Chapter 13
Biology and Ecology of Freshwater Fungi

Clement K.M. Tsui, Christiane Baschien, and Teik-Khiang Goh

Introduction

Freshwater fungi complete at least one part of their life cycle in water and distribute propagules (spores, conidia, sporangia) in or above water. It has been estimated that there are more than 3000 species of fungi occurring in the aquatic habitats (Abdel-Aziz 2008). Taxonomically, aquatic fungi comprise taxa from all fungal phyla (*Cryptomycota*, *Chytridiomycota*, *Blastocladiomycota*, *Mucoromycotina*, *Glomeromycota*, *Dikaryomycota*).

Fungal morphology in freshwater ranges from zoospores and nonmotile single cells of *Cryptomycota*, *Chytridiomycota*, *Blastocladiomycota*, yeasts, and aseptate and septate hyphae up to interwoven hyphae in more or less complex plectenchyma in higher fungi. Sporangiophores and sporangia (*Chytridiomycota*, *Blastocladiomycota*, and *Mucoromycotina*), ascomycetous and basidiomycetous

---

Our work is dedicated to John Webster (1925–2014) for his pioneer and influential work on freshwater fungi.

C.K.M. Tsui, Ph.D. (✉)
Department of Pathology and Laboratory Medicine, University of British Columbia,
Vancouver, BC, Canada, V6T 1Z4
e-mail: clementsui@gmail.com

C. Baschien, Ph.D.
Department of Microbial Ecology and Diversity, Leibniz Institute
DSMZ-German Collection of Microorganisms and Cell Cultures,
Inhoffenstr. 7 B, 38124 Braunschweig, Germany

T.-K. Goh, Ph.D.
School of Biological Sciences, Faculty of Integrative Sciences and Technology,
Quest International University Perak, No. 227, Plaza Teh Teng Seng (Level 2),
Jalan Raja Permaisuri Bainun, 30250 Ipoh, Perak Darul Ridzuan, Malaysia
e-mail: teikkhiang.goh@qiup.edu.my

D.-W. Li (ed.), *Biology of Microfungi*, Fungal Biology,
DOI 10.1007/978-3-319-29137-6_13

yeasts, conidiophores, and a high diversity of more or less conspicuous conidia (*Ascomycota* and *Basidiomycota* derived) are also visible under the microscope. In addition, complex structures such as acervuli, pycnidia, and ascocarps and basidiocarps as well as lichens can be found on substrates in freshwaters. Over the past few decades, various morphological and ecological groups of water-associated fungi have been identified (Fuller and Jaworski 1987; Goh and Hyde 1996; Hyde et al. 1997; Ingold 1975; Jones 1981). These include the zoosporic fungi, the aquatic ascomycetes, the "Ingoldian fungi," the aero-aquatics, and a great diversity of mitosporic fungi (asexual *Ascomyceta*) occurring on submerged plant materials.

Worldwide, freshwater comprises diverse habitats such as groundwater, streams, rivers, canals, and lakes but also includes amphibious habitats, such as ditches, peats, and swamps (Shearer et al. 2007). Generally, most freshwater fungi are associated with organic matter derived from decaying plants and animals. However, there are many microhabitats in and adjacent to freshwater, which provide space and possibilities for different fungal life strategies. These microhabitats include roots and other parts of submerged and riparian plants, the canopy, the ambient soil, and sediments. Indeed, freshwater fungi are recorded from the tree canopy (Ando 1992; Ando and Tubaki 1984a, b; Sridhar et al. 2009), rainwater (Gönczöl and Révay 2004), and soil (Park 1974). Also leaf litter in treeholes (Gönczöl and Révay 2003), dew drops (Tubaki et al. 1985), and honey (Magyar et al. 2005) have been identified as locality for spores of freshwater fungi. Fungi have been observed within cooling towers (Eaton and Jones 1971a, b), groundwater (Krauss et al. 2005), and potable water distribution systems (Doggett 2000; Nagy and Olson 1982) including tap water (Heinrichs et al. 2013).

Who Are the Members of Freshwater Fungi?

Traditional taxonomy and identification of fungi is mostly based on fruiting bodies and spores. Freshwater fungi are divided into various morphological and ecological groups (Shearer et al. 2007; Goh and Hyde 1996). The different groups require specialized methods to examine their biodiversity, taxonomy, distribution, population dynamics, and ecological functions. Traditionally, it has been a challenge to characterize all the different groups of freshwater fungi within a freshwater habitat.

The first group is (*I*) the aquatic hyphomycetes (more than 300 described mitosporic fungi) (Figs. 13.1 and 13.2), also known as "the Ingoldian fungi" in honor of the pioneer mycologist Prof. C. T. Ingold, which comprises conidial states of mainly *Ascomycota* and a few *Basidiomycota* (Shearer et al. 2007; Jones et al. 2014). Ingold (1942) discovered the conidia in the foam of streams and showed the connection to their associated mycelia on submerged leaves. Most aquatic hyphomycetes produce conspicuous stauroconidia (e.g., tetraradiate [*Alatospora*, *Articulospora*] or other branched forms [*Varicosporium*]) or scolecoconidia (sigmoid, curved, or straight [*Anguillospora*, *Flagellospora*]). The conidial shape is an adaptation to survival and

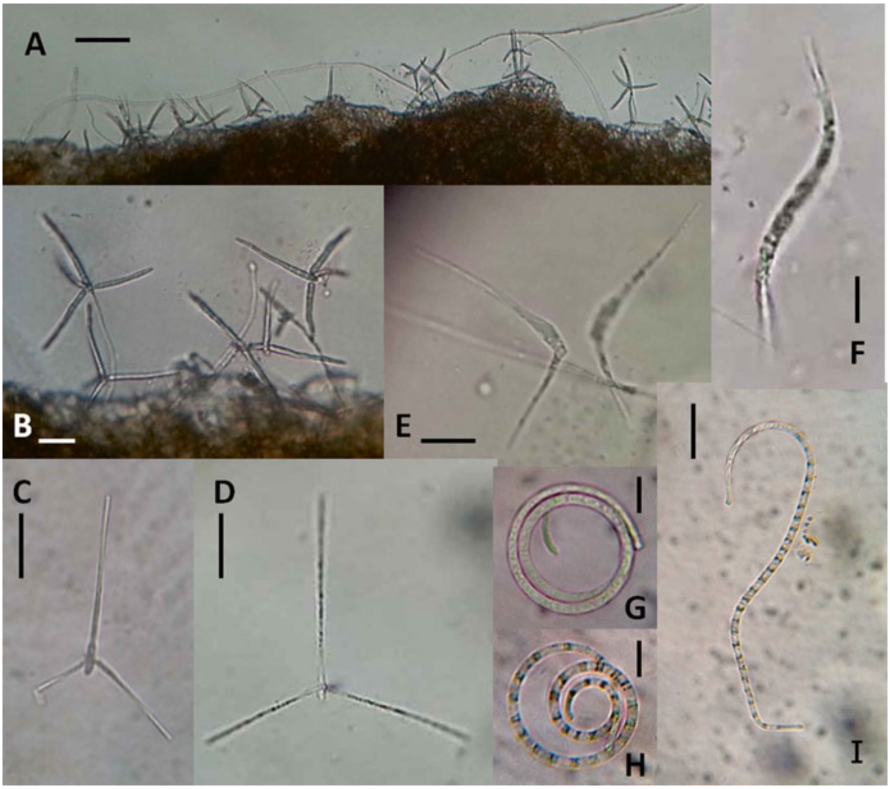

Fig. 13.1 Ingoldian fungi. (**a**, **b**) *Triscelophorus acuminatus*. Conidia production seen at the edge of submerged leaf. Each conidium has four arms. (**c**, **d**) *Triscelophorus monosporus*. Conidia with three arms. (**e**) *Lunulospora cymbiformis*. Conidia which are sickle-shaped and distinctly bent more or less at right angle. (**f**) *Anguillospora crassa*. Typical sigmoid-shaped conidium. (**g**, **h**) *Helicomyces roseus*. Typical coiled conidia. (**i**) *Helicomyces roseus*. Conidium which has uncoiled and become more or less sigmoid shaped in water. Scale bars: **a** = 50 μm; **b**−**i** = 20 μm

dispersal in aquatic habitats discussed below (Dix and Webster 1995; Webster 1959). Aquatic hyphomycetes are known as important decomposers in the turnover of leaf litter in woodland streams [overview in (Gessner et al. 2007)]

The second group is called the (*II*) aero-aquatic fungi (mitosporic ascomycetes) (~90 species described) (Fig. 13.1g, h), which are found on submerged plant litter and wood in flat lentic waters, such as woodland ponds and ditches, which may have periodical levels of water. In contrast to aquatic hyphomycetes, the aero-aquatic fungi release their propagules aerially. Therefore, they produce conspicuous air-trapping dispersal units, which can flow on the water surface; for example, some spores are helicoid in more than one plane (Fig. 13.1g, h) (e.g., *Helicoma, Helicoon*) or spiral into a sphere or a net [e.g., *Candelabrum*, *Spirosphaera* (Voglmayr 2004, 2011; Voglmayr and Delgado-Rodriguez 2003; Voglmayr et al. 2011)]. The aero-aquatic life strategy was first described by Agathe van Beverwijk (1951).

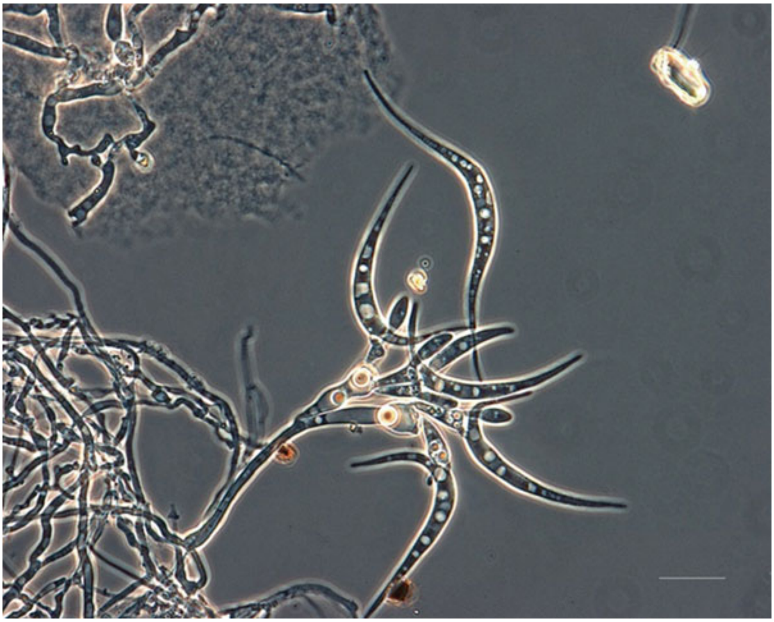

Fig. 13.2 *Lunulospora curvula*. Conidiogenesis of crescent-shaped unbranched conidia. Bar = 25 µm

The third group is named (*III*) freshwater ascomycetes (~600 species described meiosporic fungi), which comprise the sexual states of phylogenetically heterogeneous ascomycete fungi occurring worldwide in freshwater habitats on herbaceous and woody substrates (Shearer et al. 2007, 2009; Goh and Hyde 1996; Shearer 1993a; Vijaykrishna et al. 2006). In addition, they are also collected from submerged dead macrophytes (Shearer 1993a; Fallah and Shearer 2001). The morphologies in asci and ascospores are very diverse and noticeable. Asci of freshwater ascomycetes are either deliquescent, with apical apparatus (e.g., *Massarina*, *Jahnula*), or fissitunicate (ectoascus and coiling endoascus, e.g., *Kirschsteiniothelia* (transferred to *Helicascus*)) (Shearer 1993b). Many freshwater ascomycetes produce ascospores with appendages, which facilitate attachment to substrates (Shearer et al. 2007; Shearer 1993a; Wong et al. 1998). Gelatinous gel-like sheaths and/or thick-walled hyphae (Shearer et al. 2009; Ingold 1955) are thought to enhance attachment and adhesion to plant materials (Digby and Goos 1987; Ingold and Chapman 1952). However, spores borne with gelatinous sheath and the active discharge of ascospores are also present in strictly terrestrial ascomycetes. In comparison to aquatic and aero-aquatic hyphomycetes, freshwater ascomycetes seem to be less exclusively adapted to life in aquatic habitats (Vijaykrishna et al. 2006).

The fourth group of freshwater fungi is the (*IV*) zoosporic fungi (Fig. 13.3), which produce flagellate zoospores as part of their life cycle. They are known for

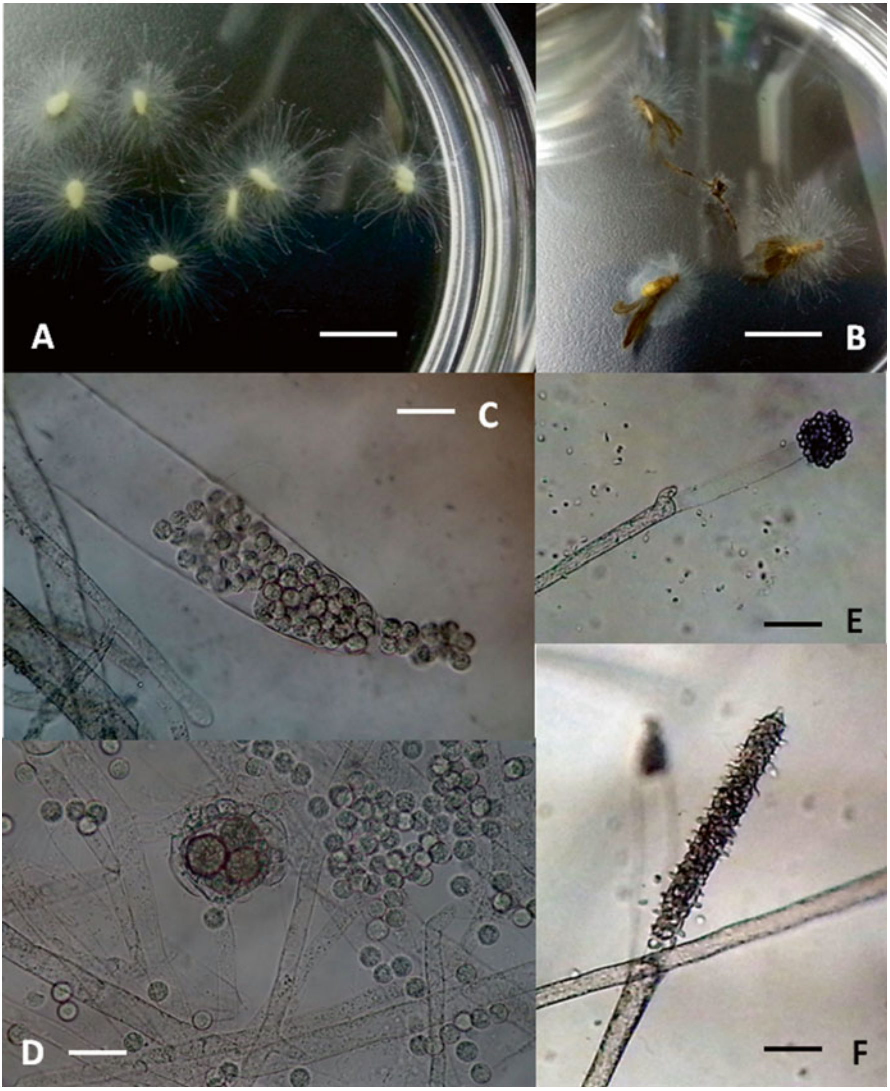

Fig. 13.3 Oomycetes. (**a**) Baiting of oomycetes, using sesame seeds. (**b**) Baiting of oomycetes, using insect carcasses. (**c**) *Saprolegnia* sp., zoosporangium releasing zoospores. (**d**) *Saprolegnia* sp., oogonium, with attached antheridia, and many encysted primary zoospores. (**e**) *Achlya* sp., zoosporangium showing discharged and encysted zoospores at the apical pore. (**f**) *Dictyuchus* sp., a dictyoid zoosporangium in the process of zoospore discharge. Scale bars: **a**, **b** = 5 mm; **c** = 10 μm; **d–f** = 20 μm

their parasitic life strategies but they are also involved in the decomposition of organic matter (Sparrow 1960). Historically, they have been known as the members of "phycomycetes," a functionally defined group. They have also been traditionally termed the "lower fungi" which basically comprises species without a septate hyphal system. With the advent of molecular studies and recent taxonomic treatments based on phylogenetics, the "phycomycetes" is in fact heterogeneous, comprising of members from the *Eumycota* ("true fungi") and the *Chromista* (*Oomycetes* and *Labyrinthulomycetes*). The biology, taxonomy, and phylogenetic relationship of these aquatic organisms have been well documented (Fuller and Jaworski 1987; Beakes 2003; Bowman et al. 1992; Buczacki 1983; Powell 1993).

The freshwater zoosporic fungi belong mostly to the *Chytridiomycetes* and the fungal-like *Oomycetes*, which are microscopic organisms not producing any fruiting bodies visible to the naked eye. Members of the *Chytridiomycetes* are generally called chytrids, whereas those belonging to the *Oomycetes* are usually called water molds. They usually reproduce asexually by means of zoospores, but in *Oomycetes*, sexual reproduction may occur by means of oogamy, resulting in the formation of oospores, which are survival structures generally resistant to adverse environmental conditions. The chytrids produce uniflagellate haploid zoospores, whereas those of the water molds are biflagellate and diploid. These taxa are associated with dead and living plant materials but also with algae, cyanobacteria (Sonstebo and Rohrlack 2011), invertebrates, fish, and amphibians (Powell 1993; Longcore et al. 1999; Powell et al. 2013).

The main orders of *Chytridiomycetes* are *Chytridiales*, *Spizellomycetales*, and *Monoblepharidales*. Furthermore members of *Neocallimastigomycota* and *Blastocladiomycota* occur in aquatic habitats (Powell and Letcher 2014). Members of *Chytridiales* and *Blastocladiales* are more frequently encountered in freshwater systems. The main orders of *Oomycetes* found in aquatic environments are the *Saprolegniales*, *Leptomitales*, and *Peronosporales*. Common genera of *Saprolegniales* frequently isolated from the aquatic systems are *Saprolegnia*, *Achlya*, and *Dictychus*.

Apart from chytrids, *Cryptomycota* is a recently discovered (Jones et al. 2011) phylum with endoparasitic lifestyle (James et al. 2013; Lazarus and James 2015). They differ from other filamentous fungi in that they lack chitinous cell walls in the trophic stage. Based on molecular markers, they have been detected in lakes and wetlands (Ishii et al. 2015; Wurzbacher et al. 2014).

The fifth group (*V*) belongs to aquatic–terrestrial hyphomycetes (mitosporic ascomycetes) (Figs. 13.4, 13.5 and 13.6) that comprise a huge morphological diversity of conidial (mitosporic) fungi growing on decaying plant material (Shearer et al. 2007; Hu et al. 2014) and capable of sporulating underwater (Bärlocher et al. 2008; Baschien et al. 2009). They are distinguished based on the features of conidia, conidiophores, and the conidiogenesis. For example, common fungi include *Dactylaria*, *Dictyochaeta, Canalisporium,* and *Sporoschisma*; some of these fungi are linked with their corresponding sexual relatives using cultural or molecular studies. Some studies also demonstrate the presence of fungi of terrestrial origin, including saprobes from plants and soil, such as *Cladosporium*, *Alternaria*, and *Penicillium* species. Fungi on leaves from the canopy (Gönczöl and Révay 2006) may fall into the water.

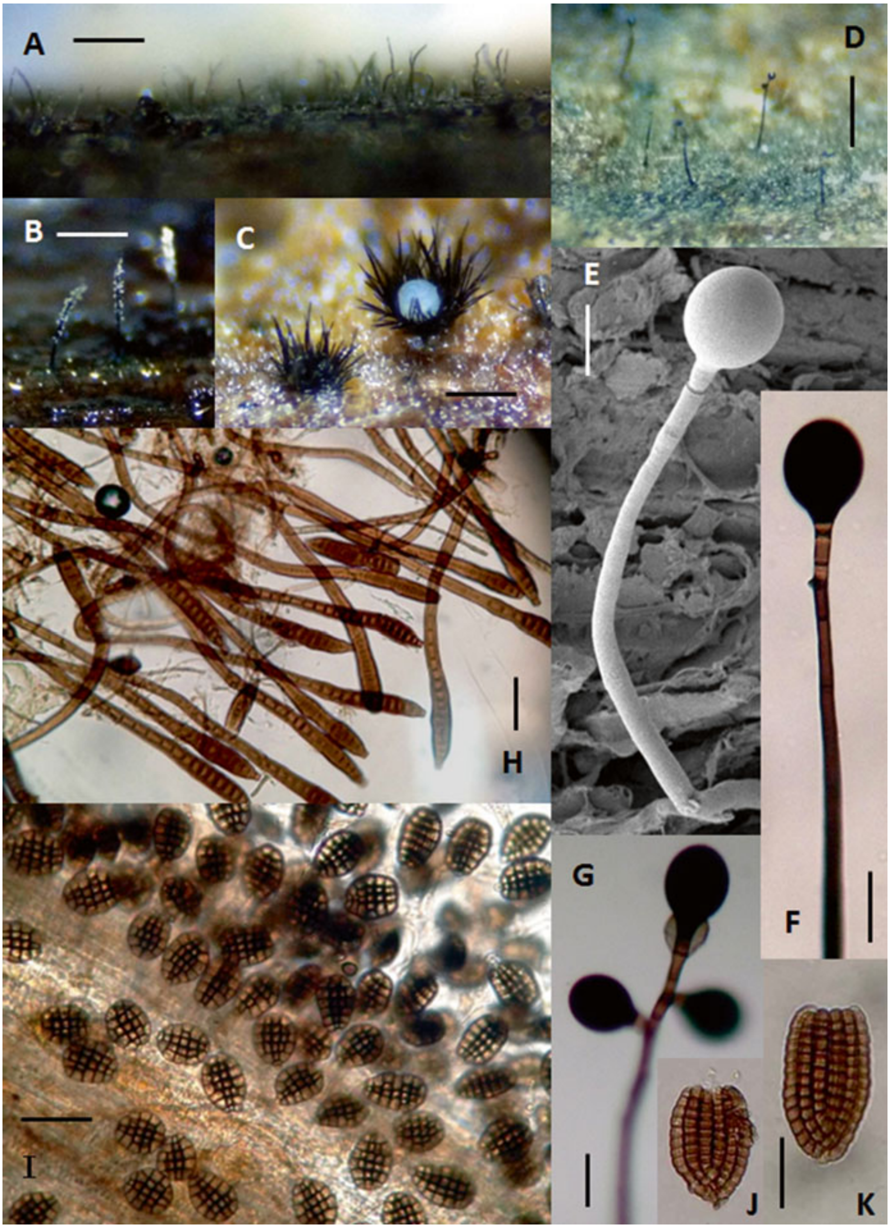

Fig. 13.4 Lignicolous hyphomycetes. (**a**) *Ellisembia adscendens*. Colony on submerged wood. Conidia are long and projecting upward on the wood surface. (**b**) *Phaeoisaria clementidis*. Colony on submerged wood. Conidiophores are in the form of long synnemata projecting upward on the wood surface. (**c**) *Vermiculariopsiella* sp. Colony on submerged wood. Conidiophores are in the form of dense sporodochia on the wood surface, surrounded by long setae and producing conidia in the form of white slimy mass. (**d**) *Monotosporella setosa*. Colony on submerged wood. Conidiophores are long, erect, and projecting from the wood surface. (**e–g**) *Monotosporella setosa*. Conidiophores producing conidia at their apex. (**h**) *Ellisembia adscendens*. Conidia. (**i**) *Canalisporium elegans*. Conidia, which were produced in the form of sporodochia on the surface of submerged wood. (**j**, **k**) *Dictyosporium elegans*. Conidia. Scale bars: **a–d** = 200 μm; **e–h**, **j**, **k** = 20 μm; **i** = 50 μm

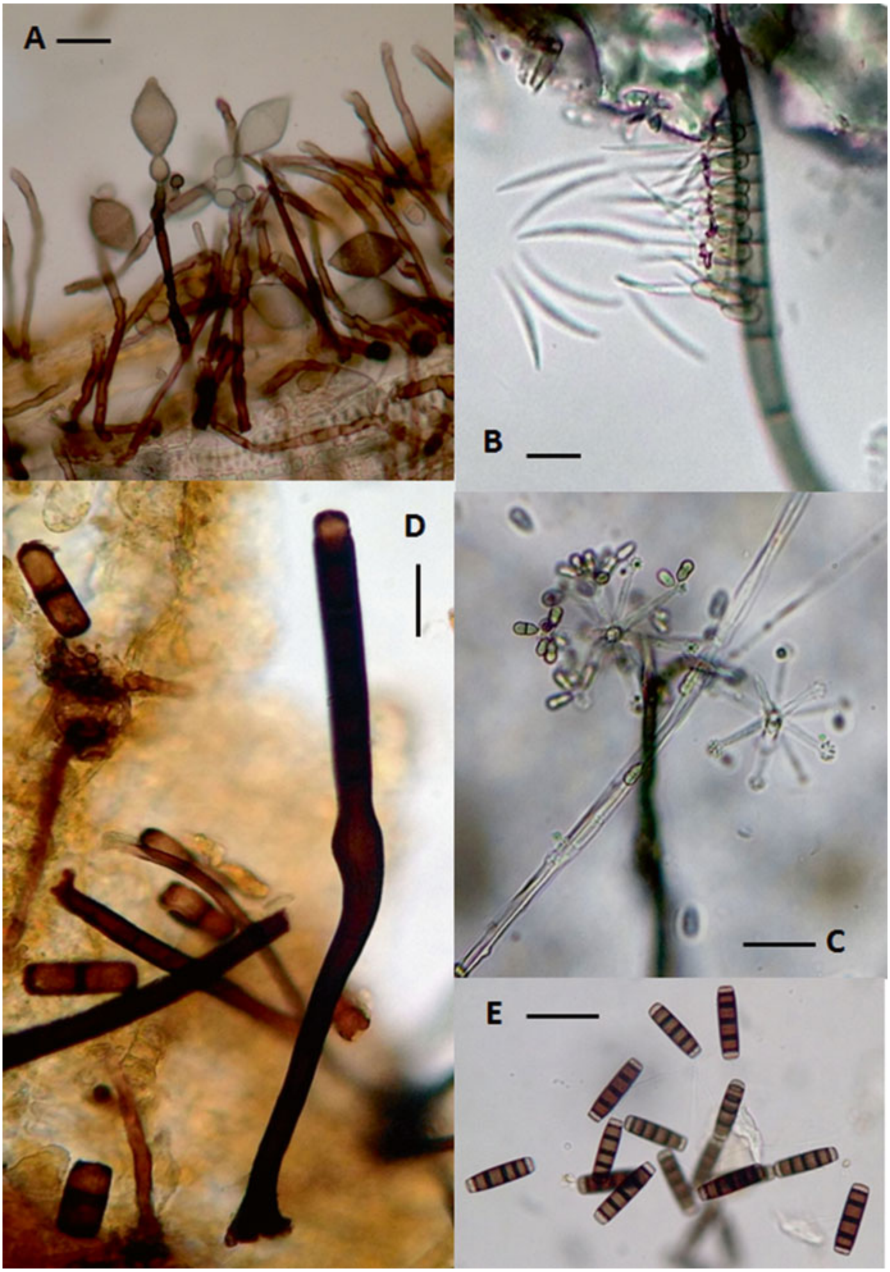

Fig. 13.5 Lignicolous hyphomycetes. (**a**) *Beltrania africana*. Conidiophores and conidia from submerged wood. (**b**) *Cryptophialoidea secunda*. Part of setiform conidiophore showing the fertile region, bearing unilateral phialidic conidiogenous cells, producing falcate conidia. (**c**) *Pseudobotrytis terrestris*. Conidiophore bearing umbellately arranged polydenticulate conidiogenous cells, producing two-celled conidia. (**d**) *Sporoschisma uniseptatum*. Conidiophore which has a swollen venter, producing endogenous conidia, usually in basipetal chains. (**e**) *Sporoschisma mirabile*. Conidia, initially borne on chains, have become disarticulated in water mount. Scale bars: **a** = 20 μm; **b** = 10 μm; **c**, **d** = 20 μm; **e** = 50 μm

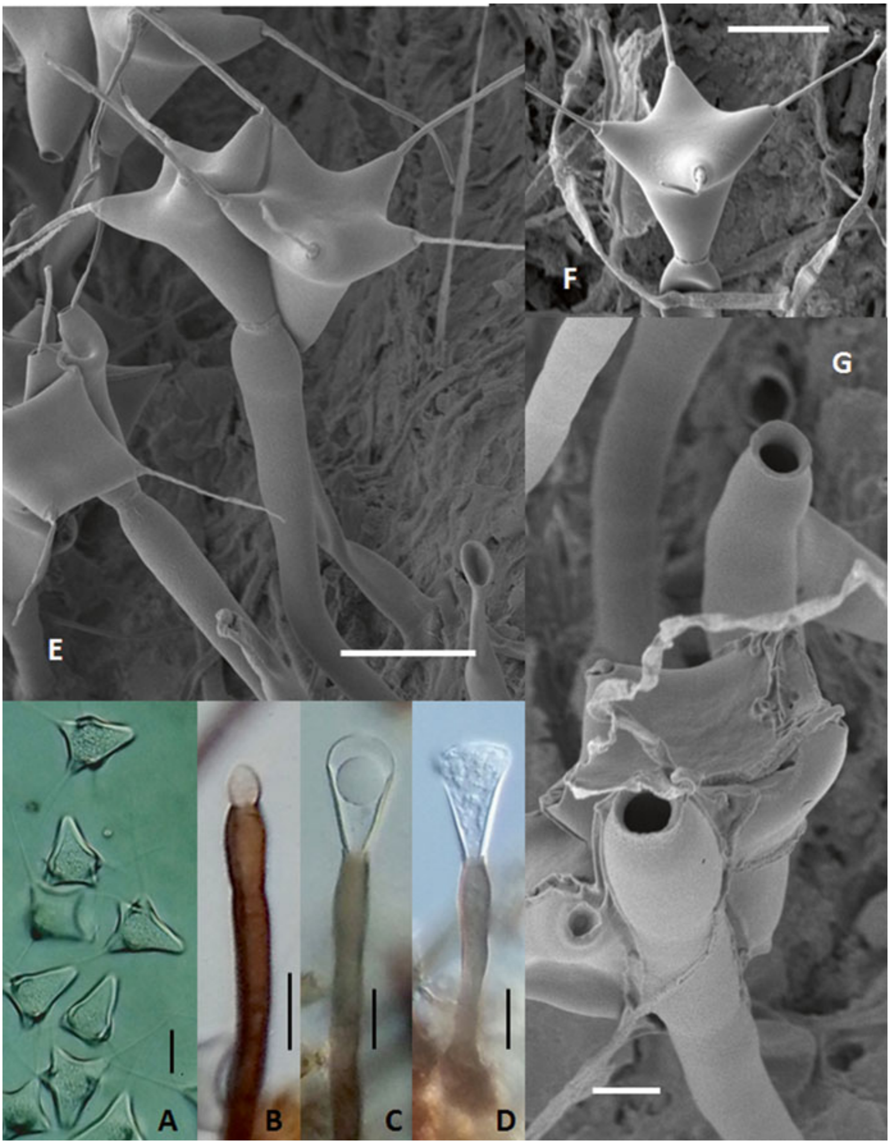

Fig. 13.6 *Nawawia quadrisetulata*. (**a**) Conidia, bearing 4–5 setulae at the corners of the distal end. (**b–d**) Conidiophores showing sequential development of conidia. (**e**, **f**) Scanning electron micrographs of setulate conidia produced at the apex of conidiophores. (**g**) Conidiophores showing the terminal phialides. Scale bars: **a–d** = 20 µm; **g** = 5 µm

How Are They Adapted to an Aquatic Lifestyle?

Spores are the dispersal propagules of fungi. Aquatic fungi need to produce spores that can be dispersed in water, and then become entrapped to, and subsequently colonize new substrates. The completion of the life cycle and hence the survival of the species is reliant on the spores.

The zoosporic fungi release motile spores that can actively disperse/swim in the lentic aquatic environments (e.g., ponds, lakes, ditches, pools, and swamps). They are usually chemotactic, being sensitively attracted to their host or substrates that release specific sugars and amino acids (Fuller and Jaworski 1987). Usually the zoospores swim for a few minutes to hours before they stop and encyst. At the initial stage of zoospore encystment, depending on the species, the flagella are either retracted or shed before the zoospore assumes a spherical shape. An important property of the zoospores in general is their ability to stick firmly to the surfaces of the substrates upon which they settle down to encyst. Adhesion ensures that the zoospore, upon reaching a favorable substrate, accidentally, or through specific tactic responses, would remain firmly attached. Evidently, this behavior has great ecological value for both saprobes and parasites as it establishes a permanent contact between the fungus and its potential food source. Swimming zoospores are for dispersal and thus are not adhesive but become so in the initial stage of encystment before a cyst wall is made. The adhesive phase lasts only about 30–60 s (Sing and Bartnicki-Garcia 1972). Apparently, the timing of the adhesive phase, coinciding with the change from motile to sessile form, provides obvious ecological advantage to the fungus. Once the cysts mature, i.e., after a well-defined wall is made, the cells lose their ability to attach themselves to solid surfaces. After successful adhesion and encystment of the spore, germination of the cyst leads to penetration and colonization of the substrate.

Besides the zoosporic fungi, most aquatic fungi are saprobes that grow/colonize on submerged wood or waterlogged leaves in freshwater. The spores of freshwater ascomycetes and Ingoldian fungi are not motile in the aquatic environment. These fungi usually occur in lotic habitats (e.g., streams, creeks, rivers, brooks), and thus they possess strategies to survive in turbulent water. Their propagules are released from conidiophores growing out of substrates and thus are able to detach from the surface of the substrates, disperse (float) in water, and eventually become entrapped (settled) or attached (adhere) to new substrates, which they can colonize by penetration of a germ tube. The mechanisms of fungal adhesion and the role of mucilage in fungal attachment in the aquatic environment have been well documented (Wong et al. 1998; Au et al. 1996; Ingold 1966; Jones 2006). An excellent review of the adaptations for dispersal in filamentous freshwater fungi is given by Goh and Hyde (1996).

Many freshwater ascomycetes have ascospores with various sheaths, appendages, or wall ornamentations, which probably function in dispersal and/or attachment of the spores. Shearer (1993a) provided a list of ascomycete species possessing ascospores surrounded by mucilaginous sheaths. There are ascospores that possess unfurling mucilaginous appendages, which uncoil in water to form long viscous threads. Several unique appendage types have now been shown to exist in freshwater ascomycetes, which account for their success in the aquatic environments (Jones 2006; Wong and Hyde 1999).

The Ingoldian fungi have been known for decades to have sigmoid or tetraradiate spores (Ingold 1975; Goh 1997). Sigmoid conidia often become attached at their sticky poles and straighten in the direction of the water current so that they are less likely to be washed away in a lotic habitat (Webster and Davey 1984). Tetraradiate and variously branched spores act as an anchor and allow their entrapment to the substrates or in surface foam (Ingold 1966). Tetraradiate spores can also effectively attach to the substrate with three "legs" forming a strongly adhesive tripod (Webster and Descals 1981). Adhesive mucilaginous material is also produced at each arm of the tetraradiate spore in contact with a surface and attaches them firmly to the substrate.

The aero-aquatic hyphomycetes, such as *Beverwykella*, *Cancellidium*, and *Clathrosphaerina*, are normally found on decaying plant materials in slow-flowing streams and stagnant ponds (Gessner et al. 2007; Voglmayr and Delgado-Rodriguez 2001, 2003; Voglmayr and Krisai-Greilhuber 1997). Their propagules are beautiful, extraordinary, and interesting as they possess a special floatation device, usually composed of intricate branching hyphal network and thus air trapping, enabling these fungi to be dispersed from one static water habitat to another. Conidia of *Helicoon* species are composed of tightly coiled filaments, which assume a barrel shape, and can trap air in water for floating (Goh and Hyde 1996). For further discussion of the adaptation strategies in the aero-aquatic fungi, see Fisher (Fisher et al. 1977) and Webster and Descals (1981).

A great diversity of dematiaceous hyphomycetes have been discovered from wood submerged in freshwater (Goh and Tsui 2003). Among these lignicolous hyphomycetes, many possess long mononematous stiptate conidiophores, which stand erect from the submerged substrates and bear masses of conidia at the apices. Examples of such hyphomycetes are *Acrogenospora*, *Cryptophiale*, and *Spadicoides*. Others produce erect synnemata (e.g., *Bactrodesmium longisporum*, *Nawawia dendroidea*, and *Phaeoisaria clematidis*) or occur as sporodochia (e.g., *Dictyosporium*, *Canalisporium*, and *Yinmingella*). Producing easily detachable conidia at the apex of long, erect conidiophores, or having conidia produced in dense masses from sporodochia, may be adaptation strategies conducive to effective spore dispersal in the aquatic habitats. Moreover, certain features observed in some of the commonly found hyphomycetes from submerged wood are worth mentioning, because they may represent special adaptation features for dispersal in the aquatic habitats. For example, *Chalara*, *Sporoschisma*, and *Sporoschismopsis* (Goh et al. 1997) produce long chains of conidia from erect conidiophores, which eventually disarticulated in water for ease of dispersal. The muriform conidia of *Canalisporium* have distinct pores or canals in the septa (Goh et al. 1998) which enable air to trap inside the conidia for floating. The various spore types of these lignicolous hyphomycetes in freshwater also are provided with modified appendages, mucilaginous sheaths, setulae, or arms (Goh 1997), and these are functionally comparable to those of aquatic ascomycetes and Ingoldian fungi.

How Did They Evolve?

The absolute age of fungal phyla is an area of active research, and only broad estimates exist for the oldest clades (Taylor and Berbee 2006). Currently, the divergence of younger phyla from the *Cryptomycota*, *Chytridiomycota*, and *Blastocladiomycota* clades—and the loss of the zoospore stage—is thought to have occurred during the Neoproterozoic, approximately 600–800 Myr (Stajich et al. 2009). The first divergence of terrestrial fungi (*Endogonales* and *Glomales*) has been estimated to have occurred about 600 Myr or even earlier, while *Ascomycota* and *Basidiomycota* separated 500 Myr (Berbee and Taylor 2001). The origin and radiation of *Euascomycetes* (whose groups commonly produce conidia adapted in aquatic habitats) may have taken place in the Mesozoic, about 240 Myr. This puts a lower limit to the earliest appearance of aquatic ascomycetes and relatives. Did the majority of the taxa appear in a brief burst of rapid radiation, or was this spread out over an extended period of time? Are new species still invading running waters today (Schlütz and Shumilovskikh 2013)?

Fungi in freshwater are grouped ecologically and morphologically, and it is not surprising that they have evolved independently from multiple lineages. Shearer (Shearer 1993a) first proposed the multiple origins of freshwater ascomycetes, which are present as endophytes, pathogens, or saprobes on plants, and have become adapted to aquatic environment when these plants invaded water. 18S rRNA data (Vijaykrishna et al. 2006; Baschien et al. 2006; Belliveau and Bärlocher 2005) showed that freshwater fungi (sexual and asexual ascomycetes) evolved from terrestrial fungi in (more than) four different classes, *Sordariomycetes*, *Dothideomycetes*, *Leotiomycetes*, and *Orbiliomycetes*. Many freshwater fungi have terrestrial relatives, supporting the fact of secondary adaptation to the freshwater environment. A comprehensive study of 84 fungi of described and undescribed freshwater *Dothideomycetes* and 85 additional ascomycetes representative of the major orders and families of *Dothideomycetes* based on ribosomal genes also confirmed the polyphyletic origins of freshwater ascomycetes (Shearer et al. 2009). Apart from these, molecular studies of fungi on submerged leaves using denaturing gradient gel electrophoresis [DGGE; (Kelly et al. 2010; Nikolcheva et al. 2003)] and the analysis of terminal restriction fragment length polymorphism [TRFLP; (Nikolcheva et al. 2003; Nikolcheva and Bärlocher 2005)] and of clone libraries (Clivot et al. 2014; Harrop et al. 2009) provided evidence for the presence of fungi of terrestrial origin.

Many genera of freshwater fungi (ascomycetes and their asexual relatives) are also not monophyletic. The polyphyletic origin of aquatic hyphomycetes has been reinforced by additional studies (Baschien et al. 2006, 2013; Campbell et al. 2006, 2009). For example, Ingoldian fungi are assigned to four classes: *Sordariomycetes* (~11 spp.), *Dothideomycetes* (~10 spp.), *Pezizomycetes* (1 sp.), *Orbiliomycetes* (3–5 spp.), and *Leotiomycetes* (>75 spp.). The morphology of tetraradiate and sigmoid conidial shape has been recognized as convergent development in unrelated aquatic hyphomycete taxa (Ingold 1966; Webster 1980). Molecular studies of ribosomal genes also reassured the convergence of the conidial shape (Baschien et al. 2006, 2013; Campbell et al. 2006; Belliveau and Bärlocher 2005). Also, the helicosporous aero-aquatic fungi have evolved from multiple lineages within the ascomycetes (Tsui and Berbee 2006).

The molecular studies mentioned above showed that many ascomycetous and basidiomycetous freshwater fungi are closely related to terrestrial fungi. A few species of the genera *Varicosporium*, *Tetracladium*, *Filosporella*, and *Anguillospora* have been isolated as endophytes from aquatic or terrestrial roots (Fisher et al. 1991; Kohout et al. 2012; Nemec 1969; Sati and Belwal 2005; Watanabe 1975). The step back from terrestrial to aquatic life cycles could have been aided by an endophytic lifestyle (Selosse et al. 2008). Furthermore, the localization of freshwater fungi inside roots or other amphibious plant parts may function as temporary reservoir during different stages within a life cycle. The production of different conidial shapes and synanamorphs may also be an adaptation to shifts between aquatic, semiaquatic, and terrestrial habitats (Baschien et al. 2013). Kohout and co-workers (Kohout et al. 2013) proposed the scenario that terrestrial ancestors of recent aquatic plants interacted with different root-associated fungi (RAF). The aquatic hyphomycetes could have evolved from non-mycorrhizal RAF that once entered aquatic habitats together with their host plants.

What Are They Doing in Freshwater Habitats?

The primary ecological role of fungi in aquatic habitats is to decompose dead plant material—both woody and herbaceous debris. When Kaushik and Hynes (1971) demonstrated the crucial role of fungi in the decomposition of plant materials to detritus in streams, limnologists recognized the important ecological function of aquatic hyphomycetes. Bärlocher and Kendrick (1974) showed that aquatic hyphomycetes condition leaf material for aquatic invertebrates (Plecoptera, Trichoptera, Coleoptera, Crustacea, Gastropoda) by increasing the palatability using exoenzymes [cellulases, pectinases, laccases; (Abdel-Raheem and Shearer 2002; Chamier 1985)]. Most aquatic fungi have the ability to decompose a wide range of organic substrates, although a few species may be limited to one or a few types of substrates. For example, Gulis (2001) showed that wood/twig substrates bear fungal communities distinct from those on leaves. In general, aquatic ascomycetes and basidiomycetes are thought to be responsible for the decomposition of woody debris while Ingoldian fungi decompose either leaves or herbaceous debris. Through decomposition, freshwater fungi can facilitate the transfer of nutrients and energy between trophic levels in the food web (Gessner et al. 2007).

Wood is a complex substance and its major chemical constituents contain cellulose, hemicellulose, and lignin. The degradation mechanisms of wood are well known in terrestrial fungi, and it is assumed that similar mechanisms are present in freshwater fungi. Cellulose hydrolysis is achieved by endoglucanases and cellobiohydrolases, collectively termed cellulases (Eaton and Hale 1993). Hydrolysis of hemicellulose, a mixed polymer, occurs via the action of hydrolytic xylanases, mannanases, and possibly other hydrolases with broad substrate specificity (Eaton and Hale 1993). The degradation of lignin involves two peroxidases, lignin peroxidase and Mn-dependent peroxidase, and a polyphenol oxidase, laccase, known as lignin-modifying enzymes (LMEs) (Pointing 2001). The vast majority of freshwater ascomycetes, regardless of eco-climate, habitat, and substrate distributions, are capable of breaking down cellobiose, hemicellulose, and xylan and starch, which are important carbon compounds in plant-based debris (Bucher et al. 2004; Simonis et al. 2008; Yuen et al. 1998).

Three fungal wood decay types are recognized on the basis of whether or not they can degrade cellulose and lignin or just cellulose alone, namely, soft rot, white rot, and brown rot (Eaton and Hale 1993). Soft rots occur in wood that has an unusually high level of moisture, which is often the case for woody substrates in aquatic environments. Most of the freshwater fungi are capable to form soft rot decay and to produce cellulases (Bucher et al. 2004; Abdel-Raheem and Shearer 2002). White-rot fungi normally have the enzymes to degrade both cellulose and lignin simultaneously. The residual material that is left behind has a somewhat fibrous appearance and is very pale in color, looking as if it had been bleached. In contrast, members of brown-rot fungi can degrade cellulose. After decomposition, wood is brown in color and tends to be broken up into cubical fragments that quickly disintegrate into a powdery brown residue. It has been questionable whether or not freshwater ascomycetes can form white rot or brown rot because the breakdown of lignin in woody debris is primarily accomplished by basidiomycetes that do not seem common in the aquatic habitat. However, Junghanns et al. (2005) showed that the aquatic hyphomycete *Clavariopsis aquatica* produced laccases. Five putative laccase genes (*lcc1* to *lcc5*) identified in *C. aquatica* were differentially expressed in response to the fungal growth stage and potential laccase inducers (Sole et al. 2012). Recently, Kerr and co-workers (2013) showed the oxidation of lignin in leaf litter by undetermined aquatic fungi using high spatial resolution infrared microspectroscopy. The modification of lignin by freshwater fungi degrades lignin into carbohydrate-depleted recalcitrant carbon, which may influence the carbon pool in aquatic environments.

Leaves and other nonwoody plant parts (e.g., fruits and seeds) represent a different type of substrate than wood and bark. In general, angiosperm leaves are readily decomposed. When a leaf falls from a tree from the riparian zone, it would be colonized by soil-inhabiting fungi—those already present in the layer of litter at the soil surface or various aquatic fungi when the leaf becomes submerged. Most aquatic hyphomycetes can degrade cellulose, various hemicelluloses, and pectin (Chamier 1985; Abdel-Raheem and Ali 2004; Chandrashekar and Kaveriappa 1991; Zemek et al. 1985). Many studies have examined the enzymatic activities of freshwater fungi and reported amylase, β-glucosidase, β-xylosidase, endoglucanase, endoxylanase, lipase, pectinase, and protease activity (Chamier 1985).

To which extent aquatic—terrestrial—hyphomycetes play an important role in aquatic systems is still unclear, although they are common on leaves and wood. It is generally assumed that the so-called aquatic–terrestrial fungi are not able to compete against aquatic hyphomycetes and hence are removed after the first 2–3 days of the decomposition process (Harrop et al. 2009; Bärlocher and Kendrick 1974; Nikolcheva et al. 2005; Perez et al. 2012). However, aquatic–terrestrial fungi are present on longer-exposed leaves in streams [e.g., (Hameed et al. 2008; Smither-Kopperl et al. 1998)]. Kelly et al. (2010) studied fungal communities on decomposing maple and aspen leaves, and his group reported that the majority of operational taxonomic units (OTUs) represented terrestrial *Cladosporium* species, whereas aquatic hyphomycete sequences were not observed. Indeed, several aquatic–terrestrial hyphomycetes are able of decomposing leaf litter (Bucher et al. 2004; Singh et al. 2014). For example, the terrestrial leaf litter ascomycete *Torula herbarum*, isolated from a tropical stream, has been found to be able to break down lignin (Bucher et al. 2004).

Few aquatic fungi form a symbiotic mycorrhizal relationship with the roots of trees and other plants and macrophytes. This association is mutually beneficial to both the plant and the fungus. The fungus enables the plant to take up nutrients that are unavailable, and the plant provides nutrition for the fungus. There are two fundamentally different types of mycorrhizal associations—ectomycorrhizal (usually involving a basidiomycete) and endomycorrhizal (most often involving a member of the *Glomeromycota*). In the former, the fungus produces a covering of hyphae (called a sheath, Hartig net, or mantle) around the outside of smaller rootlets of the host plant. Other hyphae invade the cortex of the rootlet but do not disrupt the individual cells. In endomycorrhizal associations, no sheath is formed and hyphae of the fungus actually invade cells of the cortex of the rootlet. Perhaps 80 % of all vascular plants form mycorrhizal associations with fungi. First aquatic vesicular–arbuscular mycorrhiza was discovered in *Littorella uniflora*, *Lobelia dortmanna*, and *Isoetes lacustris* by Sondergaard and Laegaard (1977). Vesicular–arbuscular mycorrhizas (VAM) in *Isoetes* plants were later also observed by Sudova et al. (2011).

Furthermore, dark septate endophytes (DSE) and fungal root associates (RAF) from aquatic habitats were reported (Kohout et al. 2012; Seena et al. 2008). Mycorrhiza and some DSE are known to be mutualistic. On the other hand, endophytism can be the balance between rather antagonistic relationships between fungus and host which may even develop into a pathogenic outcome (Schulz and Boyle 2005). Several species of aquatic hyphomycetes were isolated as endophytes from aquatic or terrestrial plants (Sati and Belwal 2005). Some aquatic hyphomycetes were also found in roots of terrestrial habitats [e.g., (Tedersoo et al. 2007)]. However, there are few reports about the transmission of freshwater fungi either vertical to the next generation of the same host or horizontal between hosts. It is not known if endophytic aquatic hyphomycetes have a harmful or beneficial effect on the hosts. Further thorough studies are needed to elucidate the aspects of endophytic life of aquatic hyphomycetes.

For instance, all the described *Minutisphaera* spp. (*M. fimbriatispora*, *M. japonica*, *M. aspera*, and *M. parafimbriatispora*) have been isolated from submerged wood in freshwater habitats so far (Ferrer et al. 2011; Raja et al. 2013), suggesting that they play an ecological role in nutrient cycling and organic matter decomposition in freshwater habitats (Pointing 2001). A recent BLAST search (Altschul et al. 1990) of newly sequenced ITS strains of *M. aspera* and *M. parafimbriatispora* in GenBank identified two ITS sequences from endophytes ("*Pleosporales* sp. 39 g," JX244063, and "*Didymosphaeria* sp. TS_04_050," HQ713763) as the top BLAST matches with high percent identity values and coverage. Based on the uncorrected p-distances calculated in PAUP*, the two ITS sequences from endophytes were identical to each other and shared 99 % sequence similarity with ITS sequences of *M. aspera*. The high ITS sequence similarity between these fungal endophytes and *M. aspera* could imply that *Minutisphaera* may have a dual mode of lifestyle as saprobes on submerged wood as well as fungal endophytes inside the roots of trees. However, additional studies are warranted to test this ecological hypothesis (Selosse et al. 2008).

In contrast to the aquatic ascomycetes (meiosporic and mitosporic fungi), which generally colonize organic matter, which are comparatively larger in size, such as fallen leaves, submerged wood, or aquatic plants, the zoosporic fungi are colonizers of smaller substrates. They are particularly fond of substrates which contain chitin, keratin, or cellulose (Wong et al. 1998). In case of small particles such as algae, pollen grains, seeds, and zooplankton carcasses, and other temporarily available substrates decomposition is achieved by the much smaller chytrids (*Chytridiomycetes*) and water molds (*Oomycetes*), rather than the aquatic hyphomycetes. This is because the zoosporic fungi are relatively simpler in structures. They do not depend on macroscale hyphal networks and thus are capable of very fast responses to changes in their environment. Being actively motile, the zoospores of these aquatic fungi actively search for adequate substrates using chemotaxis. Once a suitable substrate has been reached, the zoospore encysts. An appressorium or a penetration tube is formed and the food particle (substrate) is invaded by tiny rhizoids tapping the internal nutrient reservoirs. Zoosporogenesis can occur in a short time, producing a prolific number of zoospores from zoosporangia. Their life cycle can be completed in days, either endobiotic, epibiotic, endophytic, or ectophytic, depending on the relationship of the thallus with the host or organic substrate.

Like other aquatic fungi, the chytrids and water molds are heterotrophs. Most of the species are benign saprobes, but they often exist as parasites, sometimes as symbionts, and of course as decomposers. The aquatic systems harbor a wealth of organisms that can serve as suitable hosts for the parasitic zoosporic fungi: algae from different phyla, cyanobacteria, protists, zooplankton, fish, birds, mussels, eggs of liver flukes, nematodes, crayfish, mites, insect larvae, amphibians, mammals, plants, and other aquatic fungi. For the decomposers, resources of organic matters derived from animals include fish scales, fish eggs, carcasses, feathers, and hair, while plant-derived resources include pollen, spores, seeds, small fruits, and plant debris (Cole et al. 1990).

Chytrids are surprisingly abundant on filamentous algae, phytoplanktons, and diatoms, and some species are known to severely deplete local populations of their algal hosts. The abundance of chytrids in aquatic systems are considered much higher than traditionally thought (Kagami et al. 2014). The phytoplanktons infected with chytrid zoospores could become an excellent food source for zooplanktons in terms of size, shape, and nutritional quality, and the nutrients from within the planktons can be transferred to the zooplanktons through the "mycoloop" pathway in the aquatic ecosystems (Kagami et al. 2014). Also pollen deposited in lakes could be consumed by saprotrophic chytrids, rather than parasitic relatives (Masclaux et al. 2013).

Ibelings and co-workers studied the host–parasite interactions between freshwater phytoplankton and chytrid fungi and found that algal population was naturally regulated by the parasitism of these fungi (Ibelings et al. 2004). Encounters with these parasitic chytrids can be fatal to algae, particularly if their defense mechanism is breached by the fungal parasites. When the alga is attacked by the fungus, it undergoes a "suicide" response, which is a controlled hypersensitive reaction. This hypersensitivity is regarded as a common defense mechanism in algae. If this controlled "suicide" progress is initiated at the right moment during fungal infection, it results in the successful interruption of the fungal infection cycle, because the parasite's ability to reproduce via spore production is inhibited. This mechanism is conducive to maintaining a healthy algal population because it reduces the abundance of the deadly fungal parasite in the environment. If such control is unsuccessful, however, the parasitic chytrid prevails and thus resulting in mass mortality of the algal species. The ecological relevance of this negative interaction between the two parties is obvious. The failure of the algal "suicide" mechanism in response to fungal infection can lead to shifts in the algal community composition in a given aquatic system.

In rare, but important cases, some zoosporic fungi cause severe damage to larger aquatic organisms. They infect frogs, shrimps, fishes, or fish eggs (Chukanhom and Hatai 2004; Noga 1993) and thereby exert strong population pressure. Such damage is of great importance for aquaculture and often demands antifungal treatments. Some oomycetes, especially species of *Aphanomyces* and *Saprolegnia*, are aggressive pathogens of fish and crustacea. For example, *Aphanomyces astaci* causing the crayfish plague has driven the European crayfish population to the edge of extinction (Reynolds 1988). The most notorious parasitic chytrid is *Batrachochytrium dendrobatidis*, which cause worldwide extinction of several known and unknown species of frogs (Berger et al. 1998; Skerratt et al. 2007). Aquatic plants are also greatly affected by some oomycetes. For example, *Pythium phragmites* has been found to cause reed decline (Nechwatal et al. 2005). For more discussion on diseases of freshwater fishes caused by zoosporic fungi, see Willoughby (2003).

Distribution and Biodiversity

Distribution Pattern

Regarding the distribution pattern of freshwater fungi, some may be restricted to tropical, temperate, or cold water habitats, while others are cosmopolitan. The geographical distribution of Ingoldian mitosporic ascomycetes (=anamorph or asexual fungi) are relatively well studied compared to those of the freshwater ascomycetes. The Ingoldian fungi most commonly occur on shed leaves in streams and rivers, and they are documented by stream biologists. Some are cosmopolitan and some are restricted in distribution. Also the phylogeographic pattern varies among and within a species. Molecular barcoding (ITS) of 130 isolates of six Ingoldian fungi revealed significant genetic differentiation between continents within a single fungal species (Duarte et al. 2012). The knowledge on the distribution pattern of freshwater ascomycetes is accumulating even though most investigations are concentrating in tropical and subtropical Asia, North America, as well as the neotropics.

Some studies have reported shifts in fungal community composition by latitude and temperature (Arnold and Lutzoni 2007). Such spatial shifts/turnover in community is also expected in freshwater fungi. Wood-Eggenschwiler and Bärlocher (1985) used distribution data obtained from the literature (Webster and Descals 1981) for over 150 species of Ingoldian mitosporic fungi and they concluded, “on a worldwide scale, temperature together with its influence on vegetation in different climatic regions is the major factor in determining distribution patterns of Ingoldian mitosporic fungi.” Wood-Eggenschwiler and Bärlocher (1985) discovered that there was a higher similarity in species composition of Ingoldian fungi between geographically distinct tropical locations (South America, West Africa) than between tropical and temperate regions that were located on the same continent, either African or North and South American. Raja et al. (2009) also reported a change in species composition of freshwater ascomycetes along the temperate–subtropical latitudinal ecotone in Florida, USA.

Apart from the macroclimatic factors, microenvironmental factors also affect the distribution and abundance of freshwater fungi. Chauvet (1991) studied the distribution of Ingoldian mitosporic fungi at 27 stations in France, and he concluded that the most important environmental factors are altitude, pH, temperature, and season, although the relationship between species composition and each environmental factor is hard to establish. Longitudinal distribution patterns in freshwater fungi along a river and stream are reported for both leaf litter and woody substrates (Gönczöl 1989; Shearer and Webster 1985a, 1991; Tsui et al. 2001a). Tsui et al. (2001a) reported changes in fungal communities and taxonomic compositions from upstream to downstream in responses to salinity and riparian vegetation. Shearer and Webster (1985a) reported that Ingoldian mitosporic fungi communities in headwater streams were distinctly different from the downstream communities in the River Teign. Using water filtration, leaf pack baiting, and collection of naturally occurring substrates, lower species diversity with a lower frequency occurrence of species was observed in the headwaters (Shearer and Webster 1985a). Using molecular data of DGGE, Miura and Urabe (2014) also demonstrated that taxonomic composition and richness of epilithic fungal assemblages change along the longitudinal gradient of the river, according to the water temperature, and the spatial variation in abundance and composition of dissolved organic matter and nutrients. While species diversity could change spatially, the genetic variability within a species does not vary locally. Using eight microsatellite markers, Anderson and Shearer (2011) revealed small genetic differentiations among populations of *Tetracladium marchalianum* from Wisconsin and Illinois, USA. They concluded that the fungal populations may be highly connected in local habitats.

Substrate Preference

Freshwater fungi demonstrate substrate specialization, even though they are saprobes. For instance, of the 548 species of freshwater ascomycetes reported up to 2009 (http://fungi.life.uiuc.edu/), 60 % are reported only from submerged woody debris and about 30 % are reported only from herbaceous substrates, while only about 10 % species are reported from both submerged wood and herbaceous substrates [reviewed in (Raja et al. 2009)]. During the substrate distribution pattern investigation of freshwater ascomycetes in the Florida Peninsula (Raja et al. 2009), the results implied substrate preference among freshwater fungi. Of the 132 fungal taxa collected in freshwater habitats, 100 were reported only on woody debris, 14 species occurred exclusively on herbaceous debris, and 18 species were found on both woody and herbaceous debris (Raja et al. 2009). Cai et al. (2003) also reported substrate preferences in freshwater fungi during an investigation on the biodiversity of freshwater fungi on submerged bamboo and submerged wood in Liput River in the Philippines. Fifty-eight and 38 fungal taxa were collected on bamboo and wood, respectively, but only 16 among them were in common on both substrates (Cai et al. 2003).

Thomas et al. (1992) observed *Alatospora acuminata* more frequently on *Acacia* leaves, while *Tetrachaetum elegans* was more common on *Eucalyptus* leaves. The authors suggested five possible reasons: First, different substrates have different nutrients, favoring the growth of some fungi over others. Second, different substrates contain different inhibitory chemicals, for example, tannin, impacting sporulation and spore germination. Third, variations in the gross physical structure of substrates affect differentially the impaction efficiency of various fungal spores. Fourth, variations in fine physical structure of substrates affect penetration and colonization by fungi. Fifth, different substrates vary in their decay rate—durable substrate has a much longer exposure time to the spores and to fungal colonization. Gulis (2001) investigated five different substrate types from 92 watercourses of Belarus for aquatic hyphomycete colonization (52 species). He found specific fungal assemblages correlating with leaf litter types which suggests possible substrate preferences of aquatic hyphomycetes triggered in particular by lignin content.

Seasonal Variation

Seasonal occurrence with fluctuations in conidial numbers has been reported in many parts of the world (Thomas et al. 1989). Although most species can be collected throughout the year, their relative abundance (measured in terms of conidial production) is influenced by the seasonal availability of substrates, which is in agreement with seasonal input of deciduous tree litter in temperate regions (Bärlocher 1992). For instance, the conidial peak in summer in Australia was also highly correlated with the leaf fall of eucalypt forests in summer (Thomas et al. 1989), and the timing of conidial maxima in New Zealand streams was well correlated with the prevailing litter fall patterns (Aimer and Segedin 1985). Recent studies employing DGGE illustrated seasonal changes in fungal communities in a lake in Japan (Ishii et al. 2015).

Human Disturbance

Most freshwater habitats are vulnerable to human disturbance such as agriculture, urbanization, and industrialization. Any perturbation around the riparian environment affects significantly the in-stream fungal communities and the biogeochemical cycles through runoff processes. Organic pollution caused by the mass discharged of domestic or agricultural wastes reduces the amount of oxygen in the water. Most freshwater fungi cannot survive in such anoxic and polluted environments. For example, organic pollution reduced substantially the diversity of aquatic hyphomycetes (Raviraja et al. 1998) and ascomycetes (Tsui et al. 2001b). Toxic metal entering the rivers as a result of mining and industrialization also impact negatively the fungal communities. Spore production, biomass, and fungal diversity are severely depleted under high concentrations of coal, copper, zinc, and cadmium (Krauss et al. 2001; Niyogi et al. 2009; Sridhar et al. 2005). Similarly, the application of chemical pesticides can also change the fungal communities. For example, the antigen and biomass production of *Neonectria* (*Heliscus*) *lugdunensis* was influenced by the herbicide mecoprop (Bermingham et al. 1998). Recent pyrosequencing (metagenomics) data also showed declining fungal diversity in most eutrophic streams (Duarte et al. 2014). However, previous studies demonstrated the opposite—anthropogenic nutrients stimulated fungal spore production and mycelial biomass on leaves (Gulis and Suberkropp 2003).

Functional Biodiversity/Outlook: Who Is Doing What?

The most prominent ecological function of freshwater fungi is the decomposition of allochthonous organic matter in aquatic systems. The research of freshwater fungal ecology has been focused on stream-inhabiting aquatic hyphomycetes mostly in temperate low-order streams (Bärlocher 2010). Properties of ecosystem functions, such as fungal biomass, fungal productivity, and fungal impact on the decomposition process (Lecerf and Richardson 2010a), have been investigated in hundreds of field and laboratory (microcosm) studies [meta-analyzed in (Ferreira et al. 2014)]. These studies were accompanied by inventory biodiversity (morphological and molecular) approaches of aquatic hyphomycetes [e.g., (Nikolcheva et al. 2003; Seena et al. 2008; Duarte et al. 2014; Casas et al. 2011; Pascoal et al. 2005; Shearer and Webster 1985b)]. However, the results of studies investigating the functional consequences of biodiversity changes often remained unpredictable or inconsistent [summarized in (Graça et al. 2015)]. Within the last decade, it has become apparent that species traits and functional diversity may be better correlated with ecosystem function than taxonomic identity (Gessner et al. 2010; Lecerf and Richardson 2010b).

Nowadays we have the methods at hand to even more thoroughly elucidate species assemblages and, furthermore, investigate the possible and active traits of freshwater fungi. The progress in sequencing and annotating fungal genomes will soon shed light on the genetic diversity and metabolic potential of freshwater fungi from all fungal phyla. Transcriptomes [e.g., using RNA-seq; (Wang et al. 2009)] from single cultures or microcosm studies of freshwater fungi will enable us to study the metabolism during decomposition and/or degradation processes. For the identification of metabolic pathways, the quality of genome annotation is crucial (Kuske et al. 2015). The optimal study design is to have very well-annotated reference genomes, the transcriptome (the expressed genes), and the corresponding proteome (the produced enzymes) as shown by Hori and co-workers (2014). Freshwater fungal communities are complex assemblages of mostly filamentous fungi, single-celled chytrids, and yeasts. They are members of food webs and mediators of biogeochemical pathways for the energy transfer between different trophy levels. Future methodical improvements will hopefully ease the challenges of meta-analyses to understand the “why-is-who-doing-what” in the ecology of freshwater fungi.

Acknowledgments The authors wish to thank the following students of Professor T.K. Goh, for providing the pictures of freshwater fungi used in this chapter: Bao Yee Loh (*Oomycetes*), Huey Kei Lee (Ingoldian fungi), and Wee Kee Sim (lignicolous hyphomycetes). We are grateful to Dr. Huzefa Raja for comments and suggestions. The authors thank the master student of Christiane Baschien, Jens Schmidt for the picture of Lunulospora curvula conidiogenesis.

References

Abdel-Aziz FA (2008) Diversity of aquatic fungi on *Phragmites australis* at Lake Manzala, Egypt. Sydowia 60(1):1–14, PubMed PMID: WOS:000257909100001

Abdel-Raheem AM, Ali EH (2004) Lignocellulolytic enzyme production by aquatic hyphomycetes species isolated from the Nile’s delta region. Mycopathologia 157:277–286

Abdel-Raheem A, Shearer C (2002) Extracellular enzyme production by freshwater ascomycetes. Fungal Divers 11:1–19

Aimer RD, Segedin BP (1985) Some aquatic hyphomycetes from New Zealand streams. N Z J Bot 23:273–299

Altschul SF, Gish W, Miller W, Myers EW, Lipman DJ (1990) Basic local alignment search tool. J Mol Evol 215:403–410

Anderson JL, Shearer CA (2011) Population genetics of the aquatic fungus *Tetracladium marchalianum* over space and time. PLoS One 6(1):10. doi:10.1371/journal.pone.0015908, PubMed PMID: WOS:000286516500015

Ando K (1992) A study of terrestrial aquatic hyphomycetes. Trans Mycol Soc Jpn 33:415–425

Ando K, Tubaki K (1984a) Some undescribed hyphomycetes in rainwater draining from intact trees. Trans Mycol Soc Jpn 25:39–47

Ando K, Tubaki K (1984b) Some undescribed hyphomycetes in the rain drops from intact leaf-surface. Trans Mycol Soc Jpn 25:21–37

Arnold AE, Lutzoni F (2007) Diversity and host range of foliar fungal endophytes: are tropical leaves biodiversity hotspots? Ecology 88:541–549

Au DWT, Jones EBG, Moss ST (1996) Spore attachment and extracellular mucilage of aquatic hyphomycetes. Biofouling 10:123–140

Bärlocher F (1992) The ecology of aquatic hyphomycetes. Springer, Berlin

Bärlocher F (2010) Molecular approaches promise a deeper and broader understanding of the evolutionary ecology of aquatic hyphomycetes. J N Am Benthol Soc 29(3):1027–1041. doi:10.1899/09-081.1, PubMed PMID: WOS:000280692400021

Bärlocher F, Kendrick B (1974) Dynamics of the fungal population on leaves in a stream. J Ecol 62:761–791

Bärlocher F, Seena S, Wilson KP, Williams DD (2008) Raised water temperature lowers diversity of hyporheic aquatic hyphomycetes. Freshw Biol 53(2):368–379. doi:10.1111/j.1365-2427.2007.01899.x, PubMed PMID: WOS:000252393800013

Baschien C, Marvanová L, Szewzyk U (2006) Phylogeny of selected aquatic hyphomycetes based on morphological and molecular data. Nova Hedwigia 83(3–4):311–352. doi:10.1127/0029-5035/2006/0083-0311, PubMed PMID: WOS:000242664300003

Baschien C, Rode G, Böckelmann U, Götz F, Szewzyk U (2009) Interactions between hyphosphere-associated bacteria and the fungus *Cladosporium herbarum* on aquatic leaf litter. Microb Ecol 58(3):642–650. doi:10.1007/s00248-009-9528-6, PubMed PMID: WOS:000269928300020

Baschien C, Tsui CKM, Gulis V, Szewzyk U, Marvanová L (2013) The molecular phylogeny of aquatic hyphomycetes with affinity to the Leotiomycetes. Fungal Biol 117(9):660–672. doi:10.1016/j.funbio.2013.07.004, PubMed PMID: WOS:000324899800008

Beakes GW (2003) Lower fungi: a review of microscopial techniques for the taxonomic and ecological study of zoosporic freshwater fungi. In: Tsui CKM, Hyde KD (eds) Fungal diversity research series 10 freshwater mycology -a practical approach. Fungal Diversity Press, Hong Kong, pp 51–79

Belliveau MJ-R, Bärlocher F (2005) Molecular evidence confirms multiple origins of aquatic hyphomycetes. Mycol Res 109(12):1407–1417, PubMed

Berbee ML, Taylor JW (2001) Fungal molecular evolution: gene trees and geologic time. In: Mc Laughlin DJ and Mc Laughlin EJ, Lemke PA (eds) The mycota VII part b systematics and evolution. Springer, Berlin

Berger L, Speare R, Daszak P, Green DE, Cunningham AA, Goggin CL et al (1998) Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. Proc Natl Acad Sci USA 95(15):9031–9036. doi:10.1073/pnas.95.15.9031, PubMed PMID: WOS:000075143900110

Bermingham S, Fisher PJ, Martin A, Marriott M, Lappin-Scott H (1998) The effect of the herbicide Mecoprop on *Heliscus lugdunensis* and its influence on the preferential feeding of *Gammarus pseudolimnaeus*. Microb Ecol 35:199–204

Beverwijk AL (1951) *Candelabrum spinulosum*, a new fungus species. Anton Leeuw Int J Gen Mol Microbiol 17:9–12

Bowman BH, Taylor JW, Brown AG, Lee J, Lu SD, White TJ (1992) Molecular evolution of the fungi relationship of the basidiomycetes, ascomycetes and chytridiomycetes. Mol Biol Evol 9:285–296

Bucher VVC, Hyde KD, Pointing SB, Reddy CA (2004) Production of wood decay enzymes, mass loss and lignin solubilization in wood by marine ascomycetes and their anamorphs. Fungal Divers 15:1–14

Buczacki ST (1983) Zoosporic plant pathogens: a modern perspective. Academic, London

Cai L, Zhang KQ, McKenzie EHC, Hyde KD (2003) New species of *Dictyosporium* and *Digitodesmium* from submerged wood in Yunnan, China. Sydowia 55(2):129–135, PubMed PMID: WOS:000188231200001

Campbell J, Shearer C, Marvanová L (2006) Evolutionary relationships among aquatic anamorphs and teleomorphs: *Lemonniera*, *Margaritispora*, and *Goniopila*. Mycol Res 110:1025–1033. doi:10.1016/j.mycres.2006.04.012, PubMed PMID: WOS:000241957700003

Campbell J, Marvanová L, Gulis V (2009) Evolutionary relationships between aquatic anamorphs and teleomorphs: *Tricladium* and *Varicosporium*. Mycol Res 113:1322–1334. doi:10.1016/j.mycres.2009.09.003, PubMed PMID: WOS:000272811000009

Casas JJ, Gessner MO, Lopez D, Descals E (2011) Leaf-litter colonisation and breakdown in relation to stream typology: insights from Mediterranean low-order streams. Freshw Biol 56(12):2594–2608. doi:10.1111/j.1365-2427.2011.02686.x, PubMed PMID: WOS:000296502000014

Chamier A (1985) Cell-wall-degrading enzymes of aquatic hyphomycetes: a review. Bot J Linn Soc 91:67–81

Chandrashekar KR, Kaveriappa KM (1991) Production of extracellular cellulase by *Lunulospora curvula* and *Flagellospora penicillioides*. Folia Microbiol 36:249–255

Chauvet E (1991) Aquatic hyphomycete distribution in South-Western France. J Biogeogr 18:699–706

Chukanhom K, Hatai K (2004) Freshwater fungi isolated from eggs of the common carp (*Cyprinus carpio*) in Thailand. Mycoscience 45:42–48

Clivot H, Cornut J, Chauvet E, Elger A, Poupin P, Guerold F et al (2014) Leaf-associated fungal diversity in acidified streams: insights from combining traditional and molecular approaches. Environ Microbiol 16(7):2145–2156. doi:10.1111/1462-2920.12245, PubMed PMID: WOS:000338983600013

Cole JJ, Caraco NF, Likens GE (1990) Short-range atmospheric transport—a significant source of phosphorus to an Oligotrophic Lake. Limnol Oceanogr 35(6):1230–1237, PubMed PMID: WOS:A1990EP94300002

Digby S, Goos RD (1987) Morphology, development and taxonomy of *Loramyces*. Mycologia 79:821–831

Dix NJ, Webster J (1995) Fungal ecology. Springer, Berlin

Doggett MS (2000) Characterization of fungal biofilms within a municipal water distribution system. Appl Environ Microbiol 66(3):1249–1251. doi:10.1128/aem.66.3.1249-1251.2000, PubMed PMID: WOS:000085604800059

Duarte S, Seena S, Baerlocher F, Cassio F, Pascoal C (2012) Preliminary insights into the phylogeography of six aquatic hyphomycete species. PLoS One 7(9), e45289. doi:10.1371/journal.pone.0045289, PubMed PMID: WOS:000311313900114

Duarte S, Baerlocher F, Cassio F, Pascoal C (2014) Current status of DNA barcoding of aquatic hyphomycetes. Sydowia 66(2):191–202, PubMed PMID: WOS:000347436300003

Eaton RA, Jones EBG (1971a) The biodeterioration of timber in water-cooling towers. II. Fungi growing on wood in different positions in a water cooling system. Mater Org 6:81–92

Eaton RA, Jones EGB (1971b) The biodeterioration of timber in water cooling towers. I. Fungal ecology and the decay of wood at Connah's Quay and Ince. Mater Org 6:51–80

Eaton RA, Hale MDC (1993) Wood: decay, pests and protection. Chapman & Hall, London

Fallah PM, Shearer CA (2001) Freshwater ascomycetes: new or noteworthy species from north temperate lakes in Wisconsin. Mycologia 93(3):566–602. doi:10.2307/3761741, PubMed PMID: WOS:000168935100016

Ferreira V, Castagneyrol B, Koricheva J, Gulis V, Chauvet E, Graça MA (2014) A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol Rev. doi:10.1111/brv.12125

Ferrer A, Miller AN, Shearer CA (2011) *Minutisphaera* and *Natipusilla*: two new genera of freshwater Dothideomycetes. Mycologia 103(2):411–423. doi:10.3852/10-177, PubMed PMID: WOS:000288887400017

Fisher PJ, Sharma PD, Webster J (1977) Cellulolytic ability of aero-aquatic hyphomycetes. Trans Br Mycol Soc 69:495–496, PubMed PMID: WOS:A1977EF05300018

Fisher PJ, Petrini O, Webster J (1991) Aquatic hyphomycetes and other fungi in living aquatic and terrestrial roots of *Alnus glutinosa*. Mycol Res 95:543–547

Fuller MS, Jaworski A (1987) Zoosporic fungi in teaching and research. Southeastern Publishing Corporation, Athen, GA

Gessner MO, Gulis V, Kuehn KA, Chauvet E, Suberkropp K (2007) 17 Fungal decomposers of plant litter in aquatic ecosystems. In: Christian PK, Druzhinina IS (eds) Environmental and microbial relationships, 4th edn. Springer, Berlin

Gessner MO, Swan CM, Dang CK, McKie BG, Bardgett RD, Wall DH et al (2010) Diversity meets decomposition. Trends Ecol Evol 25(6):372–380, PubMed PMID: WOS:000278682500008

Goh TK (1997) Tropical freshwater hyphomycetes. In: Hyde KD (ed) Biodiversity of tropical microfungi. Hong Kong University Press, Hong Kong

Goh T, Hyde K (1996a) Biodiversity of freshwater fungi. J Ind Microbiol 17(5–6):328–345

Goh TK, Tsui CKM (2003) Key to common dematiaceous hyphomycetes from freshwater. In: Tsui CKM, Hyde KD (eds) Freshwater mycology. Fungal Diversity Press, Hong Kong

Goh TK, Ho WH, Hyde KD, Umali TE (1997) New records and species of *Sporoschisma* and *Sporoschismopsis* from submerged wood in the tropics. Mycol Res 101:1295–1307

Goh TK, Ho WH, Hyde KD, Whitton SR, Umali TE (1998) New records and species of *Canalisporium* (Hyphomycetes), with a revision of the genus. Can J Bot-Revue Canadienne De Botanique 76(1):142–152, PubMed PMID: WOS:000073021500017

Gönczöl J (1989) Longitudinal distribution patterns of aquatic hyphomycetes in a mountain stream in Hungary—experiments with leaf packs. Nova Hedwigia 48(3–4):391–404, PubMed PMID: WOS:A1989AD12000009

Gönczöl J, Révay A (2003) Treehole fungal communities: aquatic, aero-aquatic and dematiaceous hyphomycetes. Fungal Divers 12:19–34, PubMed PMID: WOS:000181503800003

Gönczöl J, Révay A (2004) Fungal spores in rainwater: stemflow, throughfall and gutter conidial assemblages. Fungal Divers 16:67–86, PubMed PMID: WOS:000222743900006

Gönczöl J, Révay A (2006) Species diversity of rainborne hyphomycete conidia from living trees. Fungal Divers 22:37–54, PubMed PMID: WOS:000239781700003

Graça MAS, Ferreira V, Canhoto C, Encalada AC, Guerrero-Bolano F, Wantzen KM et al (2015) A conceptual model of litter breakdown in low order streams. Int Rev Hydrobiol 100(1):1–12. doi:10.1002/iroh.201401757, PubMed PMID: WOS:000347777600001

Gulis V (2001) Are there any substrate preferences in aquatic hyphomycetes? Mycol Res 105:1088–1093. doi:10.1016/s0953-7562(08)61971-1, PubMed PMID: WOS:000171808900009

Gulis V, Suberkropp K (2003) Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshw Biol 48(1):123–134. doi:10.1046/j.1365-2427.2003.00985.x, PubMed PMID: WOS:000179693900011

Hameed AAA, El Hawarry S, Kamel MM (2008) Prevalence and distribution of airborne and waterborne fungi and actinomycetes in the Nile river. Aerobiologia 24(4):231–240. doi:10.1007/s10453-008-9101-7, PubMed PMID: WOS:000260611900006

Harrop BL, Marks JC, Watwood ME (2009) Early bacterial and fungal colonization of leaf litter in Fossil Creek, Arizona. J N Am Benthol Soc 28(2):383–396. doi:10.1899/08-068.1, PubMed PMID: WOS:000266645700011

Heinrichs G, Hübner I, Schmidt CK, de Hoog GS, Haase G (2013) Analysis of black fungal biofilms occurring at domestic water taps. I: compositional analysis using Taq-Encoded FLX Amplicon Pyrosequencing. Mycopathologia 175:387–397

Hori C, Ishida T, Igarashi K, Samejima M, Suzuki H, Master E et al (2014) Analysis of the *Phlebiopsis gigantea* genome, transcriptome and secretome provides insight into its pioneer colonization strategies of wood. PLoS Genet 10, e1004759

Hu DM, Cai L, Jones EBG, Zhang H, Boonyuen N, Hyde KD (2014) Taxonomy of filamentous asexual fungi from freshwater habitats, links to sexual morphs and their phylogeny. In: Hyde KD, Jones EBG, Pang KL (eds) Freshwater fungi: and fungal-like organisms. Walter de Gruyter GmbH & Co KG, Berlin

Hyde KD, Wong SW, Jones EBG (1997) Freshwater ascomycetes. In: Hyde KD (ed) Biodiversity of tropical microfungi Hong Kong. Hong Kong University Press, Hong Kong

Ibelings BW, De Bruin A, Kagami M, Rijkeboer M, Brehm M, van Donk E (2004) Host parasite interactions between freshwater phytoplankton and chytrid fungi (Chytridiomycota). J Phycol 40(3):437–453. doi:10.1111/j.1529-8817.2004.03117.x, PubMed PMID: WOS: 000221644400001

Ingold CT (1942) Aquatic hyphomycetes of decaying alder leaves. Trans Br Mycol Soc 25:339–417

Ingold CT (1955) Aquatic Ascomycetes: further species from the English Lake District. Trans Br Mycol Soc 38:157–168

Ingold CT (1966) The tetraradiate aquatic fungal spore. Mycologia 58(1):43–56. doi:10.2307/3756987, PubMed PMID: WOS:A19667371900002

Ingold CT (1975) Hooker lecture 1974: convergent evolution in aquatic fungi: the tetraradiate spore. Biol J Linn Soc 7(1):1–25. doi:10.1111/j.1095-8312.1975.tb00731.x

Ingold CT, Chapman B (1952) Aquatic Ascomycetes: *Loramyces juncicola* Weston and *L. macrospora* n. sp. Trans Br Mycol Soc 35:269–272

Ishii N, Ishida S, Kagami M (2015) PCR primers for assessing community structure of aquatic fungi including Chytridiomycota and Cryptomycota. Fungal Ecol 13:33–43

James TY, Pelin A, Bonen L, Ahrendt S, Sain D, Corradi N et al (2013) Shared signatures of parasitism and phylogenomics unite Cryptomycota and Microsporidia. Curr Biol 23(16):1548–1553. doi:10.1016/j.cub.2013.06.057, PubMed PMID: WOS:000323401100019

Jones EBG (1981) Observations on the ecology of lignicolous aquatic hyphomycetes. In: Wicklow DT, Carroll GC (eds) The fungal community. Marcel Dekker, New York, pp 731–742

Jones EBG (2006) Form and function of fungal spore appendages. Mycoscience 47:167–183

Jones MDM, Forn I, Gadelha C, Egan MJ, Bass D, Massana R et al (2011) Discovery of novel intermediate forms redefines the fungal tree of life. Nature 474(7350):200–203. doi:10.1038/nature09984, PubMed PMID: WOS:000291397800047

Jones EBG, Hyde KD, Pang KL (2014) Freshwater fungi and fungal-like organisms. Walter de Gruyter GmbH, Berlin

Junghanns C, Moeder M, Krauss G, Martin C, Schlosser D (2005) Degradation of the xenoestrogen nonylphenol by aquatic fungi and their laccases. Microbiology 151:45–57. doi:10.1099/mic.0.27431-0, PubMed PMID: WOS:000226352800006

Kagami M, Miki T, Takimoto G (2014) Mycoloop: chytrids in aquatic food webs. Front Microbiol 5:9. doi:10.3389/fmicb.2014.00166, PubMed PMID: WOS:000334664400001

Kaushik NK, Hynes HBN (1971) The fate of the dead leaves that fall into streams. Archiv Fur Hydrobiologie 68:465–515

Kelly JJ, Bansal A, Winkelman J, Janus LR, Hell S, Wencel M et al (2010) Alteration of microbial communities colonizing leaf litter in a temperate woodland stream by growth of trees under conditions of elevated atmospheric CO_2. Appl Environ Microbiol 76(15):4950–4959. doi:10.1128/aem.00221-10, PubMed PMID: WOS:000280266200005

Kerr JL, Baldwin DS, Tobin MJ, Puskar L, Kappen P, Rees GN et al (2013) High spatial resolution infrared micro-spectroscopy reveals the mechanism of leaf lignin decomposition by aquatic fungi. PLoS One 8, e60857

Kohout P, Sykorova Z, Ctvrtlikova M, Rydlova J, Suda J, Vohnik M et al (2012) Surprising spectra of root-associated fungi in submerged aquatic plants. FEMS Microbiol Ecol 80(1):216–235. doi:10.1111/j.1574-6941.2011.01291.x, PubMed PMID: WOS:000301051600019

Kohout P, Tesitelova T, Roy M, Vohnik M, Jersakova J (2013) A diverse fungal community associated with *Pseudorchis albida* (Orchidaceae) roots. Fungal Ecol 6(1):50–64. doi:10.1016/j.funeco.2012.08.005, PubMed PMID: WOS:000314256500007

Krauss G, Bärlocher F, Schreck P, Wennrich R, Glasser W, Krauss GJ (2001) Aquatic hyphomycetes occur in hyperpolluted waters in Central Germany. Nova Hedwigia 72(3–4):419–428, PubMed PMID: WOS:000169242400010

Krauss G, Sridhar KR, Bärlocher F (2005) Aquatic hyphomycetes and leaf decomposition in contaminated groundwater wells in Central Germany. Archiv Fur Hydrobiologie 162(3):417–429. doi:10.1127/003-9136/2005/0162/0417, PubMed PMID: WOS:000228391300009

Kuske CR, Hesse CN, Challacombe JF, Cullen D, Herr JR, Mueller RC et al (2015) Prospects and challenges for fungal metatranscriptomics of complex communities. Fungal Ecol 14:133–137

Lazarus KL, James TY (2015) Surveying the biodiversity of the Cryptomycota using a targeted PCR approach. Fungal Ecol 14:62–70

Lecerf A, Richardson JS (2010a) Biodiversity-ecosystem function research: insights gained from streams. River Res Appl 26(1):45–54. doi:10.1002/rra.1286, PubMed PMID: WOS:000274310500006

Lecerf A, Richardson JS (2010b) Litter decomposition can detect effects of high and moderate levels of forest disturbance on stream condition. For Ecol Manag 259(12):2433–2443. doi:10.1016/j.foreco.2010.03.022, PubMed PMID: WOS:000278303700022

Longcore JE, Pessier AP, Nichols DK (1999) *Batrachochytrium dendrobatidis* gen et sp. nov., a chytrid pathogenic to amphibians. Mycologia 91(2):219–227. doi:10.2307/3761366, PubMed PMID: WOS:000079317100001

Magyar D, Gönczöl J, Révay A, Grillenzoni F, Seijo-Coello MDC (2005) Stauro- and scolecoconidia in floral and honeydew honeys. Fungal Divers 20:103–120, PubMed PMID: WOS:000234463100008

Masclaux H, Perga ME, Kagami M, Desvilettes C, Bourdier G, Bec A (2013) How pollen organic matter enters freshwater food webs. Limnol Oceanogr 58:1185–1195

Miura A, Urabe J (2014) Spatial and seasonal changes in species diversity of epilithic fungi along environmental gradients of a river. Freshw Biol 60:673–685

Nagy LA, Olson BH (1982) The occurrence of filamentous fungi in drinking-water distribution-systems. Can J Microbiol 28(6):667–671, PubMed PMID: WOS:A1982NV58700017

Nechwatal J, Wielgoss A, Mendgen K (2005) *Pythium phragmitis* sp. nov., a new species close to *P. arrhenomanes* as a pathogen of common reed (*Phragmites australis*). Mycol Res 109:1337–1346. doi:10.1017/s0953756205003990, PubMed PMID: WOS:000233734000003

Nemec S (1969) Sporulation and identification of fungi isolated from root rot-diseased strawberry plants. Phytopathology 59(10):1552–1553, PubMed PMID: WOS:A1969E429700058

Nikolcheva LG, Bärlocher F (2005) Seasonal and substrate preferences of fungi colonizing leaves in streams: traditional versus molecular evidence. Environ Microbiol 7(2):270–280. doi:10.1111/j.1462-2920.2004.00709.x, PubMed PMID: WOS:000226376800013

Nikolcheva LG, Cockshutt AM, Bärlocher F (2003) Determining diversity of freshwater fungi on decaying leaves: comparison of traditional and molecular approaches. Appl Environ Microbiol 69(5):2548–2554. doi:10.1128/aem/69.5.2548.2554.2003, PubMed PMID: WOS:000182808300015

Nikolcheva LG, Bourque T, Bärlocher F (2005) Fungal diversity during initial stages of leaf decomposition in a stream. Mycol Res 109:246–253. doi:10.1017/s0953756204001698

Niyogi DK, Cheatham CA, Thomson WH, Christiansen JM (2009) Litter breakdown and fungal diversity in a stream affected by mine drainage. Fundam Appl Limnol 175(1):39–48. doi:10.1127/1863-9135/2009/0175-0039, PubMed PMID: WOS:000269326500003

Noga EJ (1993) Fungal diseases of marine and estuarine fishes. In: Couch JA, Fournie JW (eds) Pathology of marine and estuarine organisms. CRC Press, Boca Raton, FL, pp 85–110

Park D (1974) Aquatic hyphomycetes in non-aquatic habitats. Trans Br Mycol Soc 63(1): 183–187

Pascoal C, Cassio F, Marvanová L (2005) Anthropogenic stress may affect aquatic hyphomycete diversity more than leaf decomposition in a low-order stream. Archiv Fur Hydrobiologie 162(4):481–496. doi:10.1127/0003-9136/2005/0162-0481, PubMed PMID: WOS:000229072700004

Pérez J, Descals E, Pozo J (2012) Aquatic Hyphomycete communities associated with decomposing alder leaf litter in reference headwater streams of the Basque Country (northern Spain). Microb Ecol 64(2):279–290. doi:10.1007/s00248-012-0022-1, PubMed PMID: WOS:000306174700001

Pointing SB (2001) Feasibility of bioremediation by white-rot fungi. Appl Microbiol Biotechnol 57:20–33

Powell MJ (1993) Looking at mycology with a Janus face: a glimpse at Chytridiomycetes active in the environment. Mycologia 85:1–20

Powell MJ, Letcher PM (2014) 6 Chytridiomycota, Monoblepharidomycota, and Neocallimastigomycota. In: McLaughlin DJ, Spatafora JW (eds) Systematics and evolution. 7A, 2nd edn. Springer, Berlin, pp 141–175

Powell MJ, Letcher PM, Blackwell WH (2013) A new aquatic cellulose-degrading chytrid in the Chytridiales. Phytopathology 103(6):115, PubMed PMID: WOS:000322799500634

Raja HA, Schmit JP, Shearer CA (2009) Latitudinal, habitat and substrate distribution patterns of freshwater ascomycetes in the Florida Peninsula. Biodivers Conserv 18(2):419–455. doi:10.1007/s10531-008-9500-7, PubMed PMID: WOS:000262965400011

Raja HA, Oberlies NH, Figueroa M, Tanaka K, Hirayama K, Hashimoto A et al (2013) Freshwater Ascomycetes: *Minutisphaera* (Dothideomycetes) revisited, including one new species from Japan. Mycologia 105(4):959–976. doi:10.3852/12-313, PubMed PMID: WOS:000322849500014

Raviraja NS, Sridhar KR, Bärlocher F (1998) Breakdown of *Ficus* and *Eucalyptus* leaves in an organically polluted river in India: fungal diversity and ecological functions. Freshw Biol 39:537–545

Reynolds JD (1988) Crayfish extinctions and crayfish plague in central Ireland. Biol Conserv 45(4):279–285. doi:10.1016/0006-3207(88)90059-6, PubMed PMID: WOS:A1988P839500004

Sati SC, Belwal M (2005) Aquatic hyphomycetes as endophytes of riparian plant roots. Mycologia 97(1):45–49. doi:10.3852/mycologia.97.1.45, PubMed PMID: WOS:000229365800005

Schlütz F, Shumilovskikh LS (2013) On the relation of *Potamomyces armatisporus* to the fossil form-type *Mediaverrunites* and its taxonomical and ecological implications. Fungal Ecol 6(4):309–315

Schulz B, Boyle C (2005) The endophytic continuum. Mycol Res 109:661–686. doi:10.1017/s095375620500273x, PubMed PMID: WOS:000230687600001

Seena S, Wynberg N, Baerlocher F (2008) Fungal diversity during leaf decomposition in a stream assessed through clone libraries. Fungal Divers 30:1–14, PubMed PMID: WOS:000258548800001

Selosse MA, Vohnik M, Chauvet E (2008) Out of the rivers: are some aquatic hyphomycetes plant endophytes? New Phytol 178(1):3–7. doi:10.1111/j.1469-8137.2008.02390.x, PubMed PMID: WOS:000253711800002

Shearer CA (1993a) The fresh-water Ascomycetes. Nova Hedwigia 56(1–2):1–33, PubMed PMID: WOS:A1993KT94300001

Shearer CA (1993b) A new species of *Kirschsteiniothelia* (Pleosporales) with an unusual fissitunicate ascus. Mycologia 85:963–969

Shearer CA, Webster J (1985a) Aquatic hyphomycete communities in the River Teign. 1. Longitudinal distribution patterns. Trans Br Mycol Soc 84:489–501, PubMed PMID: WOS:A1985AHE9100011

Shearer CA, Webster J (1985b) Aquatic hyphomycete communities in the River Teign. 3. Comparison of sampling techniques. Trans Br Mycol Soc 84:509–518, PubMed PMID: WOS:A1985AHE9100013

Shearer CA, Webster J (1991) Aquatic hyphomycete communities in the River Teign. 4. Twig colonization. Mycol Res 95:413–420, PubMed PMID: WOS:A1991FL70400006

Shearer CA, Descals E, Kohlmeyer B, Kohlmeyer J, Marvanová L, Padgett D et al (2007) Fungal biodiversity in aquatic habitats. Biodivers Conserv 16(1):49–67. doi:10.1007/s10531-006-9120-z, PubMed PMID: WOS:000244185900004

Shearer CA, Raja HA, Miller AN, Nelson P, Tanaka K, Hirayama K et al (2009) The molecular phylogeny of freshwater Dothideomycetes. Stud Mycol 64:145–153. doi:10.3114/sim.2009.64.08, PubMed PMID: WOS:000274365900009

Simonis JL, Raja HA, Shearer CA (2008) Extracellular enzymes and soft rot decay: are ascomycetes important degraders in freshwater? Fungal Divers 31:135–146

Sing VO, Bartnicki-Garcia S (1972) Adhesion of zoospores of *Phytophthora palmivora* to solid surface. Phytopathology 62:790

Singh S, Harms H, Schlosser D (2014) Screening of ecologically diverse fungi for their potential to pretreat lignocellulosic bioenergy feedstock. Appl Microbiol Biotechnol 98(7):3355–3370. doi:10.1007/s00253-014-5563-4, PubMed PMID: WOS:000334167900045

Skerratt LF, Berger L, Speare R, Cashins S, McDonald KR, Phillott AD et al (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. EcoHealth 4(2):125–134. doi:10.1007/s10393-007-0093-5, PubMed PMID: WOS:000248231900004

Smither-Kopperl ML, Charudattan R, Berger RD (1998) Dispersal of spores of *Fusarium culmorum* in aquatic systems. Phytopathology 88(5):382–388. doi:10.1094/phyto.1998.88.5.382, PubMed PMID: WOS:000073487300002

Sole M, Muller I, Pecyna MJ, Fetzer I, Harms H, Schlosser D (2012) Differential regulation by organic compounds and heavy metals of multiple laccase genes in the aquatic Hyphomycete *Clavariopsis aquatica*. Appl Environ Microbiol 78(13):4732–4739. doi:10.1128/aem.00635-12, PubMed PMID: WOS:000305376600023

Sondergaard M, Laegaard S (1977) Vesicular-arbuscular mycorrhiza in some aquatic vascular plants. Nature 268(5617):232–233. doi:10.1038/268232a0, PubMed PMID: WOS: A1977DN97200031

Sonstebo JH, Rohrlack T (2011) Possible implications of chytrid parasitism for population subdivision in freshwater cyanobacteria of the genus *Planktothrix*. Appl Environ Microbiol 77(4):1344–1351. doi:10.1128/aem.02153-10, PubMed PMID: WOS:000287078100023

Sparrow FK (1960) Aquatic phycomycetes. University of Michigan Press, Ann Arbor, MI, 1187 p

Sridhar KR, Bärlocher F, Krauss GJ, Krauss G (2005) Response of aquatic hyphomycete communities to changes in heavy metal exposure. Int Rev Hydrobiol 90(1):21–32. doi:10.1002/iroh.200410739, PubMed PMID: WOS:000227722800002

Sridhar KR, Duarte S, Cassio F, Pascoal C (2009) The role of early fungal colonizers in leaf-litter decomposition in Portuguese streams impacted by agricultural runoff. Int Rev Hydrobiol 94(4):399–409. doi:10.1002/iroh.200811154, PubMed PMID: WOS:000269832100005

Stajich JEBM, Blackwell M, Hibbett DS, James TY, Spatafora JW, Taylor JW (2009) The fungi. Curr Biol 19:R840–R845

Sudova R, Rydlova J, Ctvrtlikova M, Havranek P, Adamec L (2011) The incidence of arbuscular mycorrhiza in two submerged Isoetes species. Aquat Bot 94(4):183–187. doi:10.1016/j.aquabot.2011.02.003, PubMed PMID: WOS:000290502100006

Taylor JW, Berbee ML (2006) Dating divergences in the fungal tree of life: review and new analyses. Mycologia 98:838–849

Tedersoo L, Pellet P, Kõljalg U, Selosse M-A (2007) Parallel evolutionary paths to mycoheterotrophy in understorey Ericaceae and Orchidaceae: ecological evidence for mixotrophy in Pyroleae. Oecologia 151(2):206–217

Thomas K, Chilvers GA, Norris RH (1989) Seasonal occurrence of conidia of aquatic hyphomycetes (fungi) in Lees Creek, Australian Capital Territory. Aust J Mar Freshwat Res 40:11–23

Thomas K, Chilvers GA, Norris RH (1992) Aquatic hyphomycetes from different substrates; substrate preference and seasonal occurrence. Aust J Mar Freshwat Res 43:491–509

Tsui CKM, Berbee ML (2006) Phylogenetic relationships and convergence of helicosporous fungi inferred from ribosomal DNA sequences. Mol Phylogenet Evol 39(3):587–597. doi:10.1016/j.ympev.2006.01.025, PubMed PMID: WOS:000238155300001

Tsui CKM, Hyde KD, Hodgkiss IJ (2001a) Longitudinal and temporal distribution of freshwater ascomycetes and dematiaceous hyphomycetes on submerged wood in the Lam Tsuen River, Hong Kong. J N Am Benthol Soc 20(4):533–549. doi:10.2307/1468086, PubMed PMID: WOS:000172517400003

Tsui CKM, Hyde KD, Hodgkiss IJ (2001b) Colonization patterns of wood-inhabiting fungi on baits in Hong Kong rivers, with reference to the effects of organic pollution. Anton Leeuw Int J Gen Mol Microbiol 79(1):33–38. doi:10.1023/a:1010210631215, PubMed PMID: WOS:000167920200004

Tubaki K, Tokumasu S, Ando K (1985) Morning dew and *Tripospermum* (Hyphomycetes). Bot J Linn Soc 91:45–50

Vijaykrishna D, Jeewon R, Hyde KD (2006) Molecular taxonomy, origins and evolution of freshwater ascomycetes. Fungal Divers 23:351–390, PubMed PMID: WOS:000243414100015

Voglmayr H (2004) *Spirosphaera cupreorufescens* sp. nov., a rare aeroaquatic fungus. Stud Mycol 50(1):221–228

Voglmayr H (2011) Phylogenetic relationships and reclassification of *Spirosphaera lignicola*, an enigmatic aeroaquatic fungus. Mycotaxon 116:191–202

Voglmayr H, Delgado-Rodriguez G (2001) *Dendroclathra caeruleofusca* gen.nov. et sp.nov., an aeroaquatic hyphomycete from Cuba. Can J Bot-Revue Canadienne De Botanique 79(9):995–1000, PubMed PMID: WOS:000171070800001

Voglmayr H, Delgado-Rodriguez G (2003) New species, notes and key to the aeroaquatic genera *Beverwykella* and *Ramicephala* gen. nov. Mycol Res 107:236–244. doi:10.1017/s0953756203007172, PubMed PMID: WOS:000182647300015

Voglmayr H, Krisai-Greilhuber I (1997) *Pseudoclathrosphaerina evamariae* gen. et sp. nov. and *Sympodioclathra globosa* gen. et sp. nov., two aeroaquatic fungi similar to *Clathrosphaerina*. Mycologia 89(6):942–951. doi:10.2307/3761115, PubMed PMID: WOS:A1997YK93200014

Voglmayr H, Park MJ, Shin HD (2011) *Spiroplana centripeta* gen. & sp. nov., a leaf parasite of *Philadelphus* and *Deutzia* with a remarkable aeroaquatic conidium morphology. Mycotaxon 116:203–216

Wang Z, Gerstein M, Snyder M (2009) RNA-Seq: a revolutionary tool for transcriptomics. Nat Rev Genet 10:57–63

Watanabe T (1975) *Tetracladium setigerum* an aquatic hyphomycetes associated with gentian and strawberry roots. Trans Mycol Soc Jpn 16:348–350

Webster J (1959) Experiments with spores of aquatic hyphomycetes I: sedimentation and impaction on smooth surfaces. Ann Bot 23:595–611

Webster J (1980) Introduction to fungi, 2nd edn. Cambridge University Press, Cambridge

Webster J, Davey RA (1984) Sigmoid conidial shape in aquatic fungi. Trans Br Mycol Soc 83:43–52, PubMed PMID: WOS:A1984TH62300005

Webster J, Descals E (1981) Morphology, distribution, and ecology of conidial fungi in freshwater habitats. In: Cole GC, Kendrick B (eds) Biology of conidial fungi. Academic, London, pp 295–335

Willoughby LG (2003) Diseases of freshwater fishes. In: Tsui CKM, Hyde KD (eds) Freshwater mycology. Fungal Diversity Press, Hong Kong, pp 111–126

Wong SW, Hyde KD (1999) *Proboscispora aquatica* gen. et sp. nov., from wood submerged in freshwater. Mycol Res 103:81–87. doi:10.1017/s0953756298006820, PubMed PMID: WOS:000078869900013

Wong MKM, Goh TK, Hodgkiss IJ, Hyde KD, Ranghoo VM, Tsui CKM et al (1998) Role of fungi in freshwater ecosystems. Biodivers Conserv 7(9):1187–1206. doi:10.1023/a:1008883716975, PubMed PMID: WOS:000078129900005

Wood-Eggenschwiler S, Bärlocher F (1985) Geographical distribution of Ingoldian fungi. Verhandlungen Internationaler nereinigung fuer Theoretische und Angewanot d Liminologie 22:2780–2785

Wurzbacher C, Rosel S, Rychla A, Grossart H-P (2014) Importance of saprotrophic freshwater fungi for pollen degradation. PLoS One 9(4), e94643

Yuen TK, Hyde KD, Hodgkiss IJ (1998) Physiological growth parameters and enzyme production in tropical freshwater fungi. Mater Org 32(1):1–16, PubMed PMID: WOS:000079120700001

Zemek J, Marvanov L, Kuniak L, Kadlecikova B (1985) Hydrolytic enzymes in aquatic hyphomycetes. Folia Microbiol 30:363–372