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Honeggeriella complexa gen. et sp. nov., a heteromerous lichen from the Lower Cretaceous of Vancouver Island (British Columbia, Canada)[1]

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- *Premise of the study:* Colonists of even the most inhospitable environments, lichens are present in all terrestrial ecosystems. Because of their ecological versatility and ubiquity, they have been considered excellent candidates for early colonizers of terrestrial environments. Despite such predictions, good preservation potential, and the extant diversity of lichenized fungi, the fossil record of lichen associations is sparse. Unequivocal lichen fossils are rare due, in part, to difficulties in ascertaining the presence of both symbionts and in characterizing their interactions. This study describes an exceptionally well-preserved heteromerous lichen from the Lower Cretaceous of Vancouver Island.
- *Methods:* The fossil occurs in a marine carbonate concretion collected from the Apple Bay locality on Vancouver Island, British Columbia, and was prepared for light microscopy and SEM using the cellulose acetate peel technique.
- *Key results:* The lichen, *Honeggeriella complexa* gen. et sp. nov., is formed by an ascomycete mycobiont and a chlorophyte photobiont, and exhibits heteromerous thallus organization. This is paired with a mycobiont-photobiont interface characterized by intracellular haustoria, previously not documented in the fossil record.
- *Conclusions: Honeggeriella* adds a lichen component to one of the richest and best characterized Early Cretaceous floras and provides a significant addition to the sparse fossil record of lichens. As a heteromerous chlorolichen, it bridges the >350 million-year gap between previously documented Early Devonian and Eocene occurrences.

Key words: Canada; Cretaceous; fossil; haustorium; heteromerous; *Honeggeriella*; lichen

Mutualistic association with photosynthetic autotrophs, in the form of lichen symbioses, is a highly successful nutritional strategy among fungi. The general perception among paleobotanists and 'neo'-botanists is that, despite the extant diversity of lichenized fungi, representation of these organisms in the fossil record remains poor. This is due in part to the challenges met in ascertaining the lichen nature of fossils, i.e., a number of authors have proposed that an unequivocal lichen fossil must show clear evidence of a stable physiological interaction between the mycobiont and photobiont (Stein et al., 1993; Taylor et al., 1997; Taylor and Krings, 2005). To date, this relationship has been demonstrated in relatively few instances, and a quick look at the fossil record reveals a spotty, albeit broad, chronostratigraphic extent of lichen and lichen-like fossils (reviewed below; see also Taylor et al., 2009).

Here we describe a new lichen, *Honeggeriella complexa* gen. et sp. nov., based on one specimen from Lower Cretaceous deposits on Vancouver Island (British Columbia). This exceptionally well-preserved, permineralized thallus fragment possesses internal stratification consisting of an upper and lower cortex, medulla, and a green algal photobiont layer. Furthermore, the lichen is characterized by haustorial mycobiont-photobiont interfaces previously not documented in the fossil record, and bridges the >350 million-year gap between previously documented Early Devonian and Eocene heteromerous chlorolichens.

MATERIALS AND METHODS

A fragment of a lichen thallus is preserved by cellular permineralization in an iron-rich carbonate concretion, as part of an allochthonous plant fossil assemblage. The concretion was collected from sandstone (greywacke) exposed on the northern shore of Apple Bay, Quatsino Sound, on the west side of Vancouver Island, British Colombia, Canada (50°36'21"N, 127°39'25"W; UTM 9U WG 951068). The concretion-containing layers are regarded as Longarm Formation equivalents and have been dated by oxygen isotope analysis to the Early Cretaceous, Valanginian-Hauterivian boundary (ca. 133 mya) (Stockey et al., 2006).

Concretions were sliced into slabs, and then peeled using the cellulose acetate peel technique (Joy et al., 1956). Slides were prepared using Eukitt xylene-soluble mounting medium (O. Kindler GmbH, Freiburg, Germany). Micrographs were taken using Nikon Coolpix E8800 and Canon PowerShot 100HS digital cameras on Nikon Eclipse E400 and Wild M20 compound microscopes.

For scanning electron microscopy parts of acetate peels containing sections of the specimen were mounted on aluminum stubs shiny-side-up. All acetate was solubilized (by immersing the SEM stub in acetone for 5-10 min) and then gently rinsed with acetone for ca. 5 min. This treatment removes the cellulose acetate completely, leaving the organic material glued to the stub in anatomical connection; rare, minute amounts of cellulose acetate residue are localized and easily recognizable in the SEM by their smooth, reflective surface. The stubs

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were coated with 100 Å Au on a Desk II sputter coater (Denton Vacuum, Moorestown, New Jersey, USA) and examined using a ABT-32 (Topcon, Paramus, New Jersey, USA) scanning electron microscope at 25 kV. Images were processed using Photoshop 7.0 (Adobe, San Jose, California, USA).

All preparations (P 13308 J top) are housed in the University of Alberta Paleobotanical Collections (UAPC-ALTA), Edmonton, Alberta, Canada.

SYSTEMATICS

Genus—*Honeggeriella* Matsunaga, Stockey et Tomescu gen. nov.

Generic diagnosis—Thallus foliose or squamulose, heteromerous, bicorticate. Upper and lower cortex plectenchymatous, outer layer dense, inner layer of looser structure. Medullary hyphae parallel to cortical layers, anastomosing. Photobiont layer between medulla and upper cortex. Mycobiont with septate ascomycetous hyphae. Photobiont a chlorophyte, cells single or in groups of two.

Etymology—*Honeggeriella* is named for Dr. Rosmarie Honegger, University of Zürich, Switzerland, in recognition of her significant contributions to the understanding of lichen structure and the mycobiont-photobiont interface.

Type species—*Honeggeriella complexa* Matsunaga, Stockey et Tomescu sp. nov.

Specific diagnosis—Thallus ca. 260 μm thick, heteromerous. Minimum thickness: upper cortex 57-86 μm, photobiont layer ca. 68 μm, medulla 92-103 μm, lower cortex 35-45 μm. Cortex plectenchymatous, a reticulum of anastomosing hyphae, 1.1-3.5 μm in diameter, dense on outside, loosely packed on inside. Medullary hyphae, 1-2.4 μm in diameter, anastomosing, parallel to cortex. Photobiont layer of single or paired algal cells, 5.8-11.6 μm in diameter. Mycobiont-photobiont interface consisting of both wall-to-wall appressions and intracellular haustoria.

Etymology—The specific epithet *complexa* emphasizes the stratified heteromerous structure of this lichen.

Holotype hic designatus—Fragment in specimen P13308 J top, peels 1-41; slides 1-5, 7-21, 23-38 and three SEM stubs containing specimens from peels 3, 7, 9, and 13; University of Alberta Paleobotanical Collections (UAPC-ALTA).

Locality—Apple Bay locality, Quatsino Sound, northern Vancouver Island, British Columbia, Canada (50°36'21"N, 127°39'25"W; UTM 9U WG 951068).

Stratigraphic position and age—Longarm Formation equivalent, Valanginian-Hauterivian boundary, Early Cretaceous.

DESCRIPTION

The specimen is a thallus fragment that is 260 μm thick, 1.1 mm wide, and at least 1.3 mm long. Transverse sections (Fig. 1A-C) reveal internal stratification consisting of two cortical layers that enclose a median layer (medulla) and a photobiont layer. One side of the fragment represents a tapering thallus margin where the upper and lower cortical layers converge around the photobiont layer, as reconstructed based on serial sections. The upper cortex is 57-86 μm thick, the underlying photobiont layer is ca. 68 μm thick, the medulla is 92-103 μm thick, and the lower cortex is 35-45 μm thick.

While the upper cortex is thicker than the lower cortex and appears to have a more uneven surface topography, both are very similar anatomically and consist of two distinct layers (Fig. 1D). The outermost layer has a compact plectenchymatous structure, consisting of thick-walled conglutinated hyphae that form the dense outer surfaces of the thallus. This region transitions into an inner cortical layer formed by a looser plectenchymatous reticulum of anastomosing hyphae that separate regular circular spaces (Fig. 1D-F). The hyphae vary in size, ranging from 1.1-3.5 μm in diameter, in both the upper and lower cortex; the thickest appear to be filaments composed of multiple conglutinated hyphae.

Although the medulla is not as well-preserved as the cortical layers, the organization of this tissue is distinct from that of the other thallus layers (Figs. 1B, C; 2C, D). The medullary hyphae are predominantly oriented parallel to the cortical layers, which makes for relatively sharp transitions between the cortex and the medulla. Medullary hyphae branch and anastomose infrequently and irregularly; they range from 1-2.4 μm in diameter; transverse septation was observed in these hyphae (Fig. 2C, D).

The photobiont layer is located between the upper cortex and medulla, and consists of evenly distributed single globose cells and pairs of tightly appressed cells (Figs. 1E, F; 2A, F, H). Thick hyphae often extend from the upper cortex into the photobiont layer (Fig. 2B). However, the majority of hyphae within the photobiont layer are comparatively thin and light in color (ca. 1 μm in diameter) (Fig. 3A-D). Photobiont cells are 5.8-11.6 μm in diameter. While many of the photobiont cells are spherical and exquisitely preserved, about half of them appear plasmolyzed or are otherwise deformed. The cell wall has a light brown color; many intact cells contain darker pigmentation inside the cell wall. A relatively small subset of the photobiont cells preserve internal structures in the form of singly-occurring opaque, spherical objects (Fig. 2E) or several larger units that are consistently 3.5 μm in diameter (Fig. 2G).

The photobiont-mycobiont interface is conspicuous for the majority of algal cells, even those appearing heavily damaged. Fungal hyphae tightly envelop the photobiont cells, forming irregular terminal and intercalary appressions, or net-like structures comprised of thin hyphae (Fig. 3). In many cases these hyphae can be found connecting multiple photobiont cells (Fig. 3A, C). In addition to wall-to-wall contact, uniformly thin hyphae (ca. 0.5 μm in diameter) can be observed protruding several microns into the cell lumens of some photobiont cells. Such hyphae are thinner than those found elsewhere in the thallus, and occur in photobiont cells that are intact and well-preserved, as well as in those that are degraded or ruptured (Figs. 2E; 3F). These hyphae appear to originate from broader hyphae that encase the photobiont cell surface. Circular punctures of a regular size and shape in the photobiont cell walls are recurrent throughout the specimen, as seen in SEM (Fig. 3E).

DISCUSSION

Recognition of lichens and the lichen fossil record—Criteria for recognizing lichens in the fossil record have been formulated by Stein et al. (1993), Taylor et al. (1997), and Taylor and

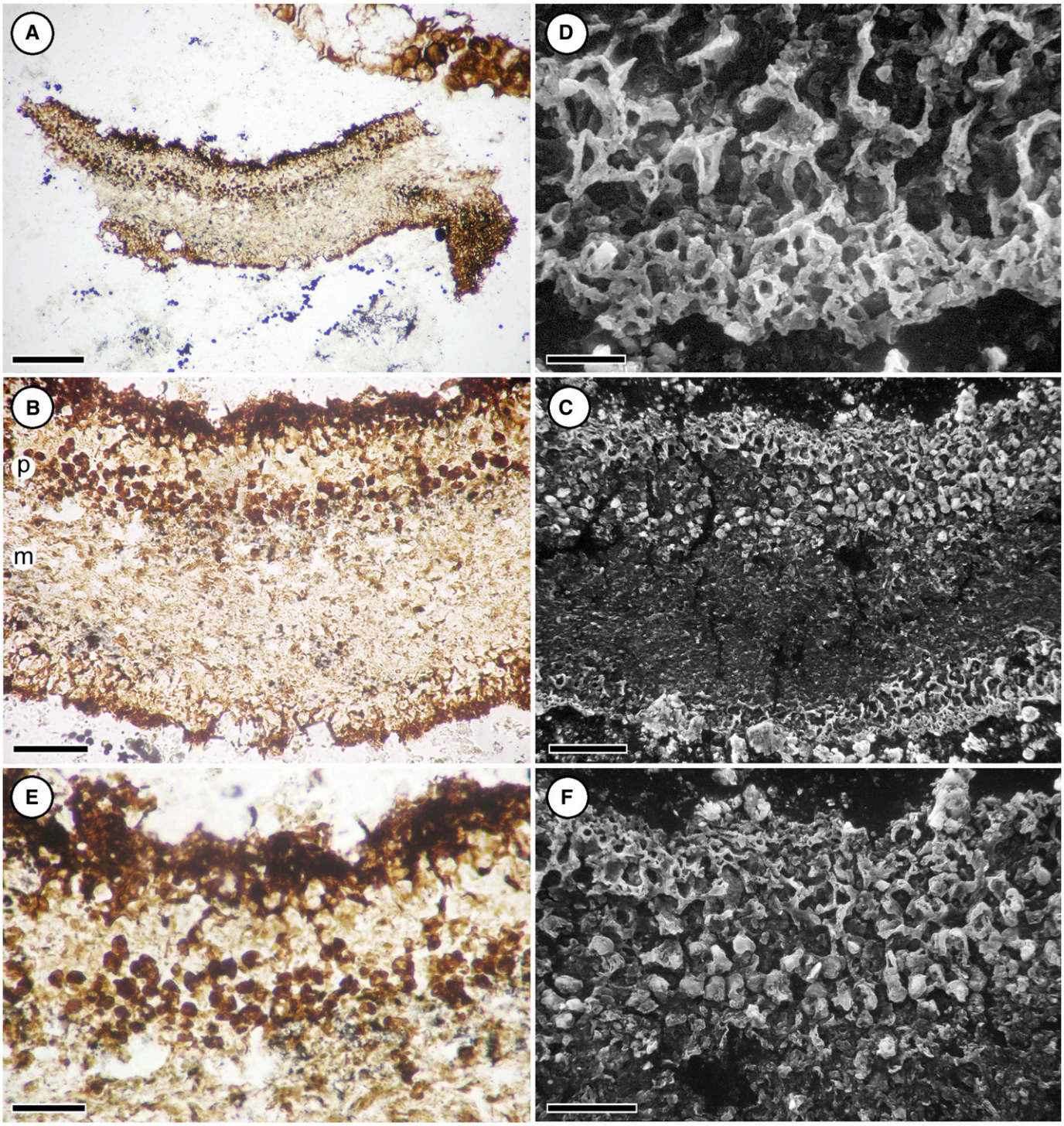

Fig. 1. *Honeggeriella complexa* gen. et. sp. nov. Holotype P13308 J top. (A) Thallus cross section; scale bar = 150 μm; peel #10. (B and C) Detail of thallus cross section showing upper and lower cortex, photobiont layer (p), and medulla (m); scale bars = 50 μm; B—peel #10; C—peel #7. (D) Detail of lower cortex showing inner layer (top) and outer layer (bottom); scale bar = 10 μm; peel #7. (E and F) Detail of upper cortex and photobiont layer; scale bars = 30 μm; E—peel #10; F—peel #7.

Krings (2005). According to these, recognition of a fossil as a lichen requires: (1) presence of a mycobiont and a photobiont; (2) recurrent evidence for physiological interaction (interdependence) between the two bionts; and (3) a body plan that is different from that of either symbiont alone. Although spotty, the fossil record of putative lichens, reviewed below, has a broad chronostratigraphic range (Table 1).

Millimeter-thick carbonaceous layers with columnar microstructures from Precambrian (ca. 2.5 Ga or billion years ago) gold-bearing deposits of the Witwatersrand Basin (South Africa)

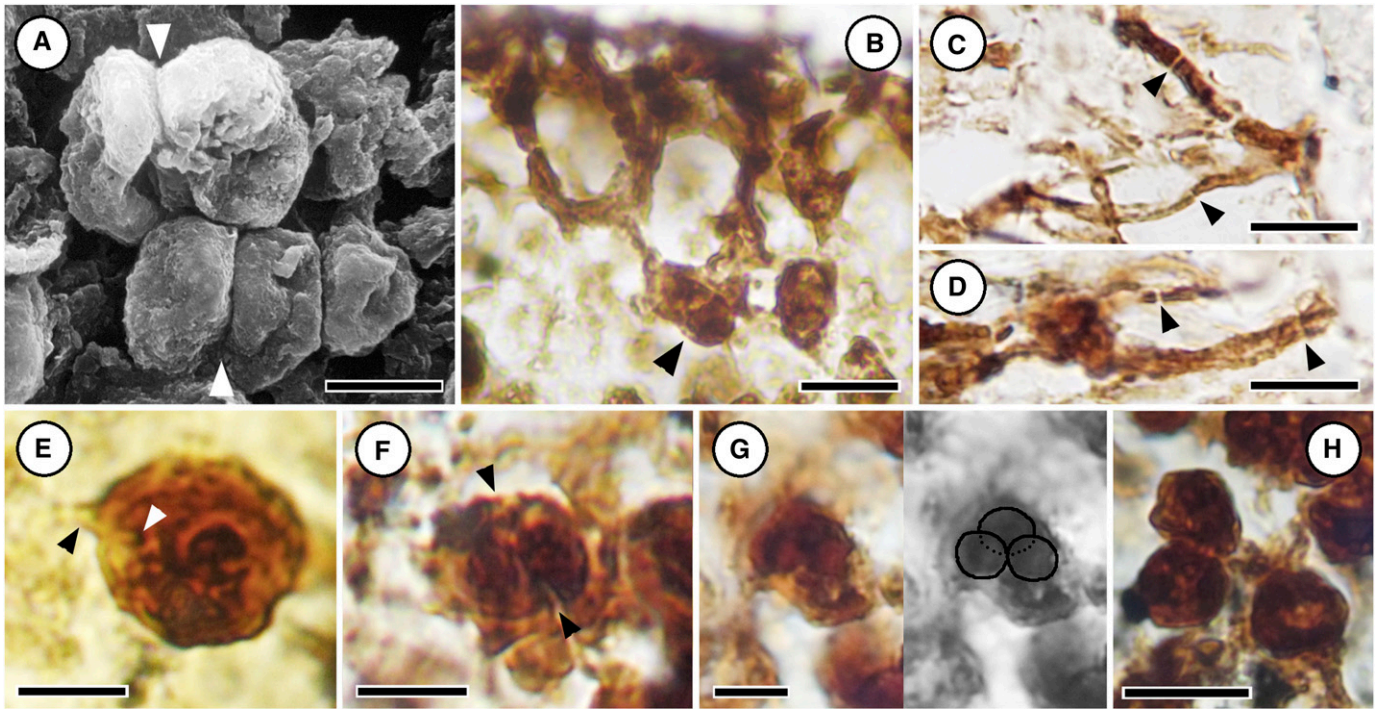

Fig. 2. *Honeggeriella complexa* gen. et. sp. nov. Holotype P13308 J top. (A) Cluster of six photobiont cells (arranged into two horizontal rows); arrowheads indicate position of latest cell divisions; scale bar = 5 μm; peel #9. (B) Thick hyphae of upper cortex (top) extending downward into photobiont layer and surrounding algal cell (arrowhead); scale bar = 10 μm; peel #10. (C and D) Medullary hyphae; arrowheads indicate septa; scale bars = 10 μm; peel #10. € Photobiont cell preserving subcellular structure (dark, at center of cell); connecting hypha (black arrowhead) produces fine branches that surround photobiont (e.g., lower left perimeter of cell); haustorium (white arrowhead) visible inside the cell, penetrates farther than shown here, as evidenced in different planes of focus; scale bar = 5 μm; peel #11. (F) Young daughter cells formed by division of photobiont cell connected along their adjacent walls (arrowheads); mycobiont hyphae encase the pair; scale bar = 5 μm; peel #4. (G) Photobiont cell with three internal structures (traced on grayscaled copy at right); scale bar = 5 μm; peel #6. (H) Photobiont cell pair; note cell at lower right with hypha appressed to it; scale bar = 10 μm; peel #8.

have been described as *Thucomyces* Hallbauer & Jahns (Hallbauer et al. 1977). The columnar units, comprised of agglutinated hyphae surrounding a central cord, were thought to have an internal organization resembling that of lichens. Although carbon geochemistry of the fossils suggests an autotrophic component, no photobiont structures were observed and the biological affinities of *Thucomyces* remain uncertain.

Neoproterozoic marine phosphorites of the Doushantuo Formation (China) preserve clusters of coccoidal cyanobacterial cells surrounded by a net-like matrix of thin, aseptate hyphal filaments (Yuan et al., 2005). The association is interpreted as mutualistic, reflecting a close physiological relationship, due to the absence of morphological abnormalities characteristic of mycoparasitism in the photobiont. However, whether these specimens represent true lichen symbioses remains questionable, as similar coccoidal thalli found in the same deposits lack fungal associates (Taylor et al., 2009).

Into the Phanerozoic, paleosols of the Grindstone Range Sandstone (South Australia), dated around the Cambrian-Ordovician boundary, host features that appear to be thalloid compressions and were named *Farghera* Retallack (2009). While the overall morphology of the features, reminiscent of dichotomously to monopodially branched thalli, suggests affinities with liverworts, algae, or lichens, the absence of any structural information precludes unequivocal assignment of *Farghera* to any of these groups. Furthermore, the biogenicity of *Farghera* has been recently questioned by Jago et al. (2012) who argued that it represents patterns produced by weathering and mobilization of iron oxides on sandstone. The Early Silurian (Llandoverian) associations of thalloid terrestrial organisms found in the Massanutten Sandstone of Virginia (Tomescu and Rothwell, 2006; Tomescu et al., 2009) comprise carbonaceous compressions some of which compare favorably with lichen thalli in terms of internal structure (Tomescu et al., 2010) but cannot be unequivocally recognized as lichens.

The Lochkovian (Early Devonian) Ditton Group of England hosts the oldest unequivocal lichens. *Cyanolichenomycites* Honegger et al. (2013) is a thallus with dorsiventral organization formed by an ascomycete and a Nostoc-like photobiont. *Chlorolichenomycites* Honegger et al. (2013) is another dorsiventrally organized thallus formed by an ascomycetous mycobiont with a photobiont of presumed algal affinities and mycobiont-photobiont interfaces consisting of wall-to-wall appositions.

Devonian rocks have yielded several other fossil taxa interpreted as lichens. Preserved by cellular permineralization in the Early Devonian (Praghian) Rhynie Chert (Scotland), *Winfrenatia* Taylor et al. (Taylor et al., 1995, 1997) is an association between cyanobacterial photobionts and mycobionts with aseptate hyphae of zygomycete or glomeromycete affinity (Taylor et al., 1997). Excellent preservation allowed for detailed characterization of the anatomy and life history of this lichen. Upon examination of additional specimens, Karatygin et al. (2009) reinterpreted *Winfrenatia* as a tripartite lichen-type association between a fungus and two types of cyanobacteria, one coccoid and the other filamentous.

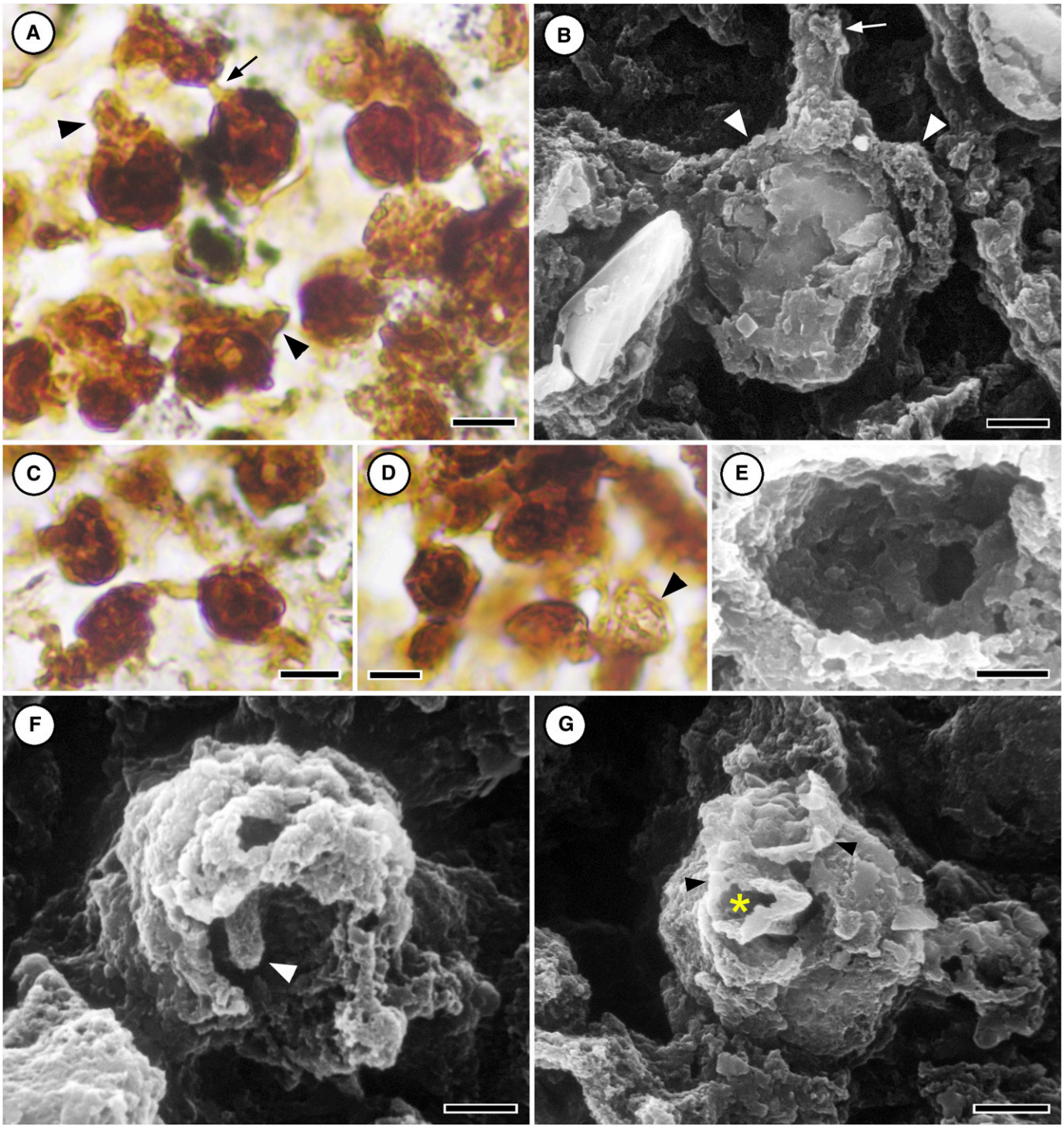

Fig. 3. *Honeggeriella complexa* gen. et. sp. nov. Holotype P13308 J top. Mycobiont-photobiont interface. (A) Detail of photobiont layer with hyphae connecting algal cells (arrow), fungal appressoria (arrowheads), and photobiont cell pair (top right); scale bar = 5 μm; peel #10. (B) Fungal hypha (arrow) produces branches (arrowheads) wrapped around photobiont cell; scale bar = 2 μm; peel #9. (C) Network of mycobiont hyphae connecting photobiont cells; scale bar = 5 μm; peel #11; (D) Net-like hyphal casing (arrowhead) from which photobiont cell has been removed by the peeling process; scale bar = 5 μm; peel #11. (E) Ruptured photobiont cell; hole left by fungal haustorium is visible across the cell lumen on the inner surface of the cell wall; scale bar = 1 μm; peel #7. (F) Rupture in photobiont cell wall exposing intracellular haustorium (arrowhead); scale bar = 1 μm; peel #7. (G) Photobiont cell with vertical track consisting of remnants of encasing fungal hypha (between arrowheads); haustorial branch (*) of missing hypha penetrates the photobiont; note mycobiont appressoria connected to the photobiont at top and bottom; scale bar = 2 μm; peel #7.

TABLE 1. Fossil lichens and lichen-like fossils.

	Recognition as lichen	Age	Rock unit	Basis for proposed lichen identity	Mycobiont identity	Photobiont identity	References
Thucomyces	incomplete evidence	Archean-Proterozoic	Carbon Leader Reef (Witwatersrand Basin), South Africa	anatomy, morphology	hyphae	photobiont not documented	Hallbauer et al., 1977; Hallbauer and van Warmelo, 1974
Lichen-like association	incomplete evidence	Neoproterozoic	Doushantuo Fm., China	anatomy	hyphae (?glomeromycete)	cyanobacteria	Yuan et al., 2005
Farghera	incomplete evidence	Cambrian-Ordovician boundary	Grindstone Range Sandstone, South Australia	morphology	mycobiont not documented	photobiont not documented	Retallack, 2009
Thalloid compressions	incomplete evidence	Early Silurian	Massanutten Sandstone, Virginia, USA	morphology, structure	mycobiont not documented	photobiont not documented	Tomescu and Rothwell, 2006; Tomescu et al., 2009
Cyanolichenomycites	accepted lichen	Early Devonian	Ditton Group, England	anatomy, morphology	ascomycete	cyanobacteria	Honegger et al., 2013
Chlorolichenomycites	accepted lichen	Early Devonian	Ditton Group, England	anatomy, morphology	ascomycete	chlorophyte	Honegger et al., 2013
Winfrenatia	accepted lichen	Early Devonian	Rhynie Chert, Scotland	anatomy, morphology	aseptate hyphae (zygomycete or glomeromycete)	cyanobacteria	Taylor et al., 1997; Karatygin et al., 2009
Flabellitha	incomplete evidence	Middle Devonian	Akbastau Fm., Kazakhstan	morphology, structure, spores	ascomycete	photobiont presence uncertain	Jurina and Krassilov, 2002
Spongiophyton	incomplete evidence	Lower-Middle Devonian	North and South America, Africa	anatomy, morphology	septate hyphae	photobiont not documented	Taylor et al., 2004; Stein et al., 1993
Thalloid compressions	incomplete evidence	Middle Triassic	Wallingarah Fm. and Basin Creek Fm., New South Wales, Australia	morphology	mycobiont not documented	photobiont not documented	Webb and Holmes, 1982
Daohugouthallus	incomplete evidence	Middle-Late Jurassic	Jiulongshan Fm., China	morphology	mycobiont not documented	photobiont not documented	Wang et al., 2010
Pelicothallos	incomplete evidence	Early Eocene	Wilcox Fm., Tennessee, USA	anatomy	absent	*Cephaleuros*-like cells (Trentepohliaceae)	Sherwood-Pike, 1985
Lichen-like fossil	incomplete evidence	Eocene	Baltic amber	morphology	?ascomycete	photobiont not documented	Garty et al., 1982
Anzia, *Alectoria*, *Calicium*, *Chaenotheca*	accepted lichen	Paleocene-Eocene	Baltic amber	anatomy, morphology	ascomycete	chlorophyte	Mägdefrau, 1957; Rikkinen and Poinar, 2002; Rikkinen, 2003
Phyllopsora, *Parmelia*	accepted lichen	Eocene-Miocene	Dominican amber	anatomy, morphology	ascomycete	chlorophyte	Poinar et al., 2000; Rikkinen and Poinar, 2008
Lobariaceae impression	accepted lichen	Miocene	Weaverville Fm., California, USA	morphology	mycobiont not documented	photobiont not documented	Peterson, 2000

Also in the Devonian, the leaf-like compression *Flabellifolium* Jurina and Putiatina described from the Givetian of Kazakhstan (Jurina and Putiatina, 2000) has been reinterpreted as a lichen under the name *Flabellitha* Jurina and Krassilov (2002). Internal anatomy preserved by authigenic cementation is reminiscent of lichens in several extant families. Ascospores and sunken apothecia were documented, but the spheroidal structures present in the subcortical layer could not be unequivocally resolved as photobiont cells. The enigmatic *Spongiophyton* Krausel, widespread during the Lower and Middle Devonian (occurrences in the Americas and Africa), has also been interpreted as a lichen (Stein et al., 1993; Taylor et al., 2004). While the fossils do possess lichen-like morphology and consist of fungal tissue, the photobiont component of *Spongiophyton* has yet to be detected.

The Mesozoic record comprises lichen-like fossils of equivocal affinities. Webb and Holmes (1982) described in the Middle Triassic of Queensland (Australia) thalloid compressions which resemble extant foliose lichens but could not be assigned to any taxonomic group due to the lack of diagnostic features. Thalloid compression-impression fossils described as *Daohugouthallus* X. Wang et al. from rocks at the Middle-Late Jurassic boundary in China, could represent thalloid liverworts, algae, or lichens. Although their nature remains unresolved, two structural features of these fossils, i.e., filiform appendages similar to lichen cilia and ruptured branch tips reminiscent of lichen soralia, point toward lichens as the more likely interpretation (Wang et al., 2010).

The Cenozoic fossil record of lichens is comparatively richer. *Pelicothallos* Dilcher, originally described from the Eocene of Tennessee as an epiphyllous microthyriaceous fungus (Dilcher, 1965) and reinterpreted as an alga (Reynolds and Dilcher, 1984), has also been suggested to bear structures comparable to those of *Cephaleuros* Kunze, a trentepohliacean alga that includes species involved in lichen symbioses (Sherwood-Pike, 1985). A handful of lichen fossils belonging to extant genera have been found in amber deposits. Baltic amber has yielded lichen-like fossils (Garty et al., 1982), as well as specimens assigned to extant genera – *Alectoria* Ach., *Anzia* Stizenb., *Calicium* Pers., and *Chaenotheca* Th. Fr. (Mägdefrau, 1957;

Rikkinen and Poinar, 2002; Rikkinen, 2003). Two *Parmelia* Ach. and one *Phyllopsora* Müll. Arg. species have been identified in Dominican amber (Poinar et al., 2000; Rikkinen and Poinar, 2008). The Early Miocene flora of Weaverville (California) has yielded a lichen impression assignable to the Lobariaceae that closely resembles *Lobaria pulmonaria* (L.) Hoffm. (Peterson, 2000).

This review of the fossil record shows that although putative lichen fossils cover a broad chronostratigraphic range that spans the entire Phanerozoic and begins as early as the Precambrian, very few of these fossils meet the criteria required for recognition of *bona fide* lichens (Table 1). These are the Devonian *Cyanolichenomycites*, *Chlorolichenomycites*, and *Winfrenatia*, and the Cenozoic amber lichens; the Miocene compression of the Weaverville Formation, although lacking any internal structures, is so closely similar to lobariaceous lichens and unlike other thalloid organisms that its lichen affinity is beyond question.

The lichen nature of Honeggeriella— The thallus of *Honeggeriella* combines two different types of organisms. One is filamentous and consists of branched, septate hyphae, whereas the other consists of globose cells. The septate organism conforms to the body plan of a fungus. Some fungi produce speroidal vesicles and other inflated structures at the tips or along their hyphae. The globose cells present in *Honeggeriella* are different from such fungal structures because: (1) the contacts between the walls of the fungal hyphae and those of globose cells are often irregular or abrupt, and do not show the continuity characteristic of fungal vesicles; and (2) the physical association between the fungal hyphae and the globose cells spans several different geometries inconsistent with fungal vesicles, including hyphae wrapped around the globose cells and hyphae that penetrate the latter (see next paragraph). The globose cells are therefore best interpreted as coccoid bacteria or algae. Consequently, the association of organisms that characterizes *Honeggeriella* conforms to the association between a fungal partner (mycobiont) and a photosynthetic partner (photobiont) seen in lichens. The types of interfaces (see next paragraph) repeatedly documented between the mycobiont and photobiont of *Honeggeriella* demonstrate recurring physiological interaction between the two bionts and are identical to those known in modern lichen-type associations. Furthermore, the stratified structure and relative positions of the photobiont and mycobiont of *Honeggeriella* reflect a thallus identical in its internal organization to those of extant heteromerous lichens. Thus, all the criteria required for ascertaining a lichen are met in *Honeggeriella* which is, therefore, a *bona fide* lichen.

Nature of the mycobiont and photobiont— Transverse septation observed in the medullary and cortical hyphae suggests mycobiont affinities with the ascomycetes or basidiomycetes. However, lichenized basidiomycetes do not form stratified thalli with the type of structure seen in *Honeggeriella*. Furthermore, careful observation has shown that clamp connections are absent from the medullary hyphae (the much tighter organization of the cortex does not allow the resolution needed for observation of such details). The fact that the finest details of hyphal branching at the mycobiont-photobiont interface are well-preserved and conspicuous, rules out preservational bias as an explanation for the lack of clamp connections. Together, these indicate that the mycobiont of *Honeggeriella complexa* is an ascomycete. The absence of reproductive structures hampers further classification of the fungal biont.

The photobiont of *Honeggeriella complexa* is represented by single cells or pairs of tightly appressed cells that appear uniformly distributed throughout the photobiont layer. In living lichens, identification of some lichen photobionts to even the genus level is difficult, if not impossible, without isolation in axenic culture (Büdel, 1992; Gartner, 1992; Friedl and Büdel, 2008). Therefore, in the absence of definitive cytological and reproductive characters, little can be said regarding the identity of the photobiont of *Honeggeriella* beyond the phylum level. A number of features indicate that the photobiont has chlorophyte rather than cyanobacterial affinities. These features include cell size, morphology, grouping, and characteristics of the mycobiont-photobiont interface, and are discussed in the next paragraph.

In *Honeggeriella*, well-preserved, undamaged photobiont cells are globose in shape, most often occur singly, and and range in size between 5.8-11.6 μm. A survey of the published literature (e.g., Honegger, 1984; Tschermak-Woess, 1988; Büdel, 1992; Hammer, 1999; Honegger, 2001; Friedl and Büdel, 2008) reveals that in extant lichens, green algal photobionts are generally larger in size (ca. 5-30 μm) while cyanobacterial photobionts are comparatively small (ca. 1-15 μm). However, there is a wide range of overlap within which cell size is not diagnostic of either of the two groups. The photobiont cells of *Honeggeriella* are relatively small in size and fall within this size range overlap. Therefore, size alone is not diagnostic of the photobionts in *Honeggeriella*. However, the chlorophyte nature of the latter cannot be excluded, as, the cells of some green algal photobionts, such as *Coccomyxa* Schmidle (ca. 4-8 μm; Honegger, 2001), are smaller than those of *Honeggeriella*, while the cells of trebouxioid chlorophyte photobionts can be as small as 10 μm.

Lichenized cyanobacteria usually form large colonies and, in coccoid taxa, numerous cells are contained within several internested gelatinous sheaths (Tschermak-Woess, 1988; Büdel, 1992; Friedl and Büdel, 2008). Chemical, structural (Helm et al., 2000), and experimental taphonomic (Bartley, 1996) studies have stressed the characteristic resistance to degradation of cyanobacterial extracellular polymeric substances (i.e., sheath and slime) in contrast to the cell contents. Despite very good cellular preservation, the photobiont of *Honeggeriella* shows no evidence of such gelatinous sheaths, e.g., adjacent photobiont cells in Fig. 2A and recurrent cell pairs (Figs. 3A, 2F, and 2H) show no evidence of a common envelope. The cells of filamentous cyanobacteria, such as *Nostoc* Vaucher ex Bornet and Flahault, are smaller (3-7 μm; Büdel, 1992) than those of *Honeggeriella.* Furthermore, *Honeggeriella* shows no evidence of large clusters of cells or filaments characteristic of cyanobacterial colonies (Tschermak-Woess, 1988; Büdel, 1992; Friedl and Büdel, 2008). Taken together, all these features are consistent with a green algal nature of the photobiont of *Honeggeriella.*

Additionally, haustorial mycobiont-photobiont interfaces are rarely found in cyanolichens (Plessl, 1963; Honegger, 1984; Galun, 1988; Honegger, 1992; Honegger, 2001). Where present, some of these interfaces conform more closely to Honegger's (1984, 1992) intraparietal haustoria (i.e., no penetration of photobiont cell wall) (Paran et al., 1971; Marton and Galun, 1976; Tschermak-Woess, 1983). True intracellular haustoria in cyanolichens have only been documented in those formed by basidiomycete fungi (Roskin, 1970; Ahmadjian, 1982). Furthermore, the haustoria formed in cyanobacteria are morphologically different from those seen in chlorolichens and in *Honeggeriella*; they are short and peg-like or highly branched arbuscule-like intrusions (Roskin, 1970; Ahmadjian, 1982), as

opposed to the long, narrow, fingerlike haustoria of chlorolichens (Honegger, 2001). Even though penetration of the photobiont wall by the mycobiont hyphae cannot be demonstrated in *Honeggeriella*, the morphology of the interface is consistent with that of the intracellular haustoria that characterize chlorolichens.

Recently divided photobiont cells are present throughout the specimen. The daughter cells appear symmetrical (Fig. 2F) and their collective size is similar to the average size of mature photobiont cells, suggesting that division was recent and little enlargement of the daughter cells had taken place. Noticeably, at this stage both cells, still connected along their adjacent walls but not enclosed in a common envelope are already surrounded by hyphae. The frequent occurrences of paired mature cells (Fig. 3A, 2H) probably represent sister cells derived from the same mitotic event.

***Subcellular structures of the photobiont*—**Some of the photobiont cells of *Honeggeriella* preserve subcellular structures. One type of structure is represented by spherical bodies whose shape suggests that they could be plasmolyzed protoplasts, cell nuclei, chloroplasts, or pyrenoids. A second type of subcellular structure consists of spheroidal units 3.5 μm in diameter, that occur in groups of three or four in photobiont cells with an irregular shape (Fig. 2G). If they are not artifacts of preservation, these structures could represent asexual reproductive propagules formed by internal cell division, i.e., zoospores, aplanospores, or autospores. Such propagules have been documented in chlorophycean photobionts including *Coccomyxa, Pseudotrebouxia* P. A. Archibald, *Dictyochloropsis* Geitler, *Myrmecia* Printz, or *Gloeocystis* Nägeli (Tschermak-Woess, 1988).

The preservation of photobiont structures at the subcellular level would not be surprising considering the quality of preservation of the specimen, as illustrated by details of the mycobiont-photobiont interface. While traditionally perceived as rare, preservation of subcellular detail is not unusual in the fossil record and numerous examples have been documented (Stewart and Rothwell, 1993). Such are the nuclei found in *Vesicaspora* (Schemel) Wilson and Venkatachala prepollen (Millay and Eggert, 1974) or the chloroplast grana observed in ultrastructural studies of Miocene leaves (Niklas and Brown, 1981). A variety of factors may have contributed to the preservation of photobiont cells in *Honeggeriella*. The location of photobiont cells inside a thallus of compact fungal tissue may have protected them against rapid degradation. This does not entirely explain how some of the best-preserved cells are located nearer the torn ends of the lichen thallus. However, a number of green algal photobionts are known to possess highly resistant sporopollenin-like biopolymers in their cell walls (*Coccomyxa*, *Elliptochlora* Tschermak-Woess; Brunner and Honegger, 1985). More generally, close association with fungi confers high resistance to external factors and greatly increases stress tolerance in their phototrophic associates (Bonfante and Genre, 2008; de Vera et al., 2008; Smith et al., 2010). All of these, combined with favorable taphonomic and diagenetic processes, would explain the excellent preservation of the *Honeggeriella* photobiont cells. This matches the high quality of preservation seen in other components of the Apple Bay fossil assemblage, which include ascomycete asci (Bronson et al., 2013 in press), moss antheridia, and bryophilous microbes.

***Mycobiont-photobiont relationship*—**Modern lichens represent a heterogeneous and polyphyletic (Nash, 2008) group of nutritional specialists that exhibit an extraordinary degree of variation in habit, morphology, and internal anatomy. Several patterns have been observed in the relationship between thallus organization and the structure of photobiont-mycobiont interfaces (Plessl, 1963; Honegger, 1986; Honegger, 1992; Galun, 1988). Heteromerous thalli that exhibit a high degree of anatomical and morphological complexity tend to form mycobiont-photobiont interfaces consisting of intraparietal haustoria wherein mycobiont hyphae do not penetrate the cell walls of the photobiont. In contrast, interfaces characterized by intracellular haustoria are found in many lichens that lack internal stratification and significant three-dimensional development, such as many crustose species (Honegger, 1986; Honegger 1990). Several exceptions to these trends have been identified. Although typically found in unstratified crustose lichens, intracellular haustoria are nevertheless characteristic of some stratified chlorolichens (e.g., *Parmelia sulcata* Taylor; Webber and Webber, 1970). Additionally, in lichens with less invasive interfaces, intracellular haustoria are often found in dead or senescent cells (Honegger, 1984). They have also been identified in individuals growing in extreme xeric conditions, in species that ordinarily exhibit only wall appositions (Ben-Shaul et al., 1969; Galun et al., 1970).

Several lines of evidence indicate that although *Honeggeriella* is a complex lichen, its mycobiont-photobiont interface consisting of intracellular haustoria represents a systemic character and not an age- or environment-related character. The frequent occurrence of intracellular haustoria in healthy photobionts suggests that they are the normal type of interface and were not restricted to senescent cells. Furthermore, in extant lichens with intracellular haustorial interfaces, not all photobiont cells are penetrated by haustoria (Galun, 1988). The composition of the allochthonous plant assemblages from the Apple Bay locality, which include coniferous gymnosperms, ferns, and bryophytes (Stockey and Rothwell, 2009), is inconsistent with xeric conditions. Growth rings observed in coniferous stems at the locality indicate a temperate seasonal climate, precluding xeric environmental conditions which are, moreover, unfavorable to plant fossil preservation.

Honeggeriella exhibits a combination of characters atypical of many modern lichens (Honegger, 1991), wherein complex thallus organization is paired with an interface characterized by intracellular haustoria. This combination has only been documented in the extant species *Parmelia sulcata* (Webber and Webber, 1970). However, detailed characterization of lichen interfaces is restricted to a handful of extant taxa. Therefore, despite being uncommon in modern lichens, this condition may be more prevalent than currently assumed.

***Affinities of* Honeggeriella—**The anatomical organization of *Honeggeriella* is so similar to that of extant lichens that it strongly suggests affinities with modern taxa. The thallus structure of *Honeggeriella* is superficially similar to that seen in many heteromerous lichen species (e.g., *Lasallia pustulata* (L.) Mérat, *Parmelia sulcata*; Honegger, 2001). The frequent occurrence of this type of thallus structure among lichens, along with a general lack of emphasis on details of internal anatomy in the diagnoses of most extant lichen genera, frustrates attempts at more narrowly circumscribing the taxonomic affinities of *Honeggeriella*. Although thallus morphology and growth habit cannot be documented due to the small size of the fragment analyzed, the complex structure and dorsiventral organization indicate that *Honeggeriella* was either a foliose or a squamulose form. Foliose lichens possess dorsiventral thalli that generally lie

flat against their substrate. Such lichens often possess specialized appendages for attachment (e.g., rhizines, cilia) on their lower cortex. Squamulose lichens grow closely appressed to their substrate and have lobes (squamules) that are free and raised above the substrate (Büdel and Scheidegger, 2008). Their thalli can be internally stratified very much like those of foliose lichens (Honegger, 2001). The lower cortex of *Honeggeriella complexa* preserves no evidence of rhizines, cilia, or tomentum, but such structures could easily have been lost during the transport process. Alternatively, even if *Honeggeriella* had rhizines or cilia, these structures could have been simply absent in the region of the thallus from which the fossilized fragment originated.

Honeggeriella *and the lichen fossil record*—Regardless of its taxonomic relationships, *Honeggeriella* is a necessary addition to the sparse Mesozoic fossil record of lichens and the first lichen described from the exceptionally rich Early Cretaceous flora from Apple Bay. Unequivocal heteromerous lichens are rare in the fossil record. They are known to date only from Cenozoic amber (55 myr or younger), which has yielded specimens assignable to modern genera (Rikkinen and Poinar, 2008) and from ca. 415 million year old Early Devonian rocks (Honegger et al., 2013). Other pre-Cenozoic fossils potentially representing heteromerous lichens, such as *Spongiophyton* or *Flabellitha*, have yet to see the presence and nature of their photobionts resolved. While *Winfrenatia* exhibits relatively complex structure, the mycobiont does not form differentiated tissues and the overall morphology of thalli is distinctly different from that of modern stratified lichens. Characterized by a thallus exhibiting a high level of organization, *Honeggeriella* is the only unequivocal heteromerous lichen formed by ascomycetes and green algae that bridges the wide gap between Cenozoic and Early Devonian heteromerous chlorolichens. The mycobiont-photobiont interface has rarely been documented to date in the fossil record—in the Devonian *Chlorolichenomycites* (Honegger et al., 2013) and the cyanolichen *Winfrenatia* (Taylor et al., 1997; Karatygin et al., 2009), and in Cenozoic amber, in *Phyllopsora dominicanus* Rikkinen and Poinar (2008). In this context, *Honeggeriella* provides the only fossil evidence to date for mycobiont-photobiont interfaces characterized by intracellular haustoria.

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