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## Freshwater and marine lichen-forming fungi

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**D.L. Hawksworth<sup>1</sup>**

MycoNova, 114 Finchley Lane, Hendon, London NW4 1DG, U.K.; e-mail: myconova@btinternet.com

Hawksworth, D.L. (2000). Freshwater and marine lichen-forming fungi. In: *Aquatic Mycology across the Millennium* (eds K.D. Hyde, W.H. Ho and S.B. Pointing). Fungal Diversity 5: 1-7.

Lichen-forming fungi can occur on river and lake margins subjected to varying water levels, and on tidal coastal rocks where they can constitute major components of the biota. There are approximately 700 species known from coastal rocks and 200 from freshwater river and lake margins. Most cannot survive constant immersion although there are exceptions. Some species are only exposed at the lowest tides or when there are exceptional droughts. Vertical zonations of lichens are characteristic of freshwater and marine habitats. The heights of zones vary according to the degree of exposure and periods of inundation. Measurements of these zones can be of value in assessments of risks due to storms and of river channel capacity. Attention is also drawn to mycophycobioses in freshwater as well as maritime situations. Most work on coastal and freshwater lichens has been in temperate regions. In the tropics lichens are less well developed on coastal rocks, but tropical stream margins are yielding species new to science. The ecophysiology and biology of these fungi is scarcely explored, but some key features are highlighted. Many fundamental aspects of these fascinating fungi remain uncertain, for example where different species of the same genus occur in both habitats. The systematics, ecology and physiology of these fascinating fungi merit increased attention by mycologists.

**Key words:** ascomycetes, freshwater, fungi, lakes, lichens, marine, rivers, tropics.

### Introduction

Lichens are mutualistic associations between a fungus and one or more extracellularly located algae or cyanobacteria. The fungus forms the outer structure and encloses the photosynthetic partner (Hawksworth and Honegger, 1994). The scientific names of lichens used are those of the fungal partner; the algal and cyanobacterial partners have independent names. About 13,500 species are currently accepted and it is estimated that the actual world total will be in the range 17-20,000 (Galloway, 1992). The fungi involved belong to a variety of mainly ascomycete orders, most of which also include non-lichenized species. Some genera even include both lichenized and saprobic or lichenicolous fungi.

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<sup>1</sup> Present address: Departamento de Biología Vegetal II, Facultad de Farmacia, Universidad Complutense, Plaza de Ramon y Cajal, Ciudad Universitaria, E-28040 Madrid, Spain.

Freshwater and marine lichen-forming fungi are rarely studied by mycologists, even by those specialising on fungi occurring in these habitats, or on fungi in lichens themselves. This contribution aims to serve as a primer to what is known of the lichens in these habitats and to indicate aspects in need of further investigation.

### **Habitat ecology and zonation**

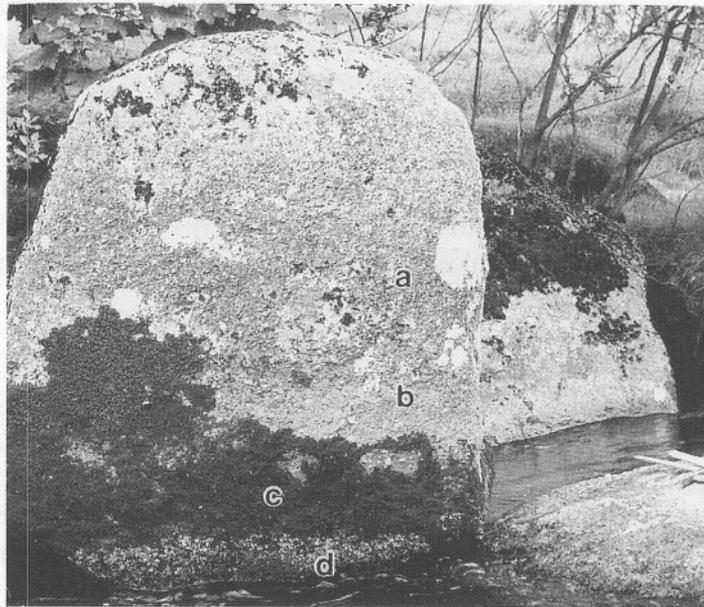
Lichen associations are primarily terrestrial and require alternate wetting and drying regimes for their survival. These circumstances occur principally on river and lake margins, subject to varying water levels, and in the tidal zones on coastal rocks. They can also arise on stabilised wood, bark, asphalt, plastic and other debris, as well as barnacles, shells, and algae. In both situations lichens can constitute major components of the biota and cover almost all rock surfaces. Around 700 species are known from tidal zones and 200 from freshwater river and lake margins, some occurring worldwide in suitable habitats (Santesson, 1939a). Most cannot survive constant immersion, although there are notable exceptions. Vertical zonation patterns develop and these correlate with different degrees of inundation, whether on a seasonal basis as in river margins or a daily basis where they are affected by tides.

### **Freshwater**

The pioneering work of Santesson (1939b) showed that lichen zonation on lake margins in Sweden was related to the periods of submersion to which the different lichens were subjected. He also recognized a "lichen line" below which foliose lichens, especially those with *Trebouxia* as their algal partner, could not survive. In some temperate regions the presence of *Parmelia conspersa* is an especially good indicator of the maximum height reached by the water in flood situations. This "lichen line" is also evident on adjacent trees where many species are eliminated at the highest water levels reached (Hale, 1984).

On acid watercourses in England, Gilbert and Giavarini (1997) recognized four zones:

1. Submerged zone, with, for example, *Collema dichotomum*, *Hymenelia lacustris*, *Placynthium flabelliforme*, *Poroscyphus kenmorensis*, *Staurothele fissa*, *Verrucaria aquatilis*, *V. funckii* and *V. praetermissa*.
2. Fluvial mesic zone, with *Aspicilia laevata*, *Bacidia inundata*, *Dermatocarpon meiophyllum*, *Ephebe lanata*, *Porpidia hydrophila*, *Verrucaria aeithiobola* and *V. latebrosa*.
3. Fluvial xeric zone, with *Aspicilia caesiocinerea*, *Catillaria chalybeia*, *Massalongia carnosa*, *Porina lectissima* and *Porpidia soredizodes*.
4. Fluvial terrestrial zone, with numerous terrestrial species, including "lichen line" indicators such as *Parmelia conspersa*.



**Fig. 1.** Granite boulder in river at Dartmeet, Dartmoor, Devon, U.K. showing vertical lichen zones characterized by *Porpidia hydrophila* (a), *Hymenelia lacustris* (b), *Ephebe lanata* (c), and *Dermatocarpon meiophilizum* (d). *Verrucaria aquatilis*, *V. funckii* and other *Verrucaria* species occur underwater below the *Dermatocarpon*. (Photograph: D.L. Hawksworth.)

An example of the distinct bands often produced is given in Fig. 1. Similar patterns are known from other parts of Europe (e.g. Ried, 1960a; Keller, 1989), and also in North America where in Idaho, Rosentreter (1984) recognized *Verrucaria* species as characterising the low-water zone and *Dermatocarpon reticulatum* the normal flood zone.

Species in the submerged zone can be exposed during summer droughts, although several can extend to 30 cm below summer water levels; and *Collema dichotomum* and *Verrucaria rheitrophila* down to 50 cm. Such species are exposed, if at all, in the most serious drought years and certainly experience several years with no direct contact with the air. The North American *Hydrothyria venosa* is also apparently always submerged.

Similar zonation patterns have been recognized around pools and water channels on granite kopjes in Zimbabwe (Scott, 1967). Here, the yellow-green *Dermatiseum thunbergii* is a particularly conspicuous upper zonal marker, with bands of *Acarospora schleicheri* and various *Heppia* species lower down. In the tropics, similar genera are involved to those in temperate regions, although it is often different species of those same genera. I recently collected an aquatic *Verrucaria* in Phuket, Thailand. McCarthy (1999) has described three *Porina*

species from aquatic and semi-aquatic habitats in that country, and noted that *Endocarpon adscendens*, and some species of *Staurothele* as well as *Verrucaria* may be present. Four aquatic *Verrucaria* species have been reported from various altitudes (500-2100 m) in Papua New Guinea (Aptroot, 1998).

The height of different vertical zones provides a measure of bankfull capacity of river channels at different times of the year, which is of potential importance in assessing risks of flooding especially where water depth is not regularly recorded. This potential was clearly recognized by Gregory (1976), but has hardly been examined since that time.

### **Marine and maritime**

The vertical zonation of lichens on rocky shores in temperate regions has been better documented than those in freshwater habitats. A detailed review of the earlier literature is included in Johnson and Sparrow (1961). Subsequently, particularly detailed investigations have been carried out on the rocky shores of Anglesey by Fletcher (1973a,b). He recognized four zones with some subzones:

1. Sublittoral.
2. Littoral (with eulittoral, e.g. *Lichina pygmaea* and *Verrucaria mucosa*; and littoral fringe, e.g. *V. maura*, subzones).
3. Supralittoral with (with mesic, e.g. *Caloplaca marina*, *Lichina confinis*; submesic, *Xanthoria parietina*; and xeric, e.g. *Anaptychia runcinata*, *Ramalina siliquosa*, subzones).
4. Terrestrial (with halophilic, e.g. *Parmelia saxatilis*; and halophobic, e.g. *P. omphalodes*, subzones).

The heights of the different zones, depends to a large degree, on exposure, with higher zones present on shores subject to the most severe storms. For example, at Start Point in Devon, *Caloplaca marina* occurs from 0-3 m above the spring tide high water level on north-facing shores and from 3.5 m to over 9 m on the more exposed south-facing shores (Hawksworth, 1980). *Lichina* species were absent on the more sheltered shores in this site. The same exposure effect has been reported from Hong Kong (Chu *et al.*, 2000). The recognition of such zones and their heights deserves more attention with respect to risk assessments due to potential storm damage in coastal sites.

Some lichen-forming fungi are only exposed at the lowest tides (e.g. *Verrucaria mucosa*), while others (e.g. *V. maura*) are exposed every day. *Pyrenocollema halodytes* partly depends on the presence of barnacle and limpet shells on which it often grows, while *P. pelvetiae* is associated only with fronds of the seaweed *Pelvetia canaliculata*.

In tropical areas coastal lichens are less developed, but when species do occur they are present in restricted vertical zones. For example Chu *et al.* (2000) found 27 species and recognised four zones on supralittoral rocks in Hong Kong, and on the east coast of Phuket, Thailand, *Verrucaria* belt occurs above a barnacle zone. In Hong Kong (Aptroot and Seaward, 1999) many non-

marine aquatic species (e.g. *Peltula* spp.) occur in the supralittoral zone where it is influenced by rain water run-off.

### **Mycophycobioses**

Mycophycobioses, in which the algal partner forms the outer structure rather than the fungus, are a particular feature of some freshwater and particularly marine associations. These are mentioned briefly here as these associations have been considered as lichens by some authors. Although falling outside the currently accepted definitions of lichens, their physiologies could well be comparable but remain to be explored in depth. On riversides in freshwater, *Phaeospora lemaneeae* grows within *Lemanea fluviatilis*, and in maritime situations *Blodgettia confervoides* is associated with *Cladophora* species (Hawksworth, 1987). Perhaps the best known mycophycobiosis is *Mycophycias ascophylli* on *Ascophyllum nodosum* and *Pelvetia canaliculata* (Kohlmeyer and Volkmann-Kohlmeyer, 1998).

### **Ecophysiology and biology**

The ecophysiology and biology of lichen-forming fungi in freshwater and marine habitats is scarcely explored. The ecological factors involved have been discussed by Ried (1960a,b) for some freshwater lichens, and by Fletcher (1980) for marine and maritime lichens. In general, the frequency and extent of submersion appear to be crucial, but in freshwater shading may also be contributory. Rock type is especially important, with very poor development of specialized communities on chalks and limestones in either habitat, although there are some specialized species in limestone streams (e.g. *Placynthium tantaleum*, *Staurothele succedens*).

In the case of the xeric supralittoral *Ramalina siliquosa*, different chemotypes distinguished by their secondary metabolites are able to occupy discrete ecological niches (Culberson and Culberson, 1967). The extent to which this kind of infraspecific specialization occurs within other lichens, and in relation to features other than metabolites, remains unclear. However, the amplitude of morphological variation in some species, especially ones that occur far inland such as *Xanthoria parietina*, is considerable and requires molecular investigation.

The photosynthetic partner in both freshwater and marine lichens, which are submerged for a substantial amount of time, is rarely *Trebouxia*, the commonest lichen-forming alga. The various genera involved include *Calothrix* (e.g. in *Lichina*), *Nostoc* (e.g. in *Pyrenocollema*), *Stichococcus* (e.g. in *Staurothele*), *Stigonema* (e.g. in *Ephebe*), and *Coccolobrya*, *Dilabifilum* and *Heterococcus* (all in *Verrucaria*).

The dispersal and establishment of lichens in freshwater and coastal situations is essentially unexplored territory. In *Staurothele*, a special strategy has developed; small algal cells grow inside the perithecium and are dispersed along with the ascospores. The ascospores of lichens in these habitats tend to be rather large and broadly ellipsoid. It is interesting to speculate whether such spores are adapted to lodge in the cracks of rocks, or are transported by grazing invertebrates. In some freshwater species in particular, either the ascospores or conidia are elongate-fusiform, acicular, or sigmoid. This is seen well in the conidia of *Lichingoldia gyalectiformis* (conidial *Bacidia inundata*; Hawksworth and Poelt, 1986). The methods of dispersal and attachment of these elongated spores may parallel those of other freshwater fungi, but this remains to be investigated.

Many research questions on fundamental aspects of these fascinating fungi remain unanswered. One topic that is especially intriguing is that some of the same genera occur in both freshwater and marine situations, but are represented by different species. Examples include *Lichina* (Henssen, 1969), *Pyrenocollema*, and *Verrucaria*. Further, in both situations the *Verrucaria* species involved vary according to the degree of inundation. Molecular studies to determine how speciation had progressed in relation to water type and tolerance of submersion would be fascinating.

This overview has been prepared to stimulate interest in these specialized fungi by mycologists. If you do decide to give them more attention, the opportunities for original work are considerable and I am sure will also prove to be stimulating.

### Acknowledgements

I am indebted to the British Mycological Society and the organizers of the 7th International Marine and Freshwater Mycology Symposium in Hong Kong for inviting me to present this paper and facilitating my participation in it; to my wife Patricia Taylor-Hawksworth for her comments on my draft manuscript; and to Mariette Cole for assisting in finalising the work for publication.

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(Received 15 July 1999, accepted 1 October 1999)