales are described each year. However, the species occurring in the aquatic environment have received little attention in recent years, with only seven species described during the last six years (Rossi et al. 2016, Das et al. 2018, Santamaria et al. 2020, Boonmee et al. 2021, Sundberg et al. 2021).

To date, molecular analysis has been carried out on a small number of genera and species from aquatic habitats, including a detailed analysis of 13 species of the genus *Chitonomyces*, all from the USA (Goldmann & Weir 2012, 2018), a few sequences from unidentified species of *Coreomyces* from various countries (Goldmann & Weir 2018, Sundberg et al. 2018), and a small number of sequences of representative aquatic genera (*Autoicomyces*, *Ceratomyces*, *Rhynchophoromyces*, *Zodiomyces*) that formed part of a larger study on the molecular phylogeny of the Laboulbeniomycetes (Goldmann & Weir 2018). Despite the low number of analyzed genera

and species, Goldmann & Weir (2018) were able to show that aquatic genera were grouped into three somewhat unresolved clades close to the base of the Laboulbeniales and were placed at some distance from the large genera *Laboulbenia* and *Rickia*, which include mostly "terrestrial" species, but also a limited number of parasites of beetles living in the freshwater environment.

The ecology of freshwater Laboulbeniales has been the subject of very few studies. Scheloske (1969) examined 23,000 arthropods collected in northern Bavaria and observed the presence of Laboulbeniales on 31.1% of the specimens of Haliplidae, 10.2% of Dytiscidae, 10.65% of Hydrophilidae (including Hydrochidae), 15.8% of Dryopidae, and 5% of Corixidae. According to our personal observations, however, in southern Europe the rates of infection are much lower. Scheloske also published two milestone papers (Scheloske 1976a, b) in which the dimorphism of two aquatic Laboulbeniales of different genera (*Eusynaptomyces* and *Hydrophilomyces*) was demonstrated and was linked to the mating behavior of the host insects. More recently, the occurrence of dimorphism in Laboulbeniales was definitively confirmed by molecular analyses in a genus (*Chitonomyces*) occurring on aquatic Coleoptera, and again it was demonstrated its link with the mating behavior of the host insects (Goldmann & Weir 2012). Dimorphism has been shown also in Laboulbeniales associated with "terrestrial" beetles (Rossi & Proaño Castro 2009, Goldmann et al. 2013), but seems to be more common in aquatic Laboulbeniales. It is certainly a very effective strategy for making more efficient the transmission of the sticky spores in the freshwater environment. For the same purpose, aquatic Laboulbeniales also display more frequently than other species two morphological features: preapical outgrowths with different shapes and sizes, that are thought to function as levers facilitating release of the spores only during mating of the host-insects (example in Fig. 19a), and outgrowths at the base of the thalli, commonly called "buffer cells" (example in Fig. 19b), that are thought to keep the thalli in the correct position to come in contact with the right portion of the body of insects of same species during mating (mainly) or other direct contacts. It is interesting to note in this regard that preapical outgrowths are not common among the hundreds of "terrestrial" species of the genus *Laboulbenia* but are quite frequent in the species of the same genus associated with insects occurring in the freshwater environment.

Table 3 Number of freshwater Laboulbeniales and their host.

Genus	**Species number**	**Family of host insects**
Autoicomyces	26	Hydrophilidae (mostly) Hydrochidae, Dytiscidae
Blasticomyces	1	1 on Hydrophilidae
Cantharomyces	7	1 on Hydrochidae; 6 on Dryopidae
Capillistichus	1	Hydrophilidae
Ceratomyces	22	Hydrophilidae
Chaetarthriomyces	3	Hydrophilidae
Chitonomyces	87	Dytiscidae, Gyrinidae, Haliplidae, Noteridae
Coreomyces	23	Corixidae
Drepanomyces	1	Hydrophilidae
Eusynaptomyces	6	Hydrophilidae
Helodiomyces	1	Dryopidae
Hydraeomyces	1	Haliplidae
Hydrophilomyces	17	Hydrophilidae, Hydraenidae
Laboulbenia	34	Gyrinidae
Limnaiomyces	3	Hydrophilidae
Phurmomyces	1	Hydrophilidae
Plectomyces	1	Hydrophilidae
Rhynchophoromyces	9	Hydrophilidae
Rickia	2	Hydrophilidae
Scepastocarpus	1	Hydrochidae

Table 3 Continued.

Genus	Species number	Family of host insects
Synaptomyces	1	Hydrophilidae
Thaumasiomyces	3	Hydrophilidae
Thripomyces	2	Hydraenidae
Zodiomyces	5	Hydrophilidae

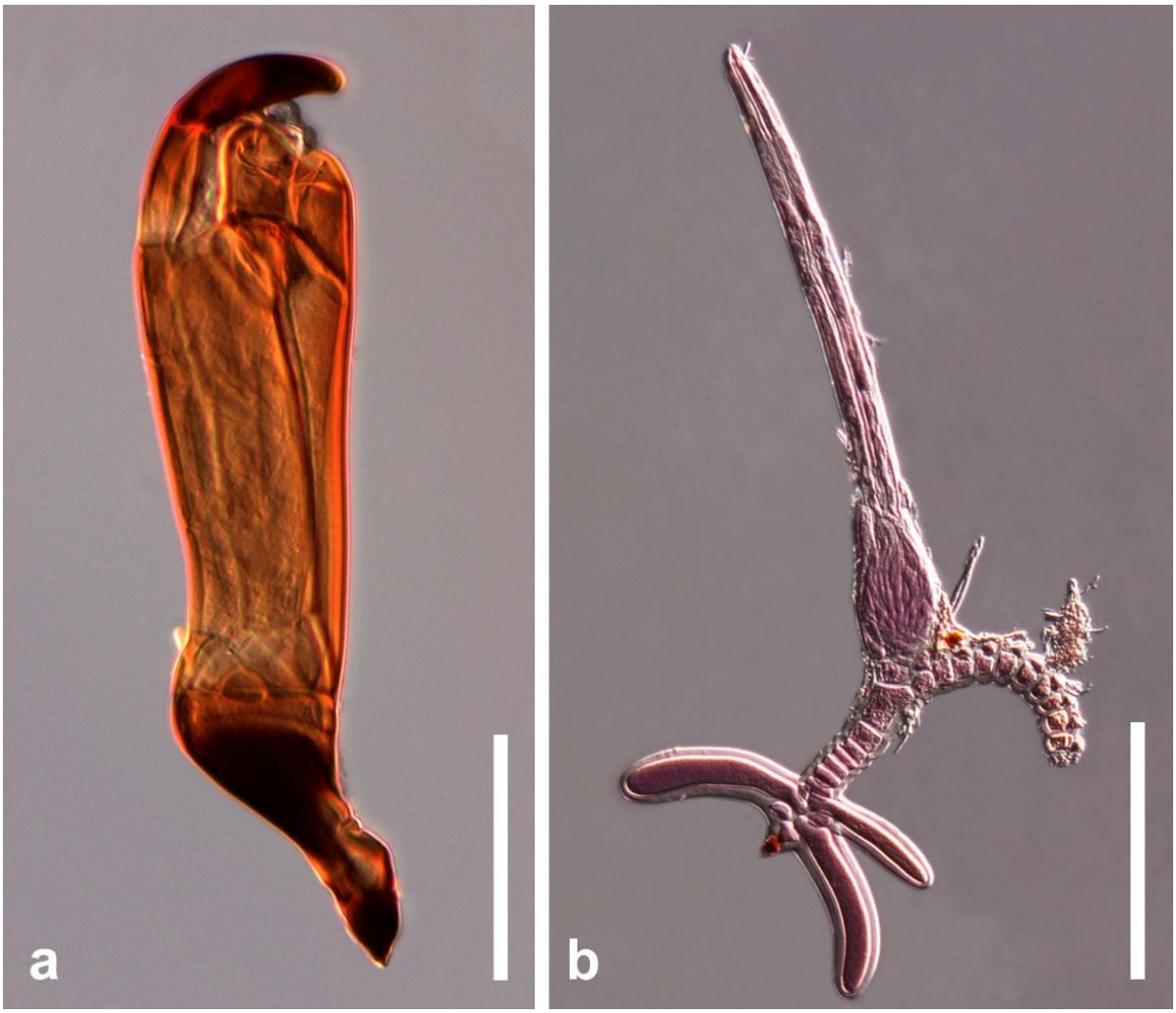


Figure 19 – Freshwater Laboulbeniales. a *Chitomomyces chinensis* bearing a large, horn-like, preapical outgrowth. b *Hydrophilomyces hydraenae*, bearing elongate buffer cells at the base of the thallus. Stained with acid fuchsin. Scale bar: a = 50 µm, b = 100 µm.

Wood Decay Fungi

Introduction

What are wood decay fungi?

A wood decay fungus is any species of fungus that digest moist wood causing it to rot (Srinivasarao & Nagadesi 2021). The decomposition phenomena of wood were first described by Hermann Schacht in 1863 (Blanchette 1991). Wood decay fungi differ from other fungi in that they can decompose lignified cell walls (Blanchette 1991). According to the symptoms, wood decay by fungi is typically classified into three types: soft rot, brown rot, and white rot (Kirk et al. 2008):

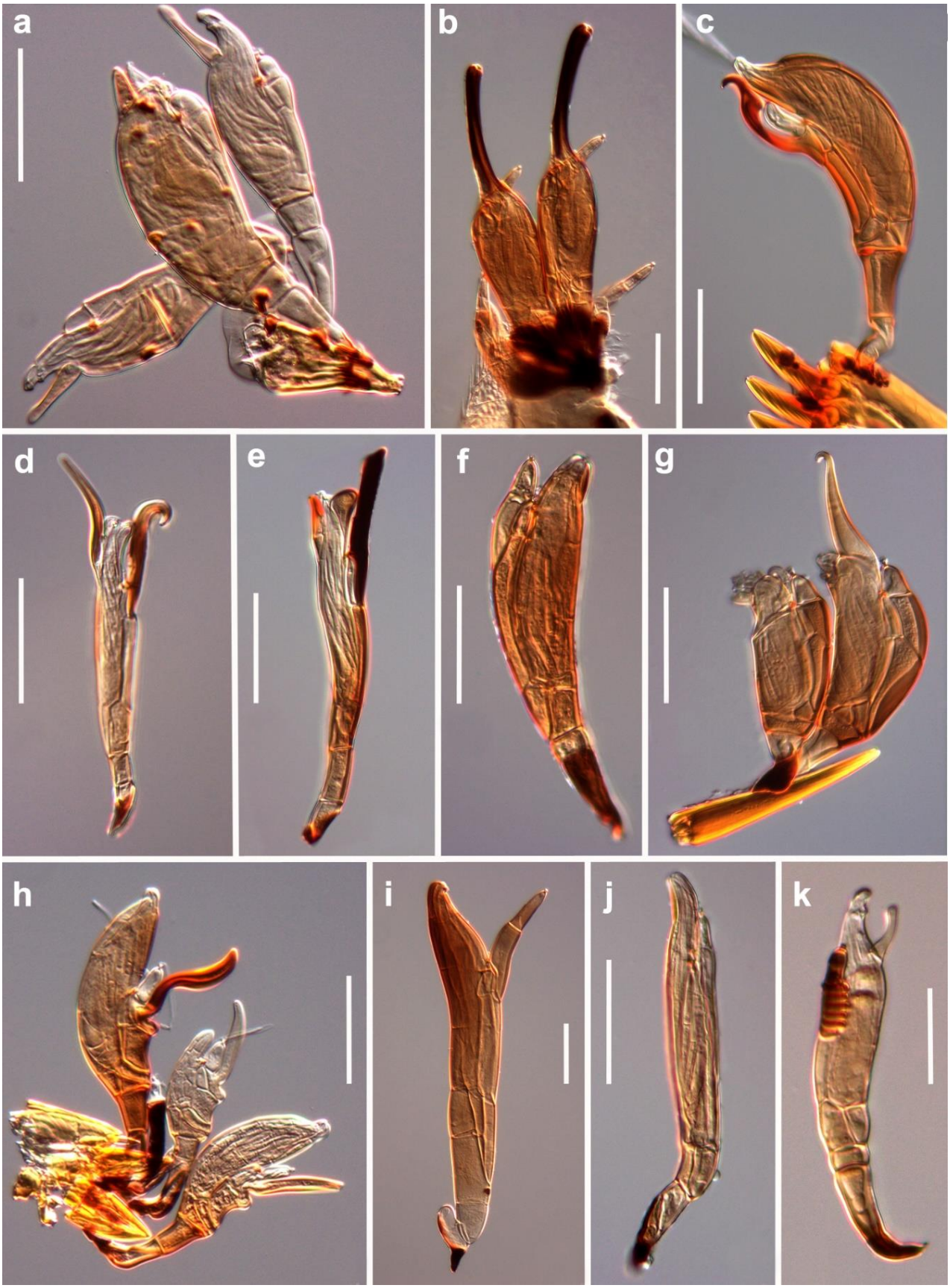


Figure 20 – Biodiversity of the genus *Chitonomyces*. a *C. appendiculatus*: typical and alternate forms growing together. b *C. bakeri*. c *C. italicus*. d *C. japanensis*. e *C. javanicus*. f *C. ordinatus*. g *C. orientalis*. h *C. spinosus*. i *C. strictus*. j *C. thaxteri*. k *C. zonatus*. Scale bars: a–j = 50 µm, k = 25 µm. Reprinted from Nova Hedwigia, Vol. 115, p. 435 (courtesy of Schweizerbart Science Publishers, Stuttgart).

1. Brown rot

The wood turns brown and with brick-shaped cracks after decay. The fungi produce enzymes to decompose the cellulose and hemicellulose of soft wood, but the lignin remains intact, hence the brown color. To date, only basidiomycetes have been reported to cause brown rot (Kirk et al. 2008). Brown-rot fungi breakdown wood polysaccharides without removing much lignin because they lack lignin-degrading enzymes.

2. White rot

The wood turns pale and fragile after decay. The fungi produce enzymes to decompose cellulose, hemicellulose, and lignin simultaneously that are usually whitish in color and fibrous in texture. Species of both Basidiomycota and Ascomycota can cause white rot (Kirk et al. 2008). White rots can degrade lignin most effectively due to the production of ligninolytic extracellular oxidative enzymes; they belong to Basidiomycota.

3. Soft rot

The texture of the wood surface turns spongy after decay. Soft rot, which is characterized by hyphal penetration of the wood cell walls resulting in the formation of diamond decay cavities in the central zone of wood cell walls, which leads to their ultimate destruction (Eaton 2000). Soft rot normally occurs in wood with a high moisture content and with available nitrogen (Kirk et al. 2008). Soft rot fungi are assigned to Ascomycota. To enzymatically break down cellulose in woody tissues, their hyphae secrete cellulases. In certain life stages, several Basidiomycota exhibit soft rot wood decay.

Most wood decay fungi reported in terrestrial habitats are basidiomycetes (Blanchette 1991, Saitta et al. 2011); however, ascomycetous wood decay fungi are mostly reported in habitats inundated with water (Hu et al. 2010, 2013, Shearer et al. 2015)

Wood decay fungi from freshwater habitats

Freshwater fungi refer to those that depend on freshwater environments for the whole or part of their life cycle (Thomas 1996). Wong et al. (1998) divided freshwater fungi into three groups:

1. Ingoldian fungi

Ingoldian fungi (Aquatic hyphomycetes) were named in the honor of the mycologist C. T. Ingold, who first reported this group of freshwater fungi (Ingold 1942, 1943, 1958, Money et al. 2010). Ingoldian fungi occur on decaying leaves in various freshwater habitats, and they are frequently collected in foam (Chan et al. 2000, Descals 2005, Fiuza & Gusmão 2013).

2. Freshwater ascomycetes and hyphomycetes

Freshwater ascomycetes and hyphomycetes are commonly reported on decaying wood submerged in various freshwater habitats, and they are also regarded as wood decay fungi or lignicolous fungi. Compared to terrestrial wood decay fungi, freshwater wood decay fungi have received less attention (Wong et al. 1998). However, recent studies on freshwater wood decay fungi have reported numerous new taxa (Dong et al. 2020b, Song et al. 2020a, b, Li et al. 2021a, Dong et al. 2021a,b, Hyde et al. 2021, Calabon et al. 2022), which greatly enriched our understanding of fungal diversity.

3. Chytrids

Chytrids and microsporidia are often reported as pathogens of fish, frogs, planktonic algae and animals but generally lack the ability to degrade cellulose (Wong et al. 1998). Microsporidia (unicellular forms that lack mitochondria) and chytrids with flagellated spores form an early-diverging clade of the fungal phylogenetic tree (James et al. 2006a).

Wood decay fungi reported from freshwater habitats are mostly ascomycetes and hyphomycetes, a specialized group which present unique physiological and ecological characteristics.

The physiology of wood decay fungi from freshwater habitats

Wood decay activity of freshwater fungi

Wood decay is affected by many factors, including temperature, pH, water potential and oxygen content. In freshwater habitats, the water saturation of wood is very high, which impedes the availability of oxygen necessary for fungal colonization and wood decay (Boddy & Rayner 1983, Schwarze 2007). Therefore, the storage of logs under water sprinklers is often used as a wood protection method in forestry (Schwarze 2007). However, many studies showed that wood can be decomposed in water (Simonis et al. 2008, Savory 1954a, Bucher et al. 2004). Sivichai et al. (2002) investigated the decay of 15 different species of wood blocks in two streams in Thailand over a three-year period and documented weight losses of 47.4–89.0% depending on the timber species. They also noted a significant difference in the extent of decay of the timbers between the two selected sites, with a lower weight loss at the peat swamp site, where water movement is less (Boonyuen et al. 2014). According to a recent study, after 11 months of decomposition, mass loss in streams was 9 % faster than on land in a lowland tropical forest in Panama where three different tree species were placed in stream and terrestrial environments (Jones et al. 2018).

As mentioned above, wood decay is usually divided into brown rot, white rot and soft rot (Kirk et al. 2008). Freshwater fungi mainly cause soft rots, and a few of them cause white rots (Table 4).

Soft rot

Savory (1954a) proposed the term soft rot for wood decay caused by cellulose-destroying microfungi to distinguish it from the brown and white rots caused by the wood-destroying basidiomycetes. The apparent symptoms of soft rot were described as follows: "*usually superficial, deep penetration occurs only in wood which is not continually waterlogged, and even then, the severity of decay progressively decreases below the surface; dull brown or blue gray discoloration, failure of the wood with a brittle fracture and softening of the surface so that it can easily be dug away with the point of a penknife are the usual indications of decay*" (Savory 1954a). When examined under a microscope, chains of diamond-shaped cavities with pointed ends could be observed in the attack zone (Savory 1954a, b).

Hale & Eaton (1985a) studied soft rot attacks continuously using time-lapse cinemicrography. Hale & Eaton (1985a) inoculated the fungi *Phialophora fastigiata* (current name: *Cadophora fastigiata*) and *P. hoffmannii* (current name: *Coniochaeta hoffmannii*) into birch and Scots pine sapwood and recorded each stage in the infection of wood cell walls on film. The findings demonstrated that the formation of soft rot cavities within wood cell walls was oscillatory and determined by successive phases of apical growth of fine hyphae; chains of soft rot cavities within wood cell walls are formed by the activities of lignolytic enzymes released along the hyphal surface (Hale & Eaton 1985a).

To further understand the decay activity, Hale & Eaton (1985b) studied the ultrastructure of fine hyphae of three soft rot fungi (i.e., *Humicola alopallonella, Monodictys putredinis* and *Phialophora hoffmannii*) in wood cell walls of birch. The results showed that fine hyphae of *P. hoffmannii* had a cell wall but were absent at the hyphal apices of *H. alopallonella* and *M. putredinis*. Hale & Eaton (1985b) found an electron-opaque region or halo in the wood cell wall around all fine hyphae, which was thought to be a precellulolytic system secreted by these hyphae. Additionally, Hale & Eaton (1985b) observed a simple organelle composition in fine soft rot hyphae and membranous organelles in T-branch and proboscis hyphae.

Hale & Eaton (1985c) showed that the hyphae of the three fungi formed cavities in the S_2 layer of birch cell walls. According to Transmission electron microscopy (TEM) sections, mature

T-branch and proboscis hyphae in cavities showed cell wall-bound hyphal compartments and an organelle composition similar to that of hyphae in wood cell lumina. Tapered cavities were produced by proboscis hyphae of *P. hoffmannii*, while *H. alopallonella* and *M. putredinis* formed cylindrical cavities. Amorphous deposits were consistently observed in the space between hyphae and cavity surfaces. Constrictions between cavities indicated inactive regions of wood cell wall dissolution around fine hyphae and were not necessarily associated with septa (Hale & Eaton 1985c). Cavity-forming soft rot hyphae may regulate the release of exocellulases and endocellulases in response to nutrient exhaustion following apical growth of the fine T-branch and proboscis hyphae (Hale & Eaton 1985c).

White rot

A few freshwater fungi cause white rots. Schmidt et al. (1997) studied the wood decay pattern of *Physisporinus vitreus* in the laboratory. The results showed that the decay occurred as small longish delignified white pockets, preferentially in the early wood. The studies of TEM and UV-microspectrophotometry results indicated the presence of lignin attacking peroxidases in the hyphal extracellular layer, on the cell wall surface and in the inner S2 layer beneath a hypha.

Decay on different timbers

Different parts and types of wood are also important factors affecting its decomposition in water. Zare-Maivan & Shearer (1988b) tested 17 species of freshwater fungi and found that most fungi caused weight loss in sapwood blocks and bark blocks, while the bark blocks decayed more rapidly than the sapwood blocks. Leightley & Eaton (1977) reported that the freshwater fungus *Neonectria lugdunensis* (≡ *Heliscus lugdunensis*) causes weight loss in beech and Scots pine wood and forms soft-rot cavities in beech wood but not in Scots pine wood. Furthermore, Jones et al. (2018) found that wood decay depended on the tree species in both streams and land habitats, suggesting that wood composition was equally important to decay in both habitats.

Freshwater fungi tested for wood decay

In previous studies, 70 freshwater fungal species (68 Ascomycota, 2 Basidiomycota) were tested for their ability to decompose wood in freshwater habitats (Table 4). Thirty-three of the 68 Ascomycota species were reported to cause soft rot of wood in freshwater habitats; one of the two Basidiomycota species (*Physisporinus vitreus*) was reported to cause white rot of wood in freshwater habitats.

Enzyme production by freshwater fungi

The ability to produce enzymes is very important for freshwater fungi to decompose wood in freshwater habitats. It is important to establish what enzymes freshwater fungi can produce, as these data may provide evidence of their individual and collective roles (Hyde & Jeewon 2003).

To study the wood-day mechanism in freshwater habitats, 58 freshwater fungi were tested for their ability to produce extracellular enzymes (Table 4). Most of the tested freshwater fungal species were capable of producing cellulase, glucosidase, laccase, and xylanase. Abdel-Raheem & Shearer (2002) screened 30 species of freshwater ascomycetes isolated from woody and/or herbaceous substrates for their ability to produce extracellular degradative enzymes with enzyme Commission Number or EC Number (IUPAC-IUBMB, 1999), including amylase or EC Number = EC 3.2.1.1), endoglucanase (EC 3.2.1.4), endoxylanase (EC 3.2.1.8), β-glucosidase (EC 3.2.1.21), laccase (EC 1.10.3.2), lipase (EC 3.1.1.3), pectinase (EC 3.2.1.15), peroxidase (EC 1.11.1.7), polygalacturonase (EC 3.2.1.15), polyphenoloxidase (EC 1.10.3.1), protease (EC 3.4.21), tyrosinase (EC 1.14.18.1) and β-xylosidase (EC 3.2. 1.37) on solid media. The results showed that all species were positive for cellulase and endoxylanase/β-xylosidase; two species [*Aquimassariosphaeria typhicola* (≡*Chaetomastia typhicola*) and *Massarina* sp. A25] tested positive for all enzyme assays. Abdel-Raheem & Ali (2004) screened 12 species of hyphomycetes isolated from woody substrates for their ability to produce extracellular lignocellulolytic enzymes,

including endoglucanase, endoxylanase, β-glucosidase, laccase, peroxidase, polyphenoloxidase, tyrosinase and β-xylosidase, on solid media. Three species, i.e., *Alatospora acuminata*, *Flagellaspora penicillioides* and *Triscelophorus monosporus*, were positive for all tested enzymes, and the ability to produce cellulase was 100% for all species, while only four species, i.e., *Alatospora acuminata*, *Flagellospora curvula*, *Flagellospora penicilloides*, *Triscelophorus monosporus*, were positive for lignin-peroxidase. The ability of the species to produce another lignocellulosic enzyme ranged from 50% to 83%.

Chamier (1985) reviewed the cell-wall-degrading enzymes of aquatic hyphomycetes, including pectinases, cellulases (EC 3.2.1.4), hemicellulases (a diverse group of enzymes that hydrolyse hemicelluloses), laminarinases (EC 3.2.1.6) and chitinases (EC 3.2.1.14), and the ability of these fungi to degrade lignin and straw, and this paper of Chamier (1985) presented new evidence of enzymic activity for 14 species.

A few studies have been reported on the enzymes of freshwater fungi, and this issue is worthy of further research. Pointing et al. (2000) considered that one of the main problems with fungal enzyme assays has been the lack of any standardized methodology; therefore, they listed detailed protocols for standardizing assays for lignocellulolytic enzyme production of marine fungi, which were recommended for the enzyme assays of freshwater fungi by Hyde & Jeewon (2003).

Table 4 Freshwater fungi tested for wood decay.

Species	Phyla	Wood decay types	Enzymes production	References
Aniptodera aquadulcis (≡ *Halosarpheia aquadulcis*)	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
A. chesapeakensis	Ascomycota	–	Cellulase, xylanase, lignin-modifying enzymes	Bucher et al. (2004)
A. nypae	Ascomycota	–	Xylanase, laccase	Bucher et al. (2004)
Annulatascus velatisporus	Ascomycota	–	Xylanase	Bucher et al. (2004)
Aquapoterium pinicola	Ascomycota	–	Cellulase, endoglucanase, β-glucosidase, xylanase, amylase, polygalacturonase	Simonis et al. (2008)
Brachiosphaera tropicalis	Ascomycota	–	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, tyrosinase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Cadophora fastigiata (≡ Phialophora fastigiata)	Ascomycota	Soft rot	Lignolytic enzymes	Hale & Eaton (1985a)
Camposporium antennatum	Ascomycota	–	Cellulase, xylanase, lignin-modifying enzymes	Bucher et al. (2004)
Chaetomium cochliodes	Ascomycota	Soft rot	–	Savory (1954a)
C. elatum	Ascomycota	Soft rot	–	Savory (1954a)
C. globosum	Ascomycota	Soft rot	–	Savory (1954a)
Clavariopsis aquatica	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)

Table 4 Continued.

Species	Phyla	Wood decay types	Enzymes production	References
Coniochaeta hoffmannii (≡ Phialophora hoffmannii)	Ascomycota	Soft rot	Ligninolytic enzymes	Hale & Eaton (1985a)
Conioscypha varia (≡*Conioscyphascus varius*)	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Dactylaria tunicata	Ascomycota	Soft rot	β-glucosidase, xylanase, amylase	Simonis et al. (2008)
Dematiohelicoma perelegans (≡ *Helicoma perelegans*)	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, amylase	Simonis et al. (2008)
Desertella fumimontarum	Ascomycota	–	Cellulases, endoglucanase, β-glucosidase, xylanase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Dichotomopilus funicola	Ascomycota	Soft rot	–	Savory (1954a)
Dictyocheirospora heptaspora (≡ *Dictyosporium heptasporum*)	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Didymella glomerata	Ascomycota	Soft rot	–	Savory (1954a)
Echria gigantospora (as Arnium gigantosporum)	Ascomycota	Soft rot	β-glucosidase, xylanase, laccase, peroxidase, amylase	Simonis et al. (2008)
Ellisembia opaca	Ascomycota	–	Xylanase	Bucher et al. (2004)
Filosporella annelidica	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)
Flabellospora multiradiata	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, tyrosinase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Fusarium solani (≡ Nectria hematococca)	Ascomycota	–	Glucosidase	Zare-Maivan & Shearer (1988b)
Halomassarina thalassiae (≡ Massarina thalassioidea)	Ascomycota	–	Cellulase, xylanase, laccase	Bucher et al. (2004)
Helicomyces roseus	Ascomycota	–	Xylanase	Bucher et al. (2004)

Table 4 Continued.

Species	Phyla	Wood decay types	Enzymes production	References
H. torquatus	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Humicola alopallonella (≡ *Trichocladium alopallonellum*)	Ascomycota	Soft rot	Ligninolytic enzymes	Hale & Eaton (1985b, c)
Jahnula bipileata	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, tyrosinase, amylase, polygalacturonase	Simonis et al. (2008)
Lindgomyces ingoldianus	Ascomycota	–	Cellulase, xylanase, laccase	Bucher et al. (2004)
L. ingoldianus (≡*Massarina ingoldiana*)	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, tyrosinase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Lophiostoma bipolare	Ascomycota	–	Cellulase, xylanase, laccase	Bucher et al. (2004)
L. purpurascens (≡ *Massarina purpurascens*)	Ascomycota	–	Cellulase, xylanase, lignin-modifying enzymes	Bucher et al. (2004)
Luttrellia guttulata	Ascomycota	Soft rot	β-glucosidase, xylanase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Megalohypha aqua-dulces	Ascomycota	–	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Mollisia gigantean (≡ Helicodendron giganteum)	Ascomycota	–	Cellulases, β-glucosidase, xylanase, laccase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Monodictys putredinis	Ascomycota	Soft rot	Ligninolytic enzymes	Hale & Eaton (1985b, c)
Nais inornata	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)
Natantispora retorquens (≡ *Halosarpheia retorquens*)	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)

Table 4 Continued.

Species	Phyla	Wood decay types	Enzymes production	References
Neohelicascus elaterascus (≡ *Kirschsteiniothelia elaterascus*)	Ascomycota	–	Cellulase, sylanase	Bucher et al. (2004)
Neojahnula australiensis (≡ *Jahnula australiensis*)	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Neonectria lugdunensis (≡*Heliscus lugdunensis*)	Ascomycota	–	Glucosidase	Zare-Maivan & Shearer (1988b)
N. lugdunensis (≡*Heliscus lugdunensis*)	Ascomycota	Soft rot	Cellulase, xylanase, and mannase	(Leightley & Eaton 1977)
Ophiobolus shoemakeri	Ascomycota	–	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Ophioceras commune	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
O. dolichostomum	Ascomycota	–	Cellulase, xylanase, laccase	Bucher et al. (2004)
Orbicula parietina	Ascomycota	Soft rot	–	Savory (1954a)
Phaeoisaria clematidis	Ascomycota	–	Xylanase, laccase	Bucher et al. (2004)
Physisporinus vitreus	Basidiomycota	White rot	–	Schmidt et al. (1997)
Porosphaerellopsis bipolaris	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, peroxidase, amylase, chitinase	Simonis et al. (2008)
Pseudohalonectria lignicola	Ascomycota	Soft rot	Glucosidase, cellulase, xylanase	Zare-Maivan & Shearer (1988b), Bucher et al. (2004)
Pseudoproboscispora aquatica	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Pseudoxylomyces elegans (≡ Xylomyces elegans)	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, tyrosinase, amylase, pectic lyase, polygalacturonase	Simonis et al. (2008)
Rigidoporus lineatus	Basidiomycota	–	–	Hood et al. (1997)

Table 4 Continued.

Species	Phyla	Wood decay types	Enzymes production	References
Savoryella aquatica	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
S. lignicola	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Sporidesmium tropicale	Ascomycota	–	B-glucosidase, xylanase, amylase	Simonis et al. (2008)
S. vagum (≡ *Ellisembia vaga*)	Ascomycota	–	–	Bucher et al. (2004)
Sporoschisma nigroseptatum	Ascomycota	–	Xylanase	Bucher et al. (2004)
S. uniseptatum	Ascomycota	–	Cellulase, xylanase	Bucher et al. (2004)
Thelonectria lucida (≡ *Nectria lucida*)	Ascomycota	–	Glucosidase	Zare-Maivan & Shearer (1988b)
Torrentispora fibrosa	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, laccase, amylase, polygalacturonase	Simonis et al. (2008)
Torula herbarum	Ascomycota	–	Cellulase, lignin-modifying enzymes	Bucher et al. (2004)
Trichocladium lignincola	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)
Trichoderma viride	Ascomycota	Soft rot	–	Savory (1954a)
Trichurus terrophilus	Ascomycota	Soft rot	–	Savory (1954a)
Vibrissea flavovirens (≡ *Anavirga dendromorpha*)	Ascomycota	Soft rot	Glucosidase	Zare-Maivan & Shearer (1988b)
Zalerion maritima	Ascomycota	Soft rot	–	Savory (1954a)
Zopfiella lundqvistii	Ascomycota	Soft rot	Cellulases, endoglucanase, β-glucosidase, xylanase, amylase	Simonis et al. (2008)

Notes: "–" indicates not mentioned in the references.

Adaptations of freshwater decay fungi

To adapt to the freshwater environment, fungi evolved spores that can be dispersed in water and then become trapped in it and subsequently colonize new substrates (Hyde & Goh 2003). Many freshwater ascomycetous species produce asci with large apical rings, ascospores with various sheaths, appendages, or wall ornamentations, which probably function in ascospore dispersal and/or attachment (Wong et al. 1998). For example, *Annulatascus velatispora*, a common freshwater lignicolous taxon, possesses asci with a large apical ring (Fig. 21a), which may help in the ejection of ascospores from asci (Fig. 21a); *Aqualignicola vaginata* and *Phaeonectriella appendiculata* produce ascospores with a sticky sheath and appendages (Fig. 21b, c), which may help the spores attach to substrates.

Freshwater hyphomycetous wood decay fungi often produce spiral or branched conidia, which are thought to aid in flotation in water or act as anchors and allow their entrapment to substrata (Ingold 1942, Wong et al. 1998). *Helicomyces roseus* and *Pleohelicoon richonis*, for example, produce spiral conidia (Fig. 21d, e), whereas *Tetraposporium* sp. develops branched conidia (Fig. 21f).

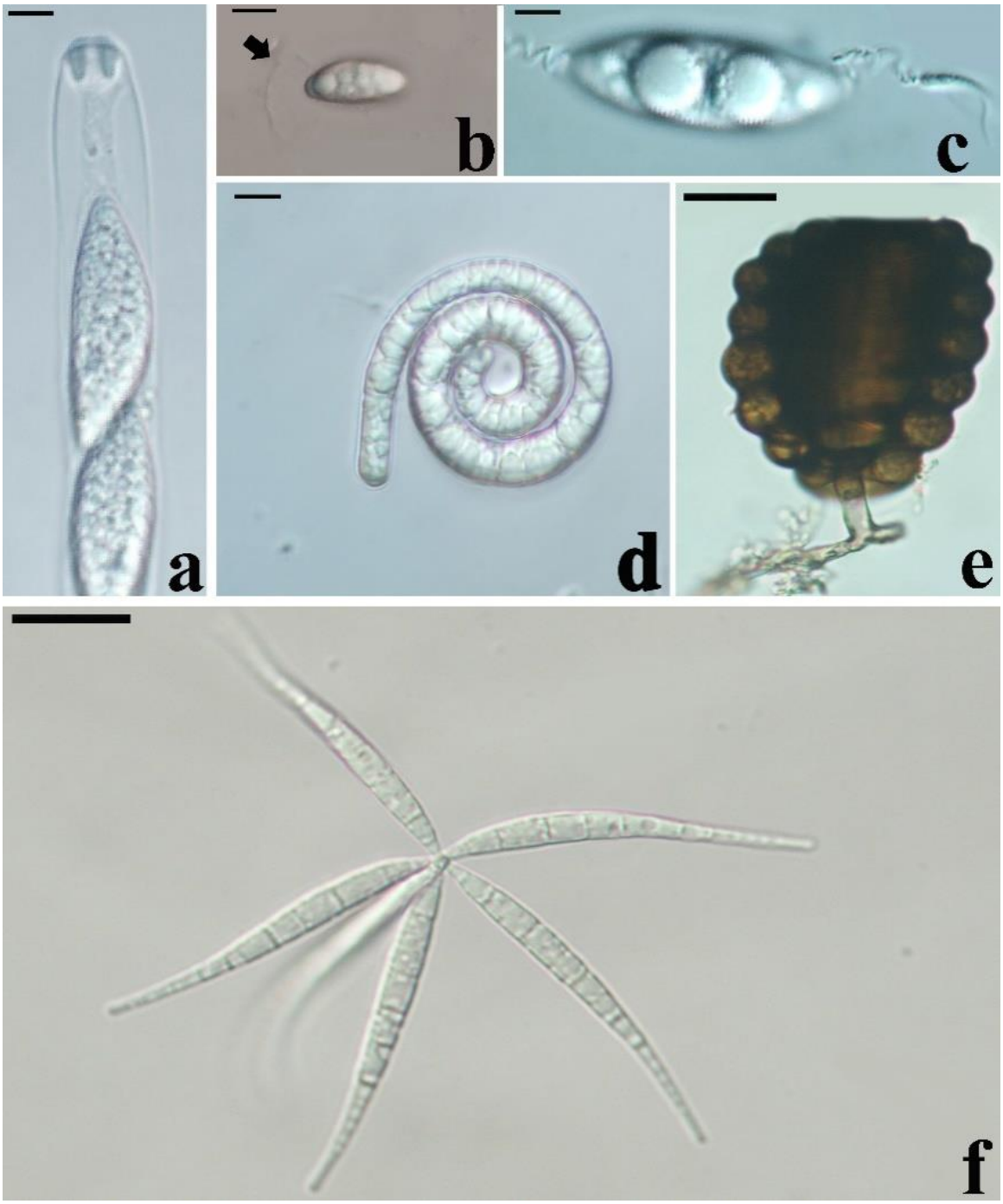


Figure 21 – Adaptive characteristics of freshwater wood decay fungi. a Apical ring of an ascus in *Annulatascus velatispora*. b Sticky sheath of an ascospore in *Aqualignicola vaginata*. c Appendages of an ascospore in *Phaeonectriella appendiculata.* d Spiral conidium of *Helicomyces roseus*. e Spiral conidium of *Helicoon richonis*. f Conidium of *Tetraposporium* sp. Scale bars: a–d = 5 μm, e–f = 20 μm.

The ecology of wood decay fungi from freshwater habitats

The role of wood decay fungi in freshwater habitats

Wood debris from terrestrial habitats is an important nutrition resource of freshwater ecosystems. It serves as a relatively stable source of fixed carbon and as a habitat for aquatic organisms (Anderson & Sedell 1979, Zare-Maivan & Shearer 1988b).

Vascular plant breakdown generally proceeds in three distinct phases: (1) an initial rapid loss due to leaching; (2) a period of microbial decomposition and conditioning; and (3) mechanical and invertebrate fragmentation (Webster & Benfield 1986).

Fungi and bacteria are the primary decomposers of wood in freshwater environment (Jones et al. 2018), and fungi play a critical role in facilitating energy and nutrient flow through detrital pathways (Tant et al. 2015). However, decay of wood in freshwater is slow and has little impact on Stream Energy budgets (Sridhar et al. 1992, Gessner & Van Ryckegem 2003). Freshwater fungi lack the ligninolytic enzymes of terrestrial fungi that cause white and brown rots of wood (Leightley & Eaton 1977).

Anthropogenic disturbance to wood decay fungi in freshwater habitats

Many human activities have an impact on freshwater ecosystems, and studies have mainly focused on freshwater animals and plants (Søndergaard & Jeppesen 2007, Dodds et al. 2013, Iversen et al. 2019, Su et al. 2021). However, little attention has been given to the impact of human activities on freshwater fungi. A few studies on the influence of anthropogenic disturbance on wood decay fungi in freshwater environments have shown that freshwater fungi are easily influenced by human disturbance (Tsui et al. 2001b, Hu et al. 2010).

Tsui et al. (2001b) studied the influence of the herbicide glyphosate on the biomass production of four freshwater fungi (*Annulatascus velatisporus*, *Camposporium antennatum*, *Massarina* sp., and *Helicosporium griseum*) obtained from submerged wood. The results showed that at 500 mg/L, inhibition from the herbicide ranged between 19 and 79% at 50 mg/L, and glyphosate stimulated the biomass production of *C. antennatum* and *H. griseum* by approximately 14%. Hu et al. (2010) discovered a dramatic decrease in species richness and diversity, with significantly changed species composition observed in the artificial lake compared to the nondammed stream, which indicated that dams might affect the wood decay fungi in freshwater habitats.

Riparian vegetation is the major source of organic input into the stream ecosystem; therefore, anthropogenic disturbance to riparian vegetation might affect the distribution of wood decay fungi in freshwater habitats (Vijaykrishna & Hyde 2006). Vijaykrishna & Hyde (2006) studied the impact and type of riparian vegetation on the biodiversity of lignicolous freshwater fungi in five tropical streams of the Barron River catchment area in Atherton Tablelands, Queensland, Australia. The findings revealed that fungal species showed limited habitat recurrence; nevertheless, major changes in species richness and abundance were observed in response to varying levels of human disturbance. Bärlocher & Graça (2002) characterized the fungal communities of eight streams in Portugal, four bordered by native deciduous forest and four bordered by pure stands of *Eucalyptus globulus*, wherein the diversity of aquatic hyphomycetes was significantly lower in eucalypt bordered streams.

Importance of wood decay fungi from freshwater habitats

Ecological importance

Wood is a major carbon input into freshwater ecosystems, but it is not an easily degraded substratum. Wood is usually low in nitrogen and phosphorus, which are two elements essential for hyphal growth (Kirk et al. 2008). Some timber (i.e., *Sequoia sempervirens*, *Quercus alba*, *Salix babylonica)* species contain tannins and phenolic compounds, which are generally toxic to fungi (Kirk et al. 2008). Most of the organic material of wood is in the form of cellulose, hemicellulose and lignin, and these components are generally resistant to enzymes (Kirk et al. 2008). As a result, only certain specialized fungi are associated with wood decay (Kirk et al. 2008).

Ferrer et al. (2020) studied the contribution of fungal and invertebrate communities to wood decay in tropical terrestrial and aquatic habitats. Divergent decay trajectories across habitats were associated with widespread order-level differences in fungal composition, with distinct communities found in freshwater, estuarine and marine environments (Ferrer et al. 2020).

Tant et al. (2015) studied the role of aquatic fungi in the transformation of organic matter mediated by nutrients and indicated that aquatic fungi play a critical role in facilitating energy and nutrient flow through detrital pathways and that their ability to mediate organic matter transformations is significantly influenced by nutrient enrichment.

Economic importance

The major economic significance of freshwater fungi was in the decay of wooden slats in water cooling towers, where water from electrically generating turbines was cooled and recycled (Savory 1954a). This led to the characterization of soft rot attack of wood by Savory (1954a, b), which led to a major study of wood decay fungi in water cooling towers by Eaton & Jones (1971a, b) and Jones (1972). The decay of wood was rapid due to the elevated temperature in cooling towers, with weight loss of beech and Scots pine test blocks of 60 and 53%, respectively, after 108 weeks of exposure (Eaton and Jones 1971b).

Freshwater wood decay fungi produce a wide variety of enzymes with broad application potential. The production of cellulase and xylanase is common among diverse freshwater ascomycetes and their hyphomycetous anamorphs (Bucher et al. 2004).

Wood decay fungi were also used for water pollution remediation. For instance, *Neonectria lugdunensis* (≡ *Heliscus lugdunensis*) is capable of biodegrading bisphenol A and utilizing it as an energy source (Omoike et al. 2013). Jia et al. (2013) studied the inhibition of freshwater algal species by coculture with two freshwater fungi, *Trichaptum abietinum* and *Porostereum spadiceum* (≡ *Lopharia spadicea*)], and these two fungi might inhibit the growth of different freshwater algal species and utilize algal cells for their growth. The findings indicated that these fungi are capable of preventing water blooms. Yang et al. (2016) tested 92 freshwater fungal strains obtained from submerged wood for their ability to decolorize seven synthetic dyes; 13 isolates demonstrated high decolorization capabilities, and some strains were highly effective in decolorization of numerous dye types.

Evolution of Freshwater Fungi

Background

Freshwater is an indispensable natural resource for sustaining terrestrial life. It is defined as the water that contains less than 1,000 milligrams per litre (ppm) of dissolved solids (Zaman & Sizemore 2017). The majority of the earth's surface is covered by water (71%), the oceans occupying about 96.5 percent, thus leaving only an estimated 3 percent as freshwater (Panchal et al. 2021). Of this estimated 3 percent, the glaciers, polar ice caps, the atmosphere, and moisture in the soil account for a reasonable share which remain unavailable (Alavian et al. 2009). This in the end works out to only 0.5 percent as available freshwater on earth. Hadean, the geologic eon of Earth's history, describes the formation of Earth about 4.54 billion years ago (Dalrymple 2001). The original land masses of the Hadean earth were the results of volcanoes emerging through a global ocean (Van Kranendonk 2010, Bada & Korenaga 2018). These land masses were analogous to Hawaii and Iceland today. About 4 billion years ago, there were abundant hydrothermal fields with multiple hot spring systems which were regularly replenished by precipitation and evaporation from the surrounding ocean (Rasmussen 2000). The distilled freshwater would percolate on the hot rocks and circulate back to the surface as springs and geysers (Damer & Deamer 2020). Hydrothermal fields provided sources of heat and chemical energy to drive polymerization reactions in films of concentrated organic solutes that were formed on the minerals (Deamer et al. 2019). Carbon dioxide and sulfur dioxide constitute the major components of volcanic gases, both of which form weak acids when dissolved in water. Early microorganisms had the ability of chemical synthesis to turn them into minerals, ultimately leading to the formation of a protocell (Damer & Deamer 2020). These were very necessary in order to adapt to the harshest environments in the early stages of Earth. Johnson & Wing (2020) hypothesized that the global-scale formation of continental soils took place after the "waterworld"

or 3.24 billion years ago based on the $_{18}O/_{16}O$ ratio through a time series of oceanic crust. The Earth had a soft mantle which was unable to support large mountain ranges until a major part of the lithosphere formed. The lithosphere creation consisted of the continental crust mantle formed between 3.6 and 2.5 billion years ago (Rao & Nara 2022). Thus, the global scale of plate tectonics initiation began no later than the estimated 3 billion years ago (Palin & Santosh 2021). Earth has experienced several ice ages, which began 2.4 million years ago. The ice ages occurred every 100,000 years and lasted until about 11,500 years ago (Rapp 2012). During the ice ages, Earth's water was trapped within the glaciers. The glaciation in the ice age caused the crust to shift, leaving open grooves and ridges to catch water. Sixty-two percent of the world's lakes fall under the territory of Canada in consequent of such glacial periods in which a large ice sheets caused by natural indentations was able to capture rainwater and other water sources (Dyke & Evans 2014, Messager et al. 2016).

The volcano eruption caused by magma flowing out, left empty land to collapse and turn into a river-ways, filling them with melting snow, rainwater, and ice, which in turn started running down the mountains. The circulation of water from the ocean and land surface represents the main source of freshwater reservoirs. Algae, *Nymphaea*, *Typha*, and numerous other plants kept water clean through the root systems, filtering away pollution and excess nutrients (Lu et al. 2018a). The earth has faced many intermissions which included the rise and fall of the sea level, perhaps paving the way for organisms from the ocean to invade the land and survive through the environmental changes (Benton & Emerson 2007). Encapsulation of genetic material in a coat of polymers into membranous compartments is an important factor in the genesis and survival through the cycles of hydration and dehydration under structures such as stromatolites (Damer & Deamer 2020). The general view is that cyanobacteria transitioned into multicellular algae (and protists and fungi) and then into non-vascular plants and possibly from them into vascular plants (Graham et al. 2014). Thus, speciation could have occurred parallelly by re-adapting to coastal or ocean from inland environments such as soil, deserts, and lakes about 3.6 to 3.2 billion years ago (Beraldi-Campesi 2013).

Fungal history

Fungal evolution is a mystery as to whether they survived the extreme weather events and conditions of the planet's development or underwent evolution billions of years ago (Berbee et al. 2017). The early stages of the Earth's biota were dominated by microscopic life that left fossil records in evidence of their tell-tale history (Demoulin et al. 2019). Fossil reports that are claimed to be of cyanobacteria possibly lived without oxygen, were trapped within 3.5 billion years old rocks (Awramik 1992). The Great Oxidation event occurred 2.4 billion years ago making significant changes in the dynamics of biological adaptations (Olejarz et al. 2021). This was believed to have played tremendously important dimensions in shaping the earth's biosphere in the prehistoric ages with the inclusion of Cyanobacteria as the by-product of photosynthesis with the use of oxygen which debatably evolved around 2.4 billion years ago or earlier (Demoulin et al. 2019). The revolutionary data demonstrate that microbes can persist and function as living organelles inside other microbes (Cavalier-Smith 2006). The speculative branch of fungal-like structures from 2.4 billion years ago in submarine basaltic fossilized lavas showed that multicellular organisms evolved in parallel with other surviving organisms (Bengtson et al. 2017). The earliest record of mutualistic symbiosis fungus was found from root tissues about 460 million years ago (Redecker et al. 2000). The Ongeluk fossils (2.4-billion-year-old) have shown bulbous protrusions, which are the common characteristics of any endolithic that inhabits a cleft within a rock (Bengtson et al. 2017). This fossil was estimated two to three times older than its estimated age of the fungal clade (1.6 to 1.0 billion-years-old) (Bengtson et al. 2017). Several researchers mentioned that fungi may have had their origin in the early evolutionary stages from the deep oceanic biosphere rather than on land (Orsi et al. 2013, Bengtson et al. 2014). This also coincided with several geological phenomena such as formation of soil, spreading of the seafloor, genesis of mountains (orogenesis), erosion of rocks and succession of lakes, which may therefore encompass

the first terrestrial association among bacteria, fungi, and algae (Fig. 22) (Gehrig et al. 1996, Evans & Johansen 1999). Microbial communities containing algae and fungi from soil were possibly the first terrestrial association between fungi and photosynthetic organisms (Gehrig et al. 1996, Evans & Johansen 1999). It is hypothesized that members of Glomeromycota played a pivotal role in the colonization process, as its members lived in symbiotic relationships with cyanobacteria or algae and were therefore necessarily symbionts of earliest land plants (Schüßler 2002, Lutzoni et al. 2018).

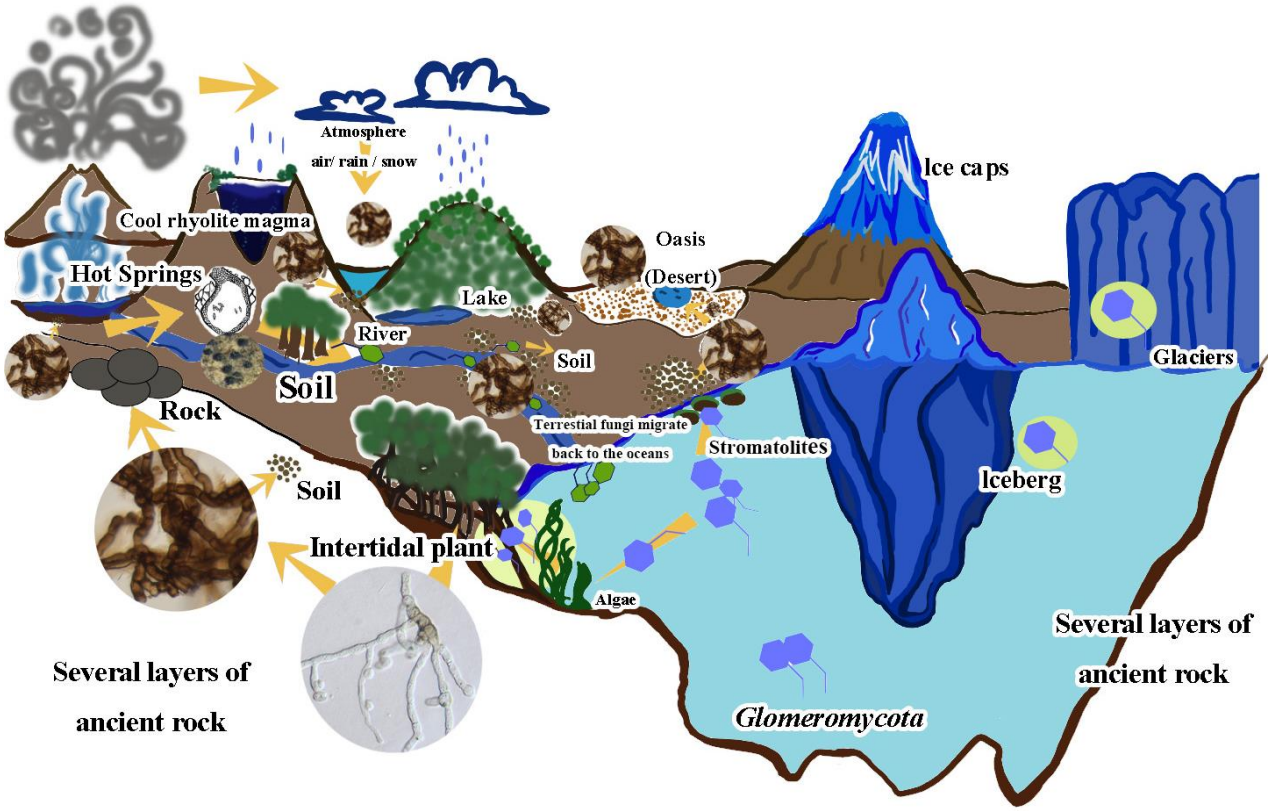


Figure 22 – Possible scenarios in the evolution of freshwater fungi. Freshwater fungi are considered to have evolved after marine and terrestrial fungi. This hypothesis is possible with the accumulation of organic matter in freshwater and fungi in these systems started to have high diversification. The figure depicts several pathways including the invasion of freshwater bodies by plants; fungi on riparian vegetation being washed into freshwater and the evolution of freshwater fungi via run-off rainwater. However, more sources of freshwaters remain to be explored.

Freshwater fungal evolution

Many studies have focused on the evolution of fungi, but their origin remains debatable (Blackwell et al. 2006). It is hypothesised that algae and major lineages of fungi were present from around 1000 MYA, whereas land plants appeared around 700 MYA (Heckman et al. 2001). Fossil evidence imply that the fungal clade is much older than previous estimates (Bengtson et al. 2017). The last common ancestor of crown-group fungi has been hypothesised to be non-filamentous, with flagellated spores, and aquatic (Bengtson et al. 2017). However, if the last common ancestor was non-marine, marine and deep-biosphere fungi would represent migrated terrestrial taxa, which is amply supported by their predominance in marine and deep-biosphere environments (Bengtson et al. 2017). Basal freshwater fungi are likely to have originated from marine ancestors (Vijaykrishna et al. 2006, Beakes & Sekimoto 2008, Jones et al. 2011). The earliest basal freshwater fungi probably migrated to estuaries and then on to land with their hosts (Beakes et al. 2012). They then probably switched hosts from nematodes to soil debris, then to plant roots (Beakes et al. 2012).

This is similar to how ancient fishes first experienced freshwater and evolved to adapt to the new environment (Takei 2015). Then, the lineage moved onto the land or re-entered the seas during evolution (Takei 2015). Similarly, terrestrial fungi are likely to have evolved to adapt to freshwater, for example, Chytridiomycota, the basal clade of fungi, is commonly found in freshwater habitats (Nagahama et al. 2011). The early lineages of Chytridiomycota are highly diverse in marine habitats and are among the earliest to diverge, which suggests that they have evolved in marine habitats (Nagahama et al. 2011, Richards et al. 2015). However, there is also evidence to support that most chytrids from freshwater are of terrestrial origin (James et al. 2006a). This makes the origin of Chytridiomycota debatable. The modern freshwater fungi probably originated from terrestrial ancestors that entered the water bodies (Beakes & Sekimoto 2008). This is supported by the presence of several terrestrial relatives among modern freshwater fungi in *Ascomycota* (Vijaykrishna et al. 2006).

Several evolutionary pathways have been proposed for freshwater fungi (Shearer 1993). It is hypothesised that fungi migrated to freshwater when plants invaded freshwater habitats, carrying with them their associated microorganisms, and these fungi adapted to aquatic habitats (Shearer 1993). The second hypothesis suggests that freshwater fungi on riparian vegetation are likely to have been washed into freshwater. This hypothesis is supported by studies that show that freshwater ascomycetes evolved directly from terrestrial species (Vijaykrishna et al. 2006). This is further supported by those freshwater genera that also have terrestrial and marine species (Vijaykrishna et al. 2006, Jones et al. 2014a, Kodsueb et al. 2016). Freshwater organisms gain water by osmosis from their environment and lose ions by diffusion to adapt to freshwater. All these pathways represent likely scenarios for the adaptation of fungi in freshwater habitats.

To our knowledge, phenotype variations such as carbonaceous versus membranous peridium structures, the polymer encapsulation sheets, the chlamydospore-like or the presence of a thick-walled mycelium are occasionally described as common characters in freshwater fungal species (Naranjo-Ortiz & Gabaldón 2019). The special peridium wall type and encapsulation of the membranous compartments may allow fungi to use the thick wall and encapsulation sheet to go through hydration and dehydration (Shearer 1993, Luo et al. 2019, Dong et al. 2020b). The chlamydospore is known as a stage of nutrient conservation in a fungal species, which renders the mycelium to survive under oxygen deficient conditions until nutrients are perforable for vegetative expansion (Lin & Heitman 2005). Most studies show that freshwater fungi occasionally share a common ancestor with fungi from terrestrial habitats or soil, instead of marine fungi (Wong et al. 1998, Jones et al. 2014a). Some freshwater fungi have been found on terrestrial plants that inhabit embankments (Mapook et al. 2016), some with ancestries as far back as the early Triassic (251 Mya) where the fluctuations in the environment was characterized by high sea surface temperatures and ocean anoxia (Song et al. 2019). Many freshwater fungi are reported from extreme environments like hot springs and have a common ancestor in the late cretaceous (~100–66 Mya) where the culmination of magmatism caused warm temperature and intense shortening in the fold-and-thrust belt of the plateau (Ariyawansa et al. 2015, Phukhamsakda et al. 2016). During the late Cretaceous, there was a transition from one of the warmest climates of the past 140 million years to cooler conditions due to declining CO_2 levels in the atmosphere (Linnert et al. 2014, Tabor et al. 2016), which could also have led to the migration of fungi to freshwater.

Conclusion

The origin of freshwater fungi remains debatable, but it is likely that they evolved from terrestrial ancestors. This is supported by divergence time studies which show that freshwater fungi have the latest development compared to marine and terrestrial fungi. However, there is a lack of information on fungi from extreme habitats like glaciers, hot springs, magma, and ancient rocks to show the exact historical development of freshwater fungi. The study of fungi inhabiting extreme habitats on land will likely enhance our understanding of fungal network drive in rivers to provide a better understanding of the evolution of freshwater fungi.

Antimicrobials from Freshwater Ascomycota

Introduction

Freshwater fungi comprise a phylogenetically diverse lineage of organisms, including members of phyla such as Ascomycota (Pezizomycotina) (Jones et al. 2014a) and Zoopagomycota (Kickxellomycotina). The Kickxellomycotina contains the orders Asellariales and Harpellales, which are associated with digestive tracts of aquatic stages of arthropods and comprise two of the four orders that have been treated previously as Trichomycetes (Spatafora et al. 2017). In addition, the zoosporic fungi, which include the Chytridiomycota (Shearer et al. 2004) and Cryptomycota (Spatafora et al. 2017, Grossart et al. 2019) are also present in freshwater habitats. Among these groups, ascomycetous fungi are known for producing a variety of bioactive secondary metabolites (Gloer 2007, El-Elimat et al. 2021).

This entry will focus on the decomposer freshwater fungi (i.e., saprobic) in the phylum Ascomycota, subphylum Pezizomycotina (Shearer 1993, Schoch et al. 2009). Of the approximately 4,145 fungi described from freshwater, the saprobic ascomycetes represent approximately 1,550 species (Jones et al. 2014a). They are the most commonly occurring group found in freshwater habitats (Raja et al. 2018). This number, however, is constantly changing as new species are being described (Shearer & Raja 2013, Calabon et al. 2020b). The freshwater fungi produce several types of extracellular enzymes, such as amylases, cellulases, pectinases, xylanases, and peroxidases, and they are capable of decomposing plant debris that falls or is washed into freshwater habitats thereby playing an important ecological role as decomposers in water (Shearer & Zare-Maivan 1988, Zare-Maivan & Shearer 1988a, b, Abdel-Raheem & Shearer 2002, Gessner & Van Ryckegem 2003, Simonis et al. 2008).

The freshwater ascomycetes (meiosporic, i.e., sexual state) are microscopic saprobic fungi that colonize and decompose submerged substrates, such as woody and herbaceous materials, in lotic habitats (i.e., running water, such as streams and rivers) and lentic habitats (i.e., standing water, such as lakes, bogs, ponds, and swamps) (Shearer 1993, 2001, Shearer & Raja 2013, Calabon et al. 2020a). In addition, the conidial ascomycetes (mitosporic, i.e., asexual state) also occur in fresh water. Collectively, these sexual and asexual fungi will be referred to as freshwater fungi. The conidial fungi can be further subdivided based on ecology into three main types, aquatic hyphomycetes (Ingold 1942), aeroaquatic hyphomycetes (Voglmayr & Delgado-Rodríguez 2001, Voglmayr 2004, Voglmayr & Yule 2006) and submerged aquatic hyphomycetes (Goh & Hyde 1996a, Wong et al. 1998, Tsui et al. 2016). A fourth asexual type producing conidiomata, referred to as coelomycetes (Magaña-Dueñas et al. 2021), is also found on submerged wood and herbaceous material in fresh water, albeit their occurrence is sporadic.

The sexual states of freshwater fungi are most involved in decomposing submerged wood (Shearer & Von Bodman 1983, Zare-Maivan & Shearer 1988a), while mitosporic forms such as the aquatic hyphomycetes are more commonly implicated in decomposing deciduous leaf litter in streams (Bärlocher & Kendrick 1974, Gessner & Van Ryckegem 2003, Gulis et al. 2009, Bärlocher 2016). Since numerous details such as definition, species numbers, systematics, collection, and isolation of freshwater fungi were recently reviewed, they will not be covered in-depth herein (Raja et al. 2018, El-Elimat et al. 2021).

Although the species numbers have dramatically increased in the last 30-40 years, little is known about the secondary metabolites (small molecules) from this ecological group of fungi. From the perspective of chemistry, both sexual and asexual states biosynthesize interesting chemical diversity of bioactive compounds.

Natural products chemistry has contributed over 500,000 secondary metabolites to organic chemistry with approximately 70,000 isolated from microbes (Bills & Gloer 2016). Among those, about 15,600 are of fungal origin. Approximately, 280 compounds are isolated from freshwater ascomycetes (El-Elimat et al. 2021). This is a very small fraction of the secondary metabolites reported from fungi in general. It is estimated that only 7% of secondary metabolites are known from all described and undescribed fungi (Bills & Gloer 2016). Although fungi are an enormous

source of new bioactive secondary metabolites, freshwater fungi are poorly investigated for this purpose (Gloer 1997, 2007, Hernández-Carlos & Gamboa-Angulo 2011, El-Elimat et al. 2021). One reason for the paucity of secondary metabolites is that few trained experts in this group of fungi have active collaborations with natural products chemists among others. A special focus of this entry, therefore, is a review of antimicrobial compounds from freshwater fungi.

Drug-resistant fungal and bacterial pathogens of humans are on the rise. There is a pressing need to meet the demands of growing microbial pathogens (Fisher et al. 2020, Nnadi & Carter 2021). The ongoing COVID-19 pandemic has only acerbated the need for new antifungal and antibacterial compounds due to the increase of secondary infections among immunocompromised patients (Fung & Babik 2021, Ripa et al. 2021). In addition, antimicrobial drugs are losing their effectiveness due to the evolution of pathogen resistance (Nnadi & Carter 2021). Thus, it is imperative to search for new antimicrobial compounds. The freshwater fungi are amenable to the discovery of new antimicrobial compounds since they regularly co-occur with other fungi and bacteria on submerged substrates (Shearer & Zare-Maivan 1988, Shearer et al. 2004).

There are three main goals in this entry: (1) highlighting the chemical structures of all antimicrobial compounds isolated from freshwater fungi with notes on the most active chemical entities that have been described; (2) providing insights into the methodology for chemical analysis of freshwater fungi and their bioactive secondary metabolites; and (3) comparing the chemical diversity and chemical space of the antimicrobial compounds from freshwater fungi and the FDA approved antimicrobial drugs. An overarching goal is to kindle interest in the discovery of new antimicrobial compounds of drug leads from freshwater fungi that could combat antibiotic and antifungal resistance.

Antimicrobial compounds from freshwater fungi

The discovery and clinical use of antimicrobial drugs revolutionized infectious disease control and contributed to the health and well-being of humankind (Travis et al. 2018, Hyde et al. 2019). Although the first antimicrobial drugs were discovered by chemical synthesis (e.g., arsphenamine and sulfa drugs), they were surpassed by more potent antibiotics from nature (e.g., penicillins, tetracyclines, macrolides, aminoglycosides, and cephalosporins) (Wright et al. 2014). However, many of these first-line defense weapons lost their effectiveness due to the emergence of resistant strains due to the overuse of antibiotics and the evolution of microbial resistance (Davies & Davies 2010, Wright et al. 2014, Travis et al. 2018).

Most antimicrobial scaffolds that were developed into drugs and are in clinical use today were discovered from natural products during the golden age of antibiotics (1950-1960) (Davies & Davies 2010, Brown & Wright 2016, Travis et al. 2018). Most subsequent efforts focused on medicinal chemistry for the preparation of new derivatives of the natural lead compounds to optimize activity and to combat resistance (Brown & Wright 2016, Travis et al. 2018). Many resistant pathogenic strains are being isolated in clinical settings implying the entrance of the post-antibiotic era. Unfortunately, modern drug discovery programs failed to uncover new antimicrobials of clinical significance (Brown & Wright 2016). Hence, to avoid any future global crisis due to resistance, there is an urgent need to find innovative methods and to explore other ways to discover new antimicrobial scaffolds. Exploring new ecological niches such as the freshwater ecosystem, specifically freshwater fungi could furnish novel antimicrobials.

Background of previous work

The first study of a secondary metabolite isolated from freshwater fungi was quinaphthin, an antibacterial compound against gram-positive bacteria, which was isolated from an aeroaquatic hyphomycetes *Helicoon richonis* (strain SY 034843) (Fisher et al. 1988). Since then, several other mycologists have studied and screened freshwater fungi against other microbial species but none of these studies isolated and identified the active chemical entities responsible for the antimicrobial activity (Fisher & Anson 1983, Gulis & Stephanovich 1999, Wai et al. 2003, Arya & Sati 2011, Pant & Sati 2021).

Ecology based strategies for isolation of antimicrobial compounds from freshwater fungi

It was not until the work of Gloer and Shearer and their students and colleagues that there was a spike in the identification and isolation of antimicrobial compounds from freshwater fungi (Poch et al. 1992, Harrigan et al. 1995, Gloer 1997, Oh et al. 1999a, b, 2001, 2003, Li et al. 2003, Reátegui et al. 2005, Jiao et al. 2006a, b). These studies laid the foundation for isolating interesting secondary metabolites from freshwater fungi using an ecological approach. It is widely accepted that natural products play important roles in the ecology of many different types of microorganisms. Principles of chemical ecology suggest that slow-growing fungi inhabiting competitive niches, or those that produce long-lived fruiting structures, would experience considerable evolutionary pressure to produce antagonistic secondary metabolites that could play important ecological roles (Harrigan et al. 1995, Shearer 1995, Fryar et al. 2001, Kusari et al. 2012). Fungal species composition and diversity vary among communities in different freshwater habitats (Raja et al. 2009, 2018, Hyde et al. 2016a). Studies by Shearer and colleagues, including others, have shown freshwater species can display interspecific competition and antagonistic effects against competing fungi (Shearer & Zare-Maivan 1988, Asthana & Shearer 1990, Yuen et al. 1999, Fryar et al. 2005). These observations from the field can be used as hypotheses to isolate secondary metabolites from freshwater fungi. Many new chemical structures with antimicrobial activities have been published based on the theme of ecology as a rationale for screening (see studies by Gloer and Shearer et al.).

Which substrate is better for isolating antimicrobial metabolites from freshwater fungi?

According to Shearer and Zare-Maivan (1988), wood-dwelling (lignicolous) freshwater sexual ascomycetes and asexual hyphomycetes are more antagonistic than leaf-dwelling (foliicolous) species because long-lasting substrates, such as submerged woody debris, favor colonization by species that are capable of defending their captured substrate by the production of antimicrobial compounds (Gloer 1995, 2007, Gulis & Stephanovich 1999). Based on these studies, it seems logical that lignicolous freshwater fungi are an obvious candidate for the isolation of antimicrobial compounds. Sexual ascomycetes, as well as the asexual fungi (aquatic, aeroaquatic, and submerged aquatic hyphomycetes, and coelomycetes), can occur on submerged woody substrates (Shearer 1992, Shearer et al. 2007, Shearer & Raja 2013). These species belong to different phylogenetic lineages such as Dothideomycetes, Sordariomycetes, and the Leotiomycetes (Belliveau & Bärlocher 2005, Luo et al. 2019, Dong et al. 2020b). Thus, the collection and isolation of freshwater fungi from submerged wood provides a large diversity of freshwater fungi species. The biodiversity of freshwater fungi at these diverse taxonomic levels should lead to a diversity of secondary metabolic pathways. This is because diversity in morphological traits among species of freshwater fungi may indicate that substantial variation also exists in this group in the production of metabolites associated with substrate decomposition and bioactivity. The work of Shearer in collaboration with Gloer on bioactive compounds from freshwater fungi supports this hypothesis (Harrigan et al. 1995, Gloer 1997, 2007, Oh et al. 1999a, b, 2001, Li et al. 2003, Reátegui et al. 2005, Jiao et al. 2006b, Mudur et al. 2006, Hosoe et al. 2010). Since few freshwater fungi have been screened, we encourage all future work to focus on as many habitats and substrate types as possible for isolation of freshwater fungi and subsequent bioassay and extraction of bioactive antimicrobial metabolites. As more freshwater fungi are screened and secondary metabolites are identified, a pattern will hopefully emerge that will guide further studies.

Methods in antimicrobial drug discovery from freshwater fungi

Methods in antimicrobial drug discovery from freshwater fungi consist of three main stages (Fig. 23): (1) the mycology stage: includes the collection of freshwater fungi, isolation, molecular identification, and culturing; (2) the chemistry stage: involves culture extraction, fungal secondary metabolites purification, and structural identification; and (3) the microbiology stage: encompasses *in vitro* methods for evaluating the antimicrobial activity of the isolated natural compounds. In the subsequent sections, the chemical and microbiological methods will be briefly reviewed. The

mycology methods have been covered previously (Shearer 1993, Shearer et al. 2004, El-Elimat et al. 2021).

Extraction, isolation, and identification of fungal natural products

Mapping secondary metabolites of fungal cultures in situ

Freshwater fungi grown in Petri dishes can be analyzed *in situ* for natural products using ambient ionization mass spectrometry such as desorption electrospray ionization (DESI), laser ablation electrospray ionization (LAESI), and the droplet-liquid microjunction-surface sampling probe (Sica et al. 2015, Oberlies et al. 2019). Such techniques can be used for the tentative identification of certain compounds *in situ* for dereplication purposes (El-Elimat et al. 2013). However, conventional methods, including extraction, purification, and structural elucidation are inevitable for any promising culture with potent activity and potential new chemistry.

Extraction of fungal cultures

Extraction involves the separation of the bioactive portions of the biomass from the inert components using selective solvents in standard extraction procedures (Kumar 2015, Nabavi et al. 2020). Many extraction methods are available and can be divided into four major types: solvent extraction, solid-phase extraction, supercritical fluid extraction, and ultrasonic-assisted extraction (Nabavi et al. 2020). Solvent extraction can be achieved using maceration, digestion, decoction, and percolation (Nabavi et al. 2020).

Cold maceration is the simplest among the listed solvent extraction techniques. In this method, the biomass is transferred into a flask and extracted sequentially at room temperature with a set of solvents of increased polarity (Heinrich et al. 2017). The potential for the degradation of natural compounds is minimal as no heat is utilized (Heinrich et al. 2017). Digestion is a form of maceration except gentle heat is used. In the decoction method, the biomass is boiled with water. This procedure is suitable for extracting water-soluble, heat-stable natural compounds. In percolation, the biomass is moistened with a proper volume of solvent and allowed to stand at room temperature for few hours. Additional solvent is then added to make a shallow layer above the biomass and the mixture is then left to macerate in the closed percolator for 24 h. The stopcock of the percolator is then slightly opened, and the solvent is allowed to drip slowly.

In the solid-phase extraction technique, the solutes were adsorbed into a solid adsorbent. The solid adsorbents came in the form of syringes or cartridges filled with beads or resins (Nabavi et al. 2020). The biomass in liquid form is forced through the cartridge under pressure or by pressing using a plunger. Purification of the biomass involves cycles of washing and elution with proper mobile phases (Nabavi et al. 2020).

Supercritical fluid extraction involves the use of certain gases at certain temperatures and pressure above their critical points. At such conditions, they behave as liquids and have solvating properties (Kumar 2015, Heinrich et al. 2017). The most used gas as an extracting fluid is carbon dioxide (Heinrich et al. 2017). It is safe, cheap, and abundant. Supercritical fluid extraction is a non-destructive extraction procedure, environmentally friendly with no solvent residues (Kumar 2015, Heinrich et al. 2017).

Ultrasonic-assisted extraction involves the use of an ultrasonic bath. The biomass is crushed and mixed with a solvent and placed in the ultrasonic bath at a specified temperature (Kumar 2015, Nabavi et al. 2020). The ultrasound waves (> 20 kHz) disrupt the cell wall of the biomass and facilitate the penetration of the solvent through the cells (Kumar 2015, Nabavi et al. 2020).

Regardless of the utilized method of extraction, the polarity of the solvents used is important. Lipophilic extracts will be obtained when using nonpolar solvents such as ethyl acetate, chloroform, and dichloromethane. Hydrophilic extracts will be obtained when using polar solvents such as acetone, methanol, and ethanol. Aqueous organic solvents are commonly used such as 70-90% ethanol and 80% methanol.

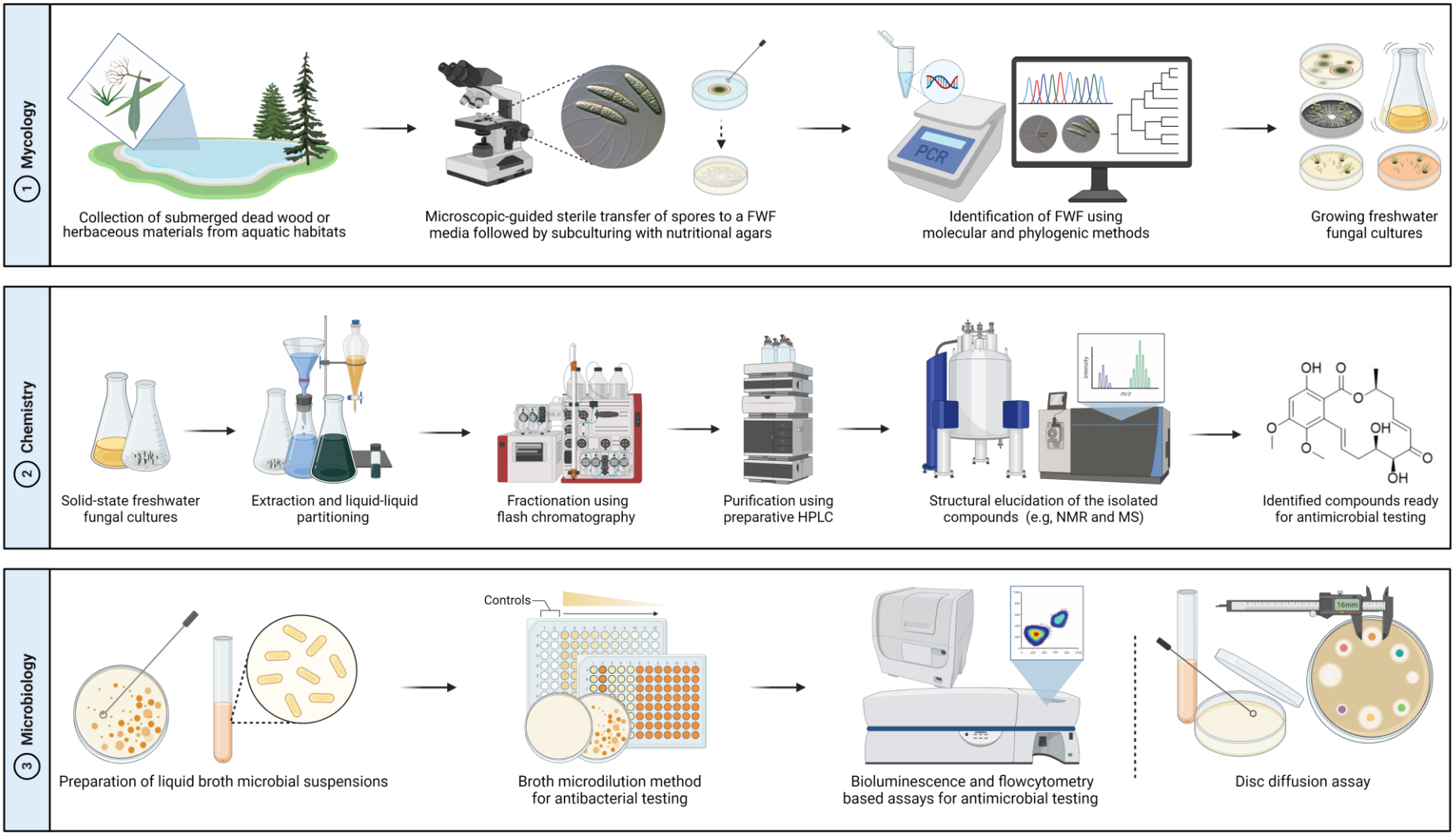


Figure 23 – Methods in antimicrobial drug discovery from freshwater fungi.

Elevated temperatures should be avoided during the extraction when data about the stability of the natural compounds in the biomass are lacking. Literature is replete with various extraction schemes that were developed by many research groups all over the world for certain classes of compounds, such as alkaloids.

The liquid extracts are then concentrated by evaporating the solvents under reduced pressure using rotary evaporators. The aliquots are then transferred into screw cap vials and left to dry under a stream of liquid nitrogen. Dried extracts are stored refrigerated until required for analysis and further purifications. For complete and efficient drying of aqueous extracts, they are freeze-dried or lyophilized.

Fractionation and purification

Once the extracts are prepared and completely dried, they are subjected to antimicrobial testing using one of the assays outlined in the next section. The extracts to show promising activity are subjected to bioactivity-guided fractionation. Only fractions with potent activity will be further purified.

One of the conventional purification processes is the sequential liquid-liquid partitioning of the extracts using two immiscible solvents of increasing polarity (Kumar 2015, Heinrich et al. 2017). For example, the use of water and hexane to separate fatty and non-polar residues, followed by partitioning with chloroform or ethyl acetate. The residual aqueous layer contains sugars and highly polar compounds (Kumar 2015, Heinrich et al. 2017).

Chromatographic methods are widely used for the purification of the active extracts. The most used techniques are column chromatography or flash chromatography, followed by preparative high-performance liquid chromatography (HPLC) (Heinrich et al. 2017). Every active fraction will go through several cycles of chromatographic purifications until one single pure compound as evidenced by analytical HPLC or ultra-performance liquid chromatography (UPLC) or by ^{1}H nuclear magnetic resonance (NMR).

Column chromatography is a versatile chromatography technique used for the separation and purification of components in a liquid mixture by interaction with a stationary phase (Smith 2004). The mixture moves through the column using eluents (mobile phase) of increased polarity. Different types of stationary phases are available that widen the application of the technique (Smith 2004). It is easy and cheap; however, it is a time-consuming technique. Flash chromatography is an automated form of column chromatography, where the mixture of components is forced to move through the stationary phase (the column) by pressure (Stevenson 2004). HPLC is an instrumental technique widely used for the identification and purification of bioactive natural compounds (Lundanes et al. 2013). It is commonly coupled with an ultraviolet-visible (UV-vis) or a photodiode array (PDA) detector (Lundanes et al. 2013). It has the capability of separating a mixture of compounds in a liquid medium depending on their interaction with a stationary phase. The column in the HPLC system is packed with versatile types of stationary phases that can be used to purify a wide array of natural compounds (Lundanes et al. 2013). The HPLC system operates at higher flow rates and higher pressure than flash chromatography. There are two types of HPLC in use, analytical and preparative. Analytical HPLC is used for the analysis and identification of compounds in small volumes and the analyzed sample is then discarded into the waste (Lundanes et al. 2013). In preparative HPLC, the system is used to purify a mixture of components in higher volumes, and the purified components in solution are then collected in separate tubes (Lundanes et al. 2013). HPLC coupled with mass spectrometry (HPLC-MS) (Lundanes et al. 2013) is now widely used as a standard analytical tool for the analysis, quantification, and dereplication of natural compounds.

Structural identification

The structure of the isolated pure compounds is then elucidated by collecting mutually supportive data using the following analytical techniques: NMR spectroscopy, MS, infrared (IR) spectroscopy, UV-vis spectroscopy, and X-ray crystallography (Nabavi et al. 2020).

NMR is a powerful analytical technique that allows nondestructive determination of the planar molecular structure of organic compounds (Silverstein et al. 2015). It provides information about the carbon skeleton of a given compound and the hydrogen atoms attached to it (i.e., carbon-hydrogen and carbon-carbon connectivity). It can be used as well for the determination of the relative (*cis*-*trans* and axial/equatorial isomerism) and absolute (*R*/*S*) configuration of organic compounds. There are two types of NMR experiments, 1D and 2D. The basic 1D NMR experiments include ^{1}H NMR that offers information about chemical shifts, coupling constants, and integrals of protons; the ^{13}C NMR provides information about the chemical shift and carbon atoms count; and the distortionless enhancement by polarization transfer (DEPT) NMR, which gives information about carbon-hydrogen connectivity via multiplicity determination (Silverstein et al. 2014). There are a plethora of 2D NMR experiments, but the most used for organic structure determination are ^{1}H-^{1}H COSY (correlated spectroscopy; *J*-coupling relationships between protons), ^{1}H-^{13}C HSQC (heteronuclear single quantum coherence; carbon multiplicities), ^{1}H-^{13}C HMBC (heteronuclear multiple bond correlation; correlations identified over two and three bonds), and ^{1}H-^{1}H NOESY (nuclear Overhauser effect spectroscopy; stereochemical analysis; configuration and conformation) (Silverstein et al. 2014).

MS is a highly sensitive yet destructive analytical technique that is used for the calculation of the mass-to-charge (*m*/*z*) ratio of molecules (Gross 2017). Such data can then be used to calculate the exact molecular weight, from which the molecular formula can be established (i.e., number and types of atoms) (Gross 2017).

IR spectroscopy is used in the realm of organic structure determination to detect the presence or absence of key functional groups (Silverstein et al. 2014). However, UV-vis spectroscopy examines the electron distribution in molecules, especially those bearing conjugated electron systems (Hattori et al. 1998).

Finally, X-ray crystallography is the most powerful among the analytical techniques described above. It determines the atomic and molecular structure of a crystal (Jones 2014). Hence, the rate-limiting step is obtaining a single crystal of the compound that is suitable for X-ray crystallography analysis.

In vitro methods for evaluating antimicrobial activity

Different antimicrobial susceptibility testing methods are available for *in vitro* evaluation of the antimicrobial activity of extracts, fractions, and pure compounds of natural compounds (Balouiri et al. 2016). The most used methods are disc diffusion and broth dilution methods (Balouiri et al. 2016). For in-depth investigation of the antimicrobial activity of a given compound, advanced methods such as bioluminescent and flow cytofluorometric methods are also being used (Balouiri et al. 2016).

Diffusion methods

The agar disk diffusion method is routinely used to test for antimicrobial susceptibility (Schumacher et al. 2018). Standard and approved procedures are published by the Clinical and Laboratory Standards Institute (CLSI) for microbial testing (Clinical and Laboratory Standards Institute). Briefly in this method, agar Petri dishes are inoculated with the test microorganism. Then a small filter paper disc with a diameter of about 6 mm containing the test compound is placed over the surface of the agar plate and left to incubate. Antimicrobial compounds will diffuse through the agar and inhibit the growth of the test microorganism. The diameter of the inhibition zone is then measured (Schumacher et al. 2018).

Other diffusion methods that can be used for testing extracts, fractions, and pure compounds of natural origin include the antimicrobial gradient method, agar well diffusion method, agar plug diffusion method, cross streak method, and poisoned food method (Balouiri et al. 2016).

Dilution methods

Broth or agar dilution methods are routinely used to estimate the minimum inhibitory concentration (MIC) values of the antimicrobial compounds against bacteria or fungi (Balouiri et al. 2016, Schumacher et al. 2018). MIC value is defined as the lowest concentration of the antimicrobial compound that inhibits the visible growth of the tested microorganism. Standard and approved bioassay procedures for the dilution methods that are published by the CLSI can be used to evaluate the clinical significance of the obtained results (Clinical and Laboratory Standards Institute).

ATP bioluminescence assay

ATP bioluminescence assay is based on the quantification of ATP to estimate the concentration of bacteria in a sample (Hattori et al. 1998). D-luciferin is converted by luciferase in presence of ATP into oxyluciferin that emits light (Hattori et al. 1998, Balouiri et al. 2016). The emitted light is measured by a luminometer, where there is a linear correlation between cell count and the light intensity (Hattori et al. 1998).

Flow cytometry

Flow cytometry can be used for antimicrobial susceptibility testing of natural compounds (Green et al. 1994, Álvarez-Barrientos et al. 2000, Balouiri et al. 2016). Damaged cells are detected using DNA dyes such as propidium iodide (Green et al. 1994, Álvarez-Barrientos et al. 2000). The use of this method is limited due to the inaccessibility of the flow cytometer in most laboratories (Álvarez-Barrientos et al. 2000).

Review of antimicrobial compounds from freshwater fungi

Natural products from fungi are both a unique source of new chemical diversity and an integral component of today's pharmacological arsenal. Compounds from freshwater fungi are not excluded, and they have shown a wide chemical diversity and a broad range of biological activities (El-Elimat et al. 2021). Over 100 natural products with antimicrobial properties have been isolated from freshwater fungi. Their structure, sources, and biological targets are shown in Figures 24–26 and Table 5 In the following paragraphs, a series of freshwater fungi compounds with significant antimicrobial activity against drug-resistant infections, fungi, and bacteria, are reviewed and discussed.

Amniculicola longissima (≡ *Anguillospora longissima*) (strain CS-869-1A)

The freshwater fungus *Amniculicola longissima* was chemically investigated as part of a systematic study by Gloer's research group to discover new biologically active natural products with antagonistic effects on bacteria and fungi (Harrigan et al. 1995). The original culture of *A. longissima* was isolated and taxonomically classified by Shearer and collaborators from birchwood baits placed in Jordan Creek (freshwater stream), a tributary of the Salt Fork River, Vermillion County, Illinois, USA. From 2 L of liquid culture of the fungus grown on potato dextrose broth (PDB) for 26 days at 150 rpm, an EtOAc extract of the culture filtrate was obtained and subjected to C_{18} semi-preparative HPLC separation. The polyketide derivative anguillosporal (**4**) was isolated as a pale-yellow oil (8 mg) and its structure was deduced using classical NMR and MS analysis, although its absolute configuration was not established (Fig. 24).

The structure of this compound is relatively unusual, and the naphthoquinones bearing an ethyl branch on the polyketide chain are proposed to be formed from the reduction of an acetyl substituent originated from acetyl-CoA. Interestingly, **4** was the only active component isolated, with MIC values of 4 μg/mL against *S. aureus* (ATCC 29213) and 58 μg/mL against *C. albicans* (ATCC 90029) (Harrigan et al. 1995). Until now, this compound is the only secondary metabolite reported from a member of the genus *Anguillospora*.

Decaisnella thyridioides (strain A-00267-2A)

From submerged decorticated wood collected in the Lemonweir River in Wisconsin, USA, the freshwater fungus *Decaisnella thyridioides* was isolated (Jiao et al. 2006b). Then, ascospores of this strain were inculcated onto rice media (250 g) and incubated for five weeks at 25 °C under 12/12 h light-dark periods. Subsequently, an EtOAc extract from the fermentation mixture was obtained. This extract showed significant antifungal activity in disk assay against *Nectria* spp., *Candida albicans*, and *Aspergillus flavus*. Chemical study of the active extract led to the isolation of active decaspirones A (**30**) and C (**31**), along with three analogs (decaspirones B, D, and E) and palmarumycin CP1 (Fig. 24). Interestingly, decaspirones possess a *trans*-decalin system instead of

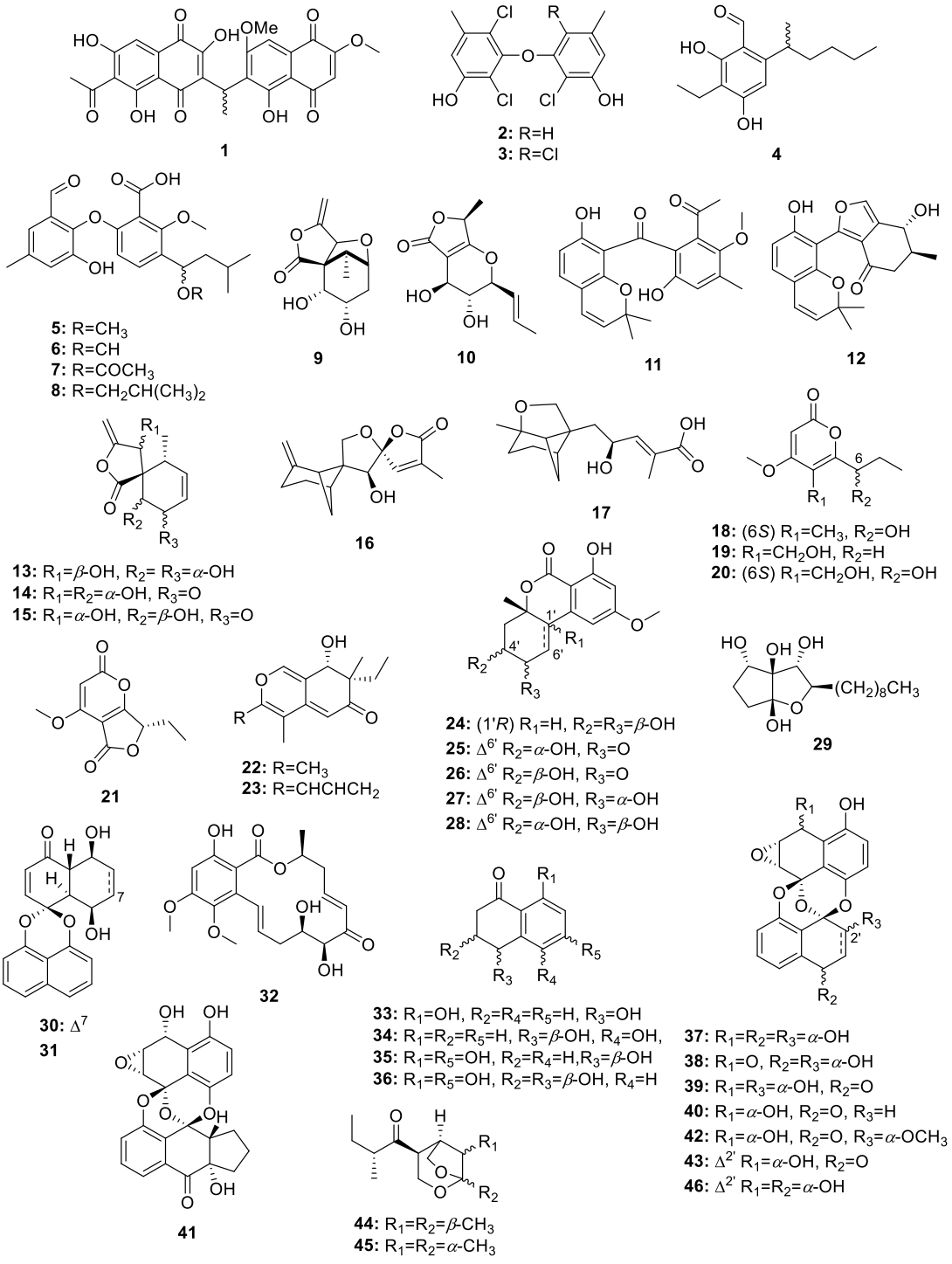


Figure 24 – Chemical structure of compounds 1–46.

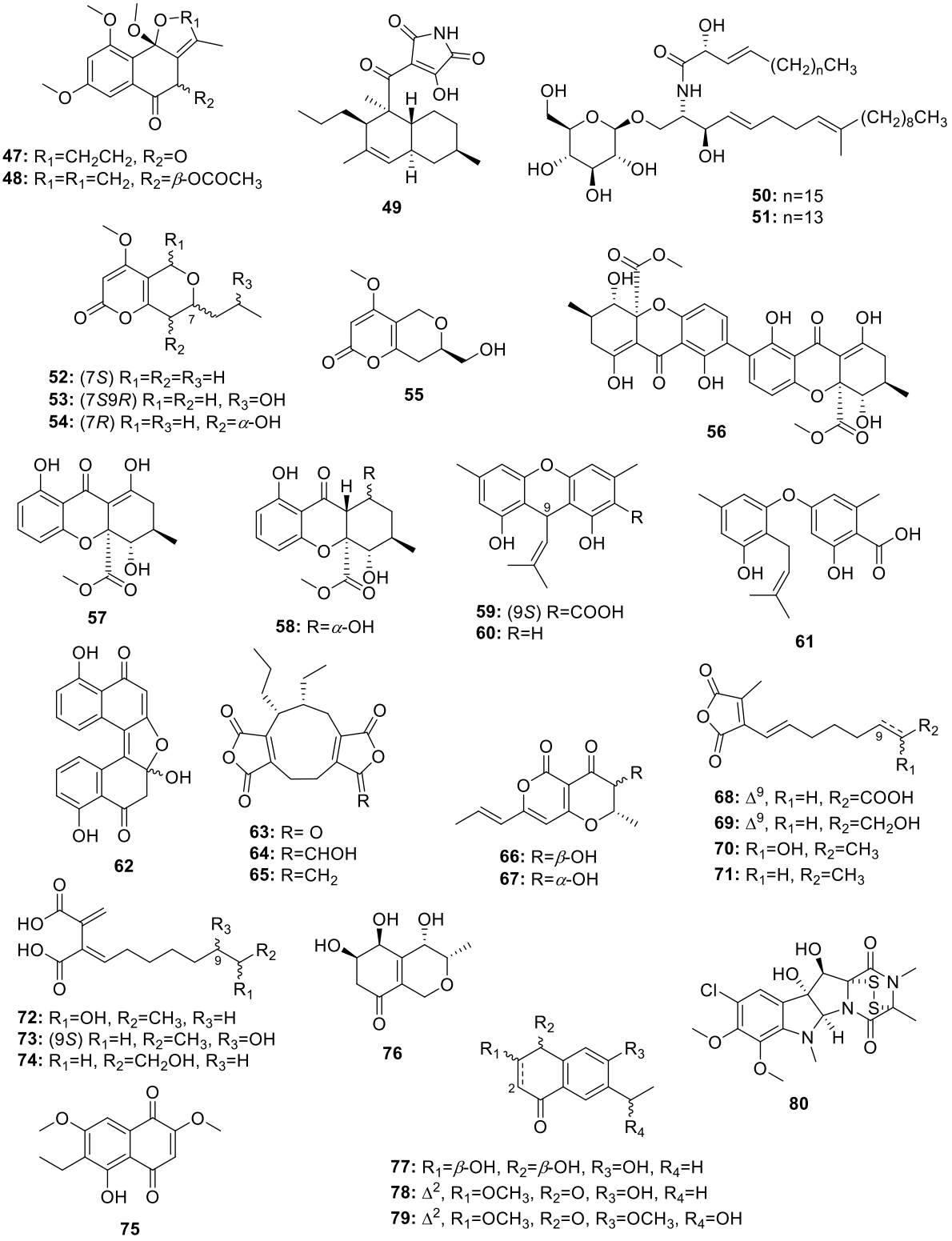


Figure 25 – Chemical structure of compounds 47–80.

a modified *cis*-decalin moiety as in the related spirodioxynaphthalenes, which includes thepalmarumycins, cladospirones, and diepoxins, among others. In general, these compounds contain a unique 1,8-dioxynaphthalene moiety linked to another portion of the molecule via a spiroketal carbon.

All decaspirones showed significant antibacterial activity against *B. subtilis* (ATCC 6051) when tested at 50 μg/disk in the disk diffusion assay. In addition, **30** was active against *S. aureus* (ATCC 29213) showing a 41 mm of inhibition when tested at 100 μg/disk. Finally, **30** and **31** displayed

MIC values against *A. flavus* (NRRL 6541) and *F. verticillioides* (NRRL 25457) of 10 and 5 μg/mL, and 25 and > 25 μg/mL, respectively (Jiao et al. 2006b). Here is yet another example where a poorly studied fungus, *D. thyridioides* afforded new chemistry in the form of these interesting spirodioxynaphthalenes analogues. To date, no other chemical studies on freshwater fungi belonging to the genera *Decaisnella* have been reported.

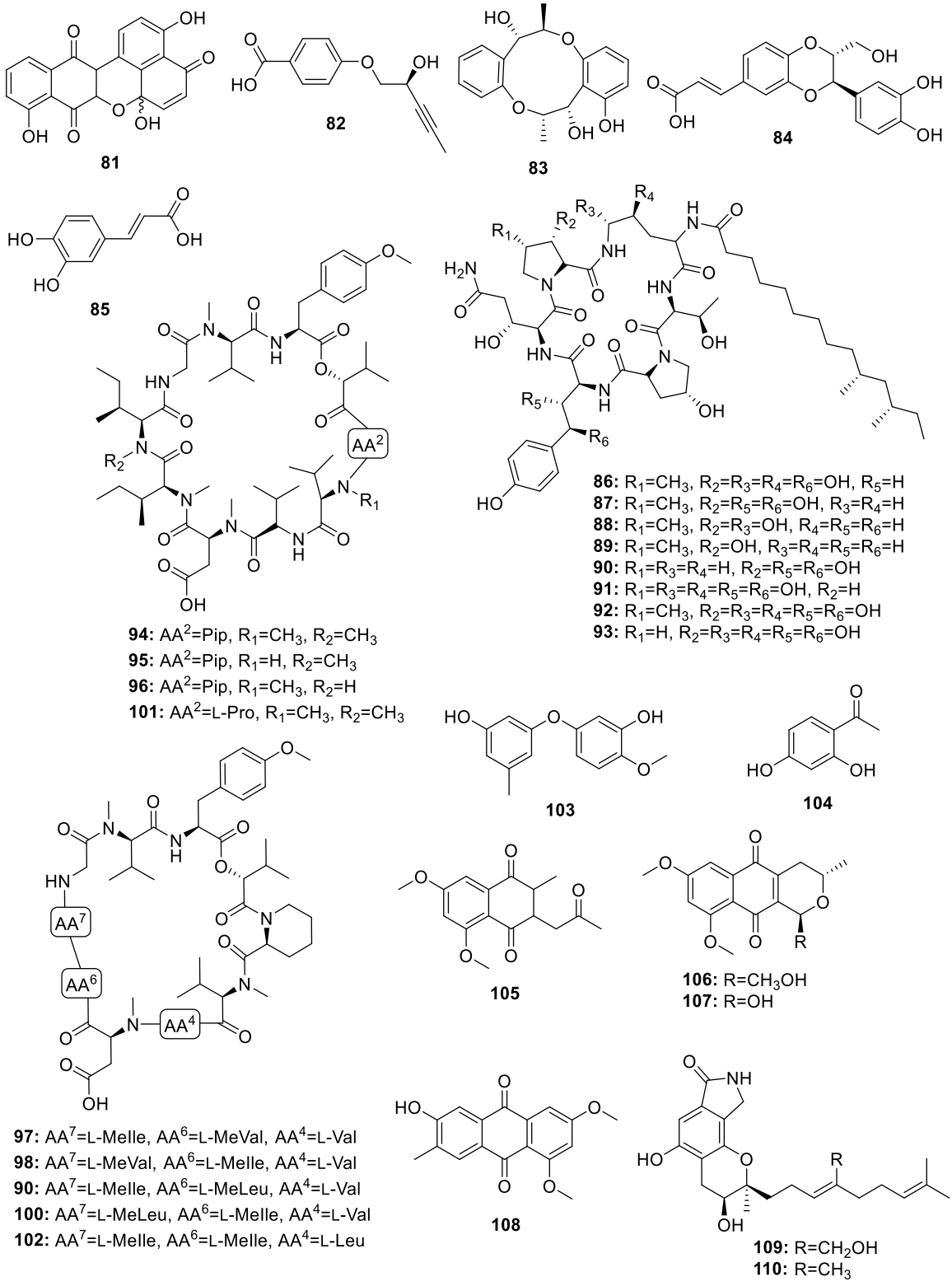


Figure 26 – Chemical structure of compounds 81–110.

Table 5 Antimicrobial metabolites from freshwater fungi.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
Kirschsteiniothelia sp. (strain C-76-1)	– Kirschsteinin (**1**) – 2,6-Dichloro,3-hydroxy,5-methyl-(2´chloro, 3´-hydroxy,5´-methyl) phenoxy benzene (**2**) – 2,6-Dichloro,3-hydroxy,5-methyl-(2´,6´-dichloro,3´-hydroxy,5´-methyl) phenoxy benzene (**3**)	– **1:** Antibacterial activity against *B. subtilis* and *S. aureus* in standard disk assay at 1 and 10 μg/disk, respectively. – **2** and **3:** Antibacterial activity against *B. subtilis* and *S. aureus* in standard disk assay at 5 and 1 μg/disk, respectively.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Anguillospora longissimi (strain CS-869-1A)	– Anguillosporal (**4**)	– MIC values of 4 and 58 μg/mL against *S. aureus* (ATCC 29213) and *C. albicans* (ATCC 90029), respectively.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Dendrospora tenella (strain CCM F-10787)	– Tenellic acids A-D (**5-8**)	– **5-8:** Antibacterial activity against *B. subtilis* (ATCC 6051) with inhibitory zones of 11, 9, 12, and 29 mm, respectively, in standard disk assay at 200 μg/disk. – **7** and **8:** Antibacterial activity against *S. aureus* (ATCC 29213) with inhibition zones of 14 and 25 mm, respectively, in standard disk assay at 200 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Massarina tunicata (strain A-25-1)	– Massarilactones A (**9**) and B (**10**) – Massarinins A (**11**) and B (**12**) – Massarigenins A (**13**), C (**14**), and D (**15**) – Massarinolins A (**16**) and B (**17**)	– **9-17:** Antibacterial activity against *B. subtilis* (ATCC 6051) with inhibitory zones of 19, 16, 17, 23, 11, 9, 14, 17, and 8 mm, respectively, in standard disk assay at 200 μg/disk. – **10-12** and **16:** Antibacterial activity against *S. aureus* (ATCC 29213) with inhibitory zones of 7, 12, 12, and 10 mm, respectively, in standard disk assay at 200 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Annulatascus triseptatus (strain A-353-1B)	– Annularins A-C (**18-20**) and F (**21**)	– **18-21:** Antibacterial activity against *B subtilis* (ATCC 6051) with inhibitory zones of 8-10 mm in standard disk assay at 200 μg/disk. – **20**: Antibacterial activity against S. aureus (ATCC 29213) with an inhibitory zone of 14 mm in standard disk assay at 200 µg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Pseudohalonectria adversaria (strain	– Pseudohalonectrins A (22) and	– **22-23**: Nematicidal activity against	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)

Table 5 Continued.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
YMF1.01019)	B (23)	*Bursaphelenchus xylophilus*.	
Unidentified species in the family *Tubeufiaceae* (strain A-00471)	– Dihydroaltenuene A (**24**) – Dehydroaltenuenes A (**25**) and B (**26**) – Isoaltenuene (**27**) – Altenuene (**28**)	– **24, 26,** and **28:** Antibacterial activity against *S aureus* (ATCC 29213) with inhibitory zones of 14, 14, and 18 mm in standard disk assay at 100 μg/disk. – **24-28:** Antibacterial activity against *B. subtilis* (ATCC 6051) with inhibitory zones of 50, 13, 20, 30, and 20 mm, respectively, in standard disk assay at 100 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Helicodendron giganteum (strain CS988-1B)	– Heliconol A (**29**)	– Antifungal activity against *F. verticillioides* (NRRL 25457) and *C. albicans* (ATCC 14053) with inhibitory zones of 15 mm (*F. verticillioides*) and 10 and 18 mm (*C. albicans*) in standard disk assay at 200, 25, and 100 μg/disk, respectively. – Antibacterial activity against *S. aureus* (ATCC 29213), and *B. subtilis* (ATCC 6051) with inhibitory zones of 23 and 35 mm, respectively, in standard disk assay at 100 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Decaisnella thyridioides (strain A-00267-2A)	– Decaspirones A (**30**) and C (**31**)	– **30:** Antibacterial activity against *S. aureus* (ATCC 29213) with an inhibitory zone of 41 mm of inhibition when tested at 100 µg/disk in standard disk assay. – **30** and **31:** Antibacterial activity against *B. subtilis* (ATCC 6051) when tested at 50 μg/disk in the disk diffusion assay. – **30** and **31:** MIC values of 10 and 5 μg/mL, and 25 and > 25 μg/mL, respectively, against *A. flavus* (NRRL 6541) and *F. verticillioides* (NRRL 25457).	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Caryospora callicarpa (strain YMF1.01026)	– Caryospomycin C (32) – (4RS)-4,8-Dihydroxy-3,4-dihydronaphthalen-1(2H)-one (33) – 4,5-Dihydroxy-3,4-	– **32-36:** Nematicidal activity *against B. xylophilus*.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)

Table 5 Continued.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
	dihydronaphthalen-1(2H)-one (34) – 4,6,8-Trihydroxy-3,4-dihydronaphthalen-1(2H)-one) (35) cis-4-Hydroxyscytalone (36)		
Unidentified species (strain YMF 1.01029)	– (4*RS*)-4,8-dihydroxy-3,4-dihydronaphthalen-1(2H)-one (**33**) – 4,6,8-trihydroxy-3,4-dihydronaphthalen-1(2H)-one) (**35**) – YMF 1029 A-E (**37-41**) – Preussomerins C (**42**) and D (**43**) – Colomitides A (**44**) and B (**45**) – Preussomerin E (**46**) – Colelomycerones A (**47**) and B (**48**)	– **37-43:** Nematicidal activity against *B. xylophilus.* – **43-48:** Antifungal and antibacterial activity against *B. maydis* (YMF 1.2094), *C. sativus* (YMF 1.2088), *F. verticillioides* (YMF 1.2076), *B. subtilis* (YMF 3.19), *B. laterosporus* (YMF 3.08), and *S. aureus* (YMF 3.17) in standard disk assay at 50 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Vaginatispora aquatica (strain HK1821)	– Oxasetin (**49**)	– Antibacterial activity against MRSA (3 strains), vancomycin-resistant *E. faecalis* (2 strains), *S. pneumoniae* (2 strains) with MIC values of 16, 16, and 16-32 μg/mL, respectively.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Paraniesslia sp. (strain YMF1.01400) and unidentified species (strain YMF 1.01029)	– (2*S*,2'*R*,3*R*,3'*E*,4*E*,8*E*)-1-*O*-(□-D-Glucopyranosyl)-3-hydroxyl-2-[*N*-2'-hydroxyl-3'-eicosadecenoyl] amino-9-methyl-4,8-octadecadiene (**50**) – Cerebroside C (**51**)	– **50-51:** Moderate nematicidal activities against *B. xylophilus.*	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Clohesyomyces aquaticus (strain G100) and *Clohesyomyces* sp. (strain G102)	– Phomopsinone A (**52**) and B (**53**) – 6-Hydroxy-7-*epi*-phomopsinone A (**54**) – Pyrenocine P (**55**) – Secalonic acid A (**56**) – 8-Hydroxyblennolide H (**57**) – cis-Dihydro-8-hydroxyblennolide H (58)	– **52-58:** Moderate inhibition of *Salmonella typhimurium* bacterial peptidyl-tRNA hydrolase (Pth1)	El-Elimat et al. (2021)
Helotiales sp. (strain G730)	– Leotiomycenes A-C (59-61)	– **59-61**: Inhibition of the production of AIP (autoinducing peptide) by the MRSA strain	El-Elimat et al. (2021)

Table 5 Continued.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
		AH1263 with IC50 values ranging from 0.3 to 12.5 μM. (quorum sensing inhibitors).	
	–	–	
Minutisphaera parafimbriatispora (strain G156-4) and *M. aspera* (strain G427)	– Sphaerolone (**62**)	– Moderate activity against *S. aureus* and *Mycobacterium smegmatis* with MIC values of 86 and 172 μM, respectively.	El-Elimat et al. (2021)
Wicklowia aquatica (strain F76-1)	– Epiheveadride (**63**) – Deoxoepiheveadride (**64**) – Dihydroepiheveadride (**65**)	– **63-64:** Antifungal activity against *F. verticillioides* (NRRL2545) – **65:** Antifungal activity against *F. verticillioides* (NRRL2545) and *A. flavus* (NRRL6541).	El-Elimat et al. (2021)
Xylomyces chlamydosporus (strain H58-1)	– Radicinin (**66**) – 3-*epi*-Radicinin (**67**)	– **66-67:** Antifungal activity against *F. verticillioides* (NRRL 25457).	El-Elimat et al. (2021)
Tricladium castaneicola (strain AJ117567)	– Tricladolides A-D (**68-71**) – Tricladic acids A-C (**72-74**)	– **68-74:** Antifungal activity against *Phytophthora* sp.	El-Elimat et al. (2021)
Delitschia corticola (strain YMF 1.01111)	– 6-Ethyl-2,7-dimethoxyjuglone (**75**) – (3*S**,4*S**,5*S**,6*R**)-4,5,6-Trihydroxy-3-methyl-3,4,6,7-tetrahydro-1H-isochromen-8 (5H)-one (**76**) – (3*R**,4*S**)-7-Ethyl-3,4,6,8-tetrahydroxy-3,4-dihydronaphthalen-1(2H)-one (**77**) – 6-Ethyl-7-hydroxyl-2-methoxyjuglone (**78**) – 6-(1-Hydroxyethyl)-2,7-dimethoxyjuglone (**79**) – Sporidesmin A (**80**)	– **75:** Antifungal activity against *Fusarium* sp. YMF 1.01996. – **76:** Antifungal activity against *Alternaria* sp. YMF 1.01991, *Sclerotium* sp. YMF 1.01993, *Fusarium* sp. YMF 1.01996, *Gibberella saubinetii* YMF 1.01989, and *Colletotrichum* sp. YMF 1.01994. – **75-80:** Antifungal activity against *B. cereus* YMF 3.19, *B. laterosporus* YMF 3.08, and *S. aureus* YMF 3.17. – **77-79:** Antifungal activity against *Alternaria* sp. YMF 1.01991. – **78:** Antifungal activity against *Sclerotium* sp. YMF 1.01993. – **80:** Antifungal activity against *G. saubinetii* YMF 1.01989, *Exserohilum turcicum* YMF 1.01990, *Alternaria* sp. YMF 1.01991, *Rhizoctonia solani*	El-Elimat et al. (2021)

Table 5 Continued.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
		– *Colletotrichum* sp. YMF 1.01994, *Phyllosticta* sp. YMF1.01995, and *Fusarium* sp. YMF 1.01996.	
Helicoon richonis (strain SY 034843)	– Quinaphthin (**81**)	– Antibacterial and antiprotozoal activity against *S. aureus* (NCTC 6571), *β*-haemolytic *Streptococcus* (DE 61), *B. subtilis*, *B. cereus* var. *mycoides*, *K. pneumonia* (NCTC 8172), *H. infiuenzae* (NCTC 4560), *Acholeplasma laidlawii* (NCTC 10116), *Mycoplasma gallisepticum* (NCTC 10115), and *Trichomonas vaginalis.*	El-Elimat et al. (2021)
Massarina tunicata (strain A25-1; ATCC 201760)	– 4-(2-Hydroxy butynoxy benzoic acid (**82**)	– Antibacterial activity against *B. subtilis* (ATCC 6051).	El-Elimat et al. (2021)
Ophioceras dolichostomum (strain YMF1.00988)	– Ophiocerol (**83**) – Isoamericanoic acid A (**84**) – Caffeic acid (**85**)	– **83-85:** Antifungal activity against *E. turcicum* (YMF 1.1990), *Fusarium* sp. (YMF 1.1996), *Paecilomyces lilacinus* (YMF 1.621), *Phyllosticta* sp. (YMF 1.1995), *Alternaria* sp. (YMF 1.1997), *A. niger* (YMF 1.46), *Coleosporium* sp. (YMF 1.2088), and *Colletotrichum* sp. (YMF 1.2099).	El-Elimat et al. (2021)
Glarea lozoyensis	– Pneumocandin A_1-A_4 (**86-89**), B_2 (**90**), C_0 (**91**), A_0 (**92**), and B_0 (**93**)	– **86-93:** Antifungal activity against *Candida* sp. and *Pneumocystis carinii* with ED_{90} values ranging from 0.15 mg/kg to >2.5 mg/kg and from 0.35 mg/kg to >6.0 mg/kg, respectively.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011), El-Elimat et al. (2021)
Clavariopsis aquatica (strain AJ117363)	– Clavariopsins A-I (**94-102**)	– **94-102:** Antifungal activity against *B. cinerea* NBc1, *Magnaporthe oryzae* Ken53-35, *C. orbiculare* 104-T, *F. oxysporum* f. sp. *lycopersici* CK3-1, *A. alternata* M-71, *A. niger* AJ117065, *C. albicans* (IFO 0583 and ATCC 10231) and *A. fumigatus* (AJ117190 and JCM1739) with MIC values ranging from 2-16 μg/mL.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011), El-Elimat et al. (2021)
Camposporium. quercicola (strain YMF1.01300)	– Tenellic acid A (**5**) – Quercilolin (**103**) – 2´,4´-Dihydroxyacetophenone (**104**)	– **5, 103,** and **104:** Antibacterial activity against *B. cereus* YMF 3.19, *B. laterosporus* YMF 3.08, and *S. aureus* YMF 3.17 with inhibitory zones of 16, 15, and 18 mm, 15, 17, and 14 mm, and 19, 13,	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)

Table 5 Continued.

Fungal strain	Isolated compounds	Antimicrobial activity	Reference
		and 16 mm, respectively, in standard disk assay at 200 μg/disk.	
Astrosphaeriella papuana (strain YMF 1.01181)	– Astropaquinones A-C (**105-107**) – 6-hydroxy-2,4-dimethoxy-7-methylanthraquinone (**108**)	– **105-108:** Antifungal and antibacterial activity against *Alternaria* spp. (YMF 1.01991 and YMF 1.01997), *B. cereus* (YMF 3.19), *B. laterosporus* (YMF 3.08), and *S. aureus* (YMF 3.17) in standard disk assay at 50 μg/disk. – **106**: Antifungal and antibacterial activity against *G. saubinetii* (YMF 1.01989), *Phyllosticta* sp. (YMF1.01995), *Fusarium* sp. (YMF 1.01996), and *E. coli* (YMF 3.16) in standard disk assay at 50 μg/disk. – **107:** Antifungal activity against *G. saubinetii* (YMF 1.01989), *Colletotrichum* sp. (YMF 1.01994), *Phyllosticta* sp. (YMF 1.01995), and *Fusarium* sp. (YMF 1.01996) in standard disk assay at 50 μg/disk.	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)
Stachybotrys sp. (strain CS-710-1)	– Stachybotrins A (**109**) and B (**110**)	– **109-110:** Antibacterial activity against *B. subtilis* (ATCC 6051) and antifungal activity against *Ascobolus furfuraceus* (NRRL 6460) and *Sorduria fimicola* (NRRL 6459).	Gloer (1997, 2007), Hernández-Carlos & Gamboa-Angulo (2011)

MIC, minimum inhibitory concentration; ED_{90}, effective dose in 90% of the population.; IC_{50}, half-maximal inhibitory concentration.

Vaginatispora aquatica (strain HK1821)

As part of a project focused on the search of new types of antibacterial agents to treat the rapid increase in bacterial resistance to antibiotics in clinical practice, the chemical investigations of the fungus of *Vaginatispora aquatica* afforded the unprecedented new 2-oxo-succinimide polyketide, oxasetin (**49**; Fig. 25) (He et al. 2002). More recently, the binomial name of this fungus was changed after molecular phylogenetic studies to *Lophiostoma vaginatispora* (Zhang et al. 2014a).

The strain was isolated from a decaying piece of wood submerged in the Lam Tsuen River in Tai Po, Hong Kong. The fermentation culture (1 liter, 10 days of growth) of the strain showed antibacterial activity using the agar diffusion method. The whole broth was extracted with methanol (biomass) and ethyl acetate (supernatant). Then, the combined extracts were separated by reversed-phase HPLC on a C_{18} column yielding about 85 mg of **49**. Interestingly, **49** exhibited moderate *in vitro* activity against Gram-positive bacteria including MRSA, vancomycin-resistant *Enterococcus faecalis*,

and *Streptococcus pneumoniae*, with MIC values of 16, 16, and 16-32 μg/mL. No activity against Gram-negative bacteria and *C. albicans* was detected for this compound (He et al. 2002). Although there are other fungal metabolites structurally related to **49**, such as the glycoside BU-4514N and the enantiomeric homologs, equisetinn and phomasetin, as well as many synthetic compounds with the 3-oxo-succinimide as a pharmacophore, this was the first natural product that bears an octahydronaphthalene moiety linked to a 2-oxo-succinimide ring.

***Helotiales* sp.** (strain G730)

In the past ten years, the Oberlies research group has systematically studied freshwater fungi from distinct locations in the USA in the search of new chemical diversity that targets virulence in MRSA (Figueroa et al. 2014). The strain G730 (order Helotiales) (Fig. 27A), isolated from submerged wood collected in a freshwater lake in Hanging Rock State Park, North Carolina, USA, showed important antivirulence activity (89% inhibition at 10 μg/mL) when tested for inhibition of AIP production against the clinical MRSA isolate, USA300 LAC (AH1263) (Paguigan et al. 2019).

Bioactivity-directed purification of the extract from rice medium led to the isolation of three new prenylated diresorcinols, leotiomycenes A-C (**59-61**; Fig. 25) (Paguigan et al. 2019). The structure of these compounds was established based on HRESIMS, NMR, and X-ray diffraction analysis, and their absolute configuration was established by TDDFT-ECD and optical rotation calculations. The anti-MRSA activity of **59-61** was established by the inhibition of AIP production by the MRSA strain AH1263 at below growth-inhibitory concentrations using a previously validated mass spectrometry-based assay. The compounds **59-61** suppressed AIP production with IC_{50} values of 0.3, 4.6, and 6.3 μM, respectively. From this, **59**, the most active compound, was further tested for the inhibition of transcription of the *agr* effector RNAIII and specific *agr*-regulated virulence factors, including phenol-soluble modulin alpha (*psmα*) and alpha-hemolysin (*hla*). Interestingly, **59** blocked transcription of RNAIII at 9.0 and 16.0 μM concentrations and suppressed the transcription of *psmα* and *hla* at 2.9, 9.0, and 16.0 μM concentrations. Notably, bacterial growth was not reduced at these concentrations of **59**, indicating this compound inhibits *S. aureus* quorum sensing by disrupting *agr* signaling and expression of virulence factors that drive invasive infections. Finally, docking studies revealed that **59** binds to the C-terminal AgrA DNA binding domain (Paguigan et al. 2019). Overall, the identification of the anti-quorum-sensing activity of **59-61**, highlights the potential of freshwater fungi as a source for new drug leads against MRSA.

Minutisphaera parafimbriatispora (strain G156-4) and ***M. aspera*** (strain G427)

Minutisphaera is a recently established genus of freshwater fungi comprising five species: *Minutisphaera aquaticum* (Thailand), *M. japonica* (Japan), and *M. fimbriatispora*, *M. aspera*, and *M. parafimbriatispora* (North Carolina, USA) (Raja et al. 2015, Bao et al. 2019).

The chemical analysis of the organic extracts of the liquid cultures of *M. aspera* (strain G427) and *M. parafimbriatispora* (strain G156-4) (Fig. 27B, C), isolated from submerged decorticated wood in the Big Beaver Island Creek, Madison, and a swampy area behind Lake Brandt, Bur-Mil Park, Greensboro, led to the isolation of the bisnaphthyl-pigment sphaerolone (**62**), along with four peptides, and isosclerone (Fig. 25) (Raja et al. 2015). The aromatic polyketide **62** was identified by comparison of its HRESIMS, NMR, and optical rotation data with those reported in the literature, and its antimicrobial activity was assessed against a set of bacteria and fungi, including *S. aureus*, *E. coli*, *M. smegmatis*, *C. albicans*, and *A. niger*. Interestingly, it showed promising activity against *S. aureus* and *M. smegmatis* with MIC values of 30 and 60 μg/mL, respectively (Raja et al. 2015).

Clavariopsis aquatica (strain AJ117363)

A series of cyclic depsipeptides, clavariopsins A-I (**94-102**) were isolated from the mycelia of the liquid culture of the aquatic hyphomycete *Clavariopsis aquatica* AJ117363 (Fig. 26) (Kaida et al. 2001, Soe et al. 2019). The aquatic hyphomycetes are usually abundant in leaf litter in streams and stream foams and release a vast number of asexual spores with characteristic shapes such as sigmoid or multiradiate forms. *Clavariopsis aquatica* was isolated from decaying leaves collected

from a mountain stream at Mt. Takao in Tokyo, Japan. The fungal spores were washed out from the leaves by bubbling air to the leaves placed in a beaker with water (Kaida et al. 2001, Soe et al. 2019).

The acetone extract of this fungus showed promising antifungal activity against *A. niger* (AJ117364) in the paper disk diffusion method. Then the extract was partitioned between EtOAc and H_2O and the organic fraction was separated using silica gel column chromatography followed by repeated reversed-phase HPLC. The planar structures of **94-102** were elucidated by HRMS and 2D NMR analyses and the absolute configurations of the amino acid residues were determined by the advanced Marfey's method and then analyzed by LC-MS (Kaida et al. 2001, Soe et al. 2019). The antifungal activities of **94-102** were broadly evaluated by a paper disk diffusion method against six plant pathogenic fungi: *Botrytis cinerea*, *M. oryzae*, *Colletotrichum orbiculare*, *F. oxysporum*, *A. alternata*, and *A. niger*. From this, **94**, **96**, and **97** showed the highest activity (minimum inhibitory dose, MID = 0.01 μg/disk) against *A. alternata*, and the remaining compounds exhibited MIDs of 0.03-0.3 μg/disk (Kaida et al. 2001, Soe et al. 2019). While no clear structure-activity relationship (SAR) was observed, the displayed activity observed, and the fact that they exhibited low cytotoxicity against human cancer cells, suggests that they are potentially safe natural pesticides.

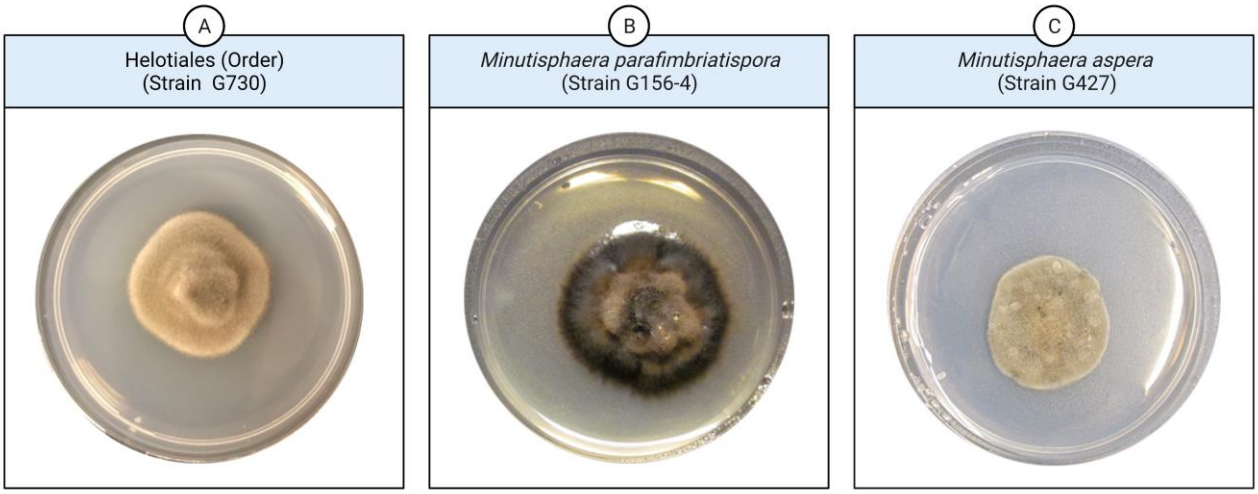


Figure 27 – Fungal strains from North Carolina, USA, grown in PDA plates.

Chemical space and diversity analysis of antimicrobial freshwater fungi secondary metabolites

Chemical space of antimicrobial freshwater fungi secondary metabolites

In cheminformatics, chemical space is considered a pivot notion in the visual representation of molecular diversity with a wide spectrum of applications mainly in the field of drug discovery (Medina-Franco et al. 2021, Lachance et al. 2012). The goal of such analysis is to explore the chemical space spanned by antimicrobial freshwater fungi secondary metabolites and their intersection with other biologically relevant agents. These metabolites with antibacterial and antifungal activity (n = 110) were combined into a single dataset namely "Freshwater Fungi DB". Two reference databases ["Antifungal Agents DB", (n = 81), accession number DBCAT000200 and "Antibacterial Agents DB", (n = 340), accession number DBCAT000104] were obtained from DrugBank 5.0 (Wishart et al. 2018). Cytotoxic antibiotics were kept in the Antibacterial Agents DB while monoclonal antibodies were excluded from the analysis. Chemical structures were drawn using ChemDraw v.16.0 software and integrated into the computational analysis as canonical simplified molecular input line entry specification (SMILES). Molecules in each dataset were subjected to structural and chemical curation as previously described (González-Medina & Medina-

Franco 2019, Al Sharie et al. 2020). In brief, the largest fragment was kept eliminating associated salts followed by charge neutralization, removal of metallic moieties, and detecting duplicates. The curation process was performed using DataWarrior (Sander et al. 2015) and KNIME (Berthold et al. 2009) aided with Vernalis nodes. Manual inspection of compounds was performed to evaluate the quality of the automated curation process as recommended by Fourches et al. (2010). Chemical spaces were visualized based on six molecular descriptors of physiological interest, namely molecular weight (MW), topological polar surface area (TPSA), octanol-water partition coefficient (cLog*P*), number of rotatable bonds (NRB), and number of hydrogen bond acceptors (HBA) and donors (HBD). Molecular descriptors were standardized, and dimension reduction was performed using principal component analysis (PCA) to generate a two-dimensional chemical space using DataWarrior software (Sander et al. 2015). Similarity and dissimilarity in the setting of inter- and intra-database diversity were investigated by the calculation of pair-wise Euclidian distances and Tanimoto coefficients, respectively using the platform of unified molecular analysis (PUMA) (González-Medina & Medina-Franco 2017).

Generated chemical space spanned by the previously mentioned datasets was visualized using two principal components, namely PC1 and PC2 recovering 75.13% and 16.92% of the diversity, respectively (Fig. 28A). The first principal component was positively correlated with all molecular descriptors except for the cLog*P*, while the second principal component was negatively associated with all descriptors except for the number of hydrogen bond donors and topological polar surface area. Per calculated diversity parameters (Fig. 28B, C), Freshwater fungi DB has the least intra-database diversity with a Euclidian distance of 2.09 followed by Antifungal Agents DB (2.19) and Antibacterial Agents DB (2.63). These findings emphasize the importance to explore the chemistry embedded within freshwater fungi since they encompass a descent shared chemical space with antibacterial and antifungal agents. Moreover, a high similarity metrics is observed between Freshwater Fungi DB and Antifungal Agents DB and Antibacterial Agents DB with Tanimoto coefficients of 0.702 and 0.673, respectively.

Molecular scaffolds of antimicrobial freshwater fungi secondary metabolites

Molecular scaffolding is considered a key concept in the field of medicinal chemistry with its impact in describing geometrical properties and structural shapes of chemical cores in relevance to substituents (Hu et al. 2016). Throughout time, the definition of scaffolds was highly subjective and ubiquitous until the introduction of Bemis and Murcko's definition in 1996; outlining scaffolds as basic cyclical cores connected by linkers (Bemis & Murcko 1996, Shelat & Guy 2007, Scott & Edith Chan 2020). Scaffolds were yielded utilizing the previously mentioned definition using DataWarrior software followed by dataset-based scaffold diversity assessment using Cyclic System Retrieval curves (CSR) parameters. CSR curves plot the fraction of scaffolds on the *x*-axis versus the fraction of compounds on the *y*-axis. Each curve was characterized by the mathematical calculation of F_{50} (fraction of scaffolds needed to acquire 50% of compounds) and AUC (area under the curve) (Medina-Franco et al. 2009, González-Medina & Medina-Franco 2019). A total of 385 chemotypes were obtained, which were distributed as follows: Antibacterial Agents DB (251), Antifungal Agents DB (66), and Freshwater Fungi DB (68). The number of acyclic compounds resistant to scaffolding was 10, which were distributed almost equally among databases. Fig. 29A represents the most frequent chemotypes in the tested databases with the benzene ring being the only shared scaffold among the three databases. Such finding has been repeatedly seen in many cheminformatics-based characterizations of chemical databases (Martínez-Mayorga et al. 2011, Tran et al. 2020, Madariaga-Mazón et al. 2021). CSR curves were plotted (Fig. 29B) illustrating that Freshwater Fungi DB curve exhibits a significant left shift away from the diagonal imaginary line indicating a lower scaffold diversity compared to other tested databases, which indicates the lowest scaffold diversity. The database with highest chemotype diversity should possess the highest F_{50} value and an AUC value closer to 0.5 (González-Medina & Medina-Franco 2017, Saldívar-González et al. 2019). Antifungal Agents DB exhibits the highest scaffold diversity with an AUC value of 0.5620 and F_{50} value of 0.4242 followed by the Antibacterial Agents DB (AUC = 0.6121,

F_{50} = 0.2267) and Freshwater Fungi DB (AUC = 0.6486, F_{50} = 0.2537), respectively. Although Freshwater Fungi DB showed relatively lower scaffold diversity, but such results can be biased taking into consideration that compounds in both the Antibacterial Agents DB and Antifungal Agents DB are a mixture of naturally occurring substances along with synthetic and semi-synthetic compounds. However, Freshwater Fungi DB originated from a single natural source. Consequently, we suggest freshwater fungi should be investigated further to isolate and characterize new biologically active agents.

Molecular fingerprints of antimicrobial freshwater fungi secondary metabolites

Molecular fingerprints are the most common and simple tool used in cheminformatics to represent molecules. It has been widely used in the field of drug discovery based on the paradigm suggesting that chemically similar agents will probably possess a similar biological profile (Fernández-De Gortari et al. 2017). The concept of fingerprints is to convert molecules into binary vectors that can be easily generated, accessed, stored, and compared (Fernández-De Gortari et al. 2017, Capecchi et al. 2020). Herein, three binary fingerprints were used, namely: extended-connectivity fingerprint with a diameter of 4 (ECFP_4), Molecular ACCess System (MACCS) keys (166-bits), and PubChem fingerprint (881-bits) in conjunction with Tanimoto index represented by cumulative distribution functions (CDFs) and median similarity values (Fig. 29C) using PUMA (González-Medina et al. 2016). ECFP_4 illustrates a slightly left-shift for the Antifungal Agents DB while the Antibacterial Agents DB and the Freshwater Fungi DB followed a similar path representing a lower diversity. Such a finding indicates the fact that such a fingerprint could not be suitable for the assessment of diversity or that the tested databases are highly diverse requiring lower resolution fingerprints (Al Sharie et al. 2020). MACCS keys fingerprint suggests that the Antifungal Agents DB has the lowest Tanimoto coefficient with a curve left-shift indicating the highest fingerprint-based diversity. However, the other databases exhibited a non-remarkable difference in the median values, in which the Freshwater Fungi DB is more diverse than the Antibacterial Agents DB. On the other hand, the PubChem fingerprint (881-bits) suggests that Freshwater Fungi DB has the lowest fingerprint diversity compared to tested databases. Consensus diversity plots (Fig. 29D) were used to visualize and summarize the findings generated within the current analysis. Consensus diversity plots represent a multi-metric visualization tool of global diversity that includes fingerprint diversity using MACCS keys fingerprint (*x*-axis), scaffold diversity represented by the AUC or F_{50} values (*y*-axis), Tanimoto coefficient based intra-database diversity (color scale), and database size (database point size) (González-Medina et al. 2016). In brief, according to the generated chemical space depended on the physiological and pharmacological properties, Freshwater Fungi DB covers a similar space to other antimicrobial databases. Hence, a growing body of the literature should be devoted to study the chemical and biological profile of freshwater fungi as potential natural source of antimicrobial agents.

A Survey of Antimicrobials Produced by Different Taxonomic Groups of Freshwater Ascomycota

Introduction

The objective of this section is to summaries antimicrobials produced by different taxonomical groups of freshwater Ascomycota as an aide to scientist in their search for the most promising taxa to study. Antimicrobial freshwater Ascomycota refers to those whose secondary metabolites have antimicrobial activity, including the inhibition of pathogenic fungi and pathogenic bacteria.

Due to its great value for antibiotic drug development, antimicrobial freshwater Ascomycota has attracted increasing attention from researchers (Sridhar 2012, Monkai et al. 2013, Han et al. 2015, Paguigan et al. 2016, Abdel-Wareth & Ghareeb 2018, Li et al. 2021b). In recent years, an increasing number of new species of freshwater.

Ascomycota have been reported (Zhang et al. 2017, 2016, Dong et al. 2018, 2020a,b, Wei et al. 2018, Yu et al. 2018, Luo et al. 2019, Wang et al. 2019, Yang et al. 2020, Calabon et al. 2021b), providing abundant taxa for the study of their biological activity and leading to greater antimicrobial freshwater Ascomycota screening.

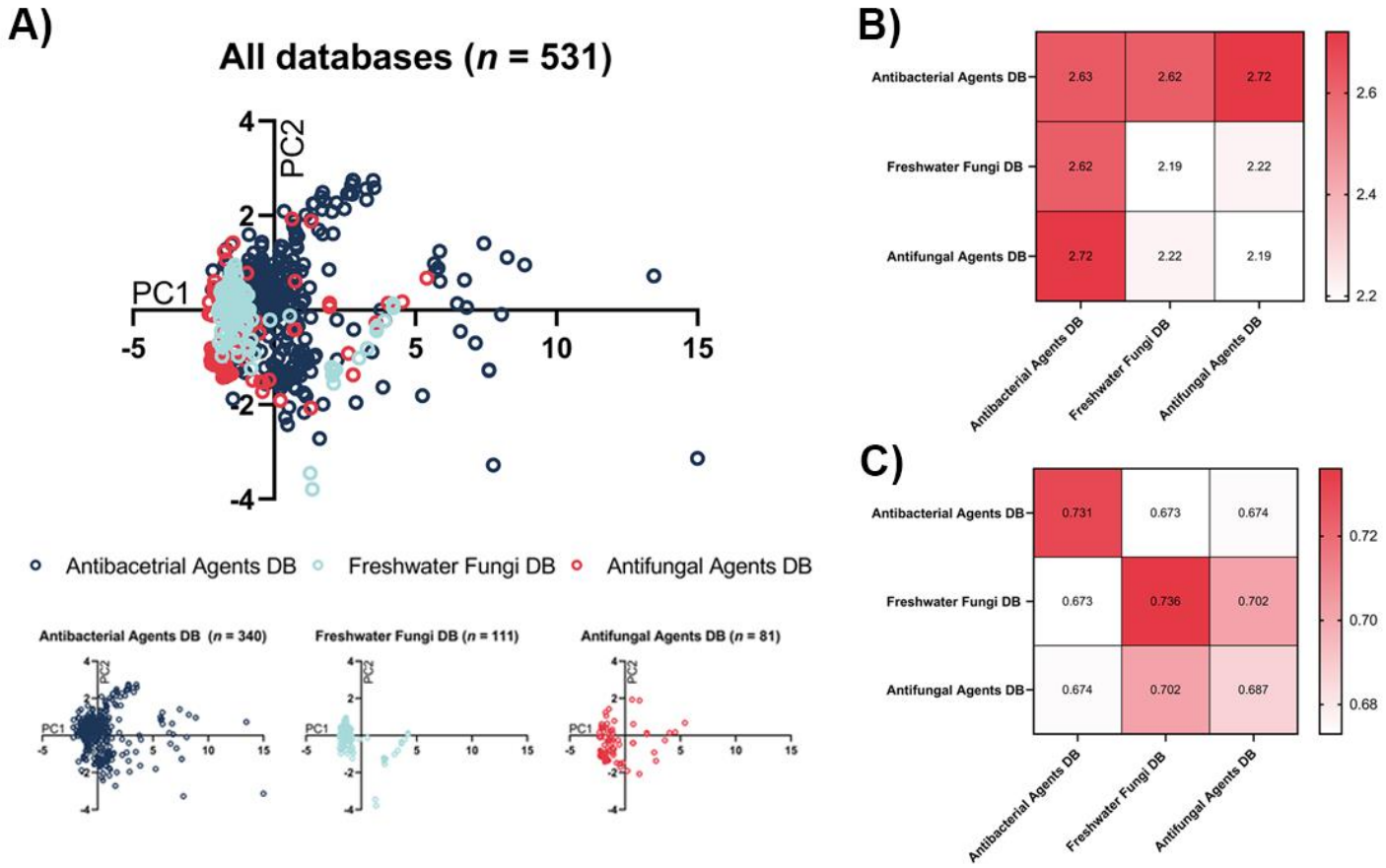


Figure 28 – Principal component analysis (PCA) of Freshwater Fungi DB compared to Antifungal Agents DB based on six molecular descriptors of physiological relevance (A). Inter- and intra-database diversity is represented by pair-wise Euclidian distances (B) and Tanimoto coefficients (C) matrices.

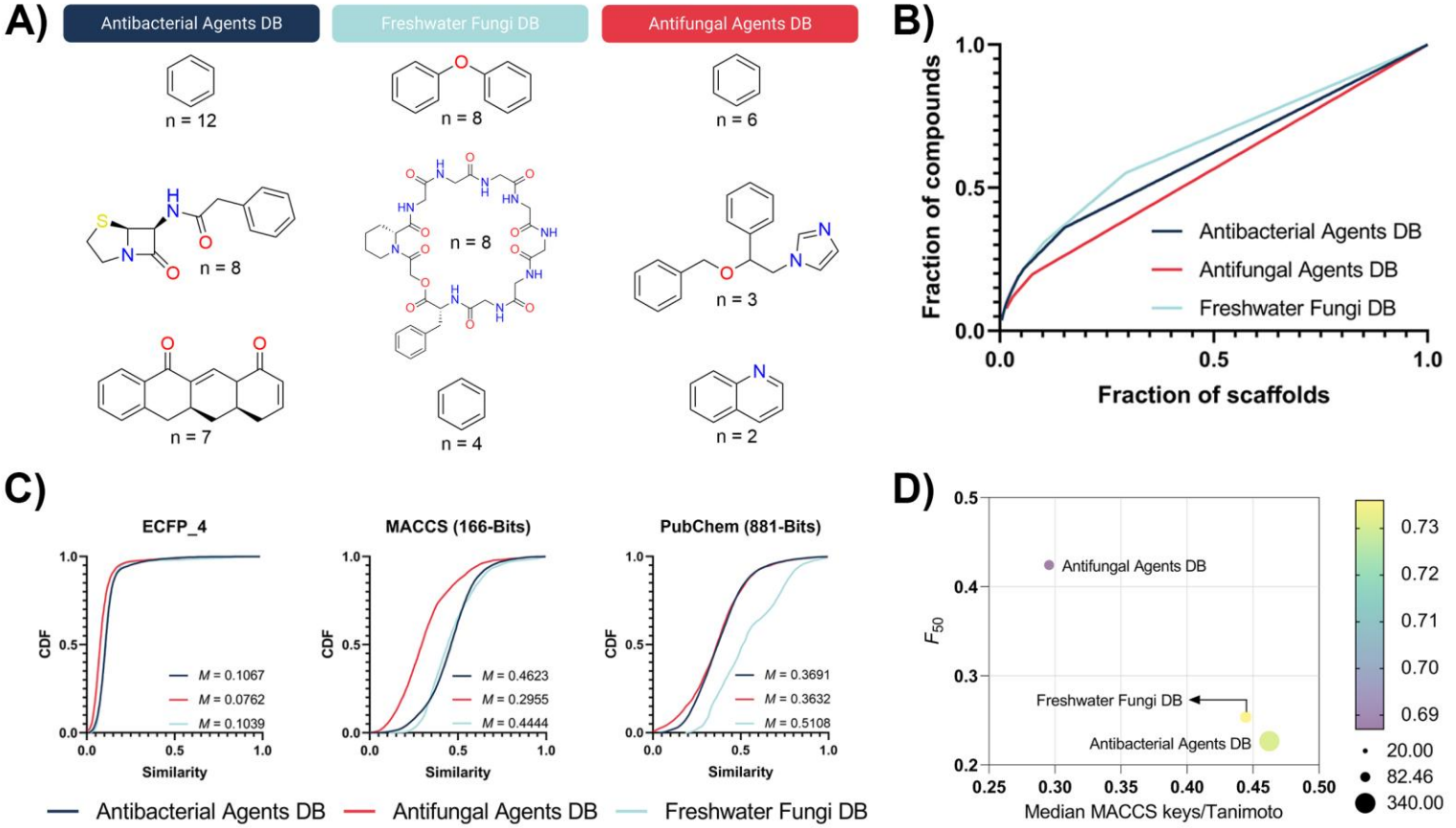


Figure 29 – Most frequent scaffolds yielded in each database (A). CSR curves (B). CDFs as a visual representation for ECFP_4, MACCS keys (166-bits), and PubChem (881-bits) binary fingerprints (C). Consensus diversity plot (D).

Review of antimicrobials by differed classes of freshwater Ascomycota

The first study on antimicrobial freshwater Ascomycota was conducted by Asthana & Shearer (1990) who reported that three strains of *Ophioceras* (Magnaporthales) could inhibit 12 pathogenic fungi, including *Phytophthora*. Since then, research on antimicrobial freshwater Ascomycota have increased annually, and a total of 112 fungal strains have been reported. All reported antimicrobial freshwater Ascomycota with

their inhibited pathogens (see Table 6 for list of pathogens) are summarized in Table 7 with their classification provided according to Wijayawardene et al. (2020). The percentages of 136 antimicrobial freshwater Ascomycota species in each order are shown in Fig. 30.

Dothideomycetes

Dothideomycetes is the most abundant class of antimicrobial freshwater Ascomycota and includes 51 species (37.5%) in six orders. Pleosporales has the largest number reported and includes 34 species (25%) in 18 families, among which Lophiostomataceae and Dictyosporiaceae yielded the greatest number of antimicrobial freshwater Ascomycota per family with four species each. The remaining species are distributed in Tubeufiales (nine species), Jahnulales (three species), Botryosphaeriales (two species), Capnodiales (one species) and Minutisphaerales (one species), as well as Dothideomycetes, genus *incertae sedis* (one species). The genus with the most abundant antimicrobial freshwater Ascomycota is *Massarina*, with three species.

Sordariomycetes

Sordariomycetes is the second most abundant class of antimicrobial freshwater Ascomycota and includes 47 species (34.56%) in 14 orders. The largest order is Magnaporthales with eleven species in two families, including three species in Pseudohalonectriaceae and eight species in Ophioceraceae. Secondly, Hypocreales yielded the second greatest number of antimicrobial freshwater Ascomycota per order with seven species. The remaining species are distributed in Chaetosphaeriales (five species), Pleurotheciales (four species), Coronophorales (three species), Microascales (two species), Savoryellales (two species), and in Amphisphaeriales, Annulatascales, Atractosporales, Distoseptisporales, Sporidesmiales, Sordariales, and Xylariales (one species each), as well as Sordariomycetes family, incertae sedis (five species) and Sordariomycetes, genus *incertae sedis* (two species). The genus with the most abundant antimicrobial freshwater Ascomycota is *Ophioceras*, with eight species.

Eurotiomycetes and other groups

A total of 20 antimicrobial freshwater Ascomycota species (14.7%) have been reported in three orders of Eurotiomycetes. Eurotiales contains 14 species (10.29%), including six species in *Paecilomyces*, five species in *Aspergillus* and three species in *Penicillium*. Onygenales contains four species in four different families, including Gymnoascaceae, Helotiaceae, Mollisiaceae, and Solenopeziaceae. The remaining two species belongs to Chaetothyriales and Mucorales, respectively.

A total of 10 antimicrobial freshwater Ascomycota species (9%) have been reported in Orbiliomycetes. They are all affiliated with Orbiliaceae (Orbiliales), including five species in *Arthrobotrys* and five species in *Dactylella*. The remaining antimicrobial freshwater Ascomycota species are affiliated with Agaricomycetes (one species), Leotiomycetes (one species), and Saccharomycetes (one species), as well as Ascomycota genus *incertae sedis* (five species).

Analyses on the distribution proportion of antimicrobial freshwater Ascomycota

The percentages of antimicrobial freshwater Ascomycota accounting for total freshwater fungi in each order are shown in Table 8. Pleosporales has the most freshwater fungi reported with 389 species, while antimicrobial freshwater Ascomycota accounts for only 8.74%. Orbiliales is the order with the highest antimicrobial freshwater Ascomycota proportion. In Orbiliales, a total of 14 species of freshwater fungi made the proportion of antimicrobial freshwater Ascomycota 71.43%, higher than those in Pleosporales. Secondly, the proportion of antimicrobial freshwater Ascomycota in Coronophorales is 60%. Jahnulales and Tubeufiales are the common orders with the most intensive freshwater fungi, while the proportions of antimicrobial freshwater Ascomycota in these two orders are 8.11% and 6.21%, respectively.

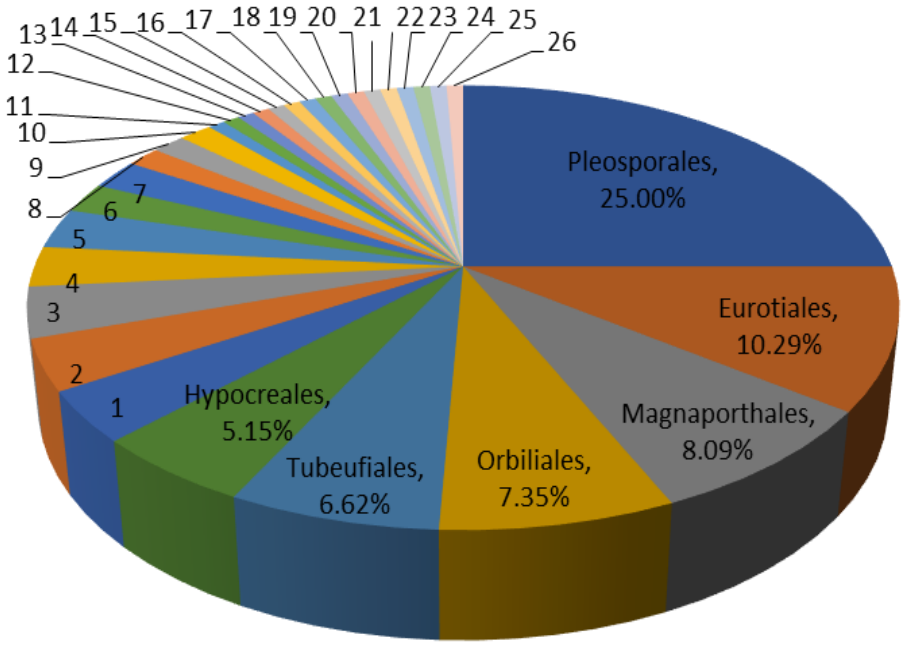


Figure 30 – The percentages of 136 antimicrobial freshwater Ascomycota species in each order. Note: 1 = Chaetosphaeriales, 3.68%; 2 = Sordariomycetes family *incertae sedis*, 3.68%; 3 = Ascomycota genera *incertae sedis*, 3.68%; 4 = Onygenales, 2.94%; 5 = Pleurotheciales, 2.94%; 6 = Jahnulales, 2.21%; 7 = Coronophorales, 2.21%; 8 = Botryosphaeriales, 1.47%; 9 = Microascales, 1.47%; 10 = Savoryellales, 1.47%; 11 = Cantharellales, 0.74%; 12 = Capnodiales, 0.74%; 13 = Minutisphaerales, 0.74%; 14 = Minutisphaerales, 0.74%; 15 = Mucorales, 0.74%; 16 = Annulatascales, 0.74%; 17 = Sordariales, 0.74%; 18 = Xylariales, 0.74%; 19 = Saccharomycetales, 0.74%; 20 = Helotiales, 0.74%; 21 = Dothideomycetes genera *incertae sedis*, 0.74%; 22 = Chaetothyriales, 0.74%; 23 = Atractosporales, 0.74%; 24 = Distoseptisporales, 0.74%; 25 = Sporidesmiales, 0.74%; 26 = Sordariomycetes genera *incertae sedis*, 0.74%.

Summary and prospective

Similar to soil and marine fungi, the secondary metabolites of freshwater fungi have great potential. However, research on the secondary metabolites of freshwater fungi with antibacterial activity is in its initial stage. The number of detected ones is less than one-fifth of the total freshwater fungi. Therefore, it remains much work to be done. Due to the different methods and indicator pathogens selected in different studies, it is difficult to conclude the inhibitory effects of antimicrobial freshwater Ascomycota on these three types of pathogens, *viz.* gram-positive bacteria, gram-negative bacteria, and pathogenic fungi. In recent years, with the continuous development of microscopic detection methods, it is possible to study the bacteriostatic mechanism of freshwater fungi from the perspective of molecules (genes) and cells, which will be helpful to improve the pertinence and efficiency of antimicrobial freshwater Ascomycota screening.

High Throughput Sequencing of Freshwater Fungi

Background

Fungi are a key component of biodiversity and fundamental for ecosystem. They exhibit different lifestyles and can be found in a wide range of habitats (Hyde et al. 2020b). They are an important part of the aquatic and terrestrial ecosystems as they can produce a range of extracellular enzymes that are involved in organic matter cycling, thus releasing key nutrients across trophic levels (Willis 2018). Fungi are considered a species-rich group (Purvis & Hector 2000), however, only 150,000 species have been named and classified so far (Hyde et al. 2020b, Bhunjun et al. 2022), with 3,870 species reported from freshwater habitats (Calabon et al. 2022).

Table 6 Test pathogens and their abbreviation used in this entry.

Scientific name	Abbreviation	Scientific name	Abbreviation
Gram-positive bacteria		**Pathogenic fungi**	
Bacillus cereus	BC	*Cunninghamella* sp.	CE
Bacillus subtilis	BS	*Colletotrichum fructicola*	CF
Clavibacter michiganensis	CM	*Cercospora arachidicola*	CI
Enterococcus faecium	EF	*Colletotrichum orbiculare*	CO
Streptococcus haemolyticus	HS	*Cochliobolus sativus*	CS
Listeria monocytogenes	LM	*Colletotrichum* sp.	CS1
Micrococcus luteus	ML	*Coleosporium* sp.	CSP
Mycobacterium smegmatis	MS	*Coprinus stercorarius*	CST
Staphylococcus aureus	SA	*Exserohilum turcicum*	ET
Sarcina lutea	SL	*Filobasidium neoformans*	FN
Streptococcus pneumonia	SP	*Fusarium oxysporum*	FO
Staphylococcus saprophyticus	SS	*Fusarium* sp.	FS
Gram-negative bacteria		*Fusarium verticillioides*	FV
Brevibacillus laterosporus	BL	*Gibberella saubinetii*	GS
Enterobacter aerogenes	EA	*Gibberella zeae*	GZ
Escherichia coli	EC	*Helicodendron giganteum*	HG
Erwinia carotovora subp. *carotovorum*	EC1	*Helicodendron triglitziense*	HT
Haemophilus influenza	HI	*Itersonilia perplexans*	IP
Klebsiella pneumonia	KP	*Microsporum gypseum*	MG
Pseudomonas aeruginosa	PA	*Magnaporthe oryzae*	MO
Pneumocystis carinii	PC	*Nectria lugdunensis*	NL
Pseudomonas fluorescens	PF	*Pythium aphanidermatum*	PA
Proteus mirabilis	PM	*Phytophthora capsica*	PC
Proteus vulgaris	PV	*Phyllosticta* sp.	PH
Shigella sonnei	SH	*Phytophthora* sp.	PH1
Shigella sp.	SS	*Phytophthora infestans*	PI
Xanthomonas campestris	XC	*Paecilomyces lilacinus*	PL
Pathogenic fungi		*Penicillium notatum*	PN
Ascobolus furfuraceus	AF	*Phytophthora palmivora*	PP
Aspergillus alternata	AA	*Phytophthora* sp.	PS
Aspergillus flavus	AF1	*Pythium ultimum*	PU
Aspergillus fumigatus	AF2	*Rhizoctonia solani*	RS
Alternaria sp.	AL	*Saccharomyces cerevisiae*	SC
Aspergillus niger	AN	*Sodaria fimicola*	SF
Allomyces javanicus	AJ	*Soprolegnia ferax*	SF1
Aspergillus sp.	AS	*Saccharomyces roseus*	SR
Alternaria sp.	AS1	*Sclerotium* sp.	SS1
Botrytis alii	BA	*Sclerotinia sclorotiorum*	SS
Botrytis cinerea	BC	*Salmonella typhimurium*	ST
Bipolaris maydis	BM	*Salmonella* sp.	SSP
Beltrania querna	BQ	*Thanatephorus cucumeris*	TC
Basidiobolus ranarum	BR	*Trichophyton gypseum*	TG
Botrytis sp.	BS	*Trichophyton mentagrophytes*	TM
Botrytis subtilis	BS1	*Trichophyton rubrum*	TR
Bursaphelenchus xylophilus	BX	*Trichoderma* sp.	TS
Candida albicans	CA	*Trichomonas vaginalis*	TV
Candida sp. 1	CAS	*Verticillium dahlia*	VD

Table 6 Continued.

Scientific name	Abbreviation	Scientific name	Abbreviation
Candida sp. 2	CA1	*Zygorhynchus moelleri*	ZM
Chaetomium dolichotrichun	CD		

Table 7 Reported antimicrobial activity of freshwater fungi with pathogen (according to taxonomic order).

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
Agaricomycetes			
Cantharellales			
Hydnaceae			
Ingoldiella hamata[1]	BS, SA	EA, EC	–
Dothideomycetes			
Botryosphaeriales			
Botryosphaeriaceae			
Sphaeropsis sp.[2]	SL	–	MG, PH1, TG, TR
Tiarosporella paludosa[3]	BC, SA	BL, EC	GS, PH, RS
Capnodiales			
Cladosporiaceae			
Cladosporium sp.[2]	SL	–	AL, BC, CA, PH1, TR
Jahnulales			
Aliquandostipitaceae			
Brachiosphaera sp.[4]	SA, LM	EC, SS	BC
Neojahnula australiensis[4]	SA, LM, BS	SS, SSP	–
Xylomyces chlamydosporus[3,5,6]	BC, SA	BL, EC	AL, ET, PH, FS, SS1, FV
Minutisphaerales			
Minutisphaeraceae			
Minutisphaera parafimbriatispora[6]	SA, MS	–	–
Pleosporales			
Amniculicolaceae			
Amniculicola longissima (≡ *Anguillospora longissima*)[7,8,9,10]	SA, CA	–	CA
Astrosphaeriellaceae			
Astrosphaeriella papuana[8,9,10,11]	BC, SA	BL, EC	AS1, GS, PS, FS, CS1
Pithomyces sp.[2]	SA, SL	EC	BC, CE, FO, PH1, TG, TR, TS
Caryosporaceae			
Caryospora minima[5]	BC, SA	BL, EC	–
Delitschiaceae			
Delitschia corticola[6,12]	BC, SA	BL, EC	AL, CS1, ET, FS, GS, PH, PS, RS, SS1
Dictyosporiaceae			
Dictyosporium cocophylum[3]	BC, SA	BL, EC	AL, CS1, ET, GS, PH, FS, RS, SS1
Dictyocheirospora heptaspora (≡ *Dictyosporium heptasporum*)[3]	BC, SA	BL, EC	AL, CS1, ET, FS, RS
Dictyocheirospora musae (≡ *Dictyosporium musae*)[3]	BC, SA	BL, EC	AL, ET, GS, PH, FS, RS, SS1
Digitodesmium bambusicola[3,5]	BC, SA	BL, EC	AL, CS1, ET, GS, PH, FS, RS, SS1
Kirschsteiniotheliaceae			
Kirschsteiniothelia sp. 1[13]	BS, SA	–	–

Table 7 Continued.

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
Kirschsteiniothelia sp. 2[8,9,10]	BS1, SA	–	–
Latoruaceae			
Pseudoasteromassaria spadicea[4]	SA, LM, BS	EC, SS	BC, RS, FO
Lindgomycetaceae			
Lindgomyces madisonensis[14]	MS, SA	EC	AN, CA
Clohesyomyces aquaticus[4,8,9,10]	SA, LM, BS	EC, SS, SSP	ST
Clohesyomyces sp.[8,9,10]	–	–	ST
Longipedicellataceae			
Longipedicellata sp.[4]	BS	SS, SSP	RS, FO
Lophiostomataceae			
Decaisnella thyridioides[8,9,10,18]	BS, BS1, SA	EC	AF1, CA, FV
Lophiostoma aquaticum (≡ *Massarina aquatica*)[3,19]	BC, SA, SS	BL, EC	AL, CS1, GS, RS, SS1 AN, BC, BQ, HG, HT, NL, PN
Lophiostoma frondisubmersum (≡ *Massarina fronsisubmersa*)[3,5]	BC, SA	BL, EC	AL, CS1, ET, FO, FS, RS, SS1
Vaginatispora aquatica[8,9,10,17]	EF, SA, SP	EC	CA
Massarinaceae			
Massarina bipolaris[3]	BC, SA	EC	AL, CS1, ET, GS, PH, RS, SS1
Massarina peerallyi[3]	BC, SA	BL	AL, CS1, ET, GS, PH, FS, RS, SS1
Massarina sp.[6,8,9,10,18](as *Massarina tunicata* in (Oh et al. 1999a), but the species is unpublished)	BS, BS1, SA	–	–
Melanommataceae			
Camposporium quercicola[3,8,9,10]	BC, SA	BL, EC	AL, CS1, ET, GS, PH, FS, RS, SS1
Morosphaeriaceae			
Helicascus thalassioideus (≡ *Massarina thalassioidea*)[3]	BC, SA	BL, EC	AL, CS1, ET, GS, RS, SS1
Helicascus sp.[4]	SA, LM, BS	SS, SSP	FO
Periconiaceae			
Periconia digitata[3]	BC, SA	BL, EC	AL, ET, GS, PH, FS, RS, SS1
Periconia minutissima[3]	BC, SA	BL, EC	AL, CS1, GS, PH, RS, SS1
Pleomonodictydaceae			
Pleohelicoon richonis (≡ *Helicoon richonis*)[6,20]	BC, BS, BS1, HS, SA, KP	HI	AL, AN, CA, MG, SC, TV
Pleosporaceae			
Alternaria. sp. 1.[2]	SA, SL	PA	CA, FO, MG, TG
Alternaria sp. 2 (= *Ulocladium* sp.)[2]	SA, SL	–	CA, PH1, TG, TR, TS
Torulaceae			
Torula graminis[3,4]	SA, BC	BL, EC	AL, CS1, ET, FO, FS, RS, SS1
Torula herbarum[3,5]	SA, BC	BL, EC	AL, CS1, ET, FO, PH, FS, SS1
Trematosphaeriaceae			
Trematosphaeria hydrela (≡ *Caryospora callicarpa*)[5,8,9,10]	BC, BX	BL	–
Tubeufiales			

Table 7 Continued.

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
Tubeufiaceae			
Aquaphila albicans[4]	SA,	SSP	RS
Helicosporium sp.[20]	BS, CM, ML, SA	KP, PM, PV, SH	AN, CA
Helicosporium talbotii[21]	SA	–	–
Helicotruncatum palmigenum[4]	LM, BS	EC, SS, SSP	FO
Tubeufia aquatica[4]	SA, LM, BS	EC, SS	RS
Tubeufia tectonae[4]	LM	EC, SS, SSP	
Tubeufia sp.[4]	SA, LM, BS	EC, SS, SSP	
Tubeufiaceae sp. A-00471[22]	BS, SA	–	–
unidentified species[8,9,10]	SA, BS1	–	–
Dothideomycetes genera *incertae sedis*			
Clavariopsis aquatic[6,8,9,10,23]	BC	–	AA, AF2, AN, CA, CAS, CO, FO, MO
Eurotiomycetes			
Chaetothyriales			
Herpotrichiellaceae			
Thysanorea thailandensis[4]	SA, BS	SS	BC
Eurotiales			
Aspergillaceae			
Aspergillus neoniveus (≡*Aspergillus niveus*)[24]	BC, SA	EC, PA	AN, CA
Aspergillus sp1.[2]	SA, SL	EC	MG, PH1, TG, TR, TS
Aspergillus sp2.[2]	SA, SL	EC	AL, BC, MG, PH1, TG, TR, TS
Aspergillus sp3.[2]	SA, SL	–	AL, BC, CA, CE, FO, MG, PH1, TG, TR, TS
Aspergillus sp4.[2]	SA	EA, PA	AL, BC, FO, MG, PH1, TG, TR, TS
Penicillium implicatum[20]	BC, SA	EC, PA	AN, CA
Penicillium sp. 1[2]	–	–	AL, CA, CE, MG, PH1, TS
Penicillium sp. 2[2]	SA, SL	EC	BC, CA, CE, FO
Thermoascaceae			
Paecilomyces sp. 1[2]	SA, SL	EA, EC, PA	CA, CE, PH1, TR, TS
Paecilomyces sp. 2[2]	SA, SL	EA, PA	AL, BC, CA, FO, MG, PH1, TR
Paecilomyces sp. 3[2]	SA, SL	EC	BC, FO, PH1, TS
Paecilomyces sp. 4[2]	SA, SL	–	AL, CA, PH1, TR, TS
Paecilomyces sp. 5[2]	SA, SL	EC	AL, CA, FO, MG, PH1, TG, TR, TS
Paecilomyces sp. 6[2]	SA, SL	EC	AL, FO, PH1, TG, TR, TS
Onygenales			
Gymnoascaceae			
Gymnoascus sp.[2]	SA, SL	EA, PA	BC, CA, CE, FO
Helotiaceae			
Glarea lozoyensis[6,8,9,10,25]	SA, BS1	–	CA, CA1, CAS, FV, PC
Mollisiaceae			
Mollisia gigantea (≡ *Helicodendron giganteum*)[8,9,10,26]	BS, BS1, SA	–	FV, CA
Solenopeziaceae			
Tricladium castaneicola[6,27]	–	–	PC, PS
Mucorales			
Rhizopodaceae			

Table 7 Continued.

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
Rhizopus sp.[2]	SA, SL	EA, EC, PA	FO, MG, TR
Leotiomycetes			
Helotiales			
Discinellaceae			
Helotiales sp.[6]	SA	–	–
Orbiliomycetes			
Orbiliales			
Orbiliaceae			
Arthrobotrys longiphorus (≡ *Monacrosporium longiphorum*)[3]	BC, SA	BL, EC	AL, GS, PH, FS, RS, SS1
Arthrobotrys microscaphoides (≡ *Monacrosporium microscaphoides*)[3]	BC, SA	BL, EC	AL, ET, GS, FS, RS, SS1
Arthrobotrys psychrophilus (≡ *Monacrosporium psychrophium*)[3]	BC, SA	BL, EC	AL, ET, GS, PH, FS, RS
Arthrobotrys reticulatus (≡ *Monacrosporium reticulatum*)[3]	BC	BL、EC	AL、ET、GS、PH、FS、RS、SS1
Arthrobotrys sphaeroides (≡ *Monacrosporium sphaeroides*)[3]	BC, SA	BL, EC	AL, ET, GS, PH, FS, RS, SS1
Dactylella intermedia[3]	BC, SA	BL, EC	AL, CS1, GS, PH, RS, SS1
Dactylella leptospora[3]	BC, SA	BL, EC	AL, CS1, ET, PH, FS, RS, SS1
Dactylella oxyspora[3]	BC, SA	BL, EC	AL, CS1, FS, SS1
Dactylellina ellipsospora (≡ *Monacrosporium ellipsosporum*)[3]	BC	BL, EC	AL, GS, PH, FS, RS, SS1
Dactylellina haptotyla (≡ *Monacrosporium sclerophyum*)[3]	BC, SA	EC	AL, PH, FS, SS1
Saccharomycetes			
Saccharomycetales			
Dipodascaceae			
Geotrichum sp.[2]	SL, SA	EC, PA	FO, MG, PH1, TG, TR, TS
Sordariomycetes			
Amphisphaeriales			
Sporocadaceae			
Hymenopleella lakefuxianensis (≡ *Dyrithiopsis lakefuxianensis*)[3]	BC, SA	BL, EC	AL, CS1, ET, PH, FS, RS, SS1
Annulatascales			
Annulatascaceae			
Annulatascus triseptatus[8,9,10,28]	BS, BS1, SA		AF1, CA
Atractosporales			
Atractosporaceae			
Atractospora thailandensis[4]	LM	EC, SS	BC
Chaetosphaeriales			
Chaetosphaeriaceae			
Chloridium sp.[29]	BS	EC, PA, PF	CA, CI, FO, PI, VD
Dictyochaeta plovercovensis[3]	BC, SA	BL, EC	AL, CS1, ET, GS, PH, FS, SS1
Dictyochaeta aquatica[4]	SA, LM, BS	EC, SS, SSP	–

Table 7 Continued.

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
Thozetella havanensis[21]	SA	–	–
Helminthosphaeriaceae			
Hilberina breviseta (≡ *Lasiosphaeria breviseta*)[3]	LM, SA	BL, EC	AL, CS1, FO, PH, RS, SS1
Coronophorales			
Ceratostomataceae			
Melanospora zamiae[3]	BC, SA	BL, EC	AL, CS1, GS, PH, FS
Coronophorales genera *incertae sedis*			
Papulaspora sp. 1[2]	SA, SL	EC	AL, CE, MG, PH1, TG, TR, TS
Papulaspora sp. 2[2]	SL, SA	EC	AL, CA, CE, FO, MG, PH1, TR, TS
Distoseptisporales			
Distoseptisporaceae			
Distoseptispora tectonae[4]	SA, LM, BS	EC, SS, SSP	–
Hypocreales			
Nectriaceae			
Nectriaceae sp.[4]	LM	SS, SSP	BC
Sarocladiaceae			
Sarocladium (≡ *Cephalosporium*) sp. 1[2]	–	–	AL, BC, FO, MG, PH1, TG, TR, TS
Sarocladium (≡ *Cephalosporium*) sp. 2[2]	SL	–	AL, BC, PH1, TG, TS
Sarocladium (≡ *Cephalosporium*) sp. 3[2]	–	EA, PA	CA, CE, FO, MG, PH1, TG, TR
Paraniesslia sp.[8,9,10]	BX	–	–
Stachybotryaceae			
Stachybotrys sp1.[30]	BS	–	AF, CA, SF
Stachybotrys sp2.[8,9,10]	BS	–	AF, SF
Magnaporthales			
Ophioceraceae			
Ophioceras leptosporum[31]	BC, SA	–	–
Ophioceras commune[3]	BC	BL, EC	AL, ET, GS, PH, RS, SS1
Ophioceras dolichostomum[3,5,6,32]	BC, SA	BL, EC	AL, AN, AS, CS, CS1, CSP, ET, FS, PL, PH, PS
Ophioceras venezuelense[33]	–	–	CA
Ophioceras sp. CS-408-2A[34]	–	–	AJ, BC, BR, CD, CST, GZ, IP, PA, PN, PH1, SF1, ZM
Ophioceras sp. CS-652[34]	–	–	AJ, BC, BR, CD, CST, GZ, IP, PA, PN, PH1, SF1, ZM
Ophioceras sp. CS-787-1A[34]	–	–	AJ, BC, BR, CD, CST, GZ, IP, PA, PN, PH1, SF1, ZM
Ophioceras sp. MFLUCC15–0982[4]	SA, BS	EC	–
Pseudohalonectriaceae			
Pseudohalonectria fuxianii[3]	BC, SA	BL, EC	AL, CS1, ET, GS, PH, RS, SS1
Pseudohalonectria lignicola[3]	BC, SA	BL, EC	AL, GS, RS, SS1
Pseudohalonectria adversaria[8,9,10]	BX	–	–
Microascales			
Halosphaeriaceae			
Halosarpheia sp.[3]	BC	BL, EC	CS1, ET, GS, PH, RS, SS1
Natantispora retorquens	BC	BL, EC	CS1, ET, PH, FS, SS1

Table 7 Continued.

Species	Pathogenic bacteria		Pathogenic fungi
	Gram-positive	Gram-negative	
(≡ *Halosarpheia retorguens*)[3]			
Pleurotheciales			
Pleurotheciaceae			
Pleurotheciella sympodia[4]	LM,	SSP	–
Phaeoisaria sp. MFLUCC15–0968[4]	SA, LM	EC, SS, SSP	FO
Savoryellales			
Savoryellaceae			
Savoryella lignicola[3]	BC	BL, EC	AL, ET, FS
Savoryella sp. MFLUCC15–0991[4]	SA, BS	EC, SSP	RS
Sordariales			
Beltraniaceae			
Beltrania rhombica[35]	SA	–	CA
Sporidesmiales			
Sporidesmiaceae			
Sporidesmium thailandense[4]	SA, LM, BS	EC, SS	–
Xylariales			
Xylariaceae			
Xylaria sp.[3] (as *Xylaria migricans* in Wang et al. (2009), but the species is unpublished)	BC, SA	BL, EC	AL, CS1, ET, GS, PH, RS
Sordariomycetes family *incertae sedis*			
Junewangiaceae			
Dictyosporella thailandensis[4]	SA, LM, BS	EC, SS, SSP	BC, RS
Papulosaceae			
Fluminicola bipolaris[3]	BC, SA	BL	AL, CS1, PH, FS, SS1
Fluminicola saprophytica (≡ *Fluminicola thailandensis*)[4]	SA, LM, BS	SS, SSP	–
Pseudoproboscisporaceae			
Neodiluviicola aquatica (≡ *Diluviicola aquatica*)[4]	SA, BS	EC, SS	–
Pseudoproboscispora thailandensis[4]	SA, LM, BS	EC, SS, SSP	BC
Sordariomycetes genera *incertae sedis*			
Saccardoëlla minuta[3]	BC, SA	BL	AL, CS1, SS1
Ascomycota genera *incertae sedis*			
Coelomycete sp1.[3]	BC, SA	BL, EC	AL, ET, GS, PH
Coelomycete sp2.[3,36]	BS, SA	BL	CS1, BS, BM, CS, FV, RS
Rosella sp.[3] (as *Rosella gnutella* in Wang et al. (2009), but the species is unpublished)	BC, SA	BL, EC	AL, CS1, ET, PH, SS1
Dendrospora tenella[8,9,10,37]	BS1, BC, SA	–	CA
Trichaegum sp.[2]	SA, SL	–	BC, FO, PH1, MG, TG, TR

References: 1. Sridhar (2012); 2. Jin et al. (2013); 3. Wang et al. (2009); 4. Li et al. (2021b); 5. Wang et al. (2008); 6. El-Elimat et al. (2021), 7. Harrigan et al. (1995); 8. Gloer (1997); 9. Gloer (2007); 10. Hernández-Carlos & Gamboa-Angulo (2011); 11. Wang et al. (2009); 12. Sun et al. (2011); 13. Poch et al. (1992); 14. Paguigan et al. (2016); 15. Jiao et al. (2006b); 16. Fisher et al. (1988); 17. He et al. (2002); 18. Oh et al. (1999a); 19. Fisher & Anson (1983); 20. Choi et al. (2012); 21. Reyes-Estebanez (2011); 22. Jiao et al. (2006a); 23. Suzuki et al. (2001); 24. Abdel-Wareth & Ghareeb (2018); 25. Bills et al. (1999); 26. Mudur et al. (2006); 27. Han et al. (2015); 28. Li et al. (2021b); 29. Kharwar et al. (2009); 30. Xu et al. (1992); 31.

Monkai et al. (2013); 32. Dong et al. (2010); 33. Reátegui et al. (2005); 34. Asthana & Shearer (1990); 35. Rukachaisirikul et al. (2005); 36. Dong et al. (2009); 37. Oh et al. (1999b).

Table 8 The percentages of antimicrobial freshwater Ascomycota accounts for total freshwater fungi in each order.

Order	Number of antimicrobial freshwater Ascomycota	Number of total freshwater fungi	Percentages
Orbiliales	10	14	71.43%
Coronophorales	3	5	60.00%
Botryosphaeriales	2	4	50.00%
Magnaporthales	11	30	36.67%
Onygenales	4	11	36.36%
Eurotiales	14	79	17.72%
Cantharellales	1	6	16.67%
Atractosporales	1	7	14.29%
Pleurotheciales	4	30	13.33%
Pleosporales	34	389	8.74%
Hypocreales	7	86	8.14%
Jahnulales	3	37	8.11%
Capnodiales	1	13	7.69%
Tubeufiales	9	145	6.21%
Savoryellales	2	35	5.71%
Minutisphaerales	1	18	5.56%
Distoseptisporales	1	22	4.55%
Sporidesmiales	1	22	4.55%
Amphisphaeriales	1	26	3.85%
Microascales	2	54	3.70%
Chaetosphaeriales	5	152	3.29%
Mucorales	1	37	2.70%
Annulatascales	1	40	2.50%
Sordariales	1	42	2.38%
Chaetothyriales	1	47	2.13%
Xylariales	1	50	2.00%
Saccharomycetales	1	158	0.63%
Helotiales	1	188	0.53%

This is much lower than the estimated 1.5 million by Hawksworth (1991) which was based on the ratio of plants to fungi (1:6). The low number of described species is mainly due to their inconspicuous nature. This has to some extent been overcome by the development of molecular High Throughput Sequencing (HTS) methods that can target fungal communities (Ritter et al. 2020, Xu et al. 2020) and even find new lineages (Nilsson et al. 2016). Baldrian et al. (2021) estimated that the number of fungal species is around six million based on HTS sequencing. Wu et al. (2019) estimated that there are 12 million fungal species based on a comparison of published literature of culture-dependent methods and culture-independent approaches from the same samples. Yet, freshwater fungi remain poorly studied despite being an ecological group with high taxonomic diversity (Wurzbacher et al. 2016). Our goal here is to provide a workflow of HTS starting from sampling to data analysis with emphasis on freshwater fungi. We also provide an overview of different HTS platforms and highlight their advantages and challenges.

What is High Throughput Sequencing?

High Throughput Sequencing is a comprehensive term used to describe a relatively new technology for obtaining information about nucleic acids (Blitz et al. 2014). High throughput sequencing differs from Sanger in sequencing volume due to its parallel sequencing technique (Reuter et al. 2015). The Sanger sequencing technology relies on chain termination signal averaged

across all amplicons, and produces a consensus read of sequences of several marker gene alleles from the target specimen (Sanger et al. 1977). High throughput sequencing approaches have enabled detailed, semi-quantitative analysis of fungal communities in large sample sets and provide ecological information that outperforms earlier approaches in terms of detail and magnitude (Lindahl et al. 2013), even at a global scale (Větrovský et al. 2020, Tedersoo et al. 2021). High throughput sequencing approaches are based on short reads (< 550 base pairs - bp) and fall under two broad categories, sequence by ligation and sequence by synthesis (Goodwin et al. 2016). The sequence by ligation approach is a straightforward enzymatic method of sequencing DNA that involves the hybridization and ligation of labelled probe and anchor sequences to a DNA strand (Ho et al. 2011). The second-generation HTS method is based on sequence by synthesis technique which requires the action of DNA polymerase (Heather & Chain 2016). The sequence by synthesis method can be based on a single molecule or real-time approach, called third-generation HTS methods, which can be performed without template amplification (Ho et al. 2011). The third-generation HTS method offers higher read lengths (>1,000 bp) than second-generation HTS method (Nilsson et al. 2019a).

Main steps in HTS studies in fungi

High throughput sequencing is fast becoming the method of choice for in-depth analysis of fungal communities as it can detect unculturable community, recently evolved species, and species complexes (Nilsson et al. 2019a). High throughput sequencing has also been used to extract DNA from ancient herbarium specimens as it can overcome the high fragmentation of ancient DNA and the occurrence of non-target DNA from contaminants (Forin et al. 2018). High throughput sequencing requires a very small amount of DNA or RNA as starting material (as little as 1 ng of DNA), which is another advantage, especially when dealing with herbarium specimens. DNA extraction from environmental samples can include dormant or dead organisms which are preserved in the samples as only a fraction of fungi present in any given environment are metabolically active (Taberlet et al. 2012). Compared to DNA, RNA has a shorter half-life which can range from minutes to hours (Kebaara et al. 2006). Therefore, transcribed messenger RNA can be analyzed using HTS to relate activity to specific gene products and eco-physiological functions as they carry coding information of functional genes (Kellner & Vandenbol 2010).

High throughput sequencing platforms follow a similar pipeline in general which involves template preparation, clonal amplification, followed by parallel sequencing (Reuter et al. 2015). Here we describe each step for fungal HTS methods focusing on environmental freshwater sampling (Fig. 31), their challenges and the recommended best practices. We also performed literature review on the bibliographic databases from Web of Science and Google Scholar on 11/03/2022 using the keywords “freshwater” AND “next-generation sequencing” OR “high throughput sequencing”. Subsequently, the literature was filtered, selecting only metabarcoding studies with freshwater fungi. We read all the articles resulting from this filtering and selected the important information, chronologically, for new advances in biogeography and ecology of freshwater fungi.

Sampling

Sample collection for HTS should follow optimal strategies based on the number and spatial distribution of samples to enable statistically robust conclusions for fungal research (Creer et al. 2016, Zinger et al. 2019). Sample collection should include replicates and sub-replicates. Careful sub-sampling and homogenization of samples are important to obtain representative samples for DNA extraction. Samples may be collected with sterile containers such as DNA-free polypropylene bottles (Matsuoka et al. 2019) or with passive filters (Cindy et al. 2021). It is also recommended to include a control sample containing distilled water which is filled in the field, to check cross-sample contamination *in situ* (Matsuoka et al. 2019). Water samples can be vacuum-filtered through glass filters prior to DNA extraction (Matsuoka et al. 2019, Cindy et al. 2021). All equipment should be carefully cleaned between samplings to avoid contamination during sampling

(Song et al. 2015). Baits, such as sterilized cellulose (thick cotton strings) can also be used for sampling (de Souza et al. 2021). The baits are left in place for few hours, months, or years, which act as a matrix for the colonization of freshwater fungi (Cindy et al. 2021, de Souza et al. 2021). It is recommended to measure physicochemical parameters such as temperature, conductivity and pH when placing the baits (de Souza et al. 2021). Sediments can be sampled using disinfected PVC pipes or PVC sediment corer following the protocol described by Ogaki et al. (2020).

Storage

Sampling may cause rapid changes in DNA composition as opportunistic growth is often induced by disturbances (Lindahl et al. 2013). It is therefore recommended to filter samples as soon as collected and to freeze filtered samples at -20 ℃ to preserve DNA and avoid community development (Delavaux et al. 2020). When using baits, they can be transferred into sterilized Whirl–Pak bags (Sigma-Aldrich, USA) and kept at -20 °C in a sterilized box (de Souza et al. 2021). The cores from sediment sampling are kept at -20 ℃ in sterilized plastic bags after collection (Ogaki et al. 2021). The cores are first thawed, and several subsamples are collected from the center of each core section for DNA extraction under strict contamination control conditions (Ogaki et al. 2021). When using filters for the water samples, they can be wrapped in commercial aluminium foil and stored at -20 °C (Matsuoka et al. 2019). If freezing is not available after sampling, the samples are kept in ethanol, while avoiding sunlight until they can be frozen. Alternatively, buffers can be used to preserve DNA and RNA (Pavlovska et al. 2021). To preserve RNA for HTS analysis, it is important to correctly store the samples due to the faster degradation of RNA. It is recommended to preserve samples for RNA extraction in the field by shock-freezing samples on dry ice or buffer or liquid nitrogen (Bernáldez et al. 2017, Pavlovska et al. 2021).

Extraction

DNA extraction usually involves mechanical cell lysis. The resulting recalcitrant chitinous cell walls and secondary metabolites can interfere with molecular analyses (Lindahl et al. 2013). Therefore, the protocol should be carefully selected based on the substrate and the target organisms as there is no universal extraction method that works for all organisms (Nilsson et al. 2019a, Pansu et al. 2021). Experimental processing after DNA extraction can sometimes be inhibited by PCR (Fujii et al. 2019). Inhibitors reduce the number of taxa detected, but they can be removed to some extent by using efficient DNA extraction kits (Fujii et al. 2019). Clean and stable DNA products can also be generated from methods that do not rely on DNA extraction kits, such as by using beads (Morrissey et al. 1989) or a phenol-chloroform method (Renshaw et al. 2015). To compare diversity or community composition, it is important to use the same DNA extraction protocol on sub-samples to avoid biases based on the efficiency of extraction methods (Tedersoo et al. 2010).

Amplification

Different primers can retrieve a large number of different fungi, so it is important to choose the best primer for a target group or community as the choice of primers dictates which fungi are recovered (Ihrmark et al. 2012, Toju et al. 2012). When using different primers, it is recommended to choose primers with similar melting temperatures and based on the optimal amplicon length of the sequencing platform. The length of amplified fragments is also a critical parameter as longer fragments are more phylogenetically informative (Nilsson et al. 2019a). However, as an increase in the length of target amplicon can negatively affect the assessments of richness using next-generation platforms (Huber et al. 2009, Engelbrektson et al. 2010). The most important step is to decide the markers that will be used in the study. The genes of the nuclear ribosomal repeat unit are highly conserved across a range of organisms, but variable enough to be phylogenetically informative. The ITS region is a commonly used marker as it is highly variable and differs even in closely related species (Djemiel et al. 2017). The more conserved LSU and SSU genes represent an alternative to the ITS region. The SSU gene is commonly used in studies focusing on aquatic fungi (Nilsson et al. 2019a). Ihrmark et al. (2012) found that the diversity and community composition

were better preserved when using the ITS2 region compared to the entire ITS region. This could be due to the lower length variation and more universal primer sites in the ITS2 region (Tedersoo et al. 2015).

PCR bias represent a major drawback to obtain accurate biodiversity data (Tedersoo et al. 2015, Wilcox et al. 2018). High Throughput Sequencing studies often design primers to amplify the taxonomic group of interest, but primer amplification bias can often lead to over-amplification of some DNA templates. This has resulted in the application of multiple PCR reactions with different primer sets, but there is still the possibility of primer bias of producing false negative results especially in GC-rich regions (Wilcox et al. 2018). Therefore, PCR-free approaches would provide a more accurate analysis of biodiversity but are high-cost option (Giebner et al. 2020). TruSeq DNA PCR-Free (Illumina) has been used in several studies to produce high quality data across the genome with reduced library bias (Rhodes et al. 2014, Riman et al. 2017, Jo et al. 2019).

It is recommended to minimize the number of PCR cycles as excessive cycles could result in preferential amplification of rare sequences and the creation of chimeric sequences (Kanagawa 2003, Haas et al. 2011). The efficiency of PCR can be improved by using markers and primers that yield short amplicons as well as using a high-fidelity polymerase to reduce the number of errors (Filges et al. 2019). It is recommended to include a negative control (no sample), a positive control (known species not likely to be present in the sample) and a mock community such as SynMock to determine the abundance and source of contamination (Nilsson et al. 2019a). A positive control ensures that the organisms can be sufficiently extracted with the used methods whereas a negative control ensures that no large-scale cross-contamination between samples takes place (Hornung et al. 2019). It is recommended to choose the most diverse mock community for the positive control to prevent overfitting of the protocol (Hornung et al. 2019). Quantitative real-time PCR (qPCR) can be used to optimize extraction protocols and PCR conditions as well as to pre-screen samples (Forootan et al. 2017). PCR products are purified to remove non-target size DNA fragments. To establish the concentration of PCR products, methods based on fluorescent DNA-binding dyes are recommended compared to UV absorbance methods due to their higher resolution as sample tubes can release UV-absorbing compounds from the plastic (Lewis et al. 2010). Specially designed normalization plates can be used to retain the same amount of DNA from each sample in case of excess PCR products. PCR products from different samples are then mixed in an equimolar amount to evenly distribute DNA sequence output before sequencing (Potapov & Ong 2017). The combined size fractionation and concentration measurements can be used to ensure a high quality of the sample and to establish the final concentration of DNA (Peck et al. 2016).

Sequencing

Tagged amplicons from samples are usually mixed and sequenced in a single run to optimise the use of HTS technologies (Esling et al. 2015). To prevent cross-contamination and to overcome misidentification, it is recommended that all tags differ by at least three nucleotides (Parameswaran et al. 2007, Faircloth & Glenn 2012). High-throughput platforms can frequently generate errors during sequencing and therefore these data must be subjected to extensive quality control measures (Kunin et al. 2010).

Data filtering

Sequenced data must be demultiplexed and raw fastq files must have the primer removed and filtered by quality, size, chimeric detection to provide operational taxonomic units (OTUs, Blaxter et al. 2005) or amplicon sequence variants (ASVs, Callahan et al. 2016). Several protocols exist for these steps (Prodan et al. 2020), including BBDuk (de Souza et al. 2021), UPARSE/USEARCH (Edgar 2013, Callahan et al. 2016), VSEARCH (Rognes et al. 2016), mBRAVE (Ratnasingham 2019), among several others. More advanced filtering methods are recommended as the standard read-score-based filtering in HTS performs poorly in detecting the number of derived sequences

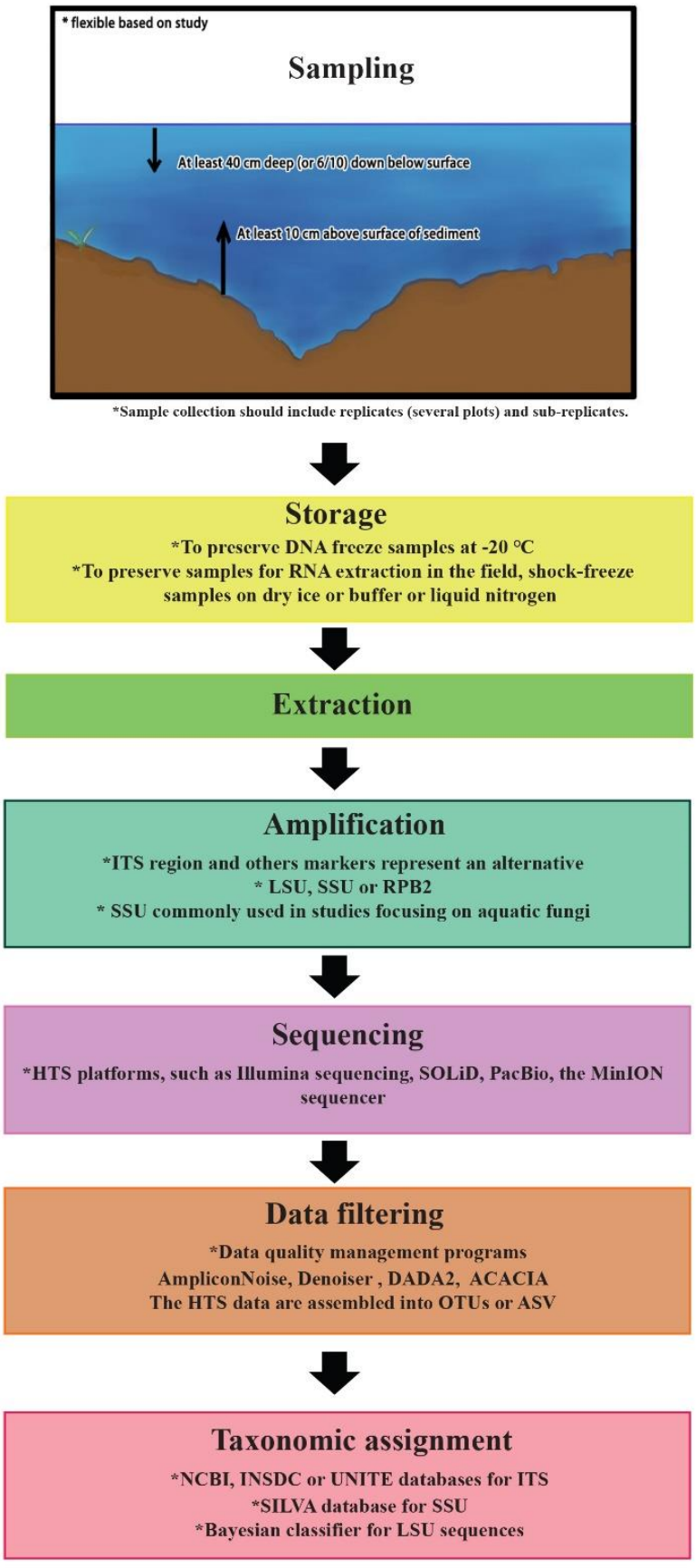


Figure 31 – Overview of the main steps involved in high-throughput sequencing of fungal communities. Fungal diversity studies include sampling, storage, DNA extraction and amplification, sequencing, data filtering and taxonomic assignment. The amplification step is not required for shotgun sequencing.

(Quince et al. 2009). Data quality management programs designed for HTS such as AmpliconNoise (Quince et al. 2011), Denoiser (Reeder & Knight 2010), DADA2 (Divisive Amplicon Denoising Algorithm) (Rosen et al. 2012), UNOISE2 (Edgar 2016) and ACACIA (Bragg et al. 2012) are recommended compared to the standard read-score-based base-pair pruning. AmpliconNoise, UNOISE2 and DADA2 can also detect sequence chimeras which can affect diversity estimates (Fonseca et al. 2012, Prodan et al. 2020). To determine sequence similarities, global alignments of markers such as LSU and SSU can be processed using packages developed to analyze community data such as Mothur (Schloss et al. 2009).

Phylogenetic distance between communities can be analyzed based on global alignment using UniFrac which can exploit similarities and differences between species (Hamady et al. 2010). However, such a method is more common with bacterial data since methods based on global alignments are not recommended for the ITS region due to its high variability and length (Tedersoo & Lindahl 2016). Pairwise alignment is more suited for ITS data and several pipelines including CLOTU (Kumar et al. 2011), LotuS (Hildebrand et al. 2014), PipeCraft (Anslan et al. 2017), PIPITS (Gweon et al. 2015), PlutoF (Abarenkov et al. 2010) and Sequence Clustering and Analysis of Tagged Amplicons (SCATA) (Durling et al. 2011) can be used to analyze ITS sequences derived from HTS. The HTS data are assembled into OTUs based on complete-linkage or single-linkage clustering (Huse et al. 2010). For a fungal community, a 98% similarity threshold is recommended and as a result, all sequences will be at most 2% different from each other in a complete-linkage clustering whereas, in single-linkage clustering a sequence is at most 2% different from any other sequence (Blaalid et al. 2013). The algorithms of complete linkage clustering are affected by the seed sequences which is based on the sequence length or frequencies whereas in single-linkage clustering, a greedy algorithm is implemented whereby clusters expand until there are no similar sequences (Zhang et al. 2000). As single-linkage clustering is not affected by the seed sequence, the same OTU is obtained regardless of the chosen sequence to define the OTU (Huse et al. 2010). Single-linkage clustering can therefore be better suited to deal with sequencing errors, but it can also result in large clusters if the OTUs are not phylogenetically well distinguished from their neighbours (Huse et al. 2010). There are also methods that can resolve ASVs, which can keep all unique sequences without a fixed dissimilarity threshold (Callahan et al. 2016, Amir et al. 2017). These methods can distinguish between sequences down to single-nucleotide difference. The ASV methods can provide finer resolution compared to OTUs (Kopylova et al. 2016). As ASVs combine the benefits of subsequent analysis of closed-reference and *de novo* OTUs, they are reproducible in future studies (Callahan et al. 2017). However, the ASVs approach keep less sequences than OTUs approach, eliminating sequences from species that are both rare and phylogenetically unique (Joos et al. 2020).

Taxonomic assignment

Taxonomic classification of OTUs and ASVs can be implemented based on phylogenetic placement or BLAST-based similarity searches in NCBI, INSDC or UNITE databases for ITS (Lücking et al. 2020), SILVA database for SSU (Pruesse et al. 2007) or a Bayesian classifier for LSU sequences (Liu et al. 2012). It is recommended to use the most common sequence in each OTU for taxonomic classification. The UNITE database offers detailed taxonomic annotation and it is recommended over INSDC and NCBI due to the presence of incorrectly annotated and chimeric entries on these database (Droege et al. 2019). To analyze ITS sequences from HTS, it is recommended to trim large part of the SSU, LSU and the 5.8S region as similarity searches on BLAST favor long sequences and conserved sequence segments (Goodwin et al. 2016). Identification of taxa based on the best BLAST hits are not always accurate (Christen 2008, Kang et al. 2010, Bhunjun et al. 2020) and accurate identification requires robust phylogenetic analyses. The taxonomic analysis software MEGAN can be used to analyse phylogenetic composition and diversity based on BLAST results (Huson et al. 2011). The Bayesian classifier assigns queried LSU sequences based on the reference database and it also provides a bootstrap value for each queried taxon (Liu et al. 2012). There is currently a lack of reference sequences in the Bayesian classifier

database, but since the LSU region is conserved, sequences from un-sequenced lineages can be assigned to higher taxonomic ranks (Xue et al. 2019). There are several packages available on the programming environment R which can be used to analyze phylogenetic composition and diversity such as adiv (Analysis of biodiversity) (Pavoine 2020), hilldiv (Alberdi & Gilbert 2019), iNEXT (Hsieh et al. 2016), metacoder (Foster et al. 2017) and phyloseq (McMurdie & Holmes 2013). The adiv package can be used to quantify species-based, trait-based and phylogenetic diversity within communities or between communities (Pavoine 2020). The hilldiv package can be used for diversity analyses using OTUs and ASVs (Alberdi & Gilbert 2019). The iNEXT package can be used to quantify species diversity in a sample by using species richness, Shannon diversity and Simpson diversity which are the most widely used species diversity measures (Hsieh et al. 2016). The metacoder package can be used to evaluate taxonomic coverage or displaying differences in taxon abundance between communities (Foster et al. 2017). The phyloseq package can be used to analyse and graphically display complex phylogenetic sequencing data that has already been clustered into OTUs (McMurdie & Holmes 2013). The SCATA pipeline provides an analysis framework for the identification of OTUs by clustering database references and sample sequences (Durling et al. 2011).

Different sequencing platforms for HTS and their impact on fungal research

The first HTS platform was the Roche 454-sequencing technique (Margulies et al. 2005) and it was used in some of the first fungal ecology studies (Buée et al. 2009, Jumpponen & Jones 2009, Öpik et al. 2009). It has also been used for shotgun sequencing of genomic DNA/cDNA and in-depth sequencing of PCR amplicons (Lindahl et al. 2013). The 454-sequencing technique can yield 1–1.5 million reads with a length of around 400–500 bases which make it ideal for covering either ITS1 or ITS2 region (Slatko et al. 2018), but it is susceptible to insertions and deletions in homopolymer-rich DNA regions (Goodwin et al. 2016). The ITS region can be subjected to extensive sequencing errors on platforms such as 454-sequencing which could be due to the occurrence of homopolymers which is the repetition of a single nucleotide (Balzer et al. 2011). Data produced with 454-sequencing can contain several sequences that represent primer dimers, random sequence data or gene segments that were not targeted (Balzer et al. 2011). The 454-sequencing platform was discontinued in 2016.

The Ion Torrent (Thermo Fisher Scientific) which was introduced in 2011, uses a similar technology to the 454-sequencing, but it is the first HTS platform without optical sensing (Goodwin et al. 2016). Compared to the 454-sequencing, the Ion Torrent has several advantages including short run-time, high yields, and competitive price (Lindahl et al. 2013). This platform measures released protons (pH) directly rather than light and the pH change is approximately proportional to the number of nucleotides detected, allowing for limited accuracy in measuring homopolymer lengths (Goodwin et al. 2016). The Ion Proton Sequencer can yield 60–80 million reads with a length of around 200 bases which make it problematic to cover the ITS region. This platform is also susceptible to errors in homopolymer repeats longer than six base pairs (Rothberg et al. 2011). To our knowledge, the Ion Torrent platform was poorly used in mycology [but see Brown et al. (2013), Geml et al. (2014), Young et al. (2014)].

Several different HTS platforms are now available, and they mainly differ in terms of quality, quantity and biases of the resulting sequence data (Reuter et al. 2015). Illumina sequencing is one of the most widely used HTS platforms due to its high-quality reads and massive throughput (Nilsson et al. 2019a). Illumina (Illumina, Inc.) sequencing has been used extensively for studies on fungal communities, but it can have limited application due to its short-read lengths of 2 x 300 bp in Illumina Miseq, 2 x 250 bp in NovaSeq or less (2 x 150 bases) in other platforms such as NextSeq and HiSeq. Illumina have an overall error rate below 0.01% across the models (Reuter et al. 2015). The MiSeq Illumina system can cover amplicons with read lengths of around 550 bases which makes it ideal for metabarcoding studies of fungi (Nilsson et al. 2019a). The sequencing platform SOLiD (Life Technologies) can yield up to 4.8 billion reads but has limited application in fungal communities' studies due to its short-read lengths. This platform is composed of a series of

probe–anchor binding, ligation, imaging, and cleavage cycles to elongate the complementary strand (Goodwin et al. 2016). The SOLiD platform displays high accuracy, but it is susceptible to errors in AT-rich and GC-rich regions (Goodwin et al. 2016). The requirement for a PCR amplification step in HTS introduces bias in read distribution, thus affecting coverage and third-generation sequencing technology were developed to address this limitation (Cao et al. 2017).

PacBio RS (Pacific Biosciences), also known as Single Molecule Real-Time (SMRT), is the first third-generation sequencing platform which was introduced in 2011. This platform is based on single-molecule and real-time sequencing which produces long read with lengths of over 10 kilobases. PacBio has a high raw error rate, but this issue is overcome by using the consensus method, which is a built-in option for PacBio and synthetic long-reads. This results in highly accurate results, but it generates fewer reads compared to Illumina platforms (Ritter et al. 2020, Tedersoo et al. 2020, Karst et al. 2021). An advantage of the PacBio real-time sequencing and detection process is that the rate of nucleotide addition can be measured during synthesis and error rates are reduced by avoiding amplification associated bias, intensity averaging, phasing, or synchronization problems (Cao et al. 2017, Slatko et al. 2018). PacBio has also been used to characterize fungal communities even at a global scale (Tedersoo et al. 2021).

The Nanopore sequencer (Oxford Nanopore Technologies) applies third-generation nanopore technology to generate long reads with a length of over two megabases (Payne et al. 2019). The MinION (Mk1B) sequencer is a lightweight, portable device that can be powered by a laptop for real-time analysis, making it ideal for field-based analyses, but it has high error rates (Reuter et al. 2015). Nanopore sequencing is regarded as one of the most promising third-generation technologies, but it has not been extensively used for fungal research due to its high average error rate (6-12%) which results from difficulty in identifying DNA bases from complex electrical signals (Weirather et al. 2017). The NanoReviser can be used to correct base-calling errors, thus reducing sequencing error rate in nanopore sequence data (Wang et al. 2020). Whole-genome sequencing is a widely used application in HTS whereby the most comprehensive view of genomic information and associated biological implications can be obtained (Goodwin et al. 2016). Over 14,000 genomes are currently in the US National Center for Biotechnology Information (NCBI) genome repositories, of which 1,090 genomes are from fungal species (Goodwin et al. 2016, Aylward et al. 2017). Bioinformatics analyses of genome data have resulted in the identification of secondary metabolism gene clusters, and this suggests that the capability of fungi to produce secondary metabolites has been underestimated as their gene clusters are silent under standard cultivation conditions (Brakhage 2013). As a result, specific biosynthetic genes can be targeted to produce novel compounds with new bioactivities (Sharma 2016). Comparative genomic analyses can provide insights about the evolution of pathogens and mechanisms of pathogenesis which could be vital for disease management (Sharma 2016).

Fungal communities detected using HTS in freshwater habitats

High throughput sequencing allows the sequencing of thousands to hundreds of thousands of fungi in a single run becoming the method of choice for in-depth analysis of fungal communities (Lindahl et al. 2013). Monchy et al. (2011) applied low-throughput (18S, ITS1, 5.8S, ITS2 and partial 28S region) and pyrosequencing approaches to analyse fungal communities from freshwater samples from lake Pavin and lake Aydat. The low-throughput approach yielded around 280 sequences from both lakes compared to around 100,000 reads from the pyrosequencing approach. Only a few species were shared between the two lakes, which suggests that fungal communities are specific to certain aquatic environments. *Chytridiomycota* species were the most abundant taxa in both approaches. High throughput sequencing was performed using the Roche 454 platform on samples from a lake in Germany (Wurzbacher et al. 2016). Over 1000 fungal OTUs were recovered in this study, but only 23% were classified to family or genus level. The phylum *Chytridiomycota* was the most abundant with the recovery of species from *Nowakowskiella*, *Chyridium* and *Betamyces*. The PacBio circular consensus sequencing (CCS) platform was used to analyse water and sediment samples from a lake using a 4500 base-pair marker which included the SSU-ITS-LSU

region (Heeger et al. 2018). Following validation using a mock community, 947 OTUs were recovered with 486 classifieds to family level, 397 to genus level and 330 to species level. Species from the fungal genera *Cladosporium, Davidiella, Leucosporidium, Penicillium* and *Saccharomyces* were recovered and species from *Chytridiomycota* were the most abundant.

It is hypothesized that nutrient concentration in freshwater systems increases from upstream to downstream as a result of nutrient transfer from terrestrial to aquatic systems via the processes of surface runoff, erosion and leaching (Peterson et al. 2001, Harner et al. 2004). Based on denaturing gradient gel electrophoresis, Liu et al. (2015a) demonstrated that tributaries have a higher fungal community but possess lower community dynamics compared to mainstream. This is supported by the hypothesis that tributaries have more efficient nutrient transport and retention process compared to mainstream (Peterson et al. 2001). However, these hypotheses have not been confirmed using HTS. High throughput technologies have often been used in combination with culture-based methods for an insight into broader-scale patterns of microbial communities in different habitats. However, there are limited studies that have used culture-dependent and culture-independent techniques to investigate the diversity of freshwater fungi. Previous studies have demonstrated that culture-dependent and culture-independent techniques are consistent in determining the dominant taxa, but the diversity is usually underestimated by culture-dependent approaches (Pitkäranta et al. 2011, Torres-Cruz et al. 2018, Deaver et al. 2019). It is also important to emphasize the need for metadata sharing and storage for scientific reproducibility and comparability across HTS studies worldwide. Global initiative for soil (e.g., Global Soil biodiversity Initiative, https://www.globalsoilbiodiversity.org/) and oceans (e.g., TaraOceans, http://ocean-microbiome.embl.de/companion.html) are already available, but the freshwater environments have been overlooked. Other initiatives are currently ongoing as part of the international network of Genomic Observatories (GOs) which will provide detailed characterization and monitoring of local biomes (Arribas et al. 2021). This is also important for developing conservation protocols as well as for comparing and understanding ecosystems. Some of the initiatives that will target metabarcoding data from water samples include 1000rivers (https://1000rivers.net/), DNAqua-Net (http://dnaqua.net/), SCANDNAnet (https://www.syke.fi/en-US/Research__Development/Research_and_development_projects/-Projects/SCANDANnet/SCANDNAnet(47361)) and VIGILIFE (https://beauvalnature-.org/en/conservation/programme/spygen-vigilife) (Arribas et al. 2021).

Challenges and future prospects of HTS for freshwater fungi

High throughput technologies have revealed an enormous and unprecedented magnitude of fungal diversity than previously estimated, as they do not only target fungi that produce fruiting bodies or fungi that can be cultured on artificial media (Wu et al. 2019). High throughput sequencing platforms such as PacBio can generate long reads which are important for OTUs classification at lower taxonomic levels (Franzén et al. 2015) and to produce high-quality data for reference databases which currently have a limited number of reference sequences especially for freshwater fungi (Hebert et al. 2018). Due to the lack of reference aquatic fungal entries, the majority of OTUs cannot be classified below the order level (Wurzbacher et al. 2016). Some of the limitations of longer reads include an increase in the possibility of chimera formation and most pipelines are optimized for shorter reads (Heeger et al. 2018). Around 15 petabytes of sequence data are generated every year and this wealth of data is proving a challenge for analysis and infrastructure, requiring innovative storage and bioinformatic approaches (Pop & Salzberg 2008, Schatz & Langmead 2013).

Inter-study comparisons are difficult due to different sampling strategies, choice of different markers, PCR target-associated biases, target sequence length, method-dependent errors, differences in data analyses approaches and presence of chimeric sequences (Quince et al. 2009, 2011, Bellemain et al. 2010, Tedersoo et al. 2010, Taylor & Houston 2011, Krüger et al. 2012, Větrovský & Baldrian 2013). We highlight that to compare fungal diversity or community composition through HTS, it is important to use standardized methods including sampling design,

DNA extraction protocol on sub-samples to avoid biases based on the efficiency of extraction methods, amplify with same markers, and sequencing equimolar DNA/RNA samples in depth (>10,000 reads per sample) (Tedersoo et al. 2010). Chimera-cleaning procedures and error-correcting procedures should be implemented to deal with sequencing errors (Quince et al. 2009, Tedersoo et al. 2010). High throughput sequencing data typically contain a considerable number of singletons which are usually omitted from statistical analyses (Tedersoo et al. 2010) as they can affect sample diversity estimates, but these singletons could represent authentic and rare taxa (Kauserud et al. 2012). Omitting singletons could also have major implication for diversity estimators such as Jackknife and Chao indices as they rely on the abundance of singletons relative to common OTUs (Dickie 2010).

However, beyond these challenges, HTS technologies have improved our understanding of the diversity (Bahram et al. 2021), distribution (Tedersoo et al. 2021), and functional roles of fungi (Nguyen et al. 2016, Bahram et al. 2018, Põlme et al. 2020), in symbiotic and pathogenic interactions with plants (Bahram et al. 2018). It is important to correctly estimate fungal diversity as they play a vital role in the ecosystem (Hyde et al. 2020b, Bhunjun et al. 2022, Phukhamsakda et al. 2022), but the functional importance of an individual fungus in nature remains unknown (Schmit & Mueller 2007). Furthermore, an increase in the number of virulent infectious diseases caused by fungi could pose a worldwide threat to food security (Hyde et al. 2018, Bhunjun et al. 2021). In this context, a better understanding of different lifestyles of fungi and their interactions is therefore important for plant biosafety. The identification of fungal pathogens undetected by earlier approaches can be important for effective quarantine measures.

The ability of HTS to target unculturable community can play a major role in the understanding of these communities, which could lead to the development of new media that can be used for their cultivation (Cao et al. 2017). An example is an axenic growth medium which was designed based on the genome data of the bacterium *Tropheryma whipplei*, which can be used for its cultivation (Renesto et al. 2003). The majority of freshwater OTUs recovered by HTS belong to *Chytridiomycota*, which is known to be dominant in freshwater samples (Sparrow 1960, Barr 2001) as parasites (Jobard et al. 2010) or as saprobe (Kagami et al. 2012), but species level classification remains problematic due to the lack of reference sequences.

There are also several annotation tool that can be used to quantify the diversity of fungi recovered from HTS (Nguyen et al. 2016). Tools such as FUNGuild and FungalTraits represent a simple and consistent way to sort HTS data into ecologically meaningful categories (Nguyen et al. 2016, Põlme et al. 2020). The guild concept refers to a group of species, whether related or unrelated, that exploit the same class of environmental resources in a similar way (Root 1967). Therefore, these tools resulted in unprecedented insights into fungal diversity and taxonomic composition in all types of complex environments (Põlme et al. 2020). However, guild assignment relies on accurate taxonomic identification of OTUs, which is problematic due to the lack of reference aquatic fungal entries (Wurzbacher et al. 2016), and several species have been misidentified on public databases such as GenBank (Nilsson et al. 2006, Bhunjun et al. 2020). Therefore, it is important accurately classify OTUs into species, genera, or higher-level taxa using curated sequence databases such as UNITE (Nilsson et al. 2019b) and ISHAM (Irinyi et al. 2015). A large number of OTUs remains unclassified for freshwater fungi and an increase of HTS analyses of freshwater habitats will allow for cross-comparison, thus providing an improved understanding of which OTU clusters represent true fungi (Richards et al. 2015). It will also be beneficial to develop standardization protocols for data analyses, pipelines for clustering and quality filtering of longer reads as most pipelines are designed for the analysis of shorter reads (Heeger et al. 2018).

Conclusion

High throughput sequencing can recover more species and provide a more comprehensive picture of fungal communities compared to traditional techniques, but methodological biases, limitations of markers and mistakes related to base reading represent important challenges which

can lead to artificial results and misleading conclusions (Lindahl et al. 2013). The application of short and long-reads HTS platforms can be used together to overcome challenges related to the characterization of fungal diversity especially in species-rich ecosystems (Ritter et al. 2020). Yet, there is currently limited HTS studies of fungal communities from freshwater habitats which suggests that rare fungal communities in these habitats remain unexplored and this also explains the low diversity of fungi from aquatic compared to terrestrial habitats.

Adaptation for Dispersal in Filamentous Freshwater Fungi

Introduction

Fungi observed from any substrate in freshwater systems, are termed freshwater fungi (Vijaykrishna et al. 2006). These fungi spend the whole or part of their life cycles in the water (Goh & Hyde 1996a). They live in lotic and lentic systems, both of which are present abundantly in riparian and large catchment areas (Goh & Hyde 1996a). The lifestyles of freshwater fungi vary. Some are saprobes of decaying dead wood and leaf litter (Kohout et al. 2012). Others are endophytes inhabiting aquatic plant tissues in submerged, immersed, and floating aquatic flora (Sati & Belwal 2005). Freshwater fungi can also be pathogens causing diseases of freshwater flora and fauna (Ibelings et al. 2004, Stentiford et al. 2013). With regards to the life cycle of their host, and environmental factors, fungi have vast diversity in the freshwater environment.

Filamentous freshwater fungi

Freshwater fungi can be zoosporic, yeasts or filamentous (Cogulet et al. 2018, Jin et al. 2018). Yeasts comprise single, round, or globular cells with or without pseudohyphae. *Aureobasidium pullulans*, *Candida albicans*, *Mrakia aquatica*, *Papiliotrema laurentii*, *Saccharomyces cerevisiae* are examples of yeasts inhabiting freshwater (Calabon et al. 2022). Filamentous fungi are mostly multicellular with thread-like, elongated hyphae. *Ascagilis and Elisembia* belong to this group of fungi. Filamentous freshwater fungi produce secondary metabolites, several of which are of biotechnological value (Jin et al. 2018). Moreover, these fungi are key players in decomposing dead plant and leaf materials. Filamentous freshwater fungi have been discovered in many types of environments and substrates (Dong et al. 2020b). These fungal groups are taxonomically rich, have broad geographic distribution, and high morphological diversity (e.g., shapes of spores: filiform, fusiform, fusoid, obovate, oval, irregular) (Raja et al. 2009, Lepère et al. 2019, Dong et al. 2020b, Bao et al. 2021).

Types of filamentous freshwater fungi

Most filamentous freshwater fungi belong to ascomycetes, though some are basidiomycetes, and both sexual and asexual morphs have been described. The latter include hyphomycetes and coelomycetes. Hyphomycetes, which produce conidia directly on hyphae without any fruiting body, are the most diverse group of freshwater fungi. Their spores have different shapes, colours, sizes and conidial arrangements (Fig. 32). Goh & Hyde (1996a) described four types of hyphomycetes mainly based on their habitats: Ingoldian fungi, which are found exclusively in freshwater, aero-aquatic, terrestrial-aquatic, and submerged-aquatic. Hyphomycetes play a significant role in the freshwater ecosystem as recyclers of a broad range of organic materials, such as cellulose and lignin (Rodrigues & Graça 1997, Duarte et al. 2016).

The asexual morphs of coelomycetes are pycnidia, and only limited number of coelomycetous species have been recorded in freshwater ecosystems (Fig. 33).

The sexual morphs of freshwater fungi produce ascospores that vary in shape, color, and size. These morphological features can be of taxonomic value (Fig. 34) (Dong et al. 2020b).

Dispersal of fungi

The movement of fungi from one habitat to another is termed fungal dispersal. Freshwater fungi possess various adaptations that enhance dispersal of their propagules. Numerous factors

affect dispersal in a positive or negative manner (Magyar et al. 2016, Langenheder & Lindström 2019).

Ingold (1971) outlined three steps with regards to dispersal of freshwater fungi emphasizing hyphomycetes: spore release, transport, and attachment (Rees & Jones 1984). Spores, both conidia and ascospores, constitute the main dispersal propagules of fungi. Upon release from the conidiophore or ascus to the water body, spores are dispersed directly or indirectly (Golan & Pringle 2017). Propagules get entrapped or attached to new substrates and start colonization by forming a germ tube. Under favorable conditions, the newly germinated and colonized fungal populations will produce sexual or asexual structures, which release mature spores into the water body (Tsui et al. 2016). These three steps of dispersal have been previously described qualitatively and quantitatively (Hyde & Goh 2003, Magyar et al. 2016). Dispersal and attachment mechanisms have been previously observed and described through microscopy (Rees & Jones 1984, Jones 1994, Hyde & Goh 2003).

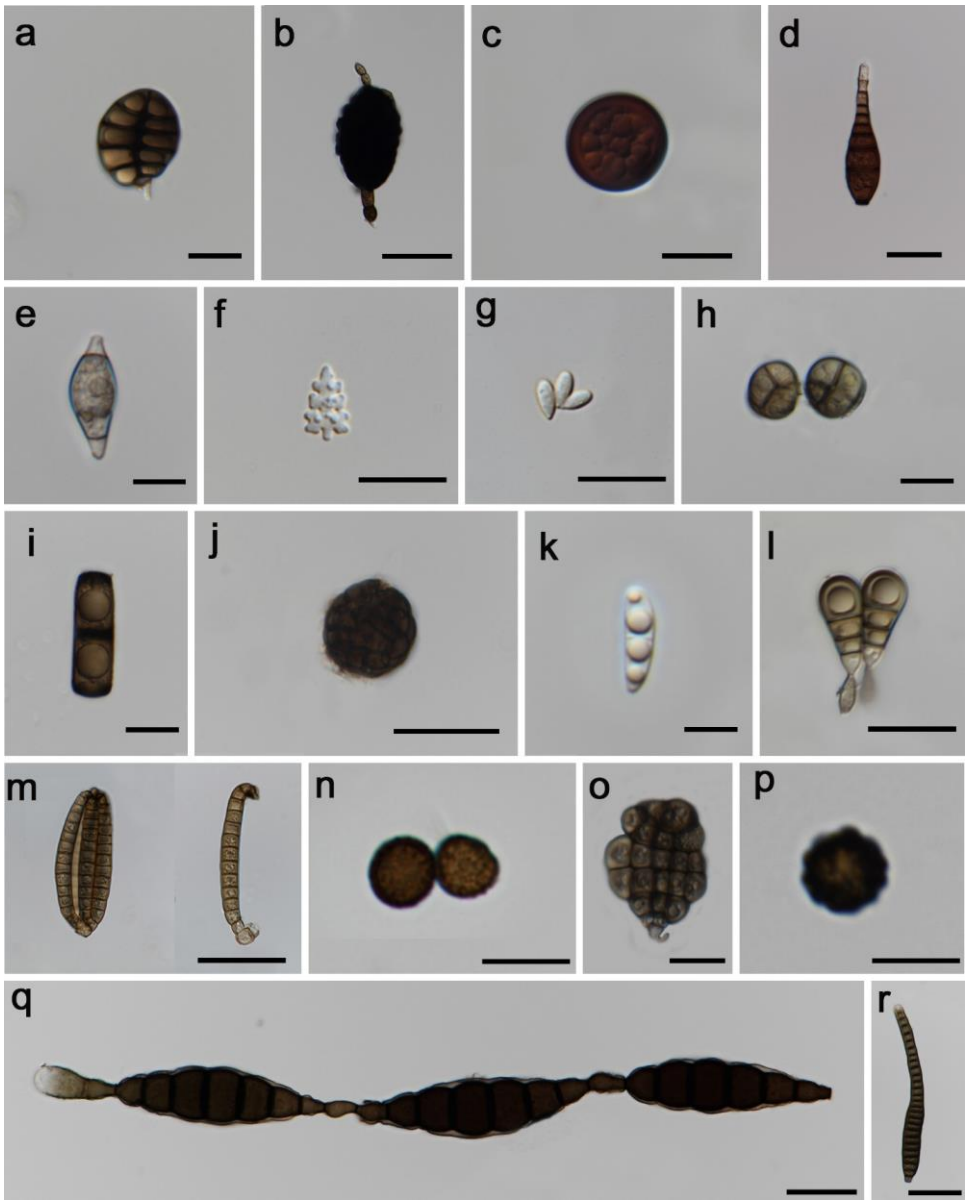


Figure 32 – Diversity of conidial form in freshwater hyphomycetes. a *Canalisporium* sp. b *Dictyospora* sp. c *Acrogenospora* sp. d *Sporidesmium* sp. e *Nakatopsis* sp. f *Dendrosporium* sp. g *Ramichloridium* sp. h Apiosporaceae. i *Sporoschisma* sp. j *Paramonodictys* sp. k *Pleurothecium* sp. l *Brachysporiella* sp. m Dictyosporiaceae. n Torulaceae. o *Canalisporium* sp. p *Memnoniella* sp. q *Taeniolella* sp. r *Distoseptispora* sp. Scale bars: a, d–p, r = 5 µm, c = 10 µm, b, q = 20 µm.

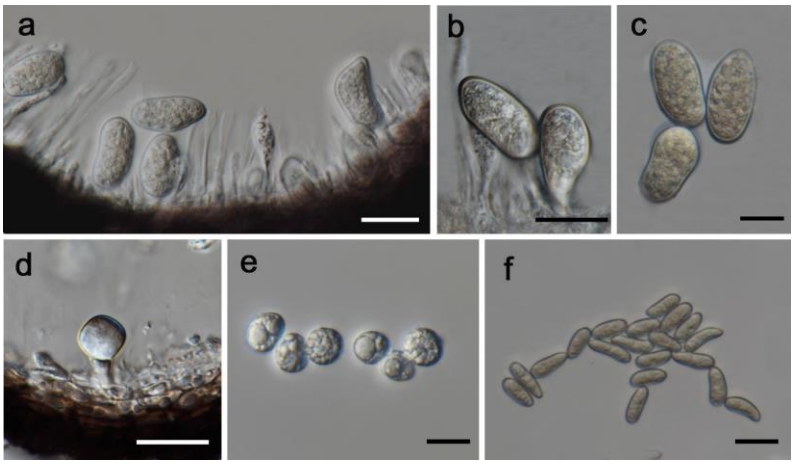


Figure 33 – Diversity of spores in freshwater coelomycetes. a–c Botryosphaeriaceae. d, e *Hongkongmyces* sp. f *Phaeocytostroma* sp. Scale bars: b-f = 5 µm, a = 10 µm.

Figure 34 – Diversity of asci and ascospores in freshwater ascomycetes. a–e Different ascal morphology. f–p Different ascospore morphology. a, g *Ophioceras* sp. b, h *Dyfrolomyces* sp. c, i *Annulatascus* sp. d, j, f Aliquandostipitaceae. e, k *Longipedicellata* sp. l *Astrosphaeriella* sp. m Pseudohalonectriaceae. n *Zopfiella* sp. o *Boerlagiomyces* sp. p *Kirschsteiniothelia* sp. Scale bars: b-p = 5 µm, a, c, k = 10 µm, d = 20 µm.

Sedimentation rate and trapping efficiency of fungal spores in aquatic environments were examined in many fungal species, such as *Anguillospora* sp., *Articulospora* sp., *Candida* sp., *Clavariopsis* sp., *Dactylella* sp., *Flagellospora* sp., and *Heliscus* sp. (Webster 1959, Webster & Davey 1975). Webster (1959) performed experiments using a trapping chamber and showed that shape of spore and water temperature influence sedimentation rate.

Webster & Davey (1984) used a flow chamber made of 50 mm long flat-faced glass capillary tubes to assess the behavior of sigmoid conidia (*Anguillospora longissima, A. furtiva, A. crassa, Flagellospora curvula, Lunulospora curvula*) for dispersal and attachment. The flow and attachment of the conidia were filmed using time-lapse photography. Conidia of *Flagellospora curvula* were initially attached to the substrate surface at one end, while the other end rotated with the water flow. Gradually the free end of the conidia moved towards the surface and also attached on the substrate. Finally, germ tubes were observed at both ends.

Read et al. (1991) investigated the strength of conidial attachment of eight freshwater hyphomycetes, which have different morphological shapes, using a radial flow chamber over a period of 24 hours. Results indicated that tetraradiate and branched conidia have stronger initial attachment to the substrate than sigmoid and ovoid conidia due to having multiple contact points with the substrate. The experiment also indicated that at the higher shear stress, appressoria increased the strength of the conidial attachment.

Importance of fungal dispersal

Most freshwater fungi are cosmopolitan. Due to their mobility and fecundity, similar fungal groups can be observed in different environments. For example, the same fungal genus might be present in both water and land. Niches of fungi overlap when multiple fungal groups share an individual substrate. Newly introduced fungi increase fungal species diversity on the substrate. This may lead to increased decomposition accompanied by rapid loss of nutrition and habitat for the native fungal species (Cadotte 2006). Alternatively, a newly arrived fungal taxon can become invasive and take over endemic taxa (Cadotte 2006, Hui & Richardson 2017). Colonization of an already inhabited substrate in a new environment may increase intra- and inter-species competition, which might lead to species extinction (Read et al. 1992b, Cadotte 2006). Dispersal of fungal spores from its native habitat to a new habitat may overcome the competition due to species extinction. The habitats of freshwater fungi overlap thus fungal species interact not only with each other, but also other taxa in the system (Bärlocher 1982, Rossi 1985, Fryar et al. 2005). These interactions include competition and predation. In the cases where fungi are negatively affected from being prey or weaker competitors, fungal spore dispersal away from the unfavorable conditions and colonization of a new freshwater habitat might confer an advantage (Holyoak 2000, Cadotte 2006).

Fungal dispersal may ensure continuation of a threatened population. Environmental changes can also put pressure on fungal populations making it difficult to maintain their niche (Kneitel & Miller 2003, Cadotte 2006). Most freshwater systems dry up or become iced for variable periods of time (Bond et al. 2008, Mosley 2015, Lennox et al. 2020). Freshwater systems are also subject to change due to natural and anthropogenic factors (Søndergaard & Jeppesen 2007, Kundzewicz & Krysanova 2010, Mosley 2015, Knouft & Ficklin 2017). These changes include eutrophication, and alterations of the physical and chemical qualities of water bodies and may negatively affect freshwater fungi (Mosley 2015, Knouft & Ficklin 2017, Bai et al. 2018).

Dispersal affects species diversity and fungal composition depending on the degree of gene flow between the original and dispersed populations (Janzen 1970, Cadotte 2006, Nathan 2006, Traveset et al. 2013, Pärtel et al. 2016, Zobel 2016, Jordano 2017, Paz et al. 2021). A high level of gene flow maintains genetic homogeneity among populations (Rogers & Rogers 1999, Choudhuri 2014). If gene flow is maintained the geographic range of a species can expand. Alternatively, disruption of gene flow results in genetic differences among populations. Interruption of gene flow occurs when habitats initially harboring populations of the same species become separated, for

example by geological events, such as earthquakes or continental movements (Choudhuri 2014). These types of events lead to isolated populations and result in speciation events.

Factors of importance in the dispersal of freshwater fungi in the ecosystem

Numerous biotic and abiotic factors are pivotal to the dispersal of fungi over long and short distances in both lotic and lentic systems (Goh & Hyde 1996a, Magyar et al. 2016, Langenheder & Lindström 2019) (Fig. 35).

The presence of suitable substrates is essential to fungal growth. Fungal dispersal relies on the type and availability of substrate. When dispersed fungal propagules become attached to suitable substrates, they can successfully colonize them. As decomposition progresses these substrates secede and may induce the rapid movement of fungi to another substrate (Bärlocher 1992a, Magyar et al. 2016). Substrates in freshwater habitats are either autochthonous or allochthonous. The former are organic materials produced in the water system itself and include photosynthetic organisms, dead aquatic animals and bacteria (Lozovik et al. 2007, Doi 2009). Allochthonous substrates refer to organic materials transferred from outside of the freshwater body, such as plant materials, animal remains and dead microorganisms and fungi (Shearer 1993, Lozovik et al. 2007, Doi 2009, Grossart & Rojas-Jimenez 2016). Examples of fungi that have been isolated from allochthonous substrates are *Apostemidium fiscellum* on willow wood, *Hyalinia* sp. on maple wood and *Flammeascoma bambusae* on bamboo wood (Shearer 1993, Dong et al. 2020b). Submerged wood and leaves constitute substrates for freshwater saprobic fungi and provides space for their colonization. For example, *Dictyosporium pandanicola, Submersispora variabilis* was found on submerged wood and *Triscelophorus acuminatus* on submerged leaves (Chan 2000, Boonmee et al. 2021). Allochthonous substrates are often already colonized by endophytic and parasitic fungi before entering a water system. However, freshwater fungi usually displace the already existing taxa, especially if the latter have low tolerance ability in the aquatic environment. Nonetheless, some of these pre-existing taxa may become adapted to the freshwater environment over time (Ingold 1942, Bärlocher 1992a, b, c, Suberkropp 1992, Magyar et al. 2016). In such cases, these taxa can be observed in both freshwater and terrestrial environments. For example, *Neovaginatispora fuckelii* and *Camposporium pellucidum* were found in both terrestrial and freshwater habitats suggesting transitions between the two habitats (Bao et al. 2019, Hyde et al. 2020a).

Fungal spores can be released into the water actively or passively. Ascospores are released passively by deliquescence, whereby the ascus wall dissolves, hence releasing the propagules. Some asci actively discharge spores through apex ruptures by creating internal pressure within the ascus. Different spore releasing mechanisms have been explored due to their diverse ascal morphology (Money 2016). *Bertia*-like fungi release spores by contraction through apical rings. After rupture, the outer wall of fissitunicate asci (e.g., *Jahnula, Ascagilis*) expands and spores are discharged. Goh & Hyde (1996a) described the active ejection of ascospores of tropical freshwater ascomycetes. However, the release mechanism of many fungi remains unclear (Golan & Pringle 2017).

In the lotic system, spores can easily be transported with moving water via leaves over short and long distances (Young et al. 1978, Prochazka et al. 1991, Magyar et al. 2016). For example, freely floating conidia of aquatic hyphomycetes can flow with the water currents over distances of hundreds of meters to a few kilometers and become successful colonizers (Iqbal & Webster 1973, Thomas et al. 1991, Sridhar & Barlocher 1994, Magyar et al. 2016).

Spiraling is the transport of particles over a certain distance in the water and may constitute the principal mechanism of fungal propagule transfer in the lotic system (Minshall et al. 1985, Mulholland et al. 1985, Magyar et al. 2016). Both dissolved and suspended solid particles are important substances for fungal attachment and transport (Bärlocher 1992a, Magyar et al. 2016). Decaying floating logs contribute to long-distance fungal dispersal in the aquatic system (Johansen & Hytteborn 2001, Hellmann et al. 2013, Rämä et al. 2014, Golan & Pringle 2017). Even though water currents comprise a transport mechanism they are likely not the only contributors to fungal

dispersal. If dispersal is dependent solely on water currents it would cause decrease and elimination of fungi from the environment, especially in the lentic system (Magyar et al. 2016). Thus, vectors are essential for fungal dispersal and include mollusks, birds, and fish (Voglino 1895, Zielinski et al. 1999, Correia et al. 2018, Vašutová et al. 2019).

Aquatic and semi-aquatic animals also contribute to fungal dispersal. Feathers, fur, extremities of aquatic vertebrates and cuticles, exoskeleton of aquatic invertebrates can be used to transport spores (Voglino 1895, Stubbs 1995, Zielinski et al. 1999, Green et al. 2008, Magyar et al. 2016, Correia et al. 2019, Vašutová et al. 2019). Spores contain adhesive or echinate surfaces and can be trapped or attached to the hairs and surface of these animals (Magyar et al. 2016). Many studies have been carried out on terrestrial spore transportation by arthropods (Ingold 1953, Upadhyay 1981, Bultman & White 1988, Abbott 2000). Thus, we can hypothesize that the same process occurs in the arthropods that live in freshwater and adjacent areas. Flying insects (damselflies, dragonflies, mayflies) that lay their eggs on decaying wood and leaf litter of freshwater bodies can act as transport vectors as spores can become trapped on their bodies. Amphibian-mediated fungal dispersal has been previously hypothesized (Golan & Pringle 2017, Vašutová et al. 2019). Analysis of gut contents and fecal samples of toads, and salamanders detected fungal spores supporting the above-mentioned hypothesis (Voglino 1895, Lilleskov & Bruns 2005). Fungal propagules can also be attached or trapped on fish scales and fins, or they can be pathogens of fish. Migratory fish provide an ideal vehicle of transport as they migrate over long distances and can thus disperse attached and infectious fungi. For example, *Exophiala pisciphila* infecting *Solmo salar*, *Candida* sp. on salmon and *Phoma* sp. infecting *Plecoglossus altivelis* can be dispersed when their fish hosts migrate (Hatai et al. 1986, Langdon & McDonald 1987, Yanong 2003). However, the precise mechanism of transport of non-infectious fungi is still unclear and requires further study. Water birds may play a role in the long-distance dispersal as fungal propagules get trapped on feathers, legs, beak, and other body parts (Simpson 2000, Magyar et al. 2016). Some terrestrial fungi survive passage through the digestive tract of herbivorous invertebrates (Bärlocher 1981, Magyar et al. 2016). One can therefore speculate that this process can also occur in the freshwater system. Terrestrial fungivorous mites disperse fungal spores directly or indirectly. Though freshwater mites including *Hydrachna conjecta*, *Limnochares aquatica* have been reported (Proctor & Pritchard 1989), their role and that of other fungivorous insects on freshwater spore dispersal remains poorly explored (Schigel 2012, Birkemoe et al. 2018).

Fungal propagules can also be transported via air currents (Golan & Pringle 2017). Terrestrial fungal spores can be deposited in bodies of water via wind (Smirnov & Smirnov 1964). Wind currents that flow across the water surface can directly carry fungal spores. When there are powerful wind currents, fungal propagules might become trapped in the clouds and disperse upon rainfall (Haga et al. 2014, Woo et al. 2018). Spores of Agaricomycetes (e.g., *Peniophora*, *Stereum*), Dothideomycetes (e. g. *Alternaria*, *Aureobasidium*) and Sordariomycetes have been collected from raindrops suggesting that these spores are present in cloud nuclei (Woo et al. 2018). When it rains, the trapped spores will be discharged away from the original water body over long distances. Despite this indirect phenomenon being important, there have been no experimental descriptions of it yet.

Adaptations of filamentous fungi

Fungi that are being dispersed spend time in between their old and new habitat. During that time, they need to survive to successfully colonize the new habitat. Thus, freshwater fungi have many adaptations that ensure safe transport (Table 9). Freshwater fungi have spores with various sheaths, appendages, or wall ornamentations that facilitate dispersal, entrapment, and attachment (Shearer 1993, Wong et al. 1998, Wong & Hyde 1999, Jones 2006, Shearer et al. 2007, Magyar et al. 2016, Tsui et al. 2016).

Spore shape and size

Spore shape and size may be vital for fungal dispersal and adherence to new substrates (Dix

& Webster 1995, Tsui et al. 2016, Golan & Pringle 2017). Fungal hyphomycetes have sigmoid, helicoid, muriform or tetraradiate spores (Fig. 36).

The tetraradiate shape of freshwater hyphomycetes spores such as *Alatospora*, *Articulospora*, and *Tetracladium* may increase the efficiency of spore dispersal, entrapment and attachment on substrates as opposed to other shapes (Webster 1959, Read et al. 1991, 1992a, b, Magyar et al. 2016). Tetraradiate conidia act like adhesive legs (Webster & Descals 1981) and their general shape may act as a tripod to help stabilize them on the substrate. Entanglement with freshwater fauna makes it easier to disperse with the water flow (Ingold 1966). However, when a substrate is suitable, the entangled conidia can produce germ tube and begin its colonization. Increased trapping efficiency has been shown experimentally by Iqbal (1995), who demonstrated that tetraradiate conidia get trapped three times more frequently than sigmoid conidia and thirty times more often than ovoid conidia (Read et al. 1992a). Dang et al. (2007) used three different freshwater hyphomycetes (e.g., *Flagellospora curvula*: curved or sigmoid conidia, *Neonectria lugdunensis:* helicoid conidia, *Tetrachaetum elegans*: tetraradiate conidia) and showed that tetraradiate have a higher trapping efficiency than the other two, supporting previous findings by Read et al. (1992a).

Table 9 Summary of adaptation of freshwater fungal spores and ascomata for their dispersal.

Adapted features	Results of adaptation
Spore	
Setula	Entrapment
Arms	Attachment
	Dispersal
	Entrapment
Polar cap-like appendages	Attachment
Pad-like appendages	Attachment
Threads-like appendages	Attachment
	Entrapment
Mucilaginous sheaths	Attachment
	Floating
Mucilaginous drop	Attachment
Sticky poles	Attachment
Air pockets	Dispersal
Coiling filamentous	Attachment
	Dispersal
	Entrapment
Lipid globules	Dispersal
	Floating
	Food storage
Ascomata	
Long neck	Long distance spore release
Setae	Dispersal
	Entrapment

The spores of some freshwater hyphomycetes contain air pockets, which trap air, providing buoyancy during dispersal via water currents in the lotic system. The muriform conidia of *Canalisporium and Cancellidium*, are examples of propagules with trapped air (Fig. 32a, o) (Tubaki 1975, Dix & Webster 1995, Goh et al. 1998, Tsui et al. 2016). *Helicoon*, *Helicomyces*, *Helicodendron and Spirosphaera* have coiled, cylindrical or barrel-shaped, hollow conidia as revealed in light and scanning electron microscopy (SEM) studies (Fig. 36d, i) (Dix & Webster 1995, Goh & Hyde 1996b, Abdullah et al. 1998, Zhao et al. 2007, Voglmayr et al. 2011, Kuo & Goh 2018).

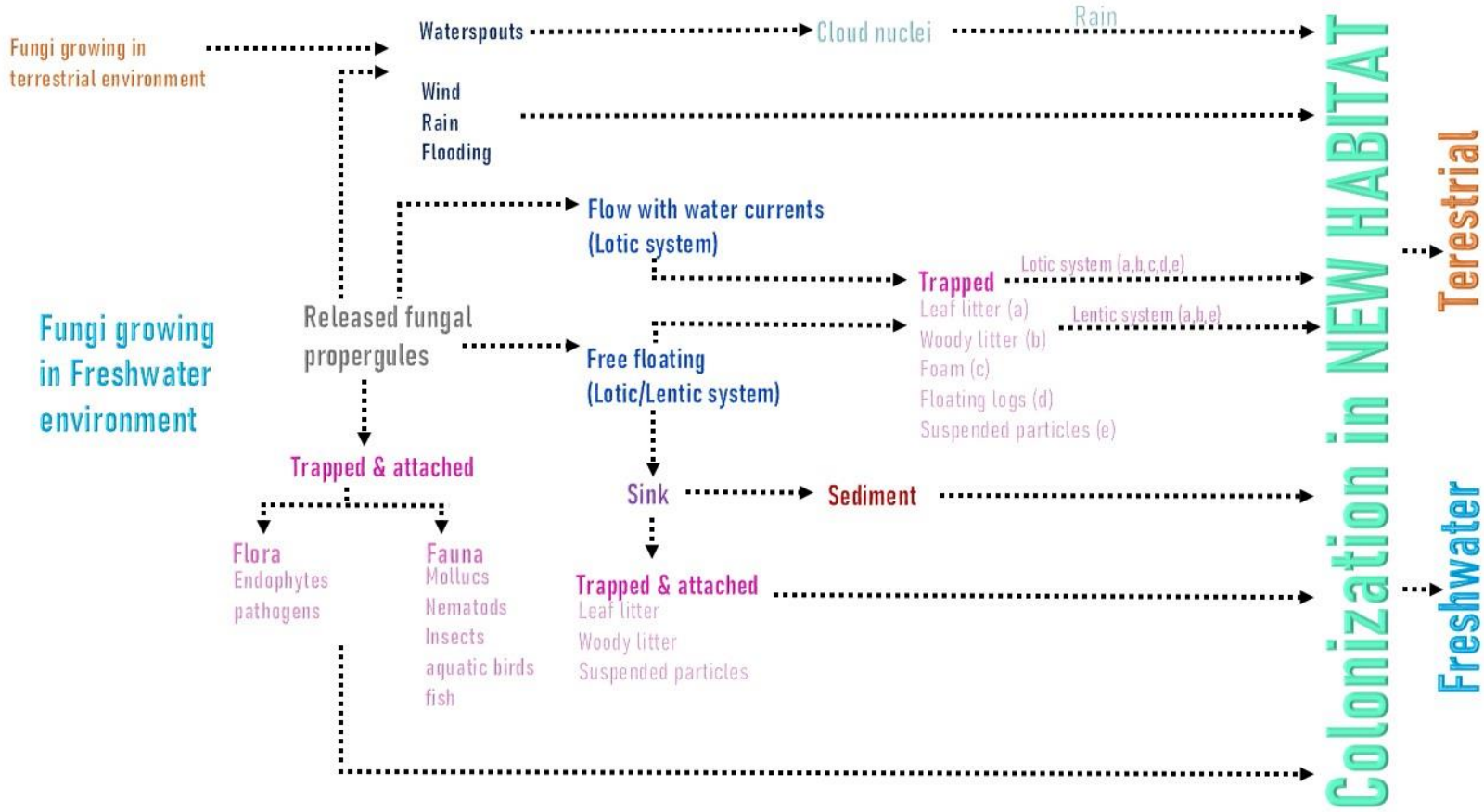


Figure 35 – Factors that are important in the dispersal of freshwater fungi in the ecosystem.

Sigmoid or curved spores flow easily with the water current. Most sigmoid freshwater hyphomycete conidia, like *Anguillospora crassa*, have sticky poles at the ends. Webster & Davey (1984) experimentally explained the movement, attachment, and the germination of sigmoid spores. Sigmoid shape conidia can roll horizontally, and this may increase the contact surface area with the substrate (Webster & Davey 1984, Hyde & Jones 1989). This shape may facilitate the trapping and attaching of the spore to the substrate (Webster & Davey 1984, Read et al. 1991, Dix & Webster 1995, Tsui et al. 2016).

Ascospores of some freshwater fungi are actively expelled from the asci. Ascospores of species, such as *Aquaticola, Annulatascus, Jahnula* and *Lophiostoma,* are wider at the center creating pressure that helps expulsion from the operculum and away from the substrate. However, ascospores have several different shapes, including those that are club-shaped (e.g., *Lasiospharaeria alexandrae*) and which are easily expelled away from the ascus and cylindrical to filiform ascospores (e.g., *Poaceascoma*, *Ophioceras*) that are dispersed and get trapped (Shearer 1993, Taylor et al. 2001, Hyde & Goh 2003). All these mechanisms may not occur while ascomata are submerged. Hyde & Goh (2003) examined the spore ejection of *Pseudohalonectrica* inside a Petri dish flooded with water and observed that the spores were lying at the base of the dish. This finding indicates that active expulsion can happen underwater. However, not all ascomycetes eject their spores underwater. The ascomata of these fungi may eject and disperse their spores during the dry season, or when the substrate washes away to the riverbank and becomes exposed (Hyde & Goh 2003).

Obovoid conidia (e.g., *Helicascus, Splanchnonema*) can easily flow with the water current and the uncommon j-shaped conidia, which are found on *Bertia convolutispora,* can become trapped and attached strongly with the substrate (Hyde 1995, Dong et al. 2020b). The shape of the ascospores itself may also provide an advantage on release and dispersal (Hyde & Goh 2003).

Mucilaginous material of spore

The ascospores and conidia of some freshwater fungi have mucilaginous sheath or appendages (37). Mucilaginous sheaths and appendages are composed of proteins and polysaccharides, but the composition may vary depending on the fungus (Au et al. 1996, 1997, Qu et al. 2017). These materials enhance the adhesive ability of the spore to the substrate (Digby & Goos 1987). Due to their sticky nature, mucilaginous materials may be used as sticky pads for attachment to new substrates. For example, the arms of tetraradiate-like spores can attach firmly to the substrata using the mucilaginous materials they produce (Read et al. 1992a, b, Tsui et al. 2016).

Conidia surrounded by mucilaginous sheath (e.g., *Dactylaria tunicala, Discula umbrinella*) are common in freshwater (Fig. 37b–e). When these spores are released, the sheath swells and increases the surface area, providing the necessary buoyancy to remain on the air-water interphase rather than sink into the sediment. Spores with sheaths can be easily attached to flowing particles and animals (Tsui et al. 2016). The sheath also protects the spore hence it can reach its destination securely (Read et al. 1992a, b). *Annulatascus, Jahnula, Kirchsteiniothelia, and Lophiostoma* are examples of ascospores with mucilaginous sheaths. For some ascospores, the sheath may act as a head and tail (*Loramyces juncicola*) when sinking into the water (Hyde & Goh 2003).

Ascospores can produce mucilaginous appendages either at one or both ends (Fig. 37g–k). These pad-like structures act as glue that adheres strongly to the substrate (Hyde & Goh 2003, Shearer et al. 2007, Tsui et al. 2016). *Annulatascus hogkongensis, Ascagilis bipolaris, Flabellascoma fusiforme, Mamillisphaeria dimorphospora, Neotrematosphaeria biappendiculata* are examples of freshwater fungi that have pad-like mucilaginous appendages (Dong et al. 2020b). The appendages of some ascospores unwind into long threads after release into the water, which may help entanglement with substrates (Fig. 37i–k). *Halosarpheia*- and *Aniptodera*-like groups have this type of appendage (Shearer 1993).

Ascospores may also release a mucilage drop at the tip (Fig. 37a). Even though this type of spore has been observed in freshwater (e.g., *Ophioceras, Pseudohalonectria*), it is primarily found in the marine environment (Taylor et al. 2001, Cai et al. 2002). When the spore reaches a substrate, the mucilage drop may act as the sticky pad for attachment (Rees & Jones 1984, Webster & Davey 1984, Hyde & Goh 2003). This may aid the spore to stand against the water flow.

Spore appendages

Many freshwater hyphomycetes bear spores with appendages, which are likely functionally important for dispersal and attachment (Hyde & Goh 2003) (Fig. 37). Some spores have setula (e.g., *Dictyocheata, Menisporopsis*), short hair-like structures, which can entrap/attach to bodies of

aquatic insects, nematodes, and mollusks (Abbott unpublished). McVey & Gerdemann (1960) demonstrated this phenomenon experimentally using *Leptodiscus terrestris*. Spores with arms (e.g., *Clavariopsis aquatica, Sporidesmiella sp.*) are well adapted for direct dispersal as they can be trapped in substrates and floating colloidal particles (Goh & Hyde 1996a). Further, arms have buoyancy ability, and that may induce floating and aid dispersal (Cunnell 1958).

Some freshwater ascomycetes (e.g., *Aniptodera*, *Halosarpheia*) have polar cap-like appendages that unravel to form viscous polar threads. These appendages may help to trap or entangle the spores themselves with living or non-living substrates and be transported along to new environments (Jones 1994). Ascospores that have filamentous, pad-like, or viscous thread-like appendages (e.g., Annulatascaceae, *Cateractispora* sp., *Phomatospora berkeleyi*, *Thailandiomyces* sp.) can get trapped onto floating particles (small leaf and woody litter debris) and become attached to new substrates (Ho & Hyde 2000, Hyde & Goh 2003) (Fig. 37).

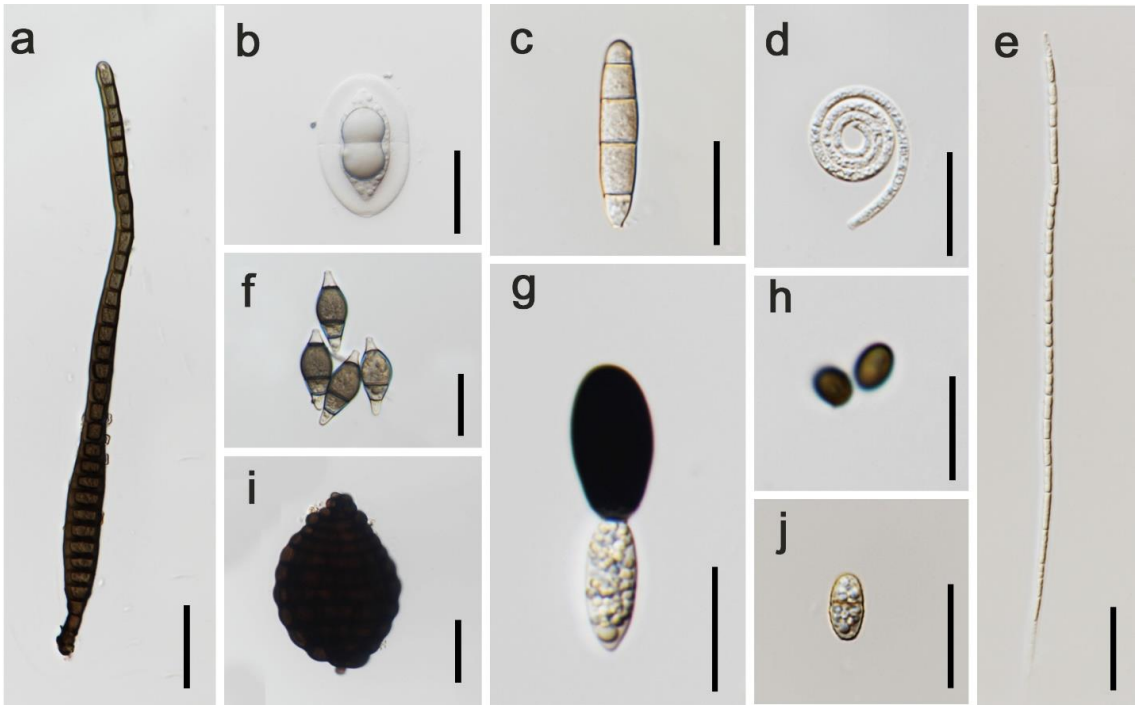


Figure 36 – Diversity of shape and size of spores. A *Distoseptispora* sp. (distoseptate, obclavate or cylindrical filamentous-like conidia). b Immature *Caryospora* sp. (fusiform to broad-ellipsoid large ascospores surrounded by mucilaginous sheath). D *Neohelicosporium* sp. (loosely coiled conidia). e *Ophioceras* sp. (filiform, fusoid to cylindrical ascospores). f *Nakatopsis* sp. (fusiform conidia). g Fuscosporellaceae (acrogenous, ellipsoidal to obovoid conidia). h Bionectriaceae (sub-globose to ovoid conidia). i *Helocoon* sp. (acrogenous, helicoid, tightly coiled conidia). j *Paraniesslia* sp. (fusoid asospores). Scale bars: c, d, f, h–j = 5 µm, a, b, e, g = 10 µm.

Lipid globules

Lipid globules within spores can act as floatation devices in the freshwater environment (e.g., *Amniculicola guttulata*, *Ascosacculus fusiformis*, *Chaetosphaeria guttulata*, *Magnisphaera spp.*, *Purpureofaciens aquatica*, *Sporoschisma* spp.). Further, these structures serve as food reserves until attachment and germination on the new substrate (Hyde & Goh 2003).

Adaptations of ascomata

Freshwater ascomata have evolved to survive in the aquatic environment and are important for spore dispersal. The ascomata of some freshwater fungi (e.g., *Aliquandostipite*, *Ascagilis*, *Megalohypha*, *Jahnula*) attach to the substrata by a stalk, which can withstand the water current. Dispersal of ascospores mainly depends on ascus dehiscence or deliquescence (Hyde & Goh 2003).

In deliquescence, release is passive, and spores can attach to the adjacent substrate. Ascomata can be either long or short necked. The likelihood of dispersal of spores released from the former is higher than that of the spores released from fungi with short neck, immersed ascomata (Hyde & Goh 2003). Spores of short neck ascomata can only reach the boundary layer when they are released actively. The spores of long neck ascomata can easily reach the boundary layer upon release and move with the water current. *Lucidascocarpa*, *Ophioceras*, *Pseudoastrosphaeriell*a, *and Pseudohalonectria* are examples of freshwater fungi with long necked ascomata (Fig. 38).

Long necks are stout and most ascospores aggregate at the end of the neck like gelatinous materials (Hyde & Goh 2003). These gelatinous materials enhance the attachment of released spores, ascomata neck or entire ascomata to the surface of the moving material.

Presence of setae around the ascomata of some freshwater fungi, such as *Chlamydotubeufia and Neoacanthostigma* like-fungi, may facilitate entrapment on the hairs of aquatic animals and induce dispersal (Abbott 2000).

In summary, freshwater fungi have developed several adaptations over evolutionary time. These are features that aid dispersal and attachment making freshwater fungi better suited to their environment.

Impact of Metal Pollution on Freshwater Fungi: From Cellular Targets to Ecosystems

Introduction

Freshwater habitats are critical natural resources, sustaining around 9.5% of the total biodiversity (Dudgeon et al. 2006, Dudgeon 2010), and accountable for about 70% of annual C flow in the planet (Battle et al. 2000, Battin et al. 2009). They comprise less than 3% of the earth's total water, with only 0.006% constituting the river network (Shiklomanov 1993). Rivers provide a wide range of cultural and economic benefits vital for survival and human well-being, such as clean drinking water, hydroelectric power, and biodiversity. Yet, rivers are one of the most exploited ecosystems around the world (Bailey et al. 2005, Vörösmarty et al. 2010), facing threats such as degradation, fragmentation, and pollution (Geist 2011, van Rees et al. 2021). Rivers are generally under-researched compared to the marine and terrestrial biodiversity, especially in ecosystem functioning and conservation strategies (Millennium Ecosystem Assessment 2005, Mazor et al. 2018). Therefore, it is pertinent to develop multilateral management policies to recover or conserve such vital ecosystems and associated services that support our society and economy (Tickner et al. 2020). But to fulfil the goals of the policies, it is imperative to attain a comprehensive understanding of the factors impacting the ecosystems.

Small streams represent around 80% of the entire river network, which are ideal for studying the impact of stressors as they are the primary interface between terrestrial (where the intense anthropogenic activity takes place) and aquatic systems (Lowe & Likens 2005, Downing et al. 2012). In forested streams, allochthonous leaf litter is the primary source of carbon and energy, maintaining food webs (Webster & Benfield 1986, Gessner et al. 1999, Richardson & Moore 2007). Leaf litter decomposition in streams is a critical functional ecosystem process, guaranteeing its integrity and health (Cummins 1973, Vannote et al. 1980, Lecerf et al. 2005, Allan & Castillo 2007). Fungi, particularly aquatic hyphomycetes, play a vital role in the transfer of energy and nutrients locked up in the leaf litter to invertebrates and higher trophic levels (Cadisch & Giller 1997, Gessner & Chauvet 2002, Canhoto & Graça 2008, Battin et al. 2009). Aquatic hyphomycetes improve leaf litter's nutritional quality and palatability via enzyme production, which is vital for invertebrates. They produce a broad spectrum of extracellular enzymes (e.g., proteases, pectinases, cellulases and hemicellulases; Krauss et al. 2011) capable of degrading a wide range of recalcitrant compounds found in the leaf litter, such as lignin, cellulose (Webster & Benfield 1986, Gessner et al. 1999), proteins and lipids (Bärlocher 1985, Zemek et al. 1985) to more labile molecules (Bärlocher 1985, Sridhar et al. 2001, Lecerf et al. 2005).

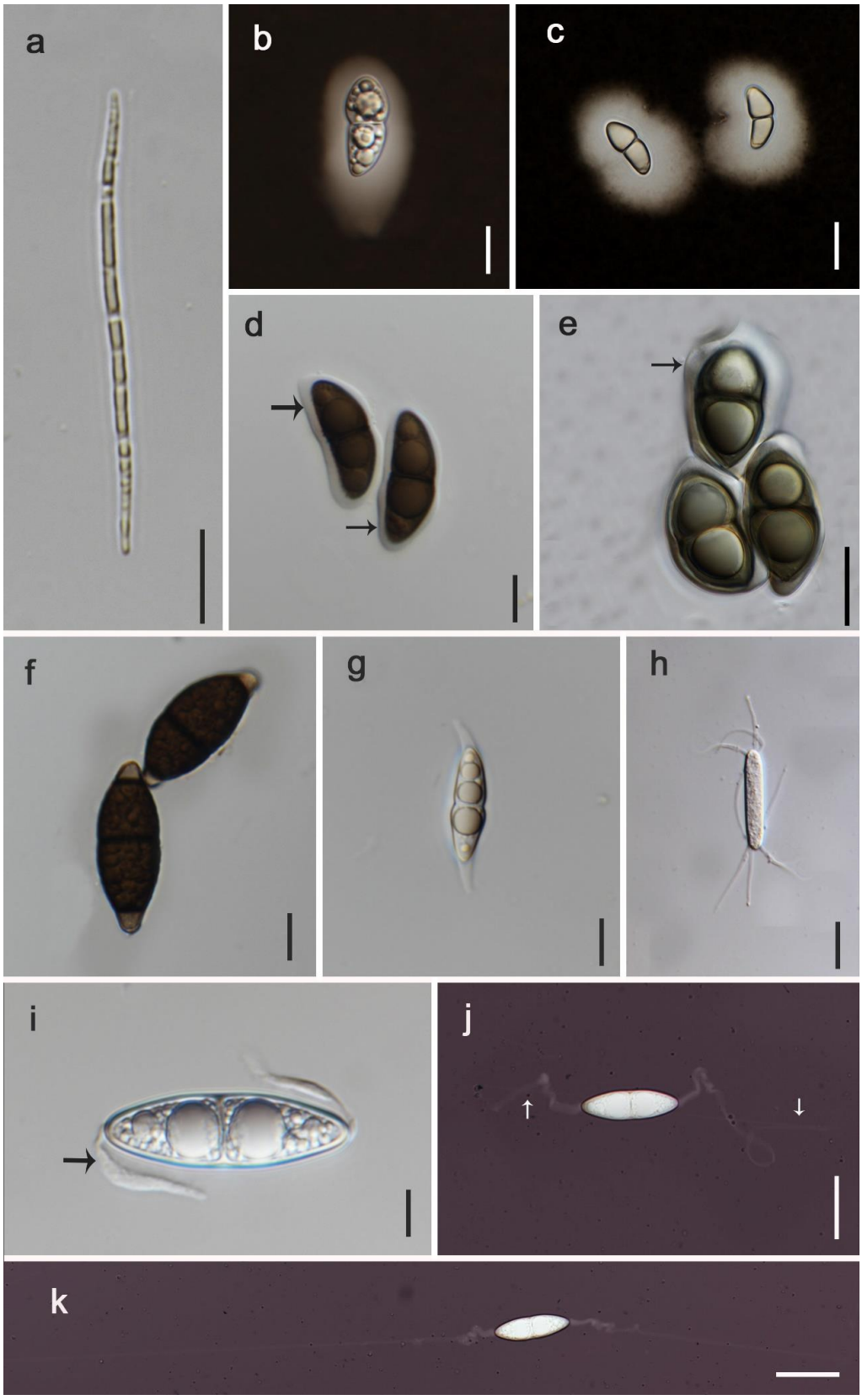


Figure 37 – Spore sheaths and appendages. a *Ophioceras* sp. b, c *Longipedicellata aquatica* (stained with Indian Ink and non-stained area indicate the sheath). d *Kirschsteiniothelia* sp. (arrow: mucilaginous sheath). e *Caryospora* sp. (arrow: mucilaginous sheath). f *Savoryella* sp. (polar hyaline end cells). g *Lophiostoma* sp. (Ascospores with bipolar appendages). h *Chaetospermum* sp. many polar appendages i-j Ascospores with appendages. i-j uncoiling appendages and formed long threads (stained). –Scale bars: a–i = 5 µm, j, k = 20 µm.

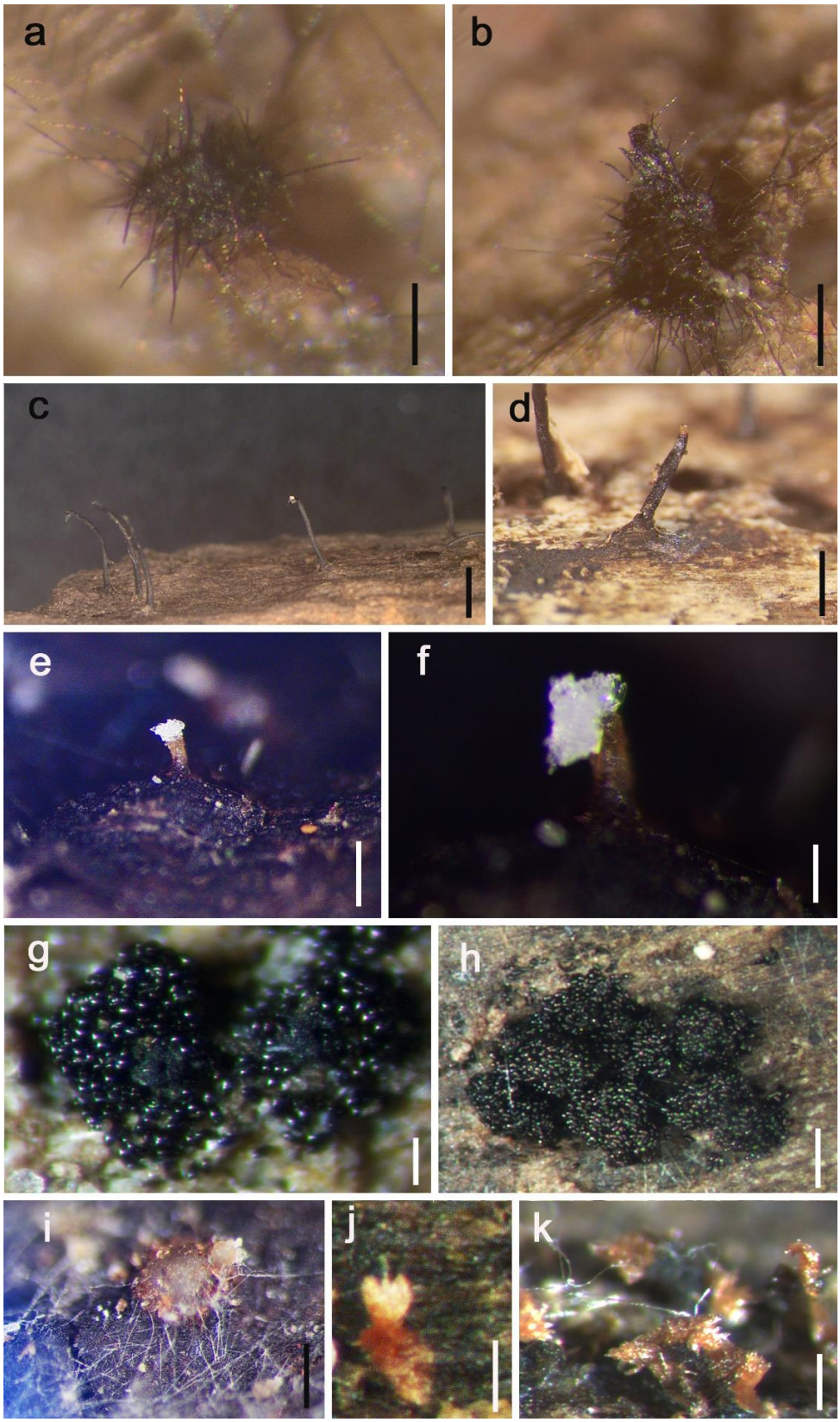


Figure 38 – Diversity of ascomata. a, b *Boerlagiomyces* sp. (seta around ascomata: easily trapped by a vector). c, d *Ophioceras* sp. (immersed ascomata with a long neck: important to long distance spore dispersal). e, f Annulatascaceae (partially immersed and occasionally soft ascomata with short ostiole; Spores come out through the ostiole). g, h *Caryospora* sp. (well clumped released spores; easy to trap on substrate and given extra protection to spores in inside clump while moving with water currents). i–k Pseudohalonectriaceae (partially superficial ascomata; releasing spores out of the fruiting body). Scale bars: a, b, i = 100 µm, c = 500 µm, d, e, h, j = 200 µm, f, g, k = 50 µm.

Aquatic environments, particularly streams, act as a terminal sink for metals discharged into the environment mainly via mining, industrial (Rand 1995), agricultural (Brown & Schroeder 1999) and domestic activities (Brown & Schroeder 1999, He et al. 2005, Geist 2011, Tchounwou et al. 2012). The most commonly occurring metal pollutants in streams are aluminium (Al), arsenic (As), cadmium (Cd), copper (Cu), gold (Au), lead (Pb), nickel (Ni) and zinc (Zn), primarily due to mining activities; metal concentrations in the streams (based on aquatic hyphomycete field experiments) impacted by mining activities are provided in Table 10. Streams impacted by mining activities are overly acidic due to the acid mine drainage system used to retrieve metals from ores. As metals are soluble in acids, it enhances their reactivity, severely impacting aquatic life (Nagajyoti et al. 2010). Metals impact aquatic hyphomycetes responses in various ways – across cells to the ecosystems (Krauss et al. 2001, Morris 2010). Metals such as Cu and Zn influence cellular processes such as inhibition or activation of enzymes and accumulation of reactive oxygen species (ROS) (Miersch et al. 1997, 2005). Other metals, like Cd (Abel & Barlocher 1984) and Al (Chamier & Tipping 1997), inhibit fungal responses, essentially aquatic hyphomycetes growth, sporulation, and biomass production (Sridhar et al. 2001). Metals also impact the aquatic hyphomycete community structure by impoverishing aquatic hyphomycetes species richness in metal-polluted streams (Bermingham et al. 1996a, Niyogi et al. 2001), which may explain why leaf litter decomposition is commonly lower in streams affected by mine drainages (Bermingham et al. 1996a, Sridhar et al. 2001, Duarte et al. 2004, 2006).

Although aquatic hyphomycetes are associated with clean and well-oxygenated waters, metal resistant species are reported to survive (Krauss et al. 2011) and sustain functional activity in polluted waters (Sridhar et al. 2001, Krauss et al. 2003b). The potential of aquatic hyphomycetes to cope with stress (Miersch et al. 1997, Pradhan et al. 2014, Quainoo et al. 2016) mainly corresponds to their ability to trigger adequate cellular defense mechanisms. In general, aquatic hyphomycetes lower cellular permeability (Gadd 1999), produces metabolites, essentially metal-binding proteins (Gadd 1994) and sequester metal in vacuoles (Miersch et al. 1997, Jaeckel et al. 2005, Braha et al. 2007). However, metal tolerance and resistance mechanisms are energy demanding processes that may affect their performance, such as reproduction, growth (Abel & Barlocher 1984, Miersch et al. 1997, Jaeckel et al. 2005, Azevedo & Cássio 2010); and their activities such as litter decomposition (Duarte et al. 2004, 2009, Sridhar et al. 2008).

The severity of aquatic hyphomycetes metal toxicity depends on several factors such as metal types, mixtures, concentration (Gadd 1994) and other stressors or components usually present in the stream water. For example, Cu was more toxic than Zn, negatively impacting aquatic hyphomycete species richness and leaf litter decomposition (Azevedo et al. 2007, Duarte et al. 2008, 2009), but not biomass. Zn and Cu mixtures promoted additive effect on leaf litter decomposition rates (Duarte et al. 2008), while metal mixture with the highest Cu concentrations subjected to a longer exposure time revealed an antagonistic effect on fungal reproduction. Other factors such as stream water chemistry may influence metal toxicity by affecting their availability; Cd supplemented soft water impacted aquatic hyphomycetes sporulation more severely than Cd amended hard waters (Abel & Barlocher 1984). Metals may also bind to essential components required for optimal functioning of aquatic hyphomycetes and influence their toxicity. For instance, Al binds to phosphate resulting in aluminium phosphate, rendering phosphate inaccessible for aquatic hyphomycetes, subsequently lowering growth, sporulation, and biomass production (Chamier & Tipping 1997).

One of the main challenges in ecotoxicology is integrating the ecological relevance of a stressor and simultaneously assessing its sensitivity responses across multiple levels of biological organization. Here, we aim to provide holistic insights on aquatic hyphomycetes response mechanisms to metals, focusing on different levels of biological organization, from aquatic hyphomycetes cellular targets to ecosystems (Fig. 39). This approach will facilitate further research into management strategies for effective and sustainable restoration. We attempt to explore aquatic hyphomycetes response to metals at 1) cellular, 2) individual (species), 3) community and 4)

ecosystem-level responses (Fig. 39) potentially to overcome the gap that most conservation strategies have been based on until now – using individual species or single-level approaches.

What are the cellular responses of aquatic hyphomycetes to metals?

Aquatic hyphomycetes interaction with metals is governed by fungal species, metal types, and environment (Gadd 2008). Aquatic hyphomycetes thrives in metal-polluted waters via mechanisms that mitigate metal toxicity by triggering extracellular and intracellular defence systems (Gadd 2008), which dictate optimal fungal functioning, survival, or death (Fig. 40). Fungi avoid the entry of metals into the cell by decreasing cell wall permeability and transport (Gadd 1994), cell wall biosorption, and the presence of extracellular polymeric substances that promote metal sequestration, precipitation, reduction, electrostatic interaction, or ion exchange (Gadd 1994, Avery 2001, Xie et al. 2020). Physiological mechanisms developed over time confer resistance to aquatic hyphomycetes against metals (Gadd 1994, Au et al. 1996, Braha et al. 2007) via efflux, intracellular compartmentation, complexation, and precipitation of metals (Gadd 1994, Avery 2001).

Extracellular barriers

The cell wall is the primary interaction site between the fungi and the environment (Latha et al. 2018), committed to providing adequate protection to the cells, especially when exposed to harmful agents (Feofilova 2010) such as metals. The cell wall maintains cellular integrity by regulating transport of metabolites, controlling cellular permeability, and protecting the cell from osmotic and mechanical stress (Latha et al. 2018). Metal biosorption by the fungal cell walls could be considered the primary defence mechanism, providing metal resistance to aquatic hyphomycetes (Gadd 1994, Latha et al. 2018). It is evidenced that Cd and Cu adsorption by *Neonectria lugdunensis* Webster, was ten times higher than the intracellular metal concentration (Jaeckel et al. 2005, Braha et al. 2007). Metal adsorption occurs by the physical adherence or bonding of ions and molecules onto the fungal cell surface mainly by electrostatic interaction (Ozdemir et al. 2003) and ion exchange (Yin et al. 2011), which promotes metal sequestration, complexation, and crystallization (Cervantes & Gutierrez-Corona 1994, Gadd 1994, Schiewer & Volesky 1996, Blaudez et al. 2000).

Aquatic hyphomycete cell walls are equipped with polymers of glucan, chitin, melanin, galactosamine, and a wide variety of extracellular polymeric substances (Schiewer & Volesky 1996), such as proteins and polysaccharides. The extracellular polymeric substances are chains of polysaccharide components, protein fractions and phenolic and carboxylic humic-like substances (Xie et al. 2020). These cell wall components provide protection (Schiewer & Volesky 1996, Avery 2001) by binding to cationic metals with different specificity and affinity (Avery 2001). The fungal cell wall encompasses cation and anion exchange (Feofilova 2010) properties, favored by various potential-binding functional groups such as free carboxyl, amino, hydroxyl, phosphate and sulfhydryl groups (Strandberg et al. 1981, Gadd 1994). This enables the cell to be a natural cation or anion exchanger, increasing metal sequestration capacity (Strandberg et al. 1981) and decreasing cell permeability (Gadd 1994). The cell wall-metal binding mechanism of aquatic hyphomycetes is not well explored; however, it is speculated to have resulted from physiological adaptation instead of evolutionary selection pressure (Garcia-Toledo et al. 1985). It is demonstrated that metal-tolerant fungal species exhibit higher metal biosorption rates than less tolerant ones (Krauss et al. 2011). For instance, the non-mutant and cobalt-mutant (achieved by cobalt exposure) isolates of a model filamentous fungus *Neurospora crassa* Shear & Dodge, demonstrated physiological differences in their Co binding capacity and transport blocking mechanisms (Latha et al. 2018). Additionally, metal sorption mechanisms are strongly affected by pH, initial metal ion concentration and exposure time (Lo et al. 1999, Azevedo 2008). A common filamentous fungus *Mucor rouxii* demonstrated a decrease in Pb sorption and the decline in pH, presumably due to the competition between metal cations and the protons for the cell wall binding sites (Lo et al. 1999).

Cell walls of filamentous fungi *Ganoderma lucidum*, and *Aspergillus niger*, respectively, were capable of Zn bioaccumulation and Pb biosorption (Lo et al. 1999). Similarly, an increase in Cd (0–0.1 mM) and Zn (0–0.3 mM) concentrations in the microcosms exacerbated the biosorption capacity of the aquatic hyphomycete *N. lugdunensis* (Jaeckel et al. 2005).

Chelation is another essential strategy conferring metal resistance, accomplished by the secretion of molecules such as enzymes (e.g., laccases) (Pradhan et al. 2014) and organic acids (e.g., citric and oxalic acid) (Gadd 1999) that binds to metal ions to form non-toxic metal complexes (Priyadarshini et al. 2021). Laccases are extracellular multi-copper-containing oxidoreductases secreted by many bacteria, plants, and fungi (Junghanns et al. 2009, Janusz et al. 2020). Due to the high redox potential, laccases play a vital role in metal-stress defence (Wesenberg et al. 2003). They are secreted in excess by fungi undergoing metals-stress; for instance, the laccase activity of the two strains of the aquatic hyphomycete *Clavariopsis aquatica*, was stimulated by Cu (0.5–50 μM of $CuSO_4$) (Solé et al. 2008); while other metals, like Zn, also enhances extracellular laccase activity in terrestrial fungi (Lebrun et al. 2011). Organic acids secretion by fungi also promotes metal detoxification (Gadd 1999) but remains under-researched in aquatic hyphomycetes. For example, wood-rotting fungi secrete both citric and oxalic acids with strong metal-chelating properties that form crystals, promoting metal resistance (Sutter et al. 1984a, b, Sutter & Jones 1985, Jarosz-Wilkolazka & Gadd 2003). The ascomycete *A. niger*

Table 10 Range of metal concentrations in the study locations pertaining to aquatic hyphomycetes field experiments impacted by mining activities.

Location	Metal (mg/L)												Reference
	Al	As	Cd	Cr	Cu	Fe	Hg	Mg	Mn	Ni	Pb	Zn	
England	0.10–2.43	nm	0.0–0.038	0.0–0.042	0.0–0.037	0.05–81.9	nm	4.83–70.4	0.05–14.8	0.0–0.092	nm	0.006–0.243	Bermingham et al. (1996a)
Germany	nm	0.002–0.014	nd–3.2	nd	0.3–13.3	0.05–0.25	nd	nm	1.5–15.3	0.05–2.1	0.0002–1.6	nd–35	Sridhar et al. (2000)
Germany	nm	0.001–0.007	<0.05–2.8	nm	<0.02–13.25	0.05–0.80	nd	nm	0.12–19.8	<0.08–2.23	<0.1 - 1.9	0.427–56.1	Krauss et al. (1998)
India	nm	nm	nm	nm	13–26	41–79	nm	nm	25–51	nm	0.6–18	43–77	Raghu et al. (2001)
Germany	nm	nd–0.007	nd–2.8	nd	nd–13.25	0.07–0.80	nd	nm	0.10–2.3	nd–2.20	nd–1.9	0.10–2600	Krauss et al. (2001)
Germany	nm	<0.09	<0.08–2.17	<0.06	0.02–16.17	<0.05	<0.0005	nm	<0.09–13.67	<0.03–1.93	<0.07–1.62	1.33–1605	Sridhar et al. (2005)
Germany	nm	0.001–0.05	<0.0001–1.57	<0.06	<0.02–15.9	<0.05–<0.5	nd	10.5–378	<0.02–12.9	<0.03–2.1	<0.07–1.5	<0.03–1430	Sridhar et al. (2008)
Germany	nm	0.000–0.026	nd–1.99	nm	nd–9.7	nd–0.06	nd - <0.0005	10–155	nd–11.6	nd–1.7	nd–0.76	nd–1228	Solé et al. (2008)
Portugal	nm	0.47–37.89*	0.09–111.7*	nm	0.83–14.95*	nm	nm	nm	nm	nm	nm	1.08×10^4–204.38*	Seena et al. (2020b)

*Values expressed in μg/L; nd- non-detectable; nm- not measured.

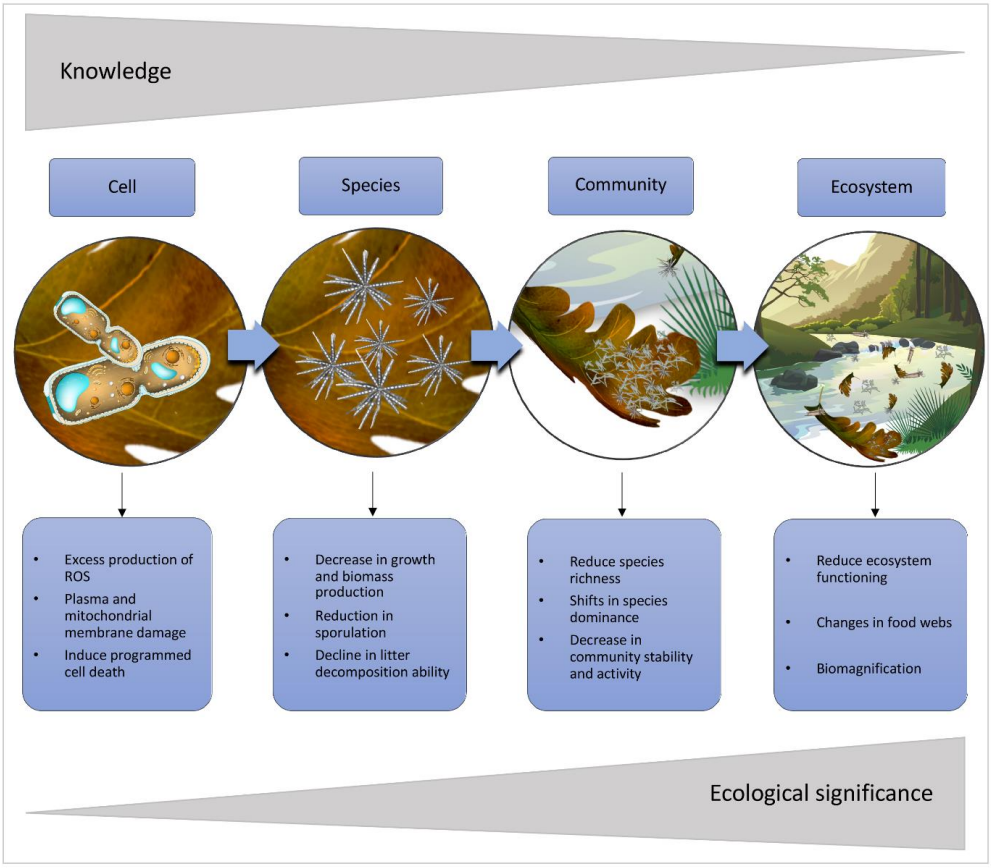


Figure 39 – Impacts of metal pollution on aquatic hyphomycetes at various levels of biological organization.

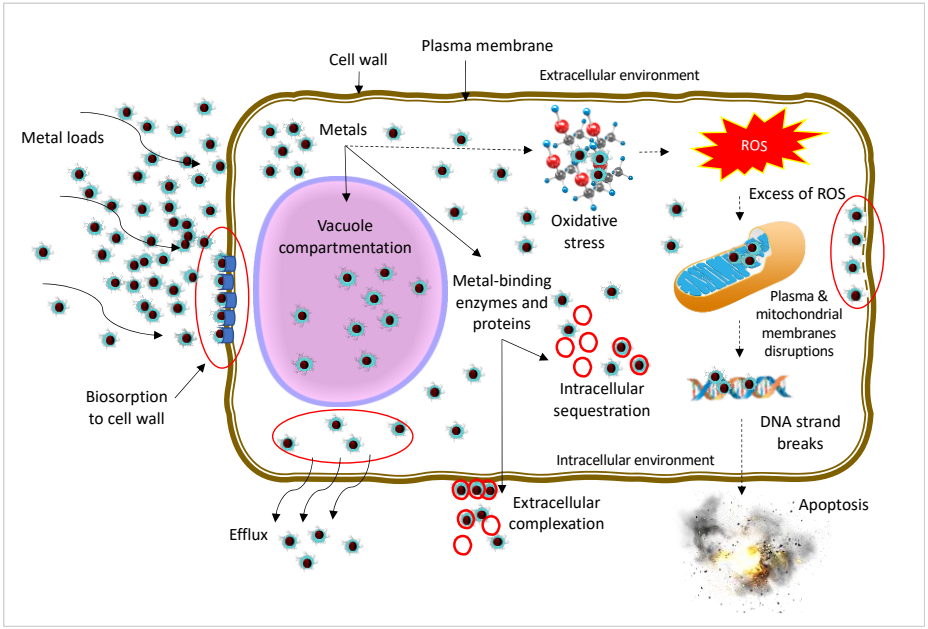


Figure 40 – Schematic representation of the aquatic hyphomycetes cellular response mechanisms to metals. Arrows indicate the potential mechanisms of fungal cells to cope with the metals (i.e., cell wall biosorption, extracellular complexation, intracellular compartmentation, sequestration, and efflux). Dotted arrows indicate possible impacts of high metal loads on fungal cells (i.e., reactive oxygen species generation, plasma and mitochondrial membrane disruptions, DNA strand breaks and ultimately apoptosis).

produces metal oxalates dihydrate crystals in the presence of Ni (Magyarosy et al. 2002), Co, Zn, Cu and Mn (Sayer & Gadd 1997).

Intracellular mechanisms

To cope with the excess metal intake, aquatic hyphomycetes may rely on a variety of intracellular defence mechanisms. Fungi have the potential to alter intracellular traffic (Gadd & Sayer 2014) by metal efflux; this mechanism was responsible for conferring resistance to Cd in *Saccharomyces cerevisiae* (Avery 2001). Metal-binding proteins, such as glutathione and phytochelatins (Guimarães-Soares et al. 2006), also play an essential role in reducing metal toxicity (White & Gadd 1986, Avery & Tobin 1992). In addition, sequestration, transport, and compartmentation of metals (Gadd 2008) in organelles, such as vacuoles (Ortiz et al. 1995), regulates metal availability within the fungal cells. The mutant strains of *S. cerevisiae* (vacuole-deficient) confirmed that the vacuole played a vital role in detoxifying several toxic metals, such as Co, Mn, Ni and Zn (Ramsay & Gadd 1997). A considerable amount of Cd was found in the vacuoles of the aquatic hyphomycete *Tetracladium marchalianum* (Miersch et al. 2005). Interestingly, fungal vacuoles may store Zn for later use, buffering intracellular Zn fluctuations (MacDiarmid et al. 2002). The intracellular mechanisms of aquatic hyphomycetes differ both inter and intra-specifically (Krauss et al. 2011) and with metal types. The plasma membrane metal uptake capacity differed among two strains of *N. lugdunensis* originating from varying heavy metal polluted sites (Braha et al. 2007), indicating distinct metal transport regulation. The aquatic hyphomycete *Varicosporium elodeae*, was more susceptible than *Heliscus submersus* to the toxic effects induced by Cu and Zn. Noticeably, in both fungi, the disruption of the plasma membrane after exposure to Cu (up to 15 mM) was more than Zn (up to 200 mM) (Azevedo et al. 2007).

One of the crucial mechanisms by which metal induces oxidative stress in fungi is by the generation of free radicals, consequently generating a high amount of reactive oxygen species (Pradhan et al. 2015, Hayyan et al. 2016). Reactive oxygen species have a high potential to cause cellular damage when generated in excess, modifying the cellular redox potential, leading to plasma membrane damage by lipid peroxidation (Lin et al. 2006, Petersen & Nelson 2010) and mitochondrial membrane depolarization (Pradhan et al. 2015). The damage caused by lipid peroxidation increases cell permeability to metals (Blackwell et al. 1995). In addition, the enzyme H+-ATPase is responsible for electrochemical protons homeostasis inside the cell (Serrano, 1988). For instance, Cu is a potent depolarizer of cell electrical potential and can inhibit the H+-ATPase at relatively low concentrations (Karamushka & Gadd 1994). In *S. cerevisiae* cells, the activation of H+-ATPase by Cu was much higher than in its absence, which is probably a counter cellular response (Fernandes et al. 2000). Ultimately, metal-induced oxidative stress may promote programmed cell death in aquatic hyphomycetes (Azevedo et al. 2009). The association between reactive oxygen species and programmed cell death was evidenced in filamentous fungi, such as *Aspergillus nidulans* G. Winter, and *Aspergillus fumigatus* Fresen (Mousavi & Robson 2003, Semighini et al. 2006).

To defend against oxidative metal stress and reactive oxygen species formation, aquatic hyphomycetes rely on antioxidant enzymes (Braha et al. 2007), metal-binding proteins, and organellar compartmentation (Avery 2001, Bellion et al. 2006, Azevedo et al. 2007). Fungal antioxidant enzymes donate electrons to neutralize free radicals. For instance, glutathione neutralizes lipid peroxidation by-products, such as hydroperoxide (H_2O_2;) to H_2O by donating an electron and a proton to form oxidized glutathione. Oxidized glutathione is converted back to its reduced form by glutathione reductase. The equilibrium between glutathione and oxidized glutathione is pertinent for regulating cellular oxidative stress (Huang et al. 2010). In addition, glutathione peroxidase converts glutathione reductase to oxidized glutathione when encountered with peroxides/hydroperoxides (Townsend & Tew 2003). Glutathione peroxidase can also act as a binding protein and react with hydroperoxides in the cytoplasm, forming H_2O. Metals such as Cd influence the aquatic hyphomycete cellular redox status by altering the glutathione pool dynamics (Braha et al. 2007). When aquatic hyphomycete species *Articulospora tetracladia* (2 strains), *N.*

lugdunensis (2 strains) and *V. elodeae* were exposed to Cd, a significant increase in glutathione was noted (Miersch et al. 1997). Similar observations were made when three strains of *T. marchalianum* were exposed to Cd, suggesting that glutathione could play an essential role in Cd detoxification (Miersch et al. 2005). In addition, fungal enzymes such as glutathione-S-transferase catalyze the conjugation of glutathione to endogenous and exogenous electrophilic compounds, protecting cellular macromolecules from reactive electrophiles (Townsend & Tew 2003). Besides, scavenging antioxidant enzymes such as superoxide dismutase and catalase convert peroxides to H_2O (Hansberg et al. 2012). Aquatic hyphomycetes antioxidant enzymes respond differently according to metal types and concentrations. Specifically, in the aquatic hyphomycetes, *H. submersus,* the superoxide dismutase and catalase activity was augmented when exposed to Cu, while in *V. elodeae,* only the catalase activity escalated while superoxide dismutase remained unaltered. Zn also enhanced the activity of catalase in both the fungal species; however, superoxide dismutase did not indicate any role in Zn stress (Azevedo et al. 2007).

Aquatic hyphomycetes also cope with metal stress by synthesising thiol peptides (Miersch et al. 2001, 2005), which confer high metal-binding affinity (Romero-Isart & Vašák 2002). The aquatic hyphomycete *Fontanospora fusiramosa* and *Flagellospora curta* amplified the production of thiol compounds as a response to Cd, Zn, and Cu exposure (Guimarães-Soares et al. 2006). Phytochelatins are γ- glutamyl peptides containing cysteine, synthetized in excess by the fungi as a response to metal exposure (Cobbett & Goldsbrough 2002); seven different phytochelatins were synthesized by the yeast *Schizosaccharomyces pombe* when treated with Cd (Grill et al. 1986). In addition, a low molecular weight, cysteine-rich proteins, namely metallothioneins, is acknowledged to play a role in fungal metal detoxification and homeostasis (Cobbett & Goldsbrough 2002). For instance, Cu induced the expression of two metallothionein genes in the ectomycorrhizal fungus *Suillus himalayensis* facilitating Cu detoxification (Kalsotra et al. 2018). Strains of *N. lugdunensis* and the terrestrial fungus *Verticillium* cf. *alboatrum* also indicated elevated production of metallothioneins and phytochelatins against Cd stress (Jaeckel et al. 2005).

Do the aquatic hyphomycetes species respond differently to metal stress?

In general, fungi are highly resistant to metal toxicity, capable of adopting several physiological strategies (Gadd 1999) to guarantee their survival. Under metal stress, aquatic hyphomycetes mainly focuses on channeling energy to maintain essential physiological functions such as metabolic activities (Abel & Barlocher 1984). Several aquatic hyphomycete species are reported from polluted streams (Krauss et al. 2001, Sridhar et al. 2001, 2008), indicating their ability to adapt or tolerate metals. Although only a few studies have attempted to study the impact of metals on aquatic hyphomycete species (Krauss et al. 2011), growing evidence suggests that aquatic hyphomycete physiological responses to metal pollution differ not only between but also within species (Azevedo et al. 2007, Braha et al. 2007, Krauss et al. 2011). Metal response studies at the species level mainly focussed on aquatic hyphomycetes growth, biomass, and sporulation (reproduction); in general, these parameters were mainly impacted by both metal exposure concentration and types, including the metal concentrations at the aquatic hyphomycetes isolation sites.

Growth rates

Growth rates of aquatic hyphomycetes species as well as strains were sensitive to metal types and concentrations. In particular, when aquatic hyphomycete species *Alatospora acuminata*, *Clavariopsis aquatica*, *Flagellospora curvula*, *N. lugdunensis*, and *T. marchalianum* were exposed to Cd ranging from 0 to 100 ppm (Abel & Barlocher 1984), all the tested species displayed a decrease in growth rate; *A. acuminata* being the most impacted. Furthermore, when the species were treated with Cd amended with Ca, Mg, and Zn (0 to100 mg/L), the impact of Cd was alleviated (except for Mg) (Abel & Barlocher 1984). When the aquatic hyphomycete species *H. submersus, T. chaetocladium* and *A. acuminata* were treated with various types of metals (Zn, Cu, Cd and Ni), Cd and Ni were more hazardous than Zn and Cu (Azevedo & Cássio 2010). In another

study, notably, Fe and Mg did not inhibit the growth rates of *A. acuminata*, *Tetrachaetum elegans* and *A. tetracladia*, while Fe stimulated fungal growth (Bermingham et al. 1996b).

The growth of *N. lugdunensis* strains differed significantly along a Cu (0–96 mg/L) gradient (Quainoo et al. 2016), implying the occurrence of metal tolerant ecotypes in the freshwaters. The aquatic hyphomycete species, *A. tetracladia* and *T. marchalianum* isolated from Cu and uranium (U) impacted streams displayed higher metal tolerance than those from non-polluted streams (Miersch et al. 1997, Bergmann & Graça 2020). An 80% growth recovery rate by aquatic hyphomycete strains (*N. lugdunensis*) was observed when metal pre-exposed fungi were transplanted to the metal-free environment (Krauss et al. 2005, Quainoo et al. 2016), indicating metal adaptability.

In addition, morphology and branching patterns also varied when the filamentous fungi *Trichoderma viride* and *Rhizopus oryzae* were exposed to 0.1 mM Cd, Cu and Zn (Gadd 2001). Similarly, the strains of the aquatic hyphomycete *N. lugdunensis* exhibited differences in morphology when exposed to Cu (Quainoo et al. 2016), as well as strains of *V. elodeae* isolated from non- and metal-polluted (U mine drainages) streams (Ferreira et al. 2010).

Biomass

Aquatic hyphomycete biomass essentially impacts the nutrition of invertebrates, and it would be worthwhile to contemplate the distinct impact of metals on fungal biomass production. Generally, the aquatic hyphomycete species were differently impacted by both metal concentrations and types. Notably, aquatic hyphomycete species *T. splendens* and *N. lugdunensis* reduced fungal biomass at 16 mg/L of U, whereas *A. tetracladia* was more resistant (up to 262 mg/L; (Bergmann & Graça 2020). In addition, the biomass of *V. elodeae*, *H. submersus*, *F. curta*, and *Y. graminea* was least impacted by Zn (EC_{50} = 75 – 152 mg/L) but was sensitive to Cu (EC_{50} = 50 – 100 mg/L) (Azevedo & Cássio 2010), whereas *V. elodeae* and *Y. graminea* were severely affected by Cd (5 mg/L) (Azevedo & Cássio 2010).

The origin of fungal strains also dictated the fungal metal resistance and biomass production. Specifically, strains of *A. tetracladia* from non-polluted streams demonstrated a pronounced reduction in biomass production ($EC_{50} \leq 31$ mg/L) than those from metal-polluted streams ($EC_{50} \geq$ 65.2 mg/L) (Pradhan et al. 2014). In addition, a concentration- and time-dependent decrease in biomass production was displayed by *A. tetracladia*, *Phoma* sp., and *C. aquatica* when exposed to Cu oxide (Pradhan et al. 2014). Likewise, the time of exposure to metals such as Cd, Cu and Zn (up to 100 µM) reduced the biomass production by the zygomycete *Mucor racemosus* (Miersch et al. 2001). Notably, in the initial phases (2 to 4 days) of metal exposure, no significant influence was observed, but after 14 days, a decrease in biomass by 90, 84, and 74% respectively to Cd, Cu, and Zn were observed (Miersch et al. 2001).

Sporulation

Sporulation (reproduction) is one of the most sensitive stress response parameters (Ferreira et al. 2016, Jain et al. 2019). Sporulation suppression is a vital aquatic hyphomycete species response against metal stress for efficient energy management (Lecerf & Chauvet 2008, Duarte et al. 2009). The type of metal is an essential factor driving the sporulation capacity of aquatic hyphomycete species. For instance, Cd was reported to be more toxic than metals such as Zn and Cu (Sridhar et al. 2001). In addition, Fe and Mg significantly reduced the aquatic hyphomycete (*A. alcuminata* and *T. elegans*) sporulation rates (Bermingham et al. 1996b). A mixture of metals had a more pronounced effect on fungal sporulation than individual metal types (Sridhar et al. 2001). In general, high metal concentrations inhibit sporulation; strikingly, low concentrations of Zn (2.5 mg/L), Cu (0.5 mg/L) and Cd (0.125 mg/L) stimulated sporulation (hormetic effect) in some aquatic hyphomycetes (*Anguillospora filiformis*, and *Anguillospora longissima*; Sridhar et al. 2001).

Besides concentration, the resistance to metals also differs between species; *V. elodeae* sporulation was inhibited by 1 mg/L of U, while *N. lugdunensis* was inhibited at 262 mg/L

(Bergmann & Graça 2020). Intraspecific differences in *N. lugdunensis* strains isolated from polluted or non-polluted streams displayed differences in conidial shape and size when subjected to Cd (50 μM $CdCl_2$) and Cu (25 μM $CuCl_2$), indicating physiologically adapted ecotypes (Braha et al. 2007).

What are the impacts of metals on the aquatic hyphomycetes community?

Growing evidence suggests that higher fungal community diversity may confer metal resistance and stability (Ferreira et al. 2010, Pascoal et al. 2010, Seena et al. 2020a). In general, the aquatic hyphomycetes community is functionally compromised if the stress-tolerant species are unable to functionally buffer the sensitive ones (Duarte et al. 2004, 2008, Batista et al. 2012). Community shifts were noted in a simplified artificial aquatic hyphomycetes community consisting of *A. tetracladia*, *F. curta*, *Geniculospora grandis*, and *Tricladium chaetocladium*, all the tested species were significantly affected when exposed to Zn (0 – 100 μM), but *A. tetracladia* displayed a clear functional advantage and was the most active species responsible for biomass production (Pascoal et al. 2010).

Metal concentration is also recognized as a determining factor modulating the aquatic hyphomycetes community response. Strikingly, low metal concentrations may stimulate litter decomposition (Batista et al. 2012) to circumvent the moderate stress imposed by the metal (Calabrese & Blain 2005). In the mining-impacted streams, under moderate (0.04 – 0.07 mg/L of Zn, Fe, Cu, Cd) metal concentrations, aquatic hyphomycete species richness was severely impacted, unlike leaf litter decomposition rates (Solé et al. 2008). However, both the parameters were severely affected under higher (Zn > 2.6 g /L; Cu, Pb, Cs, Cd > 0.01 g/L) metal concentrations (Sridhar et al. 2001). In addition, aquatic hyphomycete communities from metal-polluted streams may exhibit a higher ability to cope with stress (Braha et al. 2007). For example, when *A. tetracladia* strains from both non-polluted and metal-polluted sites belonging to an artificial community were exposed to Cd (1.5 mg/L), the strain from the metal-polluted stream appeared to be more resilient (Fernandes et al. 2009). A recent study also reinforces the vital role of intraspecific strain diversity for optimal ecosystem functioning under metal stress (Duarte et al. 2019).

Metal types and mixtures also greatly influence community behaviour (Duarte et al. 2008, Medeiros et al. 2008). When the stream colonized leaf litter was exposed separately to Cu and Zn (50 μM), Cu had a stronger impact on aquatic hyphomycete diversity, community structure and leaf litter decomposition than Zn (Duarte et al. 2008). However, when exposed to a mixture of Cu and Zn, an additive effect was observed in leaf litter decomposition rates (Duarte et al. 2008). Besides, environmental factors such as water chemistry may influence the aquatic hyphomycetes response to metals; for instance, the impact of Cd was observed to be more in soft water than hard water (Abel & Barlocher 1984).

What are the impacts of metals on the ecosystem functioning

Leaf litter decomposition in streams is one of the fundamental ecosystems processes subjected to metal stress (Niyogi et al. 2001). In the stream ecosystem, metals primarily pose risks at the aquatic hyphomycetes cellular level, which influences the impacts on higher levels of biological organization. Cellular changes govern the fitness or mortality, which reverberates in many ways across species, communities and ultimately on ecosystem processes such as organic matter decomposition, if not shielded by functional redundancy (Raviraja et al. 1998). The ecological significance of impacts is generally more at the ecosystem level, but the knowledge regarding the metal response or its effects is more profound at the lower levels of biological organization. It may be because the aquatic hyphomycetes ecotoxicological studies at the lower levels could be easily visualized using microcosm studies, hence promoting a more in-depth understanding at the lower level (Table 11, Fig. 41).

Although the geographical extent and number of the studies revolving around the impact of metals on aquatic hyphomycetes were limited (Fig. 41), lately, the significance of the effects of

metals at the ecosystem level has been receiving a lot of attention (see Ferreira et al. 2016). However, these studies are challenging as many factors are regional acting at different scales. Some of the factors can impact the ecosystem two-fold due to metal concentration and sensitivity. Various other stressors like pH or temperature modulate the metal impacts also increase the complexity (Hogsden & Harding 2012). Besides, several other factors such as pollution history may result in a stress-adapted community efficiently coping with metals. Metals may impart several direct or indirect effects across the trophic levels in the streams, which are strongly contextualized, i.e., by pollution history. Therefore, these challenges may result in a mismatch between the studies at the laboratory and field studies. Modelling studies spanning many streams over a geographical region may provide a realistic scenario to assess the impact of metal mixtures on ecosystem functioning.

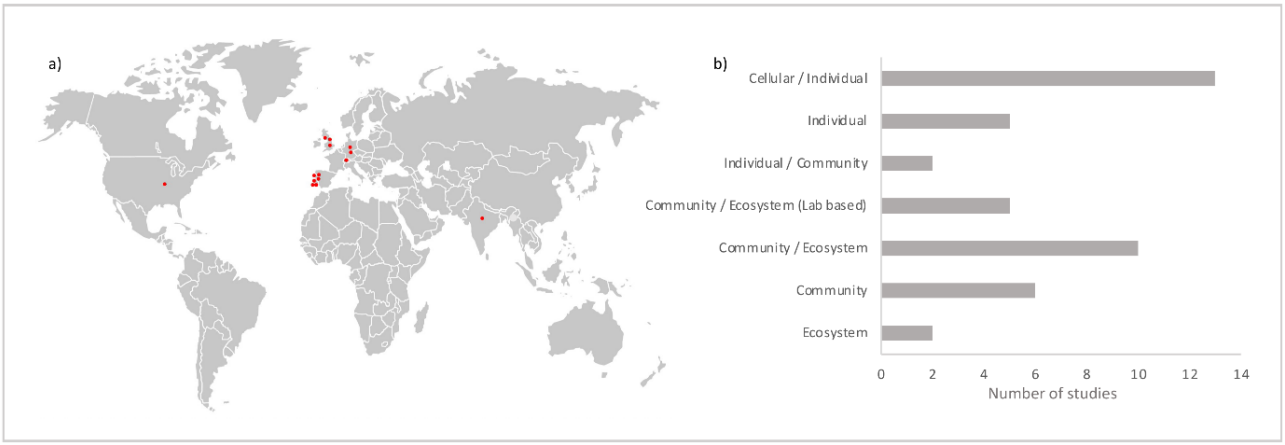


Figure 41 – a Global distribution of studies regarding metal impacts on aquatic hyphomycetes (aquatic hyphomycetes). b Number of studies at different levels of biological organization. Data were extracted from the 46 primary empirical studies (see Table 11) focusing on aquatic hyphomycetes.

The first evidence confirming the impact of metals at the ecosystem level (streams) was provided more than 35 years ago (Carpenter et al. 1983). The authors compared the effects of acid mine drainage on leaf litter decomposition in a reservoir comprising varied levels of metals and pH (6.3, 5.7 and 3.7). It was found that the litter decomposition rate decreased along with a gradient of pH (Carpenter et al. 1983), probably attributed to the different levels of acidity (Hogsden & Harding 2012, Ferreira et al. 2016). This finding was supported by two other subsequent studies in the streams impacted by coal mines (Maltby & Booth 1991, Bermingham et al. 1996a). In addition, the impact of mining effluents on the biochemical composition of the leaf litter (Maltby & Booth 1991) and the influence of exposure time on the leaf metal content was confirmed (Sridhar et al. 2001).

Table 11 Studies on impact of metals on aquatic hyphomycetes at different biological levels of organization.

Year	Type of study	Type of metal pollution	Biological level of organization	Reference
1983	Field	Acid mine drainage	Ecosystem	Carpenter et al. (1983)
1984	Field + Laboratory	Ca, Cd, Zn	Individual / Community	Abel & Barlocher (1984)
1991	Field	Metals from a coal-mine effluent	Community / Ecosystem	Maltby & Booth (1991)
1996	Field	Metals from a coal-mine effluent	Community / Ecosystem	Bermingham et al. (1996a)

Table 11 Continued.

Year	Type of study	Type of metal pollution	Biological level of organization	Reference
1996	Laboratory	Fe, Mg	Individual	Bermingham et al. (1996b)
1997	Field + Laboratory	Al	Individual	Chamier & Tipping (1997)
1997	Laboratory	Cd, Cu, Zn	Cellular / Individual	Miersch et al. (1997)
1998	Field	Cu shale mine	Individual / Community	Krauss et al. (1998)
2000	Field	Cu shale mine	Community	Sridhar et al. (2000)
2001	Field	Cu shale mine	Community	Miersch et al. (2001)
2001	Field	Iron-ore mine	Community	Raghu et al. (2001)
2001	Laboratory	Cd, Cu, Zn	Cellular / Individual	Miersch et al. (2001)
2003	Field	Groundwater of former Cu shale mine	Community	Krauss et al. (2003b)
2004	Field + Laboratory	Zn	Community / Ecosystem	Duarte et al. (2004)
2005	Field	Cu shale mine	Community / Ecosystem	(Krauss et al. (2005)
2005	Field	Cu shale mine	Community / Ecosystem	Sridhar et al. (2005)
2005	Field	Metal-polluted stream	Community / Ecosystem	Pascoal et al. (2005)
2005	Laboratory	Cd, Cu, Zn	Cellular / Individual	Miersch et al. (2005)
2005	Laboratory	Cd, Zn	Cellular / Individual	Jaeckel et al. (2005)
2006	Laboratory	Cd, Cu, Zn	Cellular / Individual	Guimarães-Soares et al. (2006)
2007	Laboratory	Cd, Cu	Cellular / Individual	Braha et al. (2007)
2007	Laboratory	Cd, Cu, Zn	Cellular / Individual	Guimarães-Soares et al. (2007)
2007	Laboratory	Cu, Zn	Cellular / Individual	Azevedo et al. (2007)
2008	Field	Gold-mining drainage	Ecosystem	Medeiros et al. (2012)
2008	Laboratory	Cd	Cellular / Individual	Miersch & Grancharov (2008)
2008	Field	Mining activity	Community	Solé et al. (2008)
2008	Field + Laboratory	Metal-polluted ponds	Community / Ecosystem	Sridhar et al. (2008)
2008	Laboratory	Cu, Zn	Community / Ecosystem	Duarte et al. (2008)
2009	Field + Laboratory	Zn	Community / Ecosystem	Fernandes et al. (2009)
2009	Laboratory	Cu, Zn	Cellular / Individual	Azevedo et al. (2009)
2009	Laboratory	Cu, Zn	Community / Ecosystem	Duarte et al. (2009)
2010	Field + Laboratory	Fe, Mn, Zn	Community / Ecosystem	Medeiros et al. (2010)
2010	Laboratory	Cu, Ni, Zn	Individual	Azevedo & Cássio (2010)
2010	Laboratory	U	Individual	Ferreira et al. (2010)
2010	Laboratory	Zn	Community	Pascoal et al. (2010)
2011	Field + Laboratory	Cd	Community / Ecosystem	Moreirinha et al. (2011)
2011	Laboratory	CuO, Ag	Community / Ecosystem	Pradhan et al. (2015)

Table 11 Continued.

Year	Type of study	Type of metal pollution	Biological level of organization	Reference
2012	Laboratory	Cd	Community / Ecosystem	Batista et al. (2012)
2012	Laboratory	Cd, Cu, Zn	Cellular / Individual	Solé et al. (2012)
2014	Laboratory	NanoCuO	Cellular / Individual	Pradhan et al. (2014)
2015	Laboratory	NanoCuO	Cellular / Individual	Pradhan et al. (2015)
2016	Laboratory	Cu	Individual	Quainoo et al. (2016)
2016	Laboratory	NanoCuO	Community / Ecosystem	Pradhan et al. (2016)
2019	Laboratory	Cd	Community / Ecosystem	(Duarte et al. 2019)
2020	Laboratory	Mine drainage	Cellular / Individual	Seena et al. (2020b)
2020	Laboratory	Uranium	Individual	Bergmann & Graça (2020)

Although metals are recognised to impact the ecological fitness of aquatic hyphomycetes in numerous ways, some species proved to be highly resistant as they were adapted to prevailing adverse stream conditions (Krauss et al. 2003b). Strikingly, in a survey of seven metal-contaminated streams in Germany, a total of 23 aquatic hyphomycete species were identified. However, metal concentration influenced species richness; > 10 species were observed at the two heavily polluted sites; *N. lugdunensis* and *T. marchalianum* were present at all study locations (Krauss et al. 2001). In addition, in a stream impacted by Cu (due to shale mining; Germany) a decrease in leaf litter decomposition rates, fungal biomass and conidia production was observed across a metal pollution gradient (Sridhar et al. 2001).

Environmental fluctuations like seasonal variations were observed in a stream impacted by iron ore mine effluents in India; the monsoon season displayed a higher species richness than the post-monsoon season and summer (Raghu et al. 2001). In addition, the influence of temperature on metal toxicity was also observed (Batista et al. 2012). Metals may interact with other stream components, such as oxygen and nutrients (Fernandes et al. 2009), impacting the ecosystem's functioning. In polluted groundwater wells with low oxygen saturation levels and high concentrations of metals (Pb, Mn, and Fe), a decline in the aquatic hyphomycetes leaf colonization capacity was observed, notably, *N. lugdunensis* and *Anguillospora* sp. was the most widespread species (Krauss et al. 2003). Similarly, mining-impacted streams with low O_2 saturation, significantly reduced aquatic hyphomycetes diversity and biomass (Solé et al. 2008). Furthermore, variations in water chemistry also contribute considerably to shaping the aquatic hyphomycetes community structure (Solé et al. 2008).

In a study targeting the food web structure in 20 streams (in New Zealand) impacted by different levels of metals and acidity, a correlation was evidenced between higher metals inputs and lower diversity of food webs (Hogsden & Harding 2012). Although the authors did not include fungi, the impact of metals on consumers feeding on detrital food resources was revealed (Hogsden & Harding 2012). Growing evidence suggests that the effects of metals on aquatic hyphomycetes may resonate at higher trophic levels (Gessner & Chauvet 2002, Canhoto & Graça 2008, Battin et al. 2009). For example, shifts in aquatic hyphomycetes communities induced by metals may indirectly promote changes in invertebrates feeding behavior and preference (Arsuffi & Suberkropp 1986), consequently lowering their fitness, which may compromise the food web structure and ecosystem functioning (Medeiros et al. 2008). Furthermore, the invertebrates' consumption of metal contaminated leaves also promoted metal accumulation in their bodies (Liu et al. 2021). This may lead to biomagnification across higher trophic levels impacting the food webs (Seena et al. 2020a, b), including humans (Lecerf & Chauvet 2008).

Conclusion

The discharge of metals into the streams is accompanied by changes in water chemistry, consequently influencing metal bioavailability (Duarte et al. 2004, Lecerf & Chauvet 2008). These events promote shifts in the aquatic food-web structure (Seena et al. 2020a), compromising the nutrient cycling and energy flow in the freshwater ecosystems (Duarte et al. 2004). Despite the wide range of studies tackling metals discharge in freshwater and their interactions with the aquatic hyphomycetes, new approaches would promote in-depth knowledge on the effects of metal pollution on aquatic hyphomycetes (Gulis et al. 2019) at multiple levels of biological organization in freshwaters. Molecular and -omics approaches have refined our understanding of many ecological aspects of aquatic hyphomycetes and opened new avenues of research. Recently, the metabolomic profiling of *N. lugdunensis* from the metal and non-metal contaminated sites revealed that triacylglycerols (TAG) could be a potential biomarker for metal stress (Seena et al. 2020b). In addition, comprehensive knowledge on the aquatic hyphomycetes genetic and cellular level may help us better understand freshwater biodiversity and ecosystem processes, allowing us to predict impacts of metal pollution before it is orchestrated at an ecosystem scale (Pietryczuk et al. 2018). Aquatic hyphomycetes are acknowledged as bioindicatos for assessing metal stress (Solé et al. 2008). Therefore, developing a multilevel study model incorporating aquatic hyphomycetes could help evaluate the effects of anthropogenic disturbances on freshwater ecosystems to assure optimal ecosystem services. Several policies are framed to reduce pollution in freshwaters via multilateral agreements such as the United Nations 2030 Agenda for Sustainable Development. But conservation strategies, particularly in streams, remain neglected (Geist 2011). For better stream ecosystem conservation and recovery strategies, it is imperative to cement the gaps between ecosystem processes and policies to control the metal discharge to the streams. Large-scale collaborative participation between local government and stakeholders and managers would also foster the implementation of successful management policies (Barmuta et al. 2011). This approach will increase the public awareness of the significance of freshwater ecosystems and their associated services sustaining our society.

Recent Progress and Future Perspectives of Freshwater Fungal Research

Our knowledge on freshwater fungi has expanded exponentially for almost century and a half of research. The classification system has been updated by using molecular phylogenetics and morphology, and by following the one fungus=one name ruling. These recent changes in fungal classification are the product of continuous exploration by aquatic mycologists of diverse habitats, studying diversity and taxonomy of freshwater fungi in worldwide laboratories (Table 12). Methodology in studying fungal communities in freshwater habitats has been improved using high-throughput sequencing that gives us a clearer picture and widens our perspectives of the overall diversity of freshwater fungi.

Pang et al. (2014) provides the direction of future research for freshwater fungi which include but are not limited to: (1) limited knowledge of fungi in various freshwater habitats like deep aquifer/groundwater, polar/subpolar areas (e.g., ice sheets, ice caps, glaciers and icebergs); (2) underexplored freshwater habitats of different areas of the world (e.g. Africa, South America, some Asian and Australasian countries); (3) rarely observed freshwater substrates (e.g. grasses, algae, planktons and macrophytes); (4) unavailability of sequence data of ex-type cultures of freshwater ascomycetes, and if available, protein genes are lacking; (5) morphological characters of freshwater fungi were not examined in detail and this might be useful in taxa delineation (e.g., peridial wall structure); (6) most of the asexual morphs lack sequence data and if this is available, linking to a named sexual morph is difficult due to the low percentage similarity with the closest match; and (7) resolution of taxonomic issues on taxon's correct name in line with the current code of fungal nomenclature. The updated information on the abovementioned challenges will be tackled in detail in the succeeding subtopics of this entry. Pang et al. (2014) concluded also that the lack of funding and trained aquatic mycologists are two factors why freshwater fungal research groups and

published works have declined over the last decades. In this entry, recent progress and challenges for the future are discussed and poorly studied areas warrant further research are also highlighted.

Table 12 A list of laboratories and their research interest on freshwater fungal research*.

Institution	Mycologist(s)	Research topics	Email address
Mae Fah Luang University, Thailand	Kevin David Hyde Saranyaphat Boonmee	Taxonomy, phylogeny, ecology	kdhyde3@gmail.com saranyaphat.boo@mfu.ac.th
Chiang Mai University, Thailand	Saisamorn Lumyong	Taxonomy and phylogeny	scboi009@gmail.com
Dali University, China	Zong-Long Luo	Taxonomy and phylogeny	luozonglongfungi@163.com
Guizhou Institute of Technology, China	Yong-Zhong Lu	Taxonomy and phylogeny	yzlu86@gmail.com
Hirosaki University, Japan	Kazuaki Tanaka	Taxonomy and phylogeny	k-tanaka@hirosaki-u.ac.jp
Jiangxi Agricultural University, China	Dian-Ming Hu	Taxonomy and phylogeny	hudianming1@163.com
King Saud University, Saudi Arabia	E.B. Gareth Jones	Taxonomy, phylogeny, and ecology	torperadgj@gmail.com
Kunming University of Science and Technology, China	Huang Zhang	Taxonomy and phylogeny	zhanghuang2002113@163.com
Mangalore University, India	Kandikere Ramaiah Sridhar	Taxonomy and phylogeny	kandikere@gmail.com
Mt. Allison University	Felix Bärlocher	Ecology	fbaerlocher@mta.ca
National Center for Genetic Engineering and Biotechnology, Thailand	Nattawut Boonyuen	Taxonomy and phylogeny	nattawut@biotec.or.th Sivichai@biotec.or.th
National Chiayi University	Teik-Khiang Goh Chang-Hsin Kuo	Taxonomy and phylogeny	chkuo@mail.ncyu.edu.tw
Real Jardín Botánico-CSIC, Spain	Alberto Miguel Stchigel Viridiana Magaña-Dueñas	Taxonomy and phylogeny	albertomiguel.stchigel@urv.cat
Sohag University, Egypt	Mohamed A. Abdel-Wahab Faten A. Abdel-Aziz	Taxonomy and phylogeny	mohamed.eisa@science.sohag.edu.eg
Universidad Nacional del Comahue, Argentina	Diego Libkind	Taxonomy and phylogeny, ecology	ibkindfd@comahue-conicet-gob.ar
University of Coimbra, Portugal	Sahadevan Seena	Ecology	seena.sahadevan@gmail.com
Universidad Nacional Autónoma de México	Mario Figueroa	Prospecting of secondary metabolites	mafiguer@unam.mx
University of North Carolina at Greensboro, USA	Huzefa A. Raja	Taxonomy, phylogeny, prospecting of secondary metabolites	huzefaraja@gmail.com; haraja@uncg.edu
Zhongkai University of Agriculture and Engineering, China	Wei Dong	Taxonomy and phylogeny	dongwei0312@hotmail.com

Table 12 Continued.

Institution	Mycologist(s)	Research topics	Email address
Federal University of Rio Grande do Norte	Patrícia Oliveira Fiuza	Taxonomy and phylogeny	patyfiuzabio@gmail.com
Federal University of Mato Grosso	Flavia Rodrigues Barbosa	Taxonomy and phylogeny	faurb10@yahoo.com.br
Nakdonggang National Institute of Biological Resources, Korea	Jaeduk Goh	Taxonomy and phylogeny	jdgoh@nnibr.re.kr
Chonnam National University, Korea	Hyang Burm Lee Thuong T. T. Nguyen	Taxonomy and phylogeny	hblee@chonnam.ac.kr
Jordan University of Science and Technology, Jordan	Tamam El-Elimat Ahmed Hesham Al Sharie	Prospecting of secondary metabolites	tamamelimat@gmail.com ahmedalsharie3@gmail.com
University of North Carolina at Greensboro, North Carolina, United States	Nicholas H. Oberlies	Prospecting of secondary metabolites	nicholas_oberlies@uncg.edu
Flinders University, Australia	Sally Fryar	Taxonomy, phylogeny, ecology	sally.fryar@flinders.edu.au
Martin-Luther-Universität Halle-Wittenberg, Germany	Gerd-Joachim Krauss	Ecology, prospecting of secondary metabolites	gerd-joachim.krauss@biochemtech.uni-halle.de

*Partial list only; additional mycologists, including their affiliated institutions, field of specializations, and contact information, will be updated in http://www.freshwaterfungi.org

Taxonomy, phylogeny, and classification

The last decade has greatly advanced our knowledge in the taxonomic and phylogenetic classification of freshwater fungi. The seminal paper of Luo et al. (2019) on freshwater Sordariomycetes outlined 127 genera in 30 orders, introduced novel taxa (two families, three genera, 47 species), and provided a strong backbone tree using combined LSU, SSU, RPB2, and TEF1α sequence dataset of Sordariomycetes. On the other hand, Dong et al. (2020b) provided a comprehensive outline of six orders of freshwater Dothideomycetes (with 43 families, 145 genera), notes, illustrations, class-level phylogenetic tree using LSU, ITS, TEF, and RPB2 sequence dataset, and introduced novel taxa (9 new genera, 33 new species) based on freshwater specimens from Thailand and China. Furthermore, Calabon et al. (2022) provided the recent numbers of freshwater fungi and totalling to 3,880 species. Unfortunately, a huge number of taxa still have uncertain placement brought upon by lack of living cultures and sequence data of the type species. For instance, 254 species (in 141 genera) are classified under Ascomycota *incertae sedis*, and 32 and 37 species of unknown placements under Sordariomycetes and Dothideomycetes, respectively (Calabon et al. 2022). Recollections of these specimens in the area where they were previously identified and obtaining sequence data, either by direct sequencing of the fruiting bodies or their isolation and mycelial extraction, can provide a better understanding of their phylogenetic placements and evolutionary relationships. In addition, a comprehensive sample collection exploring underexplored and unexploited freshwater ecosystems in different geographical regions, selecting a wider range of substrates, including aquatic plants, and their isolation and sequencing will lead to a more natural classification system of this ecological group.

For the past decades, continuous advances in sequencing technology revolutionized fungal genomics and sequences were made available in an open access online database (de Vries et al. 2014, Choi & Kim 2017). Genome sequencing, a comprehensive method for analyzing entire genomes of an organism, has become an ultimate source of biosynthetic potential and phylogenetic

placement using multilocus data that with phylogenetically informative characters that is affordable and efficient (Batley & Edwards 2009, Ma & Fedorova 2010, Hagestad et al. 2022). The availability of genome sequences provides a wealth of data on metabolic diversity within the fungal kingdom, including, but not limited, to mapping of the phenotypic traits onto their phylogeny and comparative data on the evolution of individual genes, evolutionary rates of gene sequences, gene family origins, gene presence/absence and gene duplication and loss patterns (Galagan et al. 2005, Stajich 2017). At present, numerous institutions have initiated programs to sequence the fungal genomes from throughout the kingdom (Cuomo & Birren 2010, Haridas et al. 2020). These initiatives resulted in the sequencing of several freshwater fungal genomes and includes *Amniculicola lignicola* (Haridas et al. 2020), *Aquanectria penicillioides* (Goh et al. 2019a), *Clavariopsis aquatica* (Heeger et al. 2021), *Clohesyomyces aquaticus* (Mondo et al. 2017), *Hymenoscyphus tetracladius* (Goh et al. 2018), *Lindgomyces ingoldianus* (Haridas et al. 2020), *Lentithecium fluviatile* (Haridas et al. 2020), *Lepidopterella palustris* (Peter et al. 2016) *Margaritispora aquatica* (Goh et al. 2019b), *Tetracladium* species (*T. apiense, T. furcatum, T. marchalianum, T. setigerum, Tetracladium* cf. *breve, Tetracladium* spp.) (Anderson & Marvanová 2020).

Biodiversity and ecology

The discovery rate of novel freshwater fungi from various habitats and substrates has an increasing trend and this will continue. There are published data which documents the high biodiversity of freshwater fungi (Luo et al. 2016b, 2019, Lu et al. 2018b, Bao et al. 2020, Hyde et al. 2020b, 2021, Dong et al. 2020b). The hidden diversity of freshwater fungi, especially the basal lineages (e.g., Chytridiomycota, Aphelidiomycota, Rozellomycota), have been shown also using high throughput sequencing techniques (Ishida et al. 2015, Khomich et al. 2017, Heeger et al. 2018). For instance, Ishida et al. (2015) found out that the amplified fungal sequences obtained from direct sequencing of lacustrine diatoms showed a close phylogenetic affinity with novel basal lineages of Chytridiomycota, Aphelida, Cryptomycota, and the yeast *Debaryomyces hansenii*. Planktonic fungal communities in a reservoir (Chen et al. 2018) and lake (Song et al. 2018) constitutes a large number of sequences of unclassified fungi and Ascomycota. Our knowledge on the extent of diversity and ecological habits of these unclassified fungi, popularly known as dark matter fungi, remain largely unknown and limited. To fill this gap, wider sampling of freshwater resources, and the use of reliable molecular tools (e.g., universal eukaryotic primers ITS, LSU, SSU) will yield wider understanding and less bias on specific groups of fungi (Debroas et al. 2017, Khomich et al. 2017, Tedersoo et al. 2018b, Lepère et al. 2019).

Our understanding of fungal community structure and changes in river ecosystems is still very limited. In the study of Liu et al. (2015a), using culture-dependent and -independent methods, the local climate (temperature) conditions and water eco-function in the catchment area, affects the sediment's fungal community composition. Furthermore, various nutrient elements influence the structure of freshwater fungal's community organization, dynamic, and concentration. There are limitations also in relative abundance assessment of fungal species in natural communities because some taxa have specific traits and often have a greater influence on ecosystem functioning than species number per se (Duarte et al. 2006). Hyde et al. (2021) suggested research areas to define freshwater fungal populations in unconnected river systems will enlighten us if each stream harbors distinct taxa including the species' ecology that could either be generalist or specialist.

Plant litter decomposition by fungi in streams has been the focus of research for decades. In streams, aquatic hyphomycetes degrade and utilize cellulose and hemicellulose from plant litter but little is known about the enzyme systems involved as compared with terrestrial fungi (Gulis et al. 2019). Heeger et al. (2021) sequenced the genome of *Clavariopsis aquatica* and identified laccases (of ten of which, only five had previously been identified), peroxidases (class II of the nonanimal peroxidase superfamily), and putative cytochrome P450 monooxygenases. Gene expression of *C. aquatica* on wheat straw and alder showed indication of cellulose and hemicellulose degradation wherein but the former shows an upregulation of enzymes for extracellular depolymerization. Gene

expression studies are needed to further understand the associated enzyme systems involved in lignocellulose degradation, also what regulates genes encoding this enzyme system. Another unexplored area of research in stream ecology and physiology is the role of spores in ecosystem functioning, the elucidation of physical and chemical cues, and changes that triggers sporulation of aquatic hyphomycetes (Seena et al. 2022a).

Recently, ecosystem services provided by aquatic hyphomycetes are conceptualize and categorize by Seena et al. (2022b) and as follows: (1) provisioning services for genetic and biological diversity maintenance and antimicrobial metabolites delivery; (2) regulating services, such as leaf litter decomposition and the self-cleaning ability of freshwaters; (3) supporting services, like biomonitoring, nutrient and carbon cycling, food web dynamics, and habitat maintenance; and (4) cultural services, particularly educational and inspirational values. The inclusion of freshwater hyphomycetes in conservation strategies, including threats to freshwater ecosystems and biodiversity of aquatic hyphomycetes has discussed by Barros and Seena (2022). It is also pointed out that the conservation status of most fungal species is unknown, with most of the conservation agenda restricted to macrofungi. Recently, an effort was made by Edmondstone et al. (2022) in highlighting 50 freshwater species at very high risk of extinction and to promote conservation actions for these species. Five of these species are freshwater fungal taxa namely, *Ascovaginospora stellipala Collembolispora barbata*, *Isthmosporella pulchra*, *Lepidopterella palustris,* and *Tetracladium palmatum*. Threats of these freshwater fungal species are yet to be explored given the limited knowledge of this ecological group.

Conclusions

There are still gaps in our present knowledge of freshwater fungi due to the unavailability of funds, shortage of mycologists and/or taxonomists, research priority areas, and inaccessibility of freshwater habitats. Most of the information of freshwater fungi are generated from continents like Asia, Europe, and North America resulting in a restricted and inadequate knowledge of global biodiversity and distribution patterns of freshwater fungi. There is insufficient information also on how climate change, anthropogenic pollution, and physical habitat modifications alter the composition, diversity, and functioning of fungi from aquatic habitats. It is also timely that conservation biologists include freshwater fungi as part of the conservation agenda, especially those that have restricted distributions or yet to be discovered in unexplored and underexplored aquatic habitats. Using the Web of Science (WoS) Core Collection search analytics for the topic ‘freshwater fungi’, results in 1,462 hits (articles: 1,325; review articles: 102). This is low compared to ‘marine fungi’ with 7,028 hits (articles: 6,086; review articles: 862). The number does not represent the published works, as WoS only includes the top-tier journals, but the results give an indication of research activity in freshwater fungal studies. There are still much remains to learn about higher and basal fungi in freshwater habitats and with the advent of modern technology in elucidating fungal community structure in aquatic habitats, a more systematic and in-depth investigations is underway unraveling the hidden diversity of this ecological group.

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