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Biodiversity of freshwater fungi

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There are more than 600 species of freshwater fungi with more known from temperate, as compared to tropical regions. These include *ca* 340 ascomycetes, 300 deuteromycetes, and a number of lower fungi which are not discussed here. *Aniptodera*, *Annulatascus*, *Massarina*, *Ophioceras* and *Pseudohalonectria* are common freshwater ascomycetes, which appear to be well adapted for this lifestyle either in their ascospore types or their competitive-degradative characters. The most common genera of wood-inhabiting deuteromycetes include *Cancellidium*, *Dactylaria*, *Dictyosporium* and *Helicomyces*. They are categorized into four groups depending on their form and life style: the Ingoldian hyphomycetes; the aero-aquatic hyphomycetes; the terrestrial-aquatic hyphomycetes; and the submerged-aquatic hyphomycetes. The adaptations of aquatic fungi for their dispersal and subsequent attachment to new substrates are discussed.

Keywords: hyphomycetes; ascomycetes; taxonomy; ecology; stream biology

Introduction

A broad definition of 'freshwater fungi' includes any species which, for the whole or part of their life cycle, rely on free freshwater [184]. These include any species growing on substrates that are predominantly aquatic or semi-aquatic. In other words, their habitats may be clearly of an aquatic nature or those that colonize submerged plant parts in freshwater environments. Hence, freshwater fungi are an ubiquitous and diverse group of organisms. These include representatives from different groups of fungi namely the zoosporic fungi [37], many hyphomycetes [39,80,116–133, 135–145,147–153], ascomycetes [65,86,175], basidiomycetes [134,146,154–156,170], coelomycetes [27,51], zygomycetes [30], and trichomycetes [111]. Among these fungi, the freshwater hyphomycetes (Moniliales, Deuteromycotina) are well documented and the knowledge of their ecology and diversity is more comprehensive than that of other fungal groups in the aquatic environments.

Role of fungi in freshwater ecosystems

The main role of higher fungi in freshwater ecosystems is in the degradation of dead plant material, such as *Juncus*, *Phragmites*, *Scirpus* and *Typha* and dead leaves and woody material that find their way into the water. They may also be involved in the degradation of animal parts such as insect exoskeletons, fish scales and hair. Another less significant group are pathogens of both plants and animals, while a third group, the endophytes may colonize the living tissue of aquatic plants. The decay of dead plant tissue is a result of the ability of the fungi to degrade lignocellulose. Freshwater fungi occurring on submerged woody tissue have been relatively well studied. It appears that their success in colonizing submerged woody material lies in their ability to form soft-rot cavities [175] and to be antagonistic against other fungi [173]. Their ability to soften wood may also play an important role in increasing the palatability of wood to stream invertebrates. For a detailed discussion of the role of freshwater fungi the reader should refer to Shearer [175].

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In this review of freshwater fungi we concentrate on the higher fungi, ie the Ascomycota and the mitosporic fungi. There is little available information on the lower fungi in freshwater and therefore these are not included.

Freshwater ascomycetes

In a review of the freshwater ascomycetes Shearer [175] listed 288 species. This included a wide variety of ascomycetes, encompassing discomycetes, plectomycetes, pyrenomycetes and loculoascomycetes. When Shearer published her list in 1993 only 11 of the records were from tropical locations. Several tropical freshwater ascomycetes have since been described and a total of 50 species is now known to occur in the tropics, with 16 from water cooling towers, two from high altitude ponds and 32 from tropical streams [57,65]. Many of these data have resulted from studies on the tropical freshwater ascomycetes of north Queensland or cooling towers in India [48–50,52–57,66]. Three new freshwater ascomycetes have also been described recently from temperate regions [eg 166] and the number of ascomycetes known to occur in freshwater habitats now stands at *ca* 340. These fungi are an unique group with both physiological and morphological adaptations for an aquatic lifestyle. There are many more freshwater ascomycetes awaiting discovery, both in temperate waters (Shearer, personal communication) and particularly in tropical streams, rivers and other bodies of freshwater (Ho and Hyde, personal observation). Shearer has now placed her list of freshwater ascomycetes on the World Wide Web and it can be accessed using http://www.life.uiuc.edu/plantbio/fungi.

Taxonomic aspects

Freshwater ascomycetes are not a monophyletic group and include examples from several orders in a range of classes and families. The largest group are the discomycetes with 112 representatives. The most specious family is the Heliotales with 43 genera and 103 species. Remarkably, nearly all of the records of discomycetes are from temperate regions. One hundred and twelve discomycetes are given as occurring in freshwater habitats [175], but only two (ie *Hymenoscyphus malawensis* PJ Fisher and Spooner, *Pezoloma rhodocarpa* PJ Fisher and Spooner) of these records are from tropical locations. The discomycetes *H. malawensis*, *P. rhodocarpa* and *Saccobolus beckii* Heimeri are listed for the tropics [65] and none of these were recorded in authentic tropical situations. Among the noticeable absentees from tropical freshwater habitats, are therefore, the discomycetes. In six years of collecting in tropical streams, KDH has picked up only two single discomycetes. We have no suggestions as to why there are so few tropical stream discomycetes, but the absence is most remarkable.

Another large group are the pyrenomycetes represented by 95 species. The most specious orders are the Halosphaeriales with five genera and 18 species, the Sordariales with 18 genera and 47 species and the Diaporthales with six genera and eight species. Of the 93 pyrenomycetes listed [175], only eight of these were from tropical locations. We now know that these families with unitunicate asci are also commonplace in the tropics [65] (Table 1). The loculoascomycetes (ascomycetes with bitunicate asci) also form a large group, represented by 85 species [175]. The most specious order is the Pleosporales, represented by 62 species. Of the eight loculoascomycetes listed [175] only two were tropical records. Again recent collections in tropical streams have shown that this group is well represented, although less well represented than the unitunicate ascomycetes (see Table 1).

In this section we address the question of 'how many more freshwater ascomycetes await to be discovered'. We presently know *ca* 340 species from freshwater, but if we examine the data on biogeography it is obvious that freshwater habitats have only been examined in any detail in four countries: Australia (north Queensland only), Austria (a single lake [112]), USA (Illinois) and UK (Lake District and Devon) [175]. Most other data are the result of brief studies, single collections or species descriptions [eg 66, 176]. Evidence from recent studies indicates that many new species await discovery in both temperate (Shearer, personal communication) and tropical regions [65]. Most of the tropics awaits investigation and there are also few records of ascomycetes in most temperate countries.

A comparison of the ascomycetes found on submerged wood in streams in three tropical countries can give an idea of how many new fungi may be found when a new geographical region is investigated in the tropics. KDH has recently examined 100 submerged wood samples from streams in Australia (Cape Tribulation), the Philippines (Mt Makiling) and Mauritius (Black River National Park). The fungi on these samples have been identified to genus and/or species where possible, and so it is possible to compare the numbers of ascomycetes and the numbers of identified and undescribed species at each site (Table 1).

The numbers of ascomycete species identified in each site are 26, 22 and 27 respectively. Only in Australia are half of the fungi identified to species level. In the Philippines and Mauritius only 41% and 30%, respectively, of the ascomycetes can be given species names, and probably most of these unnamed species are new to science. Only two of the unnamed species in the Philippines were also found in Mauritius. The reason for the higher numbers identified to species level in Australia is because KDH has worked on these fungi since 1989 and has described many new species. However, the most striking inference that can be made from these results is that in any new site chosen for investigation, one can presently expect that half of the fungi found will be new species. Unfortunately, there are no good modern keys to the genera of ascomycetes and in particular, no keys to the freshwater ascomycetes. Furthermore, many of the fungi collected may have been described earlier in terrestrial genera or be terrestrial species occurring in freshwater and therefore the task of identifying these unknown species is daunting. The results, do however, indicate that we are far from knowing all the freshwater fungi and presently probably only know a small fraction of the species adapted for living in freshwater habitats. The results above are from small streams in rainforests or parks and there is little to no information on the ascomycetes inhabiting other bodies of water in the tropics, such as ponds and lakes.

Common genera of freshwater ascomycetes

The most specious genera in temperate regions appear to differ from the specious genera in the tropics. In [175]

Table 1 Comparison of ascomycetes collected on submerged wood in streams at Cow Bay, Cape Tribulation, Australia, Mt Makiling, Los Baños, the Philippines and Black River, Mauritius

	Cow Bay	Mt Makiling	Black River
Discomycetes	0	0	0
Plectomycctes	0	0	0
Pyrenomycetes	17	14	18
Loculoascomycetes	9	7	8
No. genera	19	14	19
No. species	26	22	27
Identified species	13	9	8
Unidentified species	13	13	19
Overlapping unidentified species	0	2	2

where most species listed are temperate, the author records the most specious freshwater genera as *Aniptodera/Halosarpheia* (8), *Chaetomium* (8), *Hymenoscyphus* (10), *Mollisia* (13), *Ophioceras/Pseudohalonectria* (11), *Phaeosphaeria* (15) and *Vibrissia* (15). There is little information on which are the most commonly encountered species. In tropical regions the most specious genera are *Aniptodera/Halosarpheia* (10), *Annulatascus* (10) and *Savoryella* (7). However, the most frequently recorded genera in 250 collections made in Australia, Brunei, Ecuador, Malaysia and the Philippines were *Annulatascus*, *Massarina*, *Ophioceras*, *Savoryella* and *Aniptodera* [65]. The tropical ascomycetes *Aniptodera* sp, *Annulatascus* spp, *Ascagilus bipolaris*, *Bertia* sp, *Caryospora* sp, *Ophioceras dolichostomum*, *Savoryella verrucosa* and *Submersisphaeria aquatica* are discussed and illustrated below.

Annulatascus Hyde [48] has immersed to superficial, coriaceous, dark-walled ascoma (Figure 7), unitunicate cylindrical asci with a relatively massive refractive apical apparatus (Figures 6, 8, 11, 12) and unicellular or septate ascospores with various types of appendages or sheaths (Figures 9, 10, 13, 14). Three species (*A. velatispora* KD Hyde (Figures 6–10), *A. bipolaris* KD Hyde and *A. biatriisporus* KD Hyde (Figures 11–14)) are presently known and many more await publication (Hyde, unpublished).

In *Aniptodera* species ascomata are immersed, becoming erumpent, with a central small papilla. Asci are unitunicate with an apical thickening and pore (Figures 1, 2), whilst ascospores are ellispoidal or fusiform, some with polar appendages (Figures 3–5). The ascomata of *Ascagilis bipolaris* are unusual in that they comprise a peridium of large thin-walled cells (Figures 19, 20). Asci readily release their ascospores in water mounts (Figure 23) and ascospores are brown, and bicellular with polar mucilaginous pads (Figures 21, 22). In *Bertia* the ascomata are superficial and covered in warts (Figure 15). The asci have very long pedicels (Figure 16) and are released in the ascomal venter at maturity. The apex of the ascus has an apical thickening and pore (Figure 17) and the ascospores are J-shaped (Figure 18).

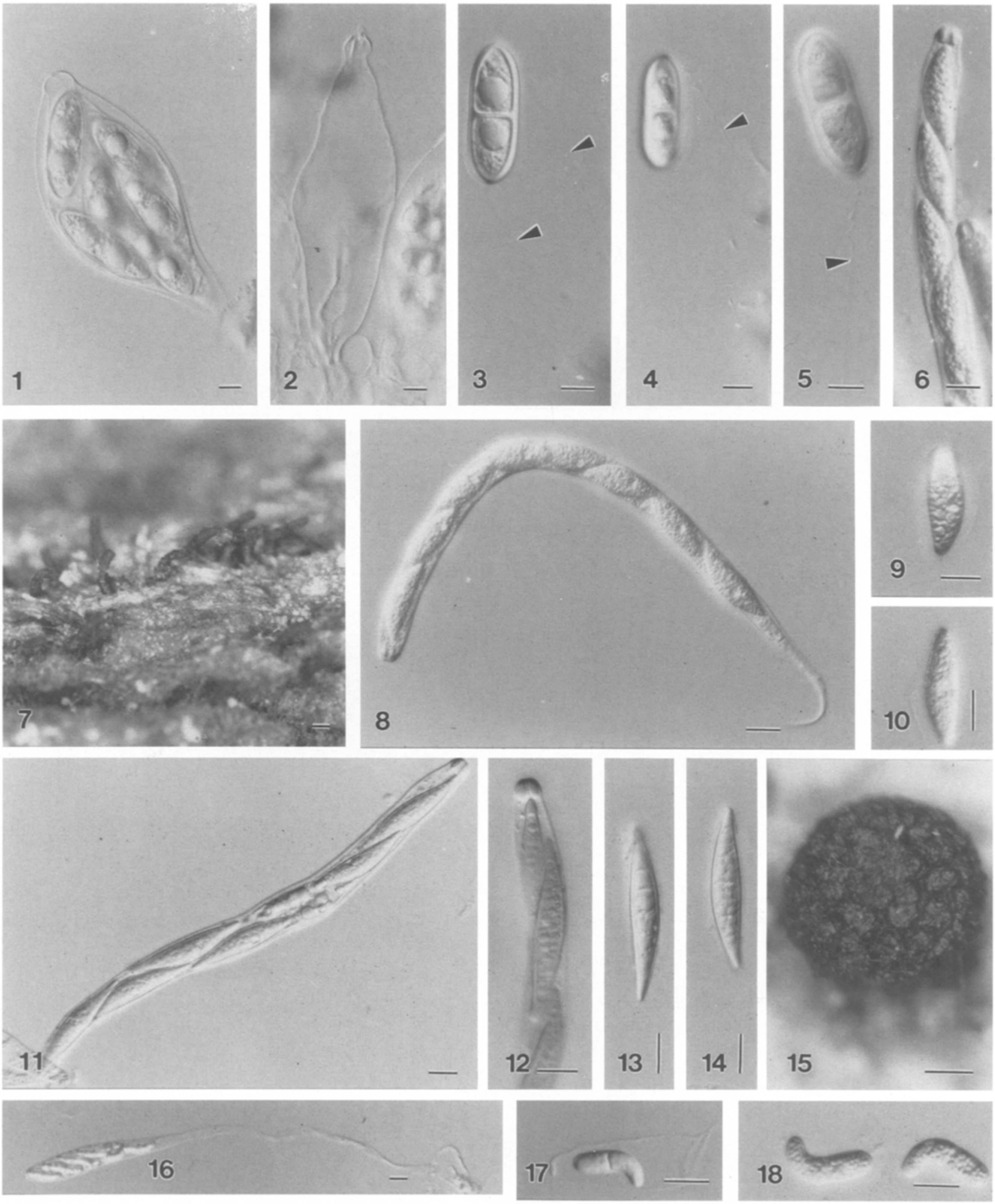
The ascomata of *Caryospora* are relatively large, black, superficial and carbonaceous (Figure 24). The asci are dark-brown, bicelled and surrounded by a mucilaginous sheath (Figure 25). In *Ophioceras dolichostomum* ascoma are immersed with long necks (Figure 36) and these can usually be seen as hair-like structures on the wood surface with the unaided eye. Asci are unitunicate and broadly cylindrical, characteristically lacking a pedicel and with a relatively small cylindrical refractive apical ring (Figures 37, 38). Ascospores are filiform with three septa and rounded ends (Figures 39, 40). In *Savoryella verrucosa* the ascomata are dark-coloured, immersed or superficial, and contain cylindrical asci with thickened apical rings with a pore (Figures 26, 27). The ascospores are four-celled, with two brown central cells and smaller hyaline end cells and a distinctly verrucose wall (Figures 28, 29). The ascomata of *Submersisphaeria aquatica* are immersed (Figure 30) and the asci (Figures 31, 34) resemble those of *Annulatascus*. The taxa, however differ, in that the ascospores in *Submersisphaeria* are brown and have apical germ pores (Figures 32–35).

Freshwater hyphomycetes

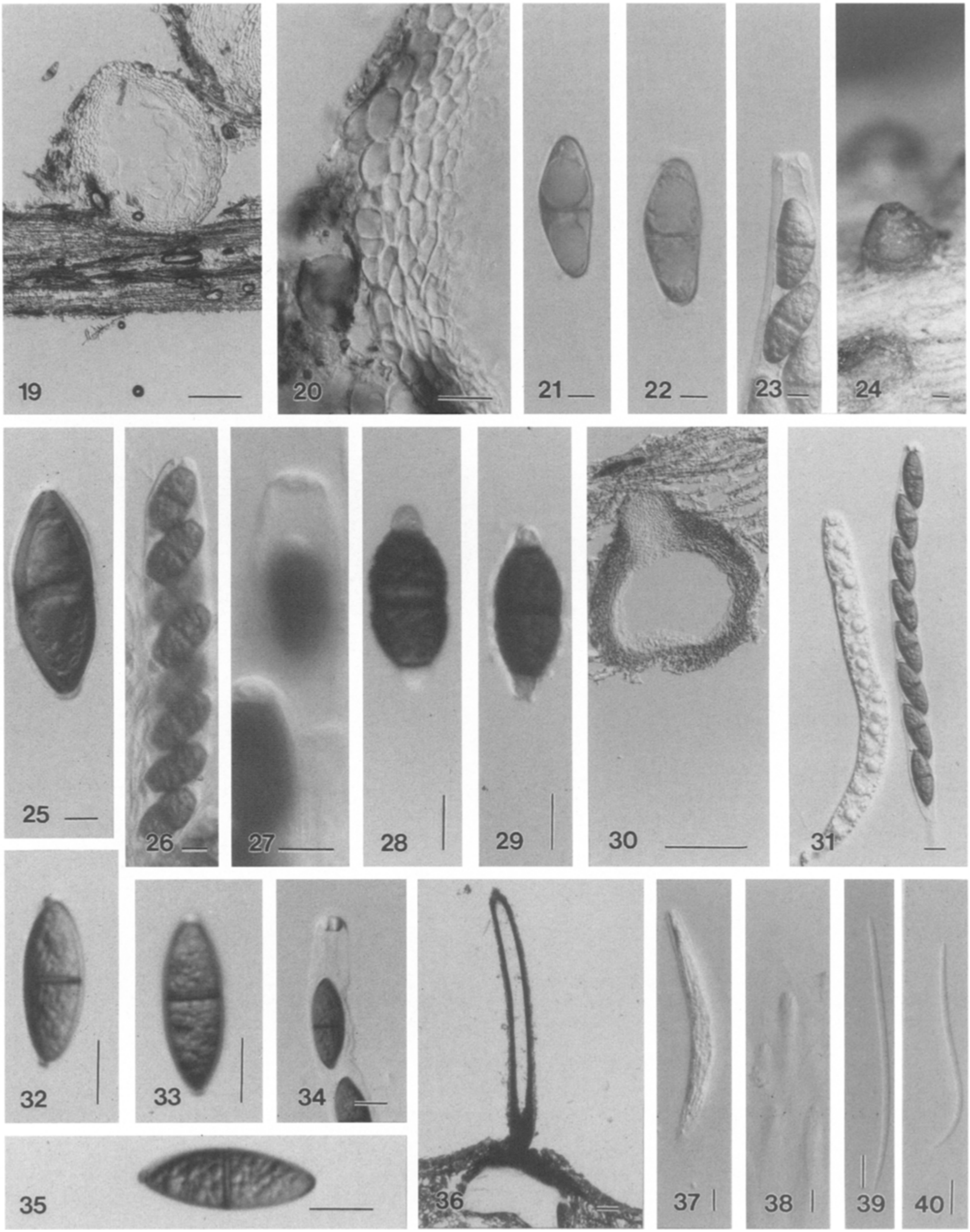
Active research on the aquatic hyphomycetes in freshwater streams and lakes began more than 50 years ago when Ingold published the first of his many papers on these fungi from England [67]. In the early 1940s it was realized [66–72] that this unique group of fungi occurs regularly on submerged decaying leaves, twigs and wood of dicotyledonous trees and shrubs. These fungi appear to be entirely absent from the needles of conifers. During the past 30 years, the majority of freshwater hyphomycetes were reported from cold and temperate regions. However, one would expect that in tropical countries, which have a rich fungal diversity, there should certainly be an equally rich diversity of freshwater hyphomycetes. It is now evident that the freshwater hyphomycetes have a worldwide distribution [3–6,16,17,22,26,31–35,39,46,47,67–72,74,76–81,92,110,113, 131,157,158,161–164,181–183,186,187]. Examples of species that are worldwide in distribution include *Anguillospora crassa* Ingold, *Campylospora chaetocladia* Ranzoni, *Flagellospora penicillioides* Ingold, *Jaculispora submersa* Hudson and Ingold, *Lunulospora curvula* Ingold, *Tetrachaetum elegans* Ingold, *Tetracladium setigerum* (Grove) Ingold, *Tricladium angulatum* Ingold, *Triscelophorus monosporus* Ingold and *Varicosporium elodeae* Kegel [200]. Nevertheless, some species appear to be localized in a given climatic zone. *Alatospora acuminata* Ingold, *Flagellospora curvula* Ingold, *Heliscella lugdunensis* Sacc and Théry, and *Lemonniera aquatica* De Wild are some of the dominant species in the high North, whereas *Angulospora aquatica* S Nilsson, *Brachiosphaera tropicalis* Nawawi, *Campylospora filicladia* Nawawi, *Ingoldiella hamata* Shaw, *Isthmotricladia gombakiensis* Nawawi, *Lunulospora cymbiformis* Miura, *Phalangispora constricta* Nawawi and Webster, *Pyramidospora casuarinae* Nilsson, *Speiropsis pedatospora* Tubaki, *Tricladiomyces malaysianum* (Nawawi) Nawawi, *Triscelophorus acuminatus* Nawawi are examples of tropical species.

To date, more than 300 species of freshwater hyphomycetes are known and the number is increasing at a rapid rate. Many new taxa have been discovered. For example, new genera published during the past few years include *Canalisporium* Nawawi and Kuthubutheen [147], *Quadricladium* Nawawi and Kuthubutheen [148], *Crucella* Marvanová and Suberkropp [115], *Nidulispora* Nawawi and Kuthubutheen [150], *Obeliospora* Nawawi and Kuthubutheen [153], *Candelosynnema* KD Hyde and Seifert [63], *Isthmophragmospora* Kuthubutheen and Nawawi [104], and *Paracryptophiale* Kuthubutheen and Nawawi [106]. Certainly, however, there are many more aquatic fungi awaiting isolation and identification.

Traditionally, the freshwater hyphomycetes are distinguishable by their biological behaviour into two groups: the *Ingoldian fungi* and the *aero-aquatic fungi*. With the broadened concept of 'aquatic fungi' given by Thomas [184], however, two additional groups of freshwater hyphomycetes can be categorized: the *terrestrial-aquatic hyphomycetes* and the *submerged-aquatic hyphomycetes* (or 'facultative-aquatic hyphomycetes'). It should be emphasized that these are 'biological groups', and, do not represent 'natural' groups in fungal systematics. Therefore, it is difficult to give them precise definition. However, these four



Figures 1–18 Light micrographs of various freshwater ascomycetes. (1–5) *Aniptodera* sp. (1, 2) Asci. Note the apical thickening and pore in 1, which has ruptured in 2. (3–5) Ascospores with fine unfurling appendages (arrowed). (6–10) *Annulatascus velatispora*. (6, 8) Asci. Note the large apical ring. (7) Necks of ascomata. (9, 10) Ascospores with mucilaginous sheath. (11–14) *Annulatascus biatriisporus*. (11, 12) Asci. Note the large thickened apical ring. (13, 14) Ascospores. (15–18) *Bertia convolutispora*. (15) Ascoma. (16, 17) Asci. Note the apical thickening. (18) J-shaped ascospores. Bars: 7, 15 = 100 μm; 1–6, 8–14, 16–18 = 10 μm.



Figures 19–40 Light micrographs of various freshwater ascomycetes. (19–23) *Ascagilis bipolaris*. (19, 20) Ascoma, illustrating large cells of peridium. (21, 22) Ascospores with bipolar mucilaginous pads. (23) Ascus. (24, 25) *Caryospora* sp. (24) Superficial ascoma. (25) Ascospore. (26–29) *Savoryella verrucosa*. (26, 27) Asci. Note the large thickened apical ring. (28, 29) Ascospores. Note the wall ornamentation and hyaline end cells. (30–35) *Submersisphaeria aquatica*. (30) Section of immersed ascoma. (31, 34) Asci. Note the large apical ring. (32, 33, 35) Ascospores. Note the polar germ pores. (36–40) *Ophioceras dolichostomum*. (36) Section of ascoma with long neck. (37, 38) Asci. Note the small apical ring. (39, 40) Filiform ascospores. Bars: 19, 24, 30, 36 = 100 μm; 20–23, 25–29, 31–35, 37–40 = 10 μm.

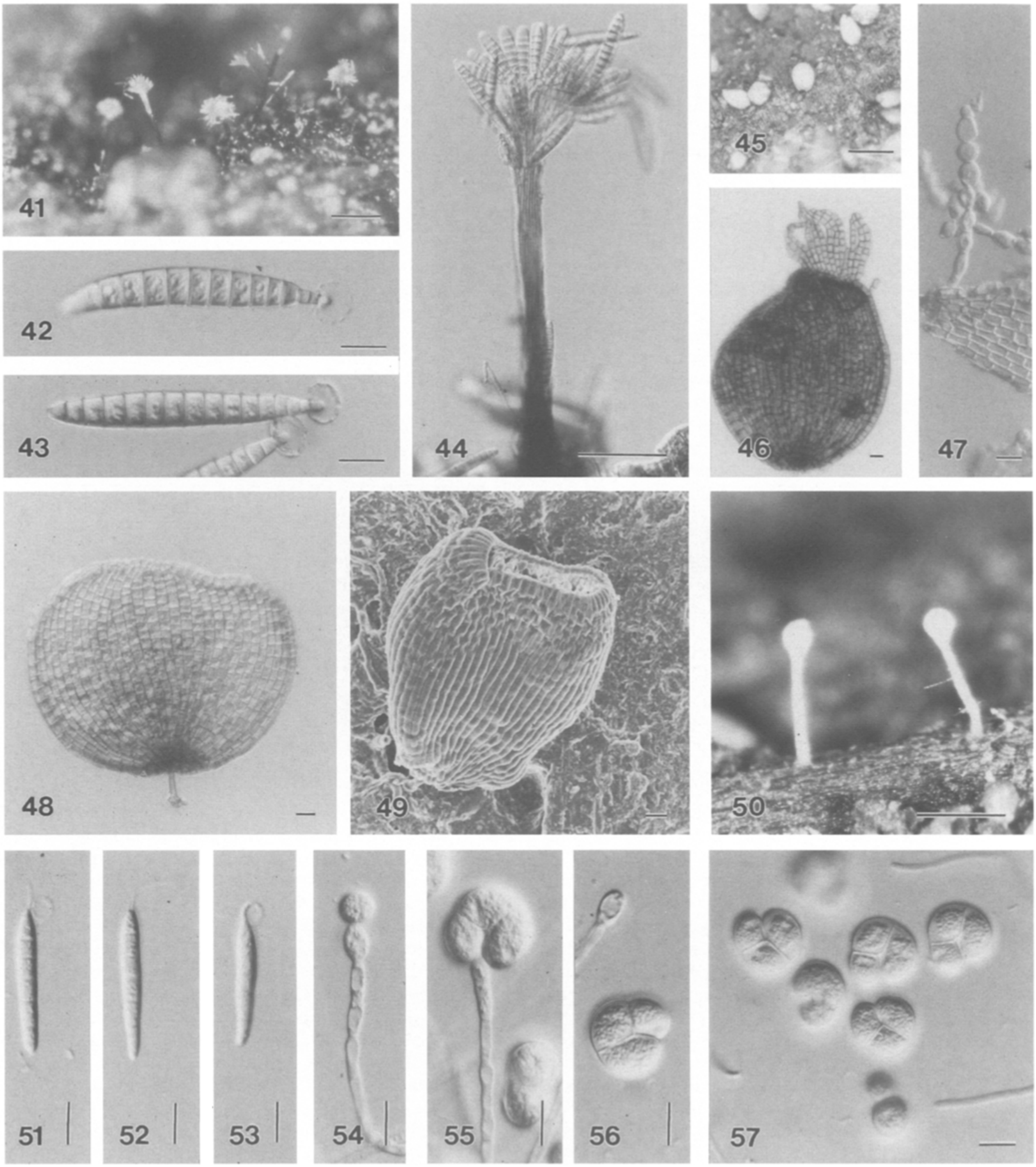
groups of freshwater hyphomycetes can be discerned as follows:

(1) The Ingoldian fungi (Figures 71–82) abound in fast-flowing tree-lined streams, babbling brooks, and well-aerated lakes, growing on submerged leaves and twigs, but are relatively more sparse on woody substrates [80,178,199]. They form conidia which are released in water and are readily trapped in foam [82,83]. They predominantly have two basic shapes of conidia: *branched* or *sigmoid*. In the great majority of these branched conidia (Figures 71–75), they are tetra-radiate, ie usually consist essentially of four long arms diverging from a common point. Examples of this spore type are found in genera such as *Alatospora*, *Actinospora*, *Articulospora*, *Campylospora*, *Clavariopsis*, *Jaculispora*, *Lemonniera*, *Tetrachaetum*, *Tetracladium*, *Tricladium* (Figures 67–69) and *Triscelophorus*. There are quite a number of branched conidia, however, that are not tetra-radiate, as in the genera *Dendrospora*, *Polycladium*, and *Varicosporium* (Figure 76). There exist also a great number of species that produce sigmoid conidia, ie long and worm-like, usually with a curvature in more than one plane. These sigmoid conidia (Figures 77–79) are seen in genera such as *Anguillospora*, *Flagellospora*, *Lunulospora* and *Mycocentrospora*. Besides these two basic shapes of conidia, other conidial shapes are occasionally found, eg variously coiled shrimp-like or flywheeled-shaped conidia (Figure 80) are represented by species of *Gyoerffyella*, and spherical or ovoid conidia (Figures 81–82) are seen in *Margaritispora*, *Dactyllela*, and *Dimorphospora*. Nevertheless, it is significant to note that nearly all the Ingoldian fungi have conidiophores and conidia that are hyaline and thin-walled. The Ingoldian fungi are extensively studied worldwide and for their monographic treatments, see [80,131,158].

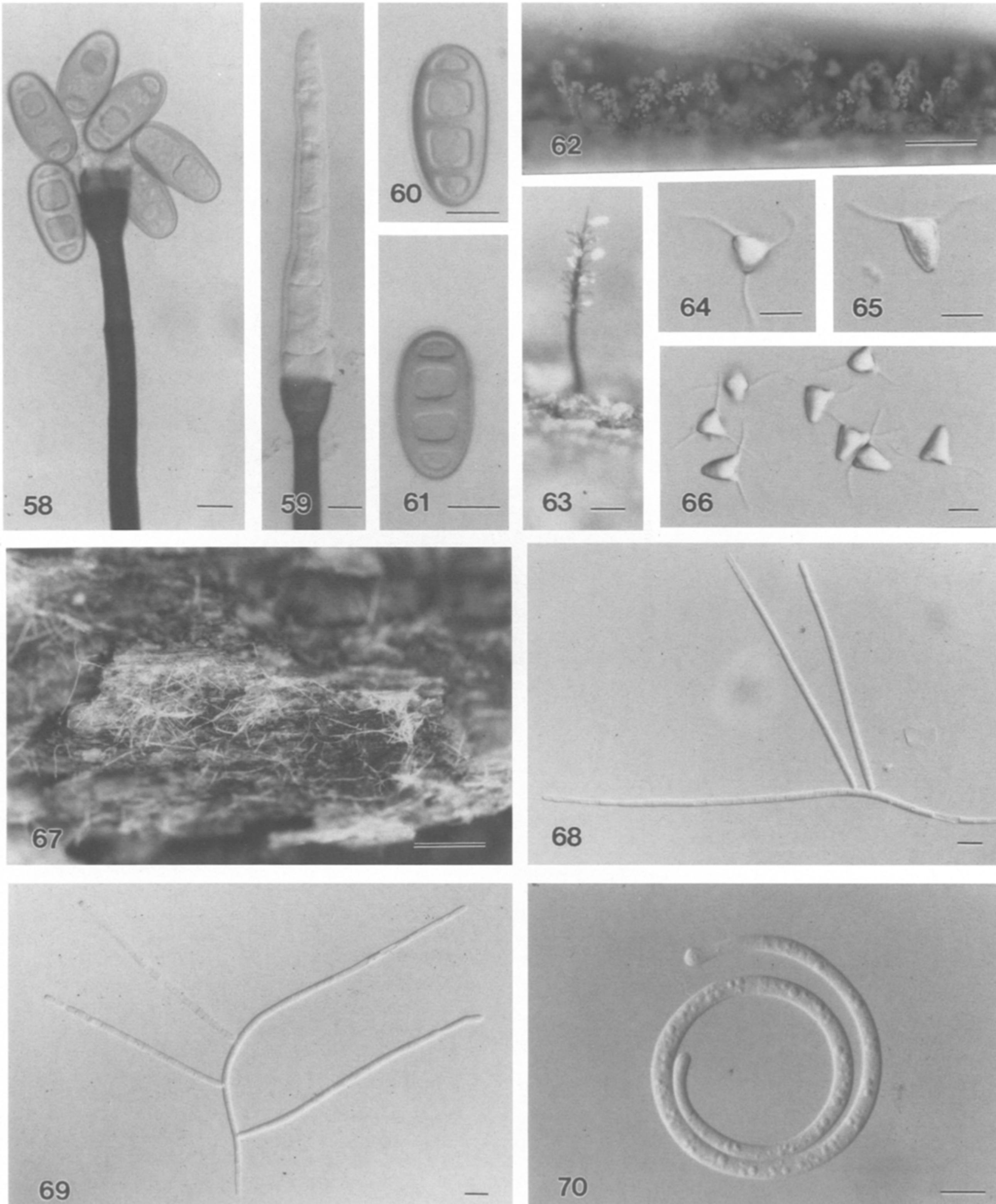
(2) The aero-aquatic hyphomycetes (Figures 83–86), termed by Beverwijk [18–21], are more usually found in stagnant ponds, ditches, or slow-running streams and are capable of vegetative growth on submerged leaves or woody substrates under semi-anaerobic conditions. Sporulation in this biological group is unique, which does not occur below water. In contrast to the Ingoldian fungi in which the whole cycle of conidium production, liberation and dispersal normally takes place below water, the aero-aquatics sporulate only when the substrate is exposed to air, when they form buoyant propagules capable of dispersal when the substrate is submerged again. The conidia, or forms of propagules, are mostly coloured. They are often tightly helicoid in more than one plane (Figures 85, 86), or equipped with a special flotation device in the form of an intricate hyphal system (Figures 45–49, 83–84). Examples of these aero-aquatic genera are *Arbuscula*, *Aegerita*, *Beverwykella*, *Cancellidium*, *Candelabrum*, *Clathrosphaerina*, *Clathrosporium*, *Cristulariella*, *Fusticeps*, *Helicodendron*, *Helicoon*, *Helicomyces* (Figure 70). *Mycoenterolobium*, *Nidulispora* and *Spirosphaera* [1,24,36,38,41,44,45,185,192].

(3) The terrestrial-aquatic hyphomycetes (Figures 87–90), termed by Ando [7], are represented by a number of conidial fungi isolated from rain drops associated with intact terrestrial plant parts, such as the leaf-surfaces [10] or rainwater draining from intact tree trunks [11]. A number of species are described from such isolations with establishments of many new genera such as *Alatosessilispora*, *Arborispora*, *Curucispora*, *Microstella*, *Ordus*, *Tricladiella*, and *Trifurcospora* [7–14]. A major characteristic of this group of hyphomycetes is that they produce staurosporous conidia similar in shape to those of the Ingoldian group, but lacking conspicuous conidiophores (ie micronematous). These conidia are mostly hyaline and thin-walled, however, some dematiaceous species were also isolated (eg *Ceratosporium cornutum* Matshushima, *Tetraploa aristata* Berk and Broome, and *Tripospermum infalcatum* Ando and Tubaki).

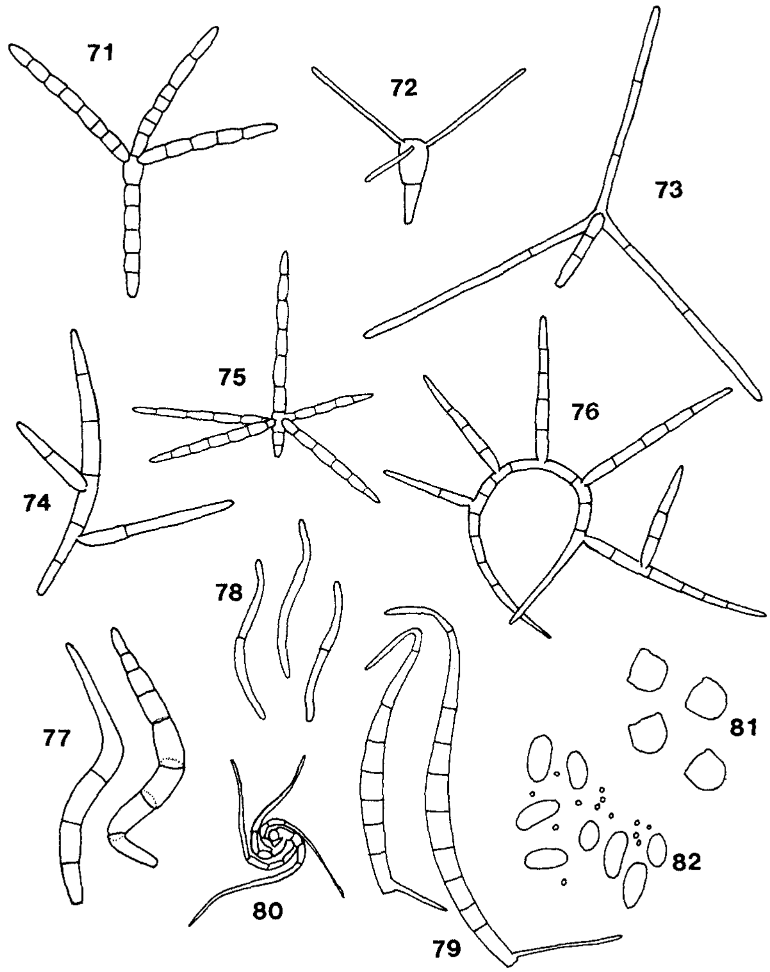
(4) The submerged-aquatic hyphomycetes (Figures 91–95), first addressed by Ingold [80], represent a heterogeneous assemblage of fungi growing on submerged decaying plant materials. Most of the species are found on wood litter blocked by rocks in fast-flowing streams or babbling brooks. These lignicolous, or to a lesser extent foliicolous, hyphomycetes are nearly all dematiaceous and produced relatively thick-walled conidiophores and/or conidia. The conidiophores are distinctly macronematous, frequently in the form of long stipes, however, they may be solitary or synnematous. The conidiogenous loci may be denticulate, cicatrized, tretic or phialidic. Although some species may sporulate under submerged conditions, a vast number sporulate when the substrates are no longer under water. Incubation of such woody substrates in moist chambers yields a great number of different species. Their conidia are capable of air dispersal or dispersed by some other mechanisms. These hyphomycetes may be regarded as 'facultative-aquatic', as compared to the aquatic Ingoldian group. The conidia of submerged-aquatic hyphomycetes are basically regular in shape, ie ovoid (Figures 58–61, 91), cylindric (Figures 51–53, 92), obclavate (Figures 41–44, 93), pyriform (Figure 94), or fusiform (Figure 95). However, branched conidia are not uncommon and may also be found in foam samples (eg conidia of *Casaresia sphagnorum*, *Pleiochaeta setosa* and *Tetraploa aristata*). Systematic studies of these submerged-aquatic hyphomycetes began about 10 years ago, mostly in Malaysia [88–109,141,142,147], and recently by Goh and Hyde with samples from Australia, Philippines, and South Africa [40–43,64]. Representative genera are *Bactrodesmium* (Figures 41–44), *Brachydesmiella*, *Brachysporiella*, *Camposporidium*, *Canalisporium*, *Cryptophiale*, *Cryptophialoidea*, *Dactylaria*, *Dendryphiosphaera*, *Dictyochaeta*, *Exserticlava* (Figures 58–61), *Kionochaeta*, *Monotosporiella*, *Nawawia* (Figures 62–66), *Phaeoisaria*, *Spadicoides*, *Sporidesmiella*, *Sporidesmium*, *Sporoschisma*, *Sporoschismopsis*, *Trichocladium* and *Xylomyces*. A few taxa, ie *Diplocladiella appendiculata* Nawawi [136], *D. scalaroides* Arnaud [136], *D. tricladioides* Nawawi [133], *Setosynnema isthmosporum* Shaw and Sutton [171], and *Triscelosporium verrucosum* Nawawi



Figures 41–57 Light micrographs of various freshwater hyphomycetes. (41–45) *Bactrodesmium longisporum*. (41) Habit on submerged wood. (42, 43) Conidia. Note the mucilaginous pads at the apex. (44) Synnema bearing conidia. (45–49) *Cancellidium applanatum*. (45) Habit on submerged wood. (46, 48) Air-trapping propagules. (47) Monilioid cells of the propagules. (49) SEM of propagule. Note the monilioid cells inside. (50–53) *Candelosynnema ranunculosporum*. (50) Synemmata. (51–53) Conidia with appendages. (54–57) *Delortia palmicola*. (54, 55) Conidiophores with developing conidia. (56, 57) Mature conidia surrounded by mucilage. Bars: 41 = 100 μm; 44 = 50 μm; 45 = 200 μm; 46 = 10 μm; 42, 43, 46–49, 51–57 = 10 μm; 50 = 500 μm.



Figures 58–70 Light micrographs of various freshwater hyphomycetes. (58–61) *Exserticlava vasiformis*. (58) Conidiophore and conidia. (59) Conidiophore showing the characteristic extension of the hyaline inner wall layer into a multiseptate, subulate structure. (60, 61) Conidia. (62–66) *Nawawia dendroides*. (62) Habit. (63) Synnema bearing conidia. (64–66) Conidia. (67–69) *Tricladium* sp. (67) Habit. (68, 69) Branched conidia. (70) Conidium of *Helicomyces* sp. Bars: 62, 67 = 1 mm; 63 = 100 μm; 58–61, 64–66, 68–70 = 10 μm.



Figures 71–82 Conidial forms of some Ingoldian fungi (drawn at various scales). (71) *Articulospora grandis*. (72) *Clavariopsis aquatica*. (73) *Lemonniera aquatica*. (74) *Tricladium splendens*. (75) *Triscelophorus magnificus*. (76) *Varicosporium helicosporum*. (77) *Anguillospora crassa*. (78) *Flagellospora penicillioides*. (79) *Mycocentrospora acerina*. (80) *Gyoerffyella speciosa*. (81) *Margaritispora aquatica*. (82) *Dimorphospora foliicola*.

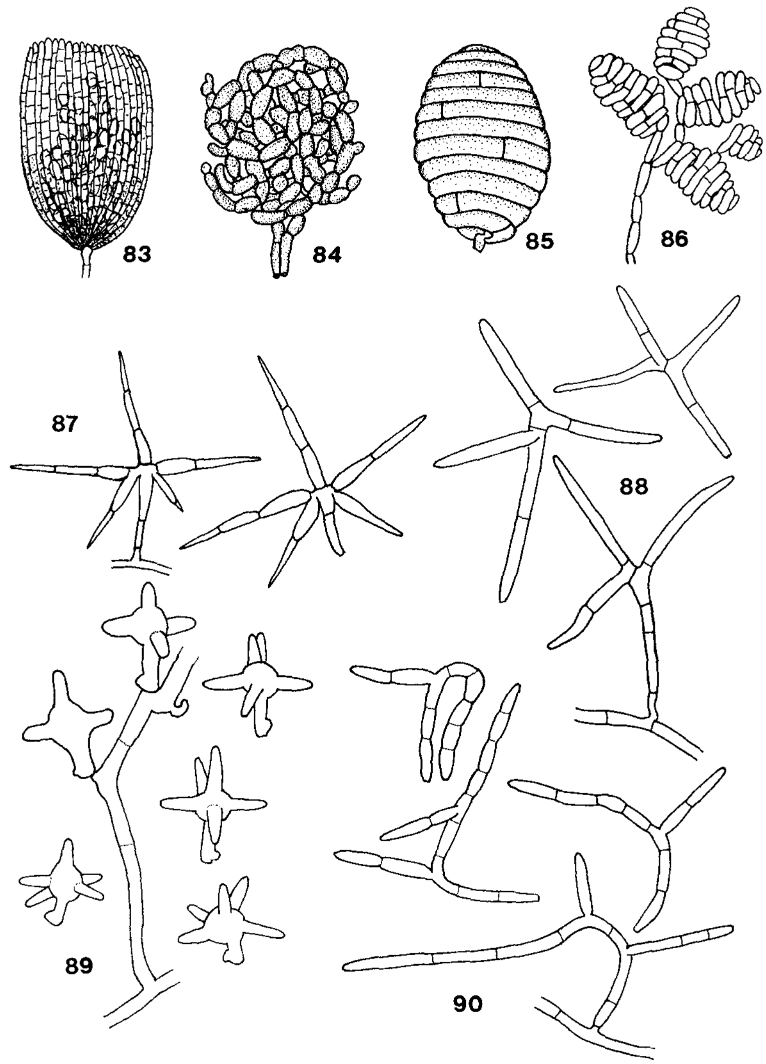
and Kuthubutheen [138], have been treated as examples of aero-aquatic species, but should be regarded as submerged-aquatic (facultative-aquatic) hyphomycetes. This is because the conidia of these species, though formed when the substrate is no longer submerged, are either filiform or branched and do not possess a flotation device.

Although the vast majority of conidia seen in foam samples almost certainly have an aquatic or stream-side origin [80], some species must come from the air spora. Indeed, it is not uncommon to see occasional conidia of such well-known terrestrial hyphomycetes as *Alternaria*, *Beltrania*, *Cladosporium*, *Drechslera*, *Epicoccum* or to encounter teliospores of smuts and uredospores of rusts.

Certain hyphomycetes have been found in aquatic habitats other than streams, lakes or ponds. Fungal species such as *Geotrichum candidum*, *Fusarium aquaeductuum*, *Aspergillus* spp and *Penicillium* spp have been recorded worldwide in water treatment plants. These records, however, are referring to those species existing in fungal films of trickling or percolating filters, in sewage, and in activated sludge. For more discussion of hyphomycetes in such unusual aquatic environments, see [25,85,182].

Anamorph-teleomorph connections of freshwater hyphomycetes

The majority of freshwater hyphomycetes are known only from their anamorphic states. Most of the known teleomorphs, however, have been shown to be associated with ascomycetes [2,190,191]. However, studies showed that many of these connections are heterogeneous, ie the ascomycetous teleomorphs include taxa of diverse relationships [191,194,195]. For example, *Flagellospora penicillioides*, which produces sigmoid conidia, and *Heliscus lugduenensis*, which produces branched conidia, both have teleomorphic connections with *Nectria* spp (Pyrenomycetes). *Anguillospora rosea* and *A. longissima* have their teleomorphic connection with *Orbilia* sp (Discomycetes) and *Massarina* sp (Loculoascomycetes), respectively. Studies of freshwater hyphomycetes in the tropics [196,197,198] demonstrated that *Tricladium indicum* Sati and Tiwari [169], isolated from a South African river, has a teleomorphic connection with the ascomycete (Leotiales) *Cudoniella indica* Webster, Eicker and Spooner [196]. These discoveries of the connections between freshwater hyphomycetes and ascomycetes or the basidiomycetes provide further evidence of the artificial nature in the taxonomy of these anamorphic genera [190,191,198].



Figures 83–90 (83–86) Propagules of some aero-aquatic fungi (drawn at various scales). (83) *Cancellidium applanatum*. (84) *Spirosphaera floriformis*. (85) *Helicoon gigantisporum*. (86) *Helicodendron tubulosum*. (87–80) Micronematous conidiophores and conidial forms of some terrestrial-aquatic hyphomycetes (drawn at various scales). (87) *Arborispora palma*. *(88) Curucispora ombrogena*. (89) *Microstella pluvioriens*. (90) *Tricladiella pluvialis*.

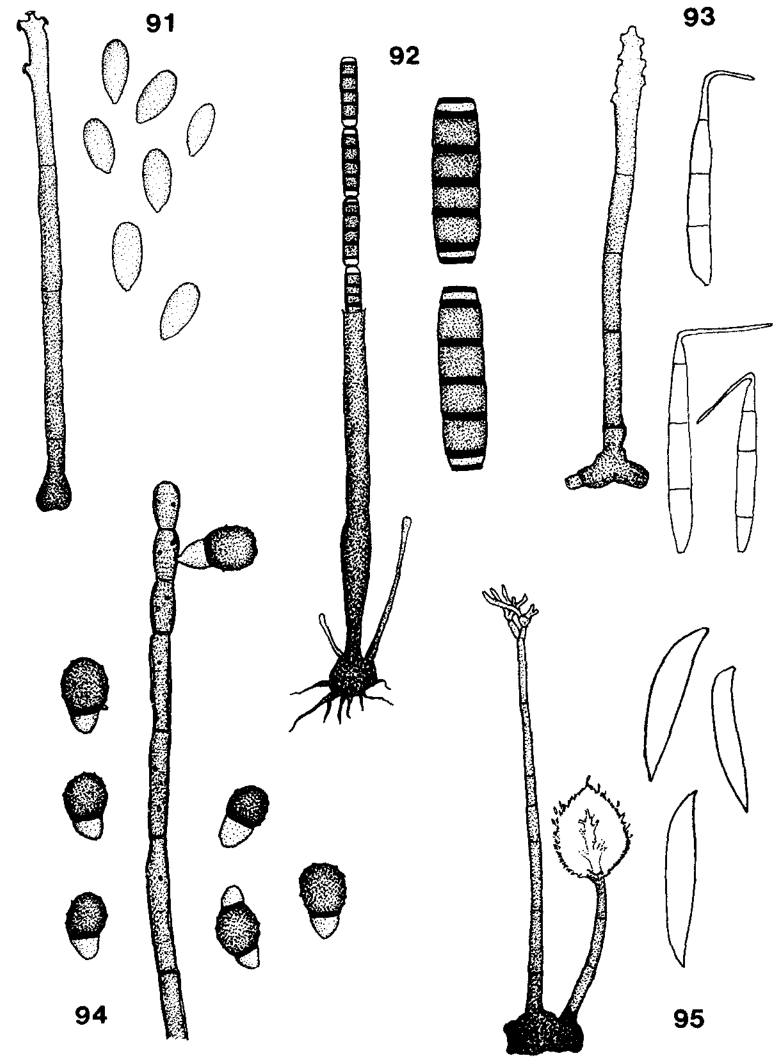
Freshwater basidiomycetes, coelomycetes and zygomycetes

In addition to a great variety of freshwater hyphomycetes, there are also many other conidial fungi that are saprotrophs or parasites on submerged parts of many reed-swamp plants (eg *Carex*, *Cladium*, *Eleocharis*, *Juncus*, *Phragmites*, *Sagittaria*, *Schoenoplectus*, and *Typha*). These hosts also provide favourable substrates for many ascomycetes and coelomycetes.

Foam surveys are extremely useful for estimation of the mycoflora of the freshwater communities at any one time, yielding longer lists than any other method known to date. Despite the rich specific variety of freshwater hyphomycetes, there do exist some other anamorphic propagules of other fungal groups, eg some basidiomycetes, coelomycetes, a few zygomycetes.

Species such as *Crucella subtilis* Marvanová and Suberkropp, *Ingoldiella hamata* Shaw, *Naiadella fluitans* Marvanová and Bandoni, *Taeniospora gracilis* Marvanová and Stalpers and *T. gracilis* var *gracilis* Marvanová and *T. gracilis* var *enecta* Marvanová have been proved to be water-borne basidiomycetes. Evidence for this is the presence of clamp connections on mycelial or conidial septa or on conidial germ tubes indicating dikaryotic propagules. Their holomorphic connections have been established in culture, and the teleomorphs are *Camptobasidium hydrophilum* (Atractiellales), *Sistotrema hamatum* (Corticiaceae), *Fibulomyces crucelliger* (Corticiaceae), *Leptosporomyces galzinii* (Bourd) Jülich (Corticiaceae), and *Fibulomyces* sp (Corticiaceae), respectively [114,115,118,132,154–156,170]. With the aid of electron microscopy and the nuclear stain ammoniacal Congo Red, two freshwater fungi have been shown to have binucleate hyphal cells with doliphore septa [134]. The basidiomycetous nature of *Varicosporium splendens* Nawawi [117] and *Tricladium malaysianum* Nawawi [121] have been confirmed with erection of new taxa, namely *Dendrosporomyces splendens* (Nawawi) Nawawi [154] and *Tricladiomyces malaysianum* (Nawawi) Nawawi [134], respectively.

Coelomycetes found in freshwater environments are not



Figures 91–95 Conidiophores and conidia of some submerged-aquatic fungi (drawn at various scales). (91) *Dictyochaeta subfuscospora*. (92) *Sporoschisma saccardoi*. (93) *Subulispora malaysiana*. (94) *Spadicoides cordanoides*. (95) *Kionochaeta nanophora*.

well-documented. These fungi occur on stream-side plants such as *Eleocharis*, *Phragmitis* and *Villarsia*, or on submerged wood litter [23,27–29,51,159,184]. Examples of these fungi are *Ascochyta arundis*. Fairm and F Lam, *Chaetospermum carneum* Tassi, *C. chaetosporium* Smith and Ramsb, *Clohesyomyces aquaticus* KD Hyde, *Hendersonia phragmitis* Desm, *H. scerpicola* Cooke and Harkn, *Melanconium sphaerospermum* (Pers) Link, *Robillarda phragmitis* Cunnell, *Septoria limnanthemi* Thüm, and *Tiarospora paludosa* (Sacc and Fiori) Höhn.

The worldwide occurrence of freshwater zygomycetes has been poorly documented. The presence of water-borne species is based on the detection of conidia along with those of aquatic hyphomycetes in foam samples. A few zygomycetes, however, from freshwater habitats have been identified, mostly belonging to the genus *Erynia* (Entomophthoraceae), which are parasitic on aquatic insects [30–31]. *Erynia conica* (Nowakowski) Remauadière and Keller, *E. plecopteri* Descals and Webster, and *E. rhizospora* Thaxter are the three species frequently encountered in foam samples [30,31,181,184]. From available records, *Entomophthora thaxteri* Brumpt (Entomophthoraceae) and *Acaulopage tetraceros* Drechsler (Zoopagaceae) have been reported to parasitise aquatic insects (Diptera) and amoebae, respectively [80]. Undoubtedly, more studies should be carried out to establish the diversity and ecology of this group of fungi in freshwater environments.

Adaptations of freshwater fungi

Fungi, which exist as a unique kingdom amongst all living things in the universe, are cosmopolitan and fascinatingly occupy various ecological niches. A general discussion of fungal adaptations to freshwater existence is given by Thomas [184]. On a continental scale, freshwater environments are very heterogeneous. These include water falls, lakes, dams, ditches, swamps, ponds, rivers, streams and creeks. Most fungi found in freshwater, however, must be able to cope with drought. There are different ways in which water-borne fungi survive during droughts, eg the zoosporic fungi form encysted spores in muds [37], the endophytes survive within substrata such as logs or in plant roots at banks, or the anamorphic fungi form thick-walled sexual propagules or chlamydosporic stages which may resist low water activity. Such fungi would become active again in the aquatic environment once conditions become favourable.

There are more studies on the ecology and mechanisms of environmental adaptation in freshwater hyphomycetes than those of other water-borne fungi [15,82,83,157,158, 165–167,177,178–180,188,189,195,199,200]. Many freshwater hyphomycetes are successful colonizers of submerged decaying leaves of a variety of deciduous dicotyledonous trees [67–70,80,189]. In the tropics, eg South Africa [46], these hyphomycetes occur on dead leaves of a variety of plants, namely, trees (eg *Celtis*, *Rhus*, *Eucalyptus*), herbaceous plants (eg *Plectranthus*), a conifer (ie *Podocarpus*), a fern (*Polystichum*), and decaying fruits of *Acacia*. It seems that these hyphomycetes seldom occur on herbaceous leaves of monocotyledons such as grasses (Poaceae), sedges (Cyperaceae), and rushes (Juncaceae). For further in-depth discussions of substratum preferences of freshwater hyphomycetes, see [160,180,181].

Freshwater hyphomycetes

The Ingoldian hyphomycetes: The Ingoldian hyphomycetes are abundant in babbling brooks and fast-flowing streams. There are several factors which may contribute to the success of these aquatic hyphomycetes [15,80,165,195], including the influence of conidial shape, mucilage secretion, and appressorium formation on attachment to substrata, rapid colonization and sporulation once substrata become available, production of a wide range of extracellular enzymes, ability to grow and sporulate at temperatures down to 0°C and an effective method of transmission between unconnected water courses or the ability to withstand drought. The unique feature of their conidial forms, invariably two- to several-armed, or sigmoid, has been shown to aid their dispersal [82]. Air bubbles generated in rapids can trap the conidia and bring them to the surface [81]. Trapping efficiency is correlatable with conidial shapes and geometry. For example, tetra-radiate conidia are trapped about three times as readily as sigmoid conidia and about 30 times as effectively as the ovoid forms.

The aero-aquatic hyphomycetes: In contrast, the aero-aquatic hyphomycetes are normally found on decaying plant materials in slow-flowing streams, stagnant ponds, or in shallow water-filled ditches subject to intermittent flooding, where the submerged substrata rest hardly a few centimetres below the water surface. This environmental condition provides excellent aeration at the substratum–water interface, inducing these hyphomycetes to sporulate vigorously when exposed to air. The propagules of these aero-aquatic hyphomycetes (eg *Beverwykella*, *Cancellidium*, *Clathrosphaerina*, *Helicoon*), represent an adaptation to their aquatic environments, as they possess a special flotation device, usually air-trapping, enabling these fungi to be dispersed from one static water habitat to another. For further ecological discussion of the aero-aquatic hyphomycetes, see [36,182,195].

The terrestrial-aquatic hyphomycetes: The term 'terrestrial-aquatic hyphomycetes' includes those species isolated from rain drops associated with intact terrestrial plant parts and producing staurosporous conidia similar in shape to the Ingoldian group [7]. One distinct characteristic of the group is that they lack conspicuous conidiophores (ie micronematous), and this may represent a means of adaptation to such terrestrial existence on plant surfaces. They need to produce their conidia quickly because their water sources, eg morning dew, mist and rain, are of unpredictable frequency and duration. The second characteristic of these hyphomycetes is their staurosporous shape of conidia, which is adapted so as to hold water around the conidium for as long as possible, thereby increasing the possibility of germination. These characteristics function to make the terrestrial-aquatic hyphomycetes better adapted to their unique environment [7].

The submerged-aquatic hyphomycetes: The submerged-aquatic hyphomycetes are a number of dematiaceous hyphomycetes growing as saprotrophs on submerged plant parts, especially on woody stems and branches, producing conidia from distinct conidiophores when the woody substrate is still underwater or when it is no longer submerged. The conidia of these hyphomycetes, however, differ from those aero-aquatics in lacking distinctive flotation devices and are capable of water dispersal and/or air-dispersal. This biological group of freshwater hyphomycetes is rather heterogeneous and they have been called the 'lignicolous terrestrial-aquatic hyphomycetes' [39], or the 'facultative-aquatics', as addressed by [80].

A number of common hyphomycete genera from submerged litter in tropical freshwater streams is listed by [92]. In fact, most of these fungi belong to the submerged aquatics. More of these lignicolous submerged aquatics from Australia have been reported [40–43]. Amongst these hyphomycetes, many possess long mononematous stipitate conidiophores, which stand erect from the submerged substrata and bear masses of conidia at the apices. Examples of such hyphomycetes are *Acrogenospora*, *Cryptophiale*, *Dictyochaeta*, *Kionochaeta*, *Monotosporiella*, *Pleurophragmium*, *Spadicoides* and *Thysanophora*. Others produce erect synnemata, such as *Bactrodesmium longisporum* Ellis (Figures 41, 44), *Candelosynnema ranunculosporum* KD Hyde & Seifert (Figures 50–53) *Didymostilbe*, *Nawawia dendroidea* KD Hyde, Goh and Steinke (Figures 62–66), and *Phaeoisaria clematidis* (Fuckel) Hughes. Perhaps these erect conidiophores are conducive to spore production and dispersal in the aquatic environment, or when the wood is exposed or dries out. In a discussion of *Setosynnema isthmosporum* [171], a synnematous hyphomycete from Papua New Guinea and Australia, it was observed that the length of the synnemata of the fungus growing on substrates in water in Petri dishes lengthened accordingly to water level in order to sporulate above the water surface. However, it is not known whether this occurs in the field, but presumably it would be quite possible for conidiophores, either mononematous or synnematous, produced on wood or on leaves stranded in shallow water near the bands of streams, or on sandbanks or on other debris, to adjust their length according to the water depth in order to sporulate above the surface.

Some of these lignicolous submerged aquatics, however, produce conidia with modified appendages, setulae, or arms and are functionally comparable to those Ingoldian hyphomycetes in the aquatic habitats. Examples for these hyphomycetes are *Dictyochaeta*, *Nawawia* (Figures 64–66), and *Obeliospora* which produce setulate conidia; *Iyengarina* and *Sporidesmiella cornuta* Kuthubutheen and Nawawi which produce conidia with arms; *Dactylaria tunicata* Goh and KD Hyde, and *Delortia palmicola* Pat (Figures 54–57), which produce conidia surrounded by a hyaline mucilaginous sheath. The occurrence of these freshwater hyphomycetes with these specialized conidial forms may be adaptations to local dispersion in the tropical rainforest habitat with its constant elevated relative humidity and persistent films of water on surfaces of the submerged substrata. For thorough discussion of aquatic hyphomycetes as successful colonizer on wood, see [164,174,178,199].

Notes on Beltrania rhombica

It is interesting that *Beltrania rhombica* Penz, normally regarded as a 'terrestrial' hyphomycete, is commonly encountered in foam samples in the tropics [60,130,131,180,183,184]. It is highly possible that this conceptually 'non-aquatic' hyphomycete can adapt to a submerged aquatic existence. Perhaps this 'terrestrial' fungus has a stream-side origin [80] in which its conidia are washed into the stream after heavy rain when water rises above parts of the bank where it is normally not submerged. Tan and Kok [183] speculated that the abundance of *B. rhombica* in the foam could not have been attributed solely to a terrestrial source because it was consistently the most or second-most abundant species of foam mycoflora observed during both dry and wet months through the period of their studies in Singapore. In India, incubation of submerged leaves of various plants yielded conidia of *B. rhombica* which showed high percentage of leaf colonization [180]. From these observations, *B. rhombica* may indeed be a 'resident' species of submerged stream litter in the tropics, and the abundance of its conidia in foam need not always imply a terrestrial origin [183].

Freshwater ascomycetes

Characteristics of freshwater fungi that are advantageous to their dispersal and subsequent attachment of new substrata, will either have been acquired from terrestrial lineages or morphologies that are preadaptive to the aquatic 'life style' or will have specifically evolved in the aquatic environment. In most freshwater ascomycetes the asci are provided with ejection mechanisms as in many terrestrial fungi (Table 2). The asci are either bitunicate with fissitunicate dehiscence (eg *Massarina* spp, *Ascagilis* spp (Figure 23)) or unitunicate with relatively massive (eg *Annulatascus* spp (Figures 6, 8, 11, 12)) or smaller (eg *Ophioceras* spp (Figures 37, 38), *Bertia* spp (Figures 16, 17)) apical rings. These fungi actively eject their ascospores in air [57], but it has not been shown conclusively that freshwater ascomycetes can eject their ascospores under water. In squash mounts the ascospores are often readily ejected, but this is hardly natural. In submerged culture, both asci and ascospores were discharged simultaneously in species of *Ophioceras* and *Pseudohalonectria* [175]. Hyde (unpublished) placed ascomata of *Pseudohalonectria* growing on a wood sliver under water in a Petri dish overnight. The following morning numerous ascospores were lying on the base of the dish around the sample, indicating that active dispersal does occur underwater. It appears that active spore ejection is an important dispersal strategy of ascomycetes in tropical freshwater streams. On the other hand, it may be that the freshwater ascomycetes have not become totally adapted to submerged conditions (or that substrates in streams are more likely to be exposed, or subjected to periods of desiccation, when ejection can occur).

In only a handful of freshwater species (eg *Halosarpheia aquatica* KD Hyde) do the asci deliquesce early to release the ascospores passively (Table 2). In only three genera, *Aniptodera* Shearer and Miller, *Halosarpheia* Kohlm and E Kohlm and *Nais* Kohlm are the spores passively released and form a cirrhus at the tip of the neck.

Floating is the next problem faced by the freshwater propagule. The lipid globules found in the ascospores of most freshwater ascomycetes (Figures 3, 21, 25), probably act as flotation devices as well as food reserves as in the marine ascomycetes.

The final obstacle faced by the propagule is entrapment and attachment and colonization of new substrates. The ascomycetes in tropical streams are mostly provided with appendaged ascospores or are sigmoid in shape. The appendages include typical to elaborate mucilaginous sheaths (ie *Massarina* spp, *Pleospora scirpicola*), polar pads (*Ascagilis bipolaris*), or uncoiling filamentous strands (*Annulatascus bipolaris*, *Halosarpheia aquatica*). An account of the various appendage types is given below. Appendaged spores do not appear to be so commonplace in temperate freshwater ascomycetes.

Five appendage types in freshwater ascomycetes are recognised (Table 3): 1) The release of a drop of mucilage (eg *Ophioceras* spp); 2) hamate or cap-like appendages which uncoil to form viscous threads (eg *Aniptodera* (Figures 3–5) and *Halosarpheia* spp). These separate from the spore and uncoil in water to form long viscous polar threads [48,50,172]. Besides mucilaginous sheaths, filamentous appendages appear to be most commonly found in ascospores of tropical freshwater ascomycetes; 3) mucilaginous sheaths (eg *A. velatispora* (Figures 9, 10), *Kirchsteiniothelia elaterascus* Shearer, *Fluviatispora reticulata* KD Hyde, *Massarina ingoldia* Shearer and KD Hyde), which may or may not have extensions; 4) pad-like attachment (eg *Ascagilis bipolaris* KD Hyde (Figures 21, 22), *Mamillisphaeria dimorphospora* KD Hyde *et al*); 5) irregular amorphous appendages without a fibrillar component (eg *Ceriospora caudaesuis* Ingold); and 6) adhesive spore wall (eg *Savoryella verrucosa* (Figures 28, 29)).

These appendage types are thought to be involved in dispersal and attachment of these freshwater propagules in a similar way to marine ascomycetes [58,59,61,62]. The mucilaginous drops at the ends of the spores of *Ophioceras* spp, probably attached the spores at one end, which then twist in the water current and lie parallel to the flow of water. These spores then stand a better chance of remaining attached as in the sigmoid hyphomycete spores [193]. The

Table 2 Ascus dehiscence and ascospore appendage types in the ten most common genera of tropical freshwater ascomycetes

Genus	Ascus dehiscence	Ascospore appendages
Aniptodera	Passive	Polar filaments
Annulatascus	Active	Sheath or various
Ascagilis	Active	Polar pads or sticky walls
Ceratosphaeria	Active	Wall ornamentations
Halosarpheia	Passive	Polar filaments
Kirschsteiniothelia	Active	Sticky walls
Mamillisphaeria	Active	Polar pads
Massarina	Active	Sheath/with modifications
Ophioceras	Active	Sigmoid
Pseudohalonectria	Active	None
Savoryella	Active	Sticky walls

Table 3 Spore adhesion types observed in tropical freshwater ascomycetes

Description	Species	Reference
1. Sticky mucilaginous sheaths	*Annulatascus velatispora* *Massarina* spp *Vaginatispora aquatica*	[49, 54, 63]
2. Polar pads	*Ascagilis bipolaris* *Mamillisphaeria dimorphaspora*	[48, 50, 66]
3. Polar filaments	*Annulatascus* spp *Aniptodera* spp *Halosarpheia* spp	[48, 50, 54] Wong, Hyde and Jones, pers. obs.
4. Adhesive spore wall	*Savoryella* spp	Ho and Hyde, pers. obs.
5. Other types or combinations of the above types	*Loramyces*	Hyde, pers. obs.

unravelling threads of *Aniptodera* and *Halosarpheia* probably serve to catch debris in the water, thus anchoring the spores to new substrates. The role of the sheath surrounding various propagules is probably two-fold. SEM micrographs illustrate that the sheaths are sticky and one function is likely to be adhesion [59]. A second function may be to hold the spore at the air water interface, perhaps allowing it to float on the surface and be dispersed in this way.

The sheath in *Massarina ingoldiana* initially envelops the ascospore, but once released in water it swells to form massive arms which appear to be highly effective in attachment. A similar massive sheath is found in *Pleospora scirpicola* (DC) Karsten [75]. In *Velatispora aquatica* KD Hyde an internal collar-like structure with an unknown function encircles the ascospore and is part of the larger sheath structure [56].

The pad-like mucilaginous appendages in *Ascagilis bipolaris* (Figures 21, 22) and *Mamillisphaeria dimorphospora* are probably sticky and function to adhere the ascospores in much the same ways as the marine species *Ceriosporopsis circumvestita* and *Ondiniella torquata* [84,87,168]. The amorphous coiled appendages at each end in *Ceriospora caudae-suis* [73] are persistent and do not appear to be the same type as those found in the genera *Aniptodera* and *Halosarpheia*. They probably, however, have the same function in trapping and sticking propagules to debris. Spore adhesion can be achieved with sticky spore walls, such as an adhesive coating or a slightly more elaborate verrucose wall. In *Savoryella verrucosa* the spore wall (Figures 28, 29) is highly verrucose. The ascospores of several other freshwater ascomycetes are provided with verrucose wall ornamentation and these probably serve to stick the spores to debris.

Active versus passive dispersal

Why do most marine unitunicate ascomycetes release their spores passively, while many tropical freshwater ascomycetes release their spores actively? Perhaps evolution has played a key role in this outcome, most marine fungi having evolved from ancestors of the *Microascales* (Spatafora, personal communication) and most *Annulatascus*-like species having evolved from other terrestrial ancestors.

Why is active spore release more common in freshwater ascomycetes? Assuming active spore release readily occurs under water then what advantage does it have over passive spore release, if any? One explanation may involve the boundary layer, which was also used to explain the attachment of sigmoid ascospores [193]. If spores are released passively they may never leave the boundary layer and become attached to the adjacent substrate. Ejected ascospores, on the other hand, may be expelled beyond the boundary layer and then dispersed in the turbulent current. The long neck found in *Ophioceras* species (Figure 36) might also achieve the same effect, but this may be fraught with inherent habitat problems (eg aquatic insects).

A simple explanation may also account for the predominance of freshwater species that actively release their spores. Streams and even rivers are subjected to periodic drying and it may be during these periods that spores are actively released. Alternatively, during heavy rains or typhoons, flash flooding may occur and it may be that during these spates the substrates are washed to the edges of the streams and exposed as the waters subside. Active spore dispersal may then occur in air.

Loculoascomycetes with fissitunicate dihiscence asci are also common in freshwater ecosystems. These asci also 'shoot' their ascospores, but whether they do this under submerged conditions or only in air is speculative. Notable spore release occurs in *Boerlagiomyces* species and *Kirchsteiniothelia elaterascus*. In *Boerlagiomyces* Butzin the bitunicate asci contain ascospores which are actively released in pairs, enveloped in a gelatinous sheath. In *K. elaterascus* the base of the ascus contains a coiled endoascus. Shearer [175] reported that it 'may be that when ascomata of *K. elaterascus* are submerged, entire, unfurled endoasci are discharged and become entangled with the substrate'. Asci of a similar type have also been recorded in an unrelated *Macroventuria*-like species from freshwater [175].

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