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# Trouble with lichen: the re-evaluation and re-interpretation of thallus form and fruit body types in the molecular era

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## ABSTRACT

Following discussions of the definition of the terms ‘lichen’ and ‘thallus’, the role of lichenization in the evolution of asco- and basidiomycetes, and divergence and convergence in fruit body types, the morphogenetic interpretation of types of thallus form in lichens is reviewed. Attention is drawn to the various morphogenetic hypotheses proposed to explain the lichen thallus, but it is concluded that it is best interpreted as a novel phenotype with no exact homologue. Similar ascomatal and thallus types are found in lichen-forming fungi of different orders and families, as now revealed by molecular phylogenetic studies. These are interpreted as examples of convergent evolution, strategies by which unrelated fungi either display captured algae to maximize photosynthetic opportunities, or to attach themselves to a substratum. Phenotypic evolution of fruit body and thallus types in the major orders and clades is summarized, and the thallus types known in each order are tabulated. An hypothesis relating the evolution of these structures to hygrosopic movements is proposed, and the critical position of lichens in developing an integrated approach to ascomycete evolution is emphasized.

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## Introduction

There has been unparalleled progress in resolving the relationships of diverse lichen-forming fungi and their integration into the overall system of fungal classification during the last five years (e.g. Lutzoni *et al.* 2001, 2004; Tehler *et al.* 2003; Reeb *et al.* 2004; Lumbsch *et al.* 2004a,b; Wedin *et al.* 2005; Miadlikowska *et al.* 2007), but how this relates to the evolution of different thallus forms has hardly been explored, except in a few specific cases (e.g. Stenroos & DePriest 1998; Myllys *et al.* 1999; Søchting & Lutzoni 2003). Thallus types have traditionally been emphasized at the family and generic levels, but the issue of convergence in these structures has not previously

been revisited across all the different lichen-forming groups in the light of the molecular phylogenetic data now available.

Here we aim to contribute to this reappraisal of ‘thallus’ forms by discussing issues related to the definition of the terms lichen and thallus, the role of lichenization in the evolution of asco- and basidiomycetes, divergence and convergence in fruit body types, morphogenetic interpretations and categorization of lichen thalli, phenotypic evolution in the major lichenized orders and clades, and consider the possible significance of photobiont specificity in the evolution of thallus forms. We also hope that this discussion will facilitate the integration of lichen-forming fungi into mainstream studies of developmental processes in fungi as a whole.

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## Trouble with 'lichen' and 'thallus'

### Lichen

There is a wide variety of relationships between fungi and algae and cyanobacteria, which complicate a precise circumscription of the term 'lichen', and this has been the cause of much debate (Hawksworth 1988a). Definitions emphasizing that the fungal partner is an exhabitant, i.e. enclosing or covering the photobiont, have been used to exclude associations where the reverse applies, the so-called mycophycobioses (e.g. *Blodgettia confervoides*, *Mycophycias ascophylli*). We adopt the following definition here, although recognizing that it has limitations: 'An ecologically obligate, stable mutualism between an exhabitant fungal partner (the mycobiont) and an inhabitant population of extracellularly located unicellular or filamentous algal or cyanobacterial cells (the photobiont)' (Hawksworth & Honegger 1994). The remark about 'extracellularly located' was specifically introduced to exclude the special endosymbiotic case of *Geosiphon pyriforme* (*Glomeromycota*) that has *Nostoc* chains within swollen vesiculate cells (Schüßler & Kluge 2001) as well as proteobacteria (Volz 2004; as bacteria-like organisms, Schüßler et al. 1994). The role played by extracellular non-photosynthetic bacteria in the lichen symbiosis in general, or on thallus evolution, still requires investigation, but recent molecular studies confirm that a diversity of bacteria live in association with lichens, and some of these bacteria prove to be nitrogen fixers, potential producers of bioactive metabolites, or involved in solubilizing phosphate (Cardinale et al. 2006; Gonzalez et al. 2005; Liba et al. 2006).

Amongst the limitations of the definition given above, are the so-called 'borderline lichens', such as *Collemopsisidium pelvetiae* and *Mastodia tesellata*, where the cyanobacteria and algae, respectively, are enveloped by fungal tissue but without the differentiation of discrete layers, which would suggest a more intimate and intricate symbiotic interaction rather than a looser co-occurrence (Kohlmeyer et al. 2004). The situation in such 'borderline lichens' is perhaps not so fundamentally different from that in *Collema* where the hyphae are dispersed amongst cyanobacterial cells in a gelatinous matrix, but also without forming a distinct cortical layer. More difficult to interpret are cases, where fruit bodies are formed amongst a consortium of different algae without apparent specificity between the symbionts, such as in *Collemopsisidium iocarpum* and similar poorly studied pyrenomycetes (Grube 2005). In other cases, the algal partners, for example when *Trentepohliales* are involved, seem to give the lichen thallus its overall shape. In certain foliicolous *Porina* species the mycobiont is merely restricted to form a reticulate mycelium beneath the colonies of *Phycopeltis* (Grube & Lücking 2002), without any differentiation of layers. The microfilamentous thalli of *Cystocolleus* and *Racodium*, and further the fan-like thalli of some *Coenogonium* species (Rivas Plata et al. 2007), are other cases where the photobiont imparts its shape to that of the symbiotic association. However, in these last cases the fungal partner is more clearly an exhabitant than in associations involving *Phycopeltis*. There are also problems with some crustose lichens growing inside bark or rock substrates,

except for their fruit bodies; the hyphae can penetrate deep into the bark layers and much deeper than the photobiont (Brodo 1974; Hawksworth 1988c), and likely also obtain nutrients from the substrate (although this has yet to be demonstrated experimentally).

It also has to be remembered that biological status can change during the lifetime of an individual, or quite rapidly in the course of evolution amongst species of the same genus. An increasing number of cases are being documented in which a fungus can start to grow as a parasite on another lichen, and subsequently develop an independent lichen thallus (e.g. Poelt & Doppelbauer 1956; Poelt & Steiner 1971; Friedl 1987; Poelt 1990). These have been called juvenile parasites, which require a specific lichen host when young, but subsequently live independently.

Some genera include both lichen-forming species as well as saprobic or lichenicolous ones, and many species studied by lichenologists are not or facultatively lichenized. There are now 53 genera known that include lichen-forming or lichenicolous species and also ones with different biologies (Hawksworth 2005a, unpubl.). Not or facultatively lichenized species traditionally studied by lichenologists include some species of *Arthonia*, *Arthopyrenia* s. str., *Biatorella*, *Leptorhaphis*, *Mycomicrothelia*, and *Stenocybe*, and many caliciaceous genera. In three species of *Stictis* (syn. *Conotrema*) it has been shown that the presence of the appropriate alga in the vicinity of the germinating ascospores determines the life habit, i.e. whether the fungus grows as a saprobe or makes a crustose lichen thallus (Wedin et al. 2004). Both lifestyles are able to form ascomata, but in other cases, the mycobiont persists saprobically on bark until they chance upon the appropriate photobionts, or associate temporarily with other photobiont(s) but without any morphological differentiation (e.g. Ott 1987). To complicate matters further, there are various fungal-algal associations with intimate if irregular connections between the bionts that are generally not considered lichens or studied by lichenologists (Hawksworth 1988a). Additional examples are *Resinicium bicolor* (Cléménçon 2004) and various primarily saprobic bracket fungi including *Trametes gibbosa* and *T. versicolor* (Zavada & Simoes 2001; Cléménçon 2004) which incorporate algae into their basidiomes. The extent to which this also occurs in facultative associations of non-lichenized ascomycetes is not known. At least, recent studies show that some non-lichenized fungi may form lichenoid associations when inoculated with coccal algae (Gorbushina et al. 2005; Brunauer et al. in press, and references therein). In order to accommodate these diverse biological situations, Hawksworth (1988a) appended 'and studied by lichenologists' to his definition of 'lichen'.

### Thallus

In classical literature, 'thallus' (Greek *θαλλός*) means a green stalk or bough. A meaning quite different from that used in biology today: 'A vegetative form of an organism which is not differentiated into stem and leaves' (Singleton & Sainsbury 2001). However, in bryology a more restricted use has developed: 'A plant body that is a flat mass of tissue' (Malcolm & Malcolm 2000). As to mycology generally, the current edition of Ainsworth & Bisby's *Dictionary of the Fungi* side-steps the

problem with: 'the vegetative body of a thallophyte', but does not now explain what a thallophyte is (Kirk *et al.* 2001). The term was formerly employed in non-lichenized fungi for 'The whole of the body that does not serve for reproduction' (Jackson 1916), which would exclude sorediate and isidiate structures of lichens, as well as ascomata or basidiomata, but has anyway now fallen out of use. Perhaps pertinently, it does not appear to be even mentioned, let alone used, in Clémençon's (2004) major work on hymenomycete structure, except in the context of the lichenized squamules of *Lichenomphalia hudsoniana*.

In practice, 'lichen thallus' is used today for: 'the vegetative and assimilative body' (Ryan *et al.* 2002) without any limitations as to the complexity or otherwise of the structure, and we adopt this concept here. It can thus embrace associations from discrete granules 10–50 µm across to pendent lichens 2 m or more in length. The term as so defined can even apply to so-called 'endokapylic' forms where a fungus develops a recognizable thallus inside another lichen thallus associating with either the photobiont of the host or a different photobiont without producing an independent morphological structure (Rambold & Triebel 1992). In cases where the host alga is involved, we cannot see a clear difference between an endokapylic lichen and a lichenicolous fungus specifically associated with the algae of the lichen host.

A further complexity is that which appears visually to be a single lichen thallus that may have arisen from either a mixture of separate propagules, such as soredia developing simultaneously (e.g. Schuster 1985), or the coalescence of originally separate thalli as they grow and fuse together (Hawksworth & Chater 1979). This means that a single thallus can in some cases comprise different mycobiont genotypes (in addition to any accessory endolichenicolous or lichenicolous fungi) and photobionts. However, detailed molecular probing or PCR amplifications from different parts of a single thallus have yet to be reported, but sampling five points on seven thalli of *Parmelia sulcata* revealed that more than one ITS rDNA class could sometimes be present in a single specimen (Crespo *et al.* 1998). Further, what appears to be a single mat of the same lichen can be a mixture of genotypically distinct individuals, as in *Cladonia chlorophaea* (DePriest 1993). In addition, instances where different species of the same genus or even of different genera grow together to form 'mechanical hybrids' have been documented (Schuster *et al.* 1985; Ott 1987).

Thallus morphology can also be somewhat variable within a species and can clearly be influenced by habitat, or in phycosymbiodemes by the photobiont type (James & Henssen 1976). This may include micromorphological characters, such as pruinosity or thickness of thallus layers, but also gross macroscopic growth form. Striking examples are a crustose morph of the normally shrubby *Ramalina siliquosa* when growing in shaded rock recesses or grazed (Hawksworth, unpubl.; Dalby & Dalby 2005). Some predominantly crustose species of *Aspicilia* such as *A. desertorum* can become more or less fruticose (see also Kunkel 1980), while the shrubby *A. californica* is crustose when it overgrows small pebbles (Sanders 1999).

Irrespective of definition, genetic variation or habitat influence, the characteristic thallus of a lichenized fungus is a unique structure, of merged physiologies, that is not found

in fungi of different life-styles. Lichen thalli are usually more or less sharply delimited at the periphery and, unlike other symbioses, more or less exposed to the sun. Moreover, symbiotic thalli are mostly long-lived and slow-growing, and may withstand stress factors, such as desiccation, much better than their separated partners (Kranter *et al.* 2005).

Interestingly, in the fungal groups forming lichens, the thallus structures are not fundamentally different. Certain features, such as internal stratification, growth forms, and others, are distributed across the taxonomic groups (see below), and the question arises as to whether these similarities are the result of independent convergent evolution or due to shared ancestral traits of early life-forms. A primary question therefore is: what is the role of lichenization in the evolution of fungi?

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## Lichenization in fungal evolution

The pioneering molecular phylogenetic studies on lichens, especially that of Gargas *et al.* (1995), suggested that lichenization had occurred independently on different occasions, and indicated that at least two lichenization events had occurred in the ascomycetes, and three such events in basidiomycetes. This led to speculation as to how many separate lichenization or delichenization events might have occurred in the course of fungal evolution as a whole (e.g. Aptroot 1998). However, as more representatives of different lichenized and non-lichenized fungi have been included in molecular studies and more gene loci sequenced, and further with the discovery of new fossil fungi, it has become obvious that the situation is very different in ascomycete as compared with basidiomycete and other fungal phyla.

### Ascomycota

Lutzoni *et al.* (2001) were the first to show convincingly by multigene molecular phylogenetic studies that different large groups of non-lichenized ascomycetes had likely been derived from lichen ancestors. This came as something of a shock to mycologists, to discover that groups like the *Chaetothyriales* were nested amongst some lichenized orders (in that case *Verucariales*). This pattern has been confirmed by subsequent studies involving representatives of more taxa and more gene loci (e.g. Lutzoni *et al.* 2004; Reeb *et al.* 2004; Wedin *et al.* 2005). Further some lichenized groups apparently occupy deep positions in the trees, such as *Lichinales*, now recognized as a separate class *Lichinomycetes*, which have cyanobacteria as photobionts (Schultz *et al.* 2001; Peršoh *et al.* 2004) and may have evolved directly from the ancestors of fruit body-forming ascomycetes (Eriksson 2005). However, it is, as yet, unclear how a lichenized ancestral ascomycete would have looked, and whether lichenization was an obligate ancestral trait or a facultative nutritional option.

The discovery of a fossil lichen from the early Devonian Rhynie Chert associated with a cyanobacterial photobiont (Taylor *et al.* 1995, 1997) added to the idea that lichenization could have occurred very early in ascomycete evolution. But even more exciting was the subsequent discovery in the same deposits of a non-lichenized fossil pyrenomycete on

a tree fern, which apparently belongs to the *Sordariomycetes* (Taylor *et al.* 2005). These fossils make clear that ascomycetes had already diversified to a very considerable extent by 410 Mya, and led Eriksson (2005) to propose the Protolichenes Hypothesis. This postulates that the first ascomycetes forming fruit bodies in the *Pezizomycotina* were lichens; the only ascomycete fruit body known outside that subphylum is the enigmatic *Neolecta* (Landvik *et al.* 1993).

The idea that the lichen life-style had a very ancient origin is far from new (Church 1921; *cfr* Hawksworth 2005b), but the new fossil and molecular evidence gives this new credence. This is not to say that any extant lichens are ancestral, as no known lichens are basal to the non-lichenized *Pezizales* and extant lichens are in terminal clades (Lutzoni *et al.* 2004). It also means that when considering phylogenetic trees of ascomycetes, these are essentially tracking changes in the loss of lichenization and diversification into other life-styles, perhaps including intermediate lichenicolous life-styles, as suggested by Lutzoni *et al.* (2001), *en route* to being plant pathogens or endophytes. To consider that some unknown lichenized forms were among the first fungal organisms that were able to endure terrestrial habitats, fits well with extant lichens that are common colonizers of bare rock surfaces, and have increased stress tolerance as a compound structure than would be possible for either partner alone.

### Basidiomycota

In contrast to the situation in the ascomycetes, the relatively small number of lichenized basidiomycetes does seem to be the result of independent and recent lichenization events in terminal branches of the basidiomycete tree, as proposed by Gargas *et al.* (1995), and so they belong to disparate orders and families predominantly comprising saprobic species. Examples are *Acantholichen* (*cfr* Corticiaceae, Jørgensen 1998), *Clavulinopsis* (Clavariaceae), *Dictyonema* (Atheliaceae), *Lentaria* (Gomphaceae), and *Lichenomphalia* (Tricholomataceae). In most cases the thalli are granular or gelatinous, or the algae are incorporated into the fruit bodies themselves (see also above), although distinctive squamules are produced in some species of *Lichenomphalia* (Cléménçon 2004).

## Morphogenetic interpretation of lichen thalli

When lichen mycobionts are grown separately in pure culture, they produce slow-growing mycelial colonies with hardly ever any indication of the development of structures recalling the thallus types seen in nature, except in the presence of a compatible photobiont (Ahmadjian 1993; Schaper 2003). An appropriate photobiont seems to initiate a morphogenetic cascade leading to layered ('stratified') thalli, following an alteration in gene expression patterns (Trembley *et al.* 2002). The detailed genetic mechanisms, first of recognition and then interaction leading to the development of complex thalli, have still to be elucidated, though algal-binding proteins and lectins may be implicated (Honegger 2001; shown for *Xanthoria parietina* by Bublrick & Galun 1980, Bublrick *et al.* 1985). Further, the situation is complicated as the same fungal partner may form completely different morphological structures depending on

whether it associates with a cyanobacterium or a green alga (James & Henssen 1976; Armaleo & Clerc 1991; Goffinet & Bayer 1997; Stenroos *et al.* 2003).

Nevertheless, various suggestions have been made as to the morphogenetic interpretation of lichen thalli, which are summarized here. The issue is whether they are homologues of, or have parallels with, other features seen in non-lichenized fungi.

### Galls

Moreau & Moreau (1918) first suggested that lichen thalli could be a gall-like response of the fungus to invasion by an alga, leading to a proliferation of distinctive tissue. This analogy was examined in detail by Hawksworth & Honegger (1994), who found ten similarities and 13 differences between insect and fungal galls produced on plants, and could not be upheld.

### Stromata

Struck by the lichen-like radiating convex lobes of the non-lichenized genus *Hypocreopsis*, the branched shrubby structures in some *Xylaria* species, and further the strap-like cords of *Thamnomyces*, Hawksworth (1988b) suggested that the possibility that such structures were homologous with lichen thalli 'should not be excluded'. Other such structures could be cited, such as the sclerotia of *Clavicipitaceae*, and there are numerous examples of complex rhizomorphs, mycelial cords, and sclerotia amongst the hymenomycetes. Interestingly, Corner (1964) had considered stromata to be an ancestral ascomycete feature. Considering that the early fruit body-forming ascomycetes could have been lichenized (see above), this hypothesis might be inverted, i.e. that some non-lichenized fungi have retained the ability to develop complex vegetative structures from ancestral 'lichen' thalli even in the absence of a photobiont.

### Expanded exciples

Antedated by Moser-Rohrhofer's (1960) observation that the upper thallus cortex is homologous to the ascomatal cortex, Poelt & Wunder (1967) were the first to propose that lichen thalli might be interpreted as modified thalline exciples of apothecia. Further support for this idea was found in the example of *Lecanora swartzii* subsp. *caulescens* (Poelt 1989), which represents a dwarf-fruticose morph that developed in an otherwise strictly crustose group. This species has a eucortex, i.e. deprived of algal remnants, that extends from the periphery of the amphithecium into the thallus, thereby replacing the phenocortex (containing remnants of algal cell walls) that is found in related crustose species. Later, Poelt (1991) asserted that: 'The foliose thallus is nothing but a precociously formed excipular structure where the development of the hymenium has been delayed'. He indicated he was to return to this theme 'in a forthcoming paper', but sadly never did. This is certainly an interesting concept for many foliose and also shrubby lichens of *Lecanorales*, as the plectenchyma are generally contiguous and similar to identical in structure, but could it be relevant to lichens that only had a true exciple (i.e. without algae)? Perhaps so, if the thalline exciple had been lost

secondarily, but there is no clear evidence and without further data this hypothesis can hardly be generalized for all lichenized ascomycetes. It is also difficult to follow this idea as the first stages of fruit body development usually comprise the formation of a hyphal plexus that develops into the internal part of the ascumata (hymenia, subhymenia, etc.), whereas the amphithecial cortex is formed later on, when the ascumata rises upwards. This idea is further challenged by squamulose and foliose pyrenocarpous lichens (e.g. *Catapyrenium* and *Dermatocarpon* spp.) where allied crustose lichens always lack a thalline exciple (e.g. groups of *Verrucaria* s. lat.).

### Lichenized stipes

Ahti (1982) argued that the erect secondary thallus structures that bore asci in cladoniiform lichens were most appropriately interpreted as lichenized apothecial stipes. This argument is especially compelling as some *Cladonia* species have apothecial stipes devoid of any photobiont and remaining translucent (e.g. *C. caespiticia*), but the homology may be restricted to the family *Cladoniaceae* in which a primary thallus precedes a secondary one that develops only after a dikaryon is established (Letrouit-Galinou 1966; Jahns 1970). It would not apply in the *Parmeliaceae*, for example, where there is no primary thallus, pycnidia occurring on the same thallus, the apothecia forming discretely and having independent exciples on both foliose (e.g. *Xanthoparmelia*) and erect shrubby or pendant thalli (e.g. *Alectoria*) with no indication of a separate stipe. The situation is similar in *Stereocaulaceae* to that in *Parmeliaceae* except that the apothecia lack a thalline margin.

### Symbiotic phenotypes

Hawksworth & Honegger (1994) concluded: '...that lichen thalli must be recognized as a particular biological phenomenon with no close exact analogue'. Honegger (2001) later referred to these as 'symbiotic phenotypes'. Recognizing the probably ancestral state of lichenization in fruit body-producing ascomycetes (see above), we see no reason not to accept lichen thalli as ancient specialized structures in their own right, perhaps developed from increasingly specialised endolithic

associations and so no necessity to search for or expect to find homologues amongst fungi derived from them.

### Categorization of lichen thalli

The issue of whether to use the term 'life-form' or 'growth form' to describe gross morphology was discussed by Barkman (1988), who after an extensive review of the literature concluded that life-forms should be related to adaptations (morphological and/or physiological) to a particular ecological factor, and growth forms to: 'plants with the same gross morphology (architecture) ... free of any hypotheses about adaptation.' He went on to endeavour to provide a comprehensive system of growth form classification for all aquatic and terrestrial 'plants' in Europe which recognized 88 main categories and also various subcategories within some of those. The categories involving lichens were mainly based on his earlier work (Barkman 1958), but three new categories were added, and rosette-forming hepatics and lichens were united. We see no value in such semantic discussions, and instead use 'categorization'. Further, although it may be of some interest to vegetation scientists to have elaborate classification schemes based on superficial appearances, this scarcely contributes to any understanding of phylogeny.

Lichenologists have traditionally used many fewer categories, notably leprose, crustose, filamentous, placodioid, squamulose, foliose, and fruticose thalli (Hawksworth & Hill 1984). Honegger (2001) uses leprose, microfilamentous, microglobose, crustose, gelatinous, foliose, and fruticose. Many further subdivisions can be attempted, for example Ryan *et al.* (2002) recognized eight categories within their concept of 'crustose', as well as various 'intermediate growth forms'. For the purposes of the analyses in this contribution (Table 1), we decided to recognize the following categories: leprose, microfilamentous, gelatinous, crustose, squamulose, placodioid, foliose, umbilicate, erect shrubby, and pendent. However, we stress that these categories represent idealized types and sometimes intergrade.

We have not attempted to consider here the different tissue types encountered in building lichen thalli, reviewed by Honegger (2001), but wish to stress that particular growth forms do not always have similar anatomical structures.

**Table 1 – Occurrence of different thallus categories within the orders of Ascomycota including lichen-forming fungi**

	Leprose	Microfilamentous	Gelatinous	Crustose	Squamulose	Placodioid	Foliose	Umbilicate	Erect shrubby	Pendent shrubby
<i>Acarosporales</i>				+	+	+				
<i>Agyriales</i>				+	+	+				
<i>Arthoniales</i>				+		+			+	+
<i>Dothideales</i>				+						
<i>Lecanorales</i>	+	+	+	+	+	+	+	+	+	+
<i>Lichinales</i>		+	+	+	+				+	
<i>Ostropales</i>	+	+		+						
<i>Peltigerales</i>			+		+		+		+	
<i>Pertusariales</i>				+						
<i>Pyrenulales</i>				+						
<i>Teloschistales</i>	+			+	+	+	+		+	+
<i>Verrucariales</i>				+	+			+		

This is true even within some closely allied groups such as the alectoroid (Hawksworth 1969) and parmelioid lichens (Hale 1973).

### Diversity of ascoma and thallus types in major groups/clades of lichen-forming fungi

Recent progress in the understanding of phenotypic evolution in the major orders of lichen-forming fungi in relation to ascoma and thallus types is presented here.

#### Acarosporales

Recent studies, such as Lutzoni *et al.* (2004) and Reeb *et al.* (2004), show that *Acarosporales* are a quite distinct lineage in *Lecanoromycetes*, and the latter introduced the subclass *Acaromycetiae* to account for this result. All members are lichenized, and most species are epilithic, whereas some also grow as specialized parasites on other lichens. The thalli are crustose to squamulose, generally associated with trebouxoid green algae, and form more or less immersed apothecia as fruit bodies.

#### Agyriales

The *Agyriales* is supported as an order by SSU rDNA analyses (Lumbsch *et al.* 2001a) and characterized by features of the asci, namely a faint amyloid reaction and the opening of the asci by eversion, rather than being rostrate as is the usual case in *Lecanorales*. The order includes both lichenized, lichen-parasitic, and non-lichenized ascomycetes, and all lichenized representatives are apotheciate and have crustose, squamulose, or placodioid thalli; photobionts are coccal green algae of the genera *Asterochloris*, *Chlorella*, and *Trebouxia*, but cyanobacteria can also be found in cephalodia in some genera (e.g. *Placopsis*).

#### Arthoniales

The second largest order of lichenized ascomycetes, which includes more than 1200 species. Members of *Arthoniales* are characterized by a peculiar ascomatal development that shares ascolocular and ascohymenial characters (Henssen & Jahns 1973; Henssen & Thor 1994; Grube & Lücking 2001). The order includes the previously separated *Opegraphales* (Grube 1998). The shape of the ascomatal structures is extremely variable, ranging from spot-like to strongly elongate (lirelliform) or branched, even within a single genus (e.g. *Arthonia*, *Opegrapha*). Substantial variation of fruit body types is found, including both apothecia (rounded, irregularly shaped or lirelliform) and perithecia, and in some cases asci arise more or less individually in the thallus without aggregation into any ascomatal structures (e.g. *Cryptothecia*, *Stirtonia*). We assume that the latter represents a loss of ascomatal structures.

The common loss of lichen symbioses, as suggested by Lutzoni *et al.* (2001), receives good support through the traditional classification of members of the order, with lichenization evidently having been lost in several lineages of the

predominantly lichenized genus *Arthonia* (Grube *et al.* 1995; Grube & Matzer 1997; Grube 1998), as well as in *Opegrapha*, *Lecanactis*, *Chiodecton*, and other genera (Tehler 1990).

Although most representatives are crustose, the fruticose *Roccellaceae* was traditionally treated as a separate family with primarily shrubby thalli, but recent studies indicate the inclusion of various crustose genera is justified (Grube 1998). SSU rDNA analyses indicated that the pendent ('fruticose') growth form may have arisen more than once and independently in the *Roccellaceae* (Myllys *et al.* 1998), and when combined with ITS data (Myllys *et al.* 1999) it became clear that this growth form and crustose lichens in this family are in some cases monophyletic (*Dirina* and *Roccella*) and have evolved multiple times in even in comparatively small groups.

#### Dothideales

The taxonomy of this order, with pseudothecia as fruit bodies, is still poorly settled, and perhaps not more than 1% of the species form lichenized associations. Most of these are placed in the family *Arthopyreniaceae*, which includes non-lichenized ('free-living'), bryophilic, lichenicolous, and lichenized species. The latter are associated with trentepohlioid photobionts, and strictly crustose (on bark) and some genera include a mixture of lichenized and saprobic species (e.g. *Mycomicrothelia*; Hawksworth 1985). The position of species that are associated with cyanobacteria is unsettled (e.g. *Collemopsisidium*; Grube 2005).

#### Lecanorales

In this order, the form of the thallus was one of the principal characters used to circumscribe families and genera in the past, and almost all conceivable thallus categories are represented within it (Table 1). However, more recent studies in different families show that various types of thallus categories may occur in closely related species (Arup & Grube 1998, 1999, 2000; Grube & Arup 2001).

Ascomata are apothecia and have functionally unitunicate asci with a complex structure and often rostrate dehiscence. Diverse subtypes of this ascus type are distinguished by the amyloid structures in the inner layers of the ascus apex, and these were used in the circumscription of families (Hafellner 1984). These different types seem to be evolutionarily derived from asci with tube-like apical structures (Wedin *et al.* 2000a,b; Ekman & Wedin 2000).

*Lecanorales* are predominantly associated with coccal green algae (i.e. *Apatococcus*, *Asterochloris*, *Chlorella*, *Dictyochloropsis*, *Elliptochloris*, *Myrmecia*, and *Trebouxia*), while some also contain cyanobacteria in cephalodia.

#### Lichinales

The *Lichinales*, with perithecioid to apothecioid fruit bodies, almost exclusively have cyanobacteria as photobionts. Molecular data indicate the order is monophyletic, and that it occupies a basal and somewhat isolated position; consequently, it has now been placed in a separate class, *Lichinomycetes* (Lutzoni *et al.* 2004) based on data from five different gene loci, although not supported by the data of Wedin *et al.* (2005).

Although the relationships to other lineages remain unresolved, and may require the analysis of further genes, the isolated position of the order is supported by the structure of the soluble polysaccharides in the cell walls (Antonio Leal *et al.*, unpubl.). Thallus types in the order vary from crustose to squamulose or peltate, and minutely coralloid to shrubby.

### Ostropales

A special type of hemiangiocarpous ontogeny is present in *Ostropales* (Henssen 1976), and the margins of the ascomata have similarities to the peridia of pyrenomycetes, especially when furnished with lateral paraphyses (Henssen 1995). The asci are thin- to thick-walled, amyloid or non-amyloid, and they may have an apical thickening, but the amyloid apical structures found in typical *Lecanorales* are absent in the order. Representatives of the order are predominantly crustose with some genera including also microfilamentous species, notably *Coenogonium* of which the crustose genus *Dimerella* is now treated as a synonym (Rivas Plata *et al.* 2007). However, more complex foliose and shrubby growth categories are not established. This order includes both lichenized and de-lichenized fungi, even in the same species complex (Wedin *et al.* 2004). Most lichenized species in this order associate with trentepohlioid algae, but *Diploschistes* predominantly forms symbioses with *Trebouxia* or *Asterochloris* in the juvenile stage of the parasitic *D. muscorum* (Friedl 1987). Molecular data show that the traditionally recognized lichenized *Graphidales*, distinguished by the elongated (lirelliform) apothecia has to be included in *Ostropales* (Winka *et al.* 1998; Kauff & Lutzoni 2002). *Graphidaceae* and *Thelotremataceae*, primarily separated by the shape of the ascomata, elongate (lirellate) in *Graphidaceae* and round to punctiform apothecia in *Thelotremataceae* are not monophyletic (Staiger *et al.* 2006). Further, Kauff & Lutzoni (2002) suggested the merger of *Agyriales*, *Gyalectales*, *Graphidales* and *Ostropales* into one large order *Ostropales*. The position of the widely recognized *Gyalectales* is still unresolved; its members are distinguished by thin-walled amyloid asci.

Lücking *et al.* (2004), based on a combined analysis of nuLSU and mtSSU rDNA sequence data, confirmed that the *Gomphillaceae* are part of the *Ostropales* *s. lat.*, and Grube *et al.* (2004a) have shown that the perithecial *Porinaceae* also belong here. Thus, a wide range of ascomatal types occurs in this order, whereas thallus form variation is rather limited.

### Peltigerales

This order is close to, and sometimes included in, *Lecanorales*, and in addition to green coccoid algae representatives associate with cyanobacteria and *Coccomyxa*-like photobionts. The study by Miadlikowska & Lutzoni (2004) suggests that bimembered association with cyanobacteria is ancestral, whereas green algae are accessed independently and multiple times and rarely followed by a loss of the cyanobiont to form a bimembered association with green algae. Phycosymbiodemes, where one mycobiont may associate with either cyanobacteria or green algae, are common in this lineage. These different morphs may have the same foliose growth habit that predominates in the order, but may then differ in colour (Brodo & Richardson 1978). In some instances cyanobacterial

morphs may form either morphologically distinct tubercles on the surface (cephalodia) or shrubby thalli with the same mycobiont (James & Henssen 1976), but also the reverse may occur, e.g. in *Peltigera venosa*.

### Pertusariales

The order includes crustose to semi-fruticose lichens with hemiangiocarpic ascoma development, thick-walled amyloid asci, relatively large ascospores, and a general association with coccoid green algal of the genera *Myrmecia* and *Trebouxia*. The fruit bodies vary from perithecioid to apothecioid (Lumbsch *et al.* 2001b). Character evolution in *Pertusariaceae* has recently been studied in detail (Lumbsch *et al.* 2006), showing that the cortical chlorinated xanthenes appear to have been lost several times. *Pertusaria* is not supported as a monophyletic group (Lumbsch & Schmitt 2001; Schmitt & Lumbsch 2004).

### Pyrenulales

The *Pyrenulales* is a predominantly corticolous tropical order of crustose species associated with trentepohlioid algae. They form a sister group to *Chaetothyriomycetes* in the phylogenetic tree of Lutzoni *et al.* (2001), but the fruit body morphology of *Pyrenulales* is quite different, being characterized, for example, by a hamathecium similar to that of members of *Pleosporales*.

### Teloschistales

Members of this order are lichenized or represent lichenicolous life-forms that develop only apothecia as fruit bodies. Most *Teloschistales* are well-characterized by anthraquinones as major secondary metabolites, which give them the typical yellow to orange colour. The position of this order is unsettled, but according to the placement of *Calicium* in Lutzoni *et al.* (2004), *Physciaceae* could be a sister group. However, the lichenized representatives display a high diversity of thallus forms, ranging from crustose to foliose and fruticose. Photobionts are generally coccalean green algae (trebouxioid).

### Verrucariales

The *Verrucariales*, characterized by perithecia, belong with the non-lichenized *Chaetothyriomycetes* (e.g. Lutzoni *et al.* 2001, 2004; Grube & Winka 2002). This placement is also supported by certain ascomatal characters, for instance the presence of periphyses. The predominantly lichenized *Verrucariales* are associated with a wide range of algae, for example *Endocarpon* with *Stichococcus*; *Verrucaria* with *Coccobotrys*, *Dilabifilum*, *Heterococcus*, *Myrmecia*, and even brown algae (Sanders *et al.* 2004). Numerous species evidently lost their lichen habit and live on other lichens (parasitizing their algae) or have uncertain symbiotic relationships (e.g. certain *Merismatium* species). Most of the species are crustose lichens, occurring preferentially on rock or soil substrates. However, *Dermatocarpon* is a foliose (umbilicate) lineage, whereas most *Endocarpon* species are more or less squamulose, with some subfruticose exceptions (*E. pulvinatum*).

## Divergence and convergence in fruit body and ascus types

It is now evident there have been many cases of divergence and convergence in fruit body and ascus types between different families and orders including lichen-forming fungi. Where families and orders have been wholly or partly based on these features, a fundamental re-appraisal of both circumscriptions and relationships has become necessary.

For example, mazaediate fruit bodies with evanescent, prototunicate asci and passive ascospore dispersal were previously used to circumscribe the *Caliciales*, which had traditionally and consistently been treated as a particularly homogeneous group of lichens. However, molecular studies showed that most predominantly lichenized *Caliciales s. lat.* (the lichenicolous and saprobic *Mycocaliciaceae* excluded, which are now regarded as belonging to a separate order, *Mycocaliciales*) evolved repeatedly within *Lecanoromycetidae*, and *Caliciaceae* did not even merit recognition as a family but belonged within *Physciaceae* (Tibell & Wedin 2000; Wedin et al. 2002). However, the name *Caliciaceae* was taken up again by Helms et al. (2003), but with a different circumscription based on ascus-type and including also non-mazaediate genera. Apart from this, the prototunicate ascus type evolved also in other lineages of ascomycetes and is found in *Arthoniomycetes* (Grube 1998, 2001), *Lichinomycetes* (Schultz et al. 2001), and *Ostropomycetidae* (*Phaeographopsis*, Frisch & Grube, unpubl.; *Nadvornikia*, Lumbsch et al. 2004a,b).

The dispersed occurrence of mazaediate ascomata in diverse ascomycete lineages is one example of the complex pattern in the evolution of ascomatal types. Although some superficially very similar fruit bodies are found in different lichen groups, the ontogeny of the ascomata is supported as an important character also by molecular work for the characterization of lichenized lineages (e.g. Henssen et al. 1981). However, the major division between loculoascomycetous and hymenoascomycetous groups of ascomycetes, which dominated classifications in the 1950s and 1960s, never found support amongst all lichenologists (e.g. Henssen & Jahns 1973) and has proved not to be sustainable (Lumbsch & Huhndorf 2007).

A major emphasis was also traditionally placed on whether fruit bodies were perithecioid or apothecioid, but it is now evident that in some cases both types can occur in the same orders and even families. For example the apothecioid *Ostropales* also contains various unrelated perithecioid lineages, including *Porinaceae* (see above) and *Belonia* (more or less closed perithecioid fruit bodies are also known from *Topeliopsis*). There is now also evidence that pyrenocarpous families *Prototelenellaceae*, *Thelenellaceae*, and *Thrombiaceae* all fall well inside *Lecanoromycetes* and may be a sister group to *Ostropales* (Schmitt et al. 2005). A similar situation exists in the family *Roccellaceae* of *Arthoniales*, where certain genera (e.g. *Dichosporidium*) with perithecioid ascomata, are clearly related to others with exposed discs (e.g. *Erythrodictyon*). Also, the formation of elongate (lirelliform) ascomata arises in orders as far apart as *Ostropales* (incl. *Graphidales*) and *Arthoniales* (incl. *Opegraphales*). In addition, the major emphasis traditionally placed on whether apothecia had a thalline exciple containing

algal cells or not is no longer sustainable as a generic criterion *per se*; both types occur in, for example, *Caloplaca*, *Lecanora s. lat.*, and *Rinodina*.

Ascus characters had been viewed as of major importance in ascomycete classification from the 1950s, and this emphasis was also applied in lichen-forming groups. However, asci were taken to unprecedented heights in the recognition of new families and fresh generic delimitations within lecanoralean lichens in particularly during the 1980s (Hafellner 1984, 1988). Numerous changes in classification and generic concepts resulted, but now these are being re-evaluated as the evolution of ascus characters proves to be more complex than previously thought in the light of molecular data. Notably, a *Lecanora*-type ascus type in the broad sense, occurs in several unrelated lineages, i.e. in *Lecanora* (*Lecanoraceae*), *Rinodina* (*Physciaceae*), and *Pleopsidium* (*Acarosporaceae*).

## Divergence of thallus form in large genera

The classification of lichen genera was traditionally led by gross morphology, and secondarily by ascospore colour and septation. The emphasis on morphology arose from variety of thallus categories (see above). This contributed to a situation with numerous well-delimited foliose (e.g. *Parmelia*, *Peltigera*, *Physcia*, *Sticta*) and shrubby genera (e.g. *Alectoria*, *Cladonia*, *Usnea*) whereas some large crustose genera (e.g. *Arthonia*, *Buellia*, *Caloplaca*, *Graphis*, *Lecanora*, *Rinodina*) are often still insufficiently understood. The relationships of the showy foliose and shrubby genera to crustose ones has been resolved to some extent by microscopic investigations of ascomatal structures, but as yet genera with different thallus types are generally kept separate. Because there was general agreement amongst lichenologists as to the heterogeneity of certain large crustose genera, smaller genera characterized by a few distinct morphological characters have been separated from the large crustose aggregates. Although some of these are definitely distinct (e.g. *Aspicilia*, *Tephromela* and *Protoparmelia* from *Lecanora*), other splits proposed seem unjustified (e.g. *Apatoplaca* from *Caloplaca*, *Arctopeltis* from *Lecanora*).

Here, we describe some case studies from different large genera that share similar types of crustose growth forms and where transitions to the foliose habit have been observed.

### *Caloplaca s. lat.* (*Teloschistaceae*)

*Caloplaca* is an extremely heterogeneous taxon with regard to thallus morphology. It is generally recognized by the presence of anthraquinones in the thallus and/or ascomata in combination with the teloschistacean ascus type as well as polarilocular ascospores. In the past, several authors attempted to distinguish smaller entities in this assemblage, although mostly below the genus level (e.g. Poelt & Hinteregger 1993).

Arup & Grube (1999) published a first phylogenetic analysis of ITS rDNA including 17 species in *Caloplaca* and three species of *Xanthoria*. This showed that *Caloplaca* and *Xanthoria*, as currently circumscribed, are not monophyletic. The primary goal of that study was to find the phylogenetic relationships of the sterile lichen *Lecanora demissa*. The species was traditionally classified as a *Lecanora*, probably due to doubtful reports of

ascospores and its lobate growth. The analysis of SSU rDNA sequence data instead indicated a monophyletic relationship with *Caloplaca*. This was somewhat surprising, mainly because the species does not produce the typical anthraquinones found in many *Teloschistaceae*, except for a sporadically detected bisanthraquinone skyrin. A closer analysis using ITS data of *Teloschistaceae*, showed that the species appears related to a lineage of greyish to dark-coloured *Caloplaca* species that lack anthraquinones in the thallus, i.e. subgenus *Pyrenodesmia*. This monophyletic group is phenotypically variable and includes several poorly understood species on different substrates, ranging from distinctly epilithic to clearly endolithic forms. A new and frequently sterile species in this group with an unusual type of endolithic thallus was recently described as *C. erodens* (Tretiach et al. 2003).

All phylogenetic analyses of *Teloschistaceae* show that growth categories are not resolved in monophyletic groups. The foliose growth form representing the genus *Xanthoria*, and traditionally distinguished from *Caloplaca* by the presence of a lower cortex, evidently evolved repeatedly (Arup & Grube 1999; Gaya et al. 2003; Søchting & Lutzoni 2003). Two main lineages can now be distinguished in *Caloplaca s. lat.* One contains the type species, *C. cerina*, and the other various *Xanthoria* species beside other *Caloplaca* species. The first group includes not only the type of *Caloplaca*, but also the subgenus *Pyrenodesmia*, including the *C. variabilis* group. The production of crystallized anthraquinones appears to be successively reduced in this main lineage. The second major group in *Caloplaca s. lat.* is more uniform with respect to the occurrence of anthraquinones, which usually occur in both the apothecia and thallus, except in *C. pyracea* and *C. lithophila* both of which may lack anthraquinones in the thallus.

#### *Lecanora s. lat. (Lecanoraceae)*

*Lecanora* is a primarily crustose genus of lichens including ca 300 species. No recent monograph exists for the whole 'genus', but some morphologically or chemically circumscribed groups have been revised, for example the *Lecanora rupicola* group characterized by the unique compound sordidone (Leuckert & Poelt 1989; Grube et al. 2004b).

Phylogenetic analyses by Arup & Grube (1998, 2000) of various crustose and lobate species suggest that the lobate growth form arose independently in different species groups of *Lecanora*. *Arctopeltis*, a monotypic genus, was earlier separated from *Lecanora* and characterized by its umbilicate growth (Poelt 1983). The ITS data suggest that this species arose from within the *Lecanora dispersa* group and that it is closely related to *L. contractula*.

Further results of Arup & Grube (2000) suggest a multiple origin of the *Rhizoplaca* morphology. In one lineage of *Rhizoplaca*, vagrant (unattached) thalli evolved and represent an alternative mode of dispersal. Some fruticose and vagrant lecanoroid lichens assigned to *Rhizoplaca* are closely related to the lobate *Lecanora novomexicana* (Arup & Grube 1999).

#### *Rinodina s. lat. (Physciaceae)*

The *Physciaceae* traditionally included only foliose members in its earlier circumscriptions. Crustose members, earlier placed

in a separate family *Buelliaceae* (e.g. Zahlbruckner 1926), are now accepted in *Physciaceae*, beside members of the *Caliciaceae* (Wedin et al. 2002); however, Helms et al. (2003) maintain *Caliciaceae* as a separate family but with a different circumscription (see p. 000). Molecular studies of the *Physciaceae* show that two main groups exist, which correlate with ascus characters. First, the *Physcia*-group with an ascus with a broad masse axiale, and spores with usually distinct endospore thickenings. This group is confirmed by molecular data (Grube & Arup 2001, Helms et al. 2003), and certain subgroups within it can be recognized – each contains crustose species placed in *Rinodina*, as well as representatives of genera with foliose, erect shrubby or pendant thallus organization (Kaschik 2006).

The highly supported monophyly of '*Buellia*' *lindingeri*, *R. lecanorina*, and *R. luridescens* suggests considerable variation in exciple types among closely related species (Kaschik 2006). The position of '*B.*' *lindingeri* agrees with its *Physcia*-type ascospores and *Lecanora*-type asci (Giralt & Matzer 1994). Similar variation of exciple types was also observed in *Phaeorrhiza* and *Rinodinella* by Mayrhofer & Poelt (1978a,b), genera that are also supported as monophyletic groups by molecular results.

Most interestingly, the molecular results shown here, and also other works (e.g. Grube & Arup 2001, Helms et al. 2001, Kaschik 2006), show that the foliose genera of the *Physciaceae* do not form monophyletic units separated from *Rinodina*, but they are rather nested in *Rinodina*. This shows that the foliose growth habit arose several times in the *Physciaceae* from rather distantly related crustose ancestors. The *Buellia* group of *Physciaceae* is much less resolved with the available data, but an independent evolution of complex growth forms from crustose groups is also suggested in this case (Helms 2003; Helms et al. 2003), e.g. for the foliose genera *Pyxine* and *Dirinaria*, as well as the fruticose *Santessonia* and the umbilicate *Dermaticum*. Nonetheless, taxon sampling in this family is still limited, and the validity of many genus names proposed by Marbach (2000) has not yet been tested.

The morphologically circumscribed genera traditionally recognized in this family clearly do not form a monophyletic group, rather the different foliose lineages evidently evolved convergently from crustose relatives to form morphologically similar groups. How this should be reflected in the formal taxonomy is still to be addressed. However, this situation does not apply to all cases of families in which more complex thallus types are produced. In *Parmeliaceae* in particular, lichens with the same parmelioid foliose thallus type (with relatively minor variations) do form a monophyletic group within the family (Wedin et al. 1999); the lichenicolous genus *Nesolechia* was also placed in the main parmelioid clade by Peršoh & Rambold (2002) on the basis of molecular evidence, but that needs further confirmation. In this case, molecular work has provided a fresh series of generic circumscriptions and the taxonomy is now much less controversial than before the advent of molecular data (e.g. Crespo et al. 2001; Blanco et al. 2004a,b, 2005, 2006; Thell et al. 2004).

There is still uncertainty in some cases as to whether more complex lichen thallus forms are derived from simpler organizational types, or vice versa. At least in *Physciaceae* and *Lecanora s. lat.* it appears that foliose and shrubby forms are derived from crustose ones, whereas the situation is inconclusive in

Teloschistaceae. Growth form transitions can also be observed in other genera, in which the reduction from shrubby to crustose forms is suspected, as in some lineages of Roccellaceae (Myllys et al. 1999), and in *Stereocaulon* (Högnabba 2006).

### Convergence in thallus evolution in unrelated lineages

Here we provide three cases of particular interest: two involving parallel loss of ascomatal structures while morphologically similar lichenized thalli were maintained, and the other parallel evolution of the umbilicate foliose thallus type.

#### Leprarioid lichens

In cases where ascomata are unknown and presumed lost, the traditional classification was often more and less uncertain or relied on the similarities in the thallus morphology and extralites (secondary metabolites) to other groups. However, molecular approaches can now be used to locate the phylogenetic position of sterile lichens in the phylogeny, and they indicate that similar morphologies of sterile thalli, serving different modes of sterile propagation, have evolved as analogies in different lineages.

The genus *Lepraria* is widespread and comprises exclusively sterile lichen species with a thallus composed entirely of granular soredia. Ekman & Tønsberg (2002) discovered that the majority of *Lepraria* represents a monophyletic lineage closely related to Stereocaulaceae, a family that encompasses primarily fruticose and fertile species. However, one of the species (*Lepraria flavescens*) was shown to be related to *Lecanora*, and is now placed under the new name *Lecanora rouxii* in the *L. rupicola* group (Grube et al. 2004b). This agrees well with the presence of the rare compound sordidone. Certain other *Lepraria* species could also be unrelated, but developed a similar morphology. For example, *Botryolepraria lesdainii* (syn. *Lepraria lesdainii*; Canals et al. 1997) is according to BLAST searches more closely related to the Verrucariales, and its relationships to the genus *Normandina* still need to be studied carefully. Morphologically similar leprarioid species (e.g. *Leproplaca chrysodeta*) but pigmented yellow or orange shades due to anthraquinone pigments have long since been accepted as a part of *Caloplaca* s. lat. (Poelt 1977), and the complete reduction to leprarioid growth is also found in further unrelated lineages (e.g. in species of *Buellia* and *Chrysothrix*).

#### Siphuloid and thamnolioid lichens

The second example is of lichens that propagate exclusively by thallus fragments and are often found in windswept habitats. The fruticose asexual genera *Siphula* and *Thamnolia* prove to belong to a clade that also includes *Icmadophila* and *Dibaeis* of Icmadophilaceae (Stenroos & DePriest 1998). Previously, *Siphula* was regarded as a natural genus of sterile species, but molecular studies including members of two species groups indicated that the genus was not monophyletic (Stenroos et al. 2002) within Icmadophilaceae. Moreover, although two monophyletic *Siphula* groups may have evolved within Icmadophilaceae, the

*S. fragilis* and the *S. complanata* group represent a monophyletic lineage within the Coccotremataceae (Grube & Kantvilas 2006).

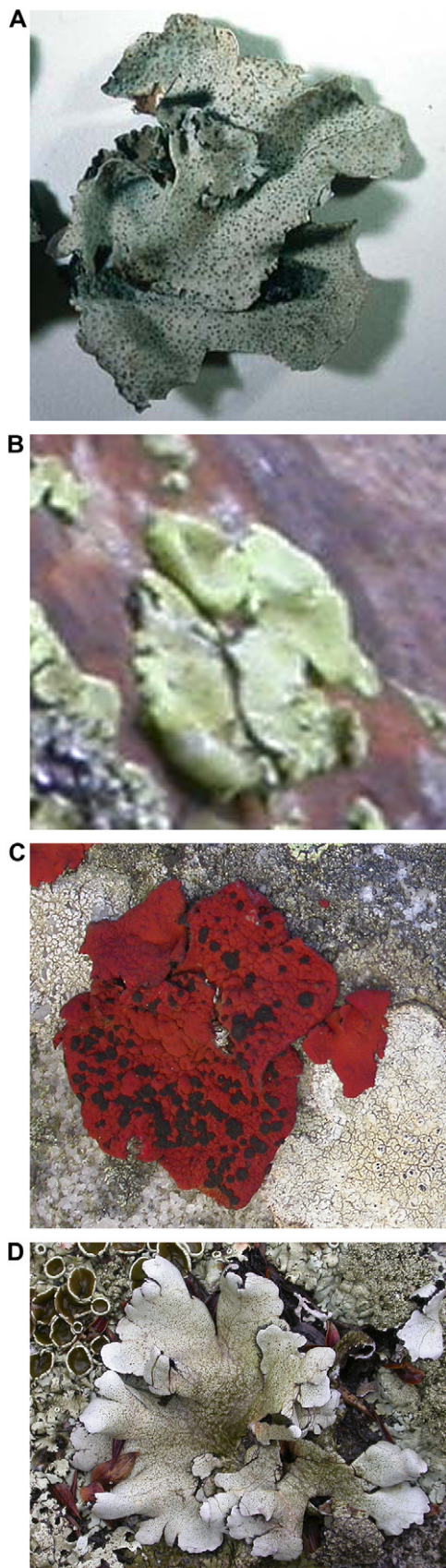
#### Umbilicate thalli

Umbilicate thalli, which have a dorsiventral foliose structure, are attached to the substratum, usually rock, only at a single central point (the 'umbilicus'). As they are not attached directly to the surface, these lichens are able to grow over the whole thallus area from the centre outward (Hestmark 1997), in contradistinction to crustose and foliose species variability attached to the substratum over almost the entire underside and which only grow at the margins. In addition, they are not constrained in their growth by the presence of adjacent lichens as the thalli just extend above any other crustose or adpressed foliose lichens that might be present and shade them out. Umbilicate thalli have a relatively large surface area from which they can absorb water from the atmosphere as both upper and lower surfaces are exposed to the air, and liquid water can be trapped underneath – especially in species that are densely covered with rhizinomorphs below (Larson 1981; Sancho & Kappen 1989). They can also take in water more rapidly than at least some foliose and shrubby lichens, but can also lose it more quickly (Larson 1981). However, there are differences in the water relations and storage amongst *Umbilicaria* species attributable to differences in the anatomy of the tissues, porosity, and internal spaces (Valladares et al. 1998).

Thalli with a similar morphology (Fig 1) occur in genera belonging to a range of lichenized families, including *Arctopeltis* (Lecanoraceae), *Dermatiscum* (Physciaceae), *Dermatocarpon* (Verrucariaceae), *Lasallia* and *Umbilicaria* (Umbilicariaceae), and *Xanthomaculina* (Parmeliaceae). The umbilicate thallus habit has consequently clearly arisen independently on at least five occasions. The ability to grow through the whole thallus area and to overreach competitors are ecological advantages, but further, many umbilicate lichens are found on rocks subject to sporadic liquid water run-off or rain, so an ability to respond quickly and take up water rapidly will also be advantageous.

### A possible role of the photobiont in the evolution of thallus types?

The majority of lichens contain eukaryotic algae of the order Trentepohliales (Ulvophyceae) and the class Trebouxiophyceae. These two groups of algae differ principally in their free-living growth habit. Although all members of Trebouxiophyceae are unicellular, Trentepohliales form often conspicuous filamentous colonies when free-living, preferentially in more humid microhabitats. Reviewing the fungal system, it appears that these different growth forms of the photobiont also influence the evolution of lichen thallus growth forms. In particular, foliose and shrubby, pendent, or other growth categories that raise the thallus from the substratum are not produced by the mycobiont in *Ostropales* associated with Trentepohliales, although the filamentous growth of the algae is often restricted in the association to few concatenated cells. In *Coenogonium* the poorly modified growth of the algal filaments determines the thallus shape entirely, and is responsible for fan-like or



filamentous thalli. Here the mycobiont merely encases the well-developed algal thraets. The situation is different in Arthoniales, where members of Roccellaceae develop conspicuous fruticose growth forms. As a consequence, we assume that the simple coccoid growth of the Trebouxiophyceae is a requirement in Lecanoromycetes to extensively evolve diverse thallus forms.

In Lecanoromycetes, other interesting correlations of photobiont selectivity have also been observed in lichens of different growth form. Piercey-Normore & DePriest (2001) found that only a few shared genotypes of *Asterochloris* occur in variously related taxa of the generally fruticose Cladoniaceae. Helms et al. (2001) showed more restricted ranges of photobionts belonging to the genus *Trebouxia* were found in foliose Physciaceae, whereas crustose groups of the same family generally had wider ranges of possible photobionts. Only two species of *Trebouxia* were observed in Scandinavian foliose Physciaceae by Dahlkild et al. (2001): *T. arboricola* was only found in *Anaptychia ciliaris*, whereas species of *Phaeophyscia*, *Physcia*, and *Physconia* were consistently associated with *T. impressa*. The strict association of this algal species is also confirmed by recent investigations that included samples from northern and southern Europe (Wornik, unpubl.). Opanowicz & Grube (2004) showed that the fruticose *Flavocetraria nivalis* only associates with *Trebouxia simplex*, and within this species complex, only with particular lineages of this algal species. Similarly, the shrubby *Letharia* associates only with particular phylogenetic lineages of *T. simplex*. Kroken & Taylor (2000) found three phylogenetic species of *T. simplex* only in California, where certain 'cryptic' species of fertile *Letharia*'s occur. Other lineages in the *T. simplex* complex detected in *Letharia* have wider geographic ranges, similar to the range of *L. vulpina*. In 27 isolates of *Parmelia sulcata*, Friedl (1989) only found *T. impressa*, whereas in 19 isolates of *Pleurosticta acetabulum* only *T. arboricola* was detected. Also, the common foliose *Xanthoria parietina* is restricted to a single clade encompassing the related morphospecies *T. decolorans*, *T. arboricola*, and *T. crenulata* (Nyati 2006).

There may be exceptions from these restricted photobiont choices, as Friedl (1989) noticed also various photobionts in different thalli of some temperate *Parmelia* and *Platismatia* species, whereas Romeike et al. (2002) found several photobionts in antarctic *Umbilicaria* species. Also, in some widespread foliose genera there can be a geographic component in the photobiont choice. *Ramalina* species select different species in the tropics as compared with species in temperate habitats (Cordeiro et al. 2005). In this case, the question arises as to whether a broad acceptance of photobionts in ancestral lineages evolved towards higher specificity in the extant species, or whether there was a more recent photobiont shift with an adaptation to different climates. The latter is likely in the case of *Physcia* (Helms 2003), where a monophyletic clade of tropical species seems to have switched to

**Fig 1 – Umbilicate growth form in lichens from different families. (A) *Dermatocarpon miniatum* (Verrucariaceae); (B) *Dermatisicum thunbergii* (Physciaceae); (C) *Lasallia rubiginosa* (Umbilicariaceae); and (D) *Xathomaculina hottentota* (Parmeliaceae). Not to scale.**

a tropical/subtropical *Trebouxia* lineage. In any event, there is clear evidence for a narrow range of selected photobionts in extant foliose and shrubby lichen species.

This seems to contrast with the situation in certain crustose lichens, where selectivity can be much lower. *Lecanora rupicola* may associate with up to six distinct lineages/species of *Trebouxia* (Blaha & Grube 2006), which could be correlated with a rather broad ecological range. Several, including as yet undescribed, *Trebouxia* species are found in thalli from the Mediterranean, whereas alpine habitats correlate with the presence of *T. simplex*. Similar patterns have been detected in alpine and Mediterranean *Tephromela atra* samples (Lucia Muggia, unpubl.), and are expected also with other euryoecious crustose species. The ubiquitous *L. muralis* is able to associate with diverse *Trebouxia* species even at the same site (Guzow-Krzeminska 2006). However, low selectivity is not generally found, and crustose lichens with more restricted ecological needs have particular partners (e.g. *Fulgensia bracteata*, Schaper 2003; *Lecanora conizaeoides*, G. Helms, pers. comm.).

These clearly indicate that the pattern of photobiont selectivity varies markedly among different lichens, and higher selectivity may commonly be associated with complex growth forms (which is also seen in foliose lichens in association with cyanobacteria, Myllys *et al.* 2007), while there is also a generally negative correlation of selectivity with ecological amplitude. The genetic background to photobiont selection certainly requires further study to assess the contribution of light-filtering compounds and taxonomic relationships to selectivity patterns. Only in a few cases have a phycobiont binding protein been found to mediate photobiont choice (Bubrick & Galun 1980; Bubrick *et al.* 1985; Legaz *et al.* 2004), and it is not yet clear whether such proteins could contribute to a generally higher selectivity in *Teloschistaceae*. Two principal strategies may be possible drivers for the evolution of symbiont selectivity patterns. Lower selectivity for symbiont lineages may increase the probability of finding an appropriate partner in varying habitats, whereas higher degree of specificity may result in an optimization of the symbiotic interaction.

## A hypothesis

Interestingly, thallus morphology has generally been interpreted by systematists without reference to changing hydration that goes along with their life in nature, notable exceptions being the study of Jahns (1984) on *Parmelia saxatilis* and those on water relations in different species of *Umbilicariaceae* (see above). However, hygroscopic thallus motion may be quite conspicuous in some cases, for example in the vagrant *Xanthoparmelia semiviridis* (syn. *Chondropsis semiviridis*), the ball-like structure of lobes folded inwardly when dry expands after wetting to form a flat structure, exposing the upper surface to the light (Rogers 1971; Lumbsch & Kothe 1988). Although a decrease in net carbon dioxide fixation in overhydrated lichens has been measured, the hydrated stage implies physiological activity and growth. Depending on the amount and structure of the intercellular polysaccharide fraction, gelatinized structures usually increase significantly in size when they are moistened; physiological activity may be sustained in thalli with such structures that may retain water,

as discussed by Jahns (1984) and Poelt (1986). Thus, although lichen thalli may generally increase in size owing to water uptake, individual layers in stratified (heteromerous) thalli may differ in this respect. Layers that are formed by distinctly gelatinized hyphal walls, also hymenia, usually swell more pronouncedly than layers that are not embedded in extracellular polysaccharides or those that are carbonized. As a consequence, the repeated swelling and shrinking of thalli under natural conditions exerts inherent mechanic forces in a growing thallus and may promote growth in certain directions. This may be especially true when the thallus is fixed to an inflexible substrate such as rock; perhaps that is the factor promoting the development of the umbilicate thallus type with a single attachment point?

Under this scenario, strictly crustose thalli with a gelatinized eucortex could be exceptional, as the hygroscopic forces in an eucortex would rather promote the development of thalli that detach from the supporting substrate surface, and are more likely to develop lobate, foliose, or shrubby forms. It is, therefore, not too surprising that growth-form transitions are observed in diverse species groups of *Lecanora* growing on rock surfaces which form variously gelatinized to eucorticate upper cortex structures, e.g. in the *Lecanora rupicola* group (*L. swartzii* subsp. *swartzii* versus subsp. *caulescens*; Poelt 1989), the *L. polytropa* group (crustose *L. polytropa* versus lobate *L. concolor*; Arup & Grube 1998) and in the *L. novomexicana* group (lobate *L. novomexicana* versus foliose *Rhizoplaca melanophthalma*; Arup & Grube 2000). The eucortex has perhaps not so much an exoskeleton function, but rather imposes a physical necessity to let the thallus grow as a detached foliose form.

Hygroscopic forces also have some effect on the functioning of sessile apothecia, and it may be hypothesized that the eucorticate thalline exciple could act to compensate for the hygroscopic motion of hymenial parts and to assist in the functionality of ascospore discharge. However, hygroscopic motions have been studied only in few lichens so far (e.g. Jahns 1984; Jahns *et al.* 1976; Büdel & Wessels 1986; Lumbsch & Kothe 1988), but they could be of interest for understanding thallus growth and evolution, as well as for functional evolution of fruit bodies. Much attention has been devoted to ascus structures and dehiscence mechanisms, but it is apparent that the ascoma in its entirety assists in the discharge of ascospores, sometimes already under moist conditions (cfr Bailey & Garrett 1968). If we consider the varying hygroscopic forces in melanized and gelatinized ascumatal parts, we face a tremendously complex evolution of discharge-assisting structures. The strongly gelatinized hymenium of a *Graphis*, for example, may develop a rather high internal pressure within its strong counter-bearing carbonized exciple. We assume a similar build-up of pressure in ascumata of *Verrucariales*, where the carbonized exciples may similarly form a rigid clamp around the distinctly swelling hymenium. Other species, for example those with biatorine or lecideine ascumata, may function differently from those with thalline (lecanorine) exciples, where a gelatinized eucorticate structure is formed to maintain the integrity of the ascoma under fluctuating water regimes. Possibly, even the notable cupular form assumed in the often quite large parmelioid ascumata could be interpreted in this context: as a counter to the swelling and shrinking hymenium.

We speculate that the role of fluctuating levels of humidity could have been underestimated in the evolution of hyphal tissue types and lichenized structures including thallus growth forms and types of ascomata. Perhaps there was a low level of differentiation in ancestral hyphal-algal aggregations, which may have been formed by the conglutination of hyphae and algae by polysaccharides derived from outer hyphal walls. The primitive thalli of *Lichinomycetes* may be reminiscent of the ancestral phenotype (see above).

## Conclusions

The traditional classification of lichen-forming fungi based on superficial similarities in fruit body and thallus types that persisted into the 1950s, started to be revolutionized through studies of ascomatal development and ascus types in the mid-1960s, and then the gradual, but then general, acceptance that their classification had to be integrated with that of all other ascomycetes in the mid-1970s. Detailed overall schemes started to be developed in the 1980s (Eriksson 1981; Hawksworth *et al.* 1983) and soon became accepted as the only possible ones for the Ascomycota (Hawksworth 1994). Molecular phylogenetic approaches have made it clear that this process is not yet complete, and that superficial similarities in fruit body and thallus types are not always reliable indicators of monophyletic groups. However, as more attention is directed to obtaining sequences from and elucidating the positions of families and genera not yet represented in the overall trees, an overall robust framework covering at least the ascomycetes that are described is in sight.

So far, molecular data in several morphologically well-circumscribed crustose genera of lichens has revealed a fundamental discrepancy between morphological diversity and sequence divergence. In large genera with high morphogenetic potential of thallus type (e.g. *Caloplaca*, *Lecanora*, *Rinodina*), different growth forms seem to have evolved rather rapidly, irrespective of what the ancestral growth form was. Substrate-detached growth forms (foliose, erect shrubby, pendent, etc.) appear morphologically more diverse than crustose forms. Yet, as the crustose (including sorediate) thallus types exhibit comparatively few diagnostic characters, these are still united in genera that now prove to be genetically diverse and paraphyletic. This situation complicates future classification schemes of lichen-forming genera, even if new or previously overlooked phenetic characters support the molecular data. In other lichens, similar challenges arise with the evolution of fruit body types, for example in *Ostropales* s. lat. (*Ostropomycetidae*) and *Arthoniales*, although the latter order is as yet little understood phylogenetically.

In the future we would also like to see attention increasingly focus on the genetic basis of development of both ascomata and thalli in lichenized groups, for example by studying the expression of functionally relevant genes, and utilizing computer simulations such as those designed for basidiomycete fruit bodies by Meškauskas *et al.* (2004) to investigate the effects of differences in timing of developmental events. An interesting aspect of such studies might be the differential reprogramming of thallus growth after spatial disturbances, as shown by the experiments of Honegger (1995). Such studies

may help explain how such similar fruit body and thallus types can develop in not closely related orders and families, and how different thallus types particularly can arise even within a single genus.

Since the mid-1990s lichen systematics has become a fast-moving and exciting research field, often yielding unexpected results, and we are pleased to have been part of that. What is also gratifying for lichenologists, who have historically tended to be side-stepped by mycologists as a whole, is that molecular phylogenetic studies have reinforced their importance in the understanding of ascomycete evolution as a whole; lichenization clearly had a key role in the ancestry of extant ascomycetes (Lutzoni *et al.* 2001; Eriksson 2005). Consequently, lichen-forming fungi merit increased attention from all concerned with ascomycetes and their evolution.

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