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The freshwater Ascomycetes

by

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With 7 figures and 3 tables

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Abstract: The freshwater Ascomycetes (exclusive of yeasts and lichenized forms) are a taxonomically diverse assemblage of species with representatives in the Plectomycetes, Discomycetes, Pyrenomycetes, and Loculoascomycetes. Over 200 species have been reported from freshwater habitats in association with aquatic and wetland macrophytes and/or as saprophytes of autochthonous and allochthonous plant debris. Various degrees of morphological adaptation to aquatic habitats are represented, ranging from adaptation of both teleomorph and anamorph, teleomorph alone, or anamorph alone. Numerous species show no obvious morphological adaptations at all. Definition, study techniques, systematics, geographical distribution, ecology, and evolution of the freshwater Ascomycetes are discussed.

Introduction

Although over 200 ascomycete taxa (exclusive of yeasts and lichenized forms) have been reported from freshwater habitats (Table 1), this group of fungi has received much less attention than the well-known marine Ascomycetes (Kohlmeyer and Kohlmeyer 1979, Kohlmeyer and Volkmann-Kohlmeyer 1991) and the freshwater Hyphomycetes (Webster and Descals 1981). Several reasons may account for this lack of attention. The freshwater Ascomycetes (FWA) comprise a taxonomically diverse group with representatives in a wide variety of families and orders (See Systematics Section). This diversity and the absence of taxonomic monographs and keys for the identification of FWA present a formidable barrier to the rapid identification of species for even the most skilled ascomycete systematist. Since many FWA also occur in terrestrial habitats or are in genera with terrestrial representatives, knowledge of terrestrial taxa is important to the successful identification of freshwater taxa. Additionally, in recent years, freshwater mycology has been dominated by the study of aquatic Hyphomycetes. Generally such studies have concerned fungi on decaying deciduous leaves from which ascomycete fructifications are largely absent (Shearer 1992). Thus FWA may have escaped detection in the majority of freshwater fungal studies. In spite of these problems, a considerable body of knowledge about FWA exists (Dudka 1985). This paper presents the current state of our knowledge of FWA with the intention of stimulating further research on their life histories, ecology, geographical distribution and systematics.

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Definition

Some of the same problems that occur in defining vascular plants as aquatic or terrestrial (Correll and Correll 1975) apply to fungi. These problems stem from the difficulty in determining what habitats should be considered aquatic and how far into the interface zones between aquatic and terrestrial habitats should be considered aquatic. The outline of types of aquatic habitats presented by Correll and Correll (1975) which is a modification of an earlier one by Mason (1957) has been used for the purpose of this review. Unlike vascular hydrophytes, however, presence in these aquatic habitats, alone, may not be appropriate to define an ascomycete as a "freshwater Ascomycete". Many Ascomycetes reported from freshwater habitats (Table 1) have also been reported from terrestrial habitats, and it is not known whether their occurrence in freshwater is simply fortuitous. Some Ascomycetes found in freshwater may be there not because they grow and reproduce while submerged, but because they enter water on allochthonous substrata. Constant recruitment of such species would be necessary to maintain their populations in water. Ascomycetes found by plating or incubation of substrata may be present in water as spores and grow and develop only when they are removed from water. Further, substrata on which FWA occur may be alternately submerged and exposed. Living and standing dead emergent macrophytes may be mostly submerged during wet times of the year and entirely exposed during dry periods. Submerged allochthonous substrata may be deposited on land during floods and remain there until they are again washed into water. In many emergent hydrophytes which serve as substrata for FWA, the upper plant parts are never submerged until well after the death of the plant. Woody debris in streams is often only partially submerged. Whether Ascomycetes should be considered aquatic when their substrata are submerged and terrestrial when they are not is problematic.

Park (1972) cogently discussed the problem of defining aquatic heterotrophic microorganisms and divided them into two categories: indwellers and immigrants. Indwellers are fully adapted to freshwater, i.e. they can maintain their biomass at a given site from year to year using substrata and nutrients at that site. A considerable number of FWA fall into this category, e.g., *Pseudohalonectria lignicola, Aniptodera rosea, Nais inornata.* Immigrants show varying degrees of adaptation to and ecological activity in aquatic habitats, but they all require immigration to maintain their presence in water. Immigrants may range from those that are very active ecologically to those that are not active at all. There may be a third category, amphibious species. Amphibious species may occur in the interfaces between land and water, e.g., edges of ponds, lakes, floodplains, backwaters of rivers or in ephemeral aquatic habitats such as temporary streams, seasonal ponds, and drainage ditches. Amphibious Ascomycetes would be adapted to fluctuating water levels. There have been so few ecological studies of FWA that it is impossible at this time to classify adequately most of the FWA as indwellers, immigrants or amphibians, let alone speculate on their ecological activity.

Definition by taxonomy is not useful because the FWA are a taxonomically diverse group with representatives in 15 different orders. For the purposes of this review,

Table I. Ascomycetes reported from submerged and/or partially submerged substrata.

Species	Substratum	Locality	Citation
PLECTOMYCETES			
Corynascella inquinata Udagawa & Süchi	sewage sludge	Japan	Udagawa and Süchi 1979
Emericellopsis terricola van Beyma	organic debris	Ireland	Park 1972
Eurotium sp.	beech wood	England	Eaton and Jones 1971b
Eurotiaceae gen. n. 4084	vegetation	USA, WI	Christiansen and Whittingham 1965
Pseudeurotium multisporum (Saito & Minoura) Stolk	beech wood	England	Eaton 1972
Pseudogymnoascus roseus Raillo (sub *Pseudogymnoascus vinaveus* Raillo)	organic debris	Ireland	Park 1972
Subbaromyces aquaticus Manoch. & Ramarao	maize baits	India	Manocharachary and Ramarao 1974
Talaromyces flavus (Klocher) Stolk & Samson var. *flavus*	leaf litter	USA, IL	Shearer and Crane 1986
	creek sand	Australia	Pitt 1979
DISCOMYCETES			
Apostemidium fiscellum (Karst.) Karst.	alder, willow and *Corylus* twigs	England, France, Sweden	Graddon 1965
	alder twigs	Hungary	Révây and Gönczöl 1990
Apostemidium fiscellum (Karst.) Karst. var. *submersum* Graddon	willow twigs	England, Germany, Sweden	Graddon 1965
Apostemidium sp.	birch twig	USA, RI	Lamore and Goos 1978
Aquadiscula appendiculata Shearer & Crane	*Acer rubrum* L. leaves	USA, IL	Shearer and Crane 1985, 1986
Belonopsis excelsior (Karst.) Rehm	*Phragmites*	Finland	Corner 1935 (not seen, cited in Nannfeldt 1985)
	Phragmites	England	Ingold 1954, 1955
Belonopsis hydrophila (Karst.) Nannf. [sub *Mollisia arundinaceae* (DC.) Phill.]	*Phragmites australis* (Cav.) Trin. ex Steud. stalks	USSR	Dudka 1963
	Phragmites australis leaves	England	Apinis et al. 1972a
	Phragmites	Czechoslovakia, Denmark, England, Finland, France, Germany, Poland Scotland, Sweden Switzerland	Nannfeldt 1985
Belonopsis mediella (Karst.) Aebi	*Phragmites*, *Schoenoplectus lacustris* L.	England, Finland, France, Germany, Ireland, Sweden, Switzerland	Nannfeldt 1985
Belonopsis retincola (Rbh.) LeGal. & Mang.	*Phragmites*, *Carex*, *Typha*	England, Finland, France, Germany Ireland, Sweden, Switzerland	Nannfeldt 1985
Bisporella citrina (Batsch:Fr.) Korf & Carpenter	wood	USA, IL	Shearer and Crane 1986
Brunnipila calycioides (Rehm) Baral	*Eriophorum vaginatum* L. *Juncus filiformis* L.	Austria	Magnes and Hafellner 1991
Cistella graminicola (Raitv.) Raitv.	*Carex rostrata* Stokes *Equisetum fluviatile* L. em. Ehrh.	Austria	Magnes and Hafellner 1991
Coleosperma lacustre Ingold	*Schoenoplectus lacustris* stalks	England	Ingold 1954
Coronellaria caricinella (Karst.) Karst.	*Carex nigra* (L.) Reichard, *Carex echinata* Murr.	Austria	Magnes and Hafellner 1991

Crocicreas megalosporum (Rea.) Carpent. var. *megalosporum* Carpent.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Cudoniella clavus (Alb. & Schw.:Fr.) Dennis	ash, alder, oak twigs	England	Willoughby and Archer 1973
Dasyscyphus controversus (Cooke) Rehm	*Phragmites australis* stems	England	Taligoola et al. 1972
	Phragmites australis stems	England	Apinis et al. 1972a
	leaves, rush stems, twigs	Germany	Eckel and Hirsch 1979
Dasyscyphus nudipes (Fuckel) Sacc.	*Phragmites australis* stems	England	Taligoola et al. 1972
Dasyscyphus c.f. *virgineus* (Batsch) S. F. Gray	wood	USA, RI	Lamore and Goos 1978
Diplonaevia emergens (Karst.) Hein	*Juncus filiformis* *Eriophorum angustifolium* Honck.	Austria	Magnes and Hafellner 1991
Diplonaevia seriata (Libert) Hein	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Gorgoniceps boltonii *(Phill.)* Dennis (sub *Pocillum boltonii* Phill.)	*Equisetum fluviatile* stems	England	Ingold 1954
	Equisetum fluviatile	Austria	Magnes and Hafellner 1991
Graddonia coracina Dennis	wood	England	Dennis 1978, Webster pers. comm.
Helotium citrinulum Karst.	*Phragmites australis* stems	England	Taligoola et al. 1972
	Phragmites australis leaves	England	Apinis et al. 1972a
	wood	USSR	Dudka 1963
Helotium sp.	*Phragmites australis* stems	England	Taligoola et al. 1972
Hyalinia sp	maple twig	USA, RI	Lamore and Goos 1978
Hyaloscypha lignicola Abdullah & Webster	twigs	England	Abdullah and Webster 1983
Hyaloscypha zalewskii Descals & Webster	catkins of *Alnus*, spine of *Castanea sativa* Miller	England	Descals and Webster 1976
Hyalotricha sp.	twigs	USA, RI	Lamore and Goos 1978
Hydrocina chaetocladia Scheuer	oak twigs	England	Webster et al. 1990
	alder twigs	England	Shearer and Webster 1991
Hymenoscyphus africanus Descals, Fisher & Webster	alder twigs	England	Descals et al. 1984
Hymenoscyphus equisetinus (Velenovsky) Dennis	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Hymenoscyphus foliicola Abdullah, Descals & Webster	*Acer pseudoplatanus* L. twigs	England	Abdullah et al. 1981
	alder twigs	Hungary	Révay and Gönczöl 1990
Hymenoscyphus malawiensis Fisher & Spooner	plant debris	Malawi	Fisher & Spooner 1987
Hymenoscyphus paradoxus Fisher and Webster	willow twigs	Switzerland	Fisher and Webster 1983
Hymenoscyphus phyllophilus (Desm.) O. Kuntze	skeletal leaves	USSR	Dudka 1963
Hymenoscyphus splendens Abdullah, Descals & Webster	beech cupules	England	Abdullah et al. 1981

Hymenoscyphus tetracladius Abdullah, Descals & Webster	beech and willow leaves	England	Abdullah et al. 1981
Hymenoscyphus varicosporoides Tubaki	twigs	Japan	Tubaki 1966
Hymenoscyphus sp.	alder twigs	Hungary	Réváy and Gönczöl 1990
Hypoderma alpinum Spooner	*Carex nigra*	Austria	Magnes and Hafellner 1991
Hysteronaevia advena (Karst.) Nannf.	*Eriophorum angustifolium*	Austria	Magnes and Hafellner 1991
Hysteronaevia olivacea (Mout.) Nannf.	*Eriphorum vaginatum*, *Carex rostrata*, *C. paupercula* Michx. *subsp. irrigua* (Wahl.) A. & D. Löve, *C. nigra*, *Juncus filiforme*	Austria	Magnes and Hafellner 1991
Hysteropeziza pusilla Hein & Scheuer	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Hysteropezizella diminuens (Karst.) Nannf.	*Carex rostrata* *C. paupercula* Michx. subsp. *irrigua* (Wahl.) A. & D. Löve	Austria	Magnes and Hafellner 1991
Hysteropezizella fuscella (Karst.) Nannf.	*Carex nigra*, *C. rostrata*	Austria	Magnes and Hafellner 1991
Hysteropezizella phragmitina (Karst. & Starb.) Nannf.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Lambertella tubulosa Abdullah & Webster	*Acer pseudoplatanus* twig	England	Abdullah and Webster 1981
Lachnum imbecille Karst.	*Eriophorum angustifolium* Honck.	Austria	Magnes and Hafellner 1991
Loramyces juncicola Weston	*Juncus*	USA, MA	Weston 1929
	dead stalks of *Scirpus*, *Eleocharis*,	England	Ingold 1955
	Equisetum, *Juncus*	USA, RI	Digby and Goos 1987
Loramyces macrospora Ingold & Chapman	internodes of *Equisetum fluviatile* L.	England	Ingold and Chapman 1952
Miladina lechithina (Cooke) Svrcek	bark of *Crategus*, *Alnus* wood	England	Descals and Webster 1978
Mitrula alba W.G.Sm.	leaves	England	Cannon et al. 1985
Mitrula paludosa Fr.	leaves, wood	England	Dennis 1978
Mollisia arundinacea (D.C.) Phill.	*Phragmites australis* leaves	England	Apinis et al. 1972a
Mollisia cinerea (Batsch) Karst.	wood	USSR	Dudka 1963
Mollisia cinerea (Batsch:Fr.) Karst. var. *minutella* Sacc. [sub *Mollisia minutella* (Sacc.) Rehm]	*Typha latifolia* L.	USSR	Dudka 1963
Mollisia gigantea Fisher & Webster	*Picea* twigs	Finland	Fisher and Webster 1983
Mollisia melaleuca (Fr.: Fr.) Sacc.	wood	USSR	Dudka 1963
Mollisia uda (Pers.:Fr.) Gill.	wood	England	Shearer and Webster unpublished
Mollisia sp.	twigs	England	Webster 1961
Mollisia sp.	skeletonized oak leaves	England	Webster and Descals 1979
Mollisia spp.	oak, ash, alder twigs	England	Willoughby and Archer 1973
Mollisia spp. 1, 2, and 3	twigs	USA, RI	Lamore and Goos 1978

Mollisia sp.	alder, ash, beech and oak twigs	Hungary	Réváy and Gönczöl 1990
Nimbomollisia eriophori (Opiz) Nannf.	*Carex rostrata*, *Eriophorum vaginatum*, *Juncus filiformis*	Austria	Magnes and Hafellner 1991
Nimbomollisia macrospora (Karst.) Nannf.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Nimbomollisia melatephroides (Rehm) Nannf.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Niptera excelsior (Karst.) Dennis [sub *Belonium excelsium* (Karst.) Boud.]	*Phragmites* stalks	England	Ingold 1954
	Phragmites culms	England	Dennis 1978
	alder and oak twigs	England	Shearer and Webster 1991
Niptera lacustris (Fr.) Fr.	*Schoenoplectus lacustris*, *Phragmites*	Scandinavia	Fries 1849 (as cited in Nannfeldt 1985)
	Scirpus, *Phragmites*	England	Dennis 1978
Niptera melanophaea Rehm.	*Schoenoplectus lacustris*	USSR	Dudka 1963
Niptera pilosa (Crossland) Boudier	*Carex*	U.K.	Dennis 1978
	Schoenoplectus lacustris	USSR	Dudka 1963
Niptera pulla (Phill. & Keith) Boud.	*Carex*, *Eleocharis*, *Juncus* *Phragmites*, *Phalaris*	England	Dennis 1978
Niptera tephromelas (Pass.) Nannf.	*Typha*	Italy	Nannfeldt 1985
Obtectodiscus aquaticus Müller, Petrini & Samuels	*Carex rostrata*	Switzerland	Müller et al. 1979
	Carex rostrata	Austria	Magnes and Hafellner 1991
	Eriophorum sp	USA, AK	Shearer unpublished
Orbilaster sp.	twigs	USA, RI	Lamore and Goos 1978
Orbilia sp.	stream foam	England	Webster and Descals 1979
Orbiliella armeniaca Kirschst.	twigs	USA, IL	Shearer and von Bodman 1983
Pachyella babingtonii (Berk.) Boud. [sub *Pachyella depressa* (Phill.) Boud.]	twigs	England	Ingold 1954
Peziza sp.	beech, Scots pine wood	England	Eaton and Jones 1971b
Pezizella sp	*Phragmites australis* stems	England	Taligoola et al 1972
Pezoloma rhodocarpa Fisher & Spooner	plant debris	Malawi	Fisher and Spooner 1987
Pezoloma sp.	stream foam	England	Webster and Descals 1979
Phaeohelotium sp	twigs	USA, IL	Shearer and von Bodman 1983
Plicaria violaceo-nigra Rehm	wood	USSR	Dudka 1963
Psilopezia aurantiaca Gill.	twigs	France	Gillet 1879
Pyrenopeziza huetteri Magnes & Hafellner	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Scutellinia scutellata (L.:Fr.) Labotte [sub *Lachnea scutellata* (L.) Gill.]	wood	USSR	Dudka 1963
Scutomollisia morvernensis Grad.	*Carex rostrata*, *Equisetum fluviatile*, *Eriophorum angustifolium*, *Glyceria fluitans* (L.) R. Br., *Juncus filiformis* L.	Austria	Magnes and Hafellner 1991
Scutomollisia punctum (Rehm) Nannf.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Stamnaria persoonii (Pers.: Fr.) Fckl.	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991

Tapesia knieffii (Wallr.) J. Kunze (sub *Belonidium rhenopalaticum* Rehm)	*Phragmites* stalks	England	Ingold 1954
Tapesia sp.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Thecotheus rivicola (Vacek) Kimbrough & Pfister	*Prunus* wood	Bohemia	Vacek 1949
Trichobelonium guestphalicum Rehm	*Schoenoplectus lacustris* and *Typha* leaf bases	England	Ingold 1954
Trichopezizella nidulus var. *hystricula* (Karst.) Haines	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Vibrissea bicolor Beaton & Weste	wood	Australia	Beaton and Weste 1977
Vibrissea decolorans (Saut.) Sánchez & Korf	twigs	Sweden, Norway	Schumacher 1976
Vibrissea dura Weste	eucalyptus logs	Australia	Beaton and Weste 1976
Vibrissea filisporia (Bon.) Korf & Sánchez f. *bouderi*	willow and alder twigs	Norway	Schumacher 1976
Vibrissea filisporia (Bon.) Korf & Sánchez f. *filisporia*	willow twigs	Norway	Schumacher 1976
Vibrissea flavovirens (Pers.:Fr.) Korf & Dixon	oak wood	Scotland	Graddon 1965
(sub *Apostemidium torrenticola* Graddon)	oak wood	England	Hamad and Webster 1987
Vibrissea guernisacii Crouan & H. Crouan	twigs	England	Ingold 1954
[sub *Apostemidium guernisaci* (Cr.) Boud.]	willow twigs	Belgium, England, France, Holland, Sweden	Graddon 1965
Vibrissea leptospora (Berk. & Br.) Phill.	*Prunus*, *Rosa*, *Ribes*, *Salix*	England, Scotland Sweden, Wales	Graddon 1965
[sub *Apostemidium leptospora* (Berk. & Br.) Boud.]	twigs	England	Willoughby and Archer 1973
Vibrissea sporogyra (Ingold) Sánchez (sub *Apostemidium* sporogyrum Ingold)	dead stalks of *Equisetum*, *Carex*, *Eleocharis*	England	Ingold 1954
Vibrissea melanochlora Beaton & Weste	eucalyptus logs	Australia	Beaton and Weste 1976
Vibrissea norvegica (Gremmen) Sánchez	*Phragmites australis*	Norway	Sánchez 1967
Vibrissea obconica (Kanouse) Sánchez f. *boudieri*	alder twigs	Scandinavia	Schumacher 1976
Vibrissea tasmanica Rodway	eucalyptus wood	Australia	Beaton and Weste 1976
Vibrissea truncorum (Alb. & Schwein.) Fr.	maple, alder, birch willow, juniper branches	Scandinavia	Kjuller 1960
Vibrissea vibrisseoides (Peck) Kjuller	wood	Scandinavia	Kjuller 1960
PYRENOMYCETES			
Aniptodera chesapeakensis Shearer & Miller	wood	USA, IL	Shearer and von Bodman 1983
	wood	USA, IL	Shearer and Crane 1986
Aniptodera fusiformis Shearer	wood	USA, IL	Shearer 1989b
Aniptodera limnetica Shearer	wood	USA, IL	Shearer 1989b
	balsa wood	Japan	Minoura and Muroi 1972
Aniptodera lignatilis Hyde	wood	Australia	Hyde unpublished
Aniptodera margarition Shearer	wood	USA, IL, England	Shearer 1989b
	Equisetum fluviatile	USA, IL	Shearer unpublished
Arnium apiculatum (Griffiths) Lundq.	*Equisetum fluviatile*	USA, IL	Shearer et al. 1980

Bombardia arachnoidea (Niessl) Cain	balsa wood	USA, MD	Shearer 1972
Calonectria sp.	wood	USA, RI	Lamore and Goos 1978
Ceratosphaeria lampadophora (Berk. & Br.) Niessl	beech wood	England	Eaton and Jones 1971a
	beech wood	England	Eaton 1972
Ceratosphaeria pusilla (Fuckel) Sacc.	wood	USA, IL	Shearer and Crane 1986
Ceratostomella sp.	alder and beech twigs	Hungary	Révây and Gönczöl 1990
	alder, ash, oak and willow twigs	England	Willoughby and Archer 1973
Cercophora sp.	twigs	USA, IL	Shearer and von Bodman 1983
	balsa wood	USA, IL	Shearer and Crane 1986
	alder & beech twigs	Hungary	Révây and Gönczöl 1990
Ceriospora caudae-suis Ingold	ash twigs	England	Ingold 1951
Ceriosporopsis sp.	*Phragmites australis* culms	England	Apinis et al. 1972b
Chaetomium aureum Chivers	wood	USA, IL	Shearer and Crane 1986
Chaetomium cochlioides Pall.	*Phragmites australis*	England	Apinis et al. 1972a
	balsa wood	USA, IL	Shearer and Crane 1986
Chaetomium funicolum Cooke	wood	USA, IL	Shearer and Crane 1986
Chaetomium elatum Kunze & Schmidt:Fr.	beech wood	England	Eaton 1972
Chaetomium globosum Kunze:Fr.	beech and Scots pine wood	England	Eaton and Jones 1971a
	beech wood	England	Eaton 1972
	balsa wood	USA, IL	Shearer and Crane 1986
	beech wood	England	Davis and Jones unpublished
Chaetomium seminudum Ames	leaf litter	USA, IL	Shearer and Crane 1986
Chaetomium trilaterale Chivers	balsa wood	USA, IL	Shearer and Crane 1986
Chaetomium spp.	*Phragmites australis* leaves	England	Apinis et al. 1972a
	wood	USA, RI	Lamore and Goos 1978
Coniochaeta kellermani (Ell. & Ev.) Munk	balsa wood	USA, MD	Shearer 1972
	wood	USA, IL	Shearer and Crane 1986
Coniochaeta leucoplaca (Berk. & Rav.) Cain	wood	USA, IL	Shearer and Crane 1986
Coniochaeta lignaria (Grev.) Cooke [sub *Coniochaeta discospora* (Auers. ex Niessl) Cain]	beech wood	England	Eaton 1972
Coniochaeta velutina (Fuckel) Munk	wood	USA, IL	Shearer and von Bodman 1983
	wood	USA, IL	Shearer and Crane 1986
Coniochaeta sp. 4022	bog vegetation	USA, WI	Christensen and Whittingham 1965
Chaetosphaeria anglica Fisher & Petrini	wood	Sudan, England	Fisher and Petrini 1983
Clypeosphaeria mamillana (Fr.) Lambotte	Scots pine wood	England	Eaton and Jones 1971b
Debaryella gracilis Munk	balsa wood	Japan	Minoura and Muroi 1978
Debaryella sp.	twigs	USA, IL	Shearer and von Bodman 1983

Ditopella sp.	Scots pine wood	England	Eaton and Jones 1971b
Gaeumannomyces graminis (Sacc.) v. Arx & Olivier	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Gnomonia papuana Sivanesan & Shaw	leaves	Papua, New Guinea	Sivanesan and Shaw 1977
Gnomonia sp.	wood	USA, IL	Shearer and Crane 1986
Griphiosphaeria corticola (Fuckel) v. Höhnel	Scots pine wood	England	Eaton and Jones 1971a
Halosarpheia lotica Shearer	twigs	USA, WI	Shearer 1984
Halosarpheia parva Shearer	monocot stem	USA, IL	Shearer unpublished
Halosarpheia retorquens Shearer & Crane	wood	USA, IL	Shearer and Crane 1980
	wood	USA, IL	Shearer and von Bodman 1983
	wood	USA, IL	Shearer and Crane 1986
Halosarpheia viscosa (Schmidt) (Schmidt) Shearer & Crane ex Kohlm. & Volkm.-Kohlm.	twigs	USA, IL	Shearer and von Bodman 1983
Hypoderma scirpinum DC.	*Schoenoplectus lacustris* stems	England	Ingold 1954
Lasiosphaeria spp.	*Schoenoplectus lacustris*	USSR	Dudka 1963
	Phragmites australis culms	England	Apinis et al. 1972b
	Phragmites australis stems	England	Taligoola et al. 1972
	twigs	USA, IL	Shearer and von Bodman 1983
Lasiosordaria lignicola (Fuckel) Chen.	beech and pine wood	England	Davis and Jones unpublished
Lejosphaerella leonensis Fisher & Petrini	wood	Africa	Fisher and Petrini 1983
Lophiotrema culmifraga Speg.	*Schoenoplectus lacustris*	USSR	Dudka 1963
Luttrellia estuarina Shearer	balsa wood	USA, MD	Shearer 1978
	twigs	USA, IL	Shearer and von Bodman 1983
	balsa wood	USA, IL	Shearer and Crane 1986
Melogramma sp.	beech, Scots pine wood	England	Apinis et al. 1972b
Micronectriella sp.	*Phragmites australis* culms	England	Eaton and Jones 1971a
	Phragmites australis stems	England	Taligoola et al. 1972
	Phragmites australis stems	England	Apinis et al. 1972
Nais inornata Kohlm.	beech, Scots pine wood	England	Eaton and Jones 1971a
	balsa wood	USA, MD	Shearer 1972
	twigs, balsa wood	USA, IL	Shearer and Crane 1978
	balsa wood	Japan	Minoura and Muroi 1978
	twigs	USA, IL	Shearer and von Bodman 1983
	balsa wood	USA, IL	Shearer and Crane 1986
Nectria coccinea (Pers.:Fr.) Fr.	beech twigs	Hungary	Révay and Gönczöl 1990
Nectria discophora (Mont.) Mont.	oak twigs	England	Shearer and Webster 1991
Nectria haematococca Berk. & Br.	twigs	USA, IL	Shearer and von Bodman 1983

Nectria lucidum Höhnel	twigs	USA, IL	Shearer and von Bodman 1983
Nectria lugdunensis Webster	twigs	England	Webster 1959
	oak, willow twigs	England	Willoughby and Archer 1973
	alder, oak twigs	England	Shearer and Webster 1991
Nectria penicillioides Ranzoni	maple leaves	USA, CA	Ranzoni 1956
Nectria spp.	beech wood	England	Eaton and Jones 1971b
	twigs	USA, RI	Lamore and Goos 1978
	alder and beech twigs	Hungary	Révây and Gönczöl 1990
Nectriella lacustris (Kirsch.) Magnes & Hafellner	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Ophioceras dolichostomum (Berk. & Curtis) Sacc.	wood	USA, FL	Conway and Barr 1977
Ophioceras leptosporum (Iqbal) Walker	plant stalks	England	Iqbal 1972
(sub *Gaumannomyces leptosporus* Iqbal)	leaves	Papua, New Guinea	Shaw 1977
Ophioceras sp. 652	twigs	Panama	Shearer unpublished
Ophioceras sp. 837	twigs	USA, IN	Shearer unpublished
Ophioceras sp. 408	twigs	USA, IL	Shearer unpublished
Phaeonectriella lignicola Eaton & Jones	beech and Scots pine wood	England	Eaton and Jones 1971a
	beech and Scots pine wood	England	Eaton 1972
Phomatospora aquatica Minoura & Muroi	balsa wood	Japan	Minoura and Muroi 1978
Phomatospora berkleyi Sacc.	*Phragmites australis*	USSR	Dudka 1963
	Carex rostrata	Austria	Magnes and Hafellner 1991
Phyllachora therophila (Desm.) v. Arx & Müller	*Juncus filiformis*	Austria	Magnes and Hafellner 1991
Physalospora aquatica Ingold	*Schoenoplectus lacustris*, *Typha angustifolia*	England	Ingold 1955
	Equisetum fluviatile	Austria	Magnes and Hafellner 1991
Plagiosphaeria nilotica Monod & Fisher	twig	Africa	Monod and Fisher 1983
Platyspora permunda (Cooke) Wehm.	*Scirpus*, *Typha*	USA, MN	Cavaliere 1975
Platyspora planispora (Ell.) Wehm.	*Scirpus*, *Typha*	USA, MN	Cavaliere 1975
Podospora setosa (Winter) Niessl	beech wood	England	Eaton 1971b
	beech wood	England	Eaton 1972
Pseudohalonectria adversaria Shearer	wood	USA, IL	Shearer 1989a
Pseudohalonectria falcata Shearer	wood	USA, IL	Shearer 1989a
Pseudohalonectria lignicola Minoura & Muroi	balsa wood	Japan	Minoura and Muroi 1972
	wood	USA, MD	Shearer 1972 (as CS-182-I)
	cottonwood, cherry and sycamore twigs	USA, IL	Shearer and von Bodman 1983
	balsa wood	USA, IL	Shearer and Crane 1986
	alder and beech twigs	Hungary	Révây and Gönczöl 1990
Pseudohalonectria longirostrum Shearer	wood	Panama	Shearer 1989a

Pseudohalonectria lutea Shearer	wood	Chile	Shearer 1989a
Pseudohalonectria phialidica Shearer	wood	USA, IL	Shearer 1989a
Pyxidiophora spinulo-rostrata Webster & Hawksworth	wood	England	Webster and Hawksworth 1986
Savoryella lignicola Jones & Eaton	beech, Scots pine and greenhart wood	England, Wales	Jones and Eaton 1969
	sycamore twigs	USA, IL	Shearer and von Bodman 1983
Savoryella verrucosa Minoura & Muroi	balsa wood	Japan	Minoura and Muroi 1972
Schizothecium sp.	beech twig	Hungary	Révay and Gönczöl 1990
Sillia ferruginea (Pers.:Fr.) Karst. (probably an *Ophioceras* sp.)	wood	England	Eaton and Jones 1971a,b; Eaton 1976
Sordaria sp. I	wood	USA, IL	Shearer and Crane 1986
Sordaria sp. II	wood	USA, IL	Shearer and Crane 1986
Thielavia sp.	*Phragmites australis* stems	England	Taligoola et al. 1972
	twigs	USA, IL	Shearer and von Bodman 1983
Zopfiella latipes (Lundq.) Malloch & Cain	balsa wood	USA, MD	Shearer 1972
	balsa wood	USA, IL	Shearer and Crane 1986
Zopfiella leucotricha (Speg.) Lundq.	balsa wood	USA, MD	Shearer 1972
Zopfiella lundqvistii Shearer & Crane	balsa wood and woody debris	USA, IL	Shearer and Crane 1978
	balsa wood and woody debris	USA, IL	Shearer and Crane 1986
Zopfiella sp.	twigs	USA, IL	Shearer and von Bodman 1983
LOCULOASCOMYCETES			
Ascagilis bipolaris Hyde	wood	Australia	Hyde in press
Bricookea sepalorum (Vleugel) Barr	*Juncus filiformis*	Austria	Magnes and Hafellner 1991
Buergenerula biseptata (E. Rostr.) H. Sydow	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Byssothecium flumineum Crane, Shearer & Huhndorf	wood	USA, IL	Shearer and von Bodman 1983 (as *Leptosphaeria* sp. 1)
	wood	USA, IL	Crane et al. in press
Caryospora callicarpa (Curry) Nitschke ex Fuckel	wood	USA, IL	Shearer unpublished
Clathrospora tirolensis Rehm ex O. Eriksson	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Delitschia bispora Eaton & Jones	beech wood	England	Eaton and Jones 1970
	beech wood	England	Eaton and Jones 1971b
	beech wood	England	Eaton 1972
Didymella equisetina (H. Sydow) Petrak	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Didymella glacialis Rehm	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Didymella spp.	*Phragmites australis* leaves	England	Apinis et al. 1972a
	Phragmites australis stems	England	Taligoola et al. 1972

Didymosphaeria sp.	beech wood	England	Eaton and Jones 1971b
	Scots pine wood	England	Davis and Jones unpublished
Diplonaevia emergens (Karst.) Hein	*Juncus filiformis* *Eriophorum angustifolium*	Austria	Magnes and Hafellner 1991
Diplonaevia seriata (Libert) Hein	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Hadrospora fallax (Mouton) Boise (sub *Trematosphaeria fallax* Mouton)	balsa wood	USA, MD	Shearer and Crane 1971
Kirschsteiniothelia sp. CS-825-1,2	woody debris	USA, IL, Chile	Shearer unpublished
Lepidopterella palustris Shearer & Crane	balsa wood	USA, IL	Shearer and Crane 1980a
Leptosphaeria acuta (Hoffm.:Fr.) Karsten	*Scirpus, Typha*	USA, MN	Cavaliere 1975
Leptosphaeria clavicarpa Ell. & Ev.	*Schoenoplectus lacustris*		USSR Dudka 1963
Leptosphaeria culmifraga (Fr.:Fr.) Ces. & deNot.	*Phragmites australis* culms	England	Apinis et al. 1972b
	Phragmites australis stems	England	Taligoola et al. 1972
Leptosphaeria lemaneae (Cohn) Sacc.	Parasitic on *Lemanea* sp.	England	Ingold 1955
Leptosphaeria sparganii (Fautrey) Munk	*Typha* leaves	England	Pugh and Mulder 1971
Leptosphaeria spp.	organic debris	Ireland	Park 1972
	birch and maple twigs	USA, RI	Lamore and Goos 1978
Lophiostoma appendiculata Fuckel	*Salix* wood	USSR	Dudka 1963
Lophiostoma arundinis (Fr.) Ces. & De Not.	*Phragmites australis*	USSR	Dudka 1963
Lophiostoma sp.	twigs	USA, IL	Shearer unpublished
Massarina amphibia Magnes & Hafellner	*Equisetum fluviatile*, *Carex rostrata*, *C. nigra*	Austria	Magnes and Hafellner 1991
Massarina aquatica Webster	twigs and roots of *Alnus glutinosa* (L.) Gaertn.	England	Webster 1965
Massarina arundinacea (Sow.:Fr.) Leuchtman (sub *Leptosphaeria arundinacea* Sow.:Fr.)	*Phragmites australis* culms	England.	Apinis et al 1972b
Massarina australiensis Hyde	wood	Australia	Hyde in press
Massarina tetraploa Scheuer	*Carex acutiformis* Ehrh.	England	Scheuer 1991
Massarina spp.	alder, ash, oak and willow twigs	England	Willoughby and Archer 1973
	twigs	England	Webster and Descals 1979
	Fagus sylvaticus L. twigs	England	Webster and Descals 1979
	twigs	USA, IL	Shearer and von Bodman 1983
	alder twigs	England	Shearer and Webster 1991
	alder and beech twigs	Hungary	Révày and Gönczöl 1990
	Carex rostrata	Austria	Magnes and Hafellner 1991
Massariosphaeria rubicunda (Müller) Crivelli	*Carex nigra*	Austria	Magnes and Hafellner 1991
Massariosphaeria scirpina (Wint.) Leuchtman (sub *Leptosphaeria scirpina* Wint.)	*Typha* leaves	USA, MN	Cavaliere 1975

Micropeltopsis nigro-annulata (Webster) Spooner & Kirk var. *papillosa* (Scheuer) Magnes & Hafellner	*Carex nigra*, *C. rostrata*, *Equisetum fluviatile*, *Eriophorum angustifolium*, *Juncus filiformis*	Austria	Magnes and Hafellner 1991
Mycosphaerella aspidii (v. Höhnel) Holm & Holm	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Mycosphaerella equiseticola Bond.-Monte.	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Mycosphaerella perexigua (Karst.) Johanson var. *minima* Johanson	*Carex rostrata*, *Eriophorum angustifolium*	Austria	Magnes and Hafellner 1991
Mycosphaerella cf. *perexigua* (Karst.) Johanson	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Nodulosphaeria modesta (Desm.) Munk ex Holm [sub *Leptosphaeria modesta* (Desm.) Auersw.]	*Typha* leaves	England	Pugh and Mulder 1971
Ophiobolus gracilis (Niessl) E. Muller	*Carex paniculata* L.	Denmark	Munk 1957
Ophiobolus typhae Feltgen	*Typha latifolia*	England	Ingold 1951
Ophiobolus sp.	*Phragmites australis*	England	Apinis et al. 1972b
Paraphaeosphaeria michotii (West.) Eriksson [sub *Leptosphaeria michotii* (West.) Sacc.]	*Typha* leaves	England	Pugh and Mulder 1971
Passeriniella obiones (Crouan & Crouan) Hyde & Mouzouras [sub *Passeriniella discors* (Sacc. & Ell.) Apinis & Chesters]	*Phragmites australis* culms	England	Apinis et al. 1972b
	Phragmites australis stems	England	Taligoola et al. 1972
	wood	USA, IL	Shearer and Crane 1986
	Typha leaves	England	Pugh and Mulder 1971
Phaeosphaeria albopunctata (West.) Shoem. [sub *Leptosphaeria albopunctata* (Westend.) Sacc.]	*Phragmites australis*	USSR	Dudka 1963
	Phragmites australis stems	England	Taligoola et al. 1972
	twigs	USA, RI	Lamore and Goos 1978
	Phragmites australis leaves	England	Apinis et al. 1972a
Phaeosphaeria alpina Leuchtm.	*Carex rostrata*, *Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Phaeosphaeria caricinella (Karst.) O. Eriksson	*Carex rostrata*, *C. paupercula* subspec. *irrigua*, *Juncus filiformis*	Austria	Magnes and Hafellner 1991
Phaeosphaeria culmorum (Auersw. in Rehm) Leuchtm.	*Carex rostrata*, *Equisetum fluviatile*, *Glyceria fluitans*	Austria	Magnes and Hafellner 1991
Phaeosphaeria eustoma (Fuckel) Holm [sub *Leptosphaeria eustoma* (Fuckel) Sacc.]	beech wood	England	Eaton 1972
	beech wood	England	Eaton and Jones 1971a
	Scirpus, *Typha*	USA, MN	Cavaliere 1975
	Carex rostrata, *Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Phaeosphaeria eustomoides (Sacc.) Shoem. (sub *Leptosphaeria eustomoides* Sacc.)	*Phragmites australis* leaves	England	Apinis et al. 1972a
Phaeosphaeria halima (Johnson) Shoem. (sub *Leptosphaeria halima* Johnson)	*Phragmites australis* stems	England	Taligoola et al. 1972
Phaeosphaeria herpotricha (Fries) Holm [sub *Ophiobolus herpotrichus* (Fries) Sacc.]	*Typha* sheaths	England	Pugh and Mulder 1971
Phaeosphaeria herpotrichoides (de Not.) Holm	beech wood	England	Eaton and Jones 1971b
	Carex rostrata	Austria	Magnes and Hafellner 1991

Phaeosphaeria juncicola (Rehm ex Winter) Holm (sub *Leptosphaeria juncicola* Rehm apud Wint.)	*Scirpus*, *Typha*	USA, MN	Cavaliere 1975
Phaeosphaeria licatensis (Sacc.) Shoem. (sub *Leptosphaeria licatensis* Sacc.)	*Typha* leaves	England	Pugh and Mulder 1971
Phaeosphaeria microscopica (Karst.) Eriksson (sub *Leptosphaeria microscopica* Karst.)	*Phragmites australis* leaves	England	Apinis et al. 1972a
	Phragmites australis stems	England	Taligoola et al. 1972
Phaeosphaeria sowerby (Fuckel) Holm [sub *Leptosphaeria sowerby* (Fuckel) Sacc.]	*Typha* leaves	USA, MN	Cavaliere 1975
Phaeosphaeria typhae (Karst.) Shoem. [sub *Leptosphaeria typhae* (Auersw.) Karst.]	*Typha* leaves	England	Pugh and Mulder 1971
	Scirpus, *Typha*	USA, MN	Cavaliere 1975
Phaeosphaeria typharum (Desm.) Holm [sub *Leptosphaeria typharum* (Desm.) Karst.]	*Typha* leaves	England	Webster 1955
	Typha leaves	USA, MN	Cavaliere 1975
	Typha leaves	England	Pugh and Mulder 1971
Physalospora aquatica Ingold	reed leaf bases	England	Ingold 1955
Pleospora gaudefroyi Pat. (sub *Pleospora lignicola* Webster & Lucas)	wood	England	Webster and Lucas 1961
Pleospora incerta Criv.	*Carex rostrata*	Austria	Magnes and Hafellner 1991
Pleospora palustris Berlese	*Scirpus maritimus* L.	England	Webster and Lucas 1961
Pleospora phaeospora (Duby) Ces. & de Not.	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991
Pleospora scirpicola (DC.) Karst.	*Schoenoplectus lacustris* stalks	England	Ingold 1955
	Schoenoplectus lacustris	USSR	Dudka 1963
Pleospora submersa Webster & Lucas	*Scirpus maritimus*	England	Webster and Lucas 1961
Pyrenophora typhaecola (Cooke) E. Müller [sub *Pleospora typhaecola* (Cke.) Sacc.]	*Typha* leaves	England	Pugh and Mulder 1971
Rebentischia unicaudata (Berk. & Br.) Sacc.	deciduous leaves	USA, IL	Shearer and Crane 1986
Rebentischia sp.	*Phragmites* stalks	England	Ingold 1955
Sphaerulina sp.	*Phragmites australis* leaves	England	Apinis et al. 1972a
Sporormia minima Auersw.	beech, Scots pine wood	England	Eaton and Jones 1971a
	beech wood	England	Eaton 1972
Sporormiella sp.	twigs	USA, IL	Shearer and von Bodman 1983
Trematosphaeria britzelmayriana (Rehm) Sacc.	twigs	Hungary	Révāy and Gönczöl 1990
Trematosphaeria circinans Fuckel [sub *Trematosphaeria vindelicorum* (Rehm) Sacc.]	alder and beech wood	Hungary	Révāy and Gönczöl 1990
Trematosphaeria hydrela (Rehm) Sacc.	immersed tree trunks	USSR	Petrak 1925
Trematosphaeria hydrophyla (Karst.) Sacc.	*Salix* wood	USSR	Dudka 1963

Trematosphaeria pertusa (Pers.:Fr.) Fuckel	beech, Scots pine wood	England	Eaton and Jones 1972
	beech, Scots pine wood	England	Eaton and Jones 1971b
	alder and beech wood	Hungary	Révảy and Gönczöl 1990
Trematosphaeria sp.	beech twigs	Hungary	Révảy and Gönczöl 1990
Tubeufia paludosa (Crouan & H. Crouan) Rossman (sub *Tubeufia helicomyces* Höhnel)	*Arrhenatherum*, *Phragmites* stems	England	Webster 1951
Wettsteinina niesslii Müller	*Phragmites australis* stalks	England	Ingold 1955
	Phragmites australis stalks	USSR	Dudka 1963
	Phragmites australis stems	England	Taligoola et al. 1972
	Phragmites australis culms	England	Apinis et al. 1972b
	balsa wood	USA, MD	Shearer 1972
Wettsteinina sp.	*Equisetum fluviatile*	Austria	Magnes and Hafellner 1991

all Ascomycetes that occur on submerged or partially submerged substrata in the aquatic habitats outlined by Correll and Corell (1975) will be considered "freshwater Ascomycetes". Much additional study is necessary before a more precise definition of the group can be made.

Study techniques

COLLECTION: FWA can be found by examining living and dead macrophytes in ponds, lakes, bogs, swamps, wetlands, drainage ditches and small temporary water bodies. Submerged woody debris is also a good source of FWA, but only a few species, eg. *Aquadiscula aquatica* (Fig. 1), *Mitrula alba* and *M. paludosa,* occur on submerged deciduous leaves. Substrata can be examined for ascomata in the field using a hand lens and promising substrata can be returned in a plastic bag to the laboratory for further study. The absence of ascomata on substrata in the field is not necessarily a good indication that FWA are not present because some species only appear after incubation in moist chambers. Thus it is a good practice to incubate field materials as well as examine them directly. Moist chambers for incubation can be constructed of glass or plastic Petri dishes containing moistened filter paper. Plastic boxes or bags containing moistened paper toweling can also be used. The choice of paper toweling is important because some types contain substances that stimulate the growth of opportunistic fungi such as *Trichoderma* and *Penicillium* which overgrow the FWA. Incubated samples should be kept at a temperature similar to that of the natural habitat and in alternating light and dark which apparently enhances sexual reproduction (Shearer and von Bodman 1983). If incubation is used, it is important to examine samples immediately after collection, prior to incubation, because some FWA deteriorate once they are removed from water.

Since it is often difficult to determine the source and length of submersion period of randomly collected substrata, baits have been employed to follow the colonization and development of FWA (Shearer, 1972; Shearer and von Bodman 1983). Baits such as twigs or wood blocks can be attached to masonry bricks or cement blocks and placed in the habitat. They also can be assembled into packs with nylon twine and attached to a line tethered to a relatively permanent structure such as a pier or a tree (Shearer 1972). Substrata such as dead macrophyte leaves and stems can be placed in nylon mesh bags and placed in the habitat as above. Given the fluctuating water levels and often muddy conditions common in freshwater habitats, a good deal of thought and planning should go into the selection of sampling sites and the method of placing and retrieving of samples. Allowances should be made for flood conditions.

Indirect collection techniques such as plating water, muds, homogenized substrata etc. are not very efficient. Ascospores of some FWA (e.g. *Aniptodera, Lepidopterella*) are difficult to germinate. Although ascospores of many FWA germinate readily, a long time period and special cultural procedures are necessary to induce reproduction. Some species do not reproduce in culture. Without reproductive structures FWA cannot be identified. Thus it is quite laborious and often futile to test the numerous isolates that result from plating techniques.

The techniques of foam examination and membrane filtration of water which are so useful for the identification and quantification of aquatic Hyphomycetes (Iqbal and Webster 1973, Shearer and Webster 1985) have little value for FWA. The ascospores of FWA occur at much lower densities than the conidia of aquatic Hyphomycetes and thus are rarely encountered on membrane filters. In addition, the ascospores of many FWA are not very morphologically distinctive and unless the investigator is already very knowledgeable about the FWA present, they cannot be identified. These limitations make it very difficult to directly quantify the spora of FWA in water.

ISOLATION: The ascospores of most FWA germinate relatively easily. FWA with closed ascomata can be isolated by crushing mature ascomata in 2-4 ml sterile distilled water to form a spore suspension. Discharged ascospores which have accumulated around ostioles can be removed a flamed, cooled needle and stirred into sterile water. Vigorous agitation of spore suspensions with a tube agitator is useful to separate ascospores and dislodge attached bacteria. Spore suspensions are poured onto antibiotic distilled water agar (AWA, agar 18 g, streptomycin sulfate 250 mg/l, penicillin G 250 mg/l, distilled water 1l). Antibiotics are added to the molten agar immediately after autoclaving. Spore suspensions on AWA plates are allowed to stand for 1-2 hr to permit settling of the ascospores. Excess water is gently decanted from the plates which are incubated at a slight angle from the upright so excess water can drain off. To isolate Discomycetes, a small piece of filter paper is attached with a drop of water to the lid of an AWA plate about 1 cm from the edge of the lid. An apothecium is removed from the substratum with a sterile needle and placed on the filter paper so that its surface is facing down toward the agar surface. The lid is placed on the bottom dish and rotated about 45° every 30 minutes so that ascospores are discharged in a circular path around the plate. This procedure can be reversed for pyrenomycetous forms with forcible ascospore discharge. A small piece of substratum with perithecia directed upward is mounted on the filter paper and the Petri dish is inverted so the agar that is on top receives upwardly discharged ascospores.

After 24 hours incubation at room temperature, plates should be examined microscopically with transmitted light and the position of germinated ascospores marked. *It is most important* that single, recognizable, uncontaminated ascospores be isolated. Thus examination and transfer of germinated ascospores within 24-48 hours is a critical step. If the plates are left for longer periods of time, the ascospores may be overgrown by contaminants or unrecognizable due to their germination and growth. Because of variation in fruiting ability among strains and the possibility that reproduction is heterothallic, at least 6-8 isolates of a given species should be made. Single germinated ascospores should be transferred from AWA to standard nutrient media such as cornmeal agar (Difco), malt extract agar (Difco), peptone, yeast extract, glucose agar (Fuller and Jaworski 1987) or yeast extract soluble starch agar (Fuller and Jaworski 1987). For the long-term storage of cultures, strips of balsa or birch wood can be added to culture tubes of the above media before autoclaving. Cultures of new or unusual species should be deposited with one or more internationally recognized culture collections such as the American Type Culture Collection or the International Mycological Institute Collection.

To induce ascomata formation, cultures are grown on alfalfa stems or wood strips. Six to eight pieces (4 cm long) are added to 50 ml sterile distilled water (filtered water from the natural habitat may also be used) in 125 ml Erlenmeyer flasks and autoclaved for one hour on three successive days. Flasks are inoculated with mycelium from stock tubes and placed on a rotary shaker (100 rpm) at 22C until substrata are visibly well-colonized. Substrata are transferred aseptically to sterile moist chambers (see above), sealed with parafilm, and incubated at 18-22C in alternating light/dark conditions. Daylight fluorescent light is acceptable and an additional black light may be useful in stimulating fruiting in some species (Webster pers. comm.). Substrata should be examined weekly for the presence of ascomata.

Aquatic hyphomycete anamorphs have been reported for several FWA (Table 2), thus all cultures should be tested for the production of such states (Webster and Descals 1979, Webster 1992). This can be done by submerging slivers of colonized agar in sterile distilled water at 15-18C for cold water species and 22-25C for warm water species. Using transmitted light, submerged cultures should be examined for conidia periodically over several weeks. If no conidia are produced in static water culture, isolates must then be tested in aerated culture. This can be done by passing air forcibly through aeration stones or Pasteur pipettes drawn out to a fine point in flasks or culture tubes. Numerous FWA produce anamorphs other than aquatic hyphomycetes, but these are usually produced on standard laboratory media so examination of stock cultures is sufficient for their detection.

EXAMINATION: For known FWA, squash mounts of ascomata are usually sufficient for identification. In the case of unknown or problematic specimens, it is necessary to section ascomata to determine anatomical details and centrum structure. Rough

Table II. Teleomorph-anamorph connections for freshwater Ascomycetes.

TELEOMORPH	ANAMORPH	REFERENCE
Vibrissea flavovirens (Pers: Fr) Korf & Dixon (sub *Apostemidium torrenticola* Graddon)	*Anavirga dendromorpha* Descals & Sutton	Hamad and Webster 1987
Gnomonia papuana Sivanesan & Shaw	*Sesquicillium* sp.	Sivanesan and Shaw 1977
Hyaloscypha lignicola Abdullah & Webster	*Pseudaegerita* sp. (corticalis?)	Abdullah and Webster 1983
Hyaloscypha zalewskii Descals & Webster	*Clathrosphaerina zalewski* v. Beverwijk	Descals and Webster 1976
Hydrocina chaetocladia Scheuer	*Tricladium chaetocladium* Ingold	Webster et al. 1991
Hymenoscyphus africanus Descals, Fisher & Webster	*Geniculospora grandis* (Greathead ex Nolan) Nilsson	Descals et al. 1984
Hymenoscyphus foliicola Abdullah, Descals & Webster	*Dimorphospora foliicola* Tubaki	Abdullah et al. 1981
Hymenoscyphus inberbis	*Anguillospora fustiformis*	Descals and Marvanová unpublished
Hymenoscyphus malawienis Fisher & Spooner	Unnamed hyphomycete	Fisher and Spooner 1987
Hymenoscyphus paradoxus Fisher & Webster	*Helicodendron paradoxum* Peyronel	Fisher and Webster 1983
Hymenoscyphus splendens Abdullah, Descals & Webster	*Tricladium splendens* Ingold	Abdullah et al. 1981
Hymenoscyphus tetracladius Abdullah, Descals & Webster	*Articulospora tetracladia* Ingold	Abdullah et al. 1981
Hymenoscyphus varicosporoides Tubaki	*Varicosporium* sp.	Tubaki 1966
Lambertella tubulosa Abdullah & Webster	*Heliocodendron tubulosum* (Reiss) Linder	Abdullah and Webster 1981
Loramyces juncicola Weston	*Anguillospora* sp.	Digby and Goos 1987
Massarina aquatica Webster	*Tumularia aquatica* (Ingold) Descals & Márv.	Webster 1965
Massarina sp.	*Clavariopsis aquatica* de Wild.	Webster and Descals 1979
Massarina sp.	*Anguillospora longissima* (Sacc. & Syd.) Ingold	Willoughby and Archer 1973
Miladina lechithina (Cooke) Svrček	*Actinospora megalospora* Ingold	Descals and Webster 1978
Mollisia gigantea Fisher & Webster	*Helicondendron giganteum* Glenn-Bott	Fisher and Webster 1983
Mollisia uda (Pers.: Fr.) Gill.	*Anguillospora crassa* Ingold	Webster 1961
Mollisia sp. 1	*Filosporella* sp.	Webster and Descals 1979
Nectria discophora (Mont.) Mont.	*Cylindrocarpon ianthothele* Wollenw.	Booth 1966
Nectria haematococca Berk. & Br.	*Fusarium solani* (Mart.) Sacc.	Booth 1960, 1971
Nectria lucidum Höhnel	*Cylindrocarpon lucidum* Booth	Booth 1966
Nectria lugdunensis Webster	*Heliscus lugdunensis* Sacc. & Théry	Webster 1959
Nectria penicillioides Ranzoni	*Flagellospora penicillioides* Ingold	Ranzoni 1956
Nectria sp.	*Flagellospora curta*	Webster unpublished
Orbilia sp.	*Anguillospora rosea* sp. ined.	Webster and Descals 1979
Pezoloma sp.	*Anguillospora furtiva* Descals	Webster and Descals 1979
Pyxidiophora spinulo-rostrata Webster	denticulate anamorphic state	Webster and Hawksworth 1986
Tubeufia paludosa (Crouan & H. Crouan) Rossman (sub *Tubeufia helicomyces* Höhnel)	*Helicosporium phragmites* Höhn.	Webster 1951
Talaromyces flavus (Klöcher) Stolk & Samson var. *flavus*	*Penicillium dangeardii* Pitt	Pitt 1979

sections of ascomata may be made with a razor blade, but more definitive work requires thin sections. The freezing microtome is useful for sectioning fresh specimens, especially Discomycetes and ascomata embedded in host or substrata. Embedding of specimens in low viscosity resin and sectioning with the ultra-microtome (Huhndorf 1991) has proved excellent for both fresh and dried specimens. In addition to sectioning material, it is important to make squash mounts of portions of the centrum in water, followed by India ink. This permits the hydration and revelation of gelatinous coatings on physes and ascospore sheaths and appendages. When no sheaths or appendages are revealed by India ink, it is necessary to remove the ink by pulling distilled water under the coverslip. The appendages of some FWA stain with ink and are only visible after excess ink is removed. It is also necessary to stain ascus tips with Meltzer's reagent and aqueous cotton blue to determine the nature of the apical apparatus and/or apex.

It is critical that both type and voucher specimens be deposited in recognized herbaria (Dennis 1978, Kohlmeyer and Kohlmeyer 1979). A published record of species occurrences is useless unless it can be validated by later investigators. Deposited specimens also should prove useful in population studies. In addition, dried ascomata can serve as a source of genetic information in the form of preserved DNA for taxonomic and population studies. As soon as cultures, sections and squash mounts have been obtained, specimens should be dried down while they are still in good condition. In dry climates, this can be done at room temperature with no special procedures. In humid areas, a desiccant may be needed along with gentle heat. High drying temperatures should be avoided as this could degrade DNA. It is extremely important to include with herbarium specimens details of habitat (e.g. standing or flowing water, water chemistry, temperature) and substratum (type and condition). This information, when compiled in the future, will be invaluable in interpreting the ecology and distribution patterns of FWA.

IDENTIFICATION: With the exception of a key to the Ascomycetes on emergent vegetation of alpine lakes (Magnes and Hafellner 1991), there are no comprehensive keys to the FWA. Thus it is necessary to collect the original descriptions of the species known from freshwater. Citations in Table 1 can be used to obtain a large part of this literature. There are several general works that are useful: Müller (1950), Holm (1957), Munk (1957), Eriksson (1967), Dennis (1978), Hedjaroude (1969), Lundqvist (1972), Korf (1973), Luttrell (1973), Müller and von Arx (1973), Barr (1978, 1987, 1990), Kohlmeyer and Kohlmeyer (1979), Kohlmeyer and Volkmann-Kohlmeyer (1991), Leuchtmann (1984), Sivanesan (1984), and Shoemaker and Babcock (1989).

Systematics

The systematics of Ascomycetes, in general, is at present controversial and taxonomic schemes abound (Hawksworth, et al. 1983). The classification system of Barr (1987, 1990) is used for the Loculoascomycetes and pyrenomycetous members of the class Hymenoascomycetes and that of Hawksworth et al. (1983) for all other taxa. Based on these systems, 275 ascomycete species in 15 orders (Eurotiales, Onygenales, Helotiales, Pezizales, Rhytismatales, Calosphaeriales, Diaporthales, Hypocreales, Halosphaeriales, Sordariales, Xylariales, Dothideales, Pleosporales, and Melanommatales) have been reported from freshwater habitats. Orders with 10 or more representatives from freshwater are the Halosphaeriales, Helotiales, Pleosporales and Sordariales. These orders represent four distinctly different evolutionary lines: the marine pyrenomycetous Hymenoascomycetes, the discomycetous Hymenoascomycetes, the Loculoascomycetes, and the pyrenomycetous Hymenoascomycetes, respectively.

The ratio of species of Plectomycetes: Discomycetes: Pyrenomycetes: Loculoascomycetes is 6:94:71:71. An interesting difference between the FWA and marine Ascomycetes is the absence of Discomycetes in marine habitats. Of 255 ascomycete taxa known from marine habitats (Kohlmeyer and Volkmann-Kohlmeyer 1991), only one belongs in the Discomycetes. The FWA differ from the marine Ascomycetes not only in the relative proportions of taxa in major ascomycete groups but also in species composition. Only eight species have been reported from both freshwater and marine (including brackish) habitats: *Aniptodera chesapeakensis, Halosarpheia retorquens, Halosarpheia viscosa, Luttrellia estuarina, Nais inornata, Phaeosphaeria halima, Savoryella lignicola,* and *Zopfiella latipes.* It appears that some aspect of the marine environment has been an extremely effective barrier to the colonization of marine habitats by freshwater Ascomycetes and vice versa. This barrier(s) has effectively isolated the two mycotas and it appears that they have evolved differently (See Evolution Section).

Geographical distribution

There are so few comprehensive studies of the FWA of different geographical areas that little can be said about this topic. At this time, distribution patterns are largely collector-linked. *Nais inornata, Pseudohalonectria lignicola* and *Wettsteinina niesslii* have each been reported from at least three widely separated geographical regions (Table 1) suggesting that they are widely distributed. Clearly much more work is needed in this area.

Ecology

FWA can be divided into two broad ecological groups based on their nutrition: (1) parasites and endophytes of aquatic macrophytes and algae, and (2) saprophytes on dead plant material. A variety of aquatic macrophytes, including *Juncus, Phragmites, Scirpus,* and *Typha,* serve as substrata for FWA. Taxa in the Loculoascomycetes were first noted in original descriptions and taxonomic treatises (Müller 1950, Holm 1957, Munk 1957, Leuchtmann 1984), but little was reported about their ecology. The first systematic effort to collect FWA on aquatic macrophytes was by Ingold (1951, 1954, 1955) and Ingold and Chapman (1952). These pioneering studies were followed by those of Webster and Lucas (1961), Dudka (1963), Pugh and Mulder (1971), Apinis et al. (1972a, b), Taligoola et al. (1972) and Magnes and Hafellner

(1991). Although Ingold (1955) predicted a rich pyrenomycetous FWA mycota on aquatic macrophytes, this group has been largely ignored. Little is known about any aspects of the biology and ecology of this group, especially the nature and specificities of their interactions with their hosts. Magnes and Hafellner (1991) recently collected Ascomycetes on emergent plants surrounding alpine lakes to determine substratum relationships. Among 52 taxa, they found one large group of species that appeared to be totally unspecialized and that occurred on a variety of plant hosts. They found 17 species that appeared to be substrate specific but they did not consider these species to be parasitic. Seven species occurred on two distantly related plants, *Carex* and *Equisetum*. Some FWA occur on living submerged stems of macrophytes (Ingold and Chapman 1952, Ingold 1955, Webster and Lucas 1961, Dudka 1963, Dennis 1968, Apinis et al. 1972b, Nannfeldt 1985). Whether these fungi are parasitic or endophytic on their hosts has not been determined. A number of species of Loculoascomycetes have been reported from dead macrophytes (Dudka 1963, Apinis et al. 1972a and b, but whether they were actively growing on their hosts before they died or colonized them saprophytically after death of the hosts is not known. In several studies, the succession of fungi on emergent macrophytes has been followed (Pugh and Mulder 1971, Apinis et al. 1972a and b, Taligoola et al. 1972). For *Typha latifolia,* during the early stages of leaf emergence, the mycota was dominated by species of yeasts and dematiaceous hyphomycetes. After the leaves died, however, species of Loculoascomycetes (*Phaeosphaeria, Paraphaeosphaeria, Leptosphaeria* and *Nodulosphaeria*) became prominent (Pugh and Mulder 1971). Ascomycetes were present in early (*Massarina* and *Wettsteinina*) and late (*Ophiobolus, Lasiosphaeria* and *Passeriniella*) stages of succession on submerged culms of *Phragmites australis* (Apinis et al. 1972b). *Massarina arundinaceae* was thought to assist in the weakening of culms of *P. australis* which results in eventual breakage at or below the water surface (Apinis et al. 1972b). How effective FWA are in decomposing macrophytes and whether they serve as a nutritional resource to detritivorous invertebrates needs to be determined. Critical studies of the life cycles of FWA on aquatic macrophytes are needed to elucidate their ecological role.

The majority of FWA have been reported from dead plant substrata. Whether this reflects a true preponderance of saprophytes over parasites and endophytes or the substratum bias of collectors is not known. Certainly there have been more studies of aquatic fungi on dead plant substrata, particularly allochthonous debris, than on living, autochthonous substrata. Thus the probability of detection may have favored saprophytic forms. Many of the saprophytic FWA in flowing water have been reported from woody debris compared to only a few from leafy debris (Table 1). The differential occurrence of FWA on these substrata has been discussed previously (Shearer 1992) and may be due to factors such as substratum longevity and/or nutrition.

Wood as a substratum for aquatic fungi has been studied relatively intensely (Dudka 1963, Shearer 1972, Willoughby and Archer 1973, Lamore and Goos 1978, Minoura and Muroi 1978, Shearer and von Bodman 1983, Shearer and Crane 1986, Révày and Gönczöl 1990, Shearer and Webster 1991) and numerous FWA have been reported from these studies. FWA have also been reported from water-saturated wood in cooling towers (Eaton and Jones 1970, 1971a and b, Eaton 1972, Eaton 1976). In addition, may new taxa of FWA have been described from wood in freshwater (Webster 1959, Webster and Lucas 1961, Webster 1965, Tubaki 1966, Jones and Eaton 1969, Eaton and Jones 1970, Iqbal 1972, Adullah and Webster 1983, Minoura and Muroi 1978, Shearer 1978, Shearer and Crane 1978a, Shearer and Crane 1980a and b, Abdullah et al. 1981, Fisher and Petrini 1983, Fisher and Webster 1983, Monod and Fisher 1983, Shearer 1984, Shearer 1989a and b, Webster et al. 1991, Crane et al. 1992, Hyde, in press).

The role of FWA in enzymatically degrading wood is largely unknown. Cultural studies of seven lignicolous FWA and an anamorph of a FWA (Zare-Maivan and Shearer 1988a) revealed that they were all enzymatically able to degrade a wide range of wood components including starch, xylose and cellulose. With the exception of two *Nectria* species and the anamorph of *N. lugdunensis, Heliscus lugdunensis* Sacc. and Théry, all species formed soft-rot cavities in balsa, ash and cottonwood. In another study of the same species (Zare-Maivan and Shearer 1988b), all were found to produce coupled cellulases, but species differed in their ability to decay wood and form soft-rot cavities. The *Nectria* species, including the anamorph, *H. lugdunensis,* and *Nais inornata* caused little weight loss in ash and cottonwood blocks compared to four other species. *Nectria* species are often the first FWA to appear on newly submerged wood and disappear at a relatively early stage of decay (Willoughby and Archer 1973, Shearer and von Bodman 1983). Since the *Nectria* species tested thus far are unable to degrade wood through the formation of soft-rot cavities, it is likely that they use components of wood other than secondary walls such as proteins, starch and soluble sugars. These substances occur in relatively small quantities compared to the cellulose, hemicelluloses and lignins of secondary walls and they disappear relatively early in the decomposition process by leaching and microbial utilization. This may explain, in part, the early disappearance of *Nectria* species from wood (Willoughby and Archer 1973, Shearer and von Bodman 1983). The early disappearance of these species also may be brought about by the antagonistic activities of more competitive species. In a study of hyphal interactions among lignicolous fungi, the same *Nectria* species discussed above were among the species least resistant to the antagonistic activities of other fungi (Shearer and Zare-Maivan 1988).

By virtue of their ability to soften wood by the formation of soft-rot cavities, lignicolous FWA may play an important role in increasing the palatability of wood to stream invertebrates. Dudley and Anderson (1982) indicate that softening is necessary before submerged wood can be used by invertebrate scrapers and gougers. They also suggest that wood borers are partially dependent on microbes for nutrition. Pereira et al. (1982) have found fungal hyphae and spores associated with wood in the gut contents of wood borers, gougers and grazers. Birchwood sticks precolonized with the FWA, *Pseudohalonectria lignicola,* and then placed in a stream showed evidence of wood gouging after eight weeks of submersion (Shearer unpublished) and *Asellus* sp. was successfully maintained in the laboratory on *P. lignicola* growing on birchwood (Shearer and Mattingly unpublished). The importance of leaf-degrading fungi to stream invertebrates has been well-documented (Suberkropp 1992); whether lignicolous FWA play a similar role awaits further investigation.

Recently, it was found that lignicolous aquatic fungi were generally more antagonistic and resistant to antagonism than their foliicolous counterparts (Shearer and Zare-Maivan 1988). These data supported the hypothesis that fungi on long-lasting substrata such as wood have more competitive strategies than those on less long-lasting substrata such as leaves (Pugh 1980). Included in this study were 10 lignicolous and 2 foliicolous FWA. Both the foliicolous and Nectriaceous lignicolous FWA were poor competitiors compared to the other FWA. Among the most competitive lignicolous FWA were four species of *Pseudohalonectria.* Species in this genus were subsequently found to be antagonistic at a distance against a wide range of fungal taxa suggesting that they produce a diffusible inhibitor (Asthana and Shearer 1990). Cultural antagonism is not always correlated with antagonism in the field (Webber and Hedger 1986). However field experiments with *P. lignicola* and *P. adversaria* demonstrated that these species were able to defend colonized substrata against invasion by other species while a weakly antagonistic species, *N. haematococca,* was not (Shearer and Bartolata unpublished). Willoughby and Archer (1973) suggested earlier that competition might occur between lignicolous FWA because rarely more than one or two species colonized a single twig. In addition, of the five FWA recorded from 41 twigs in their study, two species, *Ceratostomella* sp. and *Mollisia* sp. never occurred together. Fisher and Anson (1983) found that *Massarina aquatica,* a lignicolous FWA, produces antifungal substances in culture on natural substrata. In recent field experiments with the anamorph of *M. aquatica, Tumularia aquatica* (Ingold) Descals and Marv., this species excluded competitors from colonized wood (Shearer and Webster unpublished). These data suggest that FWA, through their antagonistic activities, may play an important role in organizing freshwater lignicolous fungal communities.

Little is known about the response of FWA to environmental parameters such as temperature, seasonality, water chemistry, flow rates, and degree of submergence. Factors influencing ascospore formation, liberation, dispersal, attachment and germination are also largely unknown. Intraspecific and interspecific interactions of FWA are also largely unstudied.

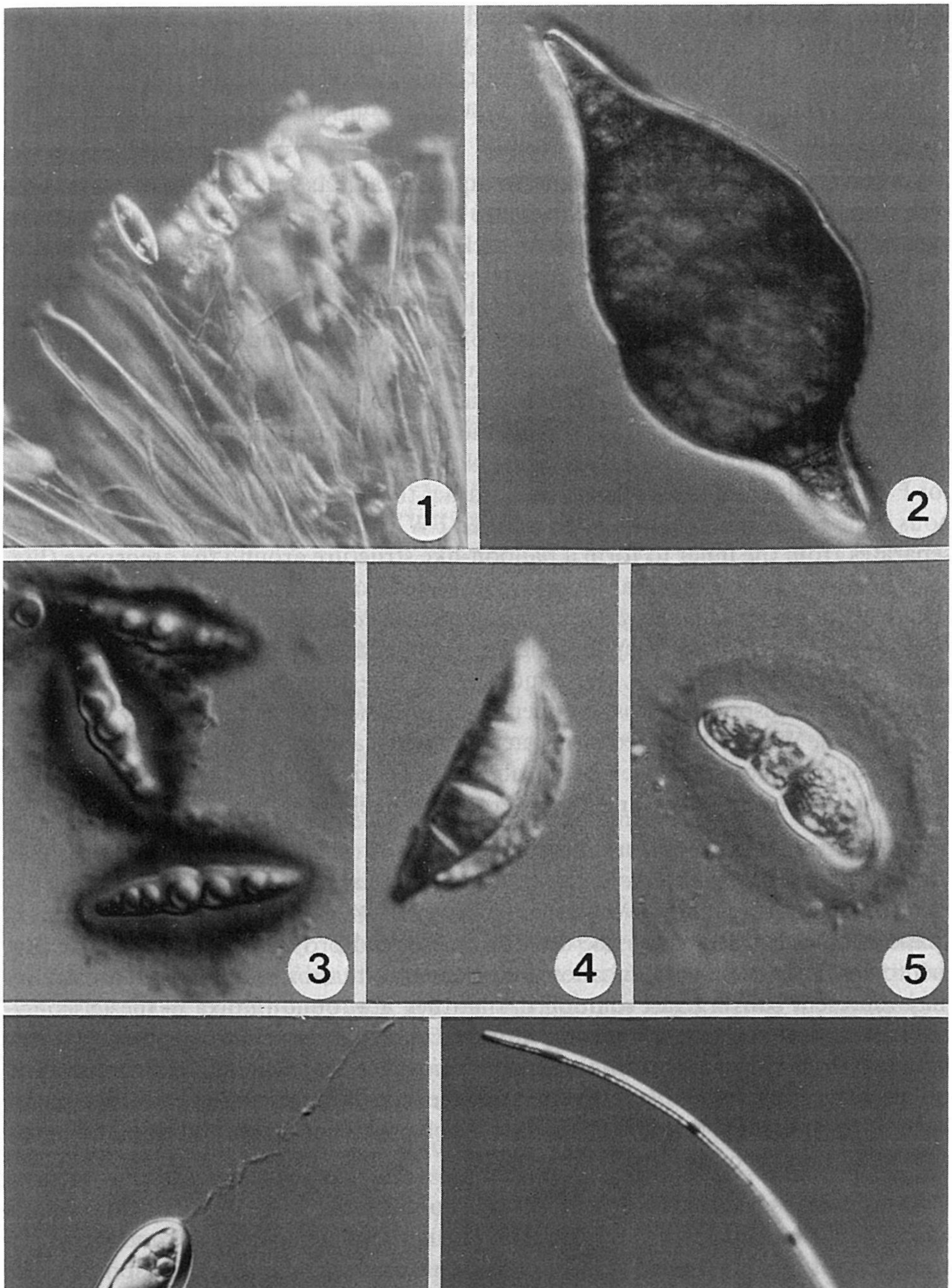
Evolution

It is likely that most FWA have evolved from terrestrial ancestors via a variety of evolutionary pathways. One pathway is as pathogens, endophytes and saprophytes of wetland and aquatic plants. As these plants invaded freshwater habitats, they no doubt brought their associated microorganisms with them. Fungal species able to survive and adapt to aquatic habitats may have been ancestral to present-day species that occur on freshwater macrophytes. Included in this group are primarily taxa in the Discomycetes and Loculoascomycetes. A second route to freshwater may have been on riparian vegetation such as tree and shrub litter. This debris carries with it a considerable complex of fungi capable of adapting to freshwater. Included in this group are species of Discomycetes, Hypocreales, Sordariales, Halosphaeriales and Loculoascomycetes. A third route to freshwater may have been through the runoff of rainwater and sediments. Included in this group may be species of Eurotiales, Sordariales and Hypocreales.

Kohlmeyer and Kohlmeyer (1979) suggested that extant marine fungi could be divided into two groups based on their origins. Primary marine fungi (Halosphaeriales, Spathulosporales) evolved directly from a marine ancestor, probably one common to both marine fungi and red algae. Secondary marine fungi originated from terrestrial ancestors and are mostly saprophytic. Kohlmeyer and Kohlmeyer (1979) agree with Saville (1968) that parasites are more ancient than saprophytes and they consider that the most ancient types of marine Ascomycetes are Spathulosporales and some parasitic Sphaeriales on marine Rhodophyta.

Some FWA taxa included in the Halosphaeriales and presumably considered by Kohlmeyer and Kohlmeyer (1979) to be of primary origin i.e., from a marine ancestor, (e.g. *Aniptodera, Halosarpheia, Nais*) occur commonly in freshwater. The occurrence of these taxa in freshwater could mean that (1) some marine Ascomycetes migrated from seawater to freshwater, or (2) some of the taxa now included in the Halosphaeriales are not of primary origin, but evolved from terrestrial or freshwater species. According to the first idea, these species could have migrated to freshwater from seawater by intertidal mixing or by travelling on the bodies of migrating waterfowl. A plausible argument, however, could be made for their terrestrial origin and subsequent migration to freshwater and then to seawater. A constant downstream movement of ascomycete substrata occurs and it is not unreasonable to expect that some terrestrial Ascomycetes adapted to freshwater and then seawater via this route. Ascomata in the above genera are made of thin-walled pseudoparenchyma and are beaked, features which are characteristic of several families in the Sordariales. They also share the lignicolous habitat with members of the Lasiosphaeriaceae in the Sordariales. Adaptations to freshwater may have included disappearance of the ascus apical apparatus, release of ascospores through the deliquescence of asci, modification of physes to form chains of enlarged cells (catenophyses), and presence of viscous ascospore appendages. In the genus *Aniptodera,* for example, various degrees of modification of the ascus apex can be seen from *A. chesapeakensis* with a distinct apical pore and thickening of the wall of the ascus apex to *A. rosea* with no pore or thickening. In *A. chesaspeakensis,* ascospores may be forcibly discharged or may accumulate outside the beak after dissolution of the asci. Environmental conditions influence the method of ascospore liberation. In *A. rosea,* asci deliquesce early to release ascospores. Compelling evidence to support either hypothesis about the evo-

Fig. 1. Asci and ascospores of *Aquadiscula aquatica* from leaves of *Acer rubrum* submerged in LaRue Swamp, Union County, Illinois. ×680. Fig. 2. Ascospore of *Caryospora callicarpa* from wood submerged in Jordan Creek, Illinois. Note thin layer of gelatinous material surrounding the ascospore. ×870. Fig. 3. Ascospores of an unidentified species of *Massarina* from wood submerged in Jordan Creek, Illinois. The thick gelatinous sheath surrounding the ascospore is stained with India ink. ×1,190. Fig. 4. Ascospore of an unidentified ascomycete from a decorticated oak twig submerged in the River Teign, Devon, England. A thin outer layer appears to separate from the ascospore wall to form a balloon-like structure. ×1,700. Fig. 5. Ascospore of *Phaeosphaeria typharum* from *Typha latifolia,* St. Anthony Head, Cornwall, England. The broad gelatinous sheath surrounding the ascospore is stained with India ink. ×1,133. Fig. 6. Ascospore of *Aniptodera chesapeakensis* with unfurling appendage from wood submerged in Jordan Creek, Illinois. ×704. Fig. 7. Filiform ascospore of *Ophioceras* sp. 652-1 from wood submerged in Allee Creek, Barro Colorado, Panama. ×800.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lution of these taxa does not now exist. More intensive collecting of FWA may reveal the existence of other taxa related to the Halosphaeriales, but because of possible convergent evolution, traditional morphology-derived systems of classification may not be indicative of the true evolutionary relationships. Biochemical and/or molecular techniques may prove to be more informative and useful.

FWA have adapted morphologically to aquatic habitats in a variety of ways. One type of modification involves the presence on ascospores of viscous, sticky appendages which may enable ascospores to stick onto substrata and remain attached in the face of water movement. Species in *Aniptodera, Aquadiscula, Ceriospora, Ceriosporopsis, Halosarpheia* and *Nais* all have ascospores equipped with viscous appendages. The appendages of species of *Halosarpheia* and *Aniptodera* (Fig. 6). unwind to form extremely long threads which may help entangle the ascospore with substrata (Shearer and Crane, 1980). Marine Ascomycetes have evolved a fascinating array of ascospore appendages involving the fragmentation and/or extension of outer ascospore walls (Jones and Moss 1978). None of the appendages reported thus far for FWA result from these mechanisms, rather they are simple, apical and mucilaginous. One exception may be an undescribed FWA with ascospores whose outer wall separates from the inner to form a balloon-like structure around the ascospore (Fig. 4). The ascospores of several loculoascomycete taxa are equipped with gelatinous sheaths (*Caryospora, Leptosphaeria, Massarina, Phaeosphaeria, Pleospora, Trematosphaeria*) (Figs. 2-3,5) or apical gelatinous appendages (*Ascalgilis, Lophiostoma, Rebentischia, Wettsteininia*). Since most of the foregoing genera contain terrestrial species with ascospore sheaths or appendages, aquatic representatives may have been pre-adapted. When introduced into water, terrestrial ancestors with ascospore sheaths or appendages may have been better able than species lacking these features to attach to substrata in water and thus were more likely to succeed.

Many FWA have long filiform ascospores (Fig. 7) which assume a sigmoid shape in water (Table 3). The sigmoid spore form as an adaptation to aquatic habitats has been discussed frequently (Webster and Davey 1984, Webster 1987). The sigmoid shape is thought to increase the area of orthogonal projection and the long, filamentous form is thought to enhance entanglement with substrata. Sigmoid ascospores may represent convergent evolution in that they are found in taxa in the Discomycetes (*Apostemidium, Loramyces, Niptera, Obtectodiscus, Vibrissea*) and Pyrenomycetes (*Ophioceras, Gaeumannomyces, Plagiosphaeria, Pseudohalonectria*) and Loculoascomycetes (*Ophiobolus*). Again, since the terrestrial taxa in some of these genera have filiform ascospores, it is difficult to resolve whether pre-adaptation or convergent evolution or both have occurred.

Ascomal and ascus structure and function do not seem to be modified for aquatic habitats. There is little difference in these structures between aquatic and terrestrial counterparts. As mentioned previously deliquescent asci are present in some genera (*Aniptodera, Halosarpheia, Nais*). It is thought that this is an adaptation to water as ascospores can be washed from ascomata and forcible discharge is not necessary. In some genera that are probably immigrants, such as *Chaetomium* and *Zopfiella*, asci are typically deliquescent. An interesting situation exists in *Pseudohalonectria* (Shearer 1989a) and *Ophioceras*, (Conway and Kimbrough 1978)in which the asci,

Table III. Spore adaptations of freshwater Ascomycetes.

A. **Adaptation of teleomorph and anamorph.**

Filiform ascospore/branched conidium - *Vibrissea flavovirens*

Filiform ascospore with gelatinous sheath/sigmoid conidium - *Loramyces juncicola*

Sheathed ascospore/knobbed conidium - *Massarina aquatica*

Sheathed ascospore/sigmoid conidium - *Massarina* sp.

Sheathed ascospore/tetraradiate conidium - *Massarina* sp.

B. **Adaptation of teleomorph.**

Sigmoid or filiform ascospores - *Apostemidium* (all species), *Gaeumannomyces graminis*, *Gorgoniceps boltonii*, *Ophioceras* (all species), *Pseudohalonectria* (all species), *Niptera excelsior*, *N. melanophaea*, *N. pulla*, *Coleosperma lacustre*, *Loramyces macrospora*, *Obtectodiscus aquaticum*, *Vibrissea* (all species), *Cudoniella clavus*, *Plagiosphaeria nilotica*.

Gelatinous appendage on ascospore - *Aniptodera chesapeakensis*, *A. lignatilis*, *Aquadiscula aquatica*, *Ascalgilis bipolaris*, *Ceriophora* sp., *Ceriospora caudae-suis*, *Ceriosporopsis* sp., *Halosarpheia lotica*, *H. parva*, *H. retorquens*, *H. viscosa*, *Lophiostoma arundinis*, *L. appendiculata*, *Rebentischia unicaudata*, *Nais inornata*, *Phaeosphaeria herpotrichoides*.

Gelatinous sheath on ascospore - *Loramyces macrospora*, *Leptosphaeria acuta*, *Massarina amphibia*, *M. aquatica*, *M. australiensis*, *M. tetraploa*, *Nectriella lacustris*, *Nimbomollisia melatephroides*, *N. eriophori*, *Phaeosphaeria alpina*, *Ph. caricinella*, *Ph. culmorum*, *Ph. eustoma*, *Ph. typharum*, *Pleospora gaudefroyi*, *P. palustris*, *P. scirpicola*, *P. submersa*, *Pyrenophora typhaecola*, *Wettsteinina niesslii*.

C. **Adaptation of anamorph.**

Aeroaquatic conidium - *Hyaloscypha lignicola*, *H. zalewski*

Branched conidium - *Hymenoscyphus africanus*, *H. splendens*, *H. tetracladius*, *H. varicosporoides*, *Miladina lechithina*, *Nectria lugdunensis*

Sigmoid conidium - *Hymenoscyphus inberbis*, *Mollisia uda*, *Mollisia* sp., *Nectria* sp., *Orbilia* sp., *Pezoloma sp.*

Helicosporous conidium - *Hymenoscyphus paradoxum*, *Lambertella tubulosum*, *Mollisia gigantea*, *Tubeufia paludosa*.

which separate from the ascogenous hyphae and assume a sigmoidal shape, are discharged from the ascomata. In some cases, filiform ascospores are released inside the ascomata and ooze out through the beak, and in some cases the ascospores are forcibly shot from the ascomata. In submerged culture, both asci and ascospores are released simultaneously. The retention of ascospores together in asci presumably would be advantageous if mating types were necessary. All of the species with this type of discharge pattern, however, are homothallic. The larger size of the ascus compared to a single ascospore may improve the chances of impaction on a substrate. The marine ascomycete, *Lignincola laevis* Höhnk, also liberates asci from ascogenous hyphae prior to ascospore discharge.

Numerous FWA may have adapted to aquatic habitats via their anamorphs. Anamorphs with branched, tetraradiate, sigmoid, helicosporous, and multicellular air-trapping conidia have been reported for FWA (Table 3). Only five species have both ascospores and conidia morphologically specialized for the aquatic habitat. The sigmoid conidial form appears to have evolved in several different evolutionary lines; it occurs in the Discomycetes, Pyrenomycetes and Loculoascomycetes. Comparable adaptation by anamorphs has not occurred in marine Ascomycetes. Only four similar teleomorph-anamorph connections have been made for marine Ascomycetes, two with tetraradiate, one with sigmoid, and one with helical conidia (Kohlmeyer and Volkmann-Kohlmeyer 1991). This is not surprising given that seawater apparently selects against conidial forms (Shearer 1972).

Conclusions

Studies of FWA are few, but they indicate that FWA comprise a diverse group consisting of indwellers and immigrants. Although there is some overlap, FWA differ taxonomically from the marine Ascomycetes. FWA vary in their degree of morphological adaptation to the aquatic habitat and have adapted morphologically primarily by ascospore modifications and/or conidial specialization. There are two major ecological groups of FWA: parasites or endophytes of aquatic and wetland macrophytes, and saprophytes of dead plant material. Additional study is needed regarding the systematics, geographical distribution, biological activities, life histories and responses to environmental factors of this challenging group.

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Usnea aurantiacoatra (Jacq.) Bory

Two collections on volcanic rock, mostly above 100 m altitude (96-09, 111-13). An Antarctic species.

Verrucaria famelica Darb. *

Rather uncommon on volcanic rock, also on concrete (79-02). This species is known only from the Antarctic region. The material from Deception Island agrees well with type material (South Shetland Islands, Nelson Island, Skottsberg 11.I.1902, BM).

Verrucaria maura Wahlenb. ex Ach. **

One collection on volcanic rock in the salt-spray zone (117-01). A cosmopolitan species.

Xanthoria candelaria (L.) Th. Fr.

Common, mostly on wood, but also on iron, asphalt paper and volcanic rock (29-04). A cosmopolitan species.

Xanthoria elegans (Link) Th. Fr.

Rather uncommon, on volcanic rock only (96-03). A cosmopolitan species.

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