



Rosmarie Honegger

Abstract

This chapter gives an overview on (1) lichen-forming fungi, lichen photobionts and peculiarities of lichen symbiosis such as gains and losses of lichenization, species concepts, specificity, morphodemes and morphotype pairs, non-lichen mutualistic fungal interactions with unicellular algae and cyanobacteria and mycophycobioses; (2) the mycobiont–photobiont interface, water relations and gas exchange, mycobiont-derived secondary metabolites and the accumulation of heavy metals or radionuclides; (3) the microbiome of lichen thalli, i.e. the bacteriome (epi- and endolichenic bacteria), lichenicolous and endolichenic fungi, lichenicolous lichens and the virome of lichens and their allies; (4) fossil lichens and their microbiome; (5) lichen–animal interactions such as the micro- and mesofauna of lichen thalli, lichenivory in invertebrates and vertebrates, endo- and epizoochory; (6) lichenomimesis in animals and flowering plants.

Keywords

Lichen symbiosis · Lichen-forming fungi · Lichen photobionts · Endolichenic fungi ·

Lichenicolous fungi · Lichenicolous lichens · Bacteriome of lichens · Virome of lichens · Fossil lichens · Lichenivory · Lichenomimesis

6.1 Introduction

Lichens are the symbiotic phenotype of nutritionally specialized fungi, ecologically obligate biotrophs which acquire fixed carbon from a population of minute photobiont cells (Honegger 1991a, b). Lichen-forming fungi (also referred to as lichen mycobionts) are, like plant or animal pathogens or mycorrhizal fungi, a polyphyletic, taxonomically diverse group of nutritional specialists, but are otherwise normal representatives of their fungal classes. They differ from non-lichenized taxa by their manifold adaptations to symbiosis with a population of minute photobiont cells (Honegger 2009). Lichenization is an ancient and very successful nutritional strategy, approximately 17% of extant fungal species being lichenized (Lücking et al. 2017a).

Lichens were the first mutualistic symbiosis discovered. The Swiss botanist Simon Schwendener (1829–1919) realized that the thallus of lichens is built up by a fungus which harbours a population of genetically different, minute green algal or cyanobacterial cells in its thalline interior (Schwendener 1867, 1869; Honegger 2000). Upon closer examination, lichen thalli represent not a dual or triple

R. Honegger (✉)
Institute of Plant and Microbiology, University of Zürich,
Zürich, Switzerland
e-mail: rohonegg@botinst.uzh.ch

symbiosis of a C-heterotrophic partner, i.e., a lichen-forming fungus (the mycobiont) and a photoautotrophic partner, either a green alga and/or a cyanobacterium (the photobiont, also termed chlorobiont or cyanobiont, respectively), but consortia with an unknown number of participants (Fig. 6.1a–b; Honegger 1991a, b) or complex ecosystems, respectively (Hawksworth and Grube 2020). Lichenicolous and endolichenic fungi and bacterial epi- and endobionts are very common and widespread, their taxonomic affiliation and potential roles for the symbiosis having been intensely studied in the last decades (see Sects. 6.5.1–6.5.5). Endolichenic fungal and actinobacterial symbionts and epithalline bacteria were already present in *Chlorolichenomycites devonicus*, a fossil lichen of the Early Devonian (ca. 415 Ma old, see Sect. 6.6.2; Honegger et al. 2013a).

As pointed out by Hawksworth (2016), there is no need to change the concept of lichen in the light of these findings. The term symbiosis, as defined by de Bary (1879), refers to genetically different organisms living together, neither the outcome of their interaction (parasitic, commensalistic or mutualistic relationships, the term mutualism having been introduced by Van Beneden in 1875) nor the number of organisms involved was defined.

Until the end of the twentieth century, the taxonomy of lichen-forming fungi and their photobionts was based on morphological, chemical and structural characters. In the twenty-first century, molecular tools, bioinformatics and rapidly growing databases facilitated the study of the inter- and intraspecific diversity of lichen-forming fungi and their photobionts, their phylogenies, but also the intrathalline

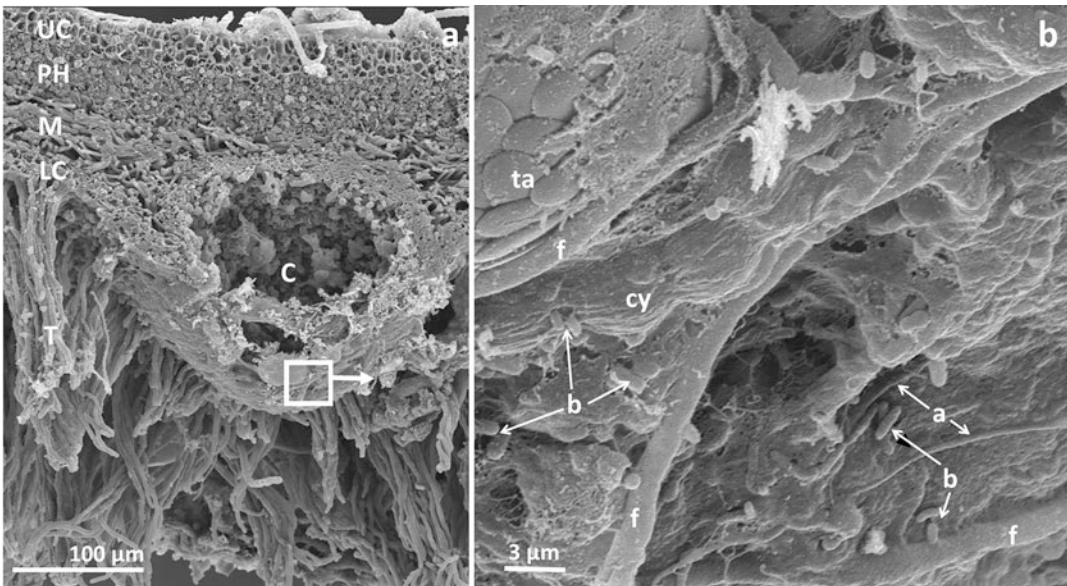


Fig. 6.1 The lichen thallus as a consortium with an unknown number of participants: (a, b) Scanning electron microscopy (SEM) micrograph of a cross-section of *Sticta sylvatica*, collected in Brittany, with bacterial, fungal, cyanobacterial and protozoan epibionts. A cyphella is tangentially sectioned, details in (b). Abbreviations thal-
lus: C: cyphella (aeration pore); UC upper cortex, PH

photobiont layer (*Nostoc* sp.); M medullary layer, LC lower cortex with tomentum (T). Abbreviations of epibionts: a actinobacteria, b bacteria, cy cyanobacterial filament, f fungal hyphae, ta testate amoeba, presumably *Assulina* sp., its shell being composed of self-made siliceous shell-plates (idiosomes)

biodiversity and the pro- and eukaryotic microbiome of lichen thalli.

6.2 Lichen-Forming Fungi (LFF)

6.2.1 Gains and Losses of Lichenization

Lichenization was repeatedly acquired (14–23 lichenization events in the Ascomycota, 6–7 in the Basidiomycota), but also repeatedly lost in favour of a saprotrophic, lichenicolous or parasitic mode of nutrition (Lücking et al. 2017a, b; Nelsen et al. 2020). Examples of relatively recently de-lichenized taxa among the Lecanoromycetes are the lichenicolous *Raesaenenia huuskonenii* (syn. *Protousnea huuskonenii*, Parmeliaceae, Lecanorales; Divakar et al. 2015; Fig. 6.6h–i) or the lignicolous *Xylographa constricta* (Baeomycetaceae, Baeomycetales; Spribille et al. 2014).

6.2.2 Species Concepts and Phylogenies

The genus and species name of a lichen refers to the fungal partner, irrespective of it being symbiotic in nature or axenically cultured apart from its photobiont (Hawksworth 2015). Attempts to refer to the aposymbiotically cultured mycobiont as *...-myces* (e.g. *Xanthoriomyces parietinae* for aposymbiotically cultured *Xanthoria parietina*; Thomas 1939) are obsolete. The photoautotrophic partner(s) of lichens have their own names and phylogenies. Traditionally, lichens were described on the basis of morphological (morphospecies) and chemical characters (secondary metabolites: chemospecies). Molecular tools provided novel insights into phylogenies, evolutionary trends and taxonomic relationships in general and in questions related to the delimitation of species in particular (Lücking et al. 2021). Many well-known morphospecies turned out to comprise either cryptic species or morphodemes (see Sects. 6.2.3 and 6.2.4).

In their 2016 classification, Lücking and colleagues listed 19,387 accepted species of lichenized fungi in 995 genera, 115 families, 39 orders and eight classes, the vast majority being ascomycetes; Lecanoromycetes, the largest and most anciently lichenized class among extant ascomycetes, comprises more than 15,100 spp. (Lücking et al. 2017a, b). Only 172 species, 15 genera, five families, five orders in one class belong to the basidiomycetes (Lücking et al. 2017a, b), but molecular data of more than 300 species of basidiolichens were not yet published. In the meantime, new taxa of basidiolichens have been described (Coca et al. 2018; Dal-Forno et al. 2019; Lücking et al. 2022). However, large numbers of species and genera of lichenized asco- and basidiomycetes await molecular analysis.

Based on molecular datasets, large numbers of new species, numerous new genera, families, few orders (e.g., the ascolichen orders Eremithallales; Lücking et al. 2008, Leprocaulales; Lendemer and Hodkinson 2013, Collemopsidales; Pérez-Ortega et al. 2016, or the basidiolichen order Leptostromatales; Hodkinson et al. 2014) and classes (e.g. Lichinomycetes; Reeb et al. 2004; Coniocybomycetes; Prieto et al. 2013) have been described. Within 6 years (2010–16), more than half of all genera of LFF were subjected to changes (Lücking et al. 2017a, b), and this work continues. Intense biodiversity analyses have been performed in areas and ecosystems which have so far been poorly investigated. An example is the TICOLICHEN project in Costa Rica, the major tropical lichen biodiversity inventory initiated in 2002 by Robert Lücking and colleagues (Lücking et al. 2004).

Molecular phylogenies give fascinating insights into evolutionary processes and biogeographic developments. Examples are (1) the calicioid ascomycetes, predominantly crustose species with prototunicate asci whose ascospores achieve maturation in a mazaedium. Their asci disintegrate before the ascospore wall is fully differentiated, spore maturation being completed in a powdery mass, the mazaedium, at the surface of the ascoma (Honegger 1985). Based on this feature, mazaediate ascomycetes were formerly

classified in the order Caliciales within the Lecanoromycetes. Today, mazaediate taxa fall into four classes: Lecanoromycetes, Eurotiomycetes, Arthoniomycetes and Coniocybomycetes (Prieto et al. 2013; Wijayawardene et al. 2020). (2) the leprose lichens with no sexual reproductive stages and morphologically very simple thalli built up by loosely interwoven hyphae which secrete interesting secondary metabolites and are in contact with green algal cells, forming a powdery mass with no stratification. Today leprose lichens of the genus *Lepraria* are classified in the Stereocaulaceae, *Leprocaulon* in the Leprocaulaceae (Lecanoromycetes; Lendemer and Hodkinson 2013), *Botryolepraria* in the Verrucariaceae (Eurotiomycetes; Kukwa and Pérez-Ortega 2010) and *Andreiomycetes* in Andreiomycetaceae (Arthoniomycetes; Hodkinson and Lendemer 2013). Moreover, leprose thalli are formed in fertile taxa such as *Chrysothrix* (rarely fertile; Chrysothrichaceae, Arthoniomycetes; Nelsen et al. 2009; Liu et al. 2018) or in *Chaenotheca furfuracea* (syn. *Coniocybe* f.; Coniocybaceae, Coniocybomycetes). (3) Phylogeographic studies provided insights into large-scale population histories, e.g., of *Lobaria pulmonaria* in North America or in the post-glacial re-colonization of the Alps (Lerch et al. 2018; Allen et al. 2021), or of the cosmopolitan *Psora decipiens* (Leavitt et al. 2018).

6.2.3 Species Pairs and Cryptic Species

The species pair concept in lichenology is based on the observation that some morphologically similar lichens differ in their reproductive mode, i.e., are either fertile or asexually reproducing, the fertile stage having been assumed to be the primary species (Crespo and Pérez-Ortega 2009). Many sexual–asexual species pairs turned out to represent a monophyletic lineage. The *Porpidia flavocoerulescens* and *P. melinodes* species pair was hypothesized to maintain asexual reproduction under optimal conditions, but sexual

reproduction and re-lichenization for escaping from a suboptimal symbiosis (Buschbom and Mueller 2006). In the presumed *Letharia columbiana* (fertile) and *L. vulpina* species pair *L. columbiana* turned out to comprise five cryptic taxa, hybridization and polyploidization included (Kroken and Taylor 2001; Altermann et al. 2016; Ament-Velásquez et al. 2021).

Many other morphospecies turned out to comprise numerous cryptic species (e.g. *Pseudocyphellaria crocata* comprising 13 spp.; Lücking et al. 2017a, b), the most extreme examples being (1) the lichenized basidiomycete *Dictyonema glabratum* (syn. *Cora pavonia*), which comprises at least 126 taxa (Lücking et al. 2014, 2016; Moncada et al. 2019); upon closer examination these hidden basidiolichen species turned out to be morphologically distinct, although the differences are recognizable to the expert's eye only. (2) the species complex of the cosmopolitan crustose lichenized ascomycete *Lecanora polytropa* comprises up to 103 cryptic species (Zhang et al. 2022).

6.2.4 Morphodemes and Morphotype Pairs (= Photosymbiodemes)

Morphodemes are formed by phylogenetically distinct taxa which differentiate the same morphotype; examples are found in the *Sticta filix* (Ranft et al. 2018) or the *Sticta weigelii* complexes (Moncada et al. 2021). On the other hand, morphologically distinct lichens, some of which had been classified in different genera, turned out to be congeneric or even conspecific. This phenomenon was first observed in tripartite lichens with a morphologically distinct cyanobacterial and a green algal morphotype, i.e., in *Ricasolia amplissima* (lobate chloromorph with cephalodia) and *Dendriscoaulon bolacinum* (fruticose cyanomorph; Dughi 1937), chimaeric forms included (James and Henssen 1976). Photosymbiodemes formed by lobate chloromorphs and fruticose, dendriscoauloid cyanomorphs occur in various peltigerean genera (*Sticta*, *Lobaria*, *Ricasolia*; Paulsrud

et al. 1998; Magain et al. 2012; Tønnsberg et al. 2016; Ranft et al. 2018). Photosymbiodemes with morphologically similar lobate chloro- and cyanomorphs occur in *Peltigera* spp. (Goffinet and Bayer 1997; see Fig. 15.1f in Honegger 2012).

Vastly different morphologies formed by the same fungal species were found in *Endocena* and *Chirleja* spp. (Icmadophilaceae); their coccoid green algal photobiont was not investigated (Fryday et al. 2017). A very peculiar morphotype pair is formed by two crustose lichens with either a trebouxoid or a trentepohlioid green algal photobiont (Ertz et al. 2018). The sterile, sorediate *Buellia violaceofusca* (formerly classified in Lecanoromycetes), which associates with different phylospesies of the genus *Trebouxia* (Trebouxiophyceae), and the fertile *Lecanographa amylacea* (Arthoniomycetes) with a *Trentepohlia* photobiont (Ulvophyceae) turned out to be conspecific. This was the first example of a lichen-forming ascomycete with a trebouxoid and a trentepohlioid morphotype. As in non-lichenized fungi the species name refers to the sexually reproducing stage (teleomorph). *Lecanographa amylacea* most likely captures trebouxoid photobiont cells from adjacent crustose or leprose lichens to form the sorediate (anamorphic) morphotype (Ertz et al. 2018).

6.2.5 Non-lichen Mutualistic Fungal Interactions with Cyanobacteria and Unicellular Green Algae

It is astonishing that no Zygomycetes, Glomeromycetes or Chytridiomycetes are among the extant LFF. However, in each of these classes, which are phylogenetically older than asco- and basidiomycetes, at least one example of a mutualistic symbiosis with either a cyanobacterial or green algal partner was reported.

The Glomeromycetes *Geosiphon pyriformis* forms a very ancient endocyanosis with *Nostoc* sp. at the soil surface, the cyanobacterial photobiont being incorporated in hyphae which subsequently differentiate a bladder at the soil

surface. The *Nostoc* filaments are kept in membrane-bound vesicles (perialgal vacuoles) in the fungal cytoplasm where they undergo cell division, are photosynthetically active and fix atmospheric N₂. The first glomeromycetan monosaccharide transporter characterized was shown to function at the symbiotic interface of *Geosiphon* with its cyanobacterial partner (Schüssler et al. 2006, 2007; review: Schüssler 2012).

Under certain environmental conditions, mutualistic interactions between non-lichenized fungi and algae are formed without prior co-evolutionary adaptation. The zygomycete *Mortierella elongata* and the unicellular green alga *Nannochloropsis oceanica* are both biotechnologically cultured on large scale to produce lipids for biofuel. In co-culture, both partners interact, the algal cells adhere to the fungal hyphae and finally become internalized, leading to a green mycelium (Du et al. 2019). This situation resembles the *Geosiphon*–*Nostoc* symbiosis, although a green alga instead of a cyanobacterium is involved.

Chytrids are saprobes or parasites of fungi, algae, plants and amphibians (reviews: Powell 2017; Longcore et al. 2020). Parasites of phytoplankton attack free-living algal species (Van den Wyngaert et al. 2018) and have a devastating effect on commercially grown algal cultures (Hoffman et al. 2008; Longcore et al. 2020). The chytrid *Rhizidium phycophilum* forms a facultative mutualism with a *Bracteacoccus* sp. (Sphaeropleales; syn. Chlorococcales) and can only be cultured in the presence of this zoosporic green algal species. The alga is not parasitized, it even grows larger and more prolific and reveals an up to eight-fold increase in biovolume in co-culture as compared to axenic culture under the same conditions. This is the first report of a mutualistic interaction between a chytrid and a green alga (Picard et al. 2013).

The ascomycetous yeast *Saccharomyces cerevisiae* (Saccharomycotina) and filamentous ascomycetes such as *Aspergillus nidulans* (Eurotiomycetes) form mutualistic interactions with the flagellate unicellular *Chlamydomonas reinhardtii* (Chlamydomonadales,

Chlorophyceae), although with different levels of productivity and without differentiating thallus-like structures as seen in lichen-forming ascomycetes (Hom and Murray 2014). However, *C. reinhardtii* cells are protected by *A. nidulans* from bacteria and their toxins (Krespach et al. 2020). Two extremely halotolerant organisms, the black yeast *Hortaea werneckii* (Teratosphaeriaceae, Capnodiales), which can switch from filamentous growth to the yeast form, and the flagellate unicellular green alga *Dunaliella atacamensis* (Chlamydomonadales), were found to interact in co-cultures (Muggia et al. 2020b). Despite close fungal–algal contacts, neither a mutual benefit, nor an antagonistic interaction was observed. Nevertheless, such heterotroph–autotroph contacts might be the beginning of a stable symbiotic interaction.

6.2.6 Mycophycobioses

Mycophycobioses are mutualistic fungal interactions with quantitatively predominant, multicellular algal hosts. *Mycophycias ascophylli* (Capnodiales incertae sedis, Dothideomycetes; Toxopeus et al. 2011; Wijayawardene et al. 2020) inhabits the intertidal brown algae *Pelvetia canaliculata* and *Ascophyllum nodosum* (Fucales, Phaeophyceae) in the upper littoral of the Atlantic, only its minute ascomata being visible at the surface of the seaweed's receptaculum (gamete-producing structure; Fig. 6.2), their very thin vegetative hyphae being best visible in ultrathin sections (Xu et al. 2008). In fresh water, *Phaeospora lemaneae* (syn. *Leptosphaeria lemaneae*; Verrucariales, Eurotiomycetes) associates with the red alga *Lemanea fluviatilis* (Batrachospermales, Rhodophyta; Brierley 1913; Hawksworth 2000). *M. ascophylli* improves the desiccation tolerance of the zygotes of its brown algal host *A. nodosum* (Garbary and London 1995). Improved desiccation tolerance was also hypothesized for the red algal host *L. fluviatilis* upon infection with *P. lemaneae* (Hill 1992), but experimental data are missing.

About 100 species of fungal endophytes of seaweeds (Phaeophyta, Rhodophyta,

Chlorophyta) were identified, some of them producing bioactive secondary metabolites (Noorjahan et al. 2021).

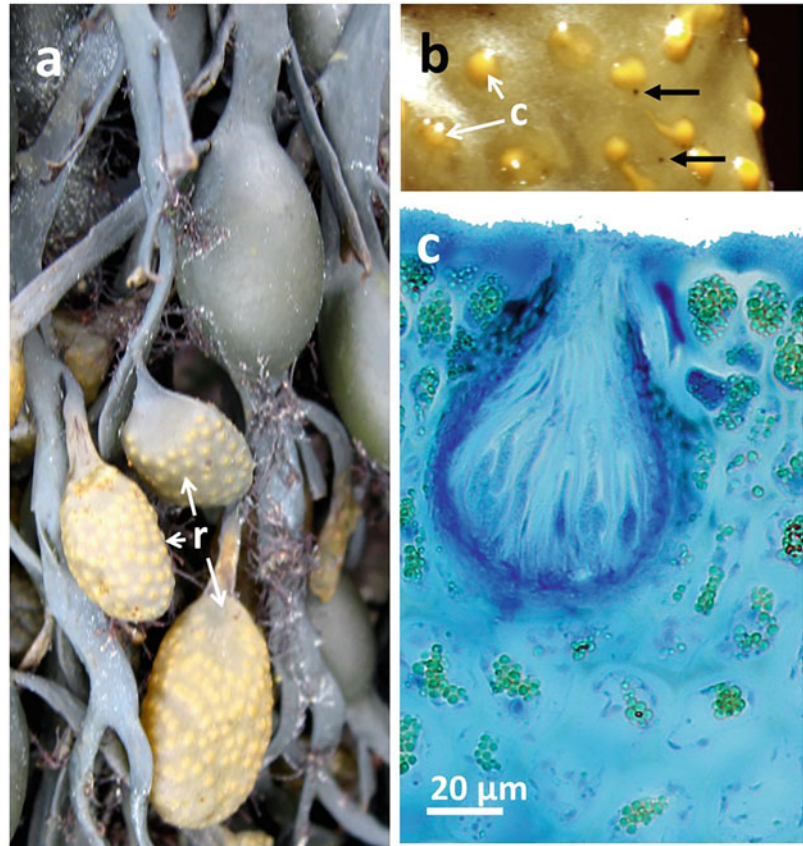
6.2.7 Secondary Metabolites

Lichen thalli are a rich source of interesting polyphenolic secondary metabolites, many of them with bioactive properties. Most of them are produced by the mycobiont, others by endolichenic fungi or by epi- or endolichenic bacteria (see below). Lichen compounds evolved early in the radiation of filamentous fungi (Armaleo et al. 2011). Polyketide synthase (PKS) genes were most likely gained by horizontal gene transfer from actinobacteria before the radiation in Leotiomyceta, which gave rise to the extant crown group of Ascomycota (Schmitt and Lumbsch 2009). PKS genes have been repeatedly lost in non-lichenized ascomycetes but retained and even duplicated in most lichenized ascomycetes (Schmitt and Lumbsch 2009). However, also in lichenized taxa were PKS gene clusters repeatedly lost (Pizarro et al. 2020).

The chemistry of mycobiont-derived secondary metabolites, the so-called lichen products, has attracted considerable interest, with a large body of literature having been published from the late nineteenth century onwards (e.g. Zopf 1896, 1907; Asahina and Shibata 1954; Culberson 1969, 1970; Culberson and Elix 1989; Culberson et al. 1977; Huneck and Yoshimura 1996; Huneck 2001; Elix and Stocker-Wörgötter 2008); a database of high-resolution tandem mass spectrometry (MS/MS) spectra for lichen metabolites is available (Olivier-Jimenez et al. 2019).

It is not known in which form the secondary metabolites are excreted by the fungal cells (possibly as glycosides?). In their soluble form, they are passively translocated into the apoplastic continuum during the wetting and drying cycles and crystallize either at on the surface of ascomata (e.g. bellidiflorin in *Cladonia* spp.; Fig. 6.3a, or haemomentosin in *Ophioparma ventosa*; Fig. 6.3b–c), on the thallus surface (e.g. anthraquinones such as parietinic or

Fig. 6.2 Mycophycobiosis in the knotted kelp (*Ascophyllum nodosum*), a common brown alga (Fucaceae, Phaeophyceae) in the littoral of the Northern Atlantic (a); its gametes are produced in conceptacles (c) in stalked receptacles (r). (b) Gametes are oozing out of the ostiole of conceptacles. Arrows point to ascomata of *Mycophycias ascophylli* (Mycosphaerellaceae, Capnodiales, Dothideomycetes), recognizable as tiny black dots between conceptacles. (c) Stained semi-thin section with ascoma (pseudothecium) of *M. ascophylli*



solorinic acid, pulvinic acid derivatives such as vulpinic or rhizocarpic acid, or depsides such as atranorin), many of them giving the thallus its characteristic colouration; others (e.g. depsidones such as physodic or protocetraric acid) crystallize on the surface of medullary hyphae and even on green algal photobiont cells in the thalline interior (Fig. 6.3d; Honegger 1986b). In soredia, mycobiont and photobiont cells are often heavily loaded with crystalline secondary metabolites which enhance their hydrophobicity (Fig. 6.3e). Crystalline lichen products are almost insoluble in aqueous systems below pH 7. Many mycobiont-derived secondary metabolites are produced in sterile, aposymbiotic culture (Thomas 1939; Yamamoto et al. 1985; Honegger and Kutasi 1990; Culberson and Armaleo 1992; Stocker-Wörgötter et al. 2013; Díaz et al. 2020; Jeong et al. 2021, etc.).

Numerous PKS gene clusters have been characterized (e.g. Miao 1999; Armaleo et al.

2011; Wang et al. 2014; Bertrand and Sorensen 2018; Bertrand et al. 2018; Calchera et al. 2019; Pizarro et al. 2020; Sveshnikova and Piercey-Normore 2021; Gerasimova et al. 2022; Singh et al. 2022), many of them being not expressed in the lichen thallus. Thus, LFF have an unexplored biosynthetic potential (Bertrand et al. 2018; Gerasimova et al. 2022).

As most LFF are slow-growing organisms, lichen-derived PKS genes were transferred into fast-growing non-lichenized ascomycetes. A *Pseudevernia furfuracea*-derived PKS gene was successfully expressed in baker's yeast (*S. cerevisiae*), the depside lecanoric acid being synthesized (Kealey et al. 2021). The transfer of lichen-derived PKS genes in filamentous ascomycetes such as *Aspergillus* spp. lead to successful transcription (Wang et al. 2016), but for unknown reasons, secondary products were often not synthesized (Gagunashvili et al. 2009; Yang et al. 2018; Bertrand and Sorensen 2019a, b).

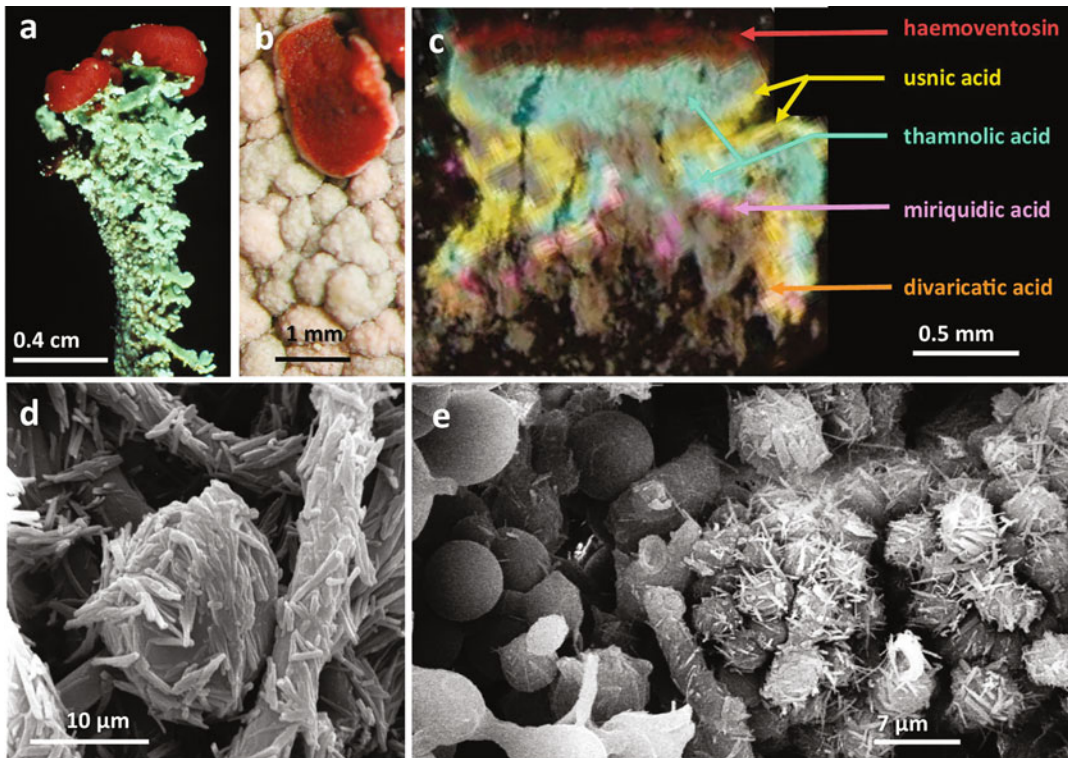


Fig. 6.3 Developmentally regulated biosynthesis of secondary metabolites. (a) *Cladonia bellidiflora* with usnic and squamatic acid in the thallus and bellidiflorin in the bright red ascomata. (b, c) The saxicolous, crustose *Ophioparma ventosa* with haemoventosin in the bright red ascomata. (c) LDI-MSI showing the tissue-specific accumulation of usnic, thamnolic, miriquidic and divaricatic acid in the thallus and haemoventosin in the epihymenial layer of the ascomal disc; from Le Pogam

et al. (2016, modified); courtesy of Pierre Le Pogam and Joël Boustie. (d) LTSEM (low temperature scanning electron microscopy) of the algal layer in in cryofixed, freeze-fractured *Cetrelia olivetorum*, with crystals of olivetoric acid on fungal hyphae and algal cell. (e) LTSEM of the margin of a soralium of *Physcia adscendens*. Secondary metabolites crystallize on hyphae and algal cells of developing soredia, thus increasing the hydrophobicity of their surfaces

Lichens have been used in traditional medicine around the globe (Crawford 2019). In the last decades, a large body of literature was published on interesting pharmaceutical properties of β -glucans such as lichenans (e.g. Caseiro et al. 2022), important cell wall components of Lecanoromycetes (Honegger and Haisch 2001), and of a wide range of lichen-derived secondary metabolites with antibiotic, anti-inflammatory, antiproliferative, antiviral, antineurodegenerative, antioxidant activities, etc. (various authors in Ranković 2019; reviews: Boustie and Grube 2005; Boustie et al. 2011; Bhattacharyya et al. 2016; Studzinska-Sroka et al. 2017; Ingelfinger

et al. 2020; Ureña-Vacas et al. 2021). Best investigated is usnic acid (Macedo et al. 2021; Xu et al. 2022), whose antibacterial properties were detected by Stoll et al. (1947).

6.3 Lichen Photobionts

6.3.1 Diversity and Specificity

In her 1988 compilation, Tschermak-Woess listed 44 genera of lichen photobionts: 15 cyanobacterial, 27 chlorophycean, one xanthophycean and one phaeophycean

(Tschermak-Woess 1988). All of these taxa had been described on the basis of morphological characters. From 1989 onwards, molecular tools, applied either to cultured (aposymbiotic) photobiont isolates or to whole thallus DNA preparations, revolutionized our knowledge of lichen photobiont diversity. In 2021, Sanders and Masumoto summarized the current state of the art. They listed 52 genera of lichen photobionts: 13 cyanobacterial, 36 chlorophycean, two xanthophycean and one phaeophycean (Sanders and Masumoto 2021). New photobiont genera had been described (e.g. *Heveochlorella*, Trebouxiophyceae; Sanders et al. 2016, or *Bracteacoccus*, Chlorophyceae; Masumoto 2020).

The Verrucariales (three families, 55 genera, >800 spp.), which comprises terrestrial, but also numerous fresh water and marine species, harbours the highest photobiont diversity. The only phaeophycean (*Petroderma maculiforme* in *Wahlenbergiella tavaresiae*) and xanthophycean photobionts (*Heterococcus* sp. in *Verrucaria* and *Hydropunctaria* spp., *Xanthonema* sp. in *Staurothele clopimoides*) are symbiotic with verrucariacean taxa (review: Sanders and Masumoto 2021). Many photobiont taxa associate exclusively with marine LFF. Examples are the cyanobacterial *Hyella* sp. in *Collembosidium halodytes* (syn. *Arthopyrenia* h., Xanthopyreniaceae) or *Rivularia* sp. in *Lichina pygmaea* and *L. confinis* (Lichinales, Lichinomycetes; see Figs. 15.1.p-r in Honegger 2012). Among marine green algal photobionts of marine Verrucariaceae are the ulvophycean *Blidingia minima* (with *Turgidosculum ulvae*; Pérez-Ortega et al. 2018), *Halophilum ramosum*, *Lithotrichon pulchrum*, *Paulbroadya petersii*, *Pseudendoclonium submarinum* and *Undulifilum symbioticum* (with *Hydropunctaria* and *Wahlenbergiella* spp.), or the trebouxiophycean *Prasiola* spp. in *Mastodia tessellata* (Sanders and Masumoto 2021; Černajová et al. 2022).

The genus *Trebouxia* harbours the most common and widespread unicellular green algal photobionts of LFF; *Trebouxia* spp. are photobionts of Parmeliaceae (>2760 spp.; Lücking et al. 2017a, b), Teloschistaceae (>810

spp.), etc. Tschermak-Woess (1988) listed seven species, Sanders and Masumoto (2021) 27 plus several unnamed phylospesies and clades, whence five had been transferred from *Pseudotrebouxia* (which no longer exists), and 19 species have been newly described from 1989 onwards. In *Asterochloris*, the second-most common genus, Tschermak-Woess (1988) listed one species, Sanders and Masumoto (2021) 18 plus several unnamed phylospesies and clades; four of these *Asterochloris* spp. had been transferred from *Trebouxia* to *Asterochloris* (*A. erici*, *A. glomerata*, *A. italiana*, *A. magna*). *Asterochloris* spp. are photobionts of *Cladonia* and *Stereocaulon* spp. and many other taxa (Sanders and Masumoto 2021), new phylogenetic lineages having been recently described (Kosecka et al. 2021).

Trebouxia and *Asterochloris* spp. are characterized by their large, lobate chloroplast with central pyrenoid. Chloroplast lobation and its interspecific variation was visualized with Confocal Laser Scanning Microscopy (CLSM; *Trebouxia*: Muggia et al. 2012; Bordenave et al. 2021; *Asterochloris*: Škaloud and Peksa 2008; Moya et al. 2015; Škaloud et al. 2015; Kim et al. 2017).

As in LFF, considerable cryptic diversity was found among lichen photobionts; examples in *Trebouxia* (Singh et al. 2019; Muggia et al. 2020a, b; Kosecka et al. 2022), *Coccomyxa* (Dariencko et al. 2015; Malavasi et al. 2016), *Dictyochloropsis* or *Symbiochloris*, respectively (Dal Grande et al. 2014; Škaloud et al. 2016), *Trebouxiophyceae* (Metz et al. 2019) or Trentepohliales (Borgato et al. 2022).

Unfortunately lichen thalli cannot be routinely resynthesized by combining cultured myco- and photobionts. Therefore, the specificity and selectivity of the symbiosis cannot yet be investigated under controlled experimental conditions. Our knowledge about the range of acceptable partners per fungal species or genotype is based on analyses of specimens collected in nature. Ideally, sampling was done over the whole geographic range of the fungal species.

Many (the majority?) of LFF with trebouxioid or trentepohlioid photobionts associate with more

than one algal species or genotype; examples are *Xanthoria parietina* with *Trebouxia decolorans* or *T. arboricola* (Nyati et al. 2014) or cosmopolitan species of *Stereocaulon*, *Cladonia* or *Lepraria*, which reveal low specificity towards their photobiont (Kosecka et al. 2021). In *Cladonia* spp., external factors such as climate or soil chemical properties have an impact on photobiont selection (Pino-Bodas and Stenroos 2021; Škvorová et al. 2022); severe heavy metal pollution even induced a switch from *Asterochloris* to *Trebouxia* spp. (Osyczka et al. 2020).

Based on light microscopy studies, the algal cell population of lichen thalli was assumed to be uniform, but molecular tools revealed intrathalline photobiont diversity. Different photobiont species or genotypes of the same photobiont may grow within the same thallus (for special relationships such as morphotype pairs, see Sect. 6.2.4, or tripartite lichens, see Sect. 6.3.2, respectively). In all thalli of *Ramalina farinacea* were two unnamed *Trebouxia* spp. found with different physiological properties (Casano et al. 2011; del Hoyo et al. 2011). In 45% of *Evernia mesomorpha* were multiple genotypes of one *Trebouxia* species found (Piercey-Normore 2006). In 30 out of 104 thalli of *Tephromela atra* or *Rhizoplaca melanophthalma*, respectively, were co-occurring *Trebouxia* spp. found (de Carolis et al. 2022). Only once were two genotypes of *T. decolorans* found in a thallus of *X. parietina* (Nyati et al. 2014).

Some *Trebouxia* photobionts were found free-living in nature (Bubrick et al. 1984), but they are not common members of aerophilic algal communities. In contrast, photobionts of the genera *Apatococcus*, *Stichococcus*, *Coccomyxa*, *Elliptochloris*, *Myrmecia*, *Symbiochloris*, *Prasiola* (all Trebouxiophyceae) or *Trentepohlia* (Ulvophyceae) are common in the free-living state, many of them having been found in soil samples along an altitudinal gradient (Stewart et al. 2021) or in biological soil crust communities (Flechtner et al. 2013; Borchhardt et al. 2017). This should be kept in mind when exploring microalgal diversity in whole thallus extracts: adhering fragments of symbiotic

propagules from other lichens or free-living algae might be included. Ideally, lichen photobionts are isolated from the algal layer of dissected thallus fragments and cultured under sterile conditions prior to genetic analysis (Nyati et al. 2013, 2014).

6.3.2 Tripartite Lichens

- (a) Lichens with a mixed photobiont layer comprising green algae and cyanobacteria. In a few lichens, the photobiont layer comprises a green algal and a cyanobacterial partner, both being photosynthetically active. Examples are (a) *Euopsis granatina* with *Trebouxia aggregata* as a green algal and *Gloeocapsa sanguinea* as cyanobacterial photobiont (Büdel and Henssen 1988); (b) *Muhria urceolata* (Jørgensen and Jahns 1987, syn. *Stereocaulon urceolatum*; Högnabba 2006) and (c) various cyanomorphs of *Pseudocyphellaria* spp. (*Ps. rufovirescens*, *Ps. lividofusca*, *Ps. dissimilis*, *Ps. hookeri*, *Ps. crocata*) and *Sticta fuliginosa*, all with *Nostoc* sp. (Henskens et al. 2012). In some of these peltigeralean species the green algal partner was detected when ribitol, the characteristic carbohydrate produced by numerous green algal photobionts (Hill 1976; Honegger 1997), was identified among the photobiont-derived mobile carbohydrates in the thalli (Henskens et al. 2012).
- (b) Cephalodiate species are green algal lichens which capture repeatedly a diazotrophic cyanobacterium as a secondary photobiont (see Fig. 15.16 a–k in Honegger 2012), either at the upper (e.g. in green algal *Peltigera* spp.) or at the lower surface (e.g. in *Solorina* spp.) or at both surfaces (*Lobaria pulmonaria*; Cornejo and Scheidegger 2013) and incorporate it in either an external (e.g. *Peltigera aphthosa*, *Stereocaulon ramulosum*) or internal cephalodium (e.g. *Solorina crocea*, *Nephroma arcticum*). Capture of a cyanobacterial partner occurs in young lobes of the green algal lichen, mature cephalodia being found in fully grown

areas of the lobes (Cornejo and Scheidegger 2013). The cyanobacterial photobionts in cephalodia are photosynthetically active, i.e., satisfy their demands of fixed carbon, but are diazotrophic, i.e., reduce atmospheric N_2 into bioavailable ammonium, highest N_2 fixation rates being achieved under microaerobic conditions. In mature cephalodia of Peltigerales with *Nostoc* as the secondary photobiont, the percentage of heterocysts, i.e., the site of N_2 fixation, is elevated (up to 55%) as compared to either cyanobacteria as primary photobiont of cyanolichens (approx. 5–8%) or free-living *Nostoc* spp. (Englund 1977; Hyvärinen et al. 2002). It is particularly interesting to see how lichen mycobionts generate microaerobic conditions, optimal for N_2 fixation, by forming a dense cortex around external cephalodia, which differs anatomically from the thalline cortex (see Fig. 15.16d–f and i–k in Honegger 2012). By 3D imaging using X-ray computed tomography at the microscopy level (Micro-CT, allowing for non-destructive analysis of the 3D-geometry in solid specimens; Elliott and Dover 1982; Hunter and Dewancke 2021), the cephalodia were quantified (Gerasimova et al. 2021); in *Lobaria pulmonaria* the internal cephalodia amounted for 0.73%, in *Peltigera leucophlebia* (external cephalodia) for 0.97% of thallus volume.

- (c) Cephalodiate species are found in all green algal Peltigerales (*Peltigera* and *Solorina* spp. etc. [Peltigeraceae] and *Lobaria*, *Sticta*, *Pseudocyphellaria* spp., etc. [Lobariaceae]), in all representatives of the genera *Stereocaulon* (Stereocaulaceae, Lecanorales), *Placopsis* (Trapeliaceae, Baeomycetales; Ott et al. 1997), but also in some crustose taxa such as *Calvitimela aglaea* (syn. *Lecidea shushanii* or *Tephromela aglaea*, respectively, Tephromelataceae, Lecanorales; Hertel and Rambold 1988; Bendiksby et al. 2015).

6.3.3 Cyanotrophy

Cyanotrophy, i.e., the close contact of lichens with free-living cyanobacterial colonies, first observed in *Bryonora* spp. (Poelt and Mayrhofer 1988), might be common and widespread among saxicolous, epiphytic and soil crust lichens (Elbert et al. 2012; Cornejo and Scheidegger 2016; Gasulla et al. 2020). The contacting lichen benefits from fixed nitrogen, as produced by diazotrophic cyanobacteria, as is also the case in bryophyte interactions with free-living cyanobacteria (Gavazov et al. 2010; Warshan et al. 2017). Epiphytic bryophyte–cyanobacteria associations can serve as a reservoir for lichen cyanobionts (Cornejo and Scheidegger 2016).

6.4 Peculiarities of Lichen Symbiosis

6.4.1 A. Symbiotic vs. Free-Living LFF

In nature, the majority of LFF are symbiotic, but physiologically they do not depend on lichenization. Soon after the discovery of lichen symbiosis by Schwendener (1867, 1869), the first culturing and resynthesis experiments with LFF and their photobionts were carried out (Stahl 1877; Bonnier 1886, 1889). From large numbers of lichen-forming ascomycetes, sterile cultures have been established, starting with either ascospores, soredia or hyphal fragments which had been scratched out of dissected thalli (e.g. Lange de la Camp 1933; Thomas 1939; Ahmadjian 1959, 1962; Honegger and Bartnicki-Garcia 1991; Crittenden et al. 1995; Stocker-Wörgötter 1995, etc.). Single-spore isolates derived from one meiosis (i.e. the content of one ascus) facilitated the analysis of mating type systems (Honegger et al. 2004a; Honegger and Zippler 2007; Scherrer et al. 2005). Thus, LFF are ecologically obligate, but physiologically facultative biotrophs. However, some LFF most likely acquire additional carbohydrates as saprotrophs. Hyphae of *Icmadophila ericetorum*

or *Baeomyces rufus* on decaying wood grow deep into the substratum and penetrate the lignified cell walls (see Figs. 12 and 14 in Honegger and Brunner 1981). In large numbers of Lecanoromycetes, a whole arsenal of genes encoding enzymes for carbohydrate degradation was identified (Resl et al. 2022).

LFF are seldom macroscopically visible in a non-lichenized state in nature. Examples are (1) juvenile developmental stages of *Rhizocarpon* spp. (Rhizocarpales), recognizable as a strongly melanized, black prothallus in search of a compatible photobiont, or (2) the optionally lichenized *Schizoxylon albescens* (Ostropales) on the bark of *Populus tremula*, which grows as a saprobe on dead wood of poplar (Muggia et al. 2011), or (3) the lichenized *Conotrema* spp. and their non-lichenized, saprotrophic stage which had been described as *Stictis* spp., optional lichenization presumably allowing to increase the ecological amplitude (Wedin et al. 2004, 2005).

6.4.2 Morphogenetic Capacity of the Mycobiont

In order to keep their photoautotrophic partner photosynthetically active, LFF have to grow at the surface of the substrate, thus exposing their thallus to temperature extremes, illumination, ultra-violet (UV) radiation included and to continuous fluctuations in water content, i.e. to regular drying and wetting cycles. Many mycobiont-derived cortical secondary metabolites such as parietin or atranorin are autofluorescent, i.e. absorb UV light and transform it into longer wavelengths (Fernandez-Marin et al. 2018); therefore, they were assumed to protect the myco- and photobiont from UV damage and to provide the photobiont cell population with wavelengths matching the absorption spectra of photosynthesis; however, the latter hypothesis was not supported by experimental approaches (Fernandez-Marin et al. 2018). The biosynthesis of secondary metabolites is enhanced by seasonally or experimentally elevated UV radiation (BeGora and Fahselt 2001; Bjerke et al. 2002,

2005; Solhaug et al. 2009). However, there are yet unknown genetic factors causing quantitative differences in cortical secondary metabolites among thalli of the same species growing side by side (Bjerke et al. 2005; Itten and Honegger 2010).

Foliose, band-shaped or fruticose lichen thalli with internal stratification are the most complex vegetative structures in the fungal kingdom. However, less than half of all lichens reveal this morphology and anatomy, the majority forming either microfilamentous, microglobose, crustose, leprose, gelatinous or squamulose thalli with no internal stratification (see Figs. 15.1a–y and 15.8 a–e in Honegger 2012). Many crustose taxa grow within the uppermost zone of the substratum where they meet their photobiont; examples are *Arthopyrenia halodytes* (syn. *Pyrenocollema h.*) with cyanobacterial photobiont (*Hyella* spp.) in the calcareous shell of limpets (*Patella* spp., Mollusca) or barnacles (Cirripedia, Crustacea), *Graphis* spp. with trentepohlioid photobiont in bark, etc. (see Fig. 15.1a–b in Honegger 2012).

6.4.3 The Mycobiont–Photobiont-Interface

In all lichenized asco- and basidiomycetes, the photoautotrophic partner is located outside the contacting fungal hyphae, with different types of mycobiont–photobiont interfaces being differentiated, ranging from simple wall-to-wall apposition to transparietal (formerly termed intracellular) or intraparietal haustoria (Honegger 1986a, b, 1991a; see micrographs in Fig. 15.13 a–l in Honegger 2012). When compared with biotrophic plant pathogenic fungi such as rusts or powdery mildews or with arbuscular mycorrhizal fungi, which form lobate or arbuscular transparietal haustoria, i.e., a large exchange surface in close contact with the plasma membrane of the host cell, the mycobiont–photobiont contact site in lichen is surprisingly simple (see Fig. 1a–f in Honegger 1993): in intraparietal haustoria, as formed by Parmeliaceae, Teloschistaceae, Cladoniaceae, etc., the mycobiont does not pierce the cellulosic cell

wall of the chlorobiont (*Trebouxia* or *Asterochloris* spp., respectively; see Fig. 15.13 a–l in Honegger 2012). A whole range of genes encoding carbohydrate-active enzymes and sugar transporters were identified in 46 representatives of Lecanoromycetes; these LFF would be able to enzymatically degrade the cellulosic cell wall of their photobiont; many of them are likely acquiring additional carbohydrates as saprotrophs (Resl et al. 2022).

Simple wall-to-wall apposition is found in asco- and basidiolichens with *Coccomyxa* or *Elliptochloris* chlorobionts; these incorporate enzymatically non-degradable, sporopollenin-like algaenans in a thin outermost cell wall layer (Honegger and Brunner 1981; Brunner and Honegger 1985; see Fig. 15.3 a–c in Honegger 2012).

6.4.4 Water Relations and Gas Exchange

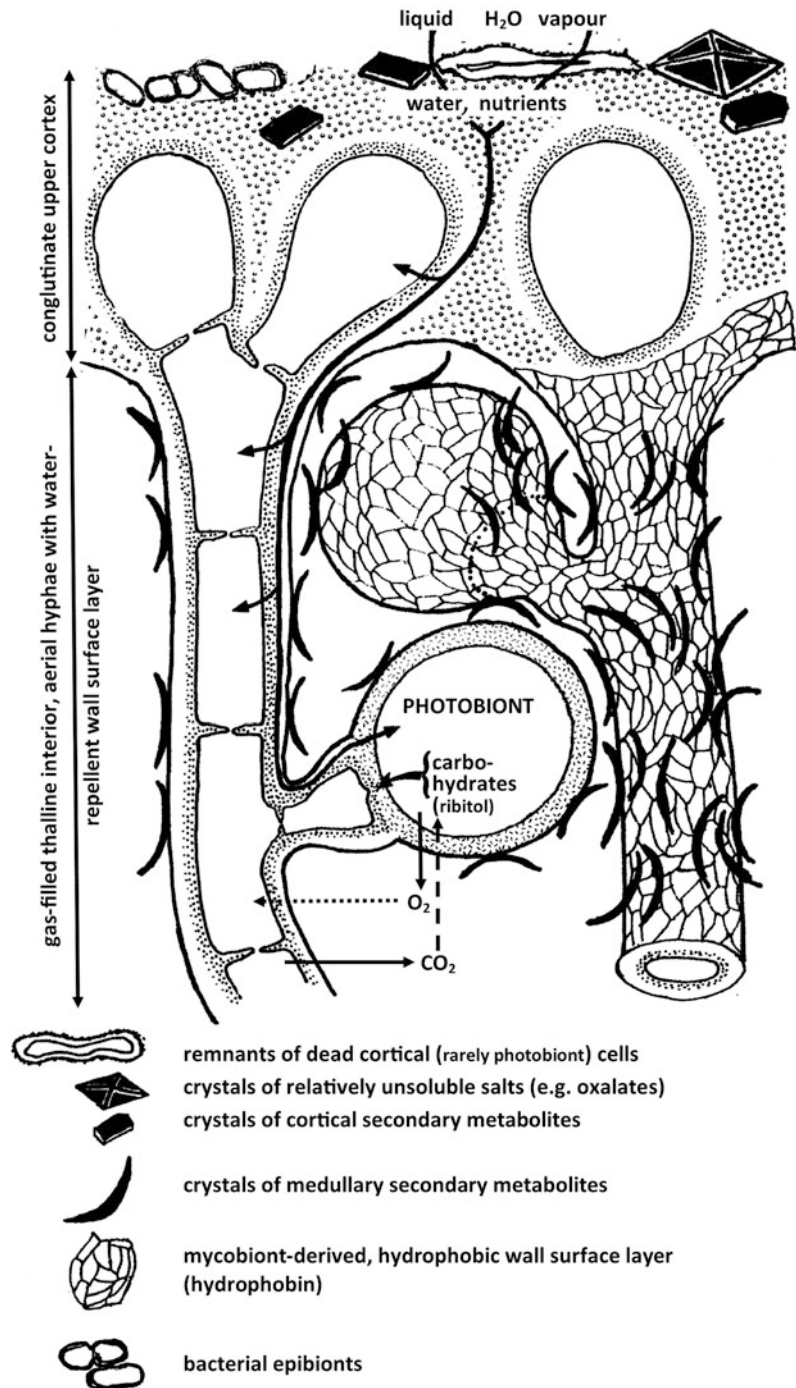
LFF and their photobionts are poikilohydrous organisms (Greek *poikilos*: variable; Greek *hydror*: water) and as such unable to control their water relations. They survive fluctuations in water content between saturation and desiccation (less than 10% water dw^{-1}) unharmed and are metabolically dormant during drought stress events, but recover within few minutes upon rehydration (Scheidegger et al. 1995). During desiccation, the cyanobacterial and green algal cells shrivel and the fungal hyphae cavitate, as seen in Low Temperature Scanning Electron Microscopy preparations of frozen-hydrated specimens, but irrespective of these dramatic changes, the cellular membrane systems remain intact, as visualized in ultrathin sections prepared from cryofixed, freeze-substituted specimens in Transmission Electron Microscopy (Honegger and Peter 1994; Honegger et al. 1996; Honegger and Hugelshofer 2000; see Fig. 16.5a–c in Honegger 2009). Poikilohydrous water relations are also characteristic of lichenicolous and endolichenic fungi and lichen-associated bacteria.

In lichen thalli water and dissolved nutrients are passively taken up at the thallus surface by the

conglutinate cortex and/or rhizinae with hydrophilic wall surfaces and passively translocated into the photobiont and medullary layers. As shown with LTSEM techniques, a flux of solutes occurs within the fungal apoplast, mostly in the thick, glucan-rich outer wall layer and underneath the thin hydrophobic wall surface layer (Honegger and Peter 1994); the latter is built up primarily by mycobiont-derived hydrophobin protein (Scherrer et al. 2000, 2002; Scherrer & Honegger, 2003), the characteristic hydrophobic lining of aerial hyphae in the fungal kingdom which self-assembles at the liquid–air interface (Wösten et al. 1993; Wessels 1997; Wösten 2001). Despite being located in the thalline interior, the hyphae of the photobiont and medullary layers are aerial, their hydrophobin layer spreads over the wall surfaces of the photobiont cell population, thus sealing the apoplastic continuum with a hydrophobic coat (Fig. 6.4). The same happens in the lichenized basidiocarp of *Dictyonema glabratum* (syn. *Cora pavonia*; Trembley et al. 2002a, b). The mycobiont-derived hydrophobic wall surface layer plays a crucial role in the functioning of the symbiosis. In co-cultures under sterile conditions, hydrophobin protein is synthesized at an early stage of thallus resynthesis at the contact site of *Usnea hakonensis* and its chlorobiont (*Trebouxia* sp.; Kono et al. 2020).

Traditionally, gas exchange of lichens was measured in the same way as in plant leaves, i.e., outside the thallus which is built up by the heterotrophic partner. However, CO_2 diffusion through the cortex is blocked in fully hydrated thalli; this was interpreted as a depression of photosynthesis at high moisture contents, and water was assumed to fill the intercellular space in the thalline interior (Lange and Tenhunen 1981). In ultrastructural studies, the hydrophobic lining of the wall surfaces in the algal and medullary layers was shown to prevent water from accumulating outside the apoplastic continuum, the algal and medullary layers being gas-filled at any level of hydration (Honegger 1991a, b). The mycobiont of macrolichens amounts to approx. 80% of thalline biomass, the photobiont cell population to approx. 20% or less. The cortex is

Fig. 6.4 Diagram illustrating the apoplastic continuum and intrathalline gas exchange in Parmeliaceae with *Trebouxia* photobiont. After Honegger (1991a), modified. The mobile carbohydrates, as produced by the different genera of green algal or cyanobacterial photobionts, are summarized by Hill (1976) and Honegger (1997)



translucent when wet, but opaque when dry, and chlorophyll fluorescence is highest in fully hydrated thalli. It was postulated that there should be enough mycobiont-derived respiratory CO₂ in

the thalline interior to secure the photosynthetic activity of the photobiont in fully hydrated thalli (Honegger 1991a). By oximetric measurements of electron transport within thalli and fluorimetric

measurements of photosynthesis in *Flavoparmelia caperata* and its *Trebouxia* chlorobiont, ten Veldhuis et al. (2019) showed that photosynthetic O₂ and photosynthates are taken up by the mycobiont and its respiratory CO₂ by the chlorobiont, the algal and fungal energy metabolism being mutually linked, a perfect recycling system.

6.4.5 Heavy Metal and Radionuclides

Lichens absorb not only water and nutrients, but also pollutants, heavy metals and radionuclides included. Thus, they are used in biomonitoring studies in urban and industrial areas (Nimis et al. 2002; Abas 2021). They have also been used as silent chronists of early nuclear weapon testing and of the Chernobyl and Fukushima accidents (Seaward 2002; Saniewski et al. 2020; Dohi et al. 2021; Anderson et al. 2022). Heavy metals are bound in insoluble complexes within the thallus. Characteristic lichen communities develop on heavy metal rich rock substrates. 5000 ppm of copper were found in the crustose thalli of *Lecanora vinetorum*: it grows on wooden supports in vineyards in South Tyrolia which, for decades, were sprayed 12 times per year with copper sulfate as a fungicide to protect the *Vitis* cultivars (Poelt and Huneck 1968); the mycobiont-derived xanthone vinetorin is assumed to form insoluble copper complexes.

6.5 The Microbiome of Lichen Thalli

6.5.1 The Bacteriome: Bacterial Epi- and Endobionts of Lichen Thalli

At least since the Early Devonian (approx. 415 Ma ago), non-photosynthetic bacteria live on the thallus surface of lichens, and filamentous actinobacteria are found on their cortex and in the thalline interior (Fig. 6.5a–b; Honegger et al. 2013b). In the twenty-first century, the taxonomic

diversity and potential role of the bacteriome for lichen symbiosis was intensely explored, as reviewed by Grube and Berg (2009), Grube et al. (2012, 2016), and Grimm et al. (2021).

Many lichens live in nutrient-poor habitats such as bare rock surfaces, steppe and desert or oligotrophic boreal-arctic ecosystems. Numerous plant-beneficial bacteria have been identified in the rhizosphere of plants (Burr et al. 1984; Davison 1988); some of them fix nitrogen, others solubilize phosphate or act as antagonists of plant pathogens and thus are important in sustainable agriculture (Romano et al. 2020). Considering the ubiquitous bacterial epi- and endobionts of lichen thalli (Fig. 6.5c–j), the question was: are there any lichen-beneficial bacteria (Honegger 1991b)? Maria Cengia Sambo (1924, 1926) was the first to culture and identify an *Azobacter* associated with lichens and referred to its potential role as a N₂-fixing partner; she introduced the term polysymbiosis. In the last decades, a whole range of nitrogen-fixing representatives of Rhizobiales and *Frankia* have been characterized as associates of lichen thalli (Hodkinson and Lutzoni 2009; Bates et al. 2011; Erlacher et al. 2015; Eymann et al. 2017; Almendras et al. 2018, etc.). Some lichen-associated Rhizobiales synthesize β-carotenes (Pankratov et al. 2020). The most common and widespread bacterial symbionts of lichens are representatives of Alphaproteobacteria. The bacterial community may change upon infection of the thallus by lichenicolous fungi or lichens (Wedin et al. 2016). Chlorolichens carry different bacterial communities than cyanolichens (Almendras et al. 2018).

In non-lichenized fungi, the intimate bacterial–fungal interaction triggers the biosynthesis of secondary metabolites such as archetypal polyketides in *A. nidulans* (Schroeckh et al. 2009) or a cryptic meroterpenoid pathway in *A. fumigatus* (König et al. 2013).

Comparative analyses of the bacteriome of lichens from different ecosystems were performed, e.g., the littoral (Sigurbjornsdottir et al. 2014; Parrot et al. 2015; West et al. 2018), high mountain areas such as alpine soil crust lichens (Muggia et al. 2013), the Andean Paramo

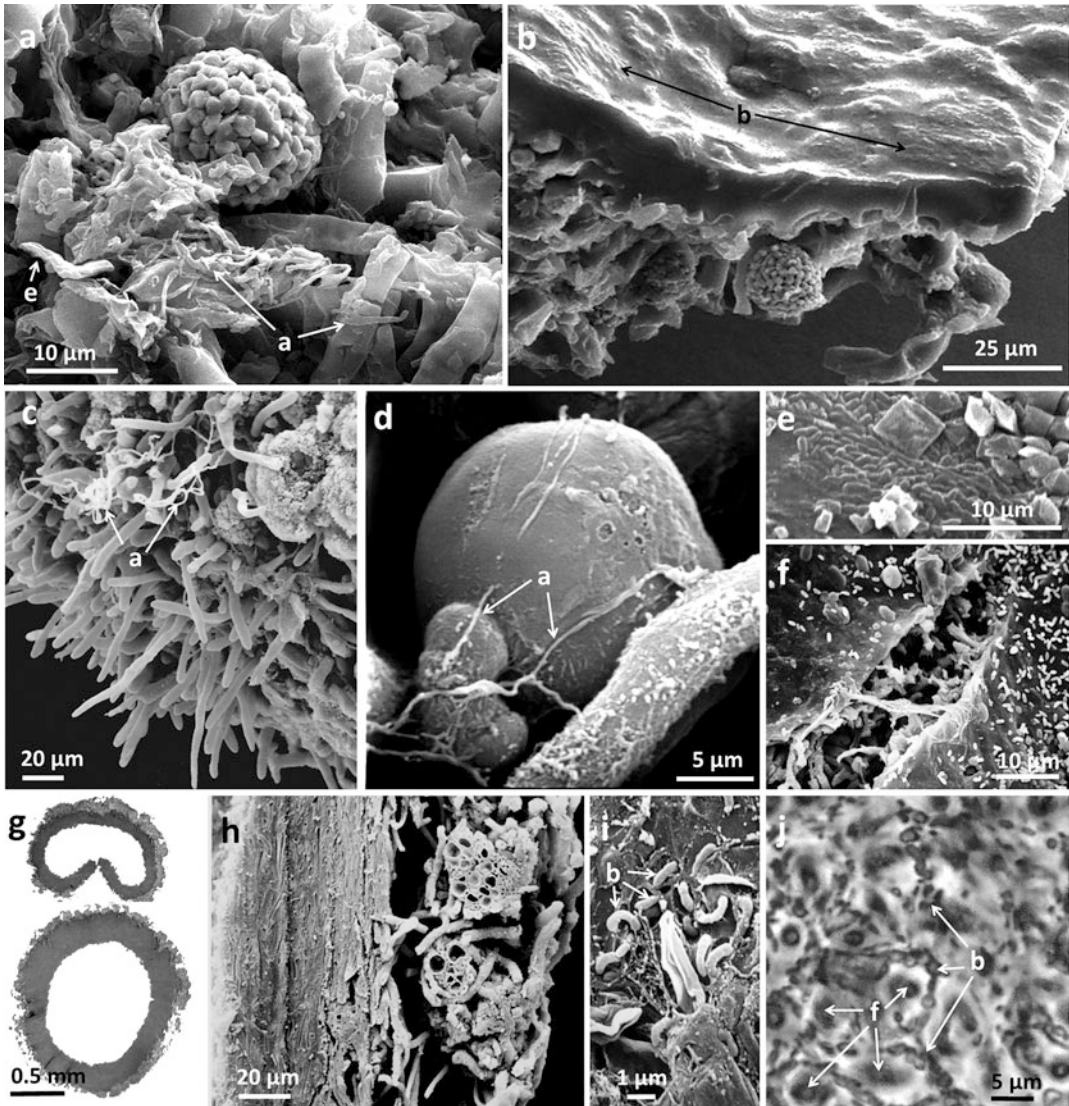


Fig. 6.5 Epi- and endolichenic bacteria past (**a, b**) and present (**c–j**). (**a, b**) Charcoalified, cross-fractured fragment of the green algal lichen *Chlorolichenomycites salopensis*, 415 Ma old, with endolichenic fungi (**e**) and actinobacterial filaments (**a**) in the thalline interior (**a**) and bacteria (**b**) on the surface of the cortex (**b**). After Honegger et al. (2013b). (**c**) Thallus margin of *Peltigera praetextata* with actinobacterial filaments (**a**) around protruding hyphae (trichogynes?). (**d**) Actinobacterial filaments (**a**) overgrowing the mycobiont-photobiont interface in the algal layer of *Pleurosticta acetabulum*. (**e, f**) Bacterial colonies growing on the surface of the

upper cortex of *Parmelia sulcata*. (**g–j**) The fruticose thallus of the reindeer lichen *Cladonia arbuscula*, a conglutinate, tubiform axis with peripheral photobiont layer and bacterial epi- and endobionts. (**g**) Cross-sections of the young (top) and older part of the thallus. (**h**) SEM of a longitudinal section, the conglutinate axis being built up by thick-walled parallel hyphae. (**i**) Bacteria growing on the inner surface of the axis near the tip of the thallus. (**j**) Cross-section of the basal, old part of the axis with large numbers of bacteria (**b**) growing between the thick walls of the fungal hyphae (**f**)

(Sierra et al. 2020), the Qinghai–Tibet Plateau (Hei et al. 2021) or tropical rainforests (Mara et al. 2011). The best investigated is the microbiome of the lung lichen, *Lobaria pulmonaria*, as reviewed by Grimm et al. (2021).

In the desiccated state, i.e., in herbaria, some bacterial symbionts retain their viability for decades (Cernava et al. 2016), whereas lichen myco- and photobionts die off within a few years of storage at room temperature (Honegger 2003). Thus, herbaria with specimens from remote areas might be a source of interesting bacterial associates of lichens, some of them with biologically interesting properties (Cernava et al. 2016). In nature, bacterial associates of lichen thalli survive drought stress unharmed (Cernava et al. 2018).

Within thalli, the species richness and cell density of lichen-associated bacteria increase from peripheral, young growing zones to older, non-growing areas. In the lobate *Xanthoparmelia*, the highest bacterial diversity was found in the centre (Mushegian et al. 2011), in the fruticose reindeer lichen *Cladonia arbuscula* or in the podetia of *Cladonia squamosa* in basal parts (Cardinale et al. 2008; Noh et al. 2020; Fig. 6.5g–i); some of the bacterial associates of old thallus areas are likely involved in biodegradative processes.

Vertical transmission of the microbiome (except the *Nostoc* cyanobiont of cephalodia) via symbiotic propagules occurs in the lung lichen (*Lobaria pulmonaria*; Aschenbrenner et al. 2014); with high probability isidia and thallus fragments of most other species also carry at least part of the microbiome at their surface, but whether soredia with very hydrophobic surfaces (Fig. 6.3e) carry bacteria remains to be seen. Lichen-inhabiting invertebrates have their own bacteriome on their surfaces (Chasiri et al. 2015).

Lichen-associated bacteria have attracted considerable interest as potential producers of novel secondary compounds with biotechnological potential, the focus being on actinobacteria (González et al. 2005; Parrot et al. 2015, 2016a, b; Suzuki et al. 2016).

6.5.2 Lichenicolous Fungi

Approximately 2320 spp. of lichenicolous asco- and basidiomycetes have been described (Fig. 6.6); 2000 spp. are obligately, 62 spp. facultatively lichenicolous and 257 spp. are lichenicolous lichens (Diederich et al. 2018), new families, new genera and species being continuously described from ecosystems which had not been previously investigated. Examples are representatives of *Pleostigmataceae* and *Melanina* spp. among the Chaetothyriomycetidae in crustose lichens from subalpine areas (Muggia et al. 2021), or *Crittendenia* spp. lichenicolous representatives of Pucciniomycotina (Basidiomycota; Millanes et al. 2021). A well-preserved lichenicolous *Lichenostigma* sp., (Arthoniomycetes, Ascomycota) was found on fossil *Ochrolechia* sp. in palaeogene amber (approx. 24 Ma old; Kaasalainen et al. 2019).

Some lichenicolous fungi have a minor impact on their host (e.g. mycocalliclean *Sphinctrina* spp. on *Pertusaria* spp., Fig. 6.6e), others have a devastating effect, killing the fungal and photoautotrophic partner (e.g. the corticialean basidiomycetes *Marchandiomyces aurantiacus* and *M. corallinus* on *Physcia* and *Parmelia* spp.; Fig. 6.6b). Only a few lichen spp. regenerate after an attack by the athelialean basidiomycete *Athelia arachnoidea* (Fig. 6.6a), whose asexual state is *Rhizoctonia carotae*, a pathogen of carrots (Adams and Kropp 1996), but the free space created by the killing effect is soon occupied by fast-growing crustose taxa such as *Biatora* spp. (Motiejūnaitė and Jucevičienė 2005).

Several lichenicolous fungi stimulate, probably via secretion of hormones, gall formations in their hosts (Hawksworth and Honegger 1994). Examples are the verrucarialean *Telogalla olivieri* on *Xanthoria parietina*, or the parmeliacean *Raesaenenia huuskonenii* on *Bryoria* spp. (Fig. 6.6h–i). The characteristic galls of members of the *Biatoropsis usnearum* complex (Tremellales, Basidiomycota; Fig. 6.6d; Millanes et al. 2016a) on *Usnea* spp. are basidiomata of the parasite. Even hyperparasitism was detected

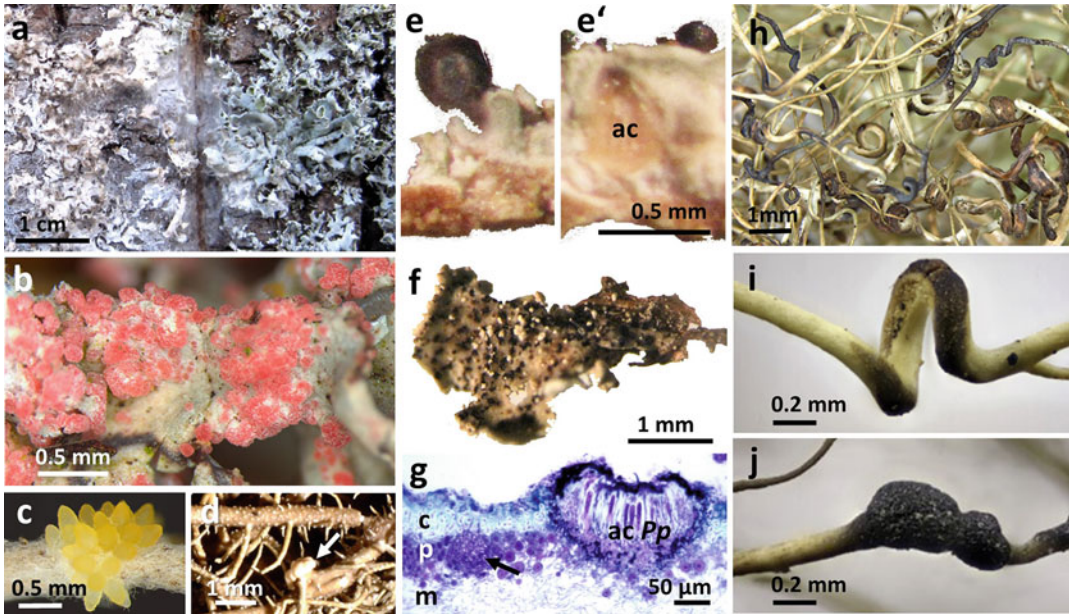


Fig. 6.6 Lichenicolous (parasitic) ascomycetes (**c, e, f, g, h, i**) and basidiomycetes (**a, b, d, j**). (**a**) *Athelia arachnoidea* (Atheliales, Agaricomycetes) killing *Physcia tenella*. (**b**) *Marchandiomyces corallinus* (Corticiales, Agaricomycetes) on *Physcia stellaris*; courtesy of Erich Zimmermann. (**c**) Ascomata of *Neobarya peltigerae* (Clavicipitaceae, Sordariomycetes) on rhizinae of *Peltigera* sp. From Zimmermann and Feusi (2018), courtesy of Erich Zimmermann. (**d**) Basidioma (arrow) of *Biatoropsis usnearum* (Tremellales, Tremellomycetes) on *Usnea ceratina*. (**e, e'**) Mazaediate ascomata of *Sphinctrina turbinata* (Mycocaliciaceae, Eurotiomycetes) on dissected *Pertusaria pertusa*; (ac) ascoma of *P. pertusa*. (**f, g**) thallus squamule of *Cladonia macrophylla* invaded by *Phaephyxis punctum* (Helotiales, Leotiomycetes), black dots in (**f**) are ascomata of the parasite, whitish dots are adhering soredia of the lichen.

(**g**) Stained semi-thin section of *C. macrophylla* with cortex (**c**), photobiont (**ph**) and medullary layer (**m**) of the lichen-forming ascomycete and ascoma of the parasite (**ac Pp**); arrows point to the primordium of an ascoma of the parasite with trichogynes protruding through the cortex of the lichen. From Honegger 2012. (**h–j**) Horsehair lichens (*Bryoria fuscescens* in **h**, *B. pikei* in **i–j**) invaded by curled gall-inducing *Raesaenenia huuskonenii* (syn. *Phacopsis* or *Protousnea huuskonenii*, respectively; Parmeliaceae, Lecanoromycetes). (**h**) Infected *Bryoria fuscescens*, from Zimmermann and Feusi (2020), courtesy of Erich Zimmermann. (**j**) basidioma of the hyperparasite *Tremella huuskonenii* (Tremellales, Tremellomycetes) developing on the gall of the lichenicolous *R. huuskonenii* on *B. pikei*. (**i, j**) From Lindgren et al. (2015), courtesy of Paul Diederich

(e.g. *Tremella huuskonenii*, parasite of *R. huuskonenii* on *Bryoria* sp., Fig. 6.6j; Lindgren et al. 2015).

Various investigators found basidiomycetous yeasts as symptomless endolichenic fungi on and in lichen thalli, belonging to the Tremellomycetes (Agaricomycotina), Cystobasidiomycetes or Agaricostilbomycetes (Pucciniomycotina; review: Diederich et al. 2018). Examples are *Fellomyces* spp. (Cuniculitremaataceae, Tremellales; Prillinger et al. 1997; Lopandic et al. 2005), the *Cyphobasidium usnicola*

complex and other *Cyphobasidium* spp. on various macrolichens (Cystobasidiales; Millanes et al. 2016b; Spribille et al. 2016), or *Lichenozyma pisutiana* in *Cladonia* spp. (Cystobasidiales; Černajová and Škaloud 2019). These basidiomycetous yeasts are widespread, but not ubiquitous in lichen thalli (Lendemer et al. 2019). Particularly interesting are tremellalean lichenicolous fungi which produce galls on their host lichen, but switch between a yeast and a hyphal stage, the former being located on and in the cortex of the lichen, as visualized with FISH (fluorescent in

situ hybridization techniques; Spribille et al. 2016). Examples are *Tremella lethariae* on *Letharia vulpina* (Tuovinen et al. 2019), *T. macrobasidiata* and *T. varia* on *Lecanora* spp. (Tuovinen et al. 2021).

Some lichenicolous fungi reduce the growth rate and the production of secondary metabolites of their host (e.g. *Plectocarpon* spp. on *Lobaria pulmonaria*; Asplund et al. 2018; Merinero and Gauslaa 2018), others degrade the secondary metabolites of their host (e.g. parietin of *Xanthoria parietina* by the capnodialean *Xanthoriicola physciae*; Edwards et al. 2017, or lecanoric acid by hypocrealean *Fusarium* spp. on *Lasallia* spp.; Lawrey et al. 1999), thus facilitating the attack of opportunistic fungi and/or enhancing the grazing pressure by lichenivorous invertebrates (Lawrey et al. 1999; Asplund et al. 2016). More and different secondary metabolites than in the lichen proper were found in *Cladonia foliacea* upon infection with the lichenicolous *Heterocephalacria bachmannii* (Filobasidiales, Tremellomycetes), the antioxidant potential of the thallus being enhanced (Khadhri et al. 2019).

6.5.3 Lichenicolous Lichens

Lichenicolous lichens (Fig. 6.7a–c) are a group of specialists whose ascospore-derived germ tubes start their development in the thallus of a host lichen, which they invade; some of them take over the photobiont host, others acquire a different green algal partner (see below). The parasitic lichen overgrows its host and differentiates its own thallus. The first known lichenicolous lichen, *Rhizocarpon lusitanicum*, parasite of *Pertusaria* spp., was described by Nylander in 1865 when lichen symbiosis was not yet defined. In their 2018 compilation, Diederich et al. listed 257 spp. of lichenicolous lichens and their hosts, representatives of 63 genera, 28 families, 16 orders and four classes of ascomycetes. The vast majority are Lecanoromycetes, the most species-rich genera being *Rhizocarpon* (33 spp.), *Acarospora* (27 spp.) and *Caloplaca* (26 spp.; Diederich et al. 2018).

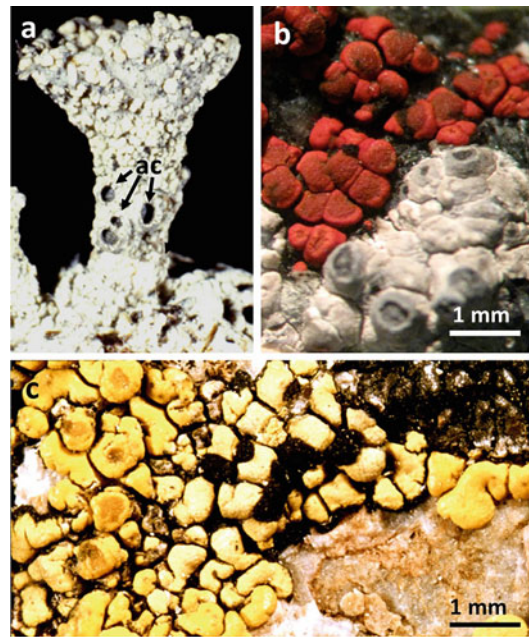


Fig. 6.7 Lichenicolous lichens. (a) *Diploschistes muscorum* (Ostropales) invading and overgrowing *Cladonia chlorophaea*. (ac) ascomata. (b) *Caloplaca anchon-phoeniceon* (Teloschistales) invading *Aspicilia calcarea*. (c) *Rhizocarpon effiguratum* (Rhizocarpaceae) invading *Acarospora oxytona*

The acquisition of the photobiont by the lichenicolous *Diploschistes muscorum* on *Cladonia* spp. was investigated using light microscopy techniques applied to symbiotic and cultured photobiont cells (Friedl 1987). In the first developmental stage on *Cladonia* sp., *D. muscorum* was shown to associate with *Asterochloris irregularis* (syn. *Trebouxia irregularis*), the unicellular green algal partner of the *Cladonia* host; subsequently algal switching occurred, *A. irregularis* being replaced by *Trebouxia showmanii* (Friedl 1987) and/or other *Trebouxia* spp. (Wedin et al. 2016). *Diploschistes* spp. associate with diverse photobiont species, as concluded from molecular investigations of *D. diacapsis* in Mediterranean soil crust communities, up to four different *Trebouxia* spp. having been found in one thallus (Moya et al. 2020).

6.5.4 Endolichenic Fungi (ELF)

Whereas the diversity of lichenicolous fungi has been intensely investigated from the nineteenth century onwards, the presence of numerous symptomless endolichenic fungi in lichen thalli was first detected towards the end of the twentieth century (Petrini et al. 1990). Today, more than 200 spp. of endolichenic fungi are known, predominantly ascomycetes, few basidio- and zygomycetes, 135 having been identified at species level; they were isolated from 114 lichen species, the majority being parmeliacean macrolichens (Chakarwanti et al. 2020).

Most ELF are saprobic generalists, but also several wood-decay asco- and basidiomycetes were found such as the xylarialean *Xylaria*, *Hypoxylon* and *Daldinia* spp., or the agaricales *Schizophyllum commune* and the russulales *Heterobasidion annosum* (Fig. 6.8). Lichen thalli as a refuge of wood-decay fungi: an unexpected result! Some ELF are plant pathogens, a few are also endophytes of plants (Arnold et al. 2009; U'Ren et al. 2010, 2012). The biology of endolichenic fungi is poorly investigated; they absorb polyols such as mycobiont-derived

mannitol from the apoplasmic continuum of the lichen thallus (Yoshino et al. 2020).

Upon isolation into sterile culture, ELF turned out to be a rich source of interesting bioactive secondary metabolites. More than 140 novel compounds have been identified, many of them with pharmaceutical potential such as antibiotic, antiviral, antifungal, anti-inflammatory, antiproliferative or antioxidant properties (reviews: Gao et al. 2016; Kellogg and Raja 2017; Tripathi and Joshi 2019; Agrawal et al. 2020; Wethalawe et al. 2021). Considering that only approximately 5% of lichen species have so far been investigated for ELF, there are lots of interesting work ahead.

6.5.5 The Virome of Lichens

Upon isolation into sterile culture, the first mycoviruses in the mycobiome of lichens were detected in the so-called dust lichens, i.e., the leprose thalli of *Lepraria incana* (Stereocaulaceae, Lecanoromycetes; LiCV1) and *Chrysothrix chlorina* (Chrysotrichaceae, Arthoniomycetes; CcCV1). LiCV1 and CcCV1 are classified in the genus *Alphachrysovirus* (family Chrysoviridae; Petrzik et al. 2019) whose host range comprises fungi, plants and possibly insects (Kotta-Loizou et al. 2020). Upon closer examination, i.e., with fluorescent *in situ* hybridization techniques, CcCV1 was located not in the lichen mycobiont proper, but in an associated *Penicillium citreosulfuratum* (Eurotiomycetes; Petrzik et al. 2019).

Lichen photobionts were shown to harbour plant viruses such as the cauliflower mosaic virus (Petrzik et al. 2013). With immunogold labelling techniques applied to ultrathin sections, viruses contained in more than 70 years old sterile cultures of *Trebouxia aggregata*, photobiont of *Xanthoria parietina*, were shown to be located in the algal cytoplasm, not in the chloroplast; upon mechanical transmission to plant host cells these phycobiont-derived viruses were infective (Petrzik et al. 2015).

In a study on virus diversity in the metagenome of the saxicolous *Umbilicaria phaea*, five novel viruses were detected, one of

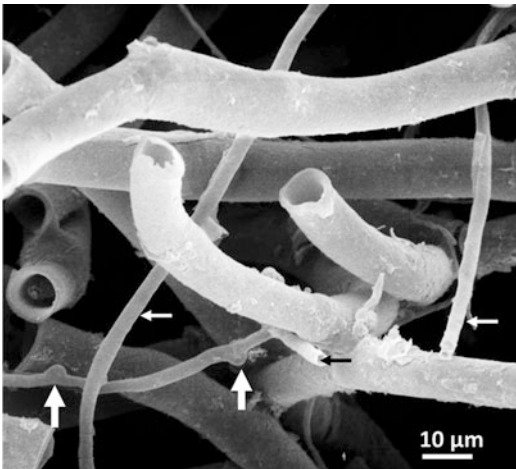


Fig. 6.8 Comparatively thin hyphae of symptomless endolichenic fungi (arrows) growing between the medullary hyphae of *Peltigera leucophlebia*. Broad arrows point to clamp connections of an endolichenic Agaricomycetes. After Honegger (2012)

them, a Caulimovirus, being associated with the *Trebouxia* photobiont and the four others, belonging to the Myoviridae, Podoviridae and Siphoviridae, with bacterial associates of the lichen, but so far, no mycoviruses have been found (Merges et al. 2021).

RNA virus diversity was investigated in an extract of a microcosm, predominantly consisting of *Cladonia* spp. and other Lecanoromycetes and their trebouxiophycean photobionts, overgrowing bryophytes, non-lichenized ascomycetes, cyanobacteria, free-living green algae, fern (spores?) and minute animals living therein, as seen in SSU rRNA sequences (Urayama et al. 2020). A total of 65 operational taxonomic units (OTUs) were achieved, 17 belonging to Partitiviridae (five to the genus *Alphapartivirus*, one to *Betapartivirus*, the host range of both genera comprising fungi and plants; Vainio et al. 2018), plus representatives of 10 additional viral families and several unclassified dsRNA and ssRNA viruses (Urayama et al. 2020).

The impact of viral infections on the biology and whether horizontal virus transfers occur between the partners of lichen symbiosis and their allies remain to be investigated.

6.6 Fossil Lichens and Their Microbiome

6.6.1 Fossil vs. Extant Lichens

Fungi colonized terrestrial environments in the Proterozoic, presumably associating with the even more ancient cyanobacteria, the latter having been present already in the Archean (approx. 2400 Ma), but colonized terrestrial habitats from the Proterozoic onwards, as concluded from fossil records and molecular clock analyses (Strother and Wellman 2016; Lutzoni et al. 2018; Demoulin et al. 2019; Garcia-Pichel et al. 2019). Trebouxiophyceae, unicellular green algae, and Trentepohliales, filamentous green algae, were present from the Proterozoic onwards, some extant taxa of both groups being the main photobionts of extant LFF (Lutzoni et al. 2018; del Cortona et al. 2020). Thus, lichenization is

assumed to be an ancient fungal lifestyle, but fossil records are very scarce and partly difficult to interpret (Fig. 6.9).

According to molecular phylogenetic datasets, the clades of ascomycetes which gave rise to extant lichens did not radiate before the Silurian (approx. 450 Ma; Lutzoni et al. 2018) or even the Mesozoic (approx. 250 Ma; Nelsen et al. 2019). According to the latter authors ascolichens, as we know them today, are younger than previously assumed, did not predate the evolution of vascular plants and were not among the (extinct) early fungal colonizers of terrestrial habitats. Nevertheless, the lichen lifestyle was most likely established in the common and widespread nematophytes and *Prototaxites* spp. (review: Selosse and Strullu-Derrien 2015). The manifold problems related to the interpretation of fungal fossils are summarized by Berbee et al. (2020).

6.6.2 Palaeozoic Fossils

An approx. 600 Ma old lichen-like association was preserved in marine phosphorite of the Doushantuo Formation in South China (Yuan et al. 2005). Mats of cyanobacterial or coccoidal algal cells were invaded by extremely thin filamentous hyphae with diameters below 1 micron, a characteristic feature of actinobacteria, not fungi (Honegger 2018); thus, the Doushantuo fossils are not lichens.

Nematophytes, an extinct phylum of presumably lichenized fungi with no modern analogues and thus not represented in molecular phylogenetic trees of living species, were common and widespread constituents of terrestrial cryptogamic ground covers from the late Silurian to the late Devonian. They comprise the families Nematothallaceae (genera *Nematothallus*, *Cosmochlaina*, *Tristratothallus*; Edwards et al. 2013, 2018) and Nematophytaceae (genera *Nematoplexus*, *Nematasketum* and the enigmatic *Prototaxites*; Edwards and Axe 2012). After long debates about their taxonomic affiliation nematophytes are currently interpreted as presumably lichenized thalloid fungal structures (Edwards et al. 2013, 2018). Cross-fractures of

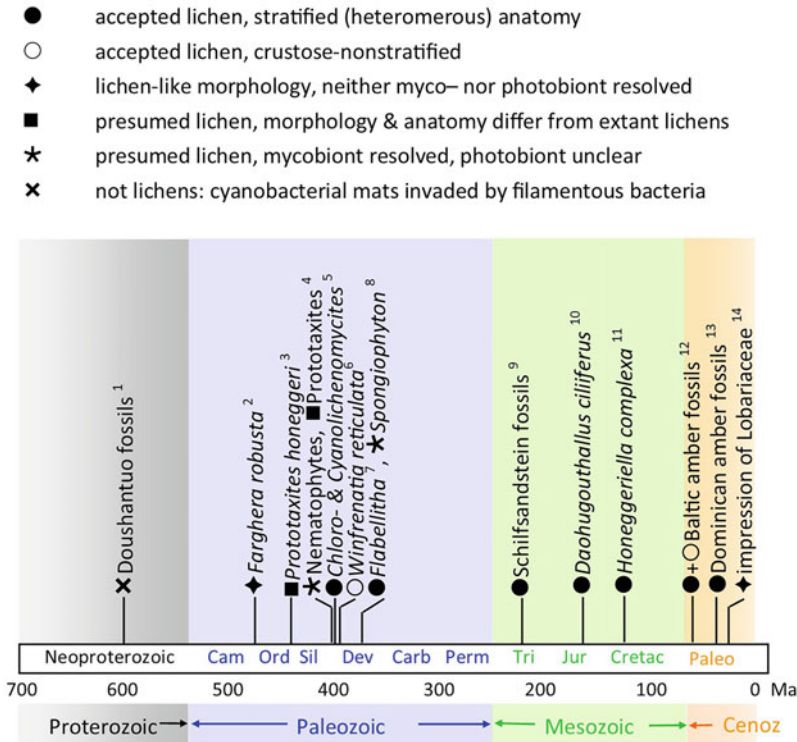


Fig. 6.9 Fossil lichens, an overview. 1. Yuan et al. (2005); 2. Retallack (2009); 3. Retallack (2020); 4. Edwards et al. (2013, 2018); Honegger et al. (2018); 5. Honegger et al. (2013a); 6. Taylor et al. (1995, 1997), Karatygin et al. (2009); 7. Jurina and Krassilov (2002); 8. Stein et al. (1993), Jahren et al. (2003); 9. Ziegler (2001); 10. Wang et al. (2010), Fang et al. (2020); 11. Matsunaga et al. (2013); 12. Mägdefrau (1957), Rikkinen and Poinar (2002), Rikkinen (2003), Hartl et al. (2015), Kaasalainen et al. (2015, 2017, 2020), Rikkinen et al. (2018);

13. Poinar Jr. et al. (2000), Rikkinen and Poinar (2008); 14. MacGinitie (1937), Peterson (2000). Chronostratigraphy (International Commission on Stratigraphy (ICS) chart 2019; Hounslow 2020): Periods in Ma. Neoproterozoic (1000-541); Cam: Cambrian (541-484); Ord: Ordovician (485-443); Sil: Silurian (443-419); Dev: Devonian (419-358); Carb: Carboniferous (358-298); Perm: Permian (298-251); Tri: Triassic (251-201); Jur: Jurassic (201-145); Cretac: Cretaceous (145-66); Paleo: Paleogene (66-23). After Honegger (2018), modified

some nematophyte fossils reveal the same stratification as found in lichens, with a conglutinate peripheral cortex and a medullary layer built up by interwoven hyphae, but photobiont cells are missing; they might have been lost during fossilization. In charcoalifying experiments with extant cyanobacterial lichens, the fungal partner was well preserved, and so were the thick mucilaginous sheaths of the *Nostoc* photobiont, but most of the cyanobacterial cells proper were lost (Honegger et al. 2013a).

Prototaxites spp., enigmatic fossils with erect axes, built up by hyphae of various diameters, ranging from pencil size dimensions as in the

mid-Ordovician (Darrivilian, approx. 460 Ma old) *P. honeggeri* (Retallack 2020) to more than 8 metres long stems, as in the mid-Devonian (early Givetian, approx. 385 Ma old) *P. loganii*, were interpreted as presumably lichenized fungi, coccoid photobiont cells having been resolved at the surface of the axes of both species (Retallack and Landing 2014; Retallack 2020). However, it remains unclear how the few coccoid algal cells should have provided enough carbohydrate to nourish these large fungal structures; nematophytes were assumed to be associated with *Prototaxites* (Selosse and Strullu-Derrien 2015). Delicate fruiting structures at the surface

of the axes were seldom retained; luckily the hymenial layer was preserved in a series of petrographic thin sections of *P. taiti* of the Kidston and Lang collection. The ascomata of *P. taiti* combine features of extant ascomycetes, i.e., Taphrinomycotina (Neoelectromycetes lacking croziers) and Pezizomycotina (epihymenial layer secreted by paraphyses), but *Prototaxites* is not an ancestor of the latter (Honegger et al. 2018).

The mid-Devonian *Spongiophyton minutissimum* is a presumed lichen, built up by a conglutinate, tissue-like, porate fungal cortex around a central cavity; a photobiont was not resolved (Taylor et al. 2004).

Winfrenatia reticulata is a permineralized fossil lichen, 10 cm long, 2 mm thick, from the Lower Devonian Rhynie chert (approx. 400 Ma old; Taylor et al. 1995, 1997). A presumed mucormycete forms a basal mat and superimposed ridges built up by parallel hyphae which are in contact with coccoid cyanobacterial cells interspersed with a filamentous cyanobacterium (Karatygin et al. 2009). However, *Winfrenatia* might be a fragment of a larger thalloid organism such as a nematophyte (Honegger, unpubl.).

The oldest lichenized ascomycetes with dorsiventrally organized, internally stratified thallus so far found are charcoalified fragments of *Cyanolichenomycites devonicus*, a cyanobacterial lichen with *Nostoc*-like photobiont (Fig. 6.10a, b), and *Chlorolichenomycites salopensis*, a presumed green algal lichen whose globular photobiont cells were retained as framboidal pyrite (Fig. 6.10c–e; Honegger et al. 2013a). Both fossils were extracted from a Lower Devonian siltstone from the Welsh Borderland (approx. 415 Ma old). Despite their striking structural similarity with extant Lecanoromycetes lichens, the taxonomic affiliation of these fossils remains unclear. They might either belong to the nematophytes or represent the earliest known members of extant lichenized ascomycetes (Hawksworth 2012; Lutzoni et al. 2018); in the latter case, some molecular clock estimates would require recalibration.

6.6.3 Mesozoic Fossils

Daohugouthallus ciliiferus, a well-preserved, band-shaped lichen resembling extant Parmeliaceae such as *Pseudevernia furfuracea*, was found in mid Jurassic sediments (approx. 165 Ma old) in north-eastern China (Inner Mongolia; Wang et al. 2010; Fang et al. 2020).

Very well preserved is the Mesozoic *Honeggeriella complexa*, a dorsiventrally organized, foliose lichen from the Early Cretaceous of Vancouver Island (Valanginian-Hauterivian boundary, ca. 133 Ma old) with distinct green algal layer and haustorial complexes at the mycobiont–photobiont interface comparable to those found in extant taxa (Matsunaga et al. 2013).

6.6.4 Cenozoic Fossils

Large numbers of well-preserved lichens were found in Cenozoic Baltic and Bitterfeld (approx. 50–35 Ma old) and in Dominican amber (approx. 16 Ma old). Excellent external and internal structural preservation allows to identify taxa similar or closely related to extant species (Hartl et al. 2015), most of them having been epiphytes on the resin-producing trees (e.g. *Pinus* spp. in N-Europe). Among the fruticose-pendulous lichens in Baltic amber are alectorioid taxa and *Usnea* spp. (Kaasalainen et al. 2015, 2020). Among the foliose lichens is *Anzia electra*, common and widespread in Baltic and Bitterfeld amber, but today extinct in Europe (Rikkinen and Poinar 2002; Schmidt et al. 2013). Very well preserved *Parmelia ambra* and *P. isidiiveteris* (Poinar Jr. et al. 2000) and *Phyllopsora dominicanus* (Rikkinen and Poinar 2008) were found in Dominican amber. Among the crustose lichens in Baltic amber are calicioid taxa (Rikkinen 2003; Rikkinen et al. 2018) and *Ochrolechia* spp. (Kaasalainen et al. 2019).

There are many more types of amber worldwide whose fossils await thorough investigation, the oldest ones dating back to the Carboniferous

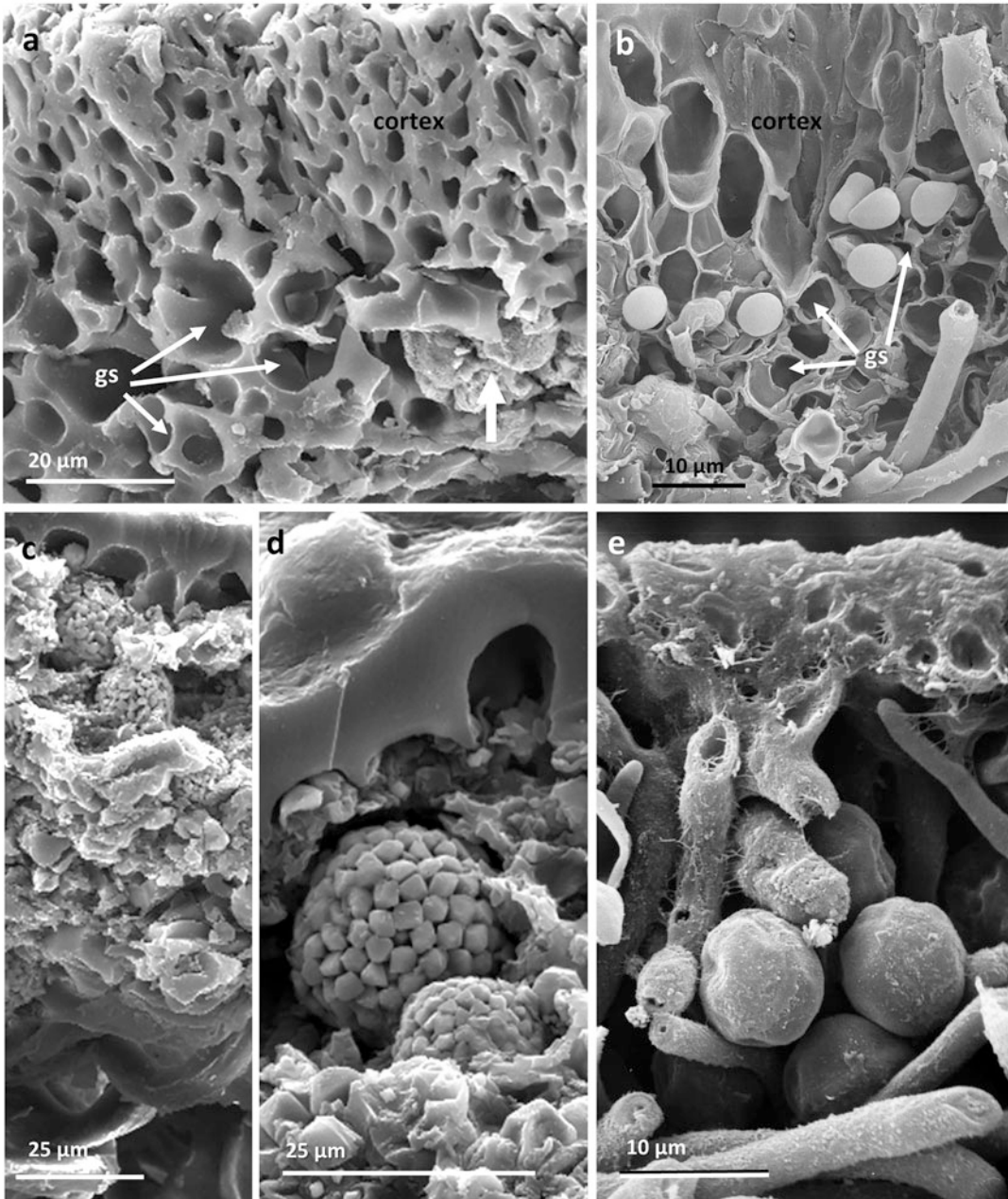


Fig. 6.10 Fossil lichens from the Lower Devonian (ca. 415 Myr old) with dorsiventrally organized, stratified thallus (**a**, **c–d**) in comparison with extant Lecanoromycetes (**b**, **e**). (**a**) *Cyanolichenomycites devonicus* with conglutinate cortex and a *Nostoc*-like cyanobiont in the photobiont layer; in contrast to the well-preserved gelatinous sheaths (*gs*) only few

cyanobacterial cells (bold arrow) are retained. (**b**) *Peltigera praetextata* (Peltigerales) with *Nostoc* sp. as cyanobiont. (**c–d**) *Chlorolichenomycites salopensis* with thin peripheral cortex and globose, presumed green algal photobiont, the latter being preserved as framboidal pyrite. (**e**) *Pleurosticta acetabulum* (Lecanorales); chlorobiont: *Trebouxia* sp. After Honegger et al. (2013a), modified

period (approx. 320 Ma old). DNA has been successfully extracted, amplified and sequenced from invertebrate and plant fossils in Dominican and Lebanese amber, the oldest ones being approx. 120–135 Ma old (Poinar 1994).

6.6.5 The Microbiome of Fossil Lichens

In the dorsiventrally organized thallus of the Lower Devonian *Chlorolichenomycites salopensis* were bacterial colonies growing on the surface of the cortex and actinobacteria and lichenicolous fungi in the thalline interior, comparable to the situation in extant lichens (Fig. 6.5a, b; Honegger et al. 2013b).

Fructifications of *Lichenostigma* sp. (Lichenostigmatales, Arthoniomycetes) were found on *Ochrolechia* sp. in palaeozoic amber (Kaasalainen et al. 2019), *Lichenostigma* spp. being common and widespread lichenicolous fungi of extant lichens (Hafellner and Calatayud 1999; Diederich et al. 2018). A wide range of filamentous fungi were found on decaying crustose lichens embedded in amber, such as well-preserved toruloid taxa, conidiomata of dematiaceous hyphomycetes resembling extant genera such as *Sporidesmium*, *Taeniolella* and *Taeniolina* (Kettunen et al. 2016, 2018).

6.7 Lichen–Animal Relations

6.7.1 The Micro- and Mesofauna of Lichen Thalli

Many interactions of lichens with protozoans, invertebrates and vertebrates have been reported. Among lichen–invertebrate interactions are rotifera, amoebae (Figs. 6.1a, b and 6.11a), ciliates, tardigrades (Fig. 6.11b), mites (Fig. 6.12a, b), spiders, nematodes, collembola and insects (springtails, barklice, lepidopterans, grasshoppers, etc.) which live between and below, some even within lichen thalli (reviews: Gerson 1973; Gerson and Seaward 1977; Sharnoff 1998; Segerer 2009). Epiphytic lichen

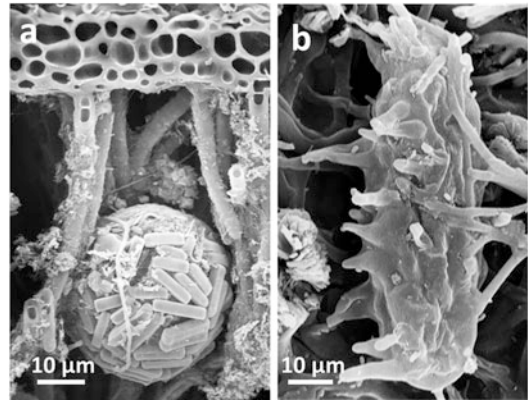


Fig. 6.11 Representatives of the microfauna of lichen thalli. (a) Testate amoeba with agglutinate shell, predominantly composed of diatoms, in the tomentum of *Sticta fuliginosa*, collected in La Réunion. (b) Tardigrade on the surface of a campylidium (conidioma) of the foliicolous *Lasioloma arachnoideum* collected in Tanzania by Edit Farkaš

biomass on oak correlated significantly with the abundance of arthropods, tardigrades and rotifera in central Maine (Stubbs 1989). The microfauna of one lichen species (*Xanthoria parietina*), collected in Lithuania, comprised 16 protozoan taxa, three tardigrades, two Nematelminthes and three rotifera (Šatkauskienė 2012). In 26 terricolous lichen samples from Svalbard and Spitzbergen, 23 species of tardigrades were identified (Zawierucha et al. 2017). On *Cladonia rei* growing on heavy metal-contaminated post-smelting dumps in Poland, 50 species of oribatid mites were recorded (Skubała et al. 2014).

Some of these allies of lichen thalli find shelter, others are lichenivorous (see below) or bacterivorous (Liu et al. 2011). Even pest insects of fruit and nut trees find shelter under epiphytic lichens; therefore, agricultural experts recommend fruit growers to control or even prevent lichen growth either mechanically or chemically in their orchards.

6.7.2 Lichenivory: Invertebrates

Lichens have always been part of terrestrial food webs. The Silurian-Devonian nematophytes, presumably lichenized fungi, were grazed by

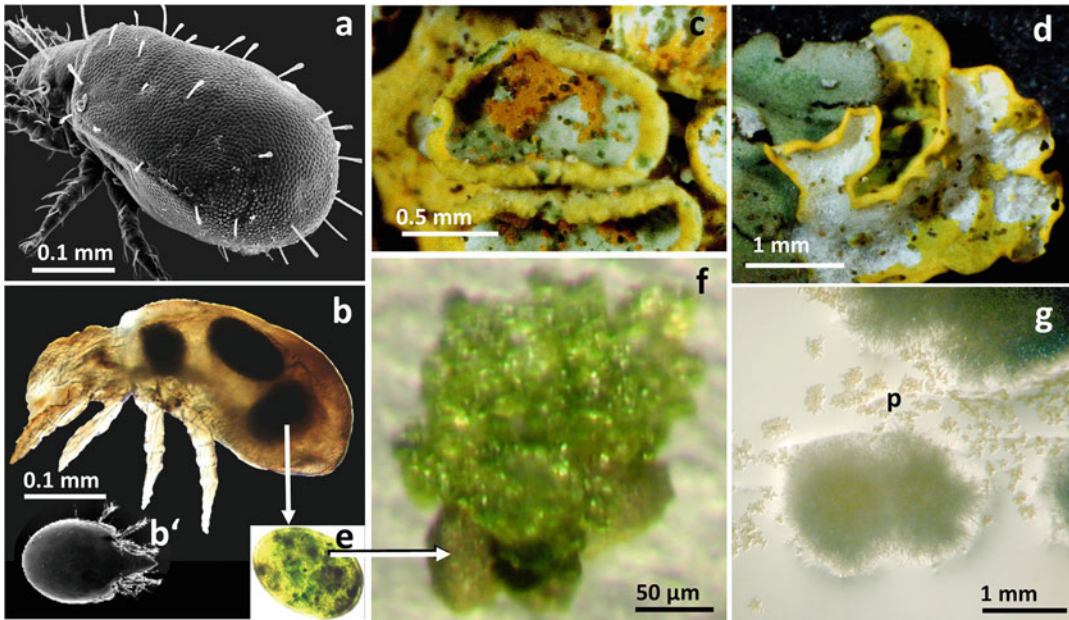


Fig. 6.12 Lichenivory and endozoochory in oribatid mites. In captivity *Trhyphochthonius tectorum* (a) and *Trichoribates trimaculatus* (b, b') were feeding on the hymenium (c) or the upper cortex and algal layer (d), respectively, of *Xanthoria parietina*; adjacent *Phycia orbicularis* was not grazed. Faecal pellets contained viable fungal and algal cells (*Trebouxia arboricola*), the latter

growing out upon incubation on Parafilm (f) in a wet chamber; mycelia grew out on agarized non-nutrient mineral medium (g). Yellow crystals of parietin (p) are formed on and around the mycelium. The identity of the fungal and algal isolates was investigated with molecular tools. After Meier et al. (2002)

arthropods, presumably millipedes, as seen in grazing marks on the thallus surface with adhering coprolites (fossil faecal pellets), some of which contain hyphae or even small fragmentary remains of the thalli (Edwards et al. 1995, 2020). Grazing marks, presumably from arthropods, and faecal pellets were found on fossil foliose lichens in Palaeogene Bitterfeld amber (Schmidt et al. 2022).

There is a large body of literature on lichenivorous invertebrates (Gerson and Seaward 1977; Rambold 1985; Sharnoff 1998; Segerer 2009). In feeding experiments, Arthropoda such as mites (Acari), springtails (Collembola), barklice (Psocoptera) or beetles (Coleoptera) and Gastropoda such as door and pillar snails (Clausiliidae, Cochliopsideae) were all shown to graze the upper cortex and algal layer of *Parmelia* and *Phycia* spp. down to the medullary layer (Schmidt et al. 2022). Lichens were assumed to

be protected from lichenivory by their content in secondary metabolites (Stahl 1904). However, many invertebrates consume even those parts of lichen thalli which contain large amounts of secondary products unharmed, crystals of these fungal metabolites passing the digestive tract unchanged (Zopf 1907; Hesbacher et al. 1995; Asplund and Wardle 2013; Gadea et al. 2019). Lichenivorous mites are selective in their food choice, some lichen species being avoided (Reutimann and Scheidegger 1987; Fröberg et al. 2003). In molluscs (slugs and snails), a preference was noted for thallus areas or even species with low contents in secondary metabolites (Benesperi and Tretiach 2004; Asplund 2011). *Arion fuscus* preferentially feeds on the large internal cephalodia of *Nephroma arcticum*, probably because these lack secondary metabolites (Asplund 2010; Asplund and Gauslaa 2010). Feeding experiments with thalli whose

secondary products had been removed by rinsing in acetone were preferentially grazed (Gauslaa 2005; Boch et al. 2011, 2015). Gall-producing lichenicolous fungi (*Plectocarpon* spp.) reduce the growth rate and the production of secondary metabolites in *Lobaria pulmonaria* (Asplund et al. 2016; Merinero and Gauslaa 2018), thus making the infected thallus areas more palatable and increasing the grazing pressure by snails (Asplund et al. 2016).

6.7.3 Lichenivory: Vertebrates

No vertebrate lives exclusively on a lichen diet, but in many regions, lichens are a substantial part of total food intake when other, preferred food such as buds, leaves, tubers and fruits are seasonally unavailable. Mat-forming terrestrial lichens such as *Cladonia* spp., and epiphytic species are a substantial part of the diet of reindeers and caribou (*Rangifer tarandus*) in Arctic tundras (Heggberget et al. 2002), but also of other ungulates such as deer, chamois or alpine *Ibex* in montane and alpine ecosystems of the Northern and Southern Hemisphere (Parrini et al. 2009; Yockney and Hickling 2000), of camelids (guanacos, llamas) in South America (Follmann 1964) and of numerous smaller mammals such as marmots, flying squirrels (Rosentreter et al. 1997), voles, etc. (reviews: Richardson and Young 1977; Sharnoff and Rosentreter 1998; Segerer 2009). Trampling damage occurs in reindeer lichen stands in subarctic and arctic tundras when large herds are feeding in dry weather; reindeer lichens (*Cladonia* spp.), like all other lichens, are elastic and flexible when wet, but very brittle in the dry state, thus being fragmented by the hooves of ungulates, recovery taking more than 30 years (Pegau 1970; den Herder et al. 2003; Théau et al. 2005; Heggnes et al. 2017, 2020).

However, trampling damage and overgrazing are not the only reasons for the decline of lichen heaths in Arctic ecosystems. In response to global warming, the Arctic is greening, deciduous shrubs and graminoids increasingly outcompete the terricolous lichen communities, as observed *in*

situ and with remote sensing technologies over time (Myers-Smith et al. 2011, 2019; Fraser et al. 2014; Aartsma et al. 2020; Berner et al. 2020). Increasing summertime temperatures are also causing the decline of cyanobacterial and other lichens in soil crust communities on the Colorado Plateau, where neither grazing nor anthropogenic disturbances are evident (Finger-Higgins et al. 2022).

Large quantities, i.e., 30–75% of total food intake of beard lichens, especially *Usnea longissima* and *Bryoria* spp., are consumed by colobine primates (snub-nosed monkeys; Fig. 6.13) of the genus *Rhinopithecus* (*R. bieti*, *R. roxellana*, *R. brelichii*) in Western China and adjacent Tibetan mountain areas (Xiang et al. 2007; Grueter et al. 2009, 2012; Li and Ang 2009; Kirkpatrick and Grueter 2010; Liu et al. 2013; Bissell 2014; Xiang 2014). The rare and endangered lowland *R. strykeri* was shown to eat 15 lichen spp. in captivity, but these amounted to less than 3% of his diet (Yang et al. 2019). Barbary macaques (*Macaca sylvanus*) in high-altitude fir forests in the Ghomaran Rif and other mountain areas in Morocco eat lichens only in harsh winters when no other food is available (Mehlman 1988).

Lichens are rich in easily digestible carbohydrates such as β -glucans in the fungal cell walls such as lichenin (Honegger & Haisch, 2001) but have only low protein content. Reindeer and caribou seasonally feed on mushrooms (Inga 2007), whereas colobines consume mushrooms, invertebrates (Xiang et al. 2007; Yang et al. 2016) and vertebrates such as flying squirrels or bird's eggs (Grueter et al. 2009), and even infanticide followed by cannibalism was observed (Xiang and Grueter 2007).

6.7.4 Endozoochory

Faecal pellets of lichenivorous invertebrates are probably common and widespread symbiotic propagules, but rarely described and experimentally investigated. Jahns (1987) reported on a novel type of symbiotic propagule in *Solorina crocea* but did not realize that these were

Fig. 6.13 Lichenivory in vertebrates. Yunnan black snub-nosed monkey (*Rhinopithecus bieti*) feeding on *Usnea longissima* and other beard lichens. Courtesy of Fabio Nodari



germinating faecal pellets of lichenivorous snails. In light microscopy studies, numerous investigators observed intact fungal and/or algal cells or thallus fragments in the intestines or faecal pellets of lichenivorous invertebrates, e.g., in oribatid mites (Acari; Lawrey 1980; Meier et al. 2002), springtails (Collembola; Lawrey 1980), butterfly larvae (Lepidoptera; Rambold 1985; Brodo et al. 2021), termites (Termitidae; Barbosa-Silva and Vasconcellos 2019; Barbosa-Silva et al. 2019b), and molluscs (snails and slugs, Gastropoda; Baur et al. 2000; Fröberg et al. 2001; Boch et al. 2011, 2015).

However, in only a few lichen–invertebrate interactions was the viability of the cells contained in faecal pellets tested with culturing experiments. Gut transmission of viable mycobiont and photobiont cells was found in oribatid mites which had been feeding on *Xanthoria parietina* (Fig. 6.12a–g); the identity of both partners in these cultures was identified

with molecular tools (Meier et al. 2002). *Physcia adscendens* and *Lobaria pulmonaria* were fed to nine gastropod species and the regeneration rate out of their faecal pellets tested. To a varying percentage, *P. adscendens* grew out of the faeces of all nine gastropod species (9/9), *L. pulmonaria* out of eight (8/9; Boch et al. 2011, 2015). No germination was observed in faecal pellets of lichenivorous snails and barklice which had been feeding on foliicolous lichens in a tropical rainforest (Lücking and Bernecker-Lücking 2000).

Various investigators report on partly severe grazing damage in saxicolous and epiphytic lichen communities (e.g. Baur et al. 1995, 2000; Gauslaa et al. 2006; Skinner 2021), but considering the high regeneration rates of lichens out of detached thallus fragments and faecal pellets of lichenivorous invertebrates, there is also a potential for rejuvenation which deserves investigation.

6.7.5 Epizoochory

Epizoochory is probably a very common and widespread mode of dispersal of symbiotic propagules, thallus fragments or faecal pellets of lichenivorous invertebrates, but only few investigations have been published. Only few viable cells of the mycobiont and photobiont are required for regenerating a new thallus. Three types of epizoochory can be distinguished:

1. Lichens growing on animals (invertebrates and vertebrates). Examples are (a) limpets (*Patella* spp., Mollusca) and barnacles (Cirripedia) in the littoral fringe whose calcareous shell is inhabited by *Pyrenocollema halodytes* (syn. *Arthroprenia halodytes*, *Collempsidium h.*) and its cyanobacterial photobiont (*Hyella caespitosa*; see Fig. 15.1a in Honegger 2012). (b) foliose lichens growing together with fungi, algae and liverworts on the back of large weevils of the genus *Gymnopholus* in New Guinea (Gressitt et al. 1965; Gressitt 1966), which are getting several years old, as concluded from the lichen growth on their back (Gressitt 1970, 1977). This epizoochory community is inhabited by mites, rotifers and nematodes; even a new family, genus and species of oribatid mites (*Symbioribatidae*, *Symbioribates papuensis*) were discovered which live among the cryptogams on the weevils' back (Aoki 1966). Liverworts, lichens and fungi were also found growing on Costa Rican Shield Mantis (*Choeradodis* spp., Mantodea; Lücking et al. 2010). (c) lichens growing on the shell of some, but by far not all Giant Tortoises (*Geochelone elephantopus*) in Galapagos (Hendrickson and Weber 1964).
2. Lichens being actively sampled for nesting or camouflage. Vertebrates: (a) Many birds such as hummingbirds, chaffinks, etc., use lichens for camouflage of their nest, which then seem to be part of the branch on which it is positioned; ideally these lichens continue to grow on the surface of the nest (Graves and Dal Forno 2018). On branches without lichen cover, fragments of bright-grey lichens on the surface of birds nests reflect light, concealment by light reflection being an important mode of camouflage (Hansell 1996). (b) Flying squirrels (*Glaucomys sabrinus*) use lichens as nesting material and food, soft *Bryoria* spp., having low contents of secondary metabolites, are preferentially collected (Rosentreter and Eslick 1993; Hayward and Rosentreter 1994). Invertebrates: (a) Larvae of bagworms (Psychidae, Lepidoptera) mount tiny fragments of the lichens on which they feed to their silk bag as a very efficient camouflage (McDonogh 1939; see Fig. 16.16a, b in Honegger 2009). (b) Barklice cover the body of their nymph with minute fragments of lichens, algae and sand granules (Henderson and Hackett 1986), and so do the larvae of the green lacewing (*Nodita pavida*; syn.), which become invisible under their load of tiny lichen fragments (Slocum and Lawrey 1976). (c) Several species of lichenivorous, terrestrial snails of the genus *Napaeus* (Gastropoda, Pulmonata) actively paste fragments of lichens to their shell (Allgaier 2007; Holyoak et al. 2011).
3. Passive sampling. Soredia, isidia and other symbiotic propagules, tiny thallus fragments or faecal pellets adhere to animal or human vectors and thus get dispersed. Examples are (a) mites carrying soredia (Stubbs 1995). (b) lichenivorous termites most likely carry fragments of lichens to their nest where a species-rich lichen community develops (Aptroot and Cáceres 2014; Barbosa-Silva et al. 2019a). (c) Woodpeckers are neither lichenivorous nor do they collect lichens for camouflage or nest building, but were found to carry vegetative propagules of lichens on their feet, chest and tail feathers in samples in a Finnish Natural History Museum (Johansson et al. 2021). (d) humans carry propagules or fragments of lichens on their clothes, as first described in cases of woodcutters disease, an allergic reaction to usnic acid containing lichens, in housewives in contact with their husbands clothes (Mitchell and Champion 1965; Aalto-Korte et al. 2005). The load of

plant seeds, moss and lichen propagules on clothes of visitors of the Antarctic was thoroughly investigated, largest amounts having been found on socks of field working scientists (Huiskes et al. 2014). However, most of these lichen propagules on human clothes likely end up in the washing machine rather than invading Antarctic ecosystems.

Long-distance anthropogenic dispersal of epiphytic lichens on economic or ornamental plants is probably quite common (Bailey 1976). An example is *Xanthoria parietina*, which was not native to Australia, but is now growing around wineries in the Barossa Valley and elsewhere. In comparative RAPD-analyses of sterile cultured isolates of the mycobiont, some of the isolates from Australia and New Zealand clustered with those from southern France and Spain (Honegger et al. 2004a, b). It could be that *X. parietina* was brought to these areas with plants or cuttings of grape wine (*Vitis vinifera*). Similarly, Brodo et al. (2021) concluded that *X. parietina* was anthropogenically transported from coastal to inland areas in Canada, presumably with trees from nurseries.

Markia, etc.; Braun 2011; Cadena-Castañeda 2011, 2013; Fig. 6.14a); one of them, *Anapolisia maculata*, even mimics foliicolous lichens in a tropical rainforest (Fig. 6.14b; Lücking and Cáceres 2002). (3) stick insects (Phasmatidae, syn. Phasmidae, such as *Extatosoma tiaratum*), or (4) spiders such as the North American Giant Lichen Orb Weaver (*Araneus bicentenarius*; Fig. 6.14d).

Among vertebrates, many frogs mimic lichens, such as the N-American *Dryophytes versicolor* (syn. *Hyla versicolor*), the Brazilian *Bokermannohyla pseudopseudis* (Leite et al. 2012) or the Australian tree frog *Litoria genimaculata* (Vanderduys 2012); the colouration may vary depending on the habitat. Follicolous lichen communities are mimicked by tree frogs in Tanzanian (*Leptopelis ulugurensis*; Farkas and Pocs 1989) and S-American rainforests (*Boana rufitela*, syn. *Hyla rufitela*; Lücking and Cáceres 2002). Lichenomimesis occurs also in reptiles such as *Rhampholeon spinosus* (Chamaeleonidae) or *Uroplatus sikorae* and other *Uroplatus* spp. (Gekkonidae).

6.8 Lichenomimesis

6.8.1 Lichenomimesis in Animals

Large numbers of invertebrates mimic lichens and are thus not easily detected by potential predators (Figs. 6.14a–e). The earliest report of lichenomimesis in insects is a moth lacewing, *Lichenipolystoechotes angustimaculatus* (Neuroptera, Ithonidae), co-occurring with the mesozoic *Daohugouthallus ciliiferus*, which beautifully mimicked the pattern of the lichen on its wings (Fang et al. 2020). Extant examples are (1) lichen moths (Arctiinae, Lepidoptera) in their caterpillar (e.g. *Catocala ilia*; Fig. 6.14c) and/or adult stage such as *Cleorodes lichenaria*, the Brussels lace moth, whose lichenivorous caterpillar and moth stage mimic epiphytic lichens; (2) various species of bush crickets (Tettigoniidae, also termed katydids, in the genera *Lichenomorphus*, *Lichenodracula*,

6.8.2 Lichenomimesis in Members of the Araceae (Flowering Plants)

A unique type of lichenomimesis occurs in petioles (leaf stalks) of some members of the *Arum* family (Araceae, monocotyledonous flowering plants). Representatives of several genera have spots on their petioles which resemble lichens (Fig. 6.15a–f); particularly interesting are *Amorphophallus* spp. (Barthlott 1995; Hejnowicz and Barthlott 2005; Claudel et al. 2019), among others *A. gigas*, the Giant Arum, which forms the largest inflorescence in the plant kingdom. One giant leaf per growing season grows out of the large tuber of these Araceae; it is fleshy and thus the vulnerable petiole resembles the stem of a lichen-covered tree, various types of crustose lichens being mimicked (Figs. 6.15a–f). This optical signal is obviously perceived by potential herbivores which assume these leaf stalks to be inedible wooden stems.

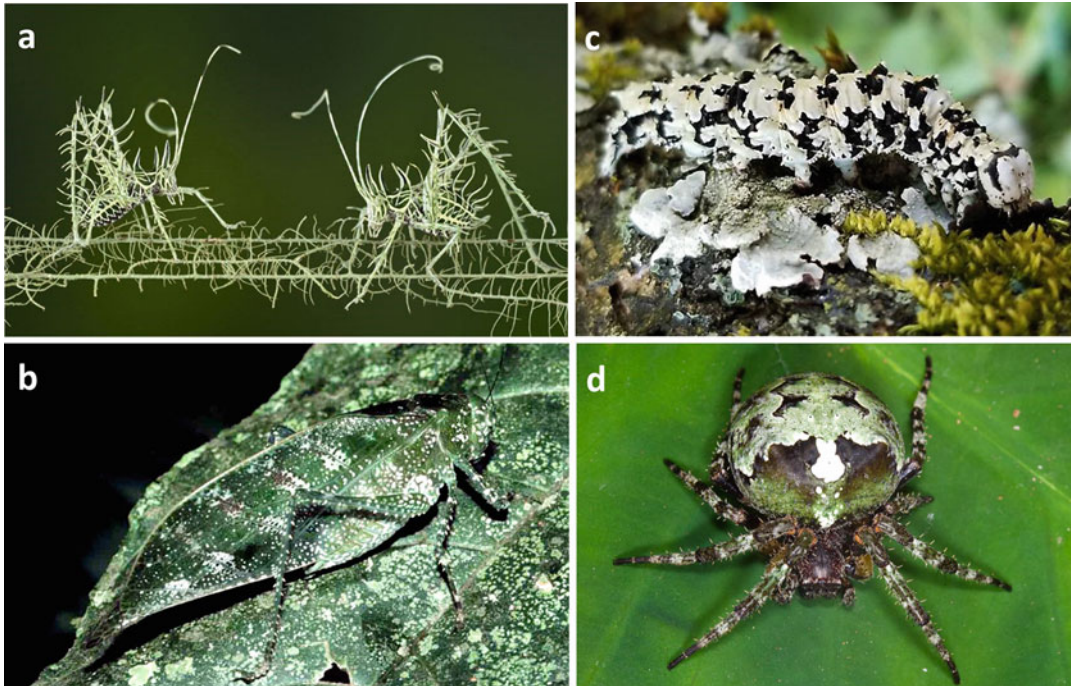


Fig. 6.14 Lichenomimesis in insects (**a–c**) and spiders (**d**). (**a–b**) Katydids (Tettigoniidae, bush crickets). (**a**) Nymphs of *Lichenodraculus matti* on beard lichen (*Usnea* sp.); courtesy of David Weiller. (**b**) *Anapolisia maculata* mimicking foliicolous lichens in a tropical rainforest in Costa

Rica; courtesy of Andrea Bernecker, in Lücking and Cáceres (2002). (**c**) Caterpillar of the Ilia Underwing Moth (*Catocala ilia*); courtesy of Erik Adams. (**d**) Giant Lichen Orb Spider (*Araneus bicentenarios*); courtesy of Jim Petranka and Becky Elkin

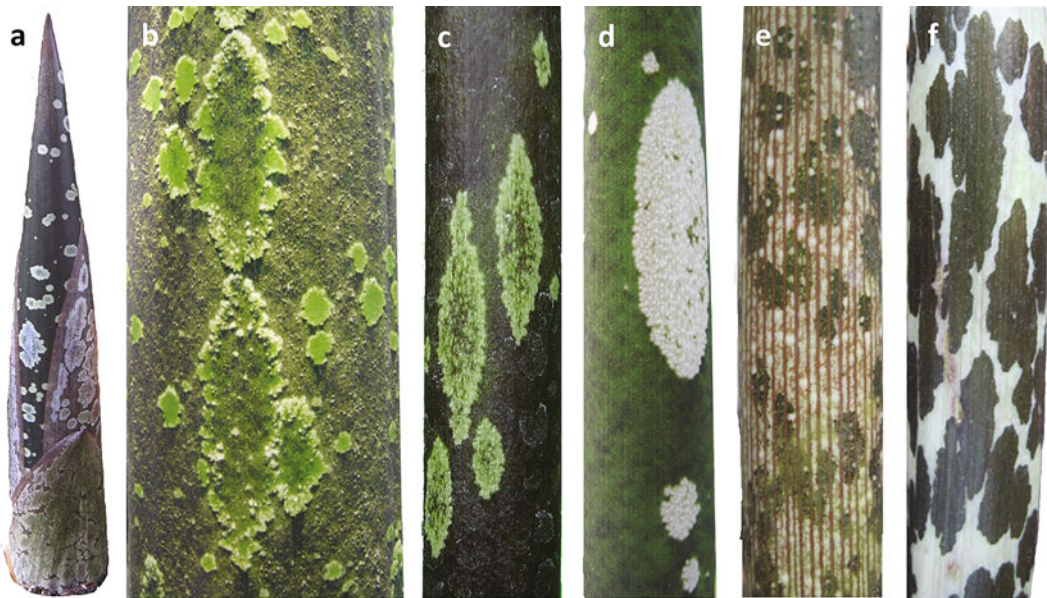


Fig. 6.15 Lichenomimesis in petioles (leaf stalks) of Araceae with characteristic patterns mimicking crustose lichens. (**a**) the bud of *Amorphophallus gigas* is protected by three ephemeral bracts. (**b**) Detail of a mature petiole of *A. gigas*. (**c**) *A. dactylifer*, mimicking representatives of

the genus *Graphis*. (**d**) *A. decus-silvae*, mimicking *Pertusaria* spp. (**e**) *A. pseudoharmandii* (syn. *Pseudodracontium harmandii*). (**f**) *Typhonium venosum*. Images taken in the Botanical Garden of the University of Zürich

Lichenomimesis is also seen in other Araceae such as *Typhonium venosum* (voodoo lily; Fig. 6.15f). The inflorescences of these Araceae emit a remarkable scent, reminiscent of decaying meat, partly intermixed with dung (e.g. horsedung in *T. venosum*), which attracts copro-necrophagous insects, some of them acting as pollinators (Claudel 2021). These plants of the *Arum* family successfully mimic elements of the fungal (i.e. lichens) and of the animal kingdoms.

6.9 Conclusions and Outlook

Molecular genetics have revolutionized our view on the biodiversity of LFF, their photobionts and their microbial associates. These investigations will continue at a global scale.

Lots of fossils, lichens and lichen-like organisms, from the Palaeozoic to the Cenozoic await thorough investigation.

The search for bioactive compounds, as produced by lichen-forming and endolichenic fungi and their bacterial associates will be intensified, several promising components having already been found. Examples are (1) usnic acid with antimicrobial, antiproliferative and antiviral properties (Macedo et al. 2021), as produced by various representatives of the Parmeliaceae in the lichenized and axenically cultured state (Yamamoto et al. 1985; Stocker-Wörgötter et al. 2013; Xu et al. 2022) and by endolichenic *Streptomyces cyaneofuscatus* (Parrot et al. 2016a); (2) antiproliferative cyaneodimycin from the same isolate of *S. cyaneofuscatus* (Parrot et al. 2016a) or (3) uncialamycin, a potent antibiotic with antiproliferative activity produced by *Streptomyces uncialis*, an endolichenic actinobacterium in *Cladonia uncialis* (Nicolau et al. 2007, 2021; Parrot et al. 2016b). It will be interesting to see whether some of these products with pharmaceutical potential will reach the clinical trial phases. The large-scale production of mycobiont-derived secondary metabolites, either by heterologous expression in fast-growing fungi or by chemical synthesis, will be a challenge. *S. uncialis*-derived uncialamycin is chemically synthesized (Nicolau et al. 2007).

Many bacterial associates of lichen thalli are in close contact with mycobiont-derived secondary metabolites with antibiotic properties, and some bacterial associates of lichens were shown to synthesize antibiotics (review: Grimm et al. 2021); an example is *Streptomyces cyaneofuscatus*, producer of usnic acid, which was isolated from the marine lichen *Lichina confinis* which does not synthesize usnic acid (Parrot et al. 2016a). The biotransformation of usnic acid into a compound with lower antibiotic activity was observed in several lichen-associated bacteria (Noël et al. 2021). The question is: are some of the epi- and endolichenic bacteria resistant to antibiotics? Bacterial antibiotic resistance emerged in the pre-antibiotic era; an example is the co-evolutionary adaptation of methicillin-resistant *Staphylococcus aureus* on hedgehogs whose skin is infected with antibiotic producing dermatophytes (Larsen et al. 2022).

Lichen-invertebrate and -vertebrate interactions deserve a closer examination as regards the dispersal of lichens and their allies. It would be interesting to see what birds carry on their feet and feathers in terms of symbiotic propagules (soredia, isidia, blastidia) or minute thallus fragments as well as faecal pellets of lichenivorous invertebrates or the minute lichenivorous mites proper. Examining the load of lichen propagules on the feathers and feet of birds with annual bipolar migration such as South Polar Skuas (*Catharacta maccormicki*, syn. *Stercorarius m.*) or Arctic Terns (*Sterna paradisaea*), which are assumed to be vectors of lichens with bipolar distribution (review: Garrido-Benavent and Pérez-Ortega 2017), would be particularly interesting. But also lichen dispersal by smaller birds, which are regularly landing on lichen-covered surfaces, should be investigated, for example, in collaboration with ornithologists during their ringing activities (Bailey and James 1979).

To conclude: there are lots of interesting work ahead, both in the field and laboratory.

Acknowledgements My sincere thanks are due to Prof. Dianne Edwards for fruitful collaboration on fossils, William Bruzgul, Paul Diederich and Robert Lücking for

valuable informations, to Andreas Valls for IT support, to Erik Adams, Andrea Bernecker, Joël Boustie, Paul Diedrich, Pierre Le Pogam, Fabio Nodari, Jim Petranka, David Weiller and Erich Zimmermann for permission to include their photos, to Prof. Ueli Grossniklaus, director of the Institute of Plant and Microbial Biology of the University of Zurich, for access to the infrastructure of the institute far beyond my retirement, IT support by Stefan Roffler included. Last but not least, I thank Barry Scott and Carl Mesarich, editors of this volume, for their kind interest, patience and help.

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