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www.freshwaterfungi.org, an online platform for the taxonomic classification of freshwater fungi

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Abstract

The number of extant freshwater fungi is rapidly increasing, and the published information of taxonomic data are scattered among different online journal archives. The only online repository, http://fungi.life.illinois.edu/, deals with freshwater ascomycetes and their asexual morphs. Other freshwater fungal groups are not included. The newly developed webpage (www.freshwaterfungi.org/) serves as a gateway to freshwater fungal systematics that provides comprehensive and updated information including detailed descriptions, photographic plates and illustrations, notes, phylogenetic trees, estimated and extant list of species, and other related information. The website is developed with user-friendly interfaces, and the usage is discussed in this paper.

Key words – Database Website – Freshwater Ascomycota – Freshwater Basidiomycota – Freshwater Chytridiomycota – Microsporidia – Molecular Phylogeny

Introduction

Freshwater fungi are an ecologically important group of fungi occurring in freshwater bodies throughout the world (Tsui & Hyde 2003, Jones et al. 2014a). There have been various definitions of freshwater fungi, but most deal with ecological groups (Table 1). In this study, we prefer to use the definition of freshwater fungi as any species which, for the whole or part of their life cycle, rely on free freshwater, or which uses any resource of a predominantly aquatic or semi-aquatic nature as a substratum (Thomas 1996). This means that all fungi found in studies on submerged organic material, freshwater, sediments, foam and animals can be considered as freshwater fungi and are

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documented. Freshwater fungi occur in lentic (ponds, pools, lakes, peat swamps) and lotic (creeks, streams, brooks, rivers) habitats (Tsui & Hyde 2003, Jones et al. 2014a). Floodplains and riparian zones are important intermediate habitats for survival and reproduction of freshwater fungi (Bärlocher 1992). Freshwater fungi also occur in artificial reservoirs such as water-cooling towers, water pipes, street gutters, wastewater treatment and sewage systems (Jones & Eaton 1969, Eaton & Jones 1970, 1971a, b, Udaiyan & Hosagoudar 1991, Kane et al. 2002, Ghate & Sridhar 2018, Grossart et al. 2019), and freshwater habitats with extreme conditions such as glacial waters (Buzzini et al. 2005, 2012, Vishniac 2006, de Garcia et al. 2007, Branda et al. 2010), ultra-oligotrophic mountain lakes exposed to increased UV radiation (Libkind et al. 2004, Libkind et al 2014), hyper-acidic aquatic environments (Nakatsu & Hutchinson 1988, López-Archilla et al. 2001, Gadanho & Sampaio 2006, Gadanho et al. 2006) and sulfur thermal springs (Chandrashekar et al. 1991, Rajashekhar & Kaveriappa 1996). The saprobic taxa are involved in the degradation of lignocellulose in woody material and cellulose in leaves (Eaton & Jones 1971a, b, Jones 1972, 1981, Ballie et al. 1998, Yuen et al. 1999, Sridhar et al. 2010, Sridhar & Sudheep 2011a, b, Sudheep & Sridhar 2011, Bärlocher & Sridhar 2014, Boonyuen et al. 2014). They are key players in the decomposition and mineralization of organic matters (Wong et al. 1998, Shearer et al. 2007, Jones et al. 2014a, Ittner et al. 2018, Raja et al. 2018). Some are parasites of aquatic plants and animals, while others are endophytes and mutualists (Srivastava & Srivastava 1978, Wong et al. 1998, Sati & Belwal 2005, Jobard et al. 2010, Ibelings et al. 2011, Gleason et al. 2014, 2015, Glockling et al. 2014, You et al. 2015, Ghate & Sridhar 2017).

Freshwater fungi divide into various morphological and ecological groups (Shearer et al. 2007, Goh & Hyde 1996). They include freshwater ascomycetes, freshwater hyphomycetes (Ingoldian fungi, aero-aquatic hyphomycetes or asexual ascomycetes, terrestrial-aquatic hyphomycetes, submerged-aquatic hyphomycetes), freshwater basidiomycetes, coelomycetes, zygomycetes, microsporidia and zoosporic fungi (Goh & Hyde 1996, Tsui et al. 2016). The estimated number of freshwater fungi and fungal-like organisms are around 3,069–4,145, but these are underestimates as some groups are not listed or do not have enough available data. In addition, many habitats and substrates are unexplored or underexplored (Jones et al. 2014a). Freshwater fungi belong to eight phyla: Aphelidiomycota, Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Monoblepharomycota, Mortierellomycota and Rozellomycota with Ascomycota being the most speciose phylum (33 orders; 622 species and excluding ascomycetous yeasts) (Hibbett et al. 2007, Zhang et al. 2012, Jones et al. 2014a, Wijayawardene et al. 2018a, Wijayawardene et al. 2020).

Several books such as *Recent Advances in Aquatic Mycology* by Jones et al. (1976); *Freshwater Mycology* by Tsui & Hyde (2003); *Genera of Freshwater Fungi* by Cai et al. (2006a); *Freshwater Fungi: and fungal-like Organisms* by Jones et al. (2014a), reviews (Shearer 1993, Goh & Hyde 1996, Hyde et al. 1997, Wong et al. 1998, Gessner & Van Ryckegem 2002, Shearer et al. 2007, Sridhar 2009, Wurzbacher et al. 2010, 2012, 2016, Chauvet et al. 2016), and monographs (Luo et al. 2019, Dong et al. 2020) of freshwater mycology have been published. The classifications have been significantly improved with the utilization of molecular data. The traditional classification of freshwater fungi was mainly based on morphological characters, such as fruit bodies and spores. However, classification has rapidly changed with the use of molecular data (Bärlocher 2010, Shearer et al. 2014, Duarte et al. 2015, Luo et al. 2019, Dong et al. 2020, Hyde et al. 2020b, Hongsanan et al. 2020). Phylogenetic analysis of extant species and the introduction of novel taxa has resulted in a modern classification system for the Kingdom Fungi (Hyde et al. 2013, Maharachchikumbura et al. 2016, Choi & Kim 2017, Tedersoo et al. 2018, Luo et al. 2019, Naranjo-Ortiz & Gabaldón 2019, Samarakoon et al. 2019, Hongsanan et al. 2020, Hyde et al. 2020b). Several new genera, families, orders, and even new subclasses of freshwater fungi have been introduced recently (Réblová et al. 2015a, b, 2016a, b, Maharachchikumbura et al. 2015, 2016, Su et al. 2016, Hongsanan et al. 2017, Wijayawardene et al. 2017, 2018a, Yang et al. 2017, 2018a, b, Zhang et al. 2017, Lu et al. 2018a, b, Bao et al. 2019a, b, Luo et al. 2019, Calabon et al. 2020a, b, c, Dong et al. 2020). Luo et al (2019) have provided a phylogenetic analysis for freshwater Sordariomycetes, while the Dothideomycetes are dealt with by Shearer et al. (2014) and Dong et al. (2020). Research on freshwater fungi has not been limited to taxonomy and identification. Researchers have also expanded knowledge through applied technology, and the future of freshwater fungal research and importance will grow (Sati & Arya 2010, Hernández-Carlos & Gamboa-Angulo 2011, Krauss et al. 2011, Paguigan et al. 2016, Sati & Pant 2018).

Table 1 Various definitions of freshwater fungi

Term	Definition	Reference
Obligate freshwater ascomycetes/Indwellers	Fully adapted in water and often adapted for dispersal in water	Park (1972)
Facultative freshwater ascomycetes/Immigrants	Originated from other habitats and must continually immigrate to maintain their population number in water; may show varying degrees of adaptation	Park (1972)
“Amphibious” freshwater ascomycetes	Found in the interface between land and water (e.g. riparian zones, floodplains); may be adapted to fluctuating water levels	Michaelides & Kendrick (1978), Shearer (1993)
Aeroaquatic hyphomycetes	Indwelling organisms characterized by the production of purely vegetative mycelium in substrates underwater and formation of conidia with special flotation devices, formed only when the substrates on which the fungus is growing are exposed to a moist environment	Fisher (1977)
Freshwater ascomycetes	All ascomycetes that occur on submerged or partially submerged substrata in aquatic habitats	Shearer (1993)
Freshwater fungi	Fungi that for the whole or part of their life cycle rely on freshwater, or which uses any resource of a predominantly aquatic or semi-aquatic nature as a substratum	Thomas (1996)
Freshwater yeasts	Those isolated from freshwater or foam	Jones & Slooff (1966)
Aquatic hyphomycetes	Hyphomycetes that able to sporulate under water and thrive on deciduous leaves decaying in streams and rivers.	Krauss et al. (2011)

Online databases serve as data repositories to amass all information in one platform (Shearer & Raja 2010, Jayasiri et al. 2015, Jayawardena et al. 2019, Jones et al. 2019, Monkai et al. 2019, Pem et al. 2019, Bundhun et al. 2020). Currently, the webpage http://fungi.life.illinois.edu/ deals with freshwater fungi, but it includes only the freshwater ascomycetes and their asexual morphs. To document all freshwater fungi at all taxonomic levels, the website www.freshwaterfungi.org is developed to provide up-to-date information for all taxa. The present paper introduces the website and discusses its features and functions.

History of freshwater fungi

Freshwater fungi, especially the freshwater hyphomycetes, have been observed as early as the 1880s. The tetraradiate, sigmoid and branched conidia were an interesting character that caught the attention of pioneer mycologists. *Heliscus lugdunensis* was the first described freshwater hyphomycete species (Saccardo 1880), while *Flagellospora penicillioides* was the first aquatic hyphomycete where the sexual state was known (Ranzoni 1956). An important contribution to aquatic hyphomycete research is that of de Wildeman (1893, 1894, 1895) who described four new fungal species, three with tetraradiate and one with sigmoid conidia, from ponds, ditches and marshy areas on different substrates (algae, willow leaves, aquatic macrophytes *Hippuris vulgaris*). The first prolific sporulation of freshwater hyphomycete *in vitro* was by Kegel (1906) for *Varicosporium elodeae*, wherein the induction of sporulation occurs when overgrown agar blocks were placed in nutrient-poor water. Some authors who worked on freshwater were Grove (1912), Fragoso (1920), Huber-Pestalozzi (1925, 1938), Brutschy (1927) and Lowe (1927). A major breakthrough occurred when Ingold (1942) discovered a typical habitat for freshwater fungi, growing on submerged decaying leaves of broad-leaved trees in well-aerated waters and introduced the taxa *Alatospora acuminata*, *Anguillospora longissima* (≡ *Amniculicola longissima*), *Articulospora tetracladia* (≡ *Hymenoscyphus tetracladius*), *Clavariopsis aquatica*, *Flagellospora curvula*, *Heliscus aquaticus* (≡ *Nectria lugdunensis*), *Heliscus longibrachiatus* (≡ *Clavatospora longibrachiata*), *Lemonniera aquatica*, *Lunulospora curvula*, *Margaritispora aquatica*, *Tetracladium marchalianum*, *Tetrachaetum elegans*, *Tetracladium setigerum*, *Tricladium angulatum*, *Tricladium splendens*, *Varicosporium elodeae*, almost 50 years after Wildeman observed their conidial morphology. At the time, Ingold was studying chytrids in a stream behind his house, and coincidentally found a large fungal spore collection trapped in scum behind a barrier of twigs (Bärlocher 1992). After a long experimental period, he discovered their structure and detailed 16 species of which ten were novel (Ingold 1942, 1953). Ainsworth (1976) considered this discovery as a "minor mycological industry" as the discovery of Ingold paved the way for an era where reports of the fungal occurrence multiplied. Presently, these hyphomycetes are popularly known as Ingoldian fungi, in honour of C.T. Ingold (Webster & Descals 1981a, b). Ingoldian fungi were previously known as "aquatic hyphomycetes" (de Wildeman 1895, Ingold 1942), freshwater hyphomycetes (Nilsson 1964), and "amphibious hyphomycetes" (Michaelides & Kendrick 1978). In the 1950s, Ingold (Ingold 1951, 1954, 1955) noted that aquatic ascomycetes were abundant in freshwater particularly on stalks of reed swamp plants with many of the ascospores with variously developed appendages (e.g. *Ceriospora caudae-suis*, *Loramyces macrospora*). A vast number of comprehensive studies were published after the initial work of Ingold (Ranzoni, 1953, Tubaki 1957, Petersen 1962, 1963a, b, Nilsson 1964, Webster & Descals 1981a, b, Dudka 1985, Goh & Hyde 1996, Chan et al. 2000, Sivichai et al. 2000, 2006, Pinnoi et al. 2006). Since Ingold's early research, numerous studies, both on sexual and asexual taxa, have been published from all over the world (Tubaki et al. 1983, Hyde 1992, Sridhar et al. 1992, Jones et al. 1999, Hyde & Wong 2000, Tsui et al. 2001b, Tsui & Hyde 2003, Pinruan et al. 2004, Shearer et al. 2004, 2007, 2014, Zhang et al. 2011, Liu et al. 2015). The most recent major publications on freshwater ascomycetes and hyphomycetes are from Shearer et al. (2014), Luo et al. (2019) and Dong et al. (2020), while those on Ingoldian fungi on leaves are by Chan et al. (2000), Selosse et al. (2008), Sudheep & Sridhar (2013), Ghate & Sridhar (2015), Fiuza et al. (2017), Fiuza et al. (2019) and Tarda et al. (2019).

Ecology

Freshwater fungi can be saprobes, mutualists and parasites (Cole et al. 1990, Wong et al. 1998, Ibelings et al. 2004, Schulz & Boyle 2005, Sati & Belwal 2005, Seena et al. 2008, Kohout et al. 2012, Masclaux et al. 2013, Karun et al. 2016, Ghate & Sridhar 2017). All these relationships are important for the decomposition process in freshwater systems. Furthermore, the fungal niches overlap with niches of different organisms such as plankton, invertebrates, insects, and fish thriving in freshwater habitats leading to direct and indirect influence of the former (Ibelings et al. 2004, Shearer et al. 2007, Roa et al. 2009, Sudheep & Sridhar 2011, Jones et al. 2014a, Gleason et al. 2014, Glockling et al. 2014, Powell & Letcher 2014).

Freshwater fungi play a key role in the transfer of nutrients and flow of energy between trophic levels in the food web by breaking down complex organic compounds into simpler inorganic materials of dead flora and fauna (Kaushik & Hynes 1971, Chamier 1985, Raviraja et al. 1996, Wong et al. 1998, Sridhar & Bärlocher 2000, Abdel-Raheem & Shearer 2002, Krauss et al. 2011, Sridhar et al. 2013, Wurzbacher et al. 2014, Tsui et al. 2016). Most aquatic fungi can decompose a wide range of organic substrates, although a few species are limited to one or a few types of substrates (Tsui et al. 2016). Most aquatic hyphomycetes can degrade cellulose, various hemicelluloses and pectins (Chamier 1985, Zemek et al. 1985, Chandrashekar & Kaveriappa 1991, Abdel-Raheem & Shearer 2002). Aquatic hyphomycetes also aid the decomposition of plant materials into detritus by producing exoenzymes that increases the palatability of substrates for shredders and collectors (Bärlocher & Kendrick 1974, Anderson & Sedell 1979, Cummins & Klug

1979, Tsui et al. 2016). In general, Ingoldian fungi are thought to decompose either leaves or herbaceous debris while ascomycetes and basidiomycetes break down woody debris (Jones 1972, 1973, Boonyuen et al. 2014). Zoosporic fungi are colonizers of smaller substrates which contain chitin, keratin or cellulose (Wong et al. 1998). Chytrids are responsible for the decomposition of small particles such as algae, zooplankton carcasses, seeds and pollen grains including other temporarily available smaller substrates (Tsui et al. 2016).

Shearer (1995) reviewed different methods used to study fungal competition and discussed the ways in which freshwater fungi defended or gained space on submerged substrates. Pre-colonization was used to determine the ability of one species to influence fungal community structure by manipulating the abundance of one or more hypothetically competing species. There are few reports on the interspecific competition among fungal species in freshwater habitats and the results suggest that the pre-colonization appears to influence the subsequent colonization of fungi on substrates (Shearer & Bartolata 1990, Sridhar & Bärlocher 1993, Fryar et al. 2001).

Few aquatic fungi form a symbiotic mycorrhizal relationship with the roots of trees and other plants and macrophytes. The latter provides nutrition for the fungus, and the former enables the plant to take up unavailable nutrients (see Søndergaard & Laegaard 1977, Seena et al. 2008, Sudová et al. 2011, Kohout et al. 2012). Some aquatic hyphomycetes have been reported as endophytes, but it is unclear if the effect on plant hosts is harmful or beneficial (Sati & Belwal 2005, Schulz & Boyle 2005). Most chytrid species are benign saprobes, but they often occur as parasites, sometimes as symbionts, and of course as decomposers (Ibelings et al. 2004). Mutualistic relationships of freshwater fungi with living hosts were observed in Trichomycetes growing in the gut of insects, crustaceans and millipedes that often breed in discrete and disjunct lentic habitats (Lichtwardt & Williams 1999, Roa et al. 2009, Lichtwardt 2014). For example, *Smittium culisetae* found in the hindgut of *Aedes aegypti* larvae could serve as a source of essential elements for insect growth, primarily of sterols and B-vitamin (Horn & Lichtwardt 1981, Lichtwardt et al. 2003). Mutualistic Trichomycetes may improve the assimilation of recalcitrant compounds directly in the gut of their hosts (Suberkropp et al. 1983). Studies on freshwater fungi with mutualistic relationships with living hosts are scarce due to their cryptic presence (e.g. some Trichomycetes belonging to Asellariales and Eccrinales remain unculturable) and related methodological difficulties (Lichtwardt et al. 2003).

Fungi can release different types of gases (e.g. CO_2, N_2, N_2O, volatile gases) into the surrounding environment (see Palmer et al. 1997, Fourest & Volesky 1997, Gulis et al. 2006). In addition, fungi act in the same role as aquatic plants for the phytoremediation process in the aquatic ecosystems (see Say et al. 2001, López & Vazquez 2003, Anand et al. 2006, Singh 2006, Iskandar et al. 2011, Harms et al. 2011, Anastasi et al. 2013). Saprobic fungi on dead particles have the potential to secrete chemicals on the substrate to induce their metabolism (see Chamier & Dixon 1982a, b, Chamier et al. 1984, Crawford 1981, Kirk et al. 1977, Singh 1982, Suberkropp & Klug 1980, Chamier 1985, Junghanns et al. 2005, Cabana et al. 2007, Solé et al. 2012, Tsui et al. 2016). Furthermore, some parasitic, endophytic and competitive fungi also secrete various chemicals to enhance their functions. These antibacterial, nematicidal, antifungal, bio-surfactant and detoxifying compounds are economically and ecologically important (Wong et al. 1998, Ho et al. 2003, Hernández-Carlos & Gamboa-Angulo 2011, Singh & Sati 2020).

The geographical distribution of freshwater fungi may be restricted to tropical, temperate, or cold-water habitats, while others are cosmopolitan (Tsui & Hyde 2003, Duarte et al. 2012, Tsui et al. 2016). Several papers reported shifts in fungal communities and taxonomic composition by latitude, altitude, pH, season, turbulence, riparian vegetation, temperature and the length of time that the substrate has been submerged (see Webster & Descals 1981a, b, Wood-Eggenschwiler & Bärlocher 1985, Gönczöl 1989, Shearer & Webster 1985, 1991, Raviraja et al. 1998, Arnold & Lutzoni 2007, Tsui et al. 2001a, Raja et al. 2009, Boonyuen et al. 2014, Hyde et al. 2016, da Silva et al 2019, Fiuza et al. 2019).

The relationship between freshwater fungi and adjacent terrestrial fungal assemblages is poorly understood. In studies that have sampled the same substrates in adjacent freshwater and terrestrial habitats, there has been low overlap in the species present and different dominant species (Wellbaum et al. 1999, Cai et al. 2006b Pinruan et al. 2007, Kodsueb et al. 2016). Although some freshwater species are found in terrestrial habitats (Bandoni 1972, Swe et al. 2009), most are only found in freshwater (Révay & Gönczöl 2011). Kodsueb et al. (2016) carried out succession studies where they placed terrestrial branches in streams and recollected them at 3 and 6 months. There was a change from terrestrial taxa to only freshwater taxa within that period. Jones & Oliver (1964) observed colonization of aquatic hyphomycetes after 6 weeks of submersion of wood test blocks/panels. Kane et al. (2002) and Sivichai et al. (2000) submerged test panels in freshwater and followed their colonization over 12 months. Sporulating fungi were observed after four weeks suggesting that samples are not examined early enough in such studies with some escaping detection. Future studies should employ high throughput sequencing of the substrates over time, starting within a few hours to establish how soon fungi colonize substrates in freshwater habitats.

Sexual-asexual connections of freshwater hyphomycetes

Studies documenting sexual-asexual connections have also revealed many links between the sexual morphs and freshwater hyphomycetes (Sivichai & Jones 2003, Hu et al. 2014, Sati & Pathak 2016, Tanney & Miller 2017, Luo et al. 2019). In 2016, there were over 300 species of extant aquatic hyphomycetes and 15% of them were linked to their sexual morphs (Sati & Pathak 2016). Hu et al. (2014) listed 77 connections of aquatic hyphomycetes to their sexual states. The number of linked morphs is now much higher and thus a further reason for developing the website so that these links can be documented in one platform.

Classification of freshwater fungi

Freshwater ascomycetes

Freshwater ascomycetes are found on fully or partly submerged substrates in freshwater habitats (Shearer 1993). Jones et al. (2014a) reported 622 species (~200 genera) of Ascomycota. Freshwater ascomycetes are composed of Arthoniomycetes, Chaetothyriomycetes, Dothideomycetes, Eurotiomycetes, Laboulbeniomycetes, Lecanoromycetes, Lecanoromycetes *incertae sedis*, Leotiomycetes, Lichinomycetes, Sordariomycetes, and Pezizomycetes (Jones et al. 2014a).

Freshwater Dothideomycetes

The freshwater Dothideomycetes comprise one third (200 species) of freshwater Ascomycota (Shearer et al. 2009). The ascostromatic fruit body and bitunicate asci often with fissitunicate dehiscence characterize this class (Hyde et al. 2013). Dothideomycetous species constitute a large group in freshwater environments and are generally isolated from submerged wood or bamboo (Zhang et al. 2012, Dong et al. 2020). The phylogenetic analysis of freshwater Dothideomycetes by Shearer et al. (2014) include 14 families in Pleosporales, of which ten accepted in Pleosporales *incertae sedis*. Jahnulales, Natipusillales and *Minutisphaera* clades were classified as Dothideomycetes *incertae sedis*. These numbers will increase as new species, genera, families and orders are being introduced (Ariyawansa et al. 2015, Raja et al. 2015, Lu et al. 2018a, b, Bao et al. 2019a, b, Boonmee et al. 2019, Calabon et al. 2020a, b, c, Boonmee et al. 2020, Dong et al. 2020, Hyde et al. 2020a, Li et al. 2020). For example, Wicklowiaceae was introduced by Ariyawansa et al. (2015) to accommodate *Wicklowia*. The *Minutisphaeria* clade was placed in Minutisphaerales, an order introduced by Raja et al. (2015) wherein two families, Acrogenosporaceae and Minutisphaeraceae (type), are accepted. The latest classification and morphological study of freshwater Dothideomycetes were by Dong et al. (2020). Dong et al. (2020) listed all the freshwater species belonging to six orders, 43 families, 145 genera in Dothideomycetes and reviewed all genera with a description, illustration, notes, freshwater distribution and a key. Among Dothideomycetes, 46 genera were unique to freshwater habitats (Dong et al. 2020).

Freshwater Sordariomycetes

Sordariomycetes are the second largest group of freshwater Ascomycota. The class is characterized by non-lichenized, perithecial ascomata and inoperculate unitunicate (Zhang et al. 2006, Kirk et al. 2008, Luo et al. 2019). Shearer & Raja (2010) reported 307 species of freshwater Sordariomycetes, nearly half of known freshwater Ascomycota at that time, which was 622 species. In a phylogenetic study, Cai et al. (2014) showed that freshwater Sordariomycetes are distributed in 13 orders (Calosphaeriales, Coniochaetales, Diaporthales, Halosphaeriales, Hypocreales, Magnaporthales, Microascales, Ophiostomatales, Phyllachorales, Savoryellales, Sordariales, Trichosphaeriales and Xylariales) under three subclasses, Sordariomycetidae, Hypocreomycetidae and Xylariomycetidae. The number has increased as new species, genera, families and orders have been introduced from freshwater habitats (Marin-Felix et al. 2018, Yang 2019, Luo et al. 2019, Boonmee et al. 2020, Hyde et al. 2020a). Luo et al. (2019) provided a comprehensive monograph of freshwater Sordariomycetes and introduced one new order (Distoseptisporales), two new families (Ceratosphaeriaceae, Triadelphiaceae), three new genera (*Aquafiliformis*, *Dematiosporium*, *Neospadicoides*), 47 new species, two new combinations and nine new records. This was incorporated in the *Refined Families of Sordariomycetes* (Hyde et al. 2020b) and *Outline of Fungi and fungus-like taxa* (Wijayawardene et al. 2020).

Freshwater ascomycetous yeasts

Ascomycetous yeasts are common inhabitants of freshwater environments, including damp mines, lakes, rivers, tundra ponds, glacial melts, and can tolerate extreme environmental conditions (Libkind et al. 2014). The most speciose order is Saccharomycetales with the genera *Candida* (e.g. *C. antarcticus* isolated from cold water stream), *Kodamaea* (e.g. *K. ohmeri* isolated from tropical lakes and rivers, Brazil) and *Mrakiella* (e.g. *M. aquatica* isolated from a lake freshwater foam, UK), and *Pichia* (e.g. *P. kluveri* isolated from Shark River, USA). Freshwater ascomycetous yeasts are less well-documented than freshwater basidiomycete yeasts.

Freshwater basidiomycetes

Basidiomycetes in freshwater habitats are taxonomically diverse including both saprobic yeasts and filamentous forms, and endophytes. Freshwater basidiomycetes thrive on various substrates such as wood (e.g. *Limnoperdon incarnatum*, *Mycocalia reticulata*, *Stauriella aquatica*, *Psathyrell aquatica* which has typical agaricoid fruit body), culms (e.g. *Mrakiella aquatica*), trapped in foam (e.g. *Crucella subtilis*, *Taeniospora gracilis*) and isolated from water columns (*Cryptococcus* spp., *Rhodotorula* spp.) (Jones & Slooff 1966, Marvanová 1977, Marvanová & Suberkropp 1990, Hyde & Goh 1998, Sivichai & Jones 2004, Brandão et al. 2011, Fell et al. 2011). Jones et al. (2014b) listed 115 species of freshwater basidiomycetes belonging to 50 genera, eight classes and 19 orders. Freshwater basidiomycetes include Ingoldian fungi such as *Crucella subtilis*, *Ingoldiella hamata*, *Naiadella fluitans* and *Taeniospora descalsii* with their known sexual morph *Camptobasidium hydrophilum* (Camptobasidiales), *Sistotrema hamatum* (Cantharellales), *Classicula fluitans* (Classiculales) and *Leptosporomyces crucelliger* (Atheliales) (Nawawi & Webster 1982, Marvanová & Bandoni 1987, Marvanová & Stalpers 1987, Marvanová & Suberkropp 1990, Bauer et al. 2003, Bernicchia & Gorjón 2010). The yeast form has the highest number of species comprising 64.35% (74 species) of the total freshwater basidiomycetes. Tremellomycetes has the highest number of species (41 species, 12 genera, five orders). The most speciose order is Tremellales with 27 species under the genera *Bullera* (2 species: *B. dendrophila*, *B. sinensis*), *Cryptococcus* (20 species: *C. albidus, C. adeliensis, C. agrionensis, C. cistialbidi, C. cylindricus, C. carnescens, C. diffluens, C. gastricus, C. gilvescens, C. heveanensis, C. laurentii, C. magnus, C. saitoi, C. spencermartinsiae, C. stepposus, C. taeanensis, C. tephrensis, C. terreus, C. victoriae, C. wieringae*), *Dioszegia* (4 species: *D. crocea, D. fristingensis, D. hungarica, D. zsoltii*) and *Xenolachne* (one species: *X. flagellifera*).

Freshwater Chytridiomycetes

Chytridiomycota is characterized by posteriorly uniflagellate zoospores which function in the dispersal of the fungus to new substrates or hosts. Most freshwater chytrids are parasitic on algae, especially plankton (Canter & Lund 1968), while others are parasites of animals: amphibians frogs/toads (*Batrachochytrium dendrobatidis, B. salamandrivorans,* Longcore et al. 1999). Many are found exclusively in freshwater and are clearly freshwater fungi, but some isolated from soil, dung and detritus in tree canopies (Wakefield et al. 2010, Simmons et al. 2012, Longcore 2005). Powell & Letcher (2014) discussed the phylogeny and characterization of freshwater Chytridiomycota. Two classes constitute freshwater chytrids, Chytridiomycetes (nine orders, 97 genera, 946 species) and Monoblepharidomycetes (one order, six genera, 50 species). The most speciose order is Chytridiales, and constitutes of 385 species under two families: Chytridiaceae (four genera: *Chytridium, Dendrochytridium, Polyphyctis, Phylctochytrium*), and Chytriomycetaceae (12 genera: *Asterophlyctis, Avachytrium, Chytriomyces, Entophlyctis, Obelidium, Odontochytrium, Phylctorhiza, Physocladia, Podochytirum, Rhizidium, Rhizoclosmatium, Siphonaria*), two *Incertae sedis* (*Delfinachytrium, Pseudorhizidium*).

Freshwater Blastocladiomycota

Blastocladiomycota, posteriorly uniflagellated zoosporic fungi, commonly found as saprotrophs and parasites of fungi, algae, plants and invertebrates of soil and freshwater, and sometimes found to be facultatively anaerobic (Sparrow 1960, Hibbett et al. 2007, James et al. 2006a, b, 2014, Powell 2017). Wijayawardene et al. (2018b) accepted two classes (Blastocladiomycetes, Physodermatomycetes) three orders (Blastocladiales, Callimastigales, Catenomycetales), eight families (Blastocladiaceae, Callimastigaceae, Catenariaceae, Catenomycetaceae, Coelomomycetaceae, Paraphysodermataceae, Physodermataceae, Porochytriaceae) and 14 genera (*Allomyces, Blastocladia, Blastocladiopsis, Callimastix, Catenomyces, Catenophlyctis, Coelomomyces, Coelomycidium, Endoblastidium, Microallomyces, Nematoceromyces, Paraphysoderma, Physoderma, Sorochytrium*) in Blastocladiomycota. Tedersoo et al. (2018) introduced the subkingdom Blastocladiomyceta and subphylum Blastocladiomycotina. All of these, except *Endoblastidium,* were reported from freshwater habitats (Hanson et al. 1945, Vavra & Joyon 1966, Sparrow 1968, Held et al. 1969, Liu & Volz 1977, Vincent 1988, El-Hissy et al. 1996, McCreadie & Adler 1999, Kiziewicz 2004, Steciow & Marano 2006, Gutman et al. 2009, Porter et al. 2011, Doweld 2014, Glockling et al. 2014, James et al. 2014, Powell 2017, Swafford & Oakley 2018, Wijayawardene et al. 2018b, Wijayawardene et al. 2020).

Freshwater Rozellomyceta (Class Microsporidia)

Of all the freshwater fungi, the least known and poorly documented are the microsporidia and require good optics for their detection. Microsporidia are spore-forming obligate intracellular parasites of eukaryotic hosts such as bony fish (Osteichyes), and arthropods (Kearney & Gleason 2014). Microsporidial spores possess a polar tube which can pierce a host cell, depositing the parasite's sporoplasm within the host cell and consumes host organelles (Larsson 1999). The sporoplasm proliferates to produce spores which are discharged to infect new hosts. Classification is based on morphology, light and electron microscopy and sequence data (ITS gene). Microsporidial classification is by referral to their generic names.

Aphelidiomycota, Monoblepharomycota, Mortierellomycota

Tedersoo et al. (2016) proposed a new classification which accepted Rozellomycota and Aphelidiomycota as phyla in the kingdom fungi. Karpov et al. (2014) describe the Aphelidiomycota as "opisthokont intracellular parasitoids of algae with phagotrophic amoeboid vegetative stage; invasive cyst with a short infective tube of penetration apparatus; zoospores with pseudopodia and/or posteriorly directed functional or rudimentary flagellum". The genera *Amoeboaphelidium* (five species), *Aphelidium* (seven species), *Paraphelidium* (two species), *Pseudaphelidium* (one species) composed in the monotypic phylum (Tedersoo et al. 2018, Wijayawardene et al. 2020). *Aphelidium*, *Amoeboaphelidium*, and *Paraphelidium* thrive in freshwater environments (Zopf 1885, Scherffel 1925, Schweikert & Schnepf 1996, Karpov et al. 2017, Letcher & Powell 2019).

Monoblepharomycota was introduced by Doweld (2001) based on *Monoblepharis* and accepted by Tedersoo et al. (2016), who proposed another class, Sanchytriomycetes, in the phylum. Three classes (Hyaloraphidiomycetes, Monoblepharidomycetes, Sanchytriomycetes), three orders (Hyaloraphidiales, Monoblepharidales, Sanchytriales), seven families (Gonapodyaceae, Harpochytriaceae, Hyaloraphidiaceae, Monoblepharidaceae, Oedogoniomycetaceae, Sanchytriaceae, Telasphaerulaceae) and seven genera (*Gonapodya*, *Harpochytrium*, *Hyaloraphidium*, *Monoblepharella*, *Monoblepharis*, *Oedogoniomyces*, *Telasphaerula*) are included in Monoblepharomycota (Wijayawardene et al. 2020). All of these genera are found in freshwater habitats (Jane 1946, Karpov et al. 2017, Wijayawardene et al. 2018b).

Mortierellomycota was upgraded to a phylum level by Tedersoo et al. (2016) and comprised one class (Mortierellomycetes), one order (Mortierellales), one family (Mortierellaceae) and six genera (*Aquamortierella*, *Dissophora*, *Gamsiella*, *Lobosporangium*, *Modicella*, *Mortierella*). Only *Aquamortierella* and *Mortierella* are known to thrive in freshwater habitats (Embree & Indoh 1967, Nguyen & Lee 2016, Nguyen et al. 2019, Wijayawardene et al. 2018b).

Need for a freshwater fungi website

Online databases are developed to compile data for general accounts of fungi (e.g. http://www.indexfungorum.org; http://www.speciesfungorum.org/; http://www.mycobank.org; http://www.facesoffungi.org; http://www.fungalgenera.org, https://www.outlineoffungi.org/), or even certain ecological (e.g. http://marinefungi.org for marine fungi; http://fungi.life.illinois.edu/ for freshwater ascomycetes and their anamorphs) and taxonomic groups (e.g. Dothideomycetes: http://www.dothideomycetes.org; Sordariomycetes: http://www.sordariomycetes.org; coelomycetes: http://www.coelomycetes.org; basidiomycetes: https://www.basidio.org). Of all the websites mentioned, the webpage http://fungi.life.illinois.edu/ focuses only on freshwater fungi. With the advent of molecular techniques and the continuous exploration of different freshwater habitats and substrates, new species, even the existing ones lacking DNA sequence data, are discovered that could change the classification scheme at certain taxonomic level, or fungal systematics as a whole. Thus, the online database for freshwater fungi, www.freshwaterfungi.org, is developed to compile all the scattered published data on freshwater fungi using a user-friendly interface and is freely accessible to public users.

The website focuses on three primary goals: (1) to provide an up-to-date outline of the freshwater fungi; (2) to give detailed notes on orders, families and genera of freshwater fungi; (3) to give an updated account of each genus keeping abreast of the current literature. The website has a valuable list of references, history and news regarding freshwater fungi.

Freshwater fungi website

The website is dedicated to the taxonomy and classification of the freshwater fungi. For speciose genera, only the description of the type species is initially provided, with a synopsis table of all the freshwater species. The rule applies to those genera whose type species were first recorded in freshwater habitats. Otherwise, if the type species is from marine or terrestrial environment, the first introduced freshwater fungus with molecular sequence data is described and the remaining freshwater species enumerated. Freshwater genera with only two or three species records will be added to the website. Once the genera and type species of all the classes are added, the remaining freshwater species will be described over time. All accounts on the taxonomy and phylogeny of freshwater fungi will be updated on the notes for each taxonomic level- from class to species. This is true to species without molecular sequence data and when the taxonomic placement is already known.

For each genus, a detailed description of the species with photographic plates, phylogenetic trees for those with molecular sequence data, and keys for more than two species are provided. The website is linked to other online databases to expand the current knowledge of freshwater fungi namely, the “Fungal Genera”, (https://www.fungalgenera.org; Monkai et al. 2019), “Outline of Fungi” (https://www.outlineoffungi.org/, Wijayawardene et al. 2020), “Faces of Fungi” (http://www.facesoffungi.org; Jayasiri et al. 2015), marine fungi (http://www.marinefungi.org; Jones et al. 2019), Dothideomycetes (https://www.dothideomycetes.org/, Pem et al. 2019), Sordariomycetes (https://sordariomycetes.org/, Bundhun et al. 2020), basidiomycetes (https://basidio.org/) and coelomycetes (https://coelomycetes.org/).

We encourage all mycologists to contribute to this web page over time and it will provide a complete one stop shop where details of freshwater fungal genera and species, molecular data as well as their roles, biosecurity issues, economic significance and industrial relevance can be sourced.

Construction

Freshwater fungi included in the website are outlined according to the most recent classification of Ascomycota (Wijayawardene et al. 2017, 2018a, 2020, Hyde et al. 2020b, Luo et al. 2019), Basidiomycota (He et al. 2019), and basal fungi (= lower fungi) (Wijayawardene et al. 2018b, 2020). The current account of Sordariomycetes and Dothideomycetes on the website follows the current outline of Luo et al. (2019) and Dong et al. (2020), respectively. The description of the species entries follows the Fungal Diversity Notes (FDN) format (Phookamsak et al. 2019). The outline, detailed description and notes of each entry in the website are carefully checked by the curators (Table 2).

Table 2 List of expert curators with their information for freshwater fungi webpage

Position	Name	Address	Contact information
Head Curator	Saranyaphat Boonmee	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	saranyaphat.boo@mfu.ac.th
Managing Curators	Sajini Chandrasiri	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	sajinichandrasiri@yahoo.com
	Mark S. Calabon	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	mscalabon@up.edu.ph
Curators	Dan-Feng Bao	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	baodanfengfungi@qq.com
	Wei Dong	Institute of Plant Health, Zhongkai University of Agriculture and Engineering, Guangzhou, Guangdong Province, People’s Republic of China	dongwei0312@hotmail.com
	Sally Fryar	College of Science and Engineering, Flinders University, GPO Box 2100, Adelaide SA 5001, Australia	sally.fryar@flinders.edu.au
	Kevin D. Hyde	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	kdhyde3@gmail.com
	E.B. Gareth Jones	Department of Botany and Microbiology, College of Science, King Saud University, P.O. Box 2455, Riyadh 11451, Kingdom of Saudi Arabia	torperadgj@gmail.com

Table 2 Continued.

Position	Name	Address	Contact information
	Yong-Zhong Lu	School of Pharmaceutical Engineering, Guizhou Institute of Technology, Guiyang, 550003, Guizhou, China	yzlu86@gmail.com
	Zong-Long Luo	College of Agriculture and Biological Sciences, Dali University, Dali, 671003, People’s Republic of China	luozonglongfungi@163.com
	Jing Yang	Center of Excellence in Fungal Research (CEFR), Mae Fah Luang University, 57100, Chiang Rai, Thailand	yangjing5633@gmail.com

Database interface and visualization

www.freshwaterfungi.org is an online platform that compiles published information on the classification and taxonomy of freshwater fungi. The website’s interface is simple and user-friendly (Fig. 1). The heading provides the eight features and functions of the website. The general information of the webpage, the contact information (*email address*: freshwaterfungi.org@gmail.com; address: Mushroom Research Foundation, 292 Moo 18 Bandu District Muang Chiang Rai, 57100 Thailand) and the publisher (Mushroom Research Foundation) is located at the footer of the webpage. The left side of the webpage lists all recent uploaded genera and species. The search toolbar is found above the *Recent Genus* of the webpage. To find the genus or taxon of interest, input the information in the search box and a pop-up suggestion appears with the target fungi including its taxonomic level (Fig. 2). Clicking on the species name will direct you to the description, notes, photographic plates and phylogenetic tree of freshwater fungi (Fig. 3). The references used in the description and notes are linked to its original source to obtain information about the species.

The website has eight different features and functions in the uppermost part. First, the *Home* tab provides the ultimate goals of the webpage, the general and specific information the website offers, and a photo slideshow of selected freshwater fungi (Fig. 1). The *Outline* provides the recent classification at all taxonomic levels of freshwater fungi (Fig. 4). Some species are automatically linked to their information on the website. The following typographical symbols are used in the website as additional information of the species in the outline: an asterisk (*) if the species has available molecular sequence data; type of habitat, + (plus) sign if the fungus is isolated in the lotic environment, and hyphen (-) if found in the lentic. Number (#) sign is added to species with sexual or asexual connections. The type of habitat where the species is isolated and if possible, the host where the fungus is associated or is recorded after the author’s name. The updated information including the descriptions, notes, photographic plates and phylogenetic tree of the specific order and families are listed in the *Archives* (Fig. 5). The *Curators* section provides the contact information and the affiliated institutions of all the curators of the website. A short historical background of freshwater mycology is on the *History* tab. The *References* is a compilation of all the published work (e.g. books, reviews, monographs and articles) on freshwater fungi. For the current year, all the available information about freshwater mycology is separated from the alphabetical list of all the references in the tab. This is to show the volume of research works done on that particular year. All activities and news related to mycology are shown in the *News*. The *Contact* tab gives the public users of the website to address any comments, suggestions and even entries.

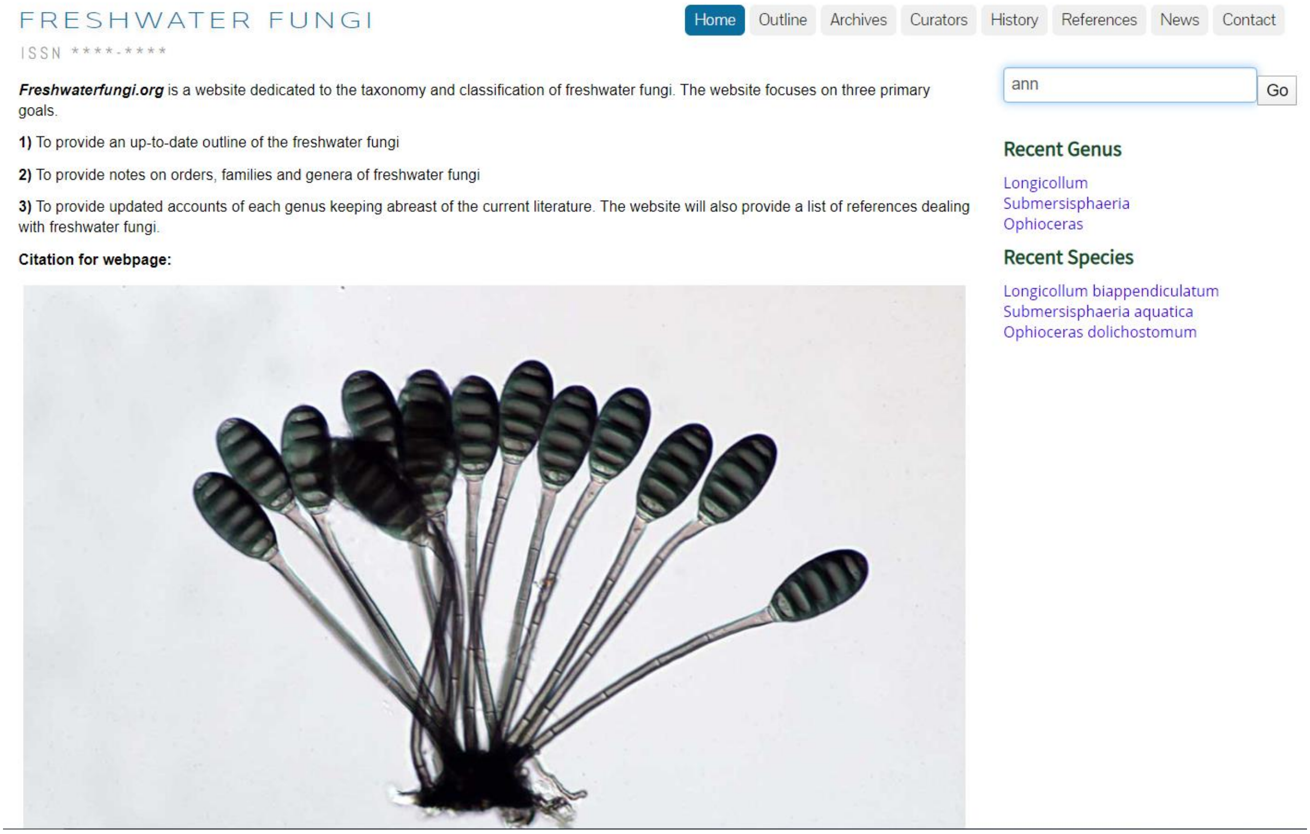

Fig. 1 – The homepage view of the freshwater fungi containing a short background of the website, the highlight of information, a photo slideshow, and the different features and functions including the search toolbar and recent uploaded data.

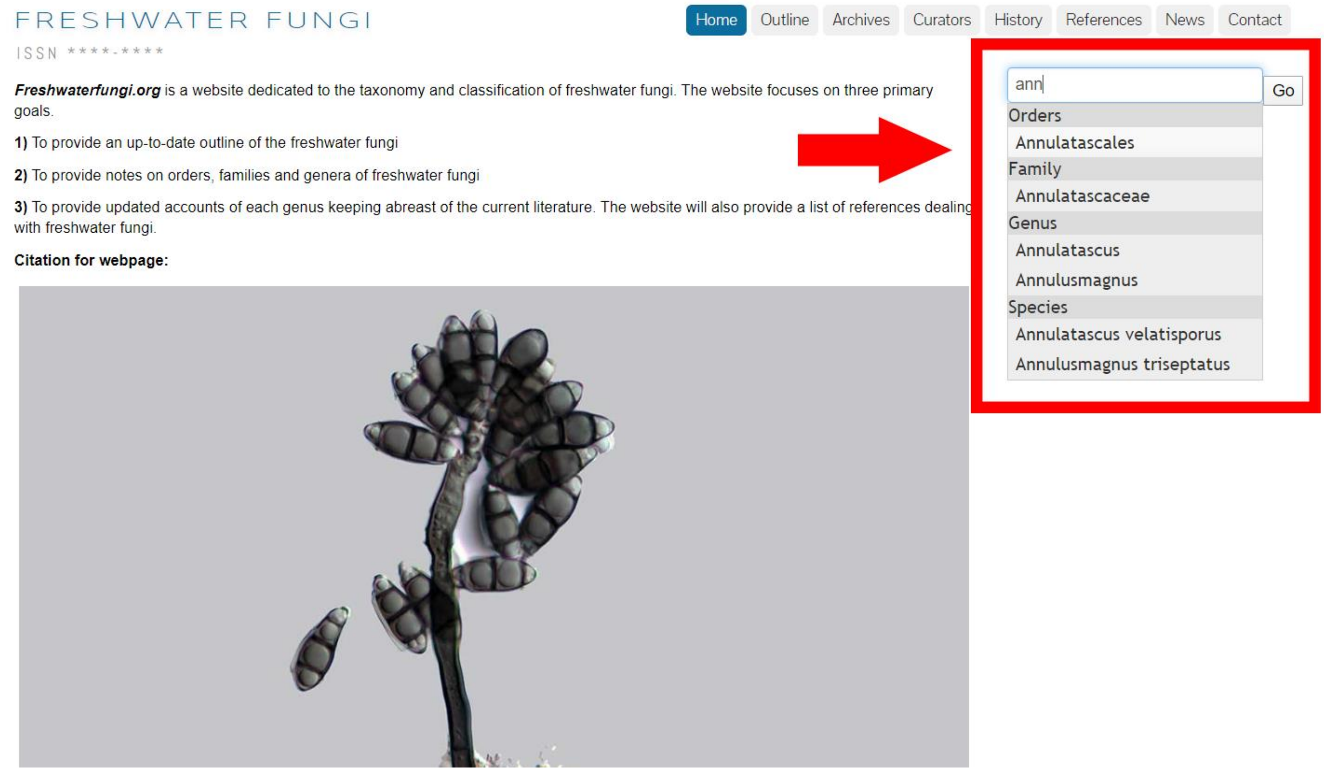

Fig. 2 – The search toolbar of the website showing some suggestions of the fungi of interest based on the user's data inputs.

FRESHWATER FUNGI

ISSN ****-****

Home | Outline | Archives | Curators | History | References | News | Cont

Magnaporthales » Ophioceraceae » Ophioceras

Ophioceras dolichostomum

Ophioceras dolichostomum (Berk. & M.A. Curtis)
Index Fungorum number: 146613

Sexual morph: *Ascomata* immersed, lenticular to conical, ostiolate, beaked, black, solitary or gregarious. *Neck* long, black, periphysate. *Paraphyses* laonger than asci, persistence, hyaline, septate, tapering, 16 µm, at the base, 4 µm at the tip, formed of cells up to 50 µm long. *Asci* 116–132 × 8–10 µm, 8-spored, cylindrical, short pedunculate, unitunicate, thin-walled, with a non-amyloid ring-like apical apparatus, 3.2– 4 µm long × 2.4–3.2 µm wide. *Ascospores* 90–104 × 2.5–3.5 µm, 4–6- celled, hyaline in mass, filiform, straight or slightly curved or twisted in the ascus, curved on release, rounded and both end and lacking mucilage. **Asexual morph:** Undetermined.

Specimen examined: AUSTRALIA, north Queensland, submerged wood (Hyde1992b); **JAPAN**, Koito River, on submerged wood (Tsui et al.2001a); **USA**, Florida, on submerged wood (Conway and Barr1977); **SEYCHELLES**, Riviere St Marie-Louis, on submerged wood (Hyde and Goh1998a).

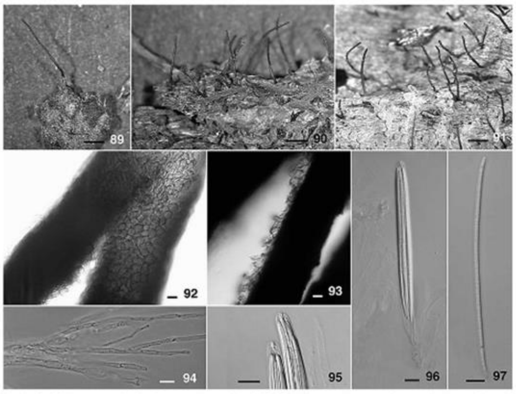

Fig 1. ***Ophioceras dolichostomum***. No. 89–91. Ascomata on the substrate. No. 92, 93. Ascomatal neck surface. No. 94. Paraphyses. No. 95. Ascus apices with rings. No. 96. Ascus. No. 97. Ascospores. No. 89–91 by photomicrography; No. 92, 93, 95–97 by DIC; 94 by PH. Scale bars: 89–91 = 1 µm, 92–97 = 10 µm. 89, 90 from NY isotype; 91–97 from SMH1888. (Photo grabbed from Huhndorf et.al 2008).

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Recent Genus

Longicollum
Submersisphaeria
Ophioceras

Recent Species

Longicollum biappendiculatum
Submersisphaeria aquatica
Ophioceras dolichostomum

Fig. 3 – A detailed description with illustration of fungi *Ophioceras dolichostomum*.

Outline

Outline of Freshwater Sordariomycetes

Phylum:	**ASCOMYCOTA**
Subphylum:	**Pezizomycotina**
Class:	**Sordariomycetes**
Subclass:	**Diaporthomycetidae** Senan et al.
Order:	**Annulatascales** D'souza et al.
Family:	**Annulatascaceae** Wong et al.

Annulatascus K.D. Hyde
Annulatascus apiculatus F.R. Barbosa & Gusmão
Annulatascus aquaticus Ho et al.
Annulatascus aquatorba Boonyuen & Sri-indrasutdhi
Annulatascus fusiformis K.D. Hyde & S.W. Wong
Annulatascus hongkongensis Ho et al.
Annulatascus joannae Tsui et al.
Annulatascus lacteus Tsui et al.
Annulatascus liputii L. Cai & K.D. Hyde
Annulatascus menglensis Hu et al.
Annulatascus nilensis Abdel-Wahab & Abdel-Aziz
Annulatascus palmietensis Goh et al.
Annulatascus saprophyticus Z.L. Luo & K.D. Hyde
Annulatascus tropicalis Ranghoo & K.D. Hyde
Annulatascus velatisporus K.D. Hyde

Annulusmagnus J. Campb. & Shearer
Annulusmagnus triseptatus (Wong et al.) J. Campb. & Shearer

Aqualignicola Ranghoo et al.
Aqualignicola hyalina Ranghoo et al.
Aqualignicola vaginata Hu et al.

Ascitendus J. Campb. & Shearer
Ascitendus aquaticus Dayarathne et al.
Ascitendus austriacus (Réblová et al.) J. Campb. & Shearer

Search Go

Recent Genus

Longicollum
Submersisphaeria
Ophioceras

Recent Species

Longicollum biappendiculatum
Submersisphaeria aquatica
Ophioceras dolichostomum

Fig. 4 – An outline of freshwater Sordariomycetes based on Luo et al. (2019)

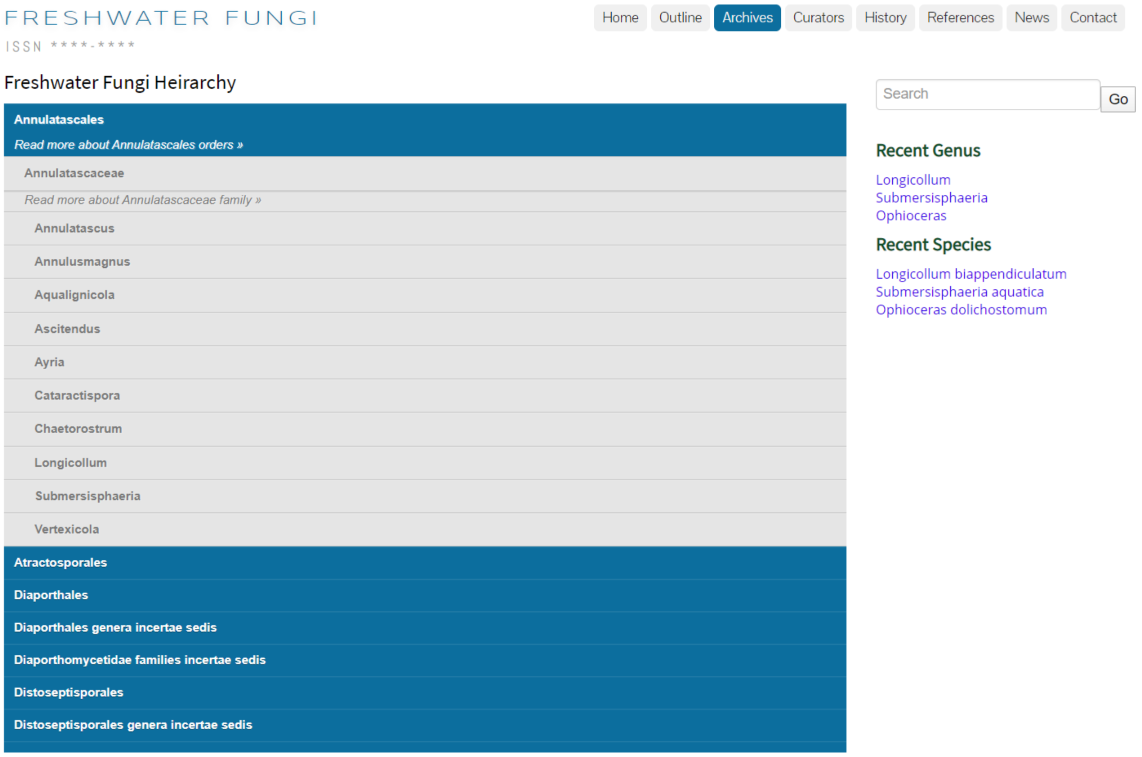

Fig. 5 – The *Archive* tab with the outline of the orders and families of freshwater fungi. These are all linked in the description of each orders and families.

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