Evolution of Lichens

H. Thorsten Lumbsch and Jouko Rikkinen

1 INTRODUCTION—THE DIVERSITY OF FUNGAL LIFESTYLES

Fungi represent one of the three major crown lineages of eukaryotes, besides plants and animals. For their nutrition, fungi either decompose organic material or form symbiotic associations with other organisms. These symbiotic relationships vary from parasitic lifestyle, such as the rice blight fungus (Partida-Martinez and Hertweck 2005), which causes damage to rice seedlings and uses endosymbiotic bacteria for toxin production, to mutualistic relationships, such as endomycorrhizal relationships, the origin of which coincides with the early evolution of land plants (Simon et al. 1993). There is a continuum among symbiotic associations, from mutualistic to parasitic lifestyles, and some fungal species are known to exhibit different kinds of relationships with different hosts, such as species in the genus *Colletotrichum,* which can form mutualistic relationships with some plants and have parasitic relationship with other hosts (Redman, Dunigan, and Rodriguez 2001). In addition, at an evolutionary scale, changes of nutritional modes (parasitism versus mutualism) and inter-kingdom host switches have been shown to be common in fungi (Spatafora et al. 2007; Arnold et al. 2009).

Given that all fungi are heterotrophic, it is not surprising that many of them have developed symbiotic relationships with photoautotrophic organisms, such as cyanobacteria, algae, and land plants. Fungal relationships with vascular plants are mostly in form of mycorrhiza, such as ectomycorrhizal (Agerer 1991; Wiemken and Boller 2002), endomycorrhizal (Bonfantefasolo and Spanu 1992), and the unique orchid mycorrhizal associations, in which plant seedlings are, from the very beginning, dependent on symbiotic fungi as carbohydrate source (Rasmussen 2002; Dearnaley 2007; Rasmussen and Rasmussen 2009). In addition, symbiotic relationships of fungi with early diverging land plants (i.e., liverworts, hornworts, and mosses) are diverse and ecologically important (Felix 1988; Davey and Currah 2006; Stenroos et al. 2010). Fungal associates with cyanobacteria and algae are just as diverse as those with plants and include not only lichen-forming fungi (Hawksworth 1988; Nash 2008) but also algicolous fungi (Hawksworth 1987; Kohlmeyer and Volkmann-Kohlmeyer 2003; Jones 2011), which are either parasites on algae or cyanobacteria (Kohlmeyer and Demoulin 1981; Sonstebo and Rohrlack 2011; Gerphagnon et al.

2013) or form mutualistic relationships, the so-called mycophycobioses (Kohlmeyer and Kohlmeyer 1972; Hawksworth 1988; Selosse and Letacon 1995; Kohlmeyer and Volkmann-Kohlmeyer 2003; Suryanarayanan et al. 2010). Another case of relationships of a fungus in the phylum Glomeromycota, which mostly includes species forming endomycorrhizal relationships, is the cyanobacterial-fungal relationship between *Geosiphon pyriforme* and *Nostoc* (Gehrig, Schussler, and Kluge 1996; Schussler and Kluge 2001; Kluge et al. 2002; Schussler 2002), in which the cyanobacteria are located within the coenocytic cell of the fungal host. If the fungal-algal/cyanobacterial relationship is exosymbiotic (versus the endosymbiotic relationship of *Geosiphon* and *Nostoc*) and the fungal partner is the exhabitant (versus inhabitant in algicolous fungi), we call this type of association a lichen. Hence, lichens are not unique symbiotic associations but merely one type of a large diversity of relationships of fungi with photoautotrophic organisms.

The majority of fungi forming lichens belong to the phylum Ascomycota, whereas a smaller number of species is also known from derived groups within Basidiomycota (Nash 2008). While the number of lichenized basidiomycetes was often assumed to be small, recent molecular studies suggest that the number of species is actually much higher—albeit drastically lower than the number of lichenized Ascomycota (Lawrey et al. 2009; Dal-Forno et al. 2013; Lücking et al. 2014). Within Ascomycota, none of the early diverging clades, such as the subphyla Taphrinomycotina, Saccharomycotina, and the Pezizomycetes, have any lichenized species (Lumbsch 2000; Hibbett et al. 2007; Schoch et al. 2009; Lumbsch and Huhndorf 2010) and other diverse clades, such as Sordariomyceta (including Leotiomycetes and Sordariomycetes), also lack lichen-forming species (Lumbsch and Huhndorf 2007). Lichen-forming ascomycetes can be found in the classes Arthoniomycetes, Coniocybomycetes (Prieto et al. 2013), Dothideomycetes, Eurotiomycetes, Lichinomycetes, and, especially, Lecanoromycetes (Hibbett et al. 2007; Schoch et al. 2009; Lumbsch and Huhndorf 2010). The latter is the second species-rich class after Dothideomycetes, with approximately 15,000 species (of the roughly 18,500 lichenized Ascomycota currently accepted [Feuerer and Hawksworth 2007]), and the vast majority of the species are lichen-forming. Only few species in this class either have a facultatively lichenized lifestyle (Wedin, Döring, and Gilenstam 2004) or are lichenicolous fungi derived from lichenized ancestors (Divakar et al. 2015).

Photosynthetic partners in the lichen symbiosis include cyanobacteria and/or algae (Friedl 1995; Friedl and Bhattacharya 2002; Rikkinen 2002; Rikkinen 2013). The majority of algae in lichen symbioses belongs to green algae (Chlorophyte), but also heterokont (Stramenopiles) algae, such as brown or yellow-green algae, are known to form associations with fungi. In addition to fungal and photosynthetic partners, bacteria and additional fungi (endolichenic and lichenicolous) are regularly found in the lichen symbiosis (Lawrey and Diederich 2003; Cardinale et al. 2008; Arnold et al. 2009; Hodkinson and Lutzoni 2009; Hodkinson et al. 2012; Erlacher et al. 2015). In many cases, their role is not well understood, but their presence is far from random and rather shows a clear pattern not only regarding phylogenetic relationships but also at an ecological scale (Hodkinson et al. 2012; U'Ren et al. 2012).

Lichen-forming species are a diverse group of fungi, with almost 20% of currently known fungal species participating in lichen associations, and they occur in all terrestrial ecosystems, from Polar Regions to the tropics. Although they are more prominent in arctic-alpine vegetation types, the diversity in the tropics, especially in wet montane forests, is actually higher (Sipman and Harris 1989; Lücking et al. 2009b). Lichens are able to grow on a wide variety of terrestrial substrates, including rocks, soil, wood, bark, and also living leaves of plants. A few species occur in the intertidal zones of coastal habitats or are submerged in mountain streams. Unlike most other fungi, lichens form extensive vegetative structures (thalli), which house the photosynthetic partners. The thalli can have different forms, including crustose, foliose, and fruticose growth forms (Figure 1). The latter resemble small shrubs; foliose lichens are distinctly flattened; and crustose species grow as a crust over or within their substrate. When isolated, lichen-forming fungi (mycobionts) do not generally form these specialized structures but grow as mold-like colonies comparable to those of many other ascomycetes. The typical growth form of each lichenforming fungus is usually species-specific, with the exception of some species that associate with both green algae and cyanobacteria and then can, in some cases, form different types of thalli with the two contrasting photobionts, such as the fruticose cyanomorphs and foliose chloromorphs of some *Sticta* species (James and Henssen 1976; Armaleo and Clerc 1991; Magain, Goffinet, and Serusiaux 2012). The conspicuous thallus structures of lichens partly explain why for a long time their symbiotic nature was not understood but they were thought to represent a separate group of organisms. DeBary and Schwendener discovered in the 1860s (Honegger 2000) that lichens are actually symbiotic entities consisting of one fungal and one to several algal/ cyanobacterial partners.

How often has the lichen lifestyle evolved in fungi? Although it is clear that lichen-forming Ascomycota and Basidiomycota originated independently, the question of lichenization within

Ascomycota is more difficult to answer. As already mentioned, lichen-forming species are not randomly distributed over the tree of the phylum but are concentrated in the derived Leotiomyceta. While some analyses suggested a single origin of lichenization—or at least could not rule it out (Lutzoni, Pagel, and Reeb 2001)—other analyses suggested multiple such events within ascomycetes (Gargas et al. 1995; Schoch et al. 2009). In this connection, some recent experiments demonstrating latent capacity for mutualism in both fungi and algae are of special interest. (Hom and Murray 2014) performed an experiment in which obligate mutualism between the nonsymbiotic model organisms *Saccharomyces cerevisiae* (ascomycetous yeast) and *Chlamydomonas reinhardtii* (green alga) was induced in an environment requiring reciprocal carbon and nitrogen exchange. Further, this capacity for mutualism was shown to be phylogenetically broad, as it was also exhibited by other species of algae and yeasts. The experiments demonstrated that under specific conditions, environmental change induced free-living species to become mutualists. This evidence is especially interesting in the context of the previously described diversity of symbiotic relationships of fungi with algae and/or cyanobacteria (parasitismmutualism and obligate or facultative mutualism) and in the context of the fact that the nature of symbiotic relationships in fungi has changed over evolutionary times (shifts between different nutritional modes, origin of lichenicolous fungi or saprobionts from lichenized ancestors, and so on). Hence, the question whether lichenization happened once or several times independently in Ascomycota may inherently require an unjustified oversimplification of biological complexity, since the plasticity of symbiotic relationships cannot really be expressed in coding schemes required for character reconstruction analyses.

2 MOLECULAR EVIDENCE

Traditionally, lichens were thought to represent an ancient group within fungi or at least within the crown group of fungi (Church 1921; Smith 1921), an idea that has been since resurrected in the “protolichenes hypothesis” (Eriksson 2005; Grube and Hawksworth 2007; Lipnicki 2015). However, lineages of Ascomycota that include lichenforming species originated sometime between the Devonian and the early Carboniferous (Lücking et al. 2009a; Gueidan et al. 2011; Prieto and Wedin 2013; Beimforde et al. 2014). Beimforde et. al. (2013) estimated the crown age of all ascomycete classes that chiefly consist of lichenized forms at or after the Carboniferous:

Arthoniomycetes in the Permian, Lecanoromycetes in the Permian or Carboniferous, and the split of Coniocybomycetes and Lichinomycetes in the Triassic or Permian. The crown ages for Dothideomycetes and Eurotiomycetes that have a smaller percentage of lichenized species were estimated as being in the Carboniferous or Permian. This indicates that lichens—at least those related to extant lichen-forming fungi—have originated during the Carboniferous and suggests that the lichen's lifestyle has evolved relatively recently in the fungal tree of life, which dates back to the Proterozoic (Lücking et al. 2009a). This means that when the first lichen-forming fungi evolved, land plants such as several bryophyte and pteridophyte groups and progymnosperms already existed. Subsequently, waves of diversification during the Jurassic and Cretaceous created the diversity at higher phylogenetic levels within the lichen-containing clades (Amo de Paz et al. 2011; Prieto and Wedin 2013). Prieto and Wedin (2013) pointed out that the major diversi.cation in Lecanoromycetes (especially the speciesrich subclasses Lecanoromycetidae and Ostropomycetidae) coincides with the major diversi.cation events in angiosperms. Angiosperms provided many new environments for epiphytic lichens. Interestingly, the two most speciesrich families of lichen-forming fungi, Parmeliaceae and Graphidaceae (together almost 5000 spp.), contain a large percentage of species growing on angiosperm bark (Jaklitsch et al. 2015). While strict substrate speci.city is relatively rare in lichens, numerous epiphytic species are more or less confined to a rather narrow range of substrates in terms of bark pH, water capacity, and hardness of the substrate (Brodo 1973; Spier, van Dobben, and van Dort 2010; Ellis 2012). Angiosperms have a higher diversity of these characters and hence may have contributed to the explosive diversification (Givnish 2015) of these two families. Graphidaceae originated during the Jurassic, whereas the family Parmeliaceae appears to be much younger and originated in the Cretaceous (Amo de Paz et al. 2011; Rivas Plata 2011; Kraichak et al. 2015). However, the relatively recent bursts in speciation contributed mainly to the current species diversity in both families. In Graphidaceae, the genus *Ocellularia,* which is unique in having sterile tissue within its hymenium, a potential key innovation (Kraichak, Luecking, and Lumbsch 2015), started to increase its diversi.cation during the early Paleogene. In Parmeliaceae, the increase in speciation rates in the genera *Usnea* and *Xanthoparmelia* (however, the latter does not include epiphytic species) appears to have started in the Oligocene (Kraichak et.al. 2015). The higher-level diversity subsequently gave rise to the current species diversity, which mostly originated between the Eocene and Pleistocene, primarily during the Neogene. The temperate to boreal genus *Biatora* is comparatively old and seems to have predominantly diversified during the Eocene and Oligocene

(Printzen and Lumbsch 2000). In contrast, much of the current species diversity in lichen-forming fungi may be much younger. The majority of studies so far have indicated major species diversi.cation during the Neogene. The main diversification was estimated to have happened during the Miocene in the temperate to boreal genus *Melanelixia* (Leavitt et al. 2012b) and the chiefly Neotropical genus *Oropogon* (Leavitt, Esslinger, and Lumbsch 2012). The genera *Flavoparmelia* (Del-Prado et al. 2013), *Melanohalea* (Leavitt et al. 2012), *Montanelia* (Divakar et.al. 2012), Macaronesian species of *Nephroma* (Sérusiaux et al. 2011), and the *Xanthoparmelia pulla* group (Amo de Paz et al. 2012) appear to have diversified during the Miocene and Pliocene.

In some lichen groups, such as the temperate to boreal genera *Letharia, Diploschistes,* and North American *Xanthoparmelia* species, the major diversifcation was estimated to have occurred in the even more recent past, during the Pleistocene (Rivas Plata 2011; Leavitt et al. 2013; Altermann et al. 2014). While improved methods of using relaxed molecular clocks have improved age estimates, and the estimates from recent studies seem to coalesce around similar times, these methods are dependent on using fossil evidence for calibration, and as discussed below, the fossil record for lichens is far from being complete or easy to interpret. In addition, it is known that branch lengths in a chronogram are not only influenced by the age of a taxon but also by other factors such as different substitution rates, which are often caused by differences in generation time (Lumbsch et al. 2008), switches of nutritional mode (Lutzoni and Pagel 1997), or frequency of founder effects in speciation processes (Wang et al. 2010). All these have been demonstrated to occur in fungi, and hence, we should keep in mind that an age estimate derived from molecular data should always be regarded only a hypothesis.

3 THE FOSSIL RECORD

The fossil record seems at odds with the molecular dating approaches, with fossils being interpreted as lichens such as *Thucomyces* (Hallbauer and van Warmelo 1974; Hallbauer, Jahns, and Beltman 1977) and lichen-like fossils (Yuan, Xiao, and Taylor 2005) from the Proterozoic, the genus *Farghera* from the Cambrian-Ordovician boundary (Retallack 2009), and thalloid impressions from the early Silurian (Tomescu and Rothwell 2006)—all of them existed well before the classes originated that contain extant lichens. In addition, the Paleozoic *Prototaxites* (Taylor and Osborn 1996; Selosse 2002; Boyce et.al. 2007; Edwards, Axe, and Honegger 2013; Retallack and Landing 2014) has been repeatedly suggested to represent a lichen-like organism.

The reasons for this incongruence of molecular and fossil evidences are multifold. First, given the relatively unspecific morphology of lichens, identifying a structure in the fossil record as a lichen is difficult and virtually impossible if both the fungal and algal partners are not present and, in addition, a thallus is formed (Taylor, Krings, and Taylor 2015). Second, the relationships of fungi and algae can vary a lot, as discussed above, and hence, the presence of fungal hyphae in close proximity of algae or cyanobacteria does not necessarily mean that this relationship was lichen-like but could also represent other types of relationships such as algicolous fungi, which are found in numerous different groups of ascomycetes. Third, even if some of the early fossils represent mutualistic relationships of fungi and algae or cyanobacteria, this does not mean that those fungi were related to extant lichenized fungi. It is logical to assume that fungi suffered mass extinctions similar to other organismal groups, but we lack the fossil evidence mainly because of the simplicity and often highly ephemeral nature of structures in these organisms. For example, within Ascomycota, the early diverging subclass Taphrinomycotina consists of only about 100 species in 5 classes with vastly different morphology and ecology (Jaklitsch et.al. 2015): Archaeorhizomycetes, which are sterile hyphae in soil; Neolectales, which are terrestrial fungi morphologically resembling Leotiales; parasites in the lungs of vertebrates that are placed in Pneumocystidomycetes; fission yeasts in Schizosaccharomycetes; and plant parasites in Taphrinomycetes. It appears that these current species are likely remnants of an originally much larger group. Hence, it cannot be ruled out that many early lichen-like associations were formed by fungi that have since become extinct.

In addition, some of the fossil evidence is incomplete and therefore difficult to interpret. For example, in *Thucomyces,* no photobiont could be found, and the structures have also been interpreted as abiotic pseudofossils or filaments of bacteria, making the report at least doubtful. The 400 Mya lichen-like fossils from the Proterozoic show a close contact of fungal hyphae and cyanobacterial cells (Yuan, Xiao, and Taylor 2005), but the exact nature of the association is unclear, since modern fungal hyphae regularly occur in cyanobacterial biofilms on soil or rocks and the fossil could also represent an algicolous fungus. In addition, the phylogenetic placement of the fungal partner in this fossil remains unclear. In the case of the genus *Farghera* (Retallack 2009), and the thallus-like impressions from the early Silurian (Tomescu and Rothwell 2006), the evidence is incomplete, since, in both cases, the presumed photobiont has not been documented and the structures have also been interpreted differently by other authors (Taylor, Krings, and Taylor 2015). Currently, there is no unambiguous evidence for the presence of lichen symbioses in the fossil record before the Devonian.

Devonian fossils that were interpreted as lichens include the genus *Winfrenatia* (Taylor, Hass, and Kerp 1997; Karatygin, Snigirevskaya, and Vikulin 2009). However, the thallus structure of this fossil is not very well defined and does not resemble that of extant lichens. Further, different types of cyanobacteria were found, and an alternative interpretation could be that the fossilized structure represents a biofilm with cyanobacterial cells and fungal hyphae. In any case the hyphae do not appear to belong to an ascomycete, since they do not show septa. In addition, the Devonian fossils *Flabellitha* (Jurina and Krassilov 2002) and *Spongiophyton* (Taylor et.al. 2004) are difficult to interpret, since the photobiont presence remains uncertain and the fungal structures do not closely resemble those of extant lichens.

The three oldest fossils that morphologically agree with extant lichens are *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis* from the Devonian (Honegger, Edwards, and Axe 2013) and *Honeggeriella* from the lower Cretaceous (Matsunaga, Stockey, and Tomescu 2013). *Cyanolichenomycites* is a sterile, dorsiventral thallus, apparently formed by an ascomycete and a nostocoid photobiont, whereas *Chlorolichenomycites,* albeit similar in structure, is formed by an ascomycete, with a photobiont that appears to be a eukaryotic alga. Both species have a stratified thallus similar to those found in extant foliose lichens. Based on the septate hyphae, they were tentatively interpreted as belonging to Pezizomycotina. These fossils were so well preserved that in *Chlorolichenomycites,* even endolichenic bacteria and fungi were identified (Honegger, Axe, and Edwards 2013). These two fossils are estimated 415 Myr. Given their age, they either could represent a clade of lichenized Pezizomycotina that became extinct or might be seen as support for the hypothesis that lichenization evolved well before the split of the major extant classes with lichenized species and that some of the crown ascomycetes would thus be derived from lichenized ancestors (Kranner and Lutzoni 1999; Lutzoni, Pagel, and Reeb 2001). Unfortunately, the next oldest fossil that has so far been confidently identified as lichen, that is, *Honeggeriella,* is more than 300 Myr younger. While it is not yet possible to trace the early evolution of lichenized ascomycetes from the fossil record, *Honegeriella* lived during the Cretaceous, when all major higher-level clades of lichenized fungi already existed (Beimforde et al. 2014). Thus, it fills an important gap between the Devonian fossils and the much younger amber fossils. *Honeggeriella* is a stratified foliose or squamulose lichenized ascomycete, with an alga as photobiont, and anatomical studies could show the mycobiont-photobiont interfaces characterized by intracellular haustoria. However, once again, its exact affinities to extant lichens cannot be determined, since it only represents a vegetative thallus, and similar thallus anatomies have independently evolved in unrelated groups of ascomycetes.

Fossils preserved in Cenozoic amber have shown that several lineages of lichen-forming fungi have conserved their morphological adaptations (Figure 2), which indicates that numerous genera have remained phenotypically stable over the last million years—this includes *Anzia, Calicium,* and *Chaenotheca* in Baltic amber (Rikkinen and Poinar 2002; Rikkinen 2003; Beimforde et al. 2014), estimated approximately 40 Myr (Poinar 1992; Standke 1998); *Phyllopsora* and parmelioid lichens in Dominican amber (Poinar, Peterson, and Platt 2000; Rikkinen and Poinar 2008), estimated to be between 15 and 20 Myr (Schlee 1990; Iturralde-Vincent and MacPhee 1996); and also an alectorioid or oropogonoid lichen in Bitterfeld amber (Kaasalainen et al. 2015), which is at least 23.8 Myr old. Hence, while even well-preserved amber fossils can be very difficult to place (Hartl et al. 2015; Kettunen et.al. 2015), the interpretation of others can be made, with some confidence, to generic level or at least groups of genera. These fossils fall within the estimated dates for diversification of those genera using molecular markers.

However, morphological similarity with extant lichens does not rule out misinterpretations. Recently, it was shown that the Baltic amber fossil *Alectoria succini* (Mägdefrau 1957), which has been used as a calibration point in molecular clock analyses (Amo de Paz et al. 2011; Prieto and Wedin 2013), is in fact not a lichen but probably root material (Kaasalainen et al. 2015). This reminds us that great care should be taken when selecting fossils, since the use of age constraints has significant effects on divergence time estimates (Taylor and Berbee 2006).

4 CONCLUSIONS

Thanks to recent spectacular discoveries of well-preserved fossils from the Devonian and Cretaceous and a series of discoveries of amber fossils, in tandem with improved molecular clock analyses and larger taxon sampling in molecular studies, our knowledge of the evolution of lichens improved dramatically over the last decades. The earliest fossils that can be unambiguously identified as lichens and the results from molecular clock approaches indicate that extant lichens may have originated during the Devonian. On the other hand, there is also a growing body of evidence that many extant lichens are not ancient but have evolved relatively recently in the fungal tree of life. In any case, there are still many uncertainties and especially the early fossils should be interpreted in a holistic framework that keeps in mind the extant diversity of symbiotic associations between fungi and phototrophic organisms. Both intensive search for fossils that bridge the large gaps between the known lichen fossils and new molecular phylogenies that include more lichenized taxa of uncertain phylogenetic placement, such as the enigmatic Aphanopsidaceae, Thelocarpaceae, and Vezdaeceae (Reeb, Lutzoni, and Roux 2004; Lumbsch, Zimmermann, and Schmitt 2009; Printzen et.al. 2012; Flakus and Kukwa 2014) or the basically unknown Moriolaceae (Hedlund 1895; Keissler 1934), will be necessary to further elucidate the evolution of these symbiotic organisms.

ACKNOWLEDGMENTS

We wish to thank our colleagues Ana Crespo (Madrid), Pradeep Divakar (Madrid), Steven Leavitt (Chicago), and Alexander R. Schmidt (Göttingen) for their collaboration and fruitful discussions on this topic over the last years.

REFERENCES

Agerer, R. 1991. Characterization of ectomycorrhiza. *Methods in Microbiology* 23:25–73.

Altermann, S., S. D. Leavitt, T. Goward, M. P. Nelsen, and H. T. Lumbsch. 2014. How do you solve a problem like *Letharia*? A new look at cryptic species in lichen-forming fungi using Bayesian clustering and SNPs from multilocus sequence data. *PLoS ONE* 9:e97556.

Amo de Paz, G., P. Cubas, P. K. Divakar, H. T. Lumbsch, and A. Crespo. 2011. Origin and diversi.cation of major clades in parmelioid lichens (Parmeliaceae, Ascomycota) during the Paleogene inferred by Bayesian analysis. *PLoS ONE* 6:e2816.

Amo de Paz, G., A. Crespo, P. Cubas, J. A. Elix, and H. T. Lumbsch. 2012. Transoceanic dispersal and subsequent diversi.cation on separate continents shaped diversity of the *Xanthoparmelia pulla* group (Ascomycota). *PLoS ONE* 7:e39683.

Armaleo, D., and P. Clerc. 1991. Lichen chimeras: DNA analysis suggests that one fungus forms two morphotypes. *Experimental Mycology* 15:1–10.

Arnold, A. E., J. Miadlikowska, K. L. Higgins et.al. 2009. A phylogenetic estimation of trophic transition networks for ascomycetous fungi: Are lichens cradles of symbiotrophic fungal diversi.cation? *Systematic Biology* 58:283–297.

Beimforde, C., K. Feldberg, S. Nylinder et.al. 2014. Estimating the phanerozoic history of the Ascomycota lineages: Combining fossil and molecular data. *Molecular Phylogenetics and Evolution* 78:386–398.

Bonfantefasolo, P., and P. Spanu. 1992. Pathogeneic and endomycorrhizal associations. *Methods in Microbiology* 24:141–168.

Boyce, C. K., C. L. Hotton, M. L. Fogel, G. D. Cody, R. M. Hazen, A. H. Knoll, and F. M. Hueber. 2007. Devonian landscape heterogeneity recorded by a giant fungus. *Geology* 35:399–402.

Brodo, I. M. 1973. Substrate ecology. In *The Lichens*, 401–441. Eds. V. Ahmadjian, and M. E. Hale. New York, Academic Press.

Cardinale, M., J. V. de Castro, Jr., H. Mueller, G. Berg, and M. Grube. 2008. *In situ* analysis of the bacterial community associated with the reindeer lichen *Cladonia arbuscula* reveals predominance of Alphaproteobacteria. *FEMS Microbiology Ecology* 66:63–71.

Church, A. H. 1921. The lichen as transmigrant and the lichen lifecycle. *Journal of Botany* 59:139–145, 164–170, 197–202, 216–221.

Dal-Forno, M., J. D. Lawrey, M. Sikaroodi, S. Bhattarai, P. M. Gillevet, M. Sulzbacher, and R. Luecking. 2013. Starting from scratch: Evolution of the lichen thallus in the basidiolichen Dictyonema (Agaricales: Hygrophoraceae). *Fungal Biology* 117:584–598.

Davey, M. L., and R. S. Currah. 2006. Interactions between mosses (Bryophyta) and fungi. *Canadian Journal of Botany* 84:1509–1519.

Dearnaley, J. D. W. 2007. Further advances in orchid mycorrhizal research. *Mycorrhiza* 17:475–486.

Del-Prado, R., O. Blanco, H. T. Lumbsch, P. K. Divakar, J. A. Elix, M. C. Molina, and A. Crespo. 2013. Molecular phylogeny and historical biogeography of the lichen-forming fungal genus *Flavoparmelia* (Ascomycota: Parmeliaceae). *Taxon* 62:928–939.

Divakar, P. K., A. Crespo, M. Wedin, et al. 2015. Evolution of complex symbiotic relationships in a morphologically derived family of lichen-forming fungi. *New Phytologist* 208:1217–1226.

Divakar, P. K., R. Del Prado, H. T. Lumbsch, M. Wedin, T. L. Esslinger, S. D. Leavitt, and A. Crespo. 2012. Diversification of the newly recognized lichen forming fungal lineage *Montanelia* (Parmeliaceae, Ascomycota) and its relation to key geological and climatic events. *American Journal of Botany* 99:2014–2026.

Edwards, D., L. Axe, and R. Honegger. 2013. Contributions to the diversity in cryptogamic covers in the mid-Palaeozoic: Nematothallus revisited. *Botanical Journal of the Linnean Society* 173:505–534.

Ellis, C. J. 2012. Lichen epiphyte diversity: A species, community and trait-based review. *Perspectives in Plant Ecology Evolution and Systematics* 14:131–152.

Eriksson, O. E. 2005. Ascomyceternas ursprung och evolution– Protolichenes-hypotesen. *Svensk Mykologisk Tidskrift* 26:22–29.

Erlacher, A., T. Cernava, M. Cardinale, J. Soh, C. W. Sensen, M. Grube, and G. Berg. 2015. Rhizobiales as functional and endosymbiontic members in the lichen symbiosis of Lobaria pulmonaria L. *Frontiers in Microbiology* 6:53.

Felix, H. 1988. Fungi on bryophytes, a review. *Botanica Helvetica* 98:239–269.

Feuerer, T., and D. L. Hawksworth. 2007. Biodiversity of lichens, including a world-wide analysis of checklist data based on Takhtajan's floristic regions. *Biodiversity and Conservation* 16:85–98.

Flakus, A., and M. Kukwa. 2014. The first squamulose *Thelocarpon* species (Thelocarpaceae, Ascomycota) discovered in the biological soil crusts in the Bolivian Andes. *Phytotaxa* 175:281–286.

Friedl, T. 1995. Inferring taxonomic positions and testing genus level assignments in coccoid green lichen algae: A phylogenetic analysis of 18S ribosomal RNA sequences from *Dictyochloropsis reticulata* and from members of the genus *Myrmecia* (Chlorophyta, Trebouxiophyceae cl. nov.). *Journal of Phycology* 31:632–639.

Friedl, T., and D. Bhattacharya. 2002. Origin and evolution of green lichen algae. In *Symbiosis: Mechanisms and Model Systems*, 343–357. Ed. J. Seckbach, Cellular Origin and Life in Extreme Habitats, Dordrecht, the Netherlands, Kluwer Academic Publishers.

Gargas, A., P. T. DePriest, M. Grube, and A. Tehler. 1995. Multiple origins of lichen symbioses in Fungi suggested by SSU rDNA phylogeny. *Science* 268:1492–1495.

Gehrig, H., A. Schussler, and M. Kluge. 1996. *Geosiphon pyriforme*, a fungus forming endocytobiosis with *Nostoc* (Cyanobacteria), is an ancestral member of the Glomales: Evidence by SSU rRNA analysis. *Journal of Molecular Evolution* 43:71–81.

Gerphagnon, M., D. Latour, J. Colombet, and T. Sime-Ngando. 2013. Fungal parasitism: Life cycle, dynamics and impact on cyanobacterial blooms. *PLoS ONE* 8(4):e60894.

Givnish, T. J. 2015. Adaptive radiation versus "radiation" and "explosive diversification": Why conceptual distinctions are fundamental to understanding evolution. *New Phytologist* 207:297–303.

Grube, M., and D. L. Hawksworth. 2007. Trouble with lichen: The re-evaluation and re-interpretation of thallus form and fruit body types in the molecular era. *Mycological Research* 111:1116–1132.

Gueidan, C., C. Ruibal, G. S. De Hoog, and H. Schneider. 2011. Rock-inhabiting fungi originated during periods of dry climate in the late Devonian and middle Triassic. *Fungal Biology* 115:987–996.

Hallbauer, D. K., H. M. Jahns, and H. A. Beltman. 1977. Morphological and anatomical observations on some Precambrian plants from the Witwatersrand, South Africa. *Geologische Rundschau* 66:477–491.

Hallbauer, D K, and K T van Warmelo. 1974. Fossilized plants in thucholite from Precambrian rocks of the Witwatersrand, South Africa. *Precambrian Research* 1:199–212.

Hartl, C., A. R. Schmidt, J. Heinrichs, L. J. Seyfullah, N. Schäfer, C. Gröhn, J. Rikkinen, and U. Kaasalainen. 2015. Lichen preservation in amber: Morphology, ultrastructure, chemofossils, and taphonomic alteration. *Fossil Record* 18:127–135.

Hawksworth, D L. 1987. Observations on three algicolous microfungi. *Notes from the Royal Botanic Garden Edinburgh* 44:549–560.

Hawksworth, D. L. 1988. The variety of fungal algal symbioses, their evolutionary significance, and the nature of lichens. *Botanical Journal of the Linnean Society* 96:3–20.

Hedlund, T. 1895. Über die Flechtengattung *Moriola*. *Botanisches Centralblatt* 64:376–377.

Hibbett, D. S., M. Binder, J. F. Bischoff et al. 2007. A higherlevel phylogenetic classi.cation of the Fungi. *Mycological Research* 111:509–547. Hodkinson, B. P., N. R. Gottel, C. W. Schadt, and F. Lutzoni. 2012. Photoautotrophic symbiont and geography are major factors affecting highly structured and diverse bacterial communities in the lichen microbiome. *Environmental Microbiology* 14:147–161.

Hodkinson, B. P., and F. Lutzoni. 2009. A microbiotic survey of lichen-associated bacteria reveals a new lineage from the Rhizobiales. *Symbiosis* 49:163–180.

Hom, E. F. Y., and A. W. Murray. 2014. Niche engineering demonstrates a latent capacity for fungal-algal mutualism. *Science* 345:94–98.

Honegger, R. 2000. Simon Schwendener (1829–1919) and the dual hypothesis of lichens. *Bryologist* 103:307–313.

Honegger, R., L. Axe, and D. Edwards. 2013. Bacterial epibionts and endolichenic actinobacteria and fungi in the Lower Devonian lichen *Chlorolichenomycites salopensis*. *Fungal Biology* 117:512–518.

Honegger, R., D. Edwards, and L. Axe. 2013. The earliest records of internally stratified cyanobacterial and algal lichens from the Lower Devonian of the Welsh Borderland. *New Phytologist* 197:264–275.

Iturralde-Vincent, M. A., and R. D. E. MacPhee. 1996. Age and paleogeographic origin of Dominican amber. *Science* 273:1850–1852.

Jaklitsch, W. M., H. O. Baral, R. Lücking, and H. T. Lumbsch. 2015. Ascomycota. In *Syllabus of Plant Families—Adolf Engler's Syllabus der Pflanzenfamilien*, 1–288. Ed. W. Frey. Stuttgart, Germany, Gebr. Borntraeger Verlagsbuchhandlung.

James, P W, and A Henssen. 1976. The morphological and taxonomic significance of cephalodia. In *Lichenology: Progress and Problems*, 27–77. Eds. D. H. Brown, D. L. Hawksworth, and R. H. Bailey. London, Academic Press.

Jones, E. B. G. 2011. Fifty years of marine mycology. *Fungal Diversity* 50:73–112.

Jurina, A. L., and V. A. Krassilov. 2002. Lichen-like fossils from the Givetian of Central Kazakhstan. *Paleontologicheskii Zhurnal* 36:541–547.

Kaasalainen, U., J. Heinrichs, M. Krings, L. Myllys, H. Grabenhorst, J. Rikkinen, and A. R. Schmidt. 2015. Alectorioid morphologies in Paleogene lichens: New evidence and re-evaluation of the fossil alectoria succini Magdefrau. *PLoS ONE* 10: e0129526.

Karatygin, I. V., N. S. Snigirevskaya, and S. V. Vikulin. 2009. The most ancient terrestrial lichen *Winfrenatia reticulata*: A new find and new interpretation. *Paleontological Journal* 43:107–114.

Keissler, K. von. 1934. Moriolaceae; Epigloeaceae. In *Kryptogamen-Flora von Deutschland, Österreich und der Schweiz*, 1–43. Ed. G. L. Rabenhorst, Leipzig, Germany, Borntraeger.

Kettunen, E., A. R. Schmidt, P. Diederich, H. Grabenhorst, and J. Rikkinen. 2015. Lichen-associated fungi from Paleogene amber. *New Phytologist* doi:10.1111/nph.13653.

Kluge, M., D. Mollenhauer, E. Wolf, and A. Schussler. 2002. The *Nostoc-Geosiphon* endocytobiosis. In: *Cyanobacteria in Symbiosis*, 19–30. Eds. A. N. Rai, B. Bergman, and U. Rasmussen, Dordrecht, the Netherlands, Kluwer Academic Publishers.

Kohlmeyer, J., and V. Demoulin. 1981. Parasitic and symbiotic fungi on marine algae. *Botanica Marina* 24:9–18.

Kohlmeyer, J., and E Kohlmeyer. 1972. Is *Ascophyllum nodosum* lichenized? *Botanica Marina* 15:109–112.

Kohlmeyer, J., and B. Volkmann-Kohlmeyer. 2003. Marine ascomycetes from algae and animal hosts. *Botanica Marina* 46:285–306.

Kraichak, E., P. K. Divakar, A. Crespo, S. D. Leavitt, M. P. Nelsen, R. Lücking, and H. T. Lumbsch. 2015. A Tale of Two Hyperdiversities: Diversification dynamics of the two largest families of lichenized fungi. *Scientific Reports* 5:e10028.

Kraichak, E., R. Luecking, and H. T. Lumbsch. 2015. A unique trait associated with increased divesification in a hyperdiverse family of tropical lichen-forming fungi. *International Journal of Plant Sciences* 176:597–606.

Kranner, I., and F Lutzoni. 1999. Evolutionary consequences of transition to a lichen symbiotic state and physiological adaptation to oxidative damage associated with poikilohydry. In *Plant Responses to Environmental Stresses: From Phytohormones to Genome Reorganization*, 591–628. Ed. H. R. E. Lerner, New York, Marcel Dekker, Inc.

Lawrey, J. D., and P. Diederich. 2003. Lichenicolous fungi: Interactions, evolution, and biodiversity. *Bryologist* 106:81–120.

Lawrey, J. D., R. Luecking, H. J. M. Sipman, J. L. Chaves, S. A. Redhead, F. Bungartz, M. Sikaroodi, and P. M. Gillevet. 2009. High concentration of basidiolichens in a single family of agaricoid mushrooms (Basidiomycota: Agaricales: Hygrophoraceae). *Mycological Research* 113:1154–1171.

Leavitt, S. D., T. L. Esslinger, P. K. Divakar, and H. T. Lumbsch. 2012a. Miocene and Pliocene dominated diversification of the lichen-forming fungal genus *Melanohalea* (Parmeliaceae, Ascomycota) and Pleistocene population expansions. *BMC Evolutionary Biology* 12:176.

Leavitt, S. D., T. L. Esslinger, P. K. Divakar, and H. T. Lumbsch. 2012b. Miocene divergence, phenotypically cryptic lineages, and contrasting distribution patterns in common lichenforming fungi (Ascomycota: Parmeliaceae). *Biological Journal of the Linnean Society* 107:920–937.

Leavitt, S. D., T. L. Esslinger, and H. T. Lumbsch. 2012. Neogenedominated diversification in neotropical montane lichens: Dating divergence events in the lichen-forming fungal genus *Oropogon* (Parmeliaceae). *American Journal of Botany* 99:1764–1777.

Leavitt, S. D., H. T. Lumbsch, S. Stenroos, and L. L. St Clair. 2013. Pleistocene speciation in North American lichenized fungi and the impact of alternative species circumscriptions and rates of molecular evolution on divergence estimates. *PLoS ONE* 8(12):e85240.

Lipnicki, L. I. 2015. The role of symbiosis in the transition of some eukaryotes from aquatic to terrestrial environments. *Symbiosis* 65:39–53.

Lücking, R., S. Huhndorf, D. H. Pfister, E. R. Plata, and H. T. Lumbsch. 2009a. Fungi evolved right on track. *Mycologia* 101:810–822.

Lücking, R., E. Rivas Plata, J. L. Chaves, L. Umaña, and H. J. M. Sipman. 2009b. How many tropical lichens are there... really? *Bibliotheca Lichenologica* 100:399–418.

Lücking, R., M. Dal-Forno, M. Sikaroodi et al. 2014. A single macrolichen constitutes hundreds of unrecognized species. *Proceedings of the National Academy of Sciences of the United States of America* 111:11091–11096

Lumbsch, H. T. 2000. Phylogeny of filamentous ascomycetes. *Naturwissenschaften* 87:335–342.

Lumbsch, H. T., A. L. Hipp, P. K. Divakar, O. Blanco, and A. Crespo. 2008. Accelerated evolutionary rates in tropical and oceanic parmelioid lichens (Ascomycota). *BMC Evolutionary Biology* 8:257.

Lumbsch, H. T., and S. M. Huhndorf. 2007. Whatever happened to the pyrenomycetes and loculoascomycetes? *Mycological Research* 111:1064–1074.

Lumbsch, H. T., and S. M. Huhndorf. 2010. Myconet Volume 14. Part One. Outline of Ascomycota–2009. *Fieldiana* (*Life and Earth Sciences*) 1:1–42.

Lumbsch, H. T., D. G. Zimmermann, and I. Schmitt. 2009. Phylogenetic position of ephemeral lichens in Thelocarpaceae and Vezdaeaceae (Ascomycota). *Bibliotheca Lichenologica* 100:389–398.

Lutzoni, F., and M. Pagel. 1997. Accelerated evolution as a consequence of transitions to mutualism. *Proceedings of the National Academy of Sciences of the United States of America* 94:11422–11427.

Lutzoni, F., M. Pagel, and V. Reeb. 2001. Major fungal lineages are derived from lichen symbiotic ancestors. *Nature* 411:937–940.

Magain, N., B. Goffinet, and E. Serusiaux. 2012. Further photomorphs in the lichen family Lobariaceae from Reunion (Mascarene archipelago) with notes on the phylogeny of Dendriscocaulon cyanomorphs. *Bryologist* 115:243–254.

Mägdefrau, K. 1957. Flechten und Moose in baltischen Bernstein. *Berichte der Deutschen Botanischen Gesellschaft* 70:433–435.

Matsunaga, K. K. S., R. A. Stockey, and A. M. F. Tomescu. 2013. *Honeggeriella complexa* gen. et sp. nov., a heteromerous lichen from the lower cretaceous of Vancouver Island (British Columbia, Canada). *American Journal of Botany* 100:450–459.

Nash, T. H. 2008. *Lichen Biology*. 2nd ed. Cambridge, UK: Cambridge University Press.

Partida-Martinez, L. P., and C. Hertweck. 2005. Pathogenic fungus harbours endosymbiotic bacteria for toxin production. *Nature* 437:884–888.

Poinar, G. 1992. *Life in Amber*. Palo Alta, CA: Stanford University Press.

Poinar, G. O., Jr, E. B. Peterson, and J. L. Platt. 2000. Fossil *Parmelia* in new world amber. *Lichenologist* 32:263–269.

Prieto, M., E. Baloch, A. Tehler, and M. Wedin. 2013. Mazaedium evolution in the Ascomycota (Fungi) and the classification of mazaediate groups of formerly unclear relationship. *Cladistics* 29:296–308.

Prieto, M., and M. Wedin. 2013. Dating the diversi.cation of the major lineages of Ascomycota (Fungi). *PLoS ONE* 8:e65576.

Printzen, C., R. Cezanne, M. Eichler, and H. T. Lumbsch. 2012. The genera *Aphanopsis* and *Steinia* represent basal lineages within Leotiomyceta. *Bibliotheca Lichenologica* 108:177–186.

Printzen, C., and H. T. Lumbsch. 2000. Molecular evidence for the diversi.cation of extant lichens in the late cretaceous and tertiary. *Molecular Phylogenetics and Evolution* 17:379–387.

Rasmussen, H. N. 2002. Recent developments in the study of orchid mycorrhiza. *Plant and Soil* 244:149–163.

Rasmussen, H. N., and F. N. Rasmussen. 2009. Orchid mycorrhiza: Implications of a mycophagous life style. *Oikos* 118:334–345.

Redman, R. S., D. D. Dunigan, and R. J. Rodriguez. 2001. Fungal symbiosis from mutualism to parasitism: who controls the outcome, host or invader? *New Phytologist* 151:705–716.

Reeb, V., F. Lutzoni, and C. Roux. 2004. Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Molecular Phylogenetics and Evolution* 32:1036–1060.

Retallack, G. J. 2009. Cambrian-Ordovician non-marine fossils from South Australia. *Alcheringa* 33:355–391.

Retallack, G. J., and E. Landing. 2014. Affinities and architecture of Devonian trunks of *Prototaxites loganii*. *Mycologia* 106:1143–1158.

Rikkinen, J. 2002. Cyanolichens: An evolutionary overview. In *Cyanobacteria in Symbiosis*, 31–72. Eds. A. N. Rain, B. Bergman, and U. E. Rasmussen, Dordrecht, the Netherlands, Kluwer Academic Publishers.

Rikkinen, J. 2003. Calicioid lichens from European Tertiary amber. *Mycologia* 95:1032–1036.

Rikkinen, J. 2013. Molecular studies on cyanobacterial diversity in lichen symbioses. *MycoKeys* 6:3–32.

Rikkinen, J., and G. O. Poinar. 2002. Fossilised *Anzia* (Lecanorales, lichen-forming Ascomycota) from European Tertiary amber. *Mycological Research* 106:984–990.

Rikkinen, J., and G. O. Poinar, Jr. 2008. A new species of *Phyllopsora* (Lecanorales, lichen-forming Ascomycota) from Dominican amber, with remarks on the fossil history of lichens. *Journal of Experimental Botany* 59:1007–1011.

Rivas Plata, E. 2011. Historical biogeography, ecology and systematics of the family Graphidaceae (Lichenized Ascomycota: Ostropales), PhD thesis, Graduate College, University of Illinois at Chicago, Chicago. Schlee, D. 1990.

Das Bernstein-Kabinett. *Stuttgarter Beiträge zur Naturkunde, Ser. C* 28:1–100.

Schoch, C. L., G. H. Sung, F. Lopez-Giraldez et al. 2009. The Ascomycota tree of life: A phylum-wide phylogeny clarifies the origin and evolution of fundamental reproductive and ecological traits. *Systematic Biology* 58:224–239.

Schussler, A. 2002. Molecular phylogeny, taxonomy, and evolution of Geosiphon pyriformis and arbuscular mycorrhizal fungi. *Plant and Soil* 244:75–83.

Schussler, A., and M. Kluge. 2001. *Geosiphon pyriforme*, an endocytosymbiosis between fungus and cyanobacteria, and its meaning as a model system for arbuscular mycorrhizal research. *Fungal Associations* IX:151–161.

Selosse, M. A. 2002. *Prototaxites*: A 400 Myr old giant fossil, a saprophytic holobasidiomycete, or a lichen? *Mycological Research* 106:642–644.

Selosse, M. A., and F. Letacon. 1995. Mutualistic associations between phototrophs and fungi–their diversity and role in land colonization. *Cryptogamie Mycologie* 16:141–183.

Sérusiaux, E., A. Villarreal J. C. Wheeler, and B. Goffinet. 2011. Recent origin, active speciation and dispersal for the lichen genus *Nephroma* (Peltigerales) in Macaronesia. *Journal of Biogeography* 38:1138–1151.

Simon, L., J. Bousquet, R. C. Levesque, and M. Lalonde. 1993. Origin and diversi.cation of endomycorrhizal fungi and coincidence with vascular land plants. *Nature* 363:67–69.

Sipman, H. J. M., and R. C. Harris. 1989. Lichens. In *Tropical Rain Forest Ecosystems*, 303–309. Eds. H. Lieth and M. J. A. Werger, Amsterdam, the Netherlands, Elsevier Science Publishers.

Smith, A. L. 1921. *A Handbook of British Lichens*. London: Printed by order of the Trustees of the British Museum.

Sonstebo, J. H., and T. Rohrlack. 2011. Possible implications of chytrid parasitism for population subdivision in freshwater cyanobacteria of the genus *Planktothrix*. *Applied and Environmental Microbiology* 77:1344–1351.

Spatafora, J. W., G. H. Sung, J. M. Sung, N. L. Hywel-Jones, and J. F. White. 2007. Phylogenetic evidence for an animal pathogen origin of ergot and the grass endophytes. *Molecular Ecology* 16:1701–1711.

Spier, L., H. van Dobben, and K. van Dort. 2010. Is bark pH more important than tree species in determining the composition of nitrophytic or acidophytic lichen floras? *Environmental Pollution* 158:3607–3611.

Standke, G 1998. Die Tertiärprofile der Samländischen Bernsteinkuste bei Rauchen. *Schriftenreihe für Geowissenschaften* 7:93–133.

Stenroos, S., T. Laukka, S. Huhtinen, P. Dobbeler, L. Myllys, K. Syrjanen, and J. Hyvonen. 2010. Multiple origins of symbioses between ascomycetes and bryophytes suggested by a five-gene phylogeny. *Cladistics* 26:281–300.

Suryanarayanan, T. S., A. Venkatachalam, N. Thirunavukkarasu, J. P. Ravishankar, M. Doble, and V. Geetha. 2010. Internal mycobiota of marine macroalgae from the Tamilnadu coast: Distribution, diversity and biotechnological potential. *Botanica Marina* 53:457–468.

Taylor, J. W., and M. L. Berbee. 2006. Dating divergences in the Fungal Tree of Life: Review and new analyses. *Mycologia* 98:838–849.

Taylor, T. N., H. Hass, and H. Kerp. 1997. A cyanolichen from the Lower Devonian Rhynie chert. *American Journal of Botany* 84:992–1004.

Taylor, T. N., S. D. Klavins, M. Krings, E. L. Taylor, H. Kerp, and H. Hass. 2004. Fungi from the Rhynie chert: A view from the dark side. *Transactions of the Royal Society of Edinburgh-Earth Sciences* 94:457–473.

Taylor, T. N., M. Krings, and E. L. Taylor. 2015. *Fossil Fungi*. London: Academic Press.

Taylor, T. N., and J. M. Osborn. 1996. The importance of fungi in shaping the paleoecosystem. *Review of Palaeobotany and Palynology* 90:249–262.

Tomescu, A. M. F., and G. W. Rothwell. 2006. Wetlands before tracheophytes: Thalloid terrestrial communities of the Early Silurian Passage Creek biota (Virginia). In *Wetlands Through Time*, 41–56. Eds. S. F. Greb and W. A. DiMichele. Boulder, CO, Geological Soc Amer Inc.

U'Ren, J. M., F. Lutzoni, J. Miadlikowska, A. D. Laetsch, and A. E. Arnold. 2012. Host and geographic structure of endophytic and endolichenic fungi at a continental scale. *American Journal of Botany* 99:898–914.

Wang, H. Y., H. T. Lumbsch, S. Y. Guo, M. R. Huang, and J. C. Wei. 2010. Ascomycetes have faster evolutionary rates and larger species diversity than basidiomycetes. *Science China, Life Sciences* 53:1163–1169.

Wedin, M., H. Döring, and G. Gilenstam. 2004. Saprotrophy and lichenization as options for the same fungal species on different substrata: Environmental plasticity and fungal lifestyles in the *Stictis-Conotrema* complex. *New Phytologist* 164:459–465.

Wiemken, V., and T. Boller. 2002. Ectomycorrhiza: Gene expression, metabolism and the wood-wide web. *Current Opinion in Plant Biology* 5:355–361.

Yuan, X. L., S. H. Xiao, and T. N. Taylor. 2005. Lichen-like symbiosis 600 million years ago. *Science* 308:1017–1020.

FIGURES

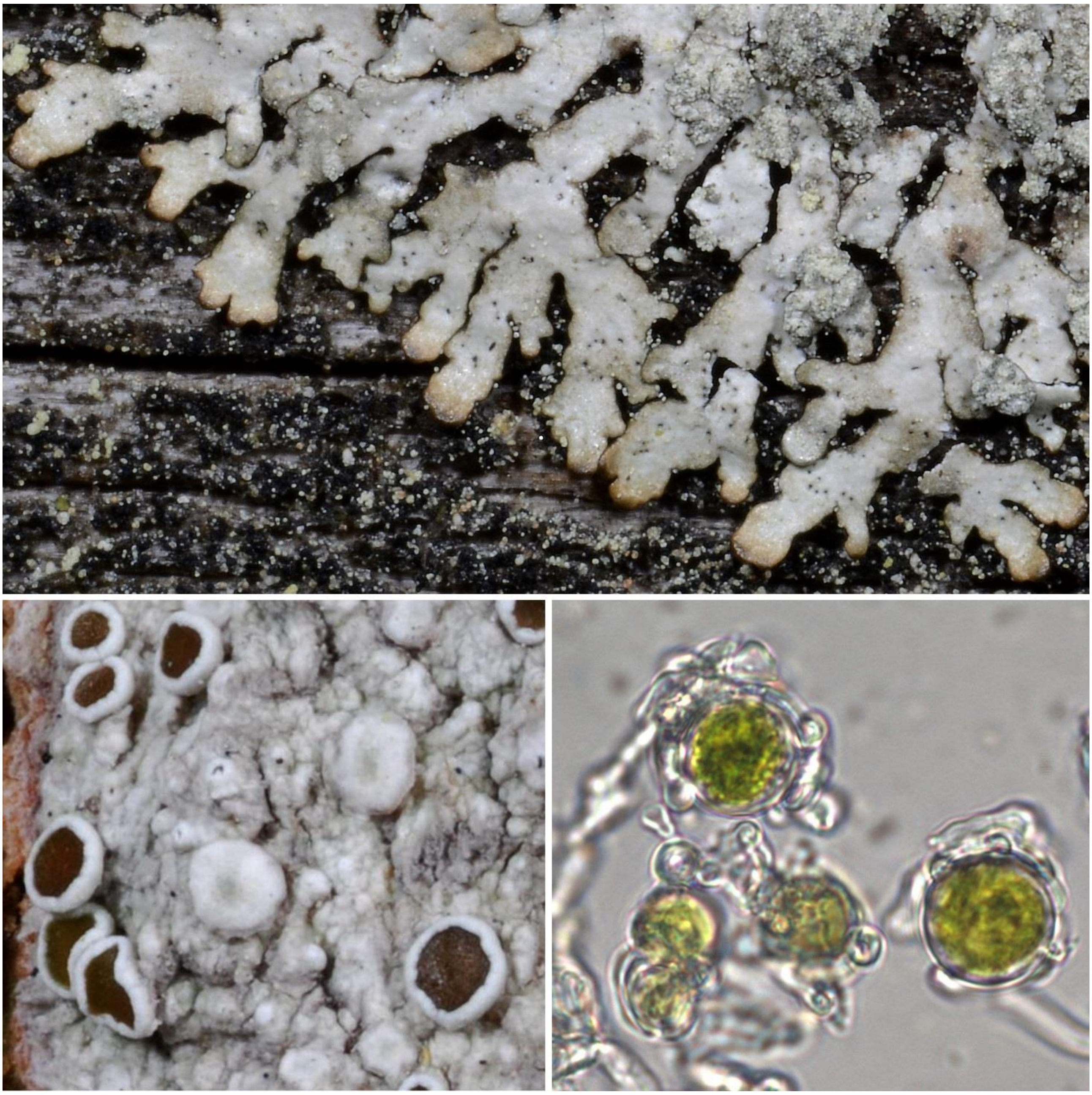

Figure 1 Examples of extant lichens. (a) Closely appressed foliose lichen (*Parmeliopsis hyperopta*, Lecanorales). (b) Apothecia of crustose epiphytic lichen (*Lecanora argentata*, Lecanorales). (c) Green algal photobionts of epiphytic lichen (*Parmelia sulcata*, Lecanorales).

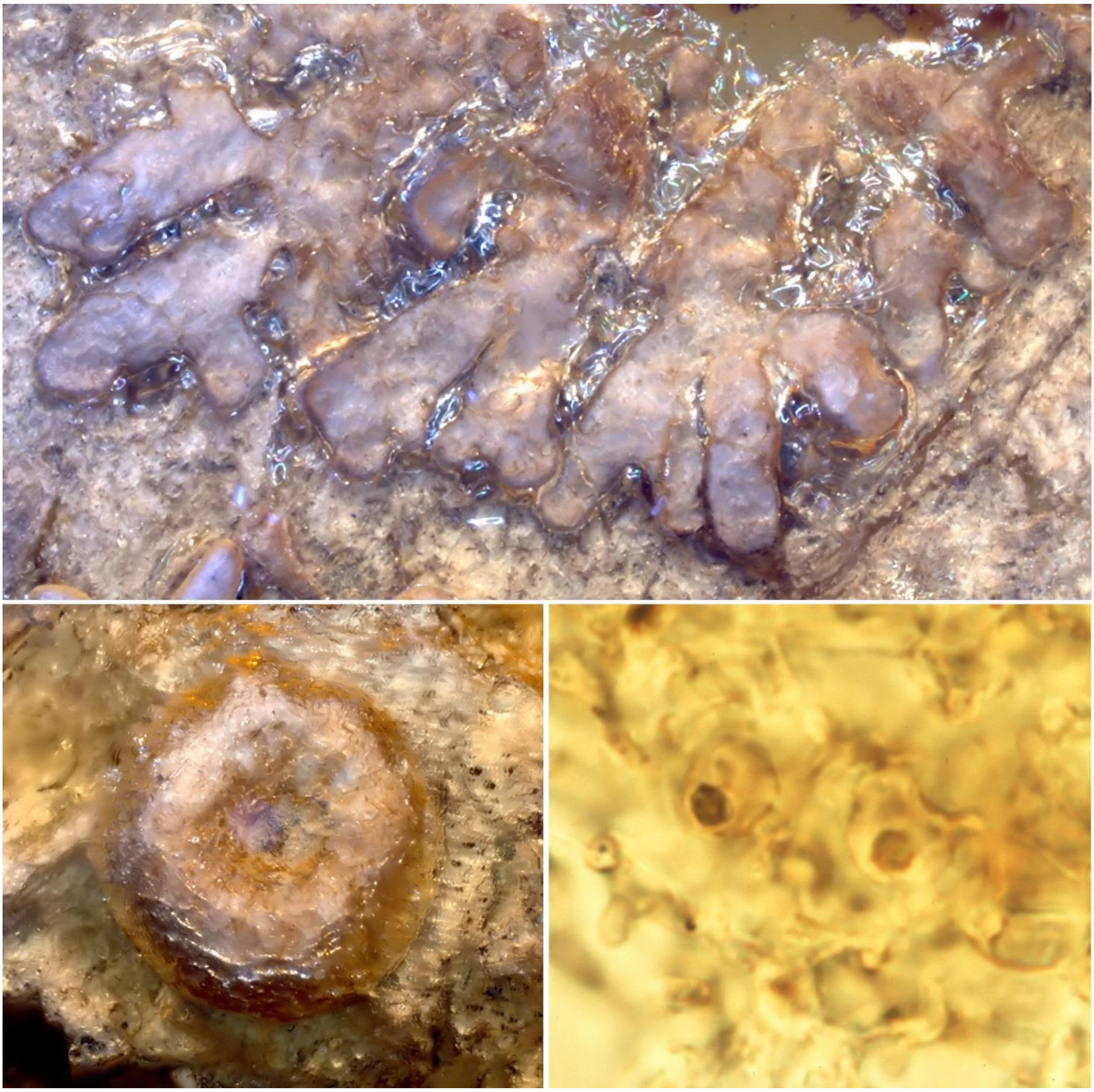

Figure 2 Examples of fossil lichens. (a) Closely appressed foliose lichen preserved in Bitterfeld amber. (b).Apothecium of crustose epiphytic lichen preserved in Bitterfeld amber. (c) Green algal photobionts of foliose epiphytic lichen (*Phyllopsora dominicanus*) preserved *in situ* in Dominican amber.