The variety of fungal–algal symbioses, their evolutionary significance, and the nature of lichens

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INTRODUCTION

The range and complexity of symbioses* between fungi and algae (or cyanobacteria) is staggering. In the last 10 years many fascinating cases have

*Symbiosis' is used here in the original sense of de Bary (1879) to refer to different organisms living together, whether in mutualistic, commensalistic, or antagonistic associations. This practice is in accord with that advocated by Starr (1975) and adopted by Cooke (1977), Ahmadjian & Paracer (1987), and Smith & Douglas (1987).
been brought to our notice which collectively both contribute to the century-old debate as to the nature of lichen associations, and provide indications as to their evolutionary significance.

In mutualistic (biotrophic) symbioses there is a stable relationship in which both partners benefit; in commensalistic symbioses one partner benefits but the other is not adversely affected or benefited; and in antagonistic (parasitic, necrotrophic) symbioses one partner benefits at the expense of the other which it often kills. These categories are not exclusive; the biological relationship may change with time from antagonistic to mutualistic, additional organisms such as bryophytes may be an integral part of the symbiosis, and rarely have the physiological, nutritional, and ultrastructural relationships been investigated. Individual fungal genera may even include species which are lichenized or not (see p.15). It is therefore only practical to discuss symbioses in terms of the number of participating organisms, or ‘bionts’ (Table 1). Poelt (1977) expressed these in terms of two-, three-, or four-membered symbioses; ‘biont’ is adopted here to conform with ‘mycobiont’ (fungal partner; Scott, 1957) and ‘photobiont’ (photosynthetic partner; Ahmadjian, 1982a).

TWO-BIONT SYMBIOSES

In mutualistic symbioses involving a single mycobiont and one photobiont, either partner may be the ‘inhabitant’ living partly or wholly inside the other, the ‘exhabitant’ (Law & Lewis, 1983). The numerous antagonistic symbioses where fungi are clearly parasitic on algae are not considered here; for further information on these see Jones (1976) and Kohlmeyer & Kohlmeyer (1979).

Mycobiont as inhabitant

The classic case of a mutualistic situation in which the mycobiont is the inhabitant or ‘endophyte’ is *Mycosphaerella asiphylli* Cotton on the brown

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seaweeds *Ascophyllum nodosum* (L.) Le Jolis and *Pelvetia canaliculata* (L.) Dcne & Thuret (Smith & Ramsbottom, 1915; Webber, 1967; Kohlmeyer & Kohlmeyer, 1972). The ascomata form mainly in the receptacles of the algae (Figs 1, 2) and the hyphae of the mycobiont ramify through the algal tissues (Fig. 3). Uninfested algae do not appear to survive in nature (Webber, 1967), but the physiology of the symbiosis remains obscure (Kingham & Evans, 1986). The algae reproduce sexually, and, contrary to the general theory of Law & Lewis (1983), the mycobiont forms both ascospores and conidia (spermatia) at the surface of the algal fronds; this suggests the symbiosis is relatively recent in origin and the selective pressure for the loss of sex is not strong in this instance. A similar situation is suspected in the case of *M. apophlaeae* Kohlm. on the red algae *Apophlaea lyallii* Hooker fil. & Harvey and *A. sinclairii* Harvey, forming circular crustose thalli with concentric growth rings (Kohlmeyer & Hawkes, 1983).

Kohlmeyer & Kohlmeyer (1972) introduced the term 'mycophycobiosis' for mutualistic associations in which the alga retained its form and continued to reproduce sexually. However, in the symbiosis between *Kohlmeyera complicatula* (Nyl.) Schatz (syn. *Mastodia tessellata* auct.) and species of the green algal genus *Prasiola* (C. Agardh) Menegh., which they also treated as a 'mycophycobiosis', the mycobiont appears to have a greater influence on the form of the alga (Brodo, 1977; Kohlmeyer & Kohlmeyer, 1979). The *Turgidosculum ulvae* Kohlm. & E. Kohlm. and *Blidingia minima* (Naegeli ex Kütz.) Kylin association, however, is closer to the *Mycosphaerella ascophylli* case, as is that between the hyphomycete *Blodgettia confervoides* Harvey and species of *Cladophora* Kütz.; in the latter case the hyphae are arranged in a roughly parallel manner within the cell walls of the photobiont (Kohlmeyer & Kohlmeyer, 1979; Feldmann, 1938; Hawksworth, 1987a). In the comparable association between *Phaeospora lemaneae* (Cohn ex Woronin) D. Hawksw. and filamentous freshwater red algae belonging to *Lemanea* Bory, both partners continue to reproduce sexually (Hawksworth, 1987a).

It must be more than coincidence that all the above examples occur in sites subject to periodic submersion. The presence of a mycobiont may therefore have an as yet unidentified key role in reducing the physiological effects of water stress and so enhancing survival. These examples may be recapitulating the process of the colonization of land by progenitors of vascular plants (Pirozynski & Malloch, 1975).

*Mycobiont as exhabitant*

Mutualistic symbioses in which the mycobiont is the sexually reproducing exhabitant and the photobiont is a cyanobacterium or an alga with repressed sexual processes encompass almost all taxa unquestionably accepted as lichens by biologists. However, the 13,500 species of fungi exhibiting this life-style are drawn from diverse systematic groups and display a range of complexity from scarcely modified bionts to dual thalli substantially different from either partner when growing alone.

The structurally simplest associations appear to be somewhat casual, as in the bark-inhabiting genera of the Arthopyreniaceae; most species in that family are not associated with any algae (e.g. *Mycomerithelia melanospora* (Hepp) D.
Hawksw.), some occasionally have small patches of *Trentepohlia* Harvey (e.g. *M. atlantica* D. Hawksw. & Coppins), while others are constantly lichenized (e.g. *M. thelena* (Ach.) D. Hawksw.) (Hawksworth, 1985a). In this family, the ascomata and hyphae are intimately mixed with the bark tissues, and the fungi involved can be expected to derive nutrients saprobically from the bark, in addition to any that may be transferred from any photobiont present.

Loose symbioses with cyanobacteria or algae not leading to any specialized morphological structures are seen in diverse fungi, for example: *Acrospermum adeanum* Hohnel (Dobbeler, 1979), *Chadefaudia corallinum* (Crouan & P. Crouan) E. Müller & v. Arx (Kohlmeier, 1973), ‘*Coniosporium* aeroalgicola’ Turian (Turian & Reymond, 1980), *Cudoniella brasiliensis* Rizz. (Rizzini, 1952), *Herpetrichia juniperi* (Duby) Petrak (Moser-Rohrheofer & Singh, 1978), *Pezizella parasitica* Velen. (Hawksworth & Sivanesan, 1976), *Pseudotrametes gibbsii* (Pers.) Bond. & Singer (Wright, 1890), and *Tricharina cretea* (Cooke) Third & Waraih (Benkert, 1981). In the associations between cyanobacteria and *Didymella lenormandii* Henssen (Henssen, 1963), ‘*Endomyces* scytonematum’ Zukal (Zukal, 1891), *Nectria phytophila* Zukal (Zukal, 1891), *Phycorrella scytonematis* Dobb. (Dobbeler, 1980), and *Pyrenothrix nigra* Riddle (Tschermak-Woess, Bartlett & Peveling, 1983), the fungi are only known in the presence of particular photobiont genera but no specialized morphological structures are formed. The cryptoendolithic associations beneath the surface of rocks in Antarctica are exceptionally specialized, but the bionts are again intimately intermixed with no specialized tissues and the algae are associated to varying degrees (Freidmann, 1982). Some species of *Epigloea* Zukal produce a more thallus-like structure, but without a differentiated cortical layer (Dobbeler, 1984). Zukal (1891) referred to such associations as half-lichens (“Halbflechten”).

The mycobiont ensheaths the photobiont filaments in *Coenogonium* Ehrenb. ex Nees, *Cystocoleus* Thwaites (Fig. 4), *Dictyonema moorei* (Nyl.) Henssen (Tschermak-Woess, 1983), *Ephete* Fr., and *Racodium* Fr. but the morphology of the photobiont is scarcely modified. However, in *Strigula elegans* (Fée) Müll. Arg. as colonies of the alga *Cephalothece siresens* Kunze are lichenized, sporangiospore production is repressed and the thallus form is modified by the mycobiont (Ward, 1884); a parallel situation occurs with foliicolous *Porina* Müll. Arg. species and algae belonging to *Physopeltis* Millardet. In the production of unlayered *Collema* Wigg, thalli, *Nostoc* Vaucher ex Bornet & Flah. colonies are modified by the mycobiont ramifying through them but this is unable to completely determine the overall structure and the photobiont cells remain dispersed through the thallus and not in a differentiated layer (Degelius, 1954; Fig. 6).

In contrast, in the majority of cases with mycobionts from exclusively or predominantly lichenized orders (e.g. Graphidales, Gyalectales, Lecanorales, Figures 1-8. Two-biont symbioses. Figs 1–3. *Mycosphaerella ascothyli*. Fig. 1. Lobe tip with ascomata, ×170. Fig. 2. Vertical section of ascoma, ×270. Fig. 3. Vertical section of thallus showing mycobiont hyphae ramifying between the cells of the photobiont, ×270. Fig. 4. *Cystocoleus ehenus* (Dillw.) Thwaites, showing septae of *Trentepohlia* and ensheathing mycobiont hyphae, ×430. Fig. 5. *Lecidella elaeochroma* (Ach.) M. Choisy, vertical section, ×270. Fig. 6. *Collema auriforme* (With.) Coppins & Laundon, vertical section, showing dispersed *Nostoc* cells, ×170. Fig. 7. *Parmelia saxatilis* (L.) Ach., vertical section showing localized *Trebouxia* cells, ×270. Fig. 8. *Byrionia fuscescens* (Geyelin) Brodo & D Hawksw., transverse section showing localized *Trebouxia* cells, ×270.
Opegraphales, Peltigerales, Teloschistales), the mycobiont appears to have the key role in determining thallus form. The inhabiting photobiont is generally limited to a well-defined layer within the thallus, whether that is crustose (Fig. 5), foliose (Fig. 7) or fruticose (Fig. 8). The great range of morphological complexity may be attributable to the mycobiont striving to achieve the shape most conducive to displaying the maximum area of photobiont cells to light, and so improve its fitness and ability to spread into otherwise hostile environments.

In pure culture mycobionts rarely produce colonies reminiscent of the composite thallus (Ahmadjian, 1967). The complex dual structures found in nature are a consequence of an interaction between the bionts in which the mycobiont has the dominant role and influences the distribution of the photobiont cells (Greenhalgh & Anglesea, 1979). Further, single mycobionts can produce similar thalli (with identical secondary metabolites) with different algae, for example either Trebouxia albuscens de Nicola & Bened. or T. decolorans Ahm. in Xanthoria parietina (L.) Th. Fr. (Piatelli & de Nicola, 1968), and Stichococcus Naegeli or Trebouxia Pyumaly in Chaenotheca eathusiae (Harm.) Lettau (Tibell, 1982). However, the same photobiont species may occur with a variety of mycobiont genera (e.g. Hildreth & Ahmadjian, 1981).

Ott (1987a) has found that X. parietina associates with foreign algae in the early stages of development as a stop-gap prior to contact with an appropriate Trebouxia species and subsequent thallus differentiation.

Differences in thallus colour in Peltigera polydactyla (Necker) Hoffm. (O. Vitikainen, unpublished data) and Sticta caulescens de Not. (D. J. Galloway & P. W. James, unpublished data) have also been attributed to their mycobionts associating with different cyanobacteria.

Whether lichen associations are truly mutualistic has often been questioned (Smith, 1975); indeed some authors assert that the photobiont is parasitized by the mycobiont (Ahmadjian, 1982b; Ahmadjian & Jacobs, 1983). As the mycobiont is generally only able to survive with the photobiont, and as the photobiont develops in environments where it could not survive alone, the symbiosis has to be viewed as mutualistic. In considering the ‘benefits’ to the photobiont it is crucial to consider the fitness of populations and not individual cells; parallel situations are familiar to sociobiologists as ‘altruism’ (e.g. Barash, 1977).

THREE-BIONT SYMBIOSES

Two photobionts: one mycobiont

The most easily recognized cases of mutualistic symbioses involving two photobionts and a single mycobiont involve both a green alga and a cyanobacterium. These occur in about 500 species dispersed through some 20 genera in five orders (James & Hennes, 1976). One of the photobionts may be contained in a separate internal layer in the thallus (e.g. Solorina crocea (L.) Ach.; Fig. 9.), as scattered internal packets (e.g. Lobaria pulmonaria (L.) Hoffm.) or in external morphologically distinct structures (‘cephalodia’). The latter vary from modified lobes (e.g. Placopsis gelida (L.) Lindsay) through convex swellings (e.g. Peltigera aphthosa (L.) Willd.; Fig. 10), to leaf-like (e.g. Sticta canariensis (L.) Bory ex Delise, S. filix (Rausch.) Nyl.; Fig. 11) or shrubby outgrowths (e.g.
Figures 9–16. Three-biont symbioses. Fig. 9. *Solorina crocea*, vertical section showing two layers with different photobionts, ×170. Fig. 10. *Peltigera aphthosa*, vertical section of ‘cephalodium’ containing cyanobacteria on an algal-containing thallus, ×170. Fig. 11. *Sticta filix*, showing foliose green-algal morph (arrow) arising from the fruticose cyanobacterial morph, ×2. Fig. 12. *Polycoccum galligenum* Vezda, forming galls on *Physcia caesia*, ×25. Fig. 13. *Nesulechia oxytropa* bleaching thallus of *Parmelia saxatilis*, ×15. Figs 14–15. *Vezdaea aestivalis*. Fig. 14. Habit on moss leaves, ×5. Fig. 15. Vertical section of moss leaf showing the subcuticular algal cells, ×170. Fig. 16. *Nectria phycophora*, surface view of ascoma showing groups of algal cells in pockets of the ascoma wall, ×430.
Lobaria amplissima (Scop.) Forss.). In Psoroma durietzii P. James & Henssen the cephalodia become sorediate and form independent cyanobacterial thalli, which in turn may capture green algae (James & Henssen, 1975).

The production of morphologically distinct structures with cyanobacteria, as opposed to algae, is of especial interest in emphasizing that the resultant thallus is a result of the interplay between the bionts. Algal and cyanobacterial morphotypes* may be found joined together or as independent two-biont thalli. They have often been given separate scientific names, and new cases of connected thalli are repeatedly coming to light (Brodo & Richardson, 1978; Renner & Galloway, 1982; Tonsberg & Holtan-Hartwig, 1983).

The second photobionts are captured from nature, and then progressively incorporated into the thallus (Jordan & Rickson, 1971). The microenvironment appears to have a key role in determining whether independent two-biont thalli develop, as described, in Sticta filix (James & Henssen, 1976). In nutrient-poor habitats the ability to incorporate a nitrogen-fixing cyanobacterium as a third biont increases the fitness of the original two-biont symbioses.

A different three-biont situation exists in Pyrenocollema pelvetiae (Sutherl.) D. Hawksw.† where the mycobiont and associated cyanobacteria grow epiphytically on Pelvetia canaliculata (Kohlmeyer, 1973; Kohlmeyer & Kohlmeyer, 1979). This is perhaps most appropriately referred to as an obligately algalcolous lichen—i.e. a mutualistic symbiosis in a commensalistic symbiosis, as the Pelvetia is presumably not advantaged. 'Pharcidia' laminaricola Kohlm. and 'P.' rhachiana Kohlm., both on Laminaria digitata (Huds.) Lamour., are similar algalcolous lichenoid associations (Kohlmeyer, 1973; Kohlmeyer & Kohlmeyer, 1979).

At least 19 lichen-forming genera include species exclusively associated with bryophytes (Poelt, 1985a). The degree of specificity varies, but many are confined to particular mosses or liverworts and must be regarded as parasitic, eventually killing the host. The thalli are generally superficial but some persist in a commensalistic symbiosis in which the algal or cyanobacterial partner grows below the cuticle of the moss leaves. In Vezdaea aestivalis (Ohl.) Tsch.-Woess & Poelt the Leptosira obovata Vischer chlorococcalean photobiont is sustained subcuticularly on living bryophyte leaves for some time before they die (Tschermak-Woess & Poelt, 1976; Figs 14–15). No mycobiont cortex is differentiated in this case, nor in the hyphomycete Velutipila poeltii D. Hawksw., also associated with chlorococcalean algae and moss leaves (Hawksworth, 1987a). In Arthopyrenia endobrya Dobb. & Poelt, Trentepohlia filaments and the mycobiont both develop together inside the leaf cells of hepatics (Dobbeler & Poelt, 1981); in Porina heterospora (Fink) R. C. Harris the mycobiont hyphae envelop and penetrate moss leaf cells (P. W. James, unpublished data); and in Vectria phycophora (Dobb.) Rossman, on leaves of Dawsonia grandis Schlieph. &

* This term is used here in preference to 'phytootype' (Swinscow, 1977) and other terms proposed (Tonsberg & Holtan-Hartwig, 1983) as the photosynthetic partner may be either an alga or a cyanobacterium. Morphological variants caused by different photobionts can be denoted by, for example, 'blue-green morphotype' or 'Corticium-morphotype' when this is desirable. If a new separate term is considered necessary 'phototype' would be one possibility, but this has been used in the printing industry since 1899.

Geh., algal cells occur in circular depressions in the ascoma wall (Döbbeler, 1978; Fig. 16).

Although the bryophyte partner in such three-biont symbioses is often naturally short-lived, it seems unlikely that it would be placed at any advantage by the additional bionts. I therefore agree with Poelt (1985a) that such associations should be regarded as parasitic bryophilous lichens, even when they can develop only in the presence of an appropriate bryophyte. These associations can be compared to subcuticular foliicolous lichens on phanerogam leaves in the tropics where the supporting leaves continue to photosynthesize and are not killed (Hawksworth, 1987b).

Two mycobionts: one photobiont

The lichenicolous fungi, some 300 genera and 1000 species, exhibit a variety of biological relationships with their host two-biont mutualistic symbioses. These range from parasitic to commensalistic*, or even mutualistic and saprophytic (Hawksworth, 1982a). Parasitic symbiotic fungi may cause extensive damage leading to thallus death (e.g. Athelzia arachnoidea (Berk.) Jülich, Lichenocodium erodens M. S. Christ. & D. Hawksw., Nectriella santessonii Lowen & D. Hawksw., Nesolechia oxySpora (Tul.) Massal.; Fig. 13) or form localized necrotic patches (e.g. Cornutispora lichenicola D. Hawksw. & B. Sutton, 'Phragmonaeia' peltigerae (Nyl.) Rehm).

In commensalistic lichenicolous fungi an additional mycobiont co-exists with the existing mutualistic symbiosis, presumably sharing the products of the photobiont either directly or indirectly but not damaging or benefiting the host mutualistic symbiosis. Amongst numerous examples (see Hawksworth, 1983) are Arthonia glaucomaria (Nyl.) Nyl. (on Lecanora rupicola (L.) Zahlbr.), Skyttea cruciata Sherw., D. Hawksw. & Coppins (on Diploicia canescens (Dickson) Massal.), Sphinctrina turbinata (Pers.) de Not. (on corticolous Pertusaria DC. species), and Weddellomyces episcleropodium (Weddell) D. Hawksw. (on placodioid Caloplaca Th. Fr. species). In other instances gall-like growths are produced as a result of the interaction, as in Bachmanniomyces unicellularis (Zopf) D. Hawksw. (on Cladorina uncialis (L.) Wigg., etc.), Guignardia olivieri (Vouaux) Sacc. (on Xanthoria parietina), Plectocarpus lichenum (Sommerf.) D. Hawksw. (on Lobaria pulmonaria (L.) DC.), Polyococcus galligenus Vězda (on Physcia caesia (Hoffm.) Furhohr; Fig. 12); and Thamnogalla crombiei (Mudd) D. Hawksw. (on Thamnolia Ach. ex Schaefer). The morphogenetic and physiological processes in these cases are obscure and promise to be a fascinating area for innovative research.

A modification of the lichenicolous habit is seen where a mycobiont initially parasitizes an existing dual association, progressively eliminates the primary mycobiont, and takes over the photobiont to produce a mutualistic thallus of its own. This phenomenon is probably more widespread than is generally assumed, and further examples are being discovered at an increasing rate now that lichenologists are aware of it. Selected instances are Arthrorhapis citrinella (Ach.) Poelt (on Baeomyces rufus (Huds.) Rebent.), Blarneya hibernica D. Hawksw., Coppins & P. James (on Enterographa Fée and Lecanactis Eschw.), Diploschistes

*Lichenicolous fungi not damaging their hosts and persisting on them have long been termed 'parasymbionts' (Zopf, 1897). However, with the broader concept of 'symbiosis' now accepted (see p. 3), this term becomes superfluous and such fungi are more appropriately referred to as 'commensalistic'.
caesioplumbeus (Nyl.) Vainio (on Lecanora gangalenoides Nyl.; Fig. 17), Lecanora preapostera Nyl. (on Aspicilia epiglypta (Norrlin ex Nyl.) Hue), and Lecidea insidiosa Th. Fr. (on Lecanora varia (Hoffm.) Ach.). In Chaenothecopsis consociata (Nádv.) A. Schmidt (on Chaenotheca chrysocephala (Turner ex Ach.) Th. Fr.), Tschermak-

Figures 17–18. Four-biont symbioses. Fig. 17. Diploschistes caesioplumbeus parasitic on Lecanora gangalenoides, showing the whitish necrotic zone of dead Lecanora tissue at the margin of the growing Diploschistes thallus, ×1.5. Fig. 18. Lecidea nodulis commensalistic on Lecanora rupicola, note the absence of a necrotic zone on the Lecanora, ×2.5.
FWoess (1980) discovered that the Chaenotheca's Trebouxia simplex Tsch.-Woess photobiont was later replaced by Dictyochloropsis symbiontica Tsch.-Woess, and in D. muscorum (Scop.) R. Sant. (on Cladonia Hill ex Browne), Friedl (1987) found that the Cladonia's photobiont, Trebouxia irregularis Hildr. & Ahm., was used initially but subsequently preferentially exchanged for T. showmanii (Hildr. & Ahm.) Gärtner. It is conceivable that several of the lichenicolous lichens discussed below start in a parallel manner.

Some of the 'mechanical hybrids' formed by fusion of propagules may also belong in the three-biont category, but as these can involve more bionts they are considered separately below (p. 14).

FOUR-BIONT SYMBIOSES

Three photobionts: one mycobiont

This situation is conclusively reported in Nephroma arcticum (L.) Torss. where a thallus was found to include two morphologically distinct cyanobacteria in separate internal patches in addition to the principal Coccomyxa Schmidle photobiont (Jordan & Rickson, 1971). Parallel cases may occur in Peltigera Willd.; Brodo & Richardson (1978) illustrate a thallus of P. aphthosa with a Nostoc which supports Coccomyxa-containing lobules which in turn have Nostoc-containing excrescences.

While instances involving three photobionts easily distinguished morphologically appear to be rare, it is probable that parallel situations involving photobionts of the same genus are much more frequent than is generally supposed (see p. 16).

Two photobionts: two mycobionts

Examples involving two photobionts each associated with a separate mycobiont are seen in the obligately lichenicolous lichenized fungi. This biological group has not been given the attention it merits in view of its widespread occurrence. Poelt & Dopplebaur (1956) listed 100 lichenicolous lichenized species, but the actual number is probably higher by a factor of two or three.

In contrast to cases such as Diploschistes where one fungus initially parasitises an already lichenized thallus (see p. 12), the lichenicolous lichens maintain a separate photobiont, often in a conspicuous thallus, as in Lecidea insularis Nyl. (on Lecanora rupicola: Fig. 18), Verrucaria aspiciliicola R. Sant. (on Aspicilia calcarea (L.) Mudd) and species of Aecaspora Massal. (Poelt & Steiner, 1972), Caloplaca Th. Fr. (e.g. C. epithallina Lynege on 13 hosts; Poelt, 1985b) and Rhizocarpon Ram. ex DC. (Poelt & Hafellner, 1982; Holtan-Hartwig & Timdal, 1987). In Xanthoria parietina, photobiont cells can be extracted from adjacent thalli of Physcia tenella (Scop.) DC. (Ott, 1987a).

In Buellia badia (Fr.) Massal. (on Parmelia annexa Kurok. and P. verruculifera Nyl.), B. pulserulenta (Anzi) Jatta (on Physconia distorta (With.) Laundon; Hafellner & Poelt, 1980), and Rhizocarpon norax Poelt & Hafellner (on Pertusaria; Poelt & Hafellner, 1982) the thallus of the lichenicolous lichen remains covered by the cortex of the host. Several other cases which may fall into this category
require further study (e.g. *Candelariella superdislans* (Nyl.) Malme on *Lecanora distans* (Pers.) Nyl.).

As the fitness of the host in all these cases is presumably not increased, such symbioses are appropriately regarded as commensalistic or parasitic lichens.

**Three mycobionts: one photobiont**

This evidently extremely rare situation may occur in the association between the hyphomycete *Trichoconis lichenicola* D. Hawksw. and galls caused by the ascomycete *Pyrenidium actinellum* Nyl. on *Peltigera collina* (Ach.) Schrader (Hawksworth, 1980).

**FIVE- OR MORE BIONT SYMBIOSES?**

That associations including five or more bionts exist in nature now seems highly probable. These may arise through the production of ‘mechanical hybrids’ (Hawksworth, 1978) in which bionts from different propagules grow together to form a single structure. This phenomenon, whose fundamental importance was stressed by Bowler (1976), and which was first documented in *Cladia* Nyl. (Jahns, 1972), could explain some complex thalli in *Alectoria* Ach. (Brodo, 1978), and has been elegantly demonstrated by scanning electron microscopy in *Hypogymnia physodes* (L.) Nyl. and *Usnea filipendula* Stirton (Schuster, 1985), and *Physcia adscendens* (Fr.) H. Olivier, *P. tenella* and *Xanthoria parietina*. In the latter cases interspecific and intergeneric mechanical hybrids have been documented (Schuster, Ott & Jahns, 1985; Ott, 1987b). Coalescence of already established independent thalli is also documented, as in *Lecanora gangaleoides* Nyl. (Hawksworth & Chater, 1979), and is a possible cause of error in lichenometry (Jochimsen, 1986).

In these, and other examples discussed by Jahns (1988), the asexual propagules growing together may be derived from the same parent thallus, in which case the bionts may be genotypically identical (i.e. from the same clone). However, Larson & Carey (1986) found that single large thalli of *Umbilicaria velsea* (L.) Ach. and *U. mammulata* (Ach.) Tuck. are not uniform with respect to physiological parameters and isoenzyme profiles; young thalli appear to be mainly monomorphic whereas older larger thalli are highly polymorphic. Their results are perhaps most plausibly explained by the ‘mechanical hybrid’ concept, supplementary mycobiont strains being incorporated with age.

Additional photobionts may be captured and integrated either by thalli growing over them (Jordan & Rickson, 1971) or as a result of their alighting on the thallus surface (Brodo & Richardson, 1978). Occurrences of this type could well be frequent, but most will remain undetected until multiple isolates of photobionts are cultured from single thalli.

**EVOLUTIONARY SIGNIFICANCE**

The formation of mutualistic symbioses with photobionts, including forest trees, orchids, endophytes of other vascular plants, liverworts, algae and cyanobacteria, is so widespread amongst the fungi that this must confer a major evolutionary advantage. At a conservative estimate, of the 64,200 species of
fungi (Hawksworth, Sutton & Ainsworth, 1983) about 30% (19,000 species) have adopted this habit: over 5000 (8%) as mycorrhizal (Malloch, Pirozynski & Raven, 1980) and 13,500 (21%) as lichen associations.

The distribution of the species entering into lichen associations amongst the major groups of fungi is far from regular: 98% belong to the Ascomycotina, but while 16 of the currently accepted 46 orders (Eriksson & Hawksworth, 1986) include at least some lichenized representatives, only six are exclusively lichenized. There are relatively few lichenized Hymenomycetes (e.g. Dictyonema C. Agardh ex Kunth., Multiclavula R. Petersen, Omphalina Quéllet p.p.), one probably mastigomycete lichen (Geosiphon pyriformes (Kütz.) Wettst.) and about 50 genera of lichen-forming conidial fungi (Vobis & Hawksworth, 1981; Hawksworth & Poelt, 1986); the latter almost all have affinities with the Ascomycotina. Further, about 20 genera include both lichenized species and ones with other nutritional modes (Hawksworth & Hill, 1984). The clear impression is of an evolutionarily significant strategy which is currently evolving in some fungi (e.g. Hymenomycetes, Helotiales) but devolving in others (e.g. certain Calicariales and Lecanorales).

The lichen life-style is very ancient, as suggested both by co-evolutionary considerations (Hawksworth, 1982b, 1988) and phytogeographic studies relating modern distributions to continental movements (Sheard, 1977; Sipman, 1983; Tehler, 1983). It seems probable that many of the primarily lichenized families, genera, and in some cases species and even chemotypes, evolved in Permo-Triassic times around 190-280 Myr B.P., before the rise to dominance of the phanerogams in the Cretaceous (65-136 Myr B.P.). In an attempt to display the orders of the Ascomycotina as a whole in relation to their biology, it was found that the Peltigerales came to occupy a somewhat central position (Dick & Hawksworth, 1985). It is interesting that this order was also highlighted as of possibly particular significance in ascomycete evolution on other grounds independently by Eriksson (1981) and Hawksworth (1982b). Further, the order includes some genera which are essentially terricolous, although able to spread onto mossy bark and trees; i.e. with primary habitats which would have existed before the rise of the phanerogams. Whether the habitats were determined by the presence of suitable photobionts, or whether lichen associations facilitated the colonization of habitats unsuited to the unprotected photobiont is a matter for conjecture. It may also be relevant that in this group of lichens the photobionts are regularly cyanobacteria; the cyanobacteria could have arisen in the Precambrian, as far back as 3500 Myr B.P. (Walsh & Lowe, 1985) and so would have been some of the first potential photobionts available for any emerging fungi.

The extent to which present-day Peltigerales, or indeed certain other anciently lichenized groups such as the Pertusariales and Teloschistales, retain features of the earliest ascomycetes is open to debate. Nevertheless, it is clear that such orders cannot be conveniently passed over by mycologists as they may prove to be central to an overall interpretation of ascomycete phylogeny. A failure to consider lichenized and non-lichenized groups together has been a key factor in hampering the development of a satisfactory taxonomy for this, the largest subdivision in the fungal kingdom (Hawksworth, 1985b).

In addition to the significance of the study of lichen-forming fungi for the classification of the Ascomycotina as a whole, co-evolution has taken place
between the bionts leading to novel morphologies, dual asexual reproductive propagules, and secondary metabolites formed only in the combined thallus (Hawksworth, 1988).

TOWARDS A DEFINITION OF 'LICHEN'

A consideration of the range of biological situations in fungal-algal symbioses is a prerequisite to attempts to provide an unequivocal definition of the term 'lichen'. Ever since the dual nature of lichens became apparent in the 1860s, biologists have struggled to produce generally acceptable forms of words:

... it is quite impossible to distinguish some lichens from fungi ...
Berkeley (in Lindsay, 1869)

... a fungus which lives during all or part of its life in parasitic relation with the algal host and also sustains a relation with an organic or an inorganic host.
Fink (1913)

... a fungus ... exclusively or sometimes living with, but not apparently harming, an alga and which is studied by lichenologists.
Hawksworth (1978)

... an association of a fungus and an alga in which the two organisms are so intertwined as to form a single thallus ...
Alexopoulos & Mims (1979)

... an association of a fungus and a photosynthetic symbiont resulting in a stable thallus of specific structure.
Ahmadjian (1982c)

... a fungal-algal association which forms a thallus that does not resemble either symbiont in the free-living (= unlichenized) state.
Ahmadjian (1982d)

... a stable self-supporting association of a fungus (mycobiont) and an alga or cyanobacterium (photobiont).
Hawksworth et al. (1983)

... associations between fungi as hosts and algae or cyanobacteria as symbionts.
Smith & Douglas (1987)

The definition of Ahmadjian (1982c), based on discussions by a committee and a subsequent poll of the International Association for Lichenology, is not satisfactory as there is then a need to define a "thallus of specific structure". On the basis of this definition, filamentous lichens such as Cystocoleus, some poorly formed leprose and crustose thalli (e.g. certain Micarea Fr. species) and many pyrenocarpous lichens immersed in bark or rock would be excluded. Debates would continue over cases such as Mycosphaerella ascophylli and Turgidosculum ulvae (the 'mycophycobioses'), and more casual associations (see p. 5). The description of the mycobiont as 'host' is inappropriate as the shape is a result of the mutualistic association and in the case of filamentous lichens it is the photobiont that has most claim to that title.

It is never likely to be feasible to produce a totally satisfactory definition in the dynamic evolving and devolving situation which confronts us. However, many lichenologists are keen to exclude mycophycobioses (and cases such as Epigloea and Velutipila) which come within the definition of Hawksworth et al. (1983). In these instances the photobiont is the exhabitant; the mycobiont...
hyphae ramify through the photobiont. If this important dichotomy is taken into account, a more acceptable definition can be provided for those still wishing to treat 'lichen' independently in floristic and ecological investigations:

A lichen is a stable self-supporting association of a mycobiont and a photobiont in which the mycobiont is the exhabitant.

It is important to emphasize that this definition does not represent a single biological type of association. In addition to mutualism with algae (or cyanobacteria) being gained in some genera and lost in others, biological strategies may be facultative or change with time. Biologists in general and mycologists in particular need to recognize that a single definition which can unequivocally categorize each mutualistic fungus–alga relationship discovered is not achievable; where possible broader symbiological terminology should be adopted.

There are numerous parallels between lichen symbioses and mycorrhizas in their definition, classification, polyphyletic nature, structure, physiology, and carbohydrate nutrition (Smith, Muscatine & Lewis, 1969; Harley, 1984; Lewis, 1987; Smith & Douglas, 1987). However, scientists working with mycorrhizas have traditionally regarded themselves primarily as mycologists or foresters rather than as mycorrhizologists. This has resulted in a broadly based and integrated approach to those mutualistic associations. In contrast, the tendency of students of lichens to regard themselves as lichenologists rather than as mycologists or phycologists has resulted in an introspective approach which has limited the development of our understanding of these biologically fascinating symbioses, as already stressed by Santesson (1967). Lichenologists are urged to view themselves first as mycologists or phycologists. Conversely, mycologists and phycologists require encouragement to integrate thoroughly lichens into their teaching and research programmes to the extent justified by their variety and numbers; they have much to contribute (Smith, 1978).

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REFERENCES


**Fungal-Algal Symbioses**


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