Fungal sporulation in a Permian plant fragment from Antarctica

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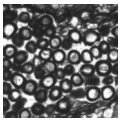

Documented evidence of fungi from the Permian of Antarctica mostly consists of dispersed remains that do not provide the whole complement of diagnostic features necessary to determine even broad systematic affinities. A dense cluster of > 250 fungal spores occurs within a degraded vascular plant (probably glossopteridalean) fragment in Permian permineralized peat from Skaar Ridge, central Transantarctic Mountains, Antarctica. Spores are spheroidal to ovoid, ~ 50 μm in diameter, and possess a massive wall composed of three wall components (wc1–3); one or two canals extend from the spore lumen to the outside. The spores are embedded in a confluent meshwork of tenuous hyphae. Structural similarities exist between the fossil spores and spores produced by certain present-day Mucoromycota, Ascomycota, and Basidiomycota; however, the precise systematic affinities of the fossils cannot be determined. The relationship between the spore producer and its also host plant remains unresolved. Nevertheless, the spatial arrangement of the spores within the plant structure suggests that the fungus required the host for sporulation, and perhaps even influenced plant development for this purpose. This discovery adds to the inventory of distinctive fungal fossils from the Permian of Antarctica and presents a new type of association/interaction between a Permian fungus and a vascular plant. • Key words: development, interaction, *Glossopteris*, parasitism, saprotrophism, spore wall.

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Structurally preserved fossils of fungi from Antarctica have to date primarily come from Triassic permineralized peat, while the record from comparable Permian-aged peat deposits remains meager. This is in spite of the fact that the Antarctic Permian deposits have yielded a number of structurally preserved plant fossils, including a moss, lycopsids, a fern, and several different seed plants (Smoot & Taylor 1986; Galtier & Taylor 1994; McLoughlin & Drinnan 1996; Slater *et al.* 2011; Ryberg *et al*. 2012a, b; McLoughlin *et al.* 2015). The vast majority (> 80% of specimens in some localities; Cúneo *et al.* 1993) of plant remains preserved in the Permian peat are disarticulated parts of glossopterid seed ferns (*e.g.*, Schopf 1970a, b, 1976; Smoot & Taylor 1986; Taylor & Taylor 1987, 1992; Klavins *et al.* 2001; Taylor *et al*. 2007; Ryberg 2009, 2010; Ryberg *et al.* 2012a; Ryberg & Taylor 2013).

The documented record of fungi from Permian peat deposits almost exclusively consists of dispersed and fragmentary remains (Holdgate *et al.* 2005; García Massini 2007; Harper *et al.* 2015, 2016; Slater *et al.* 2015), with little information available on the biology and ecology of the fungi. Permian Antarctic fungal interactions are documented almost exclusively with members of the Glossopteridales, with one notable exception with

lycopsids (McLoughlin *et al.* 2015), and include mycorrhizal associations with young *Vertebraria* rootlets, wood decay fungi, fungal hyphae and reproductive units associated with *Glossopteris* leaves, and fungi colonizing coprolitic material from inside excavated galleries in glossopterid structures (Weaver *et al.* 1997; McLoughlin *et al*. 2011; Slater *et al.* 2012, 2015; Harper *et al.* 2013, 2015, 2017a). Fungi have also been reported in association with glossopterid pollen within sporangia (Slater *et al.* 2015) from Antarctica; however, to date there are no studies that exclusively focus on fungi associated with glossopterid reproductive structures.

In this study we present a detailed account of an interesting fungus associated with a partially degraded, putative glossopterid plant fragment from the Permian permineralized peats from Skaar Ridge, central Transantarctic Mountains of Antarctica. The fungus occurs in the form of spheroidal spores with massive walls that are embedded in a confluent mycelium in the head-like, distal portion of the plant fragment. Especially interesting is the large number of spores (> 250) comprising the cluster. This discovery adds to the inventory of distinctive fungal fossils from the Permian of Antarctica and presents a new type of association/interaction of a Permian fungus with a vascular plant.

Geologic setting, materials, and methods

The fossil comes from a permineralized peat that occurs at 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. The Buckley Formation has been dated as upper Permian (260–251.9 Ma) based on palynological data (Farabee *et al.* 1990, 1991; Collinson *et al.* 2006) that correlates to the Australian APP5–APT1 biozones (Price *et al.* 1985, Mantle *et al.* 2010). The formation consists of coal measures at least 745 m thick that crop out extensively throughout the central Transantarctic Mountains (Barrett *et al*. 1986). The coal measures are informally subdivided into two members: (1) a lower, arkosic sandstone with at least 25% feldspar and (2) an upper, volcanoclastic member (Barrett *et al*. 1986, Isbell 1990, Collinson *et al*. 1994). The deposits from the lower member include permineralized (silicized) peat that is rich in anatomically preserved plant fossils, including *Glossopteris* leaves, wood traditionally assigned to *Australoxylon* (Decombeix *et al.* 2009, 2010), several seed plant reproductive structures (Taylor *et al.* 1989, Cúneo *et al*. 1993, Ryberg 2009, Ryberg *et al*. 2012a), and *Vertebraria*-type roots (Decombeix *et al.* 2009), as well as various types of microorganisms (see references *in* Harper *et al.* 2016).

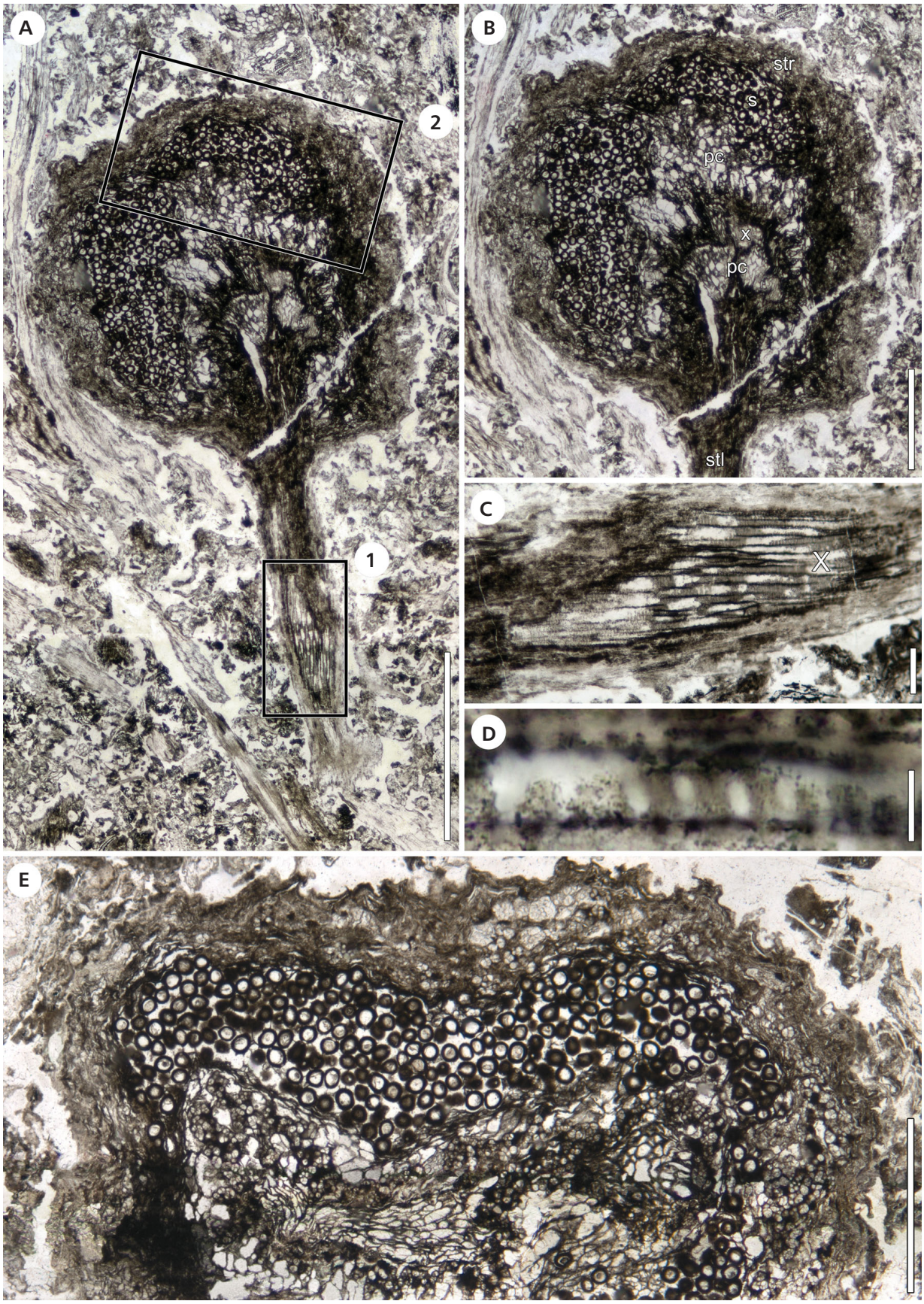
The peat block (16143 F1 bot) containing the fungus was cut into slabs with an oil-cooled lapidary saw and then individual slabs were immersed in hydrofluoric acid (conc. 48%) to dissolve the silica. Acetate peels were subsequently produced from the etched surfaces using the acetate peel technique (Joy *et al.* 1956) modified for hydrofluoric acid (Galtier & Phillips 1999) and then screened for fossilized fungal remains. Consecutive peels of the specimen used in this study were mounted on microscope slides with Eukitt® mounting medium (O. Kindler, Freiburg, Germany). The fossil was further prepared by making a single thin section. A slice of the peat was cemented with UV-cured epoxy to a glass slide and then ground thin enough to view with transmitted light. The mounted peels and thin section were analyzed using a Leica DM LB2 transmitted light microscope; 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 ×64 (©1990–2012, Adobe Systems). When necessary, multiple images of the same specimen were recorded at different focal planes and compiled to produce composite images. 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 Figs 1A–E, 2B–E, L, N, P, and Q. The specimen and slides are deposited in the Paleobotanical Collections, Biodiversity Institute, University of Kansas (KUPB) under specimen accession number KUPB 16,143 F1 bot and slide accession numbers KUPB 30,262–30,265.

Results

Surrounding matrix and morphology of the host (Figs 1A–E, 2A)

The fungal remains occur within a detached, partially degraded vascular plant structure that is 1.96 mm wide

Figure 1. Fungal sporulation in Permian plant structure – the host. • A – overview of host plant structure. Scale bar = 1 mm. • B – higher magnification of structure in Fig. 1A, stratified layer (str), fungal spores (s), parenchyma cells (pc), xylem (x), and stalk (stl). Scale bar = 500 µm. • C – higher magnification of lower box (1) in Fig. 1A, showing tracheids (x) in stalk. Scale bar = 50 µm. • D – higher magnification of tracheids with scalariform thickenings (arrowheads) in Fig. 1C. Scale bar = 10 µm. • E – overview and higher magnification of region in upper box (2) in Fig. 1A, showing head of host structure colonized by fungal spores. Scale bar = 500 µm.


A
1
2
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str
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and 3.71 mm long. The structure is composed of an enlarged distal portion (henceforth 'head') 1.96 mm wide and 1.92 mm long, and a proximal, narrow stalk (denoted 'stl' in Fig. 1B), 0.34 mm wide and 1.79 mm long. The host structure co-occurs in the peat matrix with abundant young *Vertebraria* rootlets in different stages of decomposition, woody axes, peronosporomycete oogonia, coprolites, poorly preserved, unidentifiable plant fragments and other organic matter, as well as sediment particles.

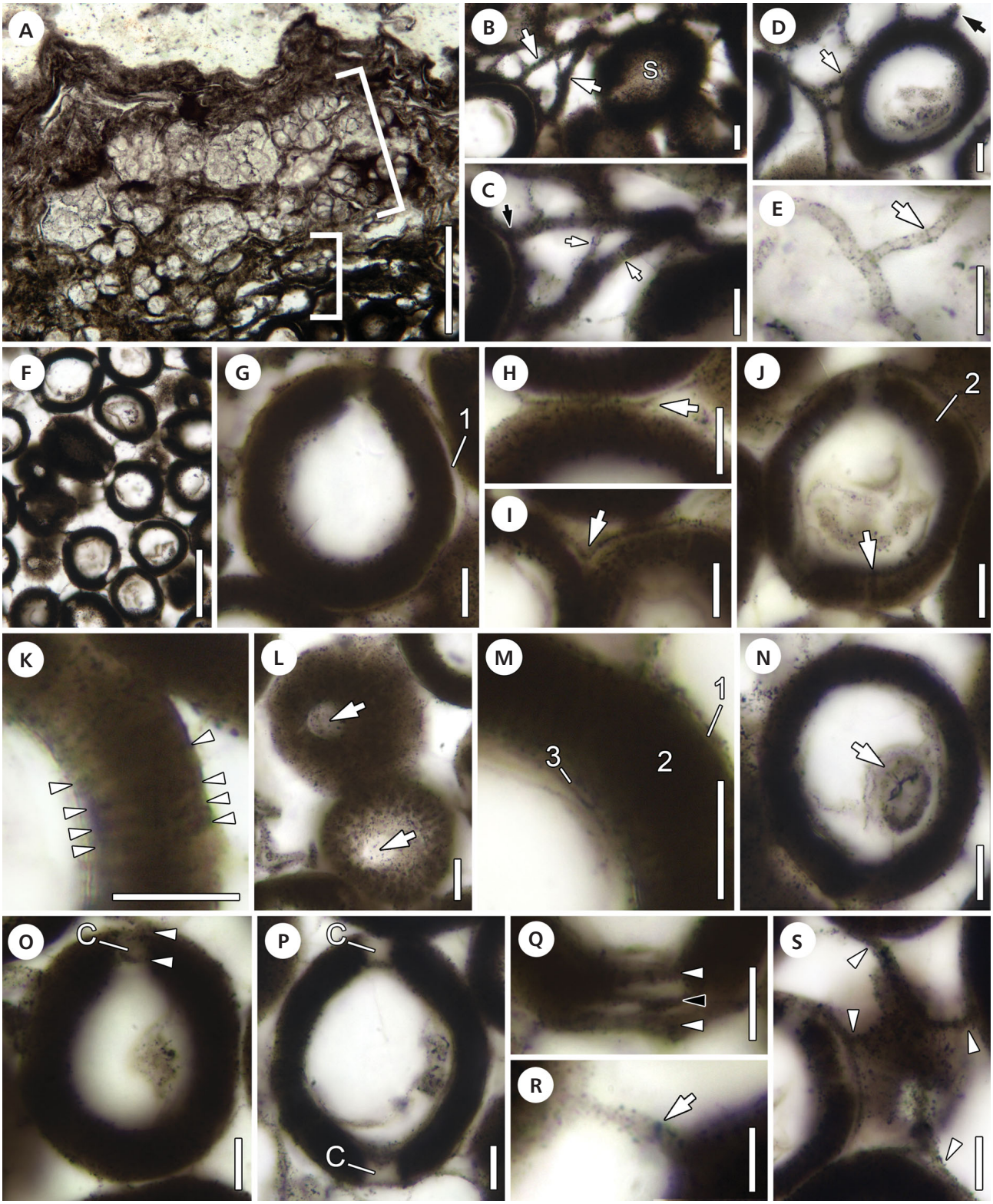
All tissues of the host structure are heavily degraded, rendering it impossible to determine internal organization. The outer surface of the head occurs in the form of a narrow, prominently undulate to irregularly wrinkled, opaque layer up to 60 μm thick (Fig. 1B). The zone extending along the inside of the surface layer ('str' in Fig. 1B) is characterized by a faint, irregular stratification and probably represents (part of) the cortex. The stratified zone is up to 165 μm wide in some areas, but on average 50–70 μm thick. Peculiar muriform structures, ranging from 6–10 μm in diameter, are scattered throughout this zone. Muriform structures are highly variable in size and shape, and display various combinations of transverse and/or longitudinal partitions resulting in the formation of 2 to 6 compartments. Two to several muriform structures together may form small groups that are 15–20 μm in diameter (lower bracket in Fig. 2A) or larger clusters 60–80 μm in diameter (upper bracket in Fig. 2A). Beneath the stratified zone is a large, more or less hemispherical void (~ 1950 μm wide and 500 μm high) that is filled with fungal spores and mycelium (see Fungi section below). The central portion of the head is dome-shaped and consists of what appear to be poorly preserved parenchyma cells ('pc' in Fig. 1B) ~ 30 μm in diameter and tracheids ('x' in Fig. 1B) that extend from the stalk into the head. The tissues of the stalk are poorly preserved and individual elements are almost indistinguishable from one another. However, one oblique section (Box 1 in Fig. 1A) reveals that a strand of tracheids (Fig. 1C) (12–15 μm individual tracheid width) with scalariform thickenings occurs in the center of the stalk (arrowheads in Fig. 1D).

Fungi (Fig. 2B–S)

Spores. – The central void in the head of the plant fragment is completely filled with fungal remains in the form of spores and mycelia (Figs 1E, 2F). Spores are spheroidal, prolate, or ellipsoidal, with an average diameter (for globose specimens) of 52 μm (n = 100), and constructed of a massive, stratified wall surrounding a central lumen (Fig. 2G; see Fig. 3A for a graphic depiction of spore morphology). The spore wall is comprised of three distinct wall components [see Fig. 3B for a graphic depiction of spore wall architecture (murograph)]; however, not all wall components are discernible in all spores, due primarily to the opacity of the specimens. The outer wall component (wc1) is a narrow (1.7–2 μm thick), irregular, perhaps ephemeral sheath (Fig. 2G). Some spores that are directly adjacent to each other appear to possess an additional, distinct boundary layer that develops between the abutting outer spore wall components (Fig. 2H, I). Wall component 2 (wc2) is the most prominent element of the spore wall (Fig. 2J), and is on average 9.4 μm thick (n = 100). Radial and transverse sections of wc2 show radial striations that are regularly arranged and extend the entire width of the component (arrowheads in Fig. 2K). However, surface views and tangential sections indicate that the striations in fact represent columns or spines (on average 1 μm wide) extending through wc2. The outer surface of the spores therefore often appears "dotted" (Fig. 2L). Spore wall component 3 (wc3) is up to 6 μm thick (Fig. 2M). Nevertheless, some of the wall component dimensions might not be natural features, but rather preservation artifacts caused by shrinkage or swelling during fossilization (see Krings & Taylor 2015), or post-mortem shrinkage prior to fossilization. The spore lumen is usually filled with amorphous matter (Fig. 2D, O), but may also be empty (Fig. 2M), or contain one to several spherical inclusions (Fig. 2N).

Approximately 27% of the spores show a single, prominent canal, 8.1–8.7 μm in diameter and 6.6–6.9 μm deep, that appears to extend through all three spore wall components (Fig. 2O), while 3% of specimens possess two canals at opposite poles (Fig. 2P). The lack of canals in the remaining 70% of spores might be a natural feature or simply

Figure 2. Fungal sporulation in Permian plant structure – the fungus. • A – faintly stratified zone of head containing large (top white bracket area) and medium-sized muriform clusters (lower white bracket area). Scale bar = 100 μm. • B – thick-walled spores (S) and dark hyphae (arrow) attached to spore. Scale bar = 10 μm. • C – high magnification of septate (white arrow) hyphae and attachment to outer spore wall component wc1 (black arrow). Scale bar = 10 μm. • D – thick-walled spore attached to thick hyphae (white arrow) and blunt hyphal attachment point (black arrow) on spore wall component wc1. Scale bar = 10 μm. • E – right-angle branching of septate (arrow) hypha. Scale bar = 10 μm. • F – high magnification of several spores. Scale bar = 50 μm. • G – thick-walled spore showing well preserved wall component 1 (1). Scale bar = 10 μm. • H – two spores with abutting wall components 1 (wc1), showing formation of separate wall components between spores (arrow). Scale bar = 10 μm. • I – two spores with abutting wall components 1 and indent (arrow) between spores. Scale bar = 10 μm. • J – spore wall component 2 (2) showing radial striations (arrow). Scale bar = 10 μm. • K – high magnification of striation in spore wall component 2 (wc2). Individual striae bracketed by arrowheads. Scale bar = 10 μm. • L – surface view of two adjacent spores with voids (arrows). Note columns or spines extending from wall component 2 (wc2) in surface view. Scale bar = 10 μm.



• M – high magnification of spore walls; wall components (wc1–3) denoted. Scale bar = 10 µm. • N – spherical content (arrow) in spore. Scale bar = 10 µm. • O – spore with one canal (C). Canal bounded by thin membranes (arrows). Scale bar = 10 µm. • P – spore showing two canals (C). Scale bar = 10 µm. • Q – high magnification of canal bounded by thin membranes (white arrows) and middle membrane (black arrow). Scale bar = 10 µm. • R – hypha with septum (arrow). Scale bar = 5 µm. • S – cruciform-branching of hypha attached to four spores (arrowheads). Note hyphae are attached to outer spore wall component 1. Scale bar = 10 µm.

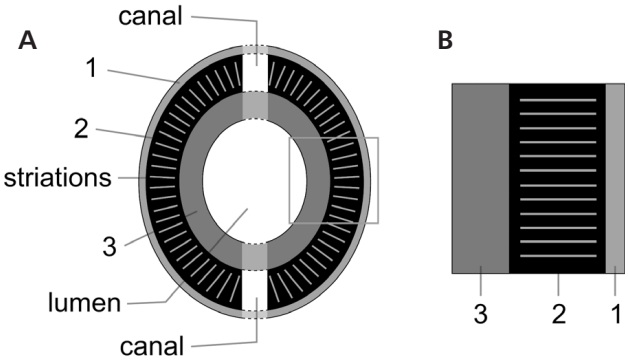


Figure 3. Reconstruction of fungal spore and spore wall components. • A – graphic depiction of spore, showing dimensions and extent of wall components (wc) 1–3, central lumen, and two canals on polar ends. Precise extent of canal unknown due to preservation limitations; spore wall components therefore dashed in region of canal. • B – spore wall architecture shown in the form of murograph. Style loosely borrowed from murographs *in* Walker (1983).

result from the plane of section. Transverse sections of spores suggest that a thin membrane occluded the canals (Fig. 2O arrowheads). There is one specimen that has a single thin membrane in the middle of the canal (Fig. 2Q black arrowhead). No collars or extensions above the outer spore wall surface are present, nor are any of the canals directly connected to hyphae.

Hyphae. – The spores are embedded in a confluent meshwork (mycelium) of narrow hyphae or filaments (1.5–2.5 µm in diameter) that branch at regular intervals and at various angles; septa are present but appear to be generally sparse (Fig. 2R arrow) and are irregularly spaced. Many hyphae appear to arise from, produce, or enter into wc1 (Fig. 2S). Each hypha is usually connected with only one spore; however, cruciform, branch-forming hyphae that are attached to 4 different spores do also occur (Fig. 2S).

An ill-defined, opaque layer that contains wide, septate, multi-branched hyphae 2–8 µm wide surrounds the cluster of spores and tenuous mycelium. Some of these hyphae are physically connected with spores from the periphery of the spore cluster (Fig. 2B–D). Other wide hyphae extend deeply into the spore cluster directly from the stratified layer of the host structure and appear to merge with wc1 of individual spores (Fig. 2B, C). Spores that are not located in close proximity to wide hyphae may still show attachment scars with diameters corresponding to the diameter of the wide hyphae (Fig. 2D black arrow). A single fragment of a septate hypha shows right angle branching (Fig. 2E).

Discussion

Determining synapomorphic characters in fungal fossils that exhibit few morphological features, and assessing the nutritional modes of these organisms represent challenging tasks that are often further compounded by the taphonomic or degradational state in which the fossils occur (Taylor *et al.* 2015). The plant part containing fungal hyphae and thick-walled spores described in this study occurs in a permineralized peat matrix. Since peat forms through the gradual accumulation and compaction of organic matter over longer periods of time, fossil plants and fungi preserved in permineralized peat are typically fragmented, partially decayed, and sometimes severely marred. Moreover, the Permian permineralized peat deposits of Antarctica appear to have developed in a 3-step process (Schopf 1971, Taylor *et al.* 1989), through which especially the more fragile structures have probably been altered secondarily. As a result, plant structures and fungal remains preserved in these rocks are particularly difficult to interpret.

The host

None of the fossil plants that have been reported to date from the Permian of Antarctica are known to produce parts that are morphologically congruent with the host structure. Overall morphology suggests that the host is some type of reproductive structure or part of a complex reproductive organ of a vascular plant. The structure is comprised of a vascularized stalk bearing an enlarged distal portion (head) (Fig. 1A). However, the fossil as a whole is ill preserved. Moreover, no spores, pollen grains, or ovules/seeds have been detected within or in close association with the structure and, as a result, render it difficult to determine affinities and, if it does come from a seed plant, whether it is a male or female reproductive structure. It is possible that the structure lacks evidence of sporangia, pollen sacs, or ovules simply because it was immature at the time of fossilization. Alternatively, it might have been post-mature, perhaps even already shed and lying on the forest floor, with sporangia, pollen sacs, or ovule(s) no longer recognizable. It is also possible that the fungus in some way modified or adversely affected the development of the host structure, perhaps in a similar manner as described for certain extant, plant-colonizing fungi that infect reproductive structures and stimulate gall formation (*e.g.*, Clay 1991, Vujanovic *et al.* 2000, Ngugi & Scherm 2006). The muriform structures interspersed throughout the fossil plant structure probably represent preservation artifacts, perhaps consolidated bubbles containing gases resulting from degradation processes (Taylor *et al.* 1997, Krings & Taylor 2015).

The vast majority of plant reproductive organs that have been described from Skaar Ridge are glossopteridalean (*e.g.*, Taylor & Taylor 1992, Ryberg *et al.* 2012a, Ryberg & Taylor 2013). Consequently, the host

structure might also be glossopteridalean. However, the host structure does not resemble any of the permineralized glossopterid ovulate or pollen organs known from Skaar Ridge, *i.e.*, *Lonchiphyllum aplospermum* Ryberg & E.L. Taylor*, Lakkosia kerasata* Ryberg*, Eretmonia natalensis* Ryberg, E.L. Taylor & T.N. Taylor, and others not formally named (see Schopf 1970a, b, 1976; Taylor & Taylor 1992; Taylor *et al.* 2007; Ryberg *et al.* 2012a; Ryberg & Taylor 2013). Nevertheless, it is possible that the host represents a permineralization equivalent of a reproductive structure described from Antarctica based on impression/compression fossils such as *Cometia, Scutum, Lidgettoniopsis, Plumsteadia, Arberiella,* or *Rigbya* (Lambrecht *et al.* 1972, Kyle 1974, Schopf 1976, McLoughlin *et al.* 1997, Rigby *et al.* 2001, Retallack *et al.* 2005, Ryberg 2009, Ryberg *et al.* 2012c), but this is impossible to know based on the specimen at hand.

Alternatively, the host might be a non-glossopteridalean reproductive structure, such as a sporophyll of lycopsid or a plant type that has not been previously documented from this locality. Non-glossopteridalean plant reproductive structures from Skaar Ridge include sporangia of the fern *Skaaripteris minuta* Galtier & T.N. Taylor (Galtier & Taylor 1994) and sporophylls of the herbaceous lycopsid *Collinsonostrobus eggertii* Ryberg, E.L. Taylor & T.N. Taylor (Ryberg *et al.* 2012b), both of which are morphologically dissimilar to and considerably larger than the structure detailed in this study.

It is also possible that the host structure represents some other plant part (*e.g.*, a root or small twig) that has been physically modified beyond recognition by the fungus (see section Affinities of the fungus, Basidiomycota). For example, the peat matrix contains abundant young *Vertebraria* rootlets characterized by a central vascular bundle surrounded by an intact parenchymatous cortex lacking lacunae, which are a feature of older roots (Decombeix *et al.* 2009). It is possible to envision that the host structure represents a *Vertebraria* rootlet that has been locally infected by a fungus and greatly enlarged in the course of fungal sporulation.

Fungal spore development

Depictions of different life history stages and ontogenetic development in fossil fungi remain rare (*e.g.*, Kettunen *et al.* 2015, Krings *et al.* 2016, Harper *et al.* 2017b). This is unfortunate because life history and ontogeny represent important diagnostic features that could be used to assess the systematic affinities and biology of these fossil organisms in the absence of molecular data. Krings *et al.* (2016) recently analyzed large sample sets (> 100 specimens) of the fungal reproductive unit *Zwergimyces vestitus* (Kidst. & W.H. Lang) M. Krings & T.N. Taylor from the Lower Devonian Rhynie chert, and used structural differences between the specimens to reconstruct ontogenetic development. Development might be used to determine the affinities of the Antarctic spores described in this study. However, all spores in the cluster appear to be mature, and no structural differences indicative of a particular developmental sequence are available.

In the Permian fossil, one peculiar feature of the spores is the presence of one or two prominent canals that extend from the spore lumen through the wall in approximately 30% of specimens. Based on this feature, together with the overall shape and wall architecture of the spores, we hypothesize that the spores represent chlamydospores, which formed on hyphae, either terminally (one polar canal) or in an intercalary position (two polar canals). Unfortunately, the structure of the parental hypha is unclear and the individual spore wall components are difficult to define precisely, rendering it impossible to determine the exact sequence of stages in spore development. Nevertheless, the initial phase might have involved an undifferentiated parental hypha (Fig. 4A) that begins to inflate, either terminally or in an intercalary position between two septa (Fig. 4B). In extant fungi, septa possess a central canal or pore to allow cytoplasmic streaming between adjacent hyphal compartments (Moore & McAlear 1962). The cytoplasm then contracts in the inflated region, and a wall component is laid down (Fig. 4C). As more wall material is amassed, new wall components and features such as the columns are produced (Fig. 4D, E). The canals connecting the lumen of the parental hypha with the lumen of the developing spore begin to close, and thus gradually disconnect the spore from the parental hypha (Fig. 4F). Upon maturation of the spore, the parental hypha disintegrates (Fig. 4G).

Arguing against this scenario are numerous spores closely associated with single hyphae that appear to enter into, or extend from, the outer wall component (wc1). We propose four hypotheses for the relationship between the spores and hyphae: (1) The hyphae might be the parental hyphae; however, they are not physically connected with the polar canals of the spores, as postulated in the hypothetical developmental sequence. Wc1 perhaps represents the inflated portion of the parental hypha, rather than a component of the spore wall proper. If this is accurate, then it is plausible that the mature spores after being disconnected from the parental hypha, moved or rotated within the inflation of the hypha, perhaps naturally or as a result of fossilization. (2) It is also possible that the hyphae, which appear to enter into or extend from wc1, do not actually merge with wc1, but rather extend along the outer circumference of the spore. Unfortunately, the latter is impossible to determine due to the opaqueness of the spores and overall poor preservation of the fossil. (3) Alternatively, the hyphae might have been produced by the spores themselves such as in modern *Glomus corymbiforme* Błaszk.

(Błaszkowski 1995), or (4) represent a type of interspore mycelium that is often found in complex spore-producing structures such as the sporocarps of *Glomus badium* Oehl, D. Redecker & Sieverd. (Oehl *et al.* 2005, Błaszkowski 2012).

Affinities of the fungus

The systematic affinities of the fungal spores described in this study cannot be determined due to the lack of diagnostic features that can be used to directly compare the fossils to modern equivalents. Moreover, the fossils display a variety of morphological features that are reminiscent of extant members in several different lineages of fungi, including Ascomycota, Basidiomycota, and Mucoromycota (Mucoromycotina and Glomeromycotina). Phylogenetic studies indicate that these groups all were well established by Permian time (Blair 2009) and fossil evidence is generally supportive of these estimates (Taylor *et al.* 2015).

Comparison with extant fungi

Ascomycota. – Many members in the Ascomycota produce complex fruiting bodies, *e.g.*, perithecia, apothecia, and cleistothecia (Spatafora *et al.* 2006, Sugiyama *et al.* 2006), but no evidence of such structures has been found in the fossil. However, species in the extant ascomycete genus *Emericella* (teleomorphs of *Aspergillus*) produce specialized, thick-walled cells (termed Hülle cells) terminally on specialized hyphae that surround the cleistothecia (Wu & Miller 1997). Hülle cells are formed in masses and vary in shape between ovoid and globular in different species (Cvetkovic & Vukic 1972, Ellis *et al.* 1973, Carvalho *et al.* 2002). The fossil spores are somewhat similar to Hülle cells, but differ in many ways. Hülle cells and the fossils share a prominent wall and are ellipsoidal to globose in shape; however, an average Hülle cell is 10–15 µm in diameter (Bayram & Braus 2012), while the fossil spores are up to 70 µm. Moreover, Hülle cells in general develop terminally on hyphae, and thus show only one attachment site, whereas some of the fossil spores clearly have two prominent canals, suggestive of intercalary development. However, figures 5 and 6 *in* Christensen *et al.* (1978) show Hülle cells with what appear to be multiple canals or hyphal attachment points. Finally, Hülle cells occur exclusively on cleistothecia, whereas the fossil fungus occurs in the form of a simple cluster of spores not surrounded by a complex ascocarp. On the other hand, the fossil spores are somewhat similar to the ascospores of certain extant ascomycetes. One of these forms is *Corynascella humicola* Arx & Hodges, which produces thick-walled spores with two germ canals at opposite poles of the spore (Arx 1973, fig. 4c; Malloch & Cain 1973); however, no evidence of ascomata or asci is present in the fossil.

Basidiomycota. – The rust (Uredinales or Pucciniales) and smut (Ustilaginomycotina) fungi are obligate biotrophs and exclusively pathogenic on vascular plants, including lycophytes, ferns, gymnosperms, and most families of angiosperms (Begerow *et al.* 2014, Helfer 2014). They are present in all modern terrestrial ecosystems containing plants. Rust and smut fungi have complex life histories; they exploit living host plant tissues in order to complete their life cycles, but can survive unfavorable conditions in dead host tissue through resting spores (teliospores). Moreover, rust and smut fungi can physically alter their plant hosts through the formation of galls (Uchida *et al.* 2003). There is considerable morphological variation in the spore types, especially teliospores, of rusts and smuts (Cummins & Hiratsuka 1984); for example, thick-walled rust teliospores can have germ pores (*Uromyces* sp.) and are produced in an intercalary manner (*Pucciniosira* sp.) (Oberwinkler 1982, 1993), features that morphologically resemble the fossil spores. Additionally, teliospores of some rust fungi such as *Puccinia* spp. are 45.9–52.1 µm in diameter (Anikster *et al.* 2005), which fits within the size range of the fossil spores that average 52 µm in diameter. On the other hand, smut teliospores are on average < 25 µm in diameter (*e.g.*, Khanna *et al.* 1966), with only a few exceptions such as *Tilletia paradoxa* Jacz., with spores up to 50 µm in diameter (Piepenbring *et al.* 1998). Prominent ornaments characterize the walls of rust and smut teliospores, often in the form of squat pyramidal structures that function as hooks to interlock the spores during development (Piepenbring *et al.* 1998, Helfer 2014). The fossil spores have columns in wc2 (Fig. 2J–L) that might be analogous to ornaments, but likely did not function as interlocking hooks. Although some rust and smut fungi can physically alter their hosts through the formation of galls, which does superficially resemble the degraded fossil host structure, we have not found any other structures characteristic of rust or smut fungi such as telia, pedicels, or sterile cells within the cluster of fossil spores (Piepenbring *et al.* 1998, Anikster *et al.* 2005, Helfer 2014).

Mucoromycota. – The fossil spores are morphologically similar in size (*i.e.*, 50–70 µm in diameter), overall shape, and wall thickness to the zygospores of *Endogone pseudopisiformis* Y.J. Yao (Yao *et al.* 1995, pl. 7, fig. 63). Another *Endogone* species that produces thick-walled zygospores is *Endogone aggregata* P.A. Tandy (Tandy 1975, fig. 4). A structural feature that can be used to positively identify fossil Mucoromycotina is the presence of specialized gametangial hyphae to form a zygospore (zygosporogenesis) within a zygosporangium, *i.e.*, gametangial fusion (O'Donnell 1979, Krings & Taylor 2012). This feature has

not been reported in members of the Glomeromycotina (Croll & Sanders 2009, Schüßler & Walker 2011). As a result, the presence of gametangia in organic connection can be accepted as proof that the affinities of a fossil lie with the Mucoromycotina, whereas the absence of gametangia cannot automatically be viewed as evidence in support of glomeromycotinan affinities (Krings & Taylor 2013). The fossil spores described in this study lack specialized gametangial hyphae and therefore cannot be directly assigned to Mucoromycotina.

The fossil spores also resemble the spores of the enigmatic *Gigaspora lazzarii* Montecchi, Ruini & G. Gross, a fungus that is formally included in the Glomeromycotina (Montecchi *et al.* 1996), but that, according to Schüßler & Walker (2010), does in fact not share any features with any taxon in the Glomeromycotina, and thus remains unresolved with regard to systematic position. *Gigaspora lazzarii* produces spores in tightly adpressed clusters (> 20 spores) sheathed by a mucilaginous gleba, all within complex structures termed sporocarps. The spores are spherical to kidney shaped, 40–50 µm in diameter, and have three wall components. *Gigaspora lazzarii*, as well as the *Endogone* species previously discussed, produces spores within sporocarps, a key feature not unequivocally demonstrable in the fossil. However, the ill-preserved zone containing wide hyphae that surrounds the spore cluster (Fig. 2A–E) might perhaps be viewed as a peridium and, accordingly, the entire structure as a sporocarp that developed within the confines of a degrading plant part.

Many present-day glomoid species produce thick-walled spores that are similar in size to the fossils, including (thickest spore wall width given in parentheses) *Funneliformis geosporum* T.H. Nicolson et Gerd., which is approximately 175 µm in diameter and produces 3 wall components (9.5 µm); the outer hyaline wall component sloughs off leaving a granular surface (Walker 1982, Roesti *et al.* 2005). *Claroideoglomus lamellosum* Dalpé, Koske & Tews is 100 µm in diameter and also produces 3 wall components (5.3 µm); the spore produces a pore that is 4.7 µm in diameter and occluded by spore wall component 3 (Dalpé *et al.* 1992). *Glomus hoi* S.M. Berch & Trappe is on average 92 µm in diameter and also produces three wall components (2.2 µm); pores are 5.1 µm in diameter and occluded by a septum (Berch & Trappe 1985). *Funneliformis geosporum, C. lamellosum,* and *G. hoi* all have three-layered walls, but are much larger than the fossil spores. Modern glomoid spores that are similar in diameter, but that do not have the same number of wall components as the fossil spores, include *Diversispora insculpta* Błaszk., which is approximately 60 µm in diameter and only has 2 wall components (Błaszkowski *et al.* 2004), and *Dominikia aurea* Oehl & Sieverd., which attains 55–65 µm in diameter and also has only 2 wall components (Oehl *et al.* 2003). Finally, it is interesting to note

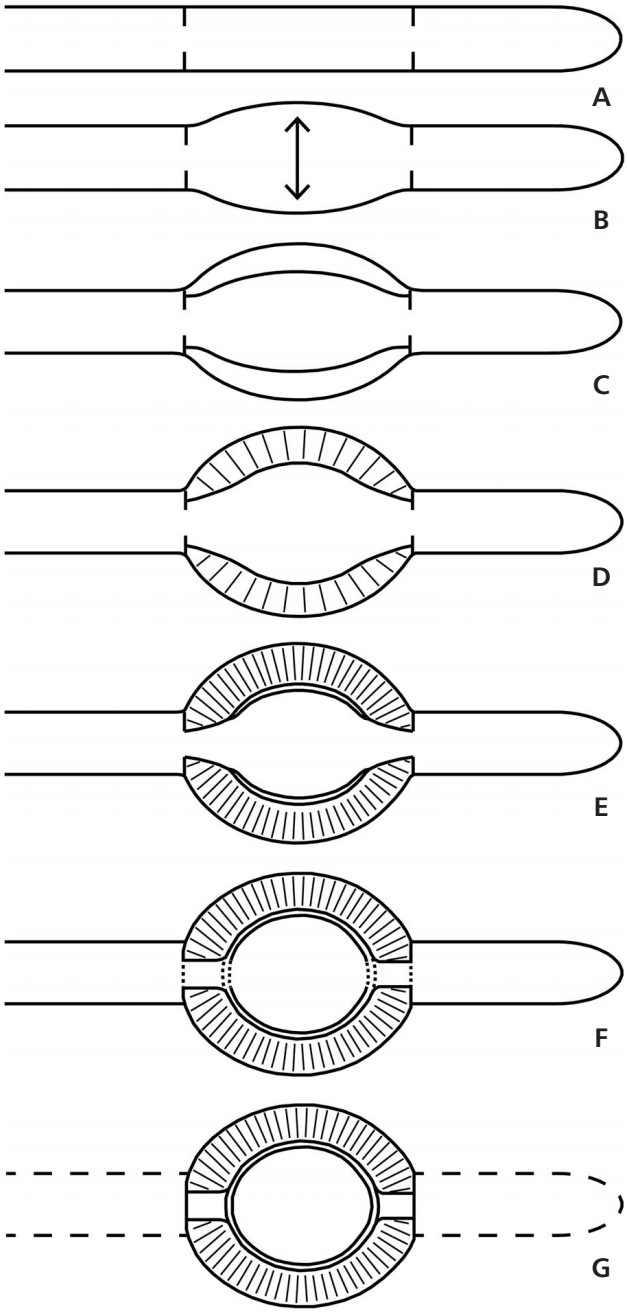


Figure 4. Fungal spore development. • A–G – hypothetical sequence of intercalary spore development (see detailed description in Discussion section – Fungal spore development).

that several extant Glomeromycotina produce spores with ornamented wall layers characterized by spines or other types of protuberances. For example, the spores of *Acaulospora spinosa* C. Walker & Trappe (Walker & Trappe 1981) are characterized by columnar- or spine-like projections extending from one of the wall components into another in a very similar pattern as that seen in wc2 of the fossil spores (Fig. 2J, K). This feature has also been documented in a fossil putative

glomeromycotinan spore from the Lower Devonian Rhynie chert (Krings *et al.* 2017).

Permian thick-walled fungal spores from Antarctica

Clusters of thick-walled spores occurring in highly degraded plant tissue (likely *Vertebraria*) have been described previously from the Skaar Ridge locality. The spores have been interpreted as terminal and intercalary glomeromycotinan chlamydospores and formally described as *Glomorphites intercalaris* García Mass. (García Massini 2007). The affinities of *G. intercalaris* to the Glomeromycotina were suggested based on morphological similarities to extant *Glomus*. Spores are ~ 40 µm in diameter and have three spore wall components, the thickest of which is 5 µm wide. There are up to four subtending hyphal attachment points (4–9 µm in diameter) on each spore. The attachment points are characterized by a thickened rim or collar with suggested septa at the base. The thick-walled spores described in this study also possess three wall components, but are larger than *G. intercalaris*. Moreover, the wall components are structurally different from the components seen in *G. intercalaris.* There is no clear indication of subtending hyphal attachment points in the spores described in this study, but rather they are embedded in a confluent mycelium or tenuous hyphae, which appear to enter into or extend from the outermost spore wall component (wc1).

Other thick-walled fungal spores that come from the Toploje Member peat of the Bainmedart Coal Measures, Prince Charles Mountains, East Antarctica, are up to 20 µm in diameter and possess a spore wall ~ 2 µm thick (Holdgate *et al.* 2005, fig. 14j). The spores are characterized by a polygonal surface pattern, and by prominent attachment points to the parental hypha. Moreover, Slater *et al.* (2015, fig. 6d) describe thick-walled spores of unknown affinities from within plant tissue that are 54 µm in diameter and possess a wall up to 5.3 µm thick. Many of these spores show prominent hyphal attachments (1–3 µm in diameter) with pronounced rims ~ 11 µm in diameter. In the same study, Slater *et al.* (2015, fig. 6e) also illustrate larger, thick-walled spores (*i.e.*, up to 64 µm in diameter) that possess a wall 9.3 µm thick and a polygonal surface pattern. Most of these spores are produced terminally on hyphae 8.8–9 µm in diameter; they occur in the matrix in close proximity to *Vertebraria* roots. The thick-walled spores described in this study differ from those described by Slater *et al.* (2015) with regard to size, mode of attachment to a parental hypha, and because they do not possess a polygonal surface pattern. However, we cannot rule out the possibility that the thick-walled spores described by Slater *et al.* (2015) represent a taphonomic and/or ontogenetic continuum of the same organism that produced the spores detailed in this study.

Nature of the plant–fungus relationship

The majority of fungal fossils preserved in the Permian Skaar Ridge permineralized peat are fragmented and dispersed, and do therefore not provide insights into fungal associations and interactions. The mass of fungal spores embedded in mycelium provides a rare opportunity to speculate on the relationship between a Permian fungus and its plant host. The large number of spores that occur densely clustered and surrounded by a confluent mycelium within a well-defined region of the host structure is suggestive of sporulation within the confines of the host (Dahlberg & Van Etten 1982), rather than spores and mycelium being washed into the degrading plant part. Support for sporulation within the host is the dark zone containing wide hyphae that envelops the spore cluster. If the hypothesis that this structure represents a gall induced by a rust- or smut-like fungus is correct, then the fungus required the (telial) host plant for sporulation to produce resting spores (teliospores). An alternative hypothesis is that the structure represents a peridium produced by a fungus that formed sporocarps within plants, perhaps in a manner similar to certain extinct Mucoromycota, including *Glomites sporocarpoides* Karatygin, Snigirevskaya, K. Demchenko & Zdebska from the Lower Devonian Rhynie chert (Karatygin *et al.* 2006). We are not aware of any modern mucoromycotan fungi that produce sporocarps within plant tissue exclusively when those plant remains are incorporated into the soil. Karatygin *et al.* (2006) suggested that, in the absence of nutrient-rich or well-established soils, *G. sporocarpoides* formed sporocarps within degrading plant parts; this may also be a plausible explanation for sporocarp formation in peat environments. The fungus in this study perhaps required a plant host in order to grow and eventually sporulate. Many modern fungi target plant reproductive structures due to their high concentration of nutritive tissues and function as parasites or require a specific plant host to complete their life cycles (*e.g.*, Banerji 1962, Barrows-Broaddus & Dwinell 1985, Clay 1991, Santini *et al.* 2008). However, the high degree of degradation prohibits determination of the precise nutritional mode of the fungus and whether the host was alive or dead at the time of fungal colonization. It is also possible that the fungus accidentally grew into or utilized the space provided by the degrading plant part lying on the forest floor or in the peat; or within a cavity excavated by a detritivore/herbivore. It is conceivable that sporulation was positively affected either by the confined space provided by the plant structure or the fungus had degraded the contents and left a void. It is interesting to note that confined spaces are known to positively affect sporulation in several modern members in the Glomeromycotina (Suwanarit *et al.* 1985, Rabatin & Rhodes 1982, Koske & Gemma 1995); similar behavior has also been suggested to occur in Glomeromy-

cotina from the Lower Devonian Rhynie chert (Krings *et al*. 2015).

Conclusions

Documented evidence of fungal fossils from the Permian of Antarctica has previously been limited to detached, morphologically simple structures. This contribution provides an additional example of fungi occurring within Permian vascular plant (possibly glossopteridalean) parts. Moreover, the fossil described in this study suggests that the fungus sporulated within the confines of the host. We leave the systematic affinities of the fossil spores open, but suggest they do share certain features with modern chlamydospores that developed terminally or in an intercalary position. We hope that more complete and better-preserved specimens showing this type of plant-fungus association and fungal sporulation within plant remains become available as exploration of Antarctic permineralized peats continues, and that these specimens will reveal structural details that can be used to resolve the systematic affinities of the host, as well as the systematic affinities and nutritional mode of the fungus. As in modern ecosystems, different microorganisms colonized different plant structures utilizing a variety of strategies. A concerted investigation of the relationships between fossil fungi and specific host-plant organs represents a largely untapped area of research, but might be a potential means of more accurately characterizing microbial diversity in the late Paleozoic high-latitude peat-forming ecosystems of Antarctica.

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