Quick guide

Lichens

François Lutzoni
and Jolanta Miadlikowska

What are lichens? The term lichen refers to a symbiotic association between a filamentous fungus, the 'mycobiont', and at least one photosynthetic organism, the 'photobiont', consisting of a micro alga, a cyanobacterium, or both (Figure 1). Although the symbiotic nature of lichens was first revealed in 1867, the development of a lichen thallus is often so integrated (Figure 1D) that they have been perceived and studied as single organisms until quite recently, and have often been referred to as the ultimate example of mutualism. The name of a 'lichen species' corresponds to the species name of the fungal partner. Only about 100 photobiont species have been reported to be associated with more than 13,500 lichen-forming fungal species, so that many different mycobiont species share the same photobiont. More than 98% of this highly diverse group of lichen-forming fungi is concentrated within the Ascomycota, the largest fungal phylum. The few remaining lichen-forming fungal species are classified within the Basidiomycota, a phylum that includes typical mushrooms. The most common lichen photobionts belong to the green algae *Trebouxia* and *Trentepohlia*, and the cyanobacterium *Nostoc*.

How successful has this symbiosis been? The lichen symbiosis is one of the most successful ways whereby fungi fulfill their requirement for carbohydrates, with nearly one fifth of all known fungal species being obligate lichen-forming species. More than 40% of all known Ascomycota species are lichenized. They are found in nearly all terrestrial habitats from the poles to the tropics, ranging from marine (littoral) and fresh water aquatic habitats to xeric environments. Lichens are the dominant life forms in about 8% of the land surface of the earth, including polar, alpine and coastal habitats where fog and water vapor are abundant. Another measure of their ecological success is their nearly ubiquitous ability to colonize various substrates. They can grow on or inside rocks (epilithic or endolithic, respectively), on or inside the bark of woody plants as epiphytes, on wood, soil, mosses, leaves of vascular plants (especially in the tropics), on other lichens, as well as on man-made substrates such as concrete, glass, metals and plastics.

How many times has the lichen symbiosis evolved? The multiple origin of the lichen symbiosis has been well-established since the 80s, with the acceptance by lichenologists that basidiomycetes associated with the same genera of green algae and cyanobacteria (basidiolichens) found in typical lichens (ascolichens) are also lichens. The controversy resides in the frequency of these independent origins and in finding in which ancestral lineages they took place during the evolution of the Ascomycota, where most of the lichen-forming fungal diversity resides. Until the end of the 90s it was widely believed that the lichen symbiosis arose independently several times, based on the mixed occurrence of lichenized and non-lichenized species in many orders of the Ascomycota. Broad multilocus phylogenetic studies of the Ascomycota during the last eight years have revealed that this tremendous diversity of lichen-forming ascomycetes might be the result of only three to five independent origins. The highly concentrated distribution of the lichen-forming species within the Ascomycota tree of life also supports the notion that this type of symbiosis originated only a few times. The implications are many and important because a low number of origins of the lichen symbiosis within the Ascomycota tree of life involves an earlier origin of this type of symbiosis and more subsequent losses, resulting in major non-lichenized clades of Ascomycota (such as the Stictidaceae, Chaetothyriales, and the Eurotiomycetidae) being derived from ancestors with a lichen symbiotic lifestyle.

How do lichens reproduce? Lichen reproduction requires the transmission of the fungal and photosynthetic partners from one generation to the next. If the mycobiont reproduces sexually, the fungal spores upon germination need to find a compatible photobiont and resynthesize the lichen symbiosis *de novo* (horizontal transmission of the photobiont). If the mycobiont reproduces asexually, the photobiont is most often transmitted to the next generation with its mycobiont through specialized vegetative propagules (such as soredia or isidia), or through thallus fragments containing both symbionts (vertical transmission of the photobiont). Because sexual reproduction of the fungal partner seems to be the most common mode of reproduction, and a large

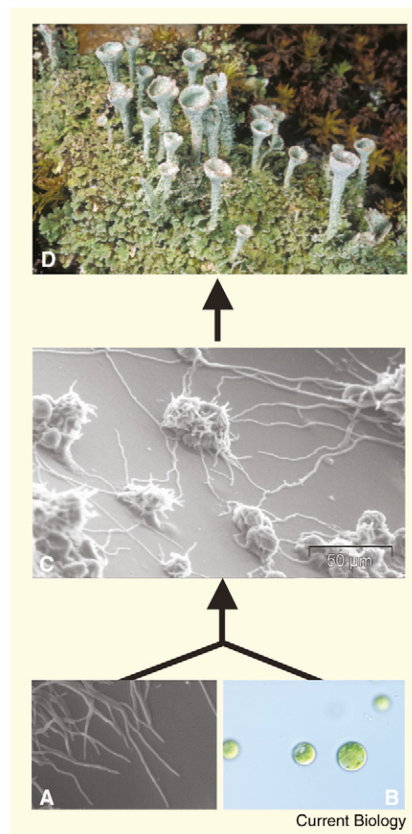

Figure 1. Lichen symbiosis.

(A) The mycobiont *Cladonia grayi* growing separately in culture (photo: S. Joneson; Joneson and Lutzoni, 2009). (B) The unicellular photobiont *Asterochloris phycobiontica* growing separately in culture (Alga Terra website). (C) *Cladonia grayi* growing with *Asterochloris* sp. in culture — clumps of algal cells overgrown by branching mycobiont and connected by mycobiont hyphae (photo: S. Joneson; Joneson and Lutzoni, 2009). (D) Mature lichen in nature resulting from the association of *Cladonia grayi* with *Asterochloris* sp. (photo: Stephen Sharnoff).

proportion of lichen photobionts (such as *Trebouxia*) are thought to be found only very rarely outside the lichen symbiosis, it has been unclear how mycobionts manage to find compatible photobionts.

From recent observations, three different mechanisms have been proposed as solutions to this enigma: first, the acquisition of compatible photobionts from vegetative symbiotic propagules generated by other lichen species or directly from other lichen thalli; second, very early association of mycobiont mycelium with a photoautotrophic organism with which it is compatible, but that is distinct from its final photobiont, extends its survival and enhances its probability to find the required photobiont; and third, the extraordinary tolerance to desiccation of the photobiont *Trebouxia*, for example, as individual or small groups of algal cells, allows their survival in a dormant state for extended periods of time, resulting in longer availability for resynthesis and production of the next generation of lichen thalli.

The last of these suggested mechanisms is consistent with the more recent view that *Trebouxia* can be common and widespread in a free-living state. Many other algae found in lichens (such as *Trentepohlia* and *Myrmecia*) are known to occur independently as epiphytes, rock-inhabiting algae, or soil algae (facultative photobionts). In contrast, nearly all lichen mycobiont species have never been reported growing without a photoautotroph — they are obligate mycobionts. For these reasons, the mycobiont is seen as the most dependent of the two symbiotic partners. With the exception of the photobionts belonging to the Trentepohliales, green algae reproduce only clonally when part of the lichen symbiosis.

What else is remarkable about lichens? Longevity, high diversity and productivity of secondary metabolites, tolerance to extreme environments, and sensitivity to pollution are among the many extraordinary traits of lichens. Reports of lichen growth rates range from less than a millimeter to a few centimeters annually, and their longevity has been estimated to be in the range of decades or centuries, up to millennia, depending on the species and environmental conditions. More than 700 secondary metabolites have been isolated from lichens, most of which (>90%) are unique to this symbiosis, and many have medically beneficial properties. These metabolites can be secreted in such large amounts by the fungal partner that they can account for more than 50% of the dry weight of some lichens. The perfume industry is responsible for the harvest of more than 8000 tonnes annually of two specific species of lichens to enhance the persistence of the fragrance on the skin. Many species thrive in polar and alpine regions where they are subjected to extreme desiccation, temperature and irradiation stresses. The same biological attributes that earned them the label 'extremophiles' are responsible in part to their high sensitivity to air pollution, which led to their extensive use in spatial and temporal monitoring of this type of pollution.

What can lichens tell us about symbiosis in general? Mutualism, commensalism and parasitism form a dynamic continuum that can be observed even between the same symbiotic partners subjected to different environmental conditions. Several pathogenic fungi have been reported as being derived from lichen ancestors. One of the most pathogen-rich clades of ascomycetes (Chaetothyriales) shares a most recent common ancestor with a clade that is mostly composed of lichen-forming species growing on rocks (Verrucariales). It was recently reported that this common ancestor was most likely an extremotolerant rock-inhabiting fungus, and that their adaptations enabling them to withstand such severe stresses facilitated the ability of members of the Chaetothyriales to colonize and infect vertebrates.

The hyperdiverse endophytic fungi that are omnipresent in healthy leaves and stems of plants can enhance plant defense against disease and herbivory, promote plant growth, influence photosynthetic efficiency and drought tolerance, and improve or inhibit the ability of plants to exploit extreme environments. It was recently discovered that the evolution of some specific lineages of endophytic fungi lies in endophyte-like (endolichenic) fungi that can be isolated from the interior of apparently healthy lichens. As for endophytes, these endolichenic fungi are hyperdiverse and have been isolated from every lichen thallus investigated so far. Interestingly, these endolichenic fungi preferentially associate with green algal photobionts in lichen thalli, which might have facilitated host switching to other land plants as they became available substrates through time. Endolichenism thus seems to be an incubator for the evolution of endophytism. In turn, endophytism is evolutionarily transient, with endophytic lineages frequently undergoing transitions to and from pathogenicity.

Is there a lichen genome project? There are currently two genome projects on lichens. The Joint Genome Institute (JGI) will sequence the genome of the lichen-forming fungus *Xanthoria parietina*; and researchers at Duke University are sequencing the genomes of both the mycobiont fungus *Cladonia grayi* and its photobiont algal partner *Asterochloris* sp. (so far they have achieved about 12x and 10x coverage for these two symbionts, respectively). There is an increasing interest in sequencing more lichen genomes with the realization that lichens can provide valuable model systems for a comprehensive understanding of fungus–plant interactions.

Where can I find more about lichens?

Arnold, A.E., Miadlikowska, J., Higgins, K.L., Sarvate, S.D., Gugger, P., Way, A., Hofstetter, V., Kauff, F., and Lutzoni, F. (2009). A phylogenetic estimation of trophic transition networks for ascomycetous fungi: Are lichens cradles of symbiotrophic fungal diversification? Syst. Biol. in press.

Culberson, W.L., Egan, R.S., and Esslinger, T.L. (2009). Recent literature on lichens. http://www.nhm.uio.no/botanisk/bot-mus/lav/sok_rll.htm.

Gueidan, C., Ruibal Villasenor, C., de Hoog, S., Gorbushina, A., Untereiner, W.A., and Lutzoni, F. (2009). An extremotolerant rock-inhabiting ancestor for mutualistic and pathogen-rich fungal lineages. Stud. Mycol. *61*, 111–119.

Joneson, S., and Lutzoni, F. (2009). Revisiting compatibility and thigmotropism in the lichen symbiosis. Symbiosis *47*, 109–115.

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

Nash, T.H. (2008). Lichen Biology, Second Edition, (New York: Cambridge University Press).

Department of Biology, Duke University, Durham, NC 27708, USA.
E-mail: flutzoni@duke.edu