AQUATIC FUNGI
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Ainsworth and Bisby (1963) define aquatic fungi as fungi living in water. The aquatic fungal populations in fresh water and seawater consist of representatives of the Phycomycetes, Fungi Imperfecti, Ascomycetes and the Basidiomycetes (Sparrow 1968; Johnson 1968). A submerged aquatic mycoflora which produces non-motile spores has been described by Ingold (1954, 1959, 1961) Nilsson (1964) and others. In the majority of species the spores are branched and the commonest type is composed of four arms diverging from or near a common point (Ingold, 1966). These tetraradiate spores occur in all the main groups of fungi, some of the Phycomycetes, although most belong to the fungi imperfecti. In a number of other aquatic species the spores are sigmoid or crescent shaped. Few aquatic species have spherical or ovoid spores, the commonest spore shape of sub-aerial species (Ingold 1959). Amongst the Phycomycetes, the aquatic species produce motile zoospores (Sparrow 1960).

From the heterotrophic nature of fungi, it seems their role in the aquatic environment is concerned with the utilization and transformation of organic matter (Sparrow 1968). Various groups of saprophytic fungi attack many kinds of submerged plant and animal debris (Johnson 1968; Sparrow 1968) but there is little information concerning the precise function of individual species. However, some aquatic fungi appear to be physiologically specialized for the destruction of specific substrates, for example; lignin, cellulose, chitin and keratin. Other aquatic
fungi, through parasitism exercise an important influence on biological productivity (Sparrow 1960).

In addition, fungi which are not normally considered part of the aquatic biota are found in aquatic habitats (Johnson and Sparrow 1961; Willoughby and Collins 1966; Anastasiou and Churchland 1969; Bridge-Cooke 1968; Newton and Hodkinson 1971; Pugh and Mulder 1971). Although of terrestrial origin, many of these fungi are associated with decaying plant material in water.

**PHYCOMYCETES**

The Phycomycetes are ordinarily considered the most primitive of the true fungi. As a whole, they include a wide diversity of forms some showing definite relationships to the flagellates, others closely resembling colorless algae, and still others being true molds. The vegetative body (thallus) may be unspecialized and entirely converted into a reproductive organ, or it may bear tapering rhizoids, or be mycelial and very extensive. In any event, the outstanding characteristic of the thallus is a tendency to be nonseptate and in most groups, multinucleate, cross walls being laid down in vigorously growing material only to delimit the reproductive organs. The unit of nonsexual reproduction the spore, is borne in a sporangium, and in the aquatic and semi-aquatic orders, is provided with a single posterior flagellum, a single anterior flagellum, or two laterally or terminally attached ones. Sexual reproduction is accomplished in
one great group, the zygomycetes by conjugation of the tips of two mycelial branches, which results in the formation of a thick-walled zygospore, only non-motile spores are formed. In the other groups generally spoken of collectively in the older literature as the oomycetes, there is great diversity in the method of sexual reproduction and as in the green algae, all gradations from isogamous planogametic to oogamous aplanogametic types occur. Moreover, the character of the sexual reproduction is not necessarily linked with the degree of thallus development.

The Phycomycetes comprise the following orders, which are here grouped in three series

Chytridiales
Blastocladiales
Monoblepharidales
Hyphochytriales
Plasmodiophorales
Saprolegniales
Leptomitales
Lagenidiales
Peronosporales

Zoosporic, aquatic

Zoosporic or conidial terrestrial except for the Pythiaceae which are amphibious

Mucorales
Entomophthorales

Conidial, terrestrial except for *Ancylistes* of the Entomophthorales
The zoosporic aquatic series, with which we are primarily concerned is composed of fungi which live as saprophytes or parasites on various plants and animals or their parts, in water or in damp soil. In this field, however, as elsewhere in biology, no hard and fast distinction can be drawn between aquatic, amphibious and terrestrial organisms. The many and diverse soil-inhabiting zoosporic types isolated in recent years are all clearly related to and usually congeneric with purely aquatic forms and have no doubt only secondarily invaded land. Another even more striking instance of what may be termed adaptive radiation is to be seen in *Ancylistes*, a member of a conidial terrestrial order (the Entomophthorales), which occurs as a parasite of desmids, a group of strictly aquatic algae. Also, this is found in the elegant series of aquatic, amphibious, and terrestrial fungi belonging to the Peronosporales, at least one genus, *Phytophthora* that is well known both to plant pathologists and to the students of aquatic fungi.

**ASCOMYCETES**

In the marine environment, Ascomycetes are important and well known colonizers of woody substrata (Kohlmeyer and Kohlmeyer 1979). With the exception of two studies (Willoughby and Archer 1973; Lamore and Goos 1978) little information is available about Ascomycetes colonizing woody substrata in fresh water.
Some Ascomycetes occurred exclusively on either bark or wood, so the rates at which twigs become debarked may have affected the patterns of occurrence of Ascomycetes. The species of Ascomycetes collected are few most of these species have been reported from other aquatic habitats of the Ascomycetes which have been reported previously from water. Aniptodera, Halosarphaea, Lutterillia, Nais, Savoryella and Zopfella have been reported from either brackish and seawater. According to Jones Savoryella lignicola also occurs in a number of fresh water habitats. Since Ascomycetes have not been collected extensively from fresh water, there are little data available for comparison to suspect that the species cited above, reported first from marine habitats, are probably regular inhabitants of fresh water habitats. In view of the constant downstream displacement of water and substrata in a seaward direction, it may be likely that these species originated in fresh water habitats and moved seaward on plant substrata or as spores released in water. A constant supply of new inoculum from fresh water rivers to brackish water habitats would provide an opportunity for selection for salt tolerant strains to occur.

Ascomycetes with appendaged or scolecosporous ascospores are very common in marine waters (Kohlmeier and Kohlmeier 1979). Such appendages are thought to be important in keeping ascospores suspended in water, thereby facilitating dispersal, and aiding in attachment of spores. Ascomycetes with ascospores having appendages similar to those of many marine Ascomycetes, exclusive of species in Halosarphaea were not found.
Direct observation of twigs yielded the lowest members and frequencies of occurrence of Ascomycetes, although frequencies increased towards the end of the study. Short term incubation of twigs in moist chambers yielded slightly more Ascomycetes than short term incubation in submerged shake cultures and both techniques yielded more species and greater frequencies of occurrence than direct observation. There are certain reports that the best technique for finding Ascomycetes on submerged substrata is incubation of substrata for long periods of time in moist chambers. Unfortunately, it is during long periods of incubation that spores and hyphae of species not normally active in the aquatic environment can grow and sporulate. In addition, the moist chamber is a much different environment than the flowing water habitat for ex: In the moist chamber, metabolic products can accumulate and may be inhibitory to certain species.

Light appears to be necessary for fruitbody formation in a number of Ascomycetes especially discomycetes and light also increases the frequency of occurrence of other species whether these effects are due to a particular wavelength of light and temperature to fruiting in fresh water Ascomycetes need to be investigated. Based on the evidences of Shearer's et al study, substrata from aquatic habitats should be incubated under light or dark conditions to obtain the most complete Ascomycete mycota.
Lamore and Goos (1978); Willoughby and Archer (1973) reported two species of *Nectria* as an early colonizer. *Leptosphaeria* also colonized twigs within 12 days of submersion. Twelve species of *Leptosphaeria* have been reported from fresh water habitats (Ingold 1955; Pugh and Nylden 1971; Apinis et al 1972; Taligoola et al 1972; Lamore and Goos 1978) of all genera reported from fresh water habitats, *Leptosphaeria* contains the most species clearly, species in this genus are important in the fresh water habitat and probably may interface with both terrestrial and aquatic habitats. Species of *Leptosphaeria* are often found on emergent aquatic or wetland macrophytes (Pugh and Mulden 1971; Apinis et al 1972; Taligoola et al 1972) subject to fluctuating water levels.

The Ascomycetes of today form essentially a group of terrestrial fungi and aquatic Ascomycetes seen such a motley through that it is easier to regard them as re-migrants from the land than as allied directly to a central stock of aquatic proto-Ascomycetes from which present day land species may also have arisen.

Aquatic Ascomycetes are abundant in fresh waters (Ingold 1951, 1954, 1955; Ingold and Chapman 1952). In the sea some Ascomycetes are rather harmless parasites of larger seaweeds. In lakes the richest sources of aquatic Ascomycetes are the submerged, dead but often in situ, stalks of reed swamp plants such as *Phragmites communis* Trin. *Schoenoplectus lacustris* (L.) palla,
Typha latifolia L. and Equisetum fluviatile L. These nearly always bear ascocarps of various species.

Many species found in lakes and rivers are aquatic species of well known terrestrial genera, such as Leptosphaeria and appear little if at all modified in relation to the aquatic environment. However, it should be emphasized at this point that the chief feature of the study of aquatic Ascomycetes is lack of knowledge. Their taxonomy needs much fuller attention.

HYPHOMYCETES

Aquatic Hyphomycetes can be found in streams from the arctic circle to the equator (Barlocher 1992b) some species are cosmopolitan, others are restricted to or more common in a narrow range of latitudes. Geographical occurrence of the fungi seem to be broadly correlated with optimal temperatures for in vitro growth and sporulation. In species common in temperate regions, vegetative growth is generally highest between 15-25°C , where as sporulation often reaches a peak at some what lower temperatures (Webster et al 1976; Suberkropp 1984; Koske and Duncan 1974).

Aquatic Hyphomycetes are fungi that most commonly occur on dead leaves in streams and rivers and sporulate under water. They are also known as fresh water Hyphomycetes (Nilsson 1964) amphibious Hyphomycetes (Michaelides and Kendrick 1978) or Ingoldian fungi (Webster and Descals 1981). A majority form tetraradiate conidia (essentially with four diverging arms) some
produce sigmoid conidia (long, worm like, generally curved in more than one plane) some have spores of more conventional shape.

The first member of this group to be described was *Heliscus lugdunensis* Sacc at Therry. It was found on pine bark near Lyon, France, and in northern Italy, presumably in a terrestrial environment (Saccardo 1880) it performs the same ecological functions as other aquatic Hyphomycetes, but its conidium is clove shaped rather than tetraradiate or sigmoid.

In the same year, Hartig (1880) described a parasite of maple seedlings as *Cercospora acerina*. Later workers established its identity with *Centrospora acerina*, it is now known as *Myacentrospora acerina* (Hartig) Deighton (Neergard and Newhall 1951; Deighton 1972). This species is remarkably widespread and versatile, it is a well known plant pathogen (Wall and Lewis 1980) has been implicated in human infections (Deighton and Mulder 1977) and is also a common stream fungus (Ingold 1975a). At least morphologically, there are no consistent differences between the various strains and Iqbal and Webster (1969) showed that strains they isolated from a stream were pathogenic to carrots and parsnips. It was already known to Hartig (1880) that the fungus grows as a saprophyte as well as a parasite and he demonstrated that desiccated mycelium can survive for up to one year. This ability is now believed to be important for the dispersal of aquatic Hyphomycetes and their continued survival in a given area. An important step forward was made by De
Wildeman (1893, 1894, 1896). He described four more species of this group, three with tetraradiate and one with sigmoid conidia. He found them in ponds, ditches and marshy areas among algae, on willow leaves and on aquatic macrophytes (e.g. *Hippuris vulgaris* L.). He correctly identified the four-armed structures as conidia. He also noticed the similarity between the spores of *Tetracladium marchalianum* and some old doubtful and poorly defined genera of algae such as *Asterothrix* and *Cerasteria*. This similarity caused much confusion among Phycologists over the next few decades, and many continued to refer to *Tetracladium marchalianum* by its algal name (Huber-Pestalozzi 1925, 1938; Brutschy 1927; Klotter 1955). The conidia were often interpreted as representing the entire fungal thallus (of a planktonic fungus) and the two central knobs as spores. It became known as the Schmerzenskind (Huber-Pestalozzi 1938) or child of sorrow (Lowe 1927) of the algologists.

In 1906, Kegel discovered *Varicosporium elodeae* on dead or dying shoots of *Elodea canadensis*. He was the first to observe that prolific sporulation can be induced when agar blocks overgrown with the fungus are brought into distilled water. *Tetracladium setigerum* was described from leaves of *Angelica sylvestris* and *Casaresia sphagnorum* on *Sphagnum* by Fragoso (1920).

A breakthrough came in 1942 when Ingold discovered the typical habitat of these fungi. At that time, he was working for chytrids, in an alder-lined stream behind his house (Barlocher...
1992b) to his utter amazement he discovered a large collection of fungal spores in scum trapped behind a barrier of twigs. It took him about 3 months to connect these conidia to mycelia growing and sporulating on alder and willow leaves. When he placed freshly collected leaves in shallow dishes of waters, rich crops of conidiophores appeared with in two days.

In his first of many papers on aquatic Hyphomycetes; Ingold illustrated sixteen species but their shapes were of two basic types: tetraradiate or sigmoid. This indicates parallel evolution and Ingold (1942, 1953) listed three possible functions of the complex spore shape 1. It might slow down sedimentation and thus ensure adequate dispersal 2. It might allow the conidium to act as an anchor and become entangled in a suitable substrate 3. The complex shape might protect the conidia against ingestion by small aquatic animals.

Webster (1959) demonstrated that the function of the spore shape of aquatic Hyphomycetes is probably to minimize down stream transport. When a tetraradiate spore makes contact with a surface it does so at three points and acts as a tripod, which represents a very stable form of attachment. Sigmoid spores in a low speed current tend to bump along the bottom, and conidial ends make frequent contact with the surface (Webster and Davey 1984). When they come to rest, they usually have two points of contact at one end and at a point along the length. The functional significance of spore shapes in fresh water and marine fungi was recently reviewed by Webster (1987).
Finally the mere fact that conidia of aquatic Hyphomycetes are comparatively large increases their probability of encountering a target (Cox 1983).

Air bubbles rising through water efficiently capture fungal spores, and examination of foam is believed to give a reasonably complete list of aquatic Hyphomycetes occurring in a given stream (Ingold 1975a).

Ingold's discovery (1942) ushered in an era where reports of the occurrence of these fungi multiplied. It has been called the starting point of a minor mycological industry (Ainsworth 1976). Among the more comprehensive studies are those dealing with California (Ranzoni 1953) Japan (Tubaki 1957) the eastern United States (Petersen 1962, 1963a, b) Scandinavia (Nilsson 1964) and the Soviet Union (Dudka 1985). The great taxonomic advances that have been made is well illustrated by Nilsson's remark (1964). Ingold continued to describe new species from all over the world (Diet et al 1985). His guide to aquatic Hyphomycetes (Ingold 1975) summarized taxonomic knowledge to that point, and contains much useful information on occurrence, ecology and techniques to study these fungi. A comprehensive, up to date monograph of aquatic Hyphomycetes is being prepared by E. Descals, L. Marvanova and J. Webster.

Aquatic Hyphomycetes occur on almost any type of plant debris and also superficially on glass and plastic, wood is of particular importance because of its long residence time, and
because it is the main site of sexual reproduction. Most commonly, dead branches and twigs serve as substrata; however aquatic Hyphomycetes also occur on or in roots (Waid 1954). They appear to be the common in roots of riparian alder trees (Fisher et al 1991).

Macrophytes sometimes replace autumn shed leaves as the major sources of detrital material in streams.

Aquatic Hyphomycetes are cosmopolitan in their distribution, extending from the arctic circle to the equator (Kobayasi et al 1967, 1971; Muller-Haeckel and Marvanova 1976, 1979; Webster and Descals 1981; Engblom et al 1986, Bhat and Chien 1990). Optimal temperatures for invitro growth and sporulation are broadly correlated with the geographical occurrence of the fungi. It is important to remember, however, that stream temperature usually declines with altitude.

By the late 1960's research into taxonomy, biology and ecology of aquatic Hyphomycetes was well advanced. Never the less, few stream ecologists were probably aware of these fungi.
SPHAEROPSIDALES

Some reference should be made to the aquatic Sphaeropsidales which are probably not uncommon on submerged dead, red swamp plants. Their taxonomy is in need of careful study. Two examples may be noted: Cunnell (1958) described Robillarda phragmitis Cunnell on submerged dead stems of Phragmites communis L. The conidia are essentially tetraradiate and are quite commonly encountered in the spora of streams both in temperate and in tropical regions. Another aquatic species with conidia having long appendages is Chaetospermum chaetosporum (Pat.) A.L. Smith et Ramsb; which de Fonseka (1960) found on a submerged decaying leaf of alder. Not too much significance should, however, be attached to the morphology of these conidia for, as already remarked contain coprophilous members of the Sphaeropsidales also have conidia of a form more usually associated with an aquatic habitat.