Fossil lichens from the Lower Devonian and their bacterial and fungal epi- and endobionts

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Abstract: A short overview on fossil lichens and lichen-like organisms from Cenozoic amber to the Proterozoic Doushantuo fossils is presented. The focus is on structural peculiarites of *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis*, fossil cyanobacterial and green algal lichens from the Lower Devonian (Lochkovian, approx. 415 Myr old), the earliest lichens with heteromerous thallus anatomy found up to now, and their bacterial and fungal epi- and endobionts, as seen in scanning electron microscopy preparations. These very small specimens had been charcoalified during wildfires before being transported by wind and rain and ending up as fluvial deposits in siltstone sediments of the Welsh borderland. The microbiome of *C. salopensis* was ultrastructurally investigated: bacterial colonies were found on the surface of the cortical layer, hyphae of endolichenic fungi between and actinobacterial filaments in close contact with medullary hyphae of the ascomycetous mycobiont. These findings are interesting since the phylogeny, biology and potential economic importance of the microbiome of extant lichens is currently intensely investigated by various teams worldwide.

1. Introduction

Extant lichen-forming ascomycetes are a diverse assembly of nutritional specialists comprising representatives of the classes Arthoniomycetes, Dothideomycetes, Lichinomycetes, Coniocybomycetes, Eurotiomycetes and Lecanoromycetes within the subphylum Pezizomycotina. During ascomycete evolution there were probably more losses than gains of lichenization, even the predominantly non-lichenized Eurotiomycetes, with many economically and medically important taxa such as *Penicillium* and *Aspergillus* spp., derive from lichenized ancestors (Lutzoni et al. 2001, 2004). Depending on the calibration of the fungal tree of life the earliest common ancestor of the main classes comprising lichenized ascomycetes was estimated to originate between the Cambrian at the earliest and the Carboniferous at the latest (Berbee & Taylor 2010, Prieto & Wedin 2013, Beimforde et al. 2014).

Terrestrial ecosystems prior to and during the advent of vascular plants most likely were dominated by epilithic microbiota and soil crust communities, i.e. extremophiles similar to the ones found in extant climatically extreme habitats such as rock surfaces, hot and dry steppe or desert sites, tundras or Arctic and Antarctic ecosystems. Late Devonian to Middle Triassic, rock-inhabiting ascomycetes were identified as ancestors of mutualistic (lichenized) and pathogen-rich lineages (Gueidan et al. 2008, 2011). Nematophytes, now being interpreted as lichens whose photobiont was not preserved during fossilization, presumably common and widespread organisms in Late Silurian to Lower Devonian terrestrial ecosystems (Edwards & Axe 2012, Edwards et al. 2013), were part of food chains, surprisingly well preserved fragments

of *Nematothallus*, *Nematosketum* und *Cosmochlaina* having been found in fecal pellets of arthropods (presumably millipedes; EDWARDS et al. 2012). Extant soil crust communities comprise mainly cyanobacteria, lichens and bryophytes (see various contributions in BELNAP & LANGE 2003, YEAGER et al. 2004, BÜDEL 2009).

Despite the presumed ancient age of lichen-forming ascomycetes the fossil records are poor. This is partly due to the fact that palaeomycologists and palaeolichenologists are a minority group among palaeontologists. While investigating fossil lichens one has to cope with problems unkown to scientists studying extant specimens. By subjecting extant lichens to simulated fossilization such as high pressure and heat (TOMESCU et al. 2010) or charring (HONEGGER et al. 2013a, see Fig. 3E–G) valuable cues were obtained for the structural interpretation of fossil samples.

Some of the difficulties are summarized as follows: 1) In contrast to tracheophytes with cutinized and/or suberized walls of dermal tissues lichen thalli comprise no compounds which resist comparatively fast microbial degradation. Nevertheless, the term "cuticle" is often used in the palaeontological literature for fragments of fungal or lichen affiliation. 2) Cyanobacterial or algal photobionts may fossilize differently than the fungal cells with their chitinous walls (examples see below) or may be lost during fossilization (e.g. in Nematophytes; EDWARDS et al. 2013). 3) The majority of fossil lichens fossilized *ex situ*, partly far away from their previous terrestrial habitats and may be intermixed with limnic (e.g. the Triassic Schilfsandstein fossils of the German Basin; ZIEGLER 1997, 2001) marine, or freshwater fossils (e.g. the Late Silurian and Lower Devonian fossils of the Red Sandstone in the Welsh Borderland, i.e. the coastal zone of the former Welsh Basin; see below); therefore nothing is known about their former distribution and habitat preference (terricolous, saxicolous, epiphytic). 4) The majority of well-preserved lichen thalli were found in the Cenozoic (amber fossils; Fig. 1), i.e. are comparatively young and morphologically and anatomically comparable with extant taxa, even lichenicolous ascomycetes having been retained (SADOWSKI et al. 2012). The geologically older the specimens are, the more difficult is their interpretation due to partly very limited or even missing similarities with extant taxa (e.g. *Prototaxites*, see below), to structural changes during fossilization (examples among Lower Devonian fossils; see below), or to presumed taxonomic affiliation either to taxa with no extant lichenized members (e.g. *Winfrenatia reticulata*, presumed lichenized Zygomycete with cyanobacterial and possibly coccoid green algal photobionts; TAYLOR et al. 1995, 1997, KARATYGIN et al. 2009) or to extict phyla (e.g. Nematophytes; EDWARDS et al. 2013), the latter problem being widespread in palaeontology.

2. Fossil lichens and lichen-like fossils: an overview

Fig. 1 summarizes published data on fossil lichens and lichen-like organisms. Only comparatively few fossils have so far been found whose fungal partner and photobiont could be adequately resolved.

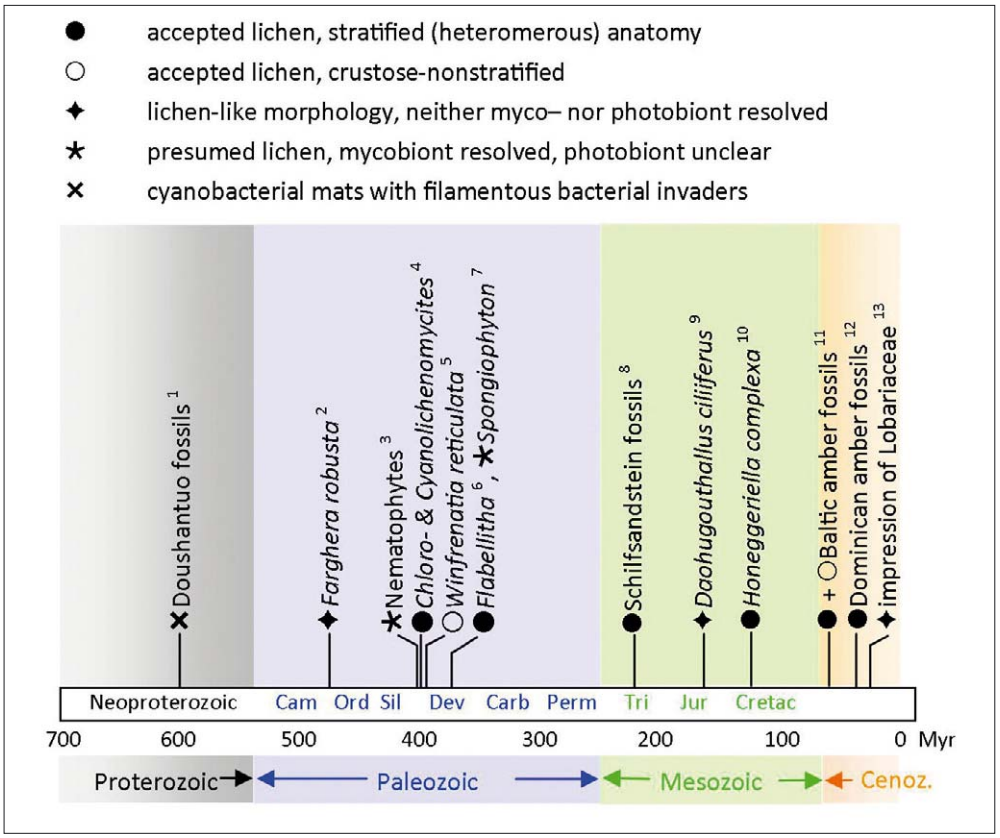

Fig. 1: Fossil lichens, an overview. 1. Yuan et al. (2005); 2. Retallack (2009); 3. Edwards & Axe (2012), Edwards et al. (2013); 4. Honegger et al. (2013a); 5. Taylor et al. (1995, 1997), Karatygin et al. (2009); 6. Jurina & Krassilov (2002); 7. Stein et al. (1993), Jahren et al. (2003), Taylor et al. (2004); 8. Ziegler (2001); 9. Wang et al. (2010); 10. Matsunaga et al. (2013); 11. Mägdefrau (1957), Rikkinen & Poinar (2002), Rikkinen (2003), Hartl et al. (2015), Kaasalainen et al. (2015); 12. Poinar et al. (2000), Rikkinen & Poinar (2008); 13. MacGinitie (1937), Peterson (2000). Chronostratigraphy (according to the International Commission on Stratigraphy, Aug. 2012. www.stratigraphy.org): Neoproterozoic Era (1000–540 Myr). Periods in Myr: Cam: Cambrian (541–484); Ord: Ordovician (485–442); Sil: Silurian (443–418); Dev: Devonian (419–356); Carb: Carboniferous (358–299); Perm: Permian (298–253); Tri: Triassic (252–202); Jur: Jurassic (201–146); Cretac: Cretaceous (145–67). Cenoz: Cenozoic era (comprising the Palaeogene, Neogene and Quarternary periods: 66–now).

The title “The oldest fossil lichen” for the Lower Devonian crustose *Winfrenatia reticulata* (Taylor et al. 1995, 1997) from the Rhynie Cherts, which is roaring through the internet, is no longer valid, since 18 years after the detection of this enigmatic fossil two lichens of the same geological era but

with distinctly more anatomical similarity with extant taxa were described: *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis* (Honegger et al. 2013a), both with internally stratified thallus resembling extant foliose Lecanoromycetes with dorsiventrally organized thallus. Similarly misleading is the statement of lichens being 600 Myr old (e.g. in Kaasalainen et al. 2015), based on the publication of Yuan et al. (2005) on the lichen-like proterozoic Doushantuo fossils. These are marine, benthic microbial mats, presumably formed by cyanobacterial colonies, which were invaded by actinobacterial filaments; hyphal diameters below 1µm, a characteristic of the Doushantuo fossils, are not features of fungal hyphae, as assumed by Yuan and colleagues, but of filamentous bacteria (Honegger et al. 2013a). Comparable cyanobacterial mats, formed by *Prattella massanuttense*, with filamentous and rod-shaped bacterial invaders were recovered from fluvial sediments in early Silurian (Llandovery; 440 Myr old) Massanutten Sandstone (Virginia, USA; Tomescu et al. 2008, 2009).

Not included in the overview, as shown in figure 1, are

– the enigmatic Precambrian (approx. 2500 Myr old) *Thuchomyces lichenoides*, as isolated from Thucholite (acronym for Thorium, Uranium, Carbon and Hydrogen [TH, U, C, H], a variety of Pyrobitumen) among gold-bearing conglomerates of the South African Witwatersrand Basin; its affiliation remains unclear ever since its first description: «The plant could …have been an alga or photosynthetic bacteria with fungal anatomy and morphology, a photosynthetical active fungus or a lichenous plant with symbiosis between a filamentous organism and an alga» (Hallbauer et al. 1977, p. 486).

– *Prototaxites* spp., (Late Silurian to Late Devonian, approx. 420–370 Myr old), terrestrial, presumably erect, branched fossils with stem-like base, partly of giant dimensions (up to > 1 m diameter, up to >8 m height). *Prototaxites* stems reveal a year-ring-like concentric zonation and tubular fine structure, at least two types of tubes being evident: unbranched thick ones (18–50 µm diameter), usually arranged longitudinally within the stem, and profusely branched thin ones (2–6 µm diameter), sometimes with a third, branched type of tubes (15–45 µm diameter). The genus *Prototaxites* was widespread, fossils having been found, e.g. in the Scottish Rhynie Cherts, in Red Sandstone of Wales, Holland, Belgium and Germany (Eifel, Taunus, etc.), in Gaspé (Canada), New York State (USA), Saudi Arabia, Australia. *Prototaxites* was interpreted as a giant marine alga, rolled carpets of liverworts, a fungus or a lichen (Edwards 1982, Hueber 2001, Selosse 2002, Graham et al. 2010, Hobbie & Boyce 2010, review: Steur 2015). Due to structural similarities with Nematophytes, an extinct, presumably lichenized group of fungi, widespread members of cryptogamic covers from the mid-Ordovician to Late Devonian, *Prototaxites* was interpreted as a member of Nematophytales (Edwards et al. 2013, Retallack & Landing 2014). Currently no-one can explain how a

predominantly fungal axis should have been able to stand more than 8 m high. The lichen hypothesis (Selosse 2002, Hobbie & Boyce 2010) gives an idea about the nutritional strategy of these extinct, impressive, presumably heterotrophic organisms.

– the foliicolous, subcuticular *Pelicothallos villosus* Dilcher (Eocene, approx. 45 Myr old), originally described as a foliicolous ascomycte (Dilcher 1965). It was interpreted as *Cephaleuros virescens*, a foliicolous green alga (Trentepohliales; Pirozynski 1976; see images in Pitaloka et al. 2015) or as a foliicolous lichen, respectively, close to extant *Strigula* spp.with *Cephaleuros* photobiont (Sherwood-Pike 1985), and finally emended as *Pelicothallus villosus* Reynolds & Dilcher (1984), a foliicolous green alga closely related to extant *Cephaleuros* spp.

3. The oldest lichens kown up to now with internally stratified (heteromerous) thallus

Lower Devonian (Lochkovian, approx. 415 Myr old) *Cyanolichenomycites devonicus* and *Chlorolichenomycites salopensis*, two ascomycetous lichens with septate hyphae, were recovered as small, charcoalified fragments of terrestrial origin from fluvial sediments (siltstone) of the Welsh borderland (Honegger et al. 2013a). These terrestrial «mini-crumbs» had been charred during wildfires and were subsequently transported by wind and rain into rivers prior to sinking into coastal sediments of the Welsh Basin; they are easily distinguishable from freshwater or marine fossils by their dark colouration (Edwards & Axe 2004, Edwards & Richardson 2004, Glasspool et al. 2004, 2006, Scott & Damblon 2010).

Charcoalification (high firing temperature at low O_2 contents) causes chemical and physical changes in organic matter (Poole et al. 2002) but, in contrast to ashing (high firing temperature at high O_2 content), leads to an astonishing structural preservation; this feature is well known to palaeontologists and archaeobotanists, the latter identifying charcoalified seeds, textile fibres or wood samples at species level ever since Oswald Heer's pioneering studies on botanical remains in neolithic lake side dwellings (Heer 1865, Figuerial & Moosbrugger 2000, Rast-Eicher & Dietrich 2015).

The holotypes of both species were extracted by subsequent incubation of the fossil-containing material (siltstone) in concentrated hydrochloric acid (HCl, 24 h) and 40 % hydrofluoric acid (HF, 72 h at room temperature), with thorough washings in between and afterwards, followed by sieving through a 250 µm polyester mesh: dissolved mineral matters passed, organic debris were retained. After drying the minute samples were examined with a dissecting microscope (Figs. 2A–B); promising samples were mounted on specimen holders for scanning electron microscopy (SEM) and sputter coated with a palla-

dium-gold alloy prior to examination. After a first round of imaging the specimens were turned over, sputter-coated, re-imagined, then broken apart with a razor-blade, sputter coated and re-imagined (protocol of Lindsey Axe, in Honegger et al. 2013a). Due to multiple sputter-coating very fine details became obscured by the comparatively thick layer of gold and palladium; this is especially true of the superficial bacterial colonies in *Chlorolichenomycites salopensis*, part of which can no longer be properly resolved. Both fossils are deposited in the Welsh National Museum at Cardiff.

The holotype of *Cyanolichenomycites devonicus* comprises a small lobule and an adjacent pycnidium with developing pycnospores (Fig. 3A–B). In the photobiont layer below the several cell layers thick peripheral cortex the majority of cyanobacterial cells were lost but the massive mucilaginous sheaths of the cyanobacterial colonies were retained, revealing the characteristic holes between adjacent cells of the cyanobacterial filaments (Fig. 3C). This photobiont very strongly resembles extant *Nostoc* spp., common and widespread diazotrophic cyanobacteria (Fig. 3D) in terrestrial and freshwater habitats, photobionts of numerous extant taxa of lichenized ascomycetes, nitrogen-fi-

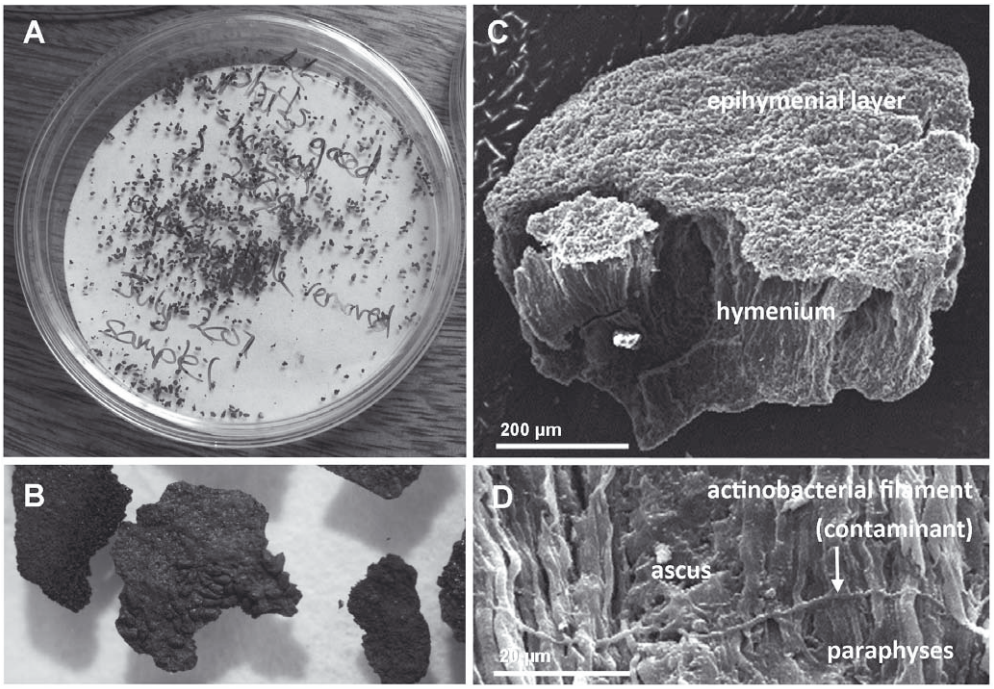

Fig. 2: Peculiarities of the charcoalified fossils from the Lower Devonian (Lochkovian), as extracted from grey siltstone of the Welsh borderland. **A**: Minute, charcoalified fragments of fossil organic material ready for mounting on specimen holders for SEM investigation; diameter of the Petri dish: 11 cm. **B**: Promising specimens are selected with the aid of a dissecting microscope. **C**–**D**: Low level of microbial contamination on the charcoalified fossils: a fragment of an apothecium with an actinobacterial contaminant growing over the the paraphyses and polysporic ascus on the hymenial layer.

xing symbionts of bryophytes (*Anthoceros*, *Phaeoceros* and *Blasia* spp.) and of the angiosperm genus *Gunnera* (Engelhardt 2014, Maldener 2014). In charring experiments with extant, freshly collected *Nostoc commune*, *Peltigera praetextata* and *Leptogium lichenoides* (two lichen-forming ascomycetes with *Nostoc* sp. as photobiont) a very similar specimen preservation was obtained (Fig. 3E–G): the cyanobacterial cells were lost during heating but their mucilaginous sheaths were retained, together with the fungal cell walls of the charred lichens (Honegger et al. 2013a).

The minute holotype of *Chlorolichenomycites salopensis* reveals a one cell layer thick cortex, built up by conglutinate, globose to ovoid cells, a photobiont layer and a medullary layer built up by loosely interwoven fungal hyphae. The photobiont cells proper, presumed coccoid green algae, are not retained, but replaced by pyrite framboids, spherical aggregates of microcrystalline iron sulfide (FeS_2); only rarely was a thin algal cell wall preserved (Fig. 4A). Organic material such as cell organelles or membranes have been identified as nucleation sites of pyrite formation (Martín-González et al. 2009), and many of these charcoalified fossils are indeed internally filled with microcrystalline pyrite. Nevertheless, the fascinating pyrite framboids were experimentally synthesized even in the absence of organic matter (Ohfuji & Rickard 2005). The globose structure and the dimensions of the presumed green algal photobiont cells resemble those of *Trebouxia* spp., the most common and widespread photobiont taxon associated with extant lichen-forming ascomycetes. A tight cell-to-cell-contact is evident at the mycobiont-photobiont interface (Fig. 4A), but neither appressorial nor haustorial structures were found, characteristic features of extant Lecanoromycetes and sites of exchange not only of either photosynthates or water with dissolved nutrients and mycobiont-derived apoplastic compounds, respectively (Honegger 1991), but also of horizontal gene transfer between lichen-forming ascomycetes and their *Trebouxia* photobionts (Beck et al. 2015).

4. The microbiome of the Lower Devonian *Chlorolichenomycites salopensis*

The thalli of extant lichens represent not dual or, as in the case of cephalodiate taxa, triple symbioses but are consortia with an unknown number of participants (Honegger 1992). Beside the lichen-forming fungus proper (mycobiont) and its green algal and/or cyanobacterial partner (photobiont) are lichenicolous (parasitic) fungi present and an astonishing diversity of symptomless endolichenic fungi, the latter being currently intensely studied not only with regard to their taxonomic affiliation and phylogeny (Arnold et al. 2009, U'Ren et al. 2012, Fleischhacker et al. 2015, Spribille et al. 2016, review: this book, Hafellner 2018), but also as potential producers of bioactive compounds (Giddings & Newman 2014, p. 67 ff.). The same is true of

bacterial epi- and endobionts, as found in association with lichen thalli worldwide (Poelt & Mayrhofer 1988, Grube et al. 2009, 2012, 2015, Hodkinson & Lutzoni 2009, Hodkinson et al. 2012, this book, Grube 2018).

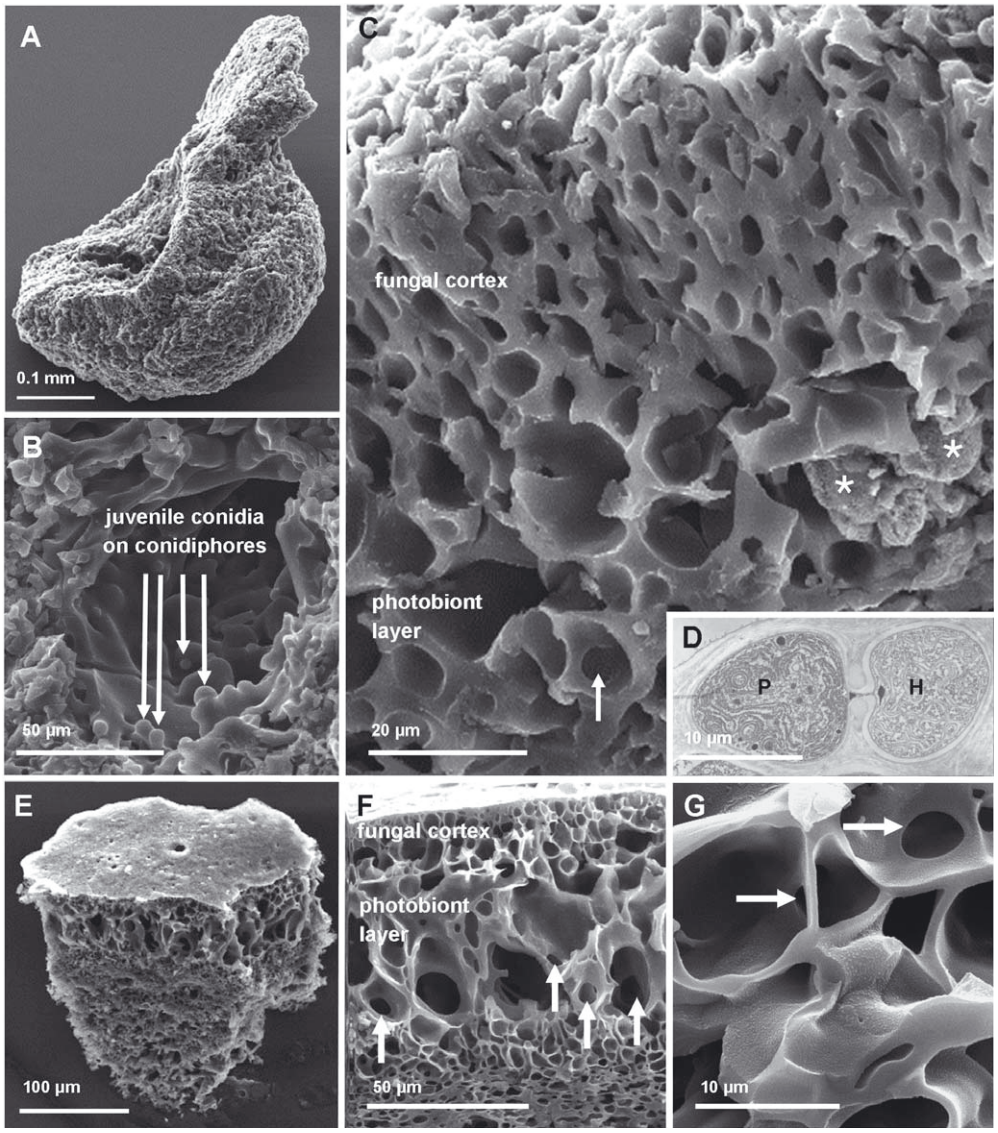

Fig. 3: SEM micrographs of the Lower Devonian fossil *Cyanolichenomycites devonicus* (A–B) in comparison with extant, charred *Peltigera canina* (E–F) and *Nostoc commune* (G). D: TEM micrograph of a photosynthetic cell (P) and adjacent heterocyst (H) of the *Nostoc* photobiont of extant *Peltigera canina*. The asterisks in C refer to two cyanobacterial cells, all others having been lost while their gelatinous sheaths are retained. Arrows in C and F–G refer to the characteristic holes in the cyanobacterial sheaths between adjacent cells of the cyanobacterial filaments. A–C and E–G from HONEGGER et al. (2013a, with permission of New Phytologist/John Wiley & Sons).

Many endolichenic fungi are recognized ultrastructurally by their dimensions and rarely by special features such as clamp connections, as observed in aphyllophoralean taxa (Fig. 4C). The fungal hyphae within the algal and medullary layers of *C. salopensis* are quite uniform but few hyphae, presumed endolichenic fungi, reveal a distinctly lower diameter (Fig. 4B).

Colonies of rod-shaped bacteria were resolved on the cortical surface of *C. salopensis* (Fig. 4A). In the thalline interior numerous actinobacterial filaments were found, partly in close contact with medullary hyphae of the mycobiont (Fig. 4B). No bacterial epibionts could be resolved on *Cyanolichenomycites devonicus* whose surface layer was lost, probably due to mechanical abrasion *post mortem*.

Facts or fiction? Are the bacterial colonies and actinobacterial filaments, as seen on and within the 415 Myr old thallus fragment of *Chlorolichenomycites salopensis*, cohabitants or contaminants? Microbial contamination after collecting the fossil-bearing rock samples can be excluded (see the chemical treatment during maceration, as summarized above). Considering the time between charring and sedimentation one might expect these fossil specimens to have been superficially colonized *post mortem* by contaminating microbes. However, in contrast to fresh fragments of lichen thalli a charred specimen has hardly any nutritional value and thus might provide a colonizable surface, but not a nutritious substrate for microbial decomposers. As concluded from other specimens (e.g. a yet undescribed apothecial fragment of the same age; Fig. 2C–D) minor contamination occurred, recognizable, e.g. as actinobacterial filaments overgrowing the surface of the fossil. Bacterial contaminants (coccoid or rod-shaped) would be found on all surfaces, not only on very localized sites, as seen on the cortex of *C. salopensis* (Fig. 4A). We are therefore confident to have imaged the microbiome of the first green algal lichen with internally stratified thallus found up to now.

Why is the detection of endolichenic fungi and of tight contact sites between endolichenic actinobacteria and medullary hyphae of this ancient lichen so exciting? Based on molecular phylogenies lichens were proposed to be ‘cradles of symbiotrophic fungal diversification’ in ascomycete evolution, and endolichenism was identified as ‘an incubator for the evolution of (fungal) endophytism’, multiple trophic transitions from endophytism to saprotrophism (and rarely *vice versa*) having been found in ascomycete evolution (Arnold et al. 2009; this book, Hafellner 2018).

The astonishing biodiversity of bacterial epi- and endobionts of lichen thalli and their biological activities are currently intensely investigated (this book, Grube 2018). Innumerable Lecanoromycetes, Eurotiomycetes and Coniocybomycetes produce interesting secondary metabolites, similar to those formed by actinobacteria. Molecular phylogenies of the enzymatic machinery, i.e. the polyketide sythetase (PKS) genes, reveal horizontal gene transfer from actino-

bacteria to ancestors of extant lichen-forming ascomycetes (SCHMITT & LUMBSCH 2009). Similarly a methylammonium permease (MEP) gene was horizontally transmitted from chemolithoautotrophic prokaryotes to early filamentous ascomycetes (Pezizomycotina; MCDONALD et al. 2012); it was subsequently lost in most linages but retained in even distantly related lichen-forming taxa. In the non-lichenized *Aspergillus nidulans* (an Eurotiomycete with lichenized ancestors) the intimate contact of bacterial cells with fungal hyphae was shown to trigger the biosynthesis of archaetypal polyketides

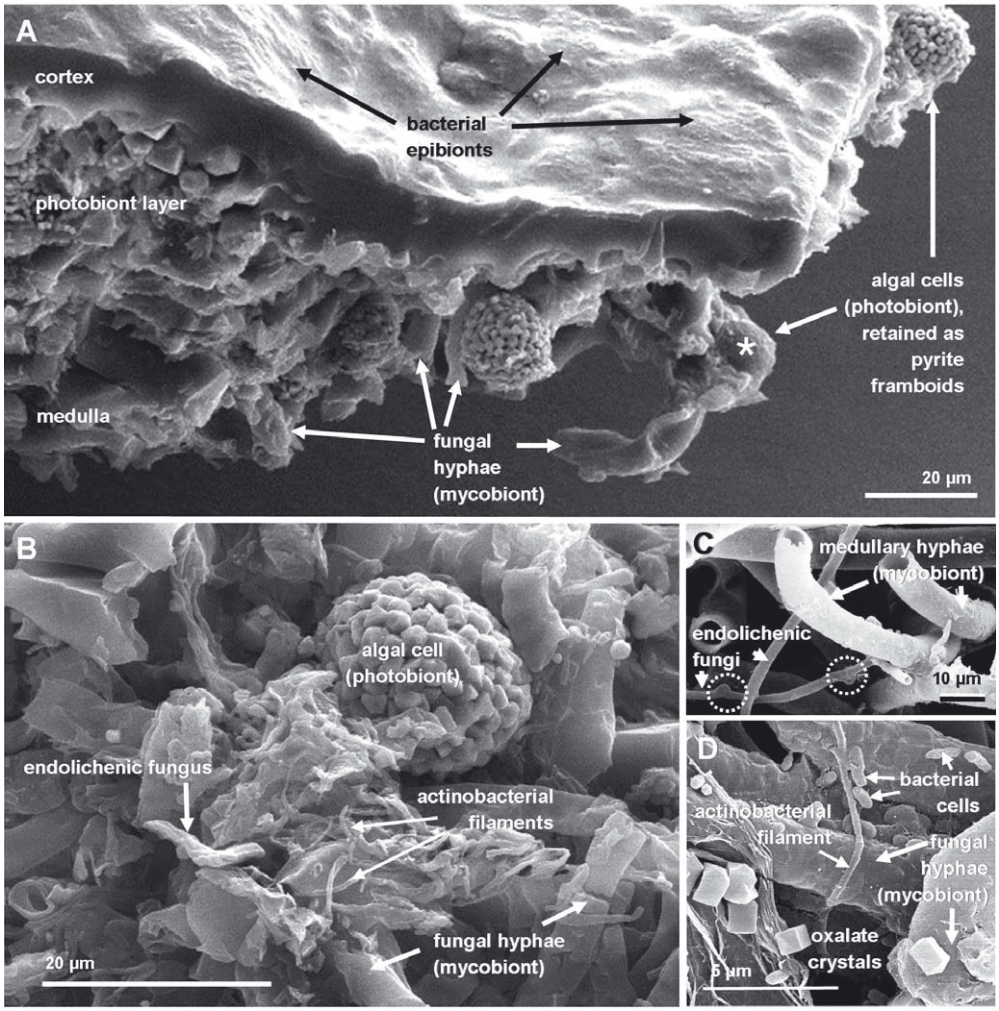

Fig. 4: Scanning electron micrographs of the Lower Devonian fossil *Chlorolichenomycites salopensis* with bacterial epi– and endobionts and endolichenic fungal hypha (A–B) in comparison with extant *Peltigera* spp. with endolichenic fungi and bacteria (C–D). The asterisk in A refers to a photobiont cell whose wall is preserved. C: Clamp connections in a hypha of an aphyllophoralean endolichenic fungus are encircled. From HONEGGER et al. (2013b, with permission of New Phytologist/John Wiley & Sons).

(SCHROECKH et al. 2009). In the light of these results, as achieved by various research teams worldwide, the more than 400 Myr old interactions of bacterial epi- and endobionts with a lichen-forming ascomycete are particularly interesting.

5. Acknowledgements

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