



Bayerische
Staatssammlung
für Paläontologie und Geologie

- Zitteliana A 55, 107 – 114
- München, xx.xx.2015
- Manuscript received
14.08.2015; revision
accepted 21.10.2015
- ISSN 1612 - 412X

Fungi associated with *Glossopteris* (Glossopteridales) leaves from the Permian of Antarctica: A preliminary report

Carla J. Harper^{1,2*}, Thomas N. Taylor², Michael Krings^{1,2} & Edith L. Taylor²

¹Department für Geo- und Umweltwissenschaften, Paläontologie und Geobiologie,
Ludwig-Maximilians-Universität, and Bayerische Staatssammlung für Paläontologie und Geologie,
Richard-Wagner-Straße 10, 80333 Munich, Germany

²Department of Ecology and Evolutionary Biology, and Natural History Museum and Biodiversity
Institute, University of Kansas, Lawrence, KS 66045-7534, USA

*Author for correspondence and reprint requests; E-mail: c.harper@lrz.uni-muenchen.de

Abstract

Fungi today occur on virtually every plant part, living and dead, and represent a significant proportion of fungal diversity. Arborescent seed ferns characterized by large, tongue-shaped leaves with reticulate venation (*Glossopteris*) represent the dominant floral element in the Permian of Gondwana. However, documented evidence of fungi associated with the leaves of these plants is exceedingly rare. Partially degraded *Glossopteris* leaves from two upper Permian permineralized peat deposits from Antarctica yield scattered evidence of fungal colonization in the form of hyphae, spores, sporangia, and mycelia. Intact leaves from the same deposits are typically free of fungi, suggesting that the fungi in the degraded leaves were saprotrophs on the forest floor, rather than colonizers of living leaves. We hypothesize that the scarcity of fungi associated with Antarctic *Glossopteris* leaves may be related to structural and physiological adaptations of the plants to the extreme conditions that governed late Paleozoic polar ecosystems.

Key words: Collinson Ridge, Gondwana, late Paleozoic, permineralization, polar forest, saprotrophism, Skaar Ridge

Zusammenfassung

Lebende und tote Pflanzenteile besiedelnde Pilze stellen heute einen großen Teil der Gesamtdiversität der Pilze dar. Baumförmige Samenfarne mit großen, zungenförmigen Blättern mit Netzervatur (*Glossopteris*) waren sehr weit verbreitet im Perm von Gondwana. Nachweise für Pilze auf und in den Blättern dieser Pflanzen sind allerdings bis heute sehr selten. Verrottete und zum Teil zerstörte *Glossopteris* Blätter aus permineralisiertem Torf von zwei Fundstellen in der Antarktis weisen Spuren einer Besiedlung durch Pilze in Form von Hyphen, Sporen, Sporangien und Myzelien auf. Intakte Blätter aus denselben Torfen sind allerdings in der Regel frei von Pilzen, was vermuten lässt, dass die Pilze in den verrotteten Blättern saprotroph waren und nicht lebende Blätter besiedelten. Das Fehlen von Pilzen auf/in intakten *Glossopteris* Blättern könnte mit bestimmten Anpassungen der Pflanzen an die extremen Bedingungen zusammenhängen, denen die jungpaläozoischen polaren Ökosysteme ausgesetzt waren.

Schlüsselwörter: Collinson Ridge, Gondwana, Jungpaläozoikum, Permineralisation, polare Wälder, Saprotrophismus, Skaar Ridge

1. Introduction

Although plant leaves constitute a harsh environment due to several abiotic and biotic factors (e.g., temporary nutrient availability, extreme fluctuations in humidity, temperature, gas exchange gradients, and ultraviolet radiation; see Goodman & Weisz 2002), they are inhabited by a remarkable variety of different organisms, including bacteria, fungi, algae, and small animals (Hill 1977; Lindow & Brandl 2003; Lill & Marquis 2004). Many of the studies investigating microbial life on and in the leaves of extant plants focus on fungi because these organisms are particularly abundant, diverse, and often play important

roles in the life history biology of their hosts (e.g., Andrews & Harris 2000; Stone et al. 2000; Arnold 2007; Rodriguez et al. 2009; Osono 2014).

The fossil record of leaf-inhabiting fungi is predominantly composed of Cenozoic epiphyllous fungi (e.g., Dilcher 1963, 1965; Selkirk 1972; Lange 1978; Phipps 2001, 2007; Phipps & Rember 2004), while there is relatively little evidence to date of pre-Cretaceous fungi associated with leaves, with the exception of several reports from the Carboniferous (Barthel 1961; Krings 2001; Krings et al. 2009, 2010, 2011; Dotzler et al. 2011). The main difficulty in studying fungi associated with pre-Cretaceous leaves is that the details needed for systematic assignment

are often not preserved or lost through fossil preparation (Taylor et al. 2011). Undeterminable hyphal fragments and propagules are usually the only evidence of the presence of fungi on/in fossil leaves.

There is only one record of fungi associated with Permian leaves from Antarctica (Holdgate et al. 2005: fig. 14i). This scarcity of documented evidence is surprising since structurally preserved Permian leaves occur in abundance in several permineralized peat deposits and have been studied intensively (e.g., Pigg 1990; Taylor & Taylor 1990; Pigg & Taylor 1993; Li et al. 1994; McLoughlin & Drinnan 1996; Pigg & McLoughlin 1997; Hilton et al. 2001; McManus et al. 2002). Moreover, foliar fungi are extremely widespread in modern ecosystems (Schulz & Boyle 2005). The most commonly found leaves in the Permian peats of Antarctica are those of *Glossopteridales*, an extinct group of seed plants that dominated the vegetation of Gondwana during the Permian (Taylor et al. 2009). *Glossopteris* leaves are lanceolate to tongue-shaped, entire margined, and characterized by a venation consisting of a strong midrib made up of multiple vascular strands, and second-order veins forming a reticulate pattern by frequent anastomoses (Pant & Singh 1974; Trivett & Pigg 1996).

Permineralized *Glossopteris* leaves and leaf mats (i.e., dense accumulations of leaves) are known from two localities in Antarctica, i.e. Skaar Ridge (Pigg 1990; Schwendemann 2010) and Collinson Ridge (McManus et al. 2002). In this study, we describe a variety of fungal remains that are associated with these leaves or occur in the peat matrix surrounding the leaves. The fungi were probably not foliar epiphytes or endophytes, but rather belonged to the community of saprotrophs that were involved in the decomposition of dead plant matter on the forest floor. This discovery contributes to a more complete understanding of the multiple associations and interactions that sustained the polar forest ecosystems of Antarctica during the Permian.

2. Material and methods

Late Permian permineralized peat containing

Glossopteris leaves comes from Skaar Ridge (84° 49' 11.8" S, 163° 20' 37.0" E; 2300 m, 8600 ft) located within the Buckley Formation near the Beardmore Glacier Area, Queen Alexandra Range, central Transantarctic Mountains, Antarctica (for details on the geological setting, refer to Barrett et al. 1986; Isbell 1990; Collinson et al. 1994). Additional material, also late Permian in age, comes from a lens of silicified peat, 6 m across and 0.6 m thick, within a medium-grained sandstone on Collinson Ridge (85° 13' S, 175° 21' W), presumably located in the lower part of the Fremouw Formation, central Transantarctic Mountains, Shackleton Glacier area (details on the geological setting can be found in Collinson & Hammer 1996; McManus et al. 2002).

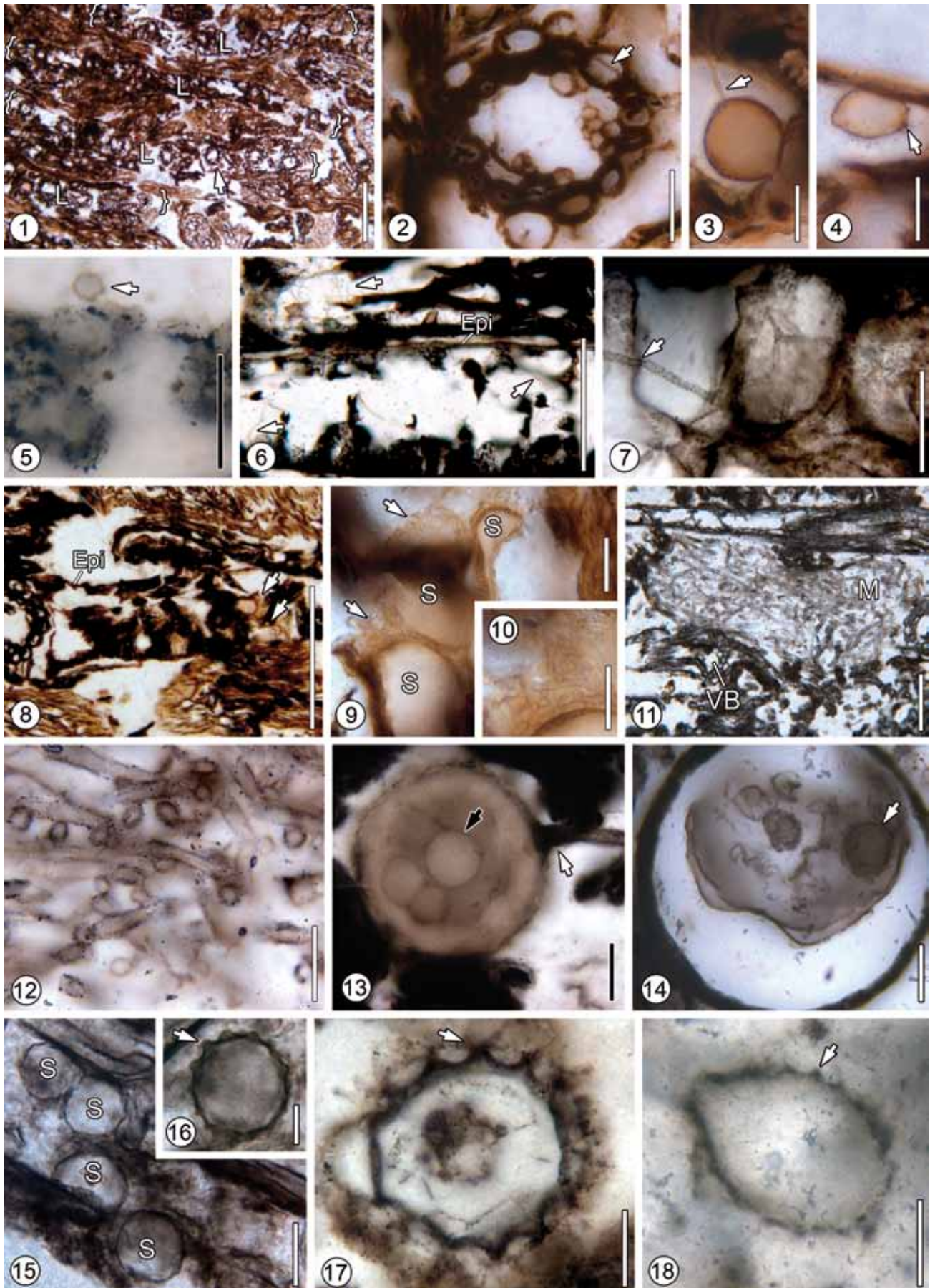
Specimens were prepared according to the standard thin-section techniques outlined in Hass & Rowe (1999). Pieces of peat were mounted on microscope slides using Hillquist 2-part A-B epoxy compound, and cut to a thickness of ~250 µm. The wafer was then ground to a thickness of ~50–65 µm and analyzed in transmitted light. Digital images were captured with a Leica DC500 digital camera and processed using Adobe Photoshop CS 6. Images of the same specimen were recorded at multiple focal planes and stacked to produce composite images (Pl. 1, Figs 2, 5–7, 9, 10, 13–17 in this study; e.g., Bercovici et al. 2009). Measurements were taken using ImageJ 1.48b software (Abràmoff et al. 2004). Specimens and slides are deposited in the Paleobotanical Collections, Biodiversity Institute, University of Kansas (KUPB) under accession numbers KUPB 15312–15375, 19967–19969, and 30713–30745.

3. Results

3.1 Host leaves

Glossopteris leaves from both localities are mostly preserved in a more or less advanced state of degradation, and thus lack diagnostic characters that could be used to assign them to a species; intact leaves also occur but are comparatively rare. Paradermal sections of the leaves show the large meshes

Plate 1: Fungal remains associated with Permian *Glossopteris* leaves from Antarctica. **(1)** Peat containing highly degraded *Glossopteris* leaves (L) in cross section; brackets denote leaf ends; slide no 30713; scale bar = 250 µm. **(2)** Vascular bundle of *Glossopteris* containing septate hypha (arrow); slide no 30713; scale bar = 25 µm. **(3)** Degraded mesophyll containing chytrid-like structure with minute filament (arrow) and possible discharge opening; slide no. 30713; scale bar = 5 µm. **(4)** Chytrid-like organism with discharge pore (arrow); slide no. 30714; scale bar = 5 µm. **(5)** Hypha in cross section on leaf surface (arrow); slide no. 30715; scale bar = 10 µm. **(6)** Leaf with preserved epidermis (Epi) showing fungal hyphae (arrows) in mesophyll and on adaxial surface; slide no. 30716; scale bar = 50 µm. **(7)** Hyphae penetrating mesophyll cell wall (arrow); slide no. 30717; scale bar = 25 µm. **(8)** Degraded *Glossopteris* leaf (epidermis of leaf = Epi) containing clusters of spores (arrow); slide no. 30714, scale bar = 250 µm. **(9)** Detail of Pl. 1, Fig. 7, showing cluster of spores (S), each enveloped in a mantle composed of septate, thickened toruloid hyphae (arrows); scale bar = 10 µm. **(10)** Detail of Pl. 1, Fig. 9, showing hyphal mantle; scale bar = 5 µm. **(11)** Fungal mycelium (M) in matrix between *Glossopteris* leaves (vascular bundle = VB); slide no. 30715; scale bar = 100 µm. **(12)** Detail of Pl. 1, Fig. 9, showing largely unbranched hyphae forming a mycelium; scale bar = 25 µm. **(13, 14)** Putative chlamydo-spores; white arrow in Pl. 1, Fig. 11 indicates hyphal attachment, black arrow in Pl. 1, Fig. 11 and white arrow in Pl. 1, Fig. 12 show internal spherules (probably reproductive units of mycoparasites); slides no. 30718 and 30719; Scale bars = 25 µm. **(15)** Small fungal spores (S); slide no. 30720; scale bar = 25 µm. **(16)** Detail of spore type in Pl. 1, Fig. 15 showing surface ornamentation (arrow); scale bar = 10 µm. **(17, 18)** *Combresomyces*-like putative peronosporomycete oogonium; arrows indicate papillations of oogonial wall bearing antler-like extensions; slides no. 30721 and 15366; scale bars = 25 µm.



that represent the second-order venation, and often also the prominent midrib, thus attesting to the affinities of the leaves to *Glossopteris*. In transverse section, the bundle sheath, when preserved, is composed of thin-walled cells that sometimes include dark contents. Stomata are rarely preserved, but when observed, they are sunken. Typically the only remaining components of the leaf that are consistently preserved are the parallel, thick-walled vascular bundles (Pl. 1, Fig. 1).

More than 200 intact leaves and leaf fragments from Skaar Ridge and 50 fragmented leaves from Collinson Ridge were examined. Fungal remains were detected in ~10% of the degraded leaves and leaf fragments from Skaar Ridge, whereas the material from Collinson Ridge yielded only a single microorganism remain. Interestingly, none of the intact *Glossopteris* leaves from either locality yielded evidence of fungal colonization.

3.2 Fungi associated with *Glossopteris* leaves

The most common fungal remains associated with degraded *Glossopteris* leaves are ramifying, septate hyphae (2–4 μm in diameter) that penetrate the walls of individual tracheids within the vascular bundles (Pl. 1, Fig. 2). Additional fungal remains in tracheids include spherical structures that fully occlude the host cells, with attachment points at the base of the spheroidal structure to the host. In the highly degraded mesophyll of several leaves, small circular to pyriform structures occur that range from 8–10 μm in diameter. Only one of these structures (Pl. 1, Fig. 3) shows what appears to be a rhizomycelial attachment or subtending hypha/filament <1 μm in diameter. An additional feature of these structures includes a putative discharge pore (Pl. 1, Fig. 4). Other leaves show fungal hyphae extending along the leaf surface (Pl. 1, Fig. 5). Many of the leaves also contain tenuous hyphae, usually less than 1 μm in diameter, that branch at right angles and are septate (Pl. 1, Fig. 6). Leaves in which the mesophyll tissue is more or less intact may also contain larger septate hyphae that directly penetrate through the cell walls (Pl. 1, Fig. 7).

Clustered spores surrounded by what appears to be a hyphal mantle or mycelium have been found in two transversely sectioned leaves (Pl. 1, Figs 8, 9). Spores are up to 37 μm in diameter, and the interwoven hyphae enveloping the spores are 2 μm in diameter (Pl. 1, Fig. 9, 10). There is also a single specimen of a larger portion of a mycelium composed of interlaced, largely unbranched septate hyphae (Pl. 1, Figs 11, 12).

3.3 Fungal remains in the matrix surrounding the *Glossopteris* leaves

Eight morphologically distinct types of fungal reproductive units, as well as several types of remains

attributable to the fungus-like Peronosporomycetes, have been discovered in the ambient peat matrix surrounding the *Glossopteris* leaves. These have been designated as numbered morphotypes because each lacks sufficient characters to assign it formally to a taxonomic category.

Fungal reproductive units that display a hyphal attachment are all terminal, and there is no evidence of the parental system on which they were produced. Morphotype 1 is ~40 μm in diameter; wall features are not discernible. Some of the units contain between 1 and 3 internal spherules, each approximately 10 μm in diameter. Morphotype 2 is slightly larger than type 1 (i.e. up to 50 μm in diameter) and the wall is up to 3 μm thick. The subtending hypha is approximately 5 μm in diameter. Internal spherules present in some of the specimens range from 6 to 10 μm in diameter (black arrow in Pl. 1, Fig. 13). Morphotype 3 is similar to type 2, up to 45 μm in diameter, but the wall is thinner (<2 μm thick). This type is only found within fragments of *Vertebraria* root tissue co-occurring with the leaves in the litter mats. Morphotype 4 is slightly pyriform, approximately 35 μm at the widest point, and possesses a wall 4–5 μm thick; a hyphal attachment may be visible at the narrow end. Morphotype 5 is ~80 μm in diameter and has a wall that is 6–8 μm thick; small spherical structures may be present in the lumen (arrow in Pl. 1, Fig. 14). Morphotype 6 ranges from 15 to 25 μm in diameter and occurs within degrading plant tissues and the matrix, and at varying focal planes reveals some surface ornamentation (Pl. 1, Figs 15, 16). Morphotype 7 is approximately 40 μm in diameter, with a distinctly two-layered wall that reaches 5–7 μm in thickness. Morphotype 8 is also characterized by a two-layered wall up to 8 μm thick, but is up to 50 μm in diameter and shows a blunt attachment point.

Pyriform to ovoid structures up to 80 μm in diameter that occur scattered throughout the peat closely resemble the fossil genus *Combresomyces*, and thus are interpreted as oogonia of members of the fungus-like Peronosporomycetes (see Dotzler et al. 2008; Schwendemann et al. 2009; Slater et al. 2013). All are characterized by a surface ornament composed of antler-like extensions positioned on hollow, column-like or broadly triangular papillations of the wall (Pl. 1, Figs 14, 17). Moreover, most occur at the tip of a short segment of the parental hypha; a septum is sometimes visible between the oogonium and subtending hypha. One specimen of this type represents the only microorganism recorded to date from the peat at Collinson Ridge (Pl. 1, Fig. 18).

4. Discussion

The fungal remains described here represent the first evidence of fungi associated with *Glossopteris* leaves from Antarctica. This discovery is important because documented evidence of fungi residing on

and in the leaves of glossopterid seed ferns, one of the dominant plant groups in Gondwana during the Permian, is generally scarce. We are aware of only two previous reports on fungal associations with *Glossopteris*, and these are from Indian compression material (Bajpai & Maheshwari 1987; Srivastava 1993).

In general, modern fungal leaf endophytes are defined functionally by their occurrence within asymptomatic (i.e., lacking visible disease symptoms at the moment of detection) tissue of living leaves (Schulz & Boyle 2005). This is problematic when studying fossil material. Krings et al. (2009) therefore offered the suggestion that, with fossils, the designation fungal endophyte should be understood as a strictly descriptive term, and used for all fungi that occur within intact plant cells or tissues in which there are no visible disease symptoms. However, when assessing the nutritional mode(s) of fungi associated with fossil leaves, it is necessary to evaluate as to whether the host leaf was alive and functional when colonized by the fungus or in the process of decay. Colonization of living leaves can be inferred by structural features such as host responses (e.g., callosities). However, without such features the condition of the host at the time of colonization cannot normally be resolved.

Although it is impossible at present to determine the nutritional mode(s) of the fungi associated with the *Glossopteris* leaves reported here, it is likely that the majority, if not all, were saprotrophs that were active in the degradation of organic matter on the forest floor, rather than colonizers of living leaves, or endophytes that acted as latent decomposers (Rajala et al. 2014). Support for this hypothesis is the absence of fungi associated with intact *Glossopteris* leaves. Leaf litter communities today include multiple phyla of fungi that exhibit different types of nutritional modes, including mutualism, saprotrophism, and parasitism (Voříšková & Baldrian 2013). The globose fungal reproductive units that occur in the peat matrix (Pl. 1, Figs 11, 13) are interpreted as chlamydospores produced by glomeromycotan fungi based on morphological similarities to the spores of certain extant Glomeromycota (e.g., Stürmer 2012). Many of the fossil chlamydospores occur in close proximity to narrow-diameter *Vertebraria*-type glossopterid rootlets that regularly co-occur with the *Glossopteris* leaves in the peat. *Vertebraria* rootlets have been shown to harbor endomycorrhizal fungi with affinities to the Glomeromycota (Harper et al. 2013), and it is therefore highly probable that some of the spores described here represent the propagules of these mycorrhizal fungi. Other fungal remains that are spheroidal might represent chytrid-like organisms based on the presence of what appear to be discharge pores (Pl. 1, Fig. 4) and rhizomycelial attachments (Pl. 1, Fig. 3). Finally, the clustered spores/sporangia enveloped in a hyphal mantle (Pl. 1, Figs 7, 8) may have affinities to the Mucoromycotina.

The general scarcity of documented evidence of

fungi associated with *Glossopteris* leaves is surprising because glossopterid seed ferns were dominant elements in many forest ecosystems across Gondwana, and have been intensely studied for more than 150 years. One simple explanation for this apparent absence of evidence may be a general lack of interest in fungi by the scientists studying *Glossopteris* leaves. Moreover, the research focus on the leaves might have created a collection bias for well-preserved specimens rather than those that are tattered or degraded. On the other hand, there might also be biological factors that have contributed to the scarcity of fungi on and in *Glossopteris* leaves, especially from Antarctica.

One factor may be the cuticle of *Glossopteris* leaves. The plant cuticle serves two principal functions, i.e., as a hydrophobic barrier that prevents desiccation, and as a structural defense against several adverse abiotic and biotic factors (Martin 1964; Kerstiens 1996; Nawarh 2006). Moreover, some leaf cuticles contain various secondary compounds that are effective as fungal deterrents (Canhoto & Graça 1999; Dominguez et al. 2011). It is therefore possible to hypothesize that perhaps the cuticle of the *Glossopteris* leaves from Antarctica contained especially high levels of substances with fungicidal properties. Geochemical analyses of *Glossopteris* leaves that might assess the chemical composition of the cuticle have not been conducted to date. However, such techniques have been used with geologically younger fungus-infected and non-infected gymnosperms to assess the lipid content in the cuticle (Tu et al. 2000). The results of this study indicate that the fungi in the infected specimens produced specific post-infection degradational compounds, and thus we can infer that biogeochemical data on fungal interactions has the potential to be extracted from fossil plants.

A second factor that may have contributed to the scarcity of leaf fungi associated with Antarctic glossopterids concerns the physiology of the Antarctic glossopterid seed ferns. Antarctica has remained in approximately the same south polar position during the majority of the Phanerozoic (Torsvik & Cocks 2013). The paleogeographic position of the continent makes the late Paleozoic forest ecosystems of Antarctica a unique setting with no modern analogue. Especially interesting are the light regimes, which would have comprised 4 months of 24-hours light exposure, 4 months of 24-hours total darkness, and 4 months of transitional light regimes (Taylor & Ryberg 2007). One of the many research questions concerning these unique high-paleolatitude forests encompasses leaf longevity in glossopterids, i.e. whether the trees were deciduous or evergreen (Gulbranson et al. 2014). The presence of *Glossopteris* leaf mats has been used to suggest that the trees were deciduous (Axelrod 1984); however, recent studies indicate that the forests contained mixed populations of evergreen and deciduous trees (Gulbranson et al. 2012, 2014). Schwendemann

(2010) suggests that *Glossopteris* plants exhibited a mixed C₃-C₄ intermediate physiology that may have played a vital role as an adaptation to the extreme light regimes. Factors such as seasonality and leaf age are known to greatly influence the abundance and diversity of leaf fungi in modern plants (e.g., Osono 2008). Low foliar fungal diversity in plants from high latitude ecosystems has been suggested to be due in part to the high amount and prolonged exposure to light in these environments (Millberg et al. 2015). It is therefore possible to envision that the extreme conditions which governed the polar Permian ecosystems had a significant effect on fungal colonization of *Glossopteris* leaves.

A third aspect concerns the fact that the permineralized *Glossopteris* leaves and leaf mats from Antarctica all represent allochthonous assemblages of plant parts that have been exposed to the peat-forming process for some time and then transported. This may have resulted in leaves being exposed to high levels of mechanical destruction prior to permineralization. The depositional setting for the peat deposits from Skaar Ridge has been interpreted as peat blocks that were rafted (prior to permineralization) into the depositional area during a flood and then became stranded on sand bars as flood waters subsided (Taylor et al. 1989). These processes might have removed or destroyed fungi that, if at all present, were only loosely attached to the leaves (e.g., epiphyllous fungi). Moreover, it is possible to speculate that the decayed and fragmented *Glossopteris* leaves probably represent a late stage in the degradation process in which they no longer provided the necessary nutrients for saprotrophic fungi, and thus were rarely colonized.

5. Conclusion

The evidence presented in this paper suggests that fungi are generally scarce as inhabitants of Permian *Glossopteris* leaves from Antarctica, and limited to saprotrophs on the forest floor. However, we are currently unable to determine whether this scarcity of evidence reflects a preservation bias, or if living Antarctic *Glossopteris* leaves were in any way colonized by fungi. Reports of what appear to be microthyriaceous fungi on *Glossopteris* from India (Bajpai & Maheshwari 1987; Srivastava 1993) suggest that at least some glossopterid leaves in vivo were inhabited by fungi. One interesting speculation suggests that the environmental conditions governing the Antarctic continent during the Permian, along with special adaptations evolved by the plants exposed to these conditions, adversely affected fungal colonization. While there is currently no evidence to support this hypothesis, geochemical analyses (e.g., biomarker analysis) represent a promising new tool with which substances related specifically to the presence of fungi may be identified in fossil leaves,

and thus would demonstrate the presence of fungi in the absence of body fossils (Harper et al. 2015). We hope that by reporting the scattered evidence that is available we will further stimulate interest in searching out fungal remains in and on leaves throughout the geologic record, and thus increase the body of data that can be used to document precisely when and how certain types of fungal associations and interactions with the phyllosphere initially evolved.

Acknowledgments

We thank Erik L. Gulbranson (Milwaukee, WI, USA) and Evelyn Kustatscher (Bolzano, Italy) for fruitful discussion, and Rudolph Serbet (Lawrence, KS, USA) for technical assistance. Financial support was provided by the Alexander von Humboldt-Foundation (3.1-USA/1160852 STP to CJH), and the National Science Foundation (EAR-0949947 to TNT and MK; OPP-0943934 to ELT and TNT). This paper greatly benefited from insightful comments and suggestions by Ari Jumpponen (Manhattan, KS, USA).

6. References

- Abràmoff MD, Magelhães PJ, Ram SJ. 2004. Image Processing with ImageJ. *Biophotonics International* 11, 36–42.
- Andrews JH, Harris RF. 2000. The ecology and biogeography of microorganisms on plant surfaces. *Annual Review of Phytopathology* 38, 145–180.
- Arnold AE. 2007. Understanding the diversity of foliar endophytic fungi: Progress, challenges, and frontiers. *Fungal Biology Reviews* 21, 51–66.
- Axelrod DI. 1984. An interpretation of Cretaceous and Tertiary biota in polar regions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 45, 105–147.
- Bajpai U, Maheshwari HK. 1987. Epiphyllous fungi from the Gondwana. *Palaeobotanist* 36, 210–213.
- Barrett PJ, Elliot DH, Lindsay JF. 1986. The Beacon Supergroup (Devonian-Triassic) and Ferrar Group (Jurassic) in the Beardmore Glacier area, Antarctica. In: MD Turner, JF Splettscoesser (Eds), *Geology of the Central Transantarctic Mountains*. Washington DC, Antarctic Research Series 36, American Geophysical Union, 339–428.
- Barthel M. 1961. Ein Pilzrest aus dem Saarkarbon. *Geologie* 10, 856–857.
- Bercovici A, Hadley A, Villanueva-Amadoz U. 2009. Improving depth of field resolution for palynological photomicrography. *Palaeontologia Electronica* 12, 12 p. [available online at: http://palaeoelectronica.org/2009_2/170/170.pdf; last accessed May 17, 2011]
- Canhoto C, Graça MAS. 1999. Leaf barriers to fungal colonization and shredders (*Tipula lateralis*) consumption of decomposing *Eucalyptus globulus*. *Microbial Ecology* 37, 163–172.
- Collinson JW, Isbell JL, Elliot DH, Miller MF, Miller JMG, Veevers JJ. 1994. Permian-Triassic Transantarctic basin. *Geological Society of America Memoir* 184, 173–222.
- Collinson JW, Hammer WR. 1996. New observations on the Triassic stratigraphy of the Shackleton Glacier region. *Antarctic Journal of the United States* 31/5, 9–12.
- Dilcher DL. 1963. Eocene epiphyllous fungi. *Science* 142, 667–669.
- Dilcher DL. 1965. Epiphyllous fungi from Eocene deposits in western Tennessee, U.S.A. *Palaeontographica* 116B, 1–54.
- Dominguez E, Cuartero J, Heredia A. 2011. An overview on plant

- cuticle biomechanics. *Plant Science* 181, 77–84.
- Dotzler N, Krings M, Agerer R, Galtier J, Taylor TN. 2008. *Combresomyces cornifer* gen. sp. nov., an endophytic peronosporomycete in *Lepidodendron* from the Carboniferous of central France. *Mycological Research* 112, 1107–1114.
- Dotzler N, Taylor TN, Galtier J, Krings M. 2011. *Sphenophyllum* (Sphenophyllales) leaves colonized by fungi from the Upper Pennsylvanian Grand-Croix cherts of central France. *Zitteliana A* 51, 3–8.
- Goodman RM, Weisz JB. 2002. Plant-microbe symbioses: An evolutionary survey. In: JT Staley, AL Reysenbach (Eds), *Biodiversity of Microbial Life. Foundation of Earth's Biosphere*. New York, NY, Wiley-Liss, Inc., 237–287.
- Gulbranson EL, Isbell JL, Taylor EL, Ryberg PE, Taylor TN, Flaig PP. 2012. Permian polar forests: Deciduousness and environmental variation. *Geobiology* 10, 479–495.
- Gulbranson EL, Ryberg PE, Decombeix A-L, Taylor EL, Taylor TN, Isbell JL. 2014. Leaf habit of Late Permian *Glossopteris* trees from high-palaeolatitude forests. *Journal of the Geological Society* 171, 493–507.
- Harper CJ, Taylor TN, Krings M, Taylor EL. 2013. Mycorrhizal symbiosis in the Paleozoic seed fern *Glossopteris* from Antarctica. *Review of Palaeobotany and Palynology* 192, 22–31.
- Harper CJ, Olcott Marshall A, Marshall CP, Taylor TN, Krings M, Taylor EL. 2015. Biomarkers in paleomycology – A case study using fungus-infected Permian woods from Antarctica. Abstract ID 337. Botanical Society of America, July 27, Edmonton, Alberta, Canada.
- Hill DJ. 1977. The role of *Anabaena* in the *Azolla-Anabaena* symbiosis. *New Phytologist* 78, 611–616.
- Hilton J, Wang SJ, Galtier J, Li CS. 2001. An Early Permian plant assemblage from the Taiyuan Formation of northern China with compression/impression and permineralized preservation. *Review of Palaeobotany and Palynology* 114, 175–189.
- Holdgate GR, McLoughlin S, Drinnan AN, Finkelman RB, Willett JC, Chiehowsky LA. 2005. Inorganic chemistry, petrography and palaeobotany of Permian coals in the Prince Charles Mountains, East Antarctica. *International Journal of Coal Geology* 63, 156–177.
- Isbell JL. 1990. Depositional architecture of the Lower Permian Weller Coal Measures, southern Victoria Land. *Antarctic Journal of the United States* 25/5, 28–29.
- Kerstiens G. 1996. Signaling across the divide: a wider perspective of cuticular structure – function relationships. *Trends in Plant Science* 1, 125–129.
- Krings M. 2001. Pilzreste auf und in den Fiedern zweier Pteridospermen aus dem Stefan von Blanzky-Montceau (Zentralfrankreich). *Geologica Saxonica – Abhandlungen des Staatlichen Museums für Mineralogie und Geologie Dresden* 46/47, 189–196.
- Krings M, Dotzler N, Taylor TN, Galtier J. 2009. A Late Pennsylvanian fungal leaf endophyte from Grand-Croix, France. *Review of Palaeobotany and Palynology* 156, 449–453.
- Krings M, Taylor TN, Galtier J, Dotzler N. 2010. Microproblematic endophytes and epiphytes of fern pinnules from the Upper Pennsylvanian of France. *Geobios* 43, 503–510.
- Krings M, Taylor TN, Dotzler N, Galtier J. 2011. Fungal remains in cordaite (Cordaitales) leaves from the Upper Pennsylvanian of central France. *Bulletin of Geosciences* 86, 777–784.
- Lange RT. 1978. Southern Australian Tertiary epiphyllous fungi, modern equivalents in the Australasian region, and habitat indicator value. *Canadian Journal of Botany* 56, 532–541.
- Li H, Tian B, Taylor EL, Taylor TN. 1994. Foliar anatomy of *Gigantoclea guizhouensis* (Gigantopteridales) from the Upper Permian of Guizhou province, China. *American Journal of Botany* 80, 678–689.
- Lill JT, Marquis RJ. 2004. Leaf ties as colonization sites for forest arthropods: An experimental study. *Ecological Entomology* 29, 300–308.
- Lindow SE, Brandl MT. 2003. Microbiology of the phyllosphere. *Applied and Environmental Microbiology* 69, 1875–1883.
- Martin JT. 1964. Role of cuticle in the defense against plant disease. *Annual Review of Phytopathology* 2, 81–100.
- McLoughlin S, Drinnan AN. 1996. Anatomically preserved Permian *Noeggerathiopsis* leaves from East Antarctica. *Review of Palaeobotany and Palynology* 92, 207–227.
- McManus HA, Taylor EL, Taylor TN, Collinson JW. 2002. A petrified *Glossopteris* flora from Collinson Ridge, central Transantarctic Mountains: Late Permian or Early Triassic. *Review of Palaeobotany and Palynology* 120, 233–246.
- Millberg H, Boberg J, Stenlid J. 2015. Changes in fungal community of Scots pine (*Pinus sylvestris*) needles along a latitudinal gradient in Sweden. *Fungal Ecology* 17, 126–139.
- Nawrath C. 2006. Unraveling the complex network of cuticular structure and function. *Current Opinions in Plant Biology* 9, 281–287.
- Osono T. 2008. Endophytic and epiphytic phyllosphere fungi of *Camellia japonica*: Seasonal and leaf age-dependent variations. *Mycologia* 100, 387–391.
- Osono T. 2014. Diversity and ecology of endophytic and epiphytic fungi of tree leaves in Japan: A review. In: VC Verma, AC Gange (Eds), *Advances in Endophytic Research*. New Delhi, India, Springer India, 3–26.
- Pant DD, Singh RS. 1974. On the stem and attachment of *Glossopteris* and *Gangamopteris* leaves. Part II. Structural features. *Palaeontographica* 147B, 42–73.
- Phipps CJ. 2001. The Evolution of Epiphyllous Fungal Communities with an Emphasis on the Miocene of Idaho. Ph.D. Dissertation. University of Kansas, Lawrence, KS, USA, 151 p.
- Phipps CJ. 2007. *Entopeltacites remberi* sp. nov. from the Miocene of Clarkia, Idaho, USA. *Review of Palaeobotany and Palynology* 145, 193–200.
- Phipps CJ, Rember WC. 2004. Epiphyllous fungi from the Miocene of Clarkia, Idaho: Reproductive structures. *Review of Palaeobotany and Palynology* 129, 67–79.
- Pigg KB. 1990. Anatomically preserved *Glossopteris* foliage from the central Transantarctic Mountains. *Review of Palaeobotany and Palynology* 66, 105–127.
- Pigg KB, Taylor TN. 1993. Anatomically preserved *Glossopteris* stems with attached leaves from the central Transantarctic Mountains, Antarctica. *American Journal of Botany* 80, 500–516.
- Pigg KB, McLoughlin S. 1997. Anatomically preserved *Glossopteris* leaves from the Bowen and Sydney basins, Australia. *Review of Palaeobotany and Palynology* 97, 339–359.
- Rajala T, Velmala SM, Vesala R, Smolander A, Pennanen T. 2014. The community of needle endophytes reflects the current physiological state of Norway spruce. *Fungal Biology* 118, 309–315.
- Rodriguez RJ, White JF, Arnold AE, Redman RS. 2009. Fungal endophytes: diversity and functional roles. *New Phytologist* 182, 314–330.
- Schulz B, Boyle C. 2005. The endophytic continuum. *Mycological Research* 109, 661–686.
- Schwendemann AB, Taylor TN, Taylor EL, Krings M, Dotzler N. 2009. *Combresomyces cornifer* from the Triassic of Antarctica: Evolutionary stasis in the Peronosporomycetes. *Review of Palaeobotany and Palynology* 154, 1–5.
- Schwendemann AB. 2012. Permian photosynthetic pathways: Form, function, and stable carbon isotopes of Antarctic *Glossopteris* leaves. Abstract ID 331. Botanical Society of America, August 2, Providence, RI, USA.
- Selkirk DR. 1972. Fossil *Manginula*-like fungi and their classification. *Proceedings of the Linnaean Society of New South Wales* 97, 141–149.
- Slater BJ, McLoughlin S, Hilton J. 2013. Peronosporomycetes (Oomycota) from a Middle Permian permineralised Peat within the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. *PLoS ONE* 8, e70707.
- Srivastava AK. 1993. Evidence of fungal parasitism in the *Glossopteris* flora of India. *Comptes Rendu XII ICC-P Buenos Aires* 2, 141–146.
- Stone JK, Bacon CW, White JF. 2000. An overview of endophytic microbes: Endophytism defined. *Microbial Endophytes* 3, 29–33.
- Stürmer SL. 2012. A history of the taxonomy and systematics of arbuscular mycorrhizal fungi belonging to the phylum Glome-

- romycota. Mycorrhiza 22, 247–258.
- Taylor EL, Taylor TN. 1990. Structurally preserved Permian and Triassic floras from Antarctica. In: TN Taylor, EL Taylor (Eds), Antarctic Paleobiology: Its Role in the Reconstruction of Gondwana. New York, NY, Springer-Verlag, 149–163.
- Taylor EL, Ryberg PE. 2007. Tree growth at polar latitudes based on fossil tree ring analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 225, 246–264.
- Taylor EL, Taylor TN, Collinson JW. 1989. Depositional setting and paleobotany of Permian and Triassic permineralized peat from the central Transantarctic Mountains, Antarctica. In: PC Lyons, B Alpern (Eds), Peat and Coal: Origin, Facies, and Depositional Models. International Journal of Coal Geology 12, 657–679.
- Taylor TN, Taylor EL, Krings M. 2009. Paleobotany: The Biology and Evolution of Fossil Plants, Second Edition. Burlington, MA, Academic Press, 1230 p.
- Taylor TN, Krings M, Dotzler N, Galtier J. 2011. The advantage of thin section preparations over acetate peels in the study of late Paleozoic fungi and other microorganisms. PALAIOS 26, 239–244.
- Torsvik TH, Cocks LRM. 2013. Gondwana from top to base in space in time. Gondwana Research 24, 999–1030.
- Trivett ML, Pigg KB. 1996. A survey of reticulate venation among fossil and living land plants. In: DW Taylor, LJ Hickey (Eds), Flowering Plant Origin, Evolution, and Phylogeny. New York, NY, Chapman and Hall, 8–31.
- Tu T, Derenne S, Largeau C, Mariotti A, Bocherens H, Pons D. 2000. Effects of fungal infection on lipid extract composition of higher plant remains: comparison of shoots of a Cenomanian conifer, uninfected and infected by extinct fungi. Organic Geochemistry 31, 1743–1754.
- Voříšková J, Baldrian P. 2013. Fungal community on decomposing leaf litter undergoes rapid successional changes. International Society for Microbial Ecology Journal 7, 477–486.
-

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Zitteliana Serie A](#)

Jahr/Year: 2015

Band/Volume: [55](#)

Autor(en)/Author(s): Harper Carla J., Taylor Thomas N., Krings Michael, Taylor Edith L.

Artikel/Article: [Fungi associated with Glossopteris \(Glossopteridales\) leaves from the Permian of Antarctica: A preliminary report 107-114](#)