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Review

# Recent studies on aero-aquatic fungi, with special reference to diversity of conidial morphology and convergent evolution

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## ABSTRACT

Aero-aquatic fungi compose an ecological group of saprophytes inhabiting the submerged decaying substrates in stagnant freshwater environment. They produce three-dimensional shaped, multi-cellular conidia, which float on water surface by holding air between conidial cells. Because the conidia show diverse morphology, genus and species level classification have been based on their features. They are mostly known as asexual morphs of Ascomycota or Basidiomycota. Recent phylogenetic study revealed the aero-aquatic fungi appeared mainly in the lineages of Leotiomycetes, Dothideomycetes, and Sordariomycetes. Furthermore, the phylogenetic tree showed the aero-aquatic fungi have polyphyletic origins and similar three-dimensional conidial morphology generated as a convergent evolution among different lineages of fungi by the selection pressure for inhabiting freshwater environment. Recent studies suggested the ancestors of the aero-aquatic fungi were terrestrial fungi.

***Keywords***: ecology, freshwater fungi, origin, polyphyly, sexual/asexual morph relationship.

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## 1. Introduction

Aero-aquatic fungi inhabit submerged litters, decaying woods or twigs in stagnant freshwater environment such as pond, pool, ditch, slow-running stream etc. where the oxygen concentration often becomes low (Webster & Descals, 1981). The most aero-aquatic fungi are known as asexual morphs of Ascomycota or Basidiomycota, and only limited number of sexual morphs are known as aero-aquatic, such as *Limnoperdon incarnatum* G.A. Escobar belonging to Basidiomycota which produces floating-type basidiomata (Escobar et al. 1976; Nakagiri & Ito, 1991; Webster et al. 1993). The term of "aero-aquatic fungi" were proposed by Beverwijk in 1951 for the fungi whose conidia (asexual spores) are produced just above the water surface and dispersed by floating on the surface of the water, though the vegetative mycelia can grow under water (Beverwijk, 1951). Park (1972) studied the ecology of heterotrophic microorganisms in freshwater including fungi. Subsequently, Fisher (1977a, 1977b) defined the term "aeroaquatic" in accordance with Park's idea as the aero-aquatic fungi were organisms indwelling substrata under water and characterized by the production of vegetative mycelium in the submerged substrates and by the formation of conidia with special flotation device only when the substrate was exposed to a moist atmosphere (Fig. 1).

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The mitosporic fungi inhabiting freshwater environment has been known as aquatic fungi (Ingoldian fungi). They are distinguished from the aero-aquatic fungi in that the aquatic fungi inhabit under flowing water such as stream and waterfall and produces conidia of S-shape, anchor-shape, and tetraradiate etc. from submerging hyphae. These conidia are released into the water and dispersed by water flow (Goh & Hyde, 1996; Ingold, 1942; Kendrick, 2000; Webster & Weber, 2007). On the other hand, the aero-aquatic fungi produce three-dimensional shaped conidia such as globose, crown shape, helicoid (doliform), clathrate etc. (Fig. 2A–G; Table 1). These types of conidia are considered to be dispersed by floating on water surface with air held in three-dimensional structure of conidia (Goh & Hyde, 1996; Kendrick, 2000; Webster & Descals, 1981; Webster & Weber, 2007).

## 2. Taxonomy

Aero-aquatic fungi have been classified based on conidial morphology as they show diverse morphological characteristics. The monographs and keys of *Helicodendron* Peyronel and *Helicoon* Morgan, both forming three-dimensionally helicoid (doliform) conidia, were provided by Goos et al. (1985, 1986), Zhao et al. (2007), and Goh and Kuo (2018), in which conidium size and color, width of conidial filament, and the number and direction of coils of a conidium were adopted as taxonomic characters. The globose, clathrate, or fan shaped conidium forming fungi including *Dendro-*

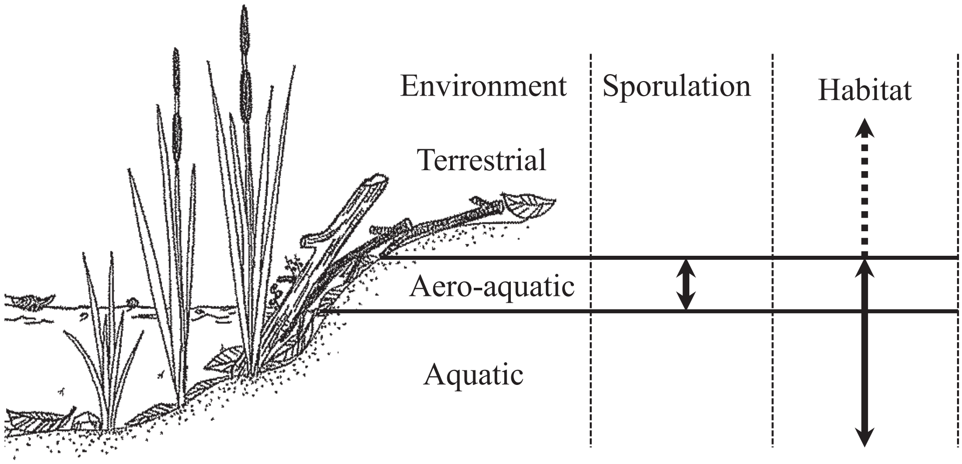


**Fig. 1.** Diagram of ecology and habitat of aero-aquatic fungi.

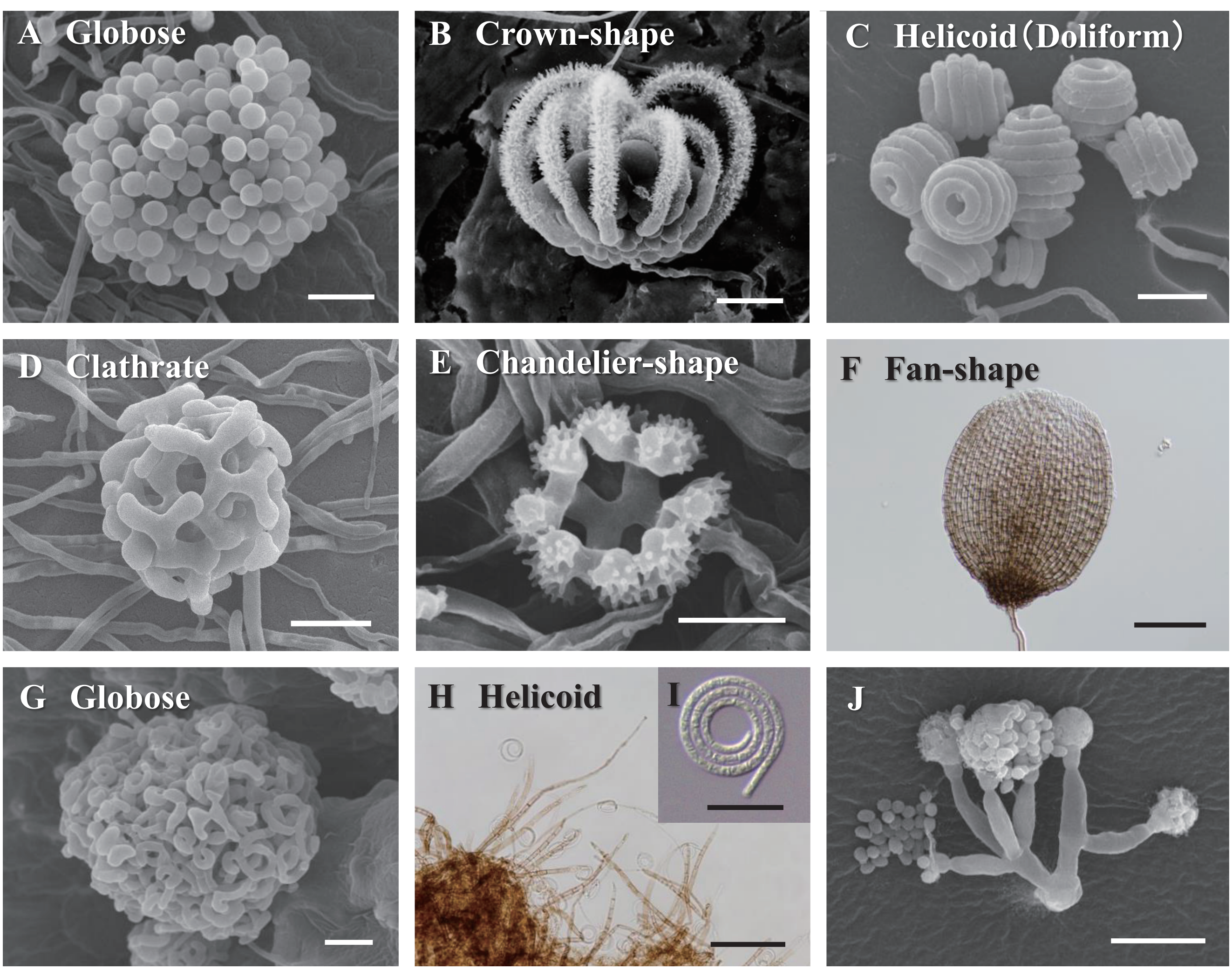


**Fig. 2.** A–G: Morphological diversity of conidia of aero-aquatic fungi. H, I: Conidial morphology of *Helicosporium*, broadly interpreted aero-aquatic fungi. Note: conidia are flat coil shaped, not three-dimensional. J: Microconidia (phialoconidia) of *Helicodendron conglomeratum*. A: *Pseudaegerita corticalis.* B: *Peyronelina glomerulata.* C: *Helicodendron conglomeratum.* D: *Pseudoclathrosphaerina* sp. E: *Candelabrum spinulosum* (current name is *Hyaloscypha spinulosa*). F: *Cancellidium applanatum.* G: *Spirosphaera floriformis.* H and I: *Helicosporium panachaeum.* J: *Helicodendron conglomeratum.* (A–E, G, J: Scanning electron micrographs. F, H, I: Light micrographs. A and D referred from the book by Mycological Society of Japan 2017. B referred from Yamaguchi et al. 2009 provided by Dr. Nakagiri. E referred from Yamaguchi et al. 2020a) *Bars*: A–D, J 10 µm; E 5 µm; F 50 µm; G, I 20 µm; H 100 µm.

*clathra* Voglmayr & G. Delgado, *Sympodioclathra* Voglmayr, *Clathrosphaerina* Beverwijk, *Pseudoclathrosphaerina* Voglmayr, *Clathrosporium* Nawawi & Kuthubutheen, *Spirosphaera* Beverwijk, *Pseudaegerita* J.L. Crane & Schoknecht, and *Beverwykella* Tubaki were reassessed on their taxonomic characters by Voglmayr and Delgado-Rodríguez (2001) focusing on the ways of the branching of the conidial filaments. Furthermore, Voglmayr (2004) reviewed the diagnostic characteristics of species in *Spirosphaera* including some species defined *Clathrosporium*, whose conidia are globose loose balls composed of interwoven coiling hyphae, and regarded conidium size, width of conidial filament, color, and conidial branching as useful traits for species taxonomy.

## 3. Ecology

The aero-aquatic fungi are decomposers of various substrates in the freshwater habitats, such as decaying wood, twigs, litters etc. Their degradation abilities of lignin and cellulose were studied by many researchers (Abdullah & Taj-Aldeen, 1989; Bergbauer et al., 1992; Fisher et al., 1977, 1983) from the 1970s to the 1990s. The aero-aquatic fungi were demonstrated as playing an important role for carbon cycling in aquatic environment by converting the substrates to palatable and nutritious food material with their mycelium for aquatic animals such as snail, frogs, tadpole etc. (Kendrick, 2000; Webster & Descals, 1981).

Studies on the geographical distribution of aero-aquatic fungi demonstrated that the fungi isolated from sub-tropical or temperate zone mainly belonged to Sordariomycetes and Dothideomycetes, while many of them from cool temperate zone were members of Leotiomycetes and Basidiomycota (Chuaseeharonnachai et al., 2013; Kageyama, 2010; Yamaguchi et al., 2020a). These distribution patterns probably correspond to their climatic preferences relating to the range of growth temperature (Větrovský et al., 2019; Wood-Eggenschwiler & Bärlocher, 1985). Verifying these distribution differences observed in specific taxonomic groups of aero-aquatic fungi is an interesting research subject in future. Further inventory studies at various geographical regions and molecular phylogeny studies based on a large number of isolates may evaluate the correlation between taxonomic groups of aero-aquatic fungi characterized by some specific characters and their geographical distribution.

## 4. Sexual/asexual morph relationship

The sexual morphs of aero-aquatic fungi have been found only in few cases (Table 1). The following sexual/asexual morphs relationships have been revealed: *Hyaloscypha zalewskii* Descals & J. Webster/*Clathrosphaerina zalewskii* Beverwijk (Descals & Webster, 1976); *Hyaloscypha lignicola* Abdullah & J. Webster [current name is *Hyaloscypha spiralis* (Velenovský) J.G. Han, Hosoya & H.D. Shin (Han et al., 2014)]/*Pseudaegerita corticalis* (Peck) J.L. Crane & Schoknecht (Abdullah & Webster, 1983; Fehrer et al., 2019); *Hyaloscypha japonensis* (Tubaki) K. Yamagychi, Huhtinen, Hosoya, Chuaseeharonnachai & Nakagiri/*Candelabrum japonense* Tubaki (Yamaguchi et al., 2020a); *Orbilia luteorubella* (Nylander) P. Karsten/*Helicoon sessile* Morgan (Pfister, 1997); *Hymenoscyphus paradoxus* P.J. Fisher & J. Webster/*Helicodendron paradoxum* Peyritsch (Fisher & Webster, 1983); *Mollisia gigantea* P.J. Fisher & J. Webster/*Helicodendron giganteum* Glen Bott (Fisher & Webster, 1983); *Lambertella tubulosa* Abdullah & J. Webster/*Helicodendron tubulosum* (Riess) Linder (Abdullah & J. Webster, 1981); *Tyrannosorus pinicola* (Petrini & P.J. Fisher) Unter. & Malloch/*Helicodendron pinicola* E. Müll., Petrini, P.J. Fisher, Samuels & Rossman ex Voglmayr & P.J. Fisher (Untereiner et al., 1995); *Bulbillomyces farinosus* (Bresàdola) Jülich/*Aegerita candida* Persoon (Webster & Weber, 2007); *Subulicystidium longisporum* (Patouillard) Parmasto/*Aegeritina tortuosa* (Bourdot & Galzin) Jülich (Webster & Weber, 2007); *Flagelloscypha* sp./*Peyronelina glomerulata* P.J. Fisher, J. Webster & D.F. Kane (Yamaguchi et al., 2009). These sexual/asexual morphs relationships were revealed mainly by finding conidium formation in culturing sexual spores or organs on the agar medium.

Recent phylogenetic studies based on the molecular phylogeny have revealed the phylogenetic positions of some species of aero-aquatic fungi (Table 1). These data give a hint of undiscovered sexual morphs. Further studies by culturing the isolates from sexual morph of the phylogenetically related group of fungi under wet or submerged condition may clarify new sexual/asexual relationships of aero-aquatic fungi.

## 5. Diversity of conidial morphology

Aero-aquatic fungi produce diverse three-dimensional shaped conidia for floating on the water surface (Fig. 2A–G; Table1). The globose conidia are produced by *Aegerita* Persoon, *Aegeritina* Jülich, *Brocchiosphaera* (Tubaki) K. Yamaguchi, Chuaseeharonnachai & Nakagiri, *Fouskomenomyces* Magaña-Dueñas, Cano, & Stchigel, *Nidulispora* Nawawi & Kuthubutheen, *Polyancora* Voglmayr & Yule, *Pseudaegerita* (Fig. 2A), *Ramicephala* Voglmayr & G. Delgado, *Spirosphaera* (Fig. 2G), *Spiroplana* Voglmayr, M.J. Park & H.D. Shin, and some species of *Trichoderma* Persoon. The detailed morphologies of this type of conidia are botryose, broccoli shape, flower-bud-shape, ball of yarn-shape, and onion flower-shape etc., all of which are composed of branched aggregate of cells. The air is trapped within the space between cells of the globose propagules. The crown shaped conidia are formed by *Peyronelina* P.J. Fisher, J. Webster & D.F. Kane (Fig. 2B) and consist of central 20–30 subglobose cells and surrounding 7–17 arms with flake-like spicules. The air is entrapped in the inside surrounded with the arms of the conidium. The spiculate ornamentation on the arms was assumed to be hydrophobic (Fisher et al., 1976; Nakagiri & Ito, 1997). The helicoid (doliform) conidia are produced by *Helicodendron* (Fig. 2C), *Helicoon*, *Pleohelicoon* Jayasiri, E.B.G. Jones & K.D. Hyde, *Pseudohelicoon* Y.Z. Lu & K.D. Hyde, *Magnohelicospora* R.F. Castañeda, Hernández-Restrepo, Gené & Guarro and *Helicoascotaiwania* Dayarathne, Maharachchikumbura & K.D. Hyde. Their barrel-shaped conidia composed of spirally coiled filamentous cells will float on water surface by keeping air inside the spiraling coil. The clathrate conidia are found in *Clathrosphaerina*, *Clathrosporium*, *Dendroclathra*, *Pseudoclathrosphaerina* (Fig. 2D), and *Sympodioclathra*. The conidia are spherical propagules consisted of interwoven conidial filaments, which repeat branching dichotomously, laterally, or spirally and trap air within the complex construction. The chandelier-shaped conidia are formed by *Candelabrum* (current name is *Hyaloscypha*) (Fig. 2E). Its conidial cells develop upward from a basal plate at the bottom of the conidium. The conidia look like flower of water lily when floating on the water. The fan-shaped conidia are produced by *Akenomyces* G. Arnaud ex D. Hornby, *Beverwykella*, and *Cancellidium* Tubaki (Fig. 2F). The elliptically flattened propagules have buoyancy by enclosing air in the inner space of conidium.

## 6. Phylogeny

Recent phylogenetic studies revealed that aero-aquatic fungi belong to diverse lineages in Ascomycota and Basidiomycota (Table 1). Major lineages are Leotiomycetes, Dothideomycetes, and

Sordariomycetes. Only a few aero-aquatic fungi belong to Basidiomycota and Orbiliomycetes. On the other hand, the aquatic mitosporic fungi (Ingoldian fungi) were also found polyphyletic among Ascomycota and Basidiomycota, while their major lineages belong to Helotiales, Leotiomycetes, followed by Dothideomycetes, Sordariomycetes, Basidiomycota and Orbiliomycetes (Duarte et al., 2013; Franco-Duarte et al., 2022). Thus, it is presumed that the almost the same groups of Ascomycota and only the small number of species of Basidiomycota have evolved to adapt to freshwater habitats as aero-aquatic fungi or aquatic fungi by applying their own strategy for conidial dispersal and colonization on substrates. For example, in the family Tricladiaceae in Helotiales, the following genera of asexual morphs inhabit aquatic environments as aero-aquatic fungi (AAF) or aquatic fungi (AF): *Helicodendron* (AAF), *Spirosphaera* (AAF), *Anguillospora* Ingold (AF), *Filosporella* Nawawi (AF), *Geniculospora* Sv. Nilsson ex Marvanová & Sv. Nilsson (AF), *Halenospora* E.B.G. Jones (AF), *Mycofalcella* Marvanová, Om-Kalthoum-Khattab & J. Webster (AF), and *Tricladium*

**Table 1.** Taxonomic positions, sexual morphs, and conidial shapes of aero-aquatic fungi.

| Higher taxa | | | Families | Genus | Sexual morph | Conidial shape | References |
|---|---|---|---|---|---|---|---|
| Ascomycota | | | Arachnopezizaceae | *Clathrosphaerina* | *Hyaloscypha?* | Clathrate | Webster & Weber (2007), Johnston et al. (2019) |
| | | | Gelatinodiscaceae | *Clathrosporium* | unknown | Clathrate | Voglmayr (2004), Johnston et al. (2019) |
| | | | Gelatinodiscaceae | *Helicodendron* | *Hymenoscyphus?* | Helicoid | Webster & Weber (2007), Johnston et al. (2019) |
| | Leotiomycetes | Helotiales | Tricladiaceae | *Helicodendron* | *Mollisia?* | Helicoid | Webster & Weber (2007), Johnston & Baschien (2020) |
| | | | Tricladiaceae | *Helicodendron* | *Lambertella?* | Helicoid | Webster & Weber (2007), Johnston & Baschien (2020) |
| | | | Tricladiaceae | *Spirosphaera* | unknown | Globose | Voglmayr (2004; 2011), Johnston & Baschien (2020) |
| | | | Hyaloscyphaceae | *Candelabrum* | *Hyaloscypha* | Chandelier-shape | Yamaguchi et al. (2020a) |
| | | | Hyaloscyphaceae | *Pseudaegerita* | *Hyaloscypha* | Globose | Webster & Weber (2007), Yamaguchi et al. (2012) |
| | | | Hyaloscyphaceae | *Pseudoclathrosphaerina* | unknown | Clathrate | Yamaguchi (2018) |
| | Dothideomycetes | Pleosporales | Amniculicolaceae | *Spirosphaera* →*Fouskomenomyces* | unknown | Globose | Voglmayr (2004), Magaña-Dueñas et al. (2020) |
| | | | Pleomassariaceae | *Beverwykella* | unknown | Fan-shape | Tian et al. (2015) |
| | | | Pleomonodictydaceae | *Helicoon* →*Pleohelicoon* | unknown | Helicoid | Jayasiri et al. (2019) |
| | | | unknown | *Clathrosporium* | unknown | Clathrate | Yamaguchi (2018) |
| | | | unknown | *Spiroplana* | unknown | Globose | Voglmayr et al. (2011) |
| | | Tubeufiales | Tubeufiaceae | *Helicoon* →*Pseudohelicoon* | unknown | Helicoid | Lu et al. (2018) |
| | | Venturiales | Venturiaceae | *Helicodendron* | *Tyrannosorus* | Helicoid | Webster & Weber (2007), Shen et al. (2020) |
| | | | Venturiaceae | *Helicoon* →*Magnohelicospora* | unknown | Helicoid | Hernández-Restrepo et al. (2017) |
| | Dothideomycetes? | Microthyriales | Microthyriaceae | *Spirosphaera* | unknown | Globose | Voglmayr et al. (2011), Liu et al. (2023) |
| | Sordariomycetes | Cancellidiales | Cancellidiaceae | *Cancellidium* | unknown | Fan-shape | Hyde et al. (2021) |
| | | Hypocreales | Hypocreaceae | *Trichoderma*** | unknown | Globose* | Yamaguchi et al. (2012) |
| | | Microascales | unknown | *Dendroclathra* | unknown | Clathrate | Voglmayr (2011) |
| | | Pisorisporiales | unknown | *Candelabrum* →*Brocchiosphaera* | unknown | Globose | Yamaguchi et al. (2020a) |
| | | Pleurotheciales | Pleurotheciaceae | *Helicoon* | *Helicoascotaiwania* | Helicoid | Reblova et al. (2020) |
| | | Xylariales | unknown | *Polyancora* | unknown | Globose or onion flower-shape | Voglmayr & Yule (2006) |
| | | unknown | unknown | *Clathrosporium* | unknown | Clathrate | Moro et al. (2015) |
| | Orbiliomycetes | Orbiliales | Orbiliaceae | *Helicoon* | *Orbilia* | Helicoid | Webster & Weber (2007) |
| Ascomycota? | unknown | unknown | unknown | *Nidulispora* | unknown | Globose or flower-bud-shape | Nawawi & Kuthubutheen (1990) |
| | unknown | unknown | unknown | *Ramicephala* | unknown | Globose | Voglmayr & Delgado-Rodríguez (2003) |
| | unknown | unknown | unknown | *Sympodioclathra* | unknown | Clathrate | Voglmayr & Krisai-Greilhuber (1997). |
| Basidiomycota | Agaricomycetes | Agaricales | Niaceae | *Akenomyces* | unknown | Fan-shape or elliptical | Yamaguchi et al. (2020b) |
| | | | Niaceae | *Peyronelina* | *Flagelloscypha* | Crown-shape | Yamaguchi et al. (2009) |
| | | Polyporales | unknown | *Aegerita* | *Bulbillomyces* | Globose | Webster & Weber (2007), Maekawa et al. (2023) |
| | | Trechisporales | Hydnodontaceae | *Aegeritina* | *Subulicystidium* | Globose | Webster & Weber (2007), Telleria et al. (2013) |

* Macroconidia, ***Trichoderma aeroaquaticum* and *Trichoderma matsushimae*.
This table was made by modifying Webster and Weber (2007) and adding data of aero-aqautic fungi described until 2022.
*Medusoides* and *Limnoperdon* in table of Webster and Weber (2007) were excluded from this table as they are Oomycota and sexual morph fungus respectively.
*Fusticeps* and helicosporous fungi except *Helicodendron* and *Helicoon* were excluded from this table, as these are not aero-aquatic fungi *s.s.*

(AF) (Johnston & Baschien, 2020). A similar situation is also found even in a genus, as some species of the genus *Orbilia* Fries (Orbiliomycetes), have asexual states formerly belonged to *Helicoon* (AAF), *Anguillospora* (AF), *Dwayaangam* Subramanian (AF), *Trinacrium* Riess (AF) etc. (Baral et al., 2020). However, it is not clear whether phylogenetic lineages are related to their ecological traits evolved as aero-aquatic fungi or aquatic fungi.

The freshwater ascomycetes, which inhabit submerged woody substrates and forming ascomata in/on the substrates and producing ascospores equipped with mucilaginous appendages, appear in only three classes (Leotiomycetes, Dothideomycetes, and Sordariomycetes) in Ascomycota (Vijaykrishna et al., 2006). Vijaykrishna et al. (2006) described that certain ascomycetes might be well adapted to freshwater habitats with their ability to degrade waterlogged wood and the superior dispersal/settlement strategies giving freshwater ascomycetes a competitive advantage in freshwater environments over their terrestrial counterparts. These physiological property and ecological advantage are also applicable to the aero-aquatic fungi and the aquatic fungi. Furthermore, the aero-aquatic fungi were rarely evolved from Eurotiomycetes and Lecanoromycetes. The Eurotiomyceteous fungi have a wide range of habitats such as soil, plant, human, food etc. and some of them grow on dry substrates with the low water activity. The species of Lecanoromycetes have affinity of algae as lichen-forming fungi. Thus, the fungi of these lineages might have chosen different niche from those for the aero-aquatic fungi.

## 7. Convergent evolution

Aero-aquatic fungi are known to have polyphyletic origins and composing an ecological group adapting to inhabit aquatic environment and produce spores at air-water interface. *Spirosphaera*, which is characteristic in forming globose conidia composed of branching, coiled, loosely interwoven conidial filaments (Fig. 2G), now includes 9 species. Voglmayr (2004) showed *Spirosphaera* species had polyphyletic origins based on phylogenetic approach, and revealed *S. floriformis* Beverwijk, the type species of *Spirosphaera,* belonged to Leotiomycetes-Sordariomycetes lineage, while *S. cupreorufescens* Voglmayr showed affinity with Dothideomycetes. Voglmayr however concluded *S. cupreorufescens* should be retained in *Spirosphaera* according to the high resemblance of conidial morphology with those of *S. floriformis* (Voglmayr, 2004). Subsequently Magaña-Dueñas et al. (2020) transferred the latter species to a new genus *Fouskomenomyces* in their phylogenetic study. Recently *S. floriformis* was proposed to assign in Tricladiaceae/Helotiales/Leotiomyces by Johnston and Baschien (2020). *Spirosphaera beverwijkiana* Hennebert and *S. minuta* Hennebert were shown assignable in Microthyriaceae/Microthyriales/Dothielomycetes by the phylogenetic analyses in Liu et al. (2023), but these two species are still retained in the genus *Spirosphaera*. In spite of unresolved taxonomic problems, these results indicate that *Spirosphaera*-like conidial morphology evolved in different phylogenetic lineages in Ascomycota as convergent evolution.

Helicosporous fungi produce coild-spores and include *Helicodendron* Peyronel, *Helicoon*, *Helicoma* Corda, *Helicomyces* Link, and *Helicosporium* Nees. *Helicodendron* and *Helicoon* produces three-dimensional doliform or barrel-shaped floating conidia on water surface (Fig. 2C). On the other hand, *Helicoma*, *Helicomyces* and *Helicosporium* inhabit aero-aquatic environment and produce floating conidia characterized by two-dimensional flat, watch spring-like spirals when the submerged substrata are exposed to the atmosphere. Therefore, these fungi are regarded aero-aquatic fungi *sensu lato*, though their conidia are not three-dimensional structure (Fig. 2H, I). Tsui and Berbee (2006) reported that helicosporous fungi including species of *Tubeufia,* sexual morph, were separated to 6 lineages (4 lineages in Dothideomycetes, each one lineage in Helotiales/Leotiomycetes and Chaetothyriales/Eurotiomycetes) in Ascomycota and that all genera of helicosporous fungi were polyphyletic. Some helicosporous fungi are suggested to have differentiated by the convergent evolution for adapting to aquatic environment by forming water surface dispersing conidia (Tsui & Berbee, 2006). The species of *Helicoon* of the different lineages from the type species of existing genera were assigned to the following newly established genera; *Pleohelicoon*, *Pseudohelicoon*, *Magnohelicospora* and *Helicoascotaiwania* by taxonomic revision based on phylogenetic analysis (Hernández-Restrepo et al., 2017; Jayasiri et al., 2019; Lu et al., 2018; Réblová et al., 2020). Furthermore *Helicoma*, *Helicomyces* and *Helicosporium* were also conducted taxonomic revision dramatically (Lu et al. 2018). *Helicodendron paradoxum,* type species of *Helicodendron* had been regarded as an asexual morph of *Hymenoscyphus paradoxus,* but recently the former species was revealed as a member of Gelatinodiscaceae in Helotiales, Leotiomycestes by Johnston et al. (2019). In addition, *Helicodendron giganteum* was treated as an asexual morph of *Mollisia gigantea,* and *Helicodendron tubulosum* was regarded as an asexual morph of *Lambertella tubulosa*, but recently these asexual morph fungi were revealed belonging to Tricladiaceae by phylogenetical revision of Solenopeziaceae in Helotiales by Johnston and Baschien (2020). These facts require further taxonomic revision and re-observation of the sexual morph morphology to clarify their classification.

*Candelabrum* Beverwijk was presumed polyphyletic due to different conidial morphology among the species (Voglmayr, 1998). The phylogenetic analysis, morphological observation and culture study indicated that several species in the *C. spinulosum* Beverwijk group, which was characterized by chandelier-shaped, hyaline to white conidia with a basal plate at the bottom of the conidium (Fig. 2E), have affinity with the sexual morph genus *Hyaloscypha* Boudier in Helotiales, Leotiomycetes, whereas other species in the *C. brocchiatum* Tubaki group, producing globose, orange, broccoli-shaped conidia without basal plate composed of dichotomously repeating branches and tiny apical projections, were found belonging to Pisorisporiales, Sordariomycetes. To accommodate the latter *C. brocchiatum* group, a new genus *Brocchiosphaera* was established along with description of a new species (Yamaguchi et al., 2020a). Thus, aero-aquatic fungi are assumed to be an ecological group generated by convergent evolution under the selection pressure for inhabiting freshwater environment.

## 8. Origins

Freshwater ascomycetes are thought to have evolved from terrestrial ancestors (Hyde et al., 2021; Shearer, 1993; Vijaykrishna et al., 2006). Aero-aquatic fungi are also presumed to have evolved from terrestrial ancestors.

*Trichoderma matsushimae* (Abdullah & J. Webster) K. Yamaguchi, Tsurumi, Chuaseeharonnachai & Nakagiri and *T. aeroaquaticum* K. Yamaguchi, Tsurumi, Chuaseeharonnachai & Nakagiri are characterized by the morphology of green colored bulbil-like propagules resembling conidia of *Pseudaegerita*. The former species was described firstly as *Papulaspora viridis* by Matsushima (1975) and subsequently assigned to *Pseudaegerita* by Abdullah and Webster (1983) based on conidial development and structure. The latter authors reported the fungus produced microconidia (phialoconidia) (Abdullah & Webster, 1983; Matsushima, 1975). Later phylogenetic analysis by Yamaguchi et al. (2012) showed this species should be assigned to the genus *Trichoderma* and the phialoconidia were true and typical conidia of *Trichoderma*. *Trichoderma* is a typical terrestrial soil-inhabiting fungus. The formation of bulbil-like propagules which float on the water is suggested some species of *Trichoderma* invaded aquatic environments. This adaptation would be a proof that aero-aquatic fungi have evolved from terrestrial fungi (Yamaguchi et al., 2012).

Some of the aero-aquatic fungi were known to produce microconidia as shown by *Pseudaegerita viridis* (Bayliss Elliot) Abdullah & J. Webster and six species of *Helicodendron*; *H. conglomeratum* Glen Bot (Fig. 2J), *H. giganteum* Glen Bott, *H. longitubulosum* Voglmayr, *H. paradoxum* Peyronel, *H. triglitziense* (Jaap) Linder, and *H. tubulosum* (Riess) Linder (Abdullah et al., 2000; Abdullah & Webster, 1983; Voglmayr, 1997). Germination of microconidia of *P. viridis* was not observed (Abdullah & Webster, 1983). The above species of *Helicodendron* were also not reported about germination of the microconidia. They were assumed spermatia, because *H. giganteum, H. paradoxum,* and *H. tubulosum* are known to have sexual morphs, i.e., *Mollisia, Hymenoscyphus,* and *Lambertella* recpectively (Field, 1979; Voglmayr, 1997). The report by Yamaguchi et al. (2012) suggests these microconidia of the aero-aquatic fungi are true conidia, while the macroconidia are special propagules for adapting aquatic environment.

*Peyronelina glomerulata*, which produces crown-shaped floating conidia (Fig. 2B), was found to have *Flagelloscypha* sexual morph, a cyphelloid basidiomycete, based on phylogenetic analysis, ultrastructure of septum and culture studies. The *Flagelloscypha* species produces terrestrial type basidiomata probably not standing from water action, but the fungus probably succeeded in invading freshwater environment by developing the aero-aquatic asexual morph, *P. glomerulata* (Yamaguchi et al., 2009). This also suggests that the aero-aquatic fungi were derived from terrestrial fungi.

## 9. Future perspectives

The aero-aquatic fungi which were described based mainly on the morphology should be reexamined by molecular phylogeny. As mentioned above, molecular phylogeny studies revealed polyphyletic situation in each genus of helicosporous fungi (*Helicodendron*, *Helicoon*, *Helicoma*, *Helicomyces*, *Helicosporium*, etc.) and of chandelier-shaped conidia forming fungi (*Candelabrum*), and led reclassification by assigning species to proper existing genera or new genera. Recent molecular phylogeny study on *Cancellidium* revealed its phylogenetic position and proposed monotypic higher taxa, Cancellidiaceae, Cancellidiales by Hyde et al. (2021). However, there are still polyphyletic taxa remain among the aero-aquatic fungi and many of them have not been reassessed by molecular phylogeny study yet. Phylogenetic study based on molecular data is also urged because taxon names need to be treated under the One Fungus One Name (1F=1N) system according to discontinuance of the dual naming system of fungi. The major factor hindering the molecular phylogenetic study is difficulty in obtaining DNA data of the type materials due to the loss of the type specimens or the absence of ex-type cultures and also the difficulty in amplifying good enough DNA sequence from the old type specimens. Therefore, new collection of specimens and cultures from type locality is required for obtaining the epi- or neotypes and DNA sequence data. In addition to the morphological and phylogenetical studies, the life history study focusing on the sexual/asexual relationships of the aero-aquatic fungi will contribute to clarifying their diversity and the way of evolution toward adaptation to the aquatic environment.

## Disclosure

The authors declare no conflicts of interest. All the experiments undertaken in this study complied with the current laws of the county where they were performed.

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