Filamentous cyanobacteria preserved in masses of fungal hyphae from the Triassic of Antarctica

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Filamentous cyanobacteria preserved in masses of fungal hyphae from the Triassic of Antarctica

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Abstract

Permineralized peat from the central Transantarctic Mountains of Antarctica has provided a wealth of information on plant and fungal diversity in Middle Triassic high-latitude forest paleoecosystems; however, there are no reports as yet of algae or cyanobacteria. The first record of a fossil filamentous cyanobacterium in this peat consists of wide, uniseriate trichomes composed of discoid cells up to 25 µm wide, and enveloped in a distinct sheath. Filament morphology, structurally preserved by permineralization and mineral replacement, corresponds to the fossil genus *Palaeolyngbya*, a predominantly Precambrian equivalent of the extant *Lyngbya* sensu lato (Oscillariaceae, Oscillatoriales). Specimens occur exclusively in masses of interwoven hyphae produced by the fungus *Endochaetophora antarctica*, suggesting that a special micro-environmental setting was required to preserve the filaments. Whether some form of symbiotic relationship existed between the fungus and cyanobacterium remains unknown.

Keywords: *Endochaetophora antarctica*, fungal reproduction, lichen, Mesozoic, Mucoromycota, Oscillariaceae, *Palaeolyngbya*, peat, symbiosis
Introduction

Cyanobacteria, one of the most successful groups of prokaryotic microorganisms on Earth, were instrumental in the oxygenation of the atmosphere and, as primary producers and nitrogen-fixers, were and are prominent contributors to Earth’s nutrient cycles (Knoll, 2008). The fossil record of these life forms is extensive and varied, with a peak of documented morphologies and formally described taxa in the Proterozoic (~2.54–0.54 Ga) (Tomitani et al., 2006; Knoll, 2008; Schopf, 2012).

Fossil cyanobacterial filaments that correspond in morphology to the modern genus *Lyngbya* (Komárek et al., 2014; Guiry & Guiry, 2019) are ordinarily assigned to *Palaeolyngbya*, a fossil taxon for wide, unbranched filaments composed of cylindrical trichomes with discoid cells several times wider than long, and colorless sheaths (e.g. Schopf, 1968). *Palaeolyngbya* is primarily Proterozoic and Cambrian in age (see references in Butterfield, Knoll & Swett, 1994; Sergeev, Sharma & Shukla, 2012). However, exquisitely preserved specimens have been reported recently from the Lower Devonian Rhynie chert (Krings, 2019), and there is also one record from the Permian of China (Liu & Li, 1986: pl. 1, fig. 5). The genus has not yet been documented from the Mesozoic, whereas Cenozoic fossils and subfossil specimens are commonly assigned to *Lyngbya*, (e.g. Waggoner, 1994; Stankevica et al., 2015).

Permineralized peat from Fremouw Peak in the central Transantarctic Mountains, Antarctica, represents a unique source of new information on Middle Triassic (240 Ma) high-latitude swamp-forest ecosystems. The peat contains an exceptionally diverse structurally preserved flora (reviewed by Escapa et al., 2011; Bomfleur et al., 2013, 2014; Decombeix et al., 2014), together with numerous examples of fungi and fungus-like organisms (reviewed by Harper et al., 2016). However, no evidence of the occurrence of photoautotrophic microorganisms, such
as cyanobacteria and eukaryotic algae, in the Fremouw Peak permineralized peat has been
discovered to date.

This paper presents the first record of a filamentous cyanobacterium from the Fremouw
Peak permineralized peat. Specimens are similar morphologically to *Palaeolyngbya kerpii* from
the Lower Devonian Rhynie chert (Krings, 2019), and to several Proterozoic species of that genus
(Schopf, 1968; Butterfield, Knoll & Swett, 1994; Sergeev, Sharma & Shukla, 2012). The Antarctic
filaments all occur within masses of interwoven hyphae produced by a fungus. This discovery is
important because it provides insights into the taphonomic circumstances that appear to be
imperative to the preservation of cyanobacteria in permineralized peat.

**Material & Methods**

Data were collected from the same locality previously described in Harper et al. (2015),
specifically the fossils occur in permineralized (silicified) peat from the Fremouw Formation in
the central Transantarctic Mountains of Antarctica (Taylor, Taylor & Collinson, 1986; Cúneo et
al., 2003). The Fremouw Formation is a 620–750-m-thick siliclastic succession deposited by low
sinuosity braided streams (Faure & Mensing, 2010). The fossils occur within several allochthonous
clasts that are at approximately the same stratigraphic level within a trough-crossbedded, medium-
grained, greenish-gray volcanioclastic sandstone. Permineralized peat is found at a single level at
the Fremouw Peak locality, approximately 30 m below the top of the formation (Figure 1). Chunks
of the peat were likely rafted into their current position during a flooding event that caused them
to be stranded on sand bars prior to permineralization (Taylor, Taylor & Collinson, 1989) and
isolated into individual lenses within the outcrop. The peat became silicified after burial; the age
of the plant remains contained in the peat is equivalent to that of the surrounding elasic sediments,
i.e. fluvial sandstone, which also contain trunks of wood of equivalent age to the peat (Decomeix et al., 2014). The silica for the permineralization is interpreted to have come from the dissolution of abundant siliceous, volcanic detritus from the upper Fremouw Formation (Taylor, Taylor & Collinson, 1989).

The exact age of the Fremouw Peak peat deposit remains uncertain. The peat and surrounding material have been dated as Anisian (early Middle Triassic) based on palynomorphs and nearby vertebrate fossils (Farabee, Taylor & Taylor, 1990; Hammer, 1990; Sidor, Damiani & Hammer 2008; Faure & Mensing, 2010). Recent detrital-zircon dating indicates that the base of member B of the Fremouw Formation is ~242.3 ± 2.3 Ma (= early Ladinian; see Elliott et al., 2017: fig. 4), but the silicified peat is located in the younger member C of the Fremouw Formation. A late Ladinian or possibly Carnian age is, therefore, more likely to be accurate for the Fremouw Peak peat deposits (Bomfleur et al., 2014; Elliot et al., 2017).

The material used in this study was collected during the 2010–2011 austral summer Antarctic field season. Peat blocks were cut into slabs and then immersed in 48% HF to dissolve the silica. Acetate peels were produced from the etched surfaces by using the technique outlined by Joy, Willis & Lacey (1956) modified for hydrofluoric acid (Galtier & Phillips, 1999). Consecutive peels of promising specimens were mounted on microscope slides in Eukitt®. Other slabs were cut into wafers and used for the preparation of thin sections (Hass & Rowe, 1999), with a thickness of 40–60 µm. Wafers of the peat were cemented to a glass slide and then ground thin enough to be viewed in transmitted light. Mounted peels and thin sections were analyzed with a Leica DM LB2 transmitted light microscope at the highest possible total magnification (400× or 1000×); digital images were captured with a Leica DFC-480 camera and processed in Adobe Photoshop CS5. When suitable specimens were identified, they were processed minimally (i.e.
contrast, brightness, and focal stacking) and measurements were taken using Adobe Photoshop
CS6 Version 13.0 x64 (©1990–2012, Adobe Systems). When necessary, multiple images of the
same specimen were recorded at different focal planes and compiled to produce composite images,
(Kerp & Bomfleur, 2011). The images were stacked in Adobe Photoshop CS6, and specific areas
were modified to reveal the complete three-dimensional image as seen in the thin section.
Composite images in this study are Figure 2A–C. Specimen and slides are deposited in the
Paleobotanical Collections, Biodiversity Institute, University of Kansas (KUPB) under specimen
accession numbers KUPB 17054, 17729 E Bot, 17729 F Top, and 18084, and slide numbers KUPB
35,009–35,018.

Results

Context and preservation

Systematic screening of permineralized peat from the Fremouw Peak locality has yielded several
hundred blocks of leaf mats that contain predominantly degraded *Dicroidium* leaves (Pigg, 1990)
(“L” in Figure 2A, B), rare pieces of fragmented *Heidiphyllum* (Axsmith, Taylor & Taylor, 1998),
degraded plant axes, and intermixed detritus. Some of the leaves are surrounded by conspicuous
whitish areas, which are elongate oval or irregular in section view, 120–590 µm high, and up to 4
cm wide. The whitish areas comprise densely interwoven, thin-walled, irregularly septate fungal
hyphae 2–6 µm wide (arrows in Figure 2C) embedded in what appears to be a gelatinous matrix.

More than 95% of these formations, henceforth called “hyphal masses,” contain one or several
specimens of the enigmatic fungal reproductive unit *Endochaetophora antarctica* (Figure 2A, B),
formally described some 30 years ago based on dispersed specimens from the same locality (White
& Taylor, 1988, 1989). For a parallel study focusing on *E. antarctica*, we analyzed more than 50
blocks of leaf mats based on thin sections, each containing between 1 and 15 hyphal masses. In these blocks, approximately 25% of the larger masses containing fungal reproductive units also contain large cyanobacterial filaments, which are described below. *Endochaetophora antarctica* is characterized by a three-layered investment from which extend numerous prominent hollow, tube-like appendages (~4.5–10 µm wide and up to 130 µm long) that branch regularly (Figure 2D, E). Because the appendages are markedly different structurally from the cyanobacterial filaments, the two structures cannot be confused. The cyanobacterial filaments are not body fossils as the hyphal masses containing the fungal reproductive units, but rather represent (partial to full) mineral infillings or coatings, which are orange to reddish or have grayish outlines (Figure 2F–J; 3A–E). Cyanobacterial filaments have not been found in the peat matrix surrounding the hyphal masses, or elsewhere in the peat.

**Cyanobacterial filaments**

In the description of the fossil cyanobacterium, we use the terminology for filamentous cyanobacteria outlined by Komárek, Kling & Komárková (2003); trichomes with sheaths are traditionally termed filaments. Preserved filament portions (arrows in Figure 2G–J) are up to 740 µm long and 17–31 µm wide, and consist of straight or somewhat curved, cylindrical, uniseriate, and probably isopolar (i.e. no evidence indicative of heteropolarity has been found) trichomes of relatively uniform, short discoid cells, enveloped in a distinct sheath (Figure 4A–C). Most of the specimens demonstrate a regular pattern of discoid cells (or cell units), which are either empty or contain homogenous opaque matter (cell contents), 22.8–25 µm wide and 3.8–5 µm high (which equals a width-to-height ratio of 5:1) (Figure 4A). Other specimens, however, are preserved as empty sheaths (Figure 4F), whereas in still others the cells are recognizable only through the
arrangement of crystals (red to orange, or gray in appearance) (Figures 2G, 3A–E, 4E). Different modes of cell and trichome preservation may also occur within the same filament (Figure 2F).

Sheaths are colorless, unornamented, and well-recognizable in all specimens. They range in thickness from 1 to 4 µm; however, sheath thickness within one filament varies only by 1–1.5 µm. Stratification of the sheath is not recognizable in any of the specimens; external constrictions or folds at cross walls are also not discernible. Most specimens represent intercalary trichome portions that end bluntly and appear to have broken off. Compelling evidence of trichome tips has not been found. There is a single poorly preserved specimen that appears to have a tapering tip with a round end; however, it is difficult to be sure that this represents an actual trichome end (Figure 3A, black arrow in 2G). Unfortunately, the preservation of the filaments by mineral replacement does not enable recognition of cell division patterns. One specimen shows possible hormogonium formation (Figure 4D, E). This filament is the only example displaying a pronounced constriction, and the cell at the constriction is umbilicated. One intercalary filament portion approximately 87 µm long might contain a necridium based on the presence of a pair of differently shaped and colored cells (Figure 4B). No evidence has been found of (false) branching and the formation of heterocysts or akinetes. For a graphical overview of the spatial distribution of cyanobacterial filaments and *E. antarctica* within one of the hyphal masses, refer to Figure 5.

**Discussion**

The Triassic permineralized peat from Fremouw Peak has been studied intensively for more than 45 years, (e.g. Schopf, 1973; Taylor, Taylor & Collinson, 1989). Plant and fungal paleodiversity have been documented in great detail based on large numbers of structurally preserved fossils (e.g. Escapa et al., 2011; Harper et al., 2016), and the paleoecosystem has been reconstructed as a
diverse peat-forming swamp forest dominated by corystospermalean seed ferns and voltzialean
conifers, with understory elements including the enigmatic Petriellales, ferns, and sphenophytes
(Taylor, Taylor & Collinson, 1989; Escapa et al., 2011; Bomfleur et al., 2014; Decombeix et al.,
2014). However, there is not a single report of cyanobacteria from Fremouw Peak despite these
organisms being regular constituents of comparable modern peat-forming ecosystems (Jackson,
Liew & Yule, 2009; Yule & Gomez, 2009; Marsid et al., 2015). Fossils of cyanobacteria have been
described from Antarctica (Priestley & David, 1912; David & Priestley, 1914; Chapman, 1916;
Gordon, 1921; Hill, 1964; Breed, 1971; Rees, Pratt & Rowell, 1989; Rowell & Rees, 1989; Riding,
1991; Wrona & Zhuravlev, 1996; Wrona, 2004); however, none come from the Mesozoic.

**Comparison and affinities**

The Fremouw Peak cyanobacterial filaments correspond in morphology to the fossil genus
*Palaeolyngbya*, a form taxon and repository for wide, unbranched, uniseriate fossil trichomes that
are composed of discoidal to cylindrical cells without any constrictions at the cross walls, and
enveloped in a prominent, uni- or multilayered, smooth sheath, and hence comparable in basic
organization to extant *Lyngbya* sensu lato (Oscillatoriaceae, Oscillatoriales; see Butterfield, Knoll
& Swett, 1994: p. 60/61; Sergeev, Sharma & Shukla, 2012: p. 300). The main criterion used to
discriminate species of *Palaeolyngbya*, according to Butterfield, Knoll & Swett (1994: p. 61), is
the width of the uncollapsed sheath (i.e. filament width); for example, (sheath width in
parentheses) *P. catenata* (10–30 µm) and *P. hebeiensis* (30–60 µm) (Butterfield, Knoll & Swett,
1994), *P. giganteus* (42–85 µm), *P. helva* (11–14 µm), and *P. barghoorniana* (≤15 µm) (Sergeev,
Sharma & Shukla, 2012), and *P. kerpii* (22–>30 µm) (Krings, 2019). The sheaths of the Fremouw
Peak filaments are 17–31 µm wide and, thus, correspond best to the recently described *P. kerpii*
from the Lower Devonian Rhynie chert. Assignment of the Triassic filaments to *P. kerpii* is conceivable. However, *P. kerpii* is preserved as a body fossil providing detailed insights into filament morphology, together with specific developmental details, whereas the Fremouw Peak fossils represent mineral replacements that provide a fair image of the filament morphology, but do not reveal any structural or developmental details. As a result, it is difficult, if not impossible, to determine whether the latter correspond to *P. kerpii* or belong to a different fossil species. Therefore, we include the Fremouw Peak filaments in open nomenclature as *Palaeolyngbya* sp.

**Cyanobacteria in Triassic permineralized peat**

One reason for the lack hitherto of documented evidence of cyanobacteria in the Triassic permineralized peat from Fremouw Peak may be that these minute life forms simply have been overlooked in cursory screenings of peels or thin sections at low magnification. Moreover, the quality of plant fossils preserved in the peat matrix depends largely on their condition (i.e. alive and fully intact, moribund but still attached, or abscised and in the process of degradation) at the time of permineralization. Evidence of microbial life appears to be generally rare in regions of the peat that contain well-preserved plant remains, but rather occurs in peat comprising (partially) degraded and tattered plant material not worthwhile for investigators interested in the plants and, thus, are often not seen (Taylor & Krings, 2010). On the other hand, the Fremouw Peak permineralized peat is interpreted to have developed in a three-step process (Schopf, 1971; Taylor, Taylor & Collinson, 1989), through which fragile structures may have been altered secondarily or destroyed (Harper et al., 2018). Finally, the lack of evidence for these organisms from permineralized peat elsewhere, (e.g. DiMichele & Phillips, 1994; Galtier, 2008; McLoughlin & Strullu-Derrien, 2015; Slater, McLoughlin & Hilton, 2015), could mean that peat-forming
paleoenvironments were perhaps generally not conducive to the preservation of cyanobacteria. The scarcity of cyanobacterial fossil in peat deposits stands in stark contrast to silicified geothermal hot spring (sinter) deposits, which often yield diverse assemblages of structurally preserved cyanobacteria (e.g. Guido et al., 2010; García Massini et al., 2012; Hamilton et al., 2019; Krings, 2019; Krings & Harper, 2019; Krings & Sergeev, 2019). Nothing is known to date about the possible influence of a hydrothermal system on the silicification process at Fremouw Peak (Taylor, Taylor & Collinson, 1989).

Cyanobacterial filaments have only been detected in the whitish hyphal masses produced by *Endochaetophora antarctica* around individual *Dicroidium* leaves on the forest floor (Harper, 2015). Because the filaments are salient structures, we rule out the possibility that they have been overlooked in the peat matrix surrounding the hyphal masses and in other types of fossils, such as hollow plant axes or decayed leaves. This peculiar pattern of spatial distribution raises the question as to why filaments are so abundant in the *E. antarctica* hyphal masses, but are absent (or cannot be traced) outside these occurrences?

One possible explanation is that a special micro-environmental setting was imperative for the filaments to become preserved intact. Research on fragile microorganisms, including cyanobacteria, exquisitely preserved elsewhere has provided evidence to suggest that certain micro-environmental settings (e.g. amber, walls of leech cocoons, interiors of hollow plant axes, small voids in the substrate, or microbial mat frameworks) had a cushioning effect on destructive mechanical forces, and hence were effective as microscopic conservation traps for delicate microbial life (Dörfelt, Schmidt & Wunderlich, 2000; Bomfleur et al., 2012, 2015; McLoughlin et al., 2016; Krings et al., 2018; Krings & Harper, 2019; Krings & Kerp, 2019). It is highly probable that special circumstances also were in play during the fossilization of the cyanobacteria from
Fremouw Peak. The hyphal masses, which are embedded in what appears to be a gelatinous matrix, may have served as a conservation trap by shielding the filaments from destructive mechanical forces, such as water movement and the taphonomic processes during peat formation, compaction, and permineralization. Moreover, certain substances excreted by the fungal hyphae into the surrounding matrix may have been biocidal and slowed down biological decomposition, or somehow facilitated the process of mineral replacement. If all this is accurate, then it raises another, equally difficult and probably even more complex question, namely as to why cyanobacterial filaments occur in large numbers within hyphal masses produced by a fungus.

Cyanobacteria in general (Dickinson, 1983; Zadorina et al., 2009; Andersen, Chapman & Artz, 2013), and certain members of *Lyngbya* in particular (Karosienė & Kasperovičienė, 2009; Koreivienė & Kasperovičienė & Karosienė, 2009), are constituents of modern peatland environments, and it would not be surprising to find these organisms also in ancient peat-forming ecosystems based on their geologic range. However, the opposite is the case. *Palaeolyngbya* filaments (and other cyanobacteria) were perhaps common and widespread on the wet forest floor covered in leaf litter interspersed with *E. antarctica* hyphal masses, in small pools of water, and maybe even on tree surfaces, but were destroyed during peat formation and the fossilization process, with the exception of those located within the protective confines of the hyphal masses (“cyanobacteria everywhere hypothesis”; see Figure 6). On the other hand, metagenomic analyses indicate that cyanobacteria represent a relatively small percentage of total microbial biomass in modern peat ecosystems, namely 0–4% in peat bogs and ~0.85% in tropical peat swamps (Gilbert & Mitchell, 2006; Kanokratana et al., 2011). Thus, it is also possible that *Palaeolyngbya* and other cyanobacteria have not been recorded more extensively because they were rare elements in this
type of paleoenvironment or occurred exclusively in certain areas of the ecosystem that are not
reflected by the silicified peat samples studied to date (see Krings & Sergeev, 2019).

Although the systematic affinity of *Endochaetophora antarctica* remains unresolved,
several authors have suggested it may belong to the Mucoromycota (see discussion by Krings,
Taylor & Dotzler, 2013). Specimens of another fossil fungus from Fremouw Peak, *Jimwhitea circumtecta*, provide the most persuasive fossil example of spores forming within a sporocarp and
embedded in what is commonly termed a gleba (Krings et al., 2012: fig. 2B–C). The hyphal masses
of *E. antarctica* are certainly not glebae in the strict sense of the definition (i.e. the central, internal
portion of a fruiting body; see Ulloa and Hanlin, 2012: p. 252), but may be analogous structures
within which the reproductive units formed. The chemical composition of glebae in
Mucoromycota is virtually unknown; however, glebae of certain present-day Basidiomycota are
composed primarily of amino acids and proteins (Oliveira & Morato, 2000). It is, therefore, a
possible, although highly speculative alternative premise at this time, that the cyanobacteria were
attracted to the components of the *E. antarctica* hyphal masses and therefore migrated into these
structures ("cyanobacteria migration hypothesis"; see Figure 7). Bearing in mind that the water in
peat-forming environments today is generally nutrient-poor and of low pH, it is possible to
envision that the cyanobacteria would gravitate towards nutritionally dense resources. Moreover,
it has been shown that, under certain stimuli or in high stress environments, some present-day
filamentous cyanobacteria actively migrate towards and assimilate specific amino acids (Gallucci
& Paerl, 1983; Michelou, Cottrell & Kirchman, 2007).

*A symbiosis?*
No direct evidence has been found to date that is suggestive of an interaction between the *Palaeolyngbya* filaments and *Endochaetophora antarctica*, nor has the nutritional mode of *E. antarctica* been deciphered. Nevertheless, the consistent co-occurrence of these two organisms begs the question as to whether this peculiar alliance may also have included some form of mutualism or parasitism. Mutualistic relationships between filamentous cyanobacteria and fungi today occur in the form of lichens (Hawksworth, 1988). The Fremouw Peak fossils concur with some of the criteria outlined by Lücking and Nelsen (2018: p. 552) for the identification of fossil lichens; the most important criterion, however, namely a physiological interdependence between the partners, cannot be evidenced. Another type of fungal symbiosis with filamentous cyanobacteria occurs in *Geosiphon pyriformis*, a fungus in the Glomeromycota that produces specialized bladders to harbor nitrogen-fixing cyanobacteria (*Nostoc* spp.) (Schüßler, 2002, 2012). *Palaeolyngbya* is non-heterocystous; however, certain non-heterocystous filamentous cyanobacteria, including *Lyngbya* under extremely stressful conditions, can also fix nitrogen (Bergman et al., 1997). In addition, some authors include *Geosiphon* within Mucoromycota (Glomeromycotina and Mucoromycotina) (Spatafora et al., 2016), to which also *E. antarctica* probably belongs. We speculate that perhaps there were extinct members of the Mucoromycota that formed non-lichen symbioses with cyanobacteria, and that the *Geosiphon-Nostoc* symbiosis represents a relic of this type of fungus-cyanobacterial symbiosis (Schüßler, 2002), which not only involved fungi interacting with endocytobiotic cyanobacteria, but perhaps also forms that house their cyanobacterial symbionts in hyphal masses. On the other hand, there is also the remote possibility that the fungus parasitized the cyanobacteria, which were somehow attracted into the hyphal masses (e.g. Arora, Filonow & Lockwood, 1983).
Conclusions

Palaeolyngbya in the Triassic permineralized peat from Fremouw Peak provides the first evidence of filamentous cyanobacteria from the Mesozoic of Antarctica. Moreover, the restricted occurrence of the cyanobacterial filaments within hyphal masses produced by a fungus suggests that special micro-environmental conditions have preserved these organisms in recognizable form, and that the fungal hyphal masses have served as microscopic conservation traps for microbial life (sensu Bomfleur et al., 2012). The recognition of cyanobacteria in microscopic conservation traps provides a search image that now can be used to trace this and other types of microorganisms in the vast amounts of permineralized peat that have been collected from Fremouw Peak. We anticipate that other cyanobacteria will be discovered as further special micro-environmental settings conducive to the preservation of microbial life are identified. The information obtained from studying the microbial component of Antarctic Mesozoic paleosystems may help to address questions pertaining specifically to the ecology of high–latitude plants and paleosystems, including such aspects of whether the only fossil cycad that has been documented to date from Antarctica, Antarctica cas schopfii (Hermsen, Taylor & Taylor, 2009), entered into a symbiotic relationship with cyanobacteria in a similar way as its relatives today (e.g. Lindblad & Bergman, 1990; Costa & Lindblad, 2002; Tajhuddin et al., 2010).

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References

Andersen R, Chapman SJ, Artz RRE. 2013. Microbial communities in natural and disturbed peatlands: A review. Soil Biology and Biochemistry 57:979–994. DOI: 10.1016/j.soilbio.2012.10.003

Arora DK, Filonow AB, Lockwood JL. 1983. Bacterial chemotaxis to fungal propagules in vitro and in soil. Canadian Journal of Microbiology 29:1104–1109. DOI: 10.1139/m83-170

Axsmith BJ, Taylor TN, Taylor EL. 1998. Anatomically preserved leaves of the conifer Notophytum krauselii (Podocarpaceae) from the Triassic of Antarctica. American Journal of Botany 85:704–713. DOI: 10.2307/2446541

Bergman B, Gallon JR, Rai AN, Stal, LJ. 1997. N_2 fixation by non-heterocystous cyanobacteria. FEMS Microbiology Reviews 19:139–185. DOI: 10.1016/S0168-6445(96)00028-9

Bomfleur B, Kerp H, Taylor TN, Moestrup Ø, Taylor EL. 2012. Triassic leech cocoon from Antarctica contains fossil bell animal. Proceedings of the National Academy of the United States of America 109:20971–20974. DOI: 10.1073/pnas.1218879109

Bomfleur B, Decombeix A-L, Escapa IH, Schwendemann AB, Axsmith B. 2013. Whole-plant concept and environment reconstruction of a Telemachus conifer (Voltziales) from the Triassic of Antarctica. International Journal of Plant Sciences 174:425–444. DOI: 10.1086/668686

Bomfleur B, Decombeix A-L, Schwendemann AB, Escapa IH, Taylor EL, Taylor TN, McLoughlin S. 2014. Habit and ecology of the Petriellales, an unusual group of seed plants
Bomfleur B, Mörs T, Ferraguti M, Reguero MA, McLoughlin S. 2015. Fossilized spermatozoa preserved in a 50-Myr-old annelid cocoon from Antarctica. Biology Letters 11:20150431. DOI: 10.1098/rsbl.2015.0431

Breed WJ. 1971. Permian stromatolites from Coalsack Col. Antarctic Journal of the United States 6(5):189–190.

Butterfield NJ, Knoll AH, Swett K. 1994. Paleobiology of the Neoproterozoic Svanbergfjellet Formation, Spitsbergen. Fossils and Strata 34:1–84. DOI: 10.1111/j.1502-3931.1994.tb01558.x

Chapman F. 1916. Report on a probable calcareous alga from the Cambrian Limestone breccia found in Antarctica at 85º South. Reports of the Scientific Investigations, British Antarctic Expedition, 1907–1909, Geology 2:81–84.

Costa JL, Lindblad P. 2002. Cyanobacteria in symbiosis in cycads. In: Rai AN, Bergman B, Rasmussen U, eds. Cyanobacteria in symbiosis. Dordrecht: Kluwer Academic, 195–206. DOI: 10.1007/0-306-48005-0_11

Cúneo NR, Taylor EL, Taylor TN, Krings M. 2003. In situ fossil forest from the upper Fremouw Formation (Triassic) of Antarctica: Paleoenvironmental setting and paleoclimate analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 197:239–261. DOI: 10.1016/S0031-0182(03)00468-1

David TWE, Priestley RE. 1914. Glaciology, physiography, stratigraphy, and tectonic geology of South Victoria Land. Reports of the Scientific Investigations, British Antarctic Expedition, 1907–1909, Geology 1:241.
Decombeix A-L, Bomfleur B, Taylor EL, Taylor TN. 2014. New insights into the anatomy, development, and affinities of corystosperm trees from the Triassic of Antarctica. Review of Palaeobotany and Palynology 203:22–34. DOI: 10.1016/j.revpalbo.2014.01.002

Dickinson CH. 1983. Micro-organisms in peatlands. In: Gore AJP, ed. Mires: swamp, bog, fen and moor: regional studies. Ecosystems of the world, Series 4B. Amsterdam: Elsevier Scientific, 225–245.

DiMichele WA, Phillips TL. 1994. Paleobotanical and paleoecological constraints on models of peat formation in the Late Carboniferous of Euramerica. Palaeogeography, Palaeoclimatology, Palaeoecology 106:39–90. DOI: 10.1016/0031-0182(94)90004-3

Dörfelt H, Schmidt AR, Wunderlich J. 2000. *Rosaria succina* spec. nov. – a fossil cyanobacterium from Tertiary amber. Journal of Basic Microbiology 40:327–332. DOI: 10.1002/1521-4028(20012)40:5/6<327::AID-JOBM327>3.0CO;2-E

Escapa IH, Taylor EL, Cúneo R, Bomfleur B, Bergene J, Serbet R, Taylor TN. 2011. Triassic floras of Antarctica: Plant diversity and distribution in high paleolatitude communities. PALAIOS 26:522–544. DOI: 10.2110/palo.2010.p10-122

Elliot DH, Fanning CM, Isbell JL, Hulett SRW. 2017. The Permo-Triassic Gondwana sequence, central Transantarctic Mountains, Antarctica: Zircon geochronology, provenance, and basin evolution. Geosphere 13:155–178. DOI: 10.1130/GES01345.1

Farabee MJ, Taylor EL, Taylor TN. 1990. Correlation of Permian and Triassic palynomorphs from the central Transantarctic Mountains Antarctica. Review of Palaeobotany and Palynology 65:257–265. DOI: 10.1016/0034-6667(90)90075-T

Faure G, Mensing TM. 2010. *The Transantarctic Mountains: Rocks, Ice, Meteorites and Water*. New York: Springer. DOI: 10.1007/978-90-481-9390-5_18
Gallucci KK, Paerl HW. 1983. *Pseudomonas aeruginosa* chemotaxis associated with blooms of N$_2$-fixing blue-green algae (Cyanobacteria). Applied and Environmental Microbiology 45:557–562.

Galtier J. 2008. A new look at the permineralized flora of Grand-Croix (Late Pennsylvanian, Saint-Etienne Basin, France). Review of Palaeobotany and Palynology 152:129–140. DOI: 10.1016/j.revpalbo.2008.04.007

Galtier J, Phillips TL. 1999. The acetate peel technique. In: Jones TP, Rowe, NP, eds. *Fossil Plants and Spores: modern techniques*. London: Geological Society, 67–70.

García Massini J, Channing A, Guido DM, Zamuner AB. 2012. First report of fungi and fungus-like organisms from Mesozoic hot springs. PALAIOS 27:55–62.

Gilbert D, Mitchell EAD. 2006. Microbial diversity in *Sphagnum* peatlands. Developments in Earth Surface Processes 13:287–318. DOI: 10.1016/S0928-2025(06)09013-4

Gordon WT. 1921. Scottish National Antarctic Expedition, 1902–1904: Cambrian organic remains from a dredging in the Weddell Sea. Transactions of the Royal Society of Edinburgh 52:681–714. DOI: 10.1017/S0080456800015957

Guiry MD, Guiry GM. 2019. ‘*Lyngbya* C. Agardh ex Gomont, 1892, nom. et typ. cons’ on AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Available at http://www.algaebase.org (accessed 9 October 2019).

Guido DM, Channing A, Campbell KA, Zamuner A. 2010. Jurassic geothermal landscapes and fossil ecosystems at San Agustín, Patagonia, Argentina. Journal of the Geological Society 167:11–20. DOI: 10.1144/0016-76492009-109

Hamilton AR, Campbell KA, Rowland JV, Barker S, Guido D. 2019. Characteristics and variations of sinters in the Coromandel Volcanic Zone: application to epithermal exploration. New
Hammer WR. 1990. Triassic terrestrial vertebrate faunas of Antarctica. In: Taylor TN, Taylor EL, eds. Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana. New York: Springer-Verlag, 42–50. DOI: 10.1007/978-1-4612-3238-4_5

Harper CJ. 2015. The diversity and interactions of fungi from the Paleozoic and Mesozoic of Antarctica. D. Phil. Thesis, University of Kansas.

Harper CJ, Taylor TN, Krings M, Taylor EL. 2015. Arbuscular mycorrhizal fungi in a voltzialean conifer from the Triassic of Antarctica. Review of Palaeobotany and Palynology 215:76–84. DOI: 10.1016/j.revpalbo.2015.01.005

Harper CJ, Taylor TN, Krings M, Taylor EL. 2016. Structurally preserved fungi from Antarctica: Diversity and interactions in late Paleozoic and Mesozoic polar forest ecosystems. Antarctic Science 28:153–173. DOI: 10.1017/S0954102016000018

Harper CJ, Taylor EL, Walker C, White JF, Serbet R, Krings M. 2018. Fungal sporulation in a Permian plant fragment from Antarctica. Bulletin of Geosciences 93:13–26. DOI: 10.3140/bull.geosci.1681

Hass H, Rowe NP. 1999. Thin sections and wafering. In: Jones TP, Rowe NP, eds. Fossil plants and spores: modern techniques. London: Geological Society, 76–81.

Hawksworth DL. 1988. The variety of fungal-algal symbioses, their evolutionary significance, and the nature of lichens. Botanical Journal of the Linnean Society 96:3–20. DOI: 10.1111/j.1095-8339.1988.tb00623.x
Hermsen EJ, Taylor EL, Taylor TN. 2009. Morphology and ecology of the *Antarcticycas* plant. Review of Palaeobotany and Palynology 153:108–123. DOI: 10.1016/j.revpalbo.2008.07.005

Hill D. 1964. *Archaeocyatha* from loose material at Plunkett Point at the head of Beardmore Glacier. In: Adie RJ, ed. *Antarctic Geology*. New York: Interscience Publishers, 609–622.

Jackson CR, Liew KC, Yule CM. 2009. Structural and functional changes with depth in microbial communities in a tropical Malaysian peat swamp forest. Microbial Ecology 57:402–412. DOI: 10.1007/s00248-008-9409-4

Joy KW, Willis AJ, Lacey WS. 1956. A rapid cellulose peel technique in palaeobotany. Annals of Botany 20:635–637. DOI: 10.1093/oxfordjournals.aob.a083546

Kanokratana P, Uengwetwanit T, Rattanachomsri U, Bunterngsook B, Nimchua T, Tangphatsornruang S, Plengvidhya V, Champreda V, Eurwilaichitr L. 2011. Insights into the phylogeny and metabolic potential of a primary tropical peat swamp forest microbial community by metagenomic analysis. Microbial Ecology 61:518–528. DOI: 10.1007/s00248-010-9766-7

Karosienė J, Kasperovičienė J. 2009. Filamentous epiphyton cyanobacteria (Oscillatoriales, Nostocales) new to algal flora of Lithuanian freshwater. Botanica Lithuanica 15:79–91.

Kerp H, Bomfleur B. 2011. Photography of plant fossils—New techniques, old tricks. Review of Palaeobotany and Palynology 166:117–151. DOI: 10.1016/j.revpalbo.2011.05.001

Knoll AH. 2008. Cyanobacteria and Earth history. In: Herrero A, Flores E, eds. *The Cyanobacteria: molecular biology, genomics, and evolution*. Norfolk: Caister Academic Press, 1–20.
Komárek J, Kling H, Komárková J. 2003. Filamentous cyanobacteria. In: Wehr JD, Sheath RG, eds. *Freshwater algae of North America ecology and classification*. London: Elsevier/Academic Press Inc., 117–196. DOI: 10.1016/B978-012741550-5/5005-2

Komárek J, Kastovsky J, Mares J, Johansen JR. 2014. Taxonomic classification of cyanoprokaryotes (cyanobacterial genera) 2014, using a polyphasic approach. *Preslia* 86:295–335.

Koreivienė J, Kasperovičienė J, Karosienė J. 2009. Cyanobacteria diversity in Kamanos raised bog (North-West Lithuania). *Botanica Lithuanica* 21:139–149. DOI: 10.1515/botlit-2015-0018

Krings M. 2019. *Palaeolyngbya kerpi* nov. sp., the largest filamentous cyanobacterium from the Lower Devonian Rhynie chert. *PalZ* 93:377–386. DOI: 10.1007/s12542-019-00475-w

Krings M, Harper CJ. 2019. A microfossil closely resembling *Merismopedia* (Cyanobacteria) from the 410-million-yr-old Rhynie and Windyfield cherts: *Rhyniococcus uniformis* revisited. *Nova Hedwigia* 108:17–35. DOI: 10.1127/nova_hedwigia/2018/0507

Krings M, Kerp H. 2019. A tiny parasite of unicellular microorganisms from the Lower Devonian Rhynie and Windyfield cherts, Scotland. *Review of Palaeobotany and Palynology* 271:104016. DOI: 10.1016/j.revpalbo.2019.104106

Krings M, Sergeev VN. 2019. A coccoid, colony-forming cyanobacterium from the Lower Devonian Rhynie chert that resembles *Eucapsis* (Synechococcales) and *Entophysalis* (Chroococcales), *Review of Palaeobotany and Palynology* 268:65–71. DOI: 10.1016/j.revpalbo.2019.06.002

Krings M, Harper CJ, Kerp H, Taylor EL. 2018. Exceptional preservation of sessile, long-stalked microorganisms in the Lower Devonian Windyfield chert (Scotland). In: Krings M, Harper CJ, Cúneo NR, Rothwell GW, eds. *Transformative Paleobotany: Commemorating the life*
501 and legacy of Thomas N. Taylor. London: Elsevier/Academic Press Inc., 519–526. DOI:
502 10.1016/B978-0-12-813012-4.00021-8

503 Krings M, Taylor TN, Dotzler N, Persichini G. 2012. Fossil fungi with suggested affinities to the
504 Endogonaceae from the Middle Triassic of Antarctica. Mycologia 104:835–844. DOI:
505 10.3852/11-384

506 Krings M, Taylor TN, Dotzler N. 2013. Fossil evidence of the zygomycetous fungi. Persoonia
507 30:1–10. DOI: 10.3767/003158513X664819

508 Lindblad P, Bergman B. 1990. The cycad–cyanobacterial symbiosis. In: Rai AN, ed. Handbook of
509 Symbiotic Cyanobacteria. Boca Raton: CRC Press, 137–159. DOI:
510 10.1201/9781351071185-6

511 Liu Z, Li H. 1986. Fossil blue-green algal community from the Upper Permian of Guangxi and its
512 significant role in forming bottom of coal beds. Acta Micropalaeontologica Sinica 3:261–
513 272.

514 Lücking R, Nelsen MP. 2018. Ediacarans, protolichens, and lichen-derived Penicillium: A critical
515 reassessment of the evolution of lichenization in fungi. In: Krings M, Harper CJ, Cúneo
516 NR, Rothwell GW, eds. Transformative Paleobotany: Commemorating the life and legacy
517 of Thomas N. Taylor. London: Elsevier/Academic Press Inc., 551–590. DOI:
518 10.1016/B978-0-12-813012-4.00023-1

519 Marsid EA, Sugiura N, Zakaria Z, Othman N, Utsumi M, Iwamoto K, Goto M, Hara
520 H. 2015. Microbial diversity in disturbed and undisturbed peat swamp forest and isolation
521 of cyanobacteria. In International Conference on Sustainability Initiatives (ICSI 2015) in
522 conjunction with 8th ASEAN Environmental Engineering Conference (AEEC), 24–25
523 August, 2015, Kuala Lumpur, Malaysia.
McLoughlin S, Strullu-Derrien C. 2015. Biota and palaeoenvironment of a high middle-latitude Late Triassic peat-forming ecosystem from Hopen, Svalbard archipelago. Geological Society, London, Special Publications 434:87–112. DOI: 10.1144/SP434.4

McLoughlin S, Bomfleur B, Mörs T, Reguero M. 2016. Fossil clitellate annelid cocoons and their microbiological inclusions from the Eocene of Seymour Island, Antarctica. Palaeontologia Electronica 19.1.11A:1–27. DOI: 10.26879/607

Michelou VK, Cottrell MT, Kirchman DL. 2007. Light-stimulated bacterial production and amino acid assimilation by cyanobacteria and other microbes in the North Atlantic Ocean. Applied and Environmental Microbiology 73:5539–5546. DOI: 10.1128/AEM.00212-07

Oliveira ML, Morato EF. 2000. Stingless bees (Hymenoptera, Meliponini) feeding on stinkhorn spores (Fungi, Phallales): robbery or dispersal? Revista Brasileira de Zoologia 17:881–884. DOI: 10.1590/S0101-81752000000300025

Pigg KB. 1990. Anatomically preserved *Dicroidium* foliage from the central Transantarctic Mountains. Review of Palaeobotany and Palynology 66:129–145. DOI: 10.1016/0034-6667(90)90031-D

Rees MN, Pratt BR, Rowell AJ. 1989. Early Cambrian reefs, reef complexes, and associated lithofacies of the Shackleton Limestone, Transantarctic Mountains. Sedimentology 36:341–361. DOI: 10.1111/j.1365-3091.1989.tb00611.x

Riding R. 1991. Cambrian calcareous Cyanobacteria and algae. In: Riding R, ed. *Calcareous Algae and Stromatolites*. Berlin: Springer-Verlag, 305–334. DOI: 10.1007/978-3-642-52335-9_16
Rowell AJ, Rees MN. 1989. Early Palaeozoic history of the upper Beardmore Glacier area: Implications for a major Antarctic structural boundary within the Transantarctic Mountains. Antarctic Science 1:249–260. DOI: 10.1017/S0954102089000374

Schopf JM. 1971. Notes on plant tissue preservation and mineralization in a Permian deposit of peat from Antarctica. American Journal of Science 271:522–543. DOI: 10.2475/ajs.271.5.522

Schopf JM. 1973. The contrasting plant assemblages from Permian and Triassic deposits in southern continents. In: Logan A, Hills LV, eds. The Permian and Triassic Systems and their mutual boundary. Memoirs of the Canadian Society of Petroleum Geology 2, 379–397.

Schopf JW. 1968. Microflora of the Bitter Springs Formation, late Precambrian, central Australia. Journal of Paleontology 42:651–688.

Schopf JW. 2012. The fossil record of cyanobacteria. In: Whitton B, ed. Ecology of Cyanobacteria II. Dordrecht: Springer, 15–36. DOI: 10.1007/978-94-007-3855-3_2

Schüßler A. 2002. Molecular phylogeny, taxonomy, and evolution of Geosiphon pyriformis and arbuscular mycorrhizal fungi. In: Smith SE, Smith FA, eds. Diversity and Integration in Mycorrhizas. Developments in Plant and Soil Sciences 94. Dordrecht: Springer, 75–83. DOI: 10.1007/978-94-017-1284-2_8

Schüßler A. 2012. The Geosiphon–Nostoc endosymbiosis and its role as a model for arbuscular mycorrhiza research. In: Hock B, ed. Fungal Associations. The Mycota (A Comprehensive Treatise on Fungi as Experimental Systems for Basic and Applied Research), vol. 9. Berlin: Springer, 77–91. DOI: 10.1007/978-3-642-30826-0_5
Sergeev VN, Sharma M, Shukla Y. 2012. Proterozoic fossil cyanobacteria. Palaeobotanist 61:189–358.

Sidor CA, Damiani R, Hammer WR. 2008. A new Triassic temnospondyl from Antarctica and a review of Fremouw Formation biostratigraphy. Journal of Vertebrate Paleontology 28:656–663. DOI: 10.1671/0272-4634(2008)28[656:ANTTFA]2.0.CO;2

Slater BJ, McLoughlin S, Hilton J. 2015. A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. Gondwana Res. 27:1446–1473. DOI: 10.1016/j.gr.2014.01.004

Spatafora JW, Chang Y, Benny GL, Lazarus K, Smith ME, Berbee ML, Bonito G, Corradi N, Grigoriev I, Gryganskyi A, James TY, O’Donnell K, Roberson RW, Taylor TN, Uehling J, Vilgalys R, White MM, Stajich JE. 2016. A phylum-level phylogenetic classification of zygomycete fungi based on genome-scale data. Mycologia 108:1028–1046. DOI: 10.3852/16-042

Stankevica K, Kalnina L, Klavins M, Cerina A, Ustupe L, Kaup E. 2015. Reconstruction of the Holocene palaeoenvironmental conditions according to the multiproxy sedimentary records from Lake Plvelis, Latvia. Quaternary International 386:102–115. DOI: 10.1016/j.quaint.2015.02.031

Tajhuddin N, Muralitharan G, Sundaramoorthy M, Ramamoorthy R, Ramachandran S, Akbarsha MA, Gunasekaran M. 2010. Morphological and genetic diversity of symbiotic cyanobacteria from cycads. Journal of Basic Microbiology 50:54–265. DOI: 10.1002/jobm.200900343
Taylor EL, Taylor TN, Collinson JW. 1989. Depositional setting and paleobotany of Permian and Triassic permineralized peat from the central Transantarctic Mountains. International Journal of Coal Geology 12:657–679. DOI: 10.1016/0166-5162(89)90068-2

Taylor TN, Krings M. 2010. Paleomycology: The rediscovery of the obvious. PALAIOS 25:283–286. DOI: 10.2110/palo.2010.S03

Taylor TN, Taylor EL, Collinson JW. 1986. Paleoenvironment of Lower Triassic plants from the Fremouw Formation. Antarctic Journal of the United States 21(5):26–27. DOI: 10.1007/978-1-349-07805-9_4

Tomitani A, Knoll AH, Cavanaugh CM, Ohno T. 2006. The evolutionary diversification of cyanobacteria: Molecular–phylogenetic and paleontological perspectives. Proceedings of the National Academy of the United States of America 103:5442–5447. DOI: 10.1073/pnas.0600999103

Ulloa M, Hanlin RT. 2012. Illustrated Dictionary of Mycology, Second Edition. St. Paul: APS [American Phytopathological Society] Press.

Waggoner BM. 1994. An aquatic microfossil assemblage from Cenomanian amber of France. Lethaia 27:77–84. DOI: 10.1111/j.1502-3931.1994.tb01559.x

White JF, Taylor TN. 1988. Triassic fungus from Antarctica with possible Ascomycetous affinities. American Journal of Botany 75:1495–1500. DOI: 10.1002/j.1537-2197.1988.tb11223.x

White JF, Taylor TN. 1989. An evaluation of sporocarp structure in the Triassic fungus Endochaetophora. Review of Palaeobotany and Palynology 61:341–345. DOI: 10.1016/0034-6667(89)90038-9
Wrona R. 2004. Cambrian microfossils from glacial erratics of King George Island, Antarctica. Acta Palaeontologica Polonica 49:13–56.

Wrona R, Zhuravlev A Yu. 1996. Early Cambrian archaeocyaths from glacial erratics of King George Island (South Shetland Islands), Antarctica. In: Gaidzicki A, ed. Palaeontological Results of the Polish Antarctic Expedition. Part II. Palaeontologia Polonica 55:9–36.

Yule CM, Gomez LN. 2009. Leaf litter decomposition in a tropical peat swamp forest in Peninsular Malaysia. Wetlands Ecology and Management 17:231–241. DOI: 10.1007/s11273-008-9103-9

Zadorina EV, Siobodova NV, Boulygina ES, Kolganova TV, Kravchenko IK, Kuznetsov BB. 2009. Analysis of the diversity of diazotrophic bacteria in peat soil by cloning of the nifH gene. Microbiology 78:218–226. DOI: 10.1134/S0026261709020131

**Figure captions**

**Figure 1.** Geographic occurrence and stratigraphic position of the Fremouw Peak permineralized peat; modified from Bomfleur et al. (2014: fig. 1). A. Overview of collection area in the Central Transantarctic Mountains, South Victoria Land, Antarctica. B. Boxed area and arrow in Fig. 1A. Detail of Fremouw Peak locality with arrow indicating collecting site. C. Stratigraphic column of Fremouw Peak locality with arrow indicating position of permineralized peat.

**Figure 2.** Overview of *Endochaetophora antarctica* hyphal masses and *Palaeolyngbya* sp. in permineralized peat. A. Three hyphal masses (arrows) in leaf mats (L); slide KUPB 35,009; scale bar=1 cm. B. Higher magnification of Fig. 2A, showing hyphal mass (between arrowheads) and
**E. antarctica** reproductive units (F); slide KUPB 35,009; scale bar=500 µm. C. High magnification of densely spaced hyphae comprising hyphal mass; arrows indicate septa; slide KUPB 35,017; scale bar=10 µm. D. Comparison of appendages (black arrows) of **E. antarctica** fungal reproductive unit (F) to adjacent *Palaeolyngbya* filament (white arrow); slide KUPB 35,017; scale bar=50 µm. E. High magnification of **E. antarctica** appendage; portion of appendage extending into hyphal mass and base of appendage in wall of **E. antarctica** (arrow); slide KUPB 35,018; scale bar=10 µm. F. Hyphal mass containing **E. antarctica** (F) and fragmented cyanobacterial filaments; note different mineral replacement, reddish-orange filaments (black arrows) and gray mineral (white arrow); slide KUPB 35,009; scale bar=250 µm. G. Hyphal mass with **E. antarctica** (F) and long cyanobacterial filaments (arrows); slide KUPB 35,010; scale bar=250 µm. H. Assemblage of cyanobacterial filaments in hyphal mass; filaments in cross (black arrow) and longitudinal section views (white arrow); slide KUPB 35,010; scale bar=250 µm. I. Assemblage of cyanobacterial filaments preserved as reddish-orange mineral replacements; note detail of discoid cells (arrow); slide KUPB 35,011; scale bar=500 µm. J. Well preserved filament in hyphal mass (arrow); slide KUPB 35,009; scale bar=500 µm.

**Figure 3.** Range of preservation states of cyanobacterial filaments. All scale bars=50 µm. A. Clear mineral replacement with barely visible discoid cells. Note rounded (possible) filament tip; slide KUPB 35,009. B. Clear mineral replacement with discoid cells well recognizable; slide KUPB 35,009. C. Reddish-orange mineral replacement; slide KUPB 35,011. D. Cell lumina filled with opaque matter; slide KUPB 35,010. E. Filaments with fine granular opaque matter; slide KUPB 35,010.
**Figure 4.** Details of *Palaeolyngbya* sp. filaments. **A.** Overview of trichome with prominent sheath (arrowheads) and discoid cells (arrow); slide KUPB 35,009; scale bar=50 µm. **B.** Filament portion with possible necridium (arrow); slide KUPB 35,009; scale bar=50 µm. **C.** High magnification of Fig. 4A, showing filament with discoid cells (black arrow) and prominent sheath (arrowheads); slide KUPB 35,009; scale bar=10 µm. **D.** Filament with constriction (arrow); slide KUPB 35,012; scale bar=50 µm. **E.** High magnification of constriction in Fig. 4D; slide KUPB 35,012; scale bar=5 µm. **F.** Filament showing portion of trichome in which cells are not preserved (arrow); slide KUPB 35,012; scale bar=50 µm.

**Figure 5.** Association of *Endochaetophora antarctica* with *Palaeolyngbya* sp. in permineralized peat. **A.** Photograph of *Endochaetophora antarctica* and *Palaeolyngbya* sp. in permineralized peat. **B.** Graphical representation of association between *Endochaetophora antarctica* and *Palaeolyngbya* sp. in permineralized peat. Scale bars=500 µm.

**Figure 6.** Graphical representation of “cyanobacteria everywhere” hypothesis. **A.** Filaments occur everywhere in matrix and hyphal mass. **B.** Filaments not preserved in peat but in hyphal mass. **C.** Filaments found exclusively in hyphal mass. Scale bars=500 µm.

**Figure 7.** Graphical representation of the “cyanobacteria migration” hypothesis. **A.** Filaments occur exclusively in matrix. **B.** Filaments migrate into hyphal mass. **C.** Filaments found exclusively in hyphal mass. Refer to key in Figure 6. Scale bars=500 µm.
Figure 1

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Overview of *Endochaetophora antarctica* hyphal masses and *Palaeolyngbya* sp. in permineralized peat.

**A.** Three hyphal masses (arrows) in leaf mats (L); slide KUPB 35,009; scale bar=1 cm. **B.** Higher magnification of Fig. 2A, showing hyphal mass (between arrowheads) and *E. antarctica* reproductive units (F); slide KUPB 35,009; scale bar=500 µm. **C.** High magnification of densely spaced hyphae comprising hyphal mass; arrows indicate septa; slide KUPB 35,017; scale bar=10 µm. **D.** Comparison of appendages (black arrows) of *E. antarctica* fungal reproductive unit (F) to adjacent *Palaeolyngbya* filament (white arrow); slide KUPB 35,017; scale bar=50 µm. **E.** High magnification of *E. antarctica* appendage; portion of appendage extending into hyphal mass and base of appendage in wall of *E. antarctica* (arrow); slide KUPB 35,018; scale bar=10 µm. **F.** Hyphal mass containing *E. antarctica* (F) and fragmented cyanobacterial filaments; note different mineral replacement, reddish-orange filaments (black arrows) and gray mineral (white arrow); slide KUPB 35,009; scale bar=250 µm. **G.** Hyphal mass with *E. antarctica* (F) and long cyanobacterial filaments (arrows); slide KUPB 35,010; scale bar=250 µm. **H.** Assemblage of cyanobacterial filaments in hyphal mass; filaments in cross (black arrow) and longitudinal section views (white arrow); slide KUPB 35,010; scale bar=250 µm. **I.** Assemblage of cyanobacterial filaments preserved as reddish-orange mineral replacements; note detail of discoid cells (arrow); slide KUPB 35,011; scale bar=500 µm. **J.** Well preserved filament in hyphal mass (arrow); slide KUPB 35,009; scale bar=500 µm.
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Range of preservation states of cyanobacterial filaments.

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Association of *Endochaetophora antarctica* with *Palaeolyngbya* sp. in permineralized peat.

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**B.** Graphical representation of association between *Endochaetophora antarctica* and *Palaeolyngbya* sp. in permineralized peat. Scale bars=500 µm.
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Figure 6

Graphical representation of “cyanobacteria everywhere” hypothesis.

**A.** Filaments occur everywhere in matrix and hyphal mass. **B.** Filaments not preserved in peat but in hyphal mass. **C.** Filaments found exclusively in hyphal mass. Scale bars=500 µm.
Figure 7

Graphical representation of the “cyanobacteria migration” hypothesis.

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