

## Lichen-Forming Fungi, Diversification of

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### Glossary

**Ascoma** A fruiting body bearing meiosporangia (sporangia in which meiosis occurs) known as asci.

**Ascospore** Meiospore of ascomycetes is called ascospore.

**Columella** Sterile tissue in the hymenium of some tropical crustose lichens.

**Crustosen** Crust-like growth form of the vegetative thallus in lichens.

**Cupulate exciple** It is a type of ascomatal margin forming a cupula.

**Diaspore** A vegetative propagule.

**Endolichenic** Growing inside a lichen.

**Foliose** Leaf-like growth form of the vegetative thallus in lichens.

**Fruticose** Growth form with pendulous or upright branches of the vegetative thallus in lichens.

**Heterokont** Having two morphologically different flagellae.

**Hymenium** A layer consisting of meiosporangia and sterile elements.

**Isidium** Corticated outgrowth of the thallus surface for vegetative dispersal of both partners in a lichen.

**Lichenicolous** Growing on a lichen.

**Neoendemic** A species that originated recently and is indigenous to a certain environment.

**Periderm** Cork-like outer layer of a plant stem.

**Perithecium** Pear-shaped ascoma opening with a small pore.

**Photobiont** Algal or cyanobacterial partner in a lichen symbiosis.

**Soredium** Powdery, non-corticated structures on the thallus surface for vegetative dispersal of both partners in a lichen.

**Synapomorphy** Shared derived character.

**Thallus** Plant-like vegetative body that lacks differentiation of stem, leaves, and roots.

Lichen-forming fungi form stable symbiotic associations with photosynthetic partners, such as algae and/or cyanobacteria. The fungi mostly belong to Ascomycota and to a lesser extent to Basidiomycota. Most algae in lichen symbioses belong to green algae, but heterokont (Stramenopiles) algae, such as brown algae or yellow-green algae, are also known to form stable associations with fungi. In addition, bacteria and additional fungi (endolichenic and lichenicolous) are found in the lichen symbiosis but their roles in the symbiosis are currently not fully understood. Lichen-forming fungi are a successful group, with almost 20% of all known fungi forming lichen associations, and they occur in all ecosystems: from the polar regions to the tropics. They are able to grow on all sorts of terrestrial substrates, including rocks, soil, wood, bark, and also living leaves. They are unusual for fungi in forming extensive vegetative structures, so-called thalli that have crustose, foliose, or fruticose growth forms (Figure 1). The vegetative structures provide space for the photosynthetic partners that provide nutrients in the form of sugar or sugar alcohols to the fungal partner.

Although some molecular clock-based studies suggested an origin of lichens (Heckman *et al.*, 2001) as early as the Precambrian, other studies suggest a later evolution (Lücking *et al.*, 2009; Beimforde *et al.*, 2014). Part of the problem is the uncertainty with interpreting the fossil species *Paleopyrenomyces devonius*, which has been widely used to calibrate the fungal tree of life (Berbee and Taylor, 1993; Taylor *et al.*, 1999; Taylor and Berbee, 2006; Berbee and Taylor, 2010). The interpretation of the morphological structures has varied, with the ascoma-type and ascus interpreted differently, either as



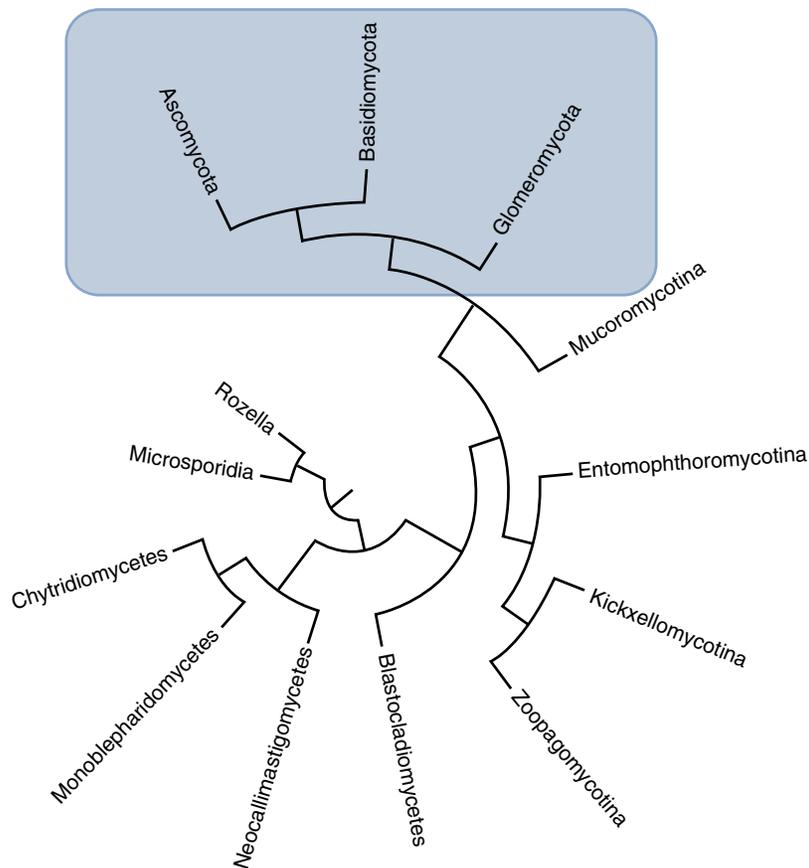
**Figure 1** Growth forms of lichens. (a) and (b). Crustose lichens ((a) – *Ochrolechia* on siliceous rocks, (b) – *Lecanora* on mosses and detritus). (c) and (d). Foliose lichens ((c) – *Menegazzia* on bark, (d) – *Hypogymnia* on twigs). (e). Fruticose lichen (*Cladia* on soil). Photos (c) and (d) by Todd Widhelm, photo (e) by Sittiporn Parmen.

being a perithecium with unitunicate asci placing them in the derived Sordariomycetes (Taylor and Berbee, 2006) or as a perithecioid ascoma with operculate asci placing them in the early diverging Pezizomycetes (Lücking *et al.*, 2009). The earliest fossils of lichens are from the lower Devonian (Taylor *et al.*, 1997), which is consistent with a later evolution of this type of fungal symbiosis. In fact, there are no lichenized taxa in basal groups of Ascomycota or Basidiomycota (Lutzoni *et al.*, 2004; Schoch *et al.*, 2009; Prieto and Wedin, 2013), which together with the mostly mycorrhizal Glomeromycota (Redecker and Raab, 2006) form the crown group of fungi (Figure 2). The latter group and all other fungal phyla lack any lichenized species.

Within Ascomycota, stable, symbiotic relationships with algae and/or cyanobacteria evolved within the derived Leotiomyceta probably during the Carboniferous (Schwartzman, 2010; Prieto and Wedin, 2013). Although the major Ascomycota lineages with lichenized species originated then, successive waves of diversification in the Jurassic and Cretaceous created the diversity at higher phylogenetic levels (Amo de Paz *et al.*, 2011; Prieto and Wedin, 2013). This subsequently gave rise to the current species diversity that originated between the Eocene and Pleistocene (see below). The diversification of major clades in lichenized fungi, especially in Lecanoromycetidae and Ostropomycetidae, is probably correlated with the major diversification events in angiosperms (Prieto

and Wedin, 2013). The angiosperms provided many new environments for epiphytic lichens. Three of the four most diverse families of lichenized fungi, Parmeliaceae (c. 2800 spp.), Graphidaceae (c. 2100 spp.), and Ramalinaceae (c. 800 spp.) are especially diverse on angiosperm bark (Jaklitsch *et al.*, 2015). Although substrate specificity is rare in lichens, a number of species are confined to similar substrates in terms of bark pH, water capacity, and bark hardness (Brodo, 1973). Recent estimates suggest the origin of angiosperms either in the lower Jurassic to lower Cretaceous (Bell *et al.*, 2005; Bell *et al.*, 2010) or in the Triassic to early Jurassic (Clarke *et al.*, 2011).

It is unclear whether lichenization within Leotiomyceta originated once (Lutzoni *et al.*, 2001) or several times (Gargas *et al.*, 1995; Schoch *et al.*, 2009). Experiments suggest that there is a latent capacity for mutualism in fungi and algae (Hom and Murray, 2014). In an experiment, obligate mutualism between the non-symbiotic model organisms *Saccharomyces cerevisiae* (yeast) and *Chlamydomonas reinhardtii* (alga) was induced in an environment requiring reciprocal carbon and nitrogen exchange. This capacity for mutualism was shown to be phylogenetically broad, including other *Chlamydomonas* and yeast species. These experiments showed that under specific conditions, environmental change induces free-living species to become mutualists. Also some fungi occurring in boreal ecosystems were shown to be facultatively lichenized



**Figure 2** Cartoon tree of the phylogenetic relationships of phyla and other major clades within the fungal kingdom. The crown group of fungi indicated by a blue box.

(Wedin *et al.*, 2004). Phylogenetic analyses showed intermixed groups of lichenized and saprotrophic specimens, suggesting that these related species can undergo their sexual lifecycle either as lichens or as saprotrophs. The flexibility of nutritional modes allows separate individuals to exploit different niches during forest succession. These studies suggest that there is more plasticity in nutritional modes of fungi than previously thought. This is not surprising, given that nutritional modes (parasitism vs. mutualism) and interkingdom host switches have been demonstrated to be common at an evolutionary scale in fungi (Spatafora *et al.*, 2007; Arnold *et al.*, 2009). Some fungi growing on lichens, so-called lichenicolous fungi, have originated from lichenized ancestors, such as the genera *Nesolechia* and *Phacopsis*, which evolved during the Miocene (Divakar *et al.*, 2015). It was even hypothesized that lichenicolous fungi may represent a 'halfway house' to explain evolution of non-symbiotic fungi from lichenized ancestors (Lutzoni *et al.*, 2001; Arnold *et al.*, 2009).

### The Evolution of Current Species Diversity in Space and Time

A number of studies have demonstrated that diversification events occurred during periods of climatic changes. For example, in the temperate to boreal crustose genus *Biatora*, the main diversification occurred during phases of climatic cooling when new types of forest vegetation and the arctic-alpine vegetation evolved (Printzen and Lumbsch, 2000). Likewise, the diversification of *Montanelia* was estimated to have occurred during a period of cooling and the development of marked thermal seasonality during the Miocene (Divakar *et al.*, 2012). In the genus *Melanohalea* it was shown that Pleistocene glaciations were not inherently unfavorable for some species and even indicated that some populations were able to expand during Pleistocene glacial cycles (Leavitt *et al.*, 2012a). Molecular data also suggest that closely related species may have experienced different demographic histories. In the genus *Xanthomendoza*, two closely related species with arctic-alpine to montane temperate distributions were studied (Leavitt *et al.*, 2013a). Whereas the data suggested a Late Pleistocene population expansion in *Xanthomendoza montana*, there was evidence for a long-term stability in the demographic history of the bipolar *Xanthomendoza borealis*, which suggests that the latter species was able to survive climatic oscillations without major contraction of its population size. In a study focusing on the phylogeography of *Ramalina menziesii*, a lichen occurring along the west coast of North America, from Baja California to Alaska, multiple lineages were found within the species (Sork and Werth, 2014). Localized lineages were found to be ancient, while some recent lineages were found to be widespread and some of the populations such as the ones in Baja California, were relatively isolated. This study provided evidence that both population persistence and dispersal contribute to the wide range of a genetically diverse species.

The fossil record for lichenized fungi is rather poor and largely restricted to Paleogene amber (Kaasalainen *et al.*, 2015). However, molecular clock approaches have been widely used to address the question of when the current diversity of species found in lichenized fungi evolved. An early

study on *Biatora*, which occurs in temperate to boreal habitats mainly of the northern hemisphere, showed that species predominantly diversified during the Eocene and Oligocene (Printzen and Lumbsch, 2000). However, there is a growing body of evidence that a large portion of the current species diversity in lichen-forming fungi is much younger and most studies indicate major diversification happened during the Neogene. During the Neogene period the climate became cooler and drier and mountain systems developed with the uplift of the Himalayas, Alps, and Rocky Mountains, resulting in the alteration of air circulation and weather patterns. These processes likely had a major impact on diversification patterns. In the temperate-to-boreal genus *Melanelixia* (Leavitt *et al.*, 2012b) and the mostly Neotropical genus *Oropogon* (Leavitt *et al.*, 2012c) the main diversification was estimated to have occurred during the Miocene. Interestingly, in these two genera, cryptic species, which are delimited based on DNA sequence divergence, were detected that originated during the Miocene. This indicates that phenotypically cryptic species in lichenized fungi can be relatively ancient and do not necessarily represent recent divergence events. Diagnosable phenotypic differences may be absent even millions of years after their divergence, suggesting that our understanding of morphology and chemistry in these organisms is poor.

The main diversification during the Miocene and Pliocene was found in the genera *Flavoparmelia* (Del-Prado *et al.*, 2013), *Melanohalea* (Leavitt *et al.*, 2012a), *Montanelia* (Divakar *et al.*, 2012), the *Xanthoparmelia pulla* group (Amo de Paz *et al.*, 2012), and the Macaronesian species of *Nephroma* (Sérusiaux *et al.*, 2011). The former three genera all belong to the family Parmeliaceae, which is one of the largest families of lichen-forming fungi (Thell *et al.*, 2012; Kraichak *et al.*, 2015a). *Melanohalea* and *Montanelia* have their centers of diversity in temperate to arctic-alpine regions of the northern hemisphere, whereas *Flavoparmelia* – although being a cosmopolitan genus – has its center of diversity in Australasia. The latter genus occurs in temperate to subtropical areas mostly on tree bark. The *Xanthoparmelia pulla* group, which also belongs to Parmeliaceae, occurs worldwide in areas dominated by a Mediterranean (winter rain) climate. Traditionally, these species were distinguished using phenotypical characters and were assumed to have a subcosmopolitan distribution. However, molecular data, similar to results in the *Parmelina quercina* group (Arguello *et al.*, 2007), demonstrated that distinct lineages were correlated with geographical distributions (Amo de Paz *et al.*, 2012). Five major clades were found, two clades occurring in South Africa and one clade in the Mediterranean basin, Macaronesia, and California, whereas two clades had disjunct distributions, occurring in Australia and South America, and California and South America, respectively. These disjunctions were explained by long-distance dispersal (in the most recent California–South America disjunction it was estimated at 3.44 Ma). In a few genera of Parmeliaceae, molecular data suggest that the diversification predominantly occurred even more recently. In the fruticose genus *Letharia*, which occurs in temperate to boreal areas of western North America, continental parts of Eurasia, and montane areas of northern Africa, the major speciation was estimated to have occurred during the Pleistocene (Altermann *et al.*, 2014).

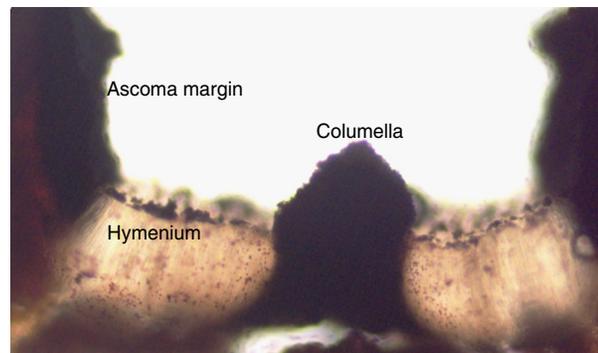
The genus *Xanthoparmelia* is the most speciose among lichenized fungi with over 800 species (Theell *et al.*, 2012). A clade of *Xanthoparmelia* species occurring in North America has been shown to have diversified mainly during the Pleistocene (Leavitt *et al.*, 2013b). Recently diverged lineages are generally more difficult to separate using molecular data due to incomplete lineage sorting, requiring a large sampling of markers (Leavitt *et al.*, 2013b; Altermann *et al.*, 2014). Whereas this has been a limiting factor examining these species complexes using Sanger sequencing, it is likely that next generation sequencing will allow more of these recently evolved complexes to be thoroughly studied.

The studies addressing diversification events of species complexes in lichens suggest that lichen-forming fungi are not unique, in that diversification is similar in land plants clades of similar age (Linder, 2008). However, lichenized fungi tend to have wider distributional ranges than land plants. This is true although molecular data have demonstrated that cryptic species are commonly found hidden within phenotypically circumscribed species (Crespo and Lumbsch, 2010; Lumbsch and Leavitt, 2011) and helped to revise species delimitation in these fungi. The wider distributional ranges are likely due to the higher distributional capacity of the relatively small ascospores or vegetative diaspores (soredia or isidia) that allow dispersal of the photosynthetic partner simultaneously with the fungal partner. Indeed, long-distance dispersal has been shown to have occurred commonly in lichenized fungi (Divakar *et al.*, 2010; Geml *et al.*, 2010; Otálora *et al.*, 2010; Amo de Paz *et al.*, 2011; Fernandez-Mendoza *et al.*, 2011; Amo de Paz *et al.*, 2012; Leavitt *et al.*, 2012a; Parmen *et al.*, 2012).

Local diversification has been found in a clade of *Umbilicaria* species endemic to the central Andes (Hestmark *et al.*, 2011). All endemic species found in this region share a common ancestor in the *Umbilicaria vellea* group that has a worldwide distribution and contains several asexually reproducing species. The authors interpreted independent reversals to sexual reproduction as an explanation for different ascoma morphologies in this monophyletic endemic lineage. In a different study on the genus *Nephroma*, all species endemic to the north-west African archipelago of Macaronesia were shown to represent neoendemics that originated from a common ancestor shared with a widely distributed species (Sérusiaux *et al.*, 2011). The endemics are estimated to have reached the archipelago via long-distance dispersal.

### Adaptive Radiation and Explosive Diversification

Across the entire tree of life, large disparities can be seen in species richness. Explosive diversification (Gittenberger, 1991; Givnish, 2015) or adaptive radiation (Osborn, 1902; Gavrilits and Losos, 2009; Rundell and Price, 2009) are well known to cause dramatic differences in species numbers among clades, and prominent examples of radiations include African cichlid fishes (Seehausen, 2006), Darwin finches (Grant, 1981; Lamichhane *et al.*, 2015), or the Hawaiian silverswords (Baldwin and Sanderson, 1998). Adaptive radiation is usually explained as being driven by divergent selection caused by competition among closely related, ecologically similar species (Givnish, 1997). In lichenized fungi our understanding of the



**Figure 3** Cross section through an ascoma of the genus *Ocellularia* showing the columella, a sterile dark structure in the center of the hymenium.

impact of trait evolution on diversification is not well understood and the few studies addressing this issue focus on specific genera. Despite the fact that some hyper-diverse families, such as Parmeliaceae, have distinct morphological synapomorphies, such as the cupulate exciple (Divakar *et al.*, 2013, 2015), the relationship of these traits and diversification are not well understood. However, the remarkable phenotypic disparity in the genus *Cladia* (including crustose, foliose, and fruticose species) has been explained by adaptive radiation (Lumbsch *et al.*, 2010) in temperate Australia. Explosive diversification has resulted in hyper-diverse groups, such as the genera *Ocellularia*, *Parmotrema*, *Usnea*, and *Xanthoparmelia* (Kraichak *et al.*, 2015a,b). The former genus belongs to a hyper-diverse family but even within the family, *Ocellularia* has a significantly accelerated rate of diversification (Kraichak *et al.*, 2015a,b). In this genus, the accelerated diversification rate was significantly associated with the presence of a unique sterile tissue in the hymenium (Figure 3) that often covers most parts of the ascomata, the so-called columella (Kraichak *et al.*, 2015b; Rivas Plata and Lumbsch, 2011). Hence the columella was interpreted as a key innovation, which is a trait that enabled a lineage to proliferate (Simpson, 1953). The function of the columella, however, is less clear and this underlines the poor state of knowledge of trait evolution in lichenized fungi. Hypotheses of its function include being a 'battering ram' to push through the outer periderm of these tropical epiphytic lichens (Redinger, 1936) or defense against fungivores, since the structure fills almost the entire hymenium and hence potentially protects the ascospores (Lücking and Bernecker-Lücking, 2000).

### Association of Rates of Diversification and Evolutionary Rates

Similar to the way rates of diversification fluctuate over time and among clades, differences in evolutionary rates have been shown to be common across the tree of life (Langley and Fitch, 1974; Britten, 1986; Arbogast *et al.*, 2002; Bromham and Penny, 2003). A number of causes have been invoked to explain the observed differences, most commonly body size and metabolic rate (Martin and Palumbi, 1993; Bromham, 2002), generation time (Gu and Li, 1992; Ohta, 1992), symbiotic association (Lutzoni and Pagel, 1997; Woolfit and Bromham,

2003), or environmental conditions (Bromham and Cardillo, 2003). Disparities of evolutionary rates have also been shown among lichen-forming fungi (Lumbsch *et al.*, 2008; Otálora *et al.*, 2013). In addition, theory also predicts a correlation between rates of substitution changes and diversification (Jobson and Albert, 2002). In the presence of a founder effect (Mayr, 1963), i.e., when speciation takes place in small, peripheral populations, genetic drift will cause rapid genetic change resulting in longer branches in phylogenetic trees (Pagel *et al.*, 2006). Evidence from various organismal groups support the correlation of evolutionary rates and rates of diversification (Barraclough *et al.*, 1996; Barraclough and Savolainen, 2001; Webster *et al.*, 2003) and has also been shown for Ascomycota (Wang *et al.*, 2010). Approximately a third of all Ascomycota species are lichen-forming. However, currently the frequency of speciation that experienced founder effects is poorly understood.

### The Diversity of the Photobiont in the Lichen Symbiosis

Most studies to date have focused on the fungal partner in the lichen symbiosis. However, there is evidence for strong phylogenetic signals in the occurrence of photobionts in clades of lichenized fungi (Rambold *et al.*, 1998; Dahlkild *et al.*, 2001; Helms *et al.*, 2001; Persoh *et al.*, 2004; Buckley *et al.*, 2014; Lindgreen *et al.*, 2014; Leavitt *et al.*, 2015). At the same time, it was shown that some lichenized fungi are able to adapt to different habitats by forming symbiotic relationships with ecologically distinct photosynthetic partners (Del Campo *et al.*, 2010, 2013). It was hypothesized that ecological diversification and speciation of lichen symbionts in different habitats includes a transient phase consisting of associations with more than one photobiont in individual thalli (Del Campo *et al.*, 2013) and that such a diversification might be promoted by different physiological backgrounds. An alternative interpretation sees the ability to form association with ecologically different photobionts as an adaptive strategy to expand the potential geographical range of a species (Sadowska-Des *et al.*, 2014). Studies addressing photobiont diversity and selectivity of the fungal partner, however, are currently in their infancy and additional studies will undoubtedly shed more light in the complex interplay of partners in these fascinating symbiotic systems.

*See also:* Endophytic Microbes, Evolution and Diversification of Mutualism, the Evolutionary Ecology of

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