

Structurally preserved fungi from Antarctica: diversity and interactions in late Palaeozoic and Mesozoic polar forest ecosystems

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Abstract: Chert and silicified wood from the Permian through Cretaceous of Antarctica contain abundant information on fungal diversity and plant–fungal interactions. The chert deposits represent a particularly interesting setting for the study of plant–fungal interactions because they preserve remains of distinctive high latitude forest ecosystems with polar light regimes that underwent a profound climate change from icehouse to greenhouse conditions. Moreover, some of the cherts and wood show the predominance of extinct groups of seed plants (e.g. Glossopteridales, Corystospermales). Over the past 30 years, documentation of fossil fungi from Antarctica has shifted from a by-product of plant descriptive studies to a focused research effort. This paper critically reviews the published record of fungi and fungal associations and interactions in the late Palaeozoic and Mesozoic cherts and silicified wood from Antarctica; certain fungal palynomorphs and fungal remains associated with adpression fossils and cuticles are also considered. Evidence of mutualistic (mycorrhizal), parasitic and saprotrophic fungi associated with plant roots, stems, leaves and reproductive organs is presented, together with fungi occurring within the peat matrix and animal–fungus interactions. Special attention is paid to the morphology of the fungi, their systematic position and features that can be used to infer fungal nutritional modes.

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Introduction

Extant plants enter into multiple types of associations with other organisms, including bacteria, viruses, algae, fungi and animals (Chapman & Good 1983, Palukaitis *et al.* 2008, Herrera & Pellmyr 2009, Soto *et al.* 2009, Southworth 2012). Of these, fungi are capable of profoundly affecting the plants and environments in which they occur through the formation of permanent or temporary interactions that range from mutualistic to parasitic (Redman *et al.* 2001). Moreover, fungi act as the principal decomposers of lignified plant parts (Kirk & Farrell 1987). Numerous types of fungal interactions that occur with plants also exist with animals (e.g. Lawrence & Milner 1996). Moreover, fungi serve as the primary food source for certain animals (Fogel & Trappe 1978), and many animals, especially arthropods, are effective as vectors in the distribution of fungal spores (e.g. Bultman & Mathews 1996).

Since fungal interactions are prevalent in modern ecosystems, it would be reasonable to assume that these interactions also existed in ancient ecosystems and,

consequently, can be documented from the fossil record. Although fossil evidence of fungal associations and interactions is generally rather rare, the examples reported to date suggest that fungi in fact played important roles in ancient ecosystems and in the evolutionary history of life (Pirozynski & Malloch 1975, Hawksworth 1991, Taylor *et al.* 2015). Until relatively recently, fossil fungi found in association with other organisms have mostly been described cursorily and rarely been placed into a palaeoecological context. Today, however, the importance of fungal interactions as a driving force in modern ecosystems is widely acknowledged and, consequently, palaeobiologists take increased effort to document fossil fungal associations and interpret the roles these organisms may have played in the ecosystems in which they lived.

Plants may become preserved as fossils in a variety of modes (Schopf 1975), each demonstrating a different complement of information on the organism. However, only three of these preservation types can provide details of the internal organization (anatomy, histology) of a plant, i.e. petrifications, permineralizations and, to a

Table 1. (Continued)

Age	Stratigraphy	Locality	Plant organ or matrix	Species or fungal description	Major fungal phyla										Reference(s)		
					Chytridiomycota	Blastocladiomycota	Zygomycetes	Glomeromycota	Ascomycota	Basidiomycota	Unknown Affinity	Lichen	Fungal Spores	Fungal Interactions		Peronosporomycetes	Mycetozoa
				<i>Sclerocystis</i> -like fungus													Stubblefield et al. 1987a
				<i>Endochoetophora antarctica</i>													White & Taylor 1988, 1989a, Harper 2015
				<i>Mycocarpon asterineum</i>													Taylor & White 1989
				Fungal type No. 2 "sporocarp" with mycelial peridium with internal spores													
				Fungal type No. 3 "sporocarp" with mycelial peridium with internal mantled spores													
				Fungal type No. 5 Subglobose sporangium													
				Fungal type No. 6 Subglobose sporangium with a radially orientated striated cell wall													White & Taylor 1989b
				Trichomycete-like fungus													
				Fossil 1 "sporocarp" composed of irregularly thick interwoven hyphae													White & Taylor 1989c
			matrix	Fossil 2 trilayer "sporocarp"													
				Fossil 3 globose "sporocarp" surrounded with interwoven mycelium with internal septate hyphae													
				Fossil 4 ovate "sporocarp" surrounded with interwoven mycelium with internal septate hyphae													
				Fossil 6 "sporocarp" surrounded with interwoven mycelium													
				Fossil 7 Multiple cell wall "sporocarp" with inner acellular layer with internal spores													
				Fossil 8 double isodiametric cell wall "sporocarp" with internal spores													
				Fossil 9 double cell wall "sporocarp" with membranous contents													
				Fossil 10 thick wall "sporocarp" with internal spores													
				<i>Combesomyces cornifer</i>													Schwendemann et al. 2009
				<i>Jimwhitea circumtecta</i>													Krings et al. 2012
				Fungal type No. 1 Globose spores in clusters													
			matrix; roots	Fungal type No. 4 Trilayer "sporocarp" with internal globose spores with possible gametangia													White & Taylor 1989b
				Fossil 5 possible chlamydospore with mycoparasite													White & Taylor 1991
			multiple organs	<i>Palaeyfibulus antarctica</i>													Osborn et al. 1989
				Fungal spores in <i>Spiculinodium collinsonii</i> bud													Osborn et al. 2000, Schwendemann et al. 2010b
			reproductive structure	<i>Mycocarpon asterineum</i> in <i>Parasciadophlys aequata</i>													Schwendemann et al. 2010a
				Fungal hyphae in <i>Parasciadophlys aequata</i>													
				Hyphae in ovules of <i>Ignatosperrum</i>													Perovich & Taylor 1989
				Chytrid-like structure in <i>Gleichenopteris antarctica</i> spores													Phipps et al. 2000
				Chytrid-like structures in pollen grains													Harper 2015

Table I. (Continued)

Age	Stratigraphy	Locality	Plant organ or matrix	Species or fungal description	Major fungal phyla										Reference(s)										
					Chytridiomycota	Blastocladiomycota	Zygomycetes	Glomeromycota	Ascomycota	Basidiomycota	Unknown Affinity	Lichen	Fungal Spores	Fungal Interactions		Peronosporomycetes	Mycetozoa	Bacteria							
Middle to Late Triassic (Anisian)	Fremouw Formation, Victoria Group, Upper Beacon Supergroup	Fremouw Peak, Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains of Antarctica	roots	Mycorrhizae in <i>Antarctocyclus schopffii</i>														Stubblefield <i>et al.</i> 1987b,c							
				<i>Gigasporites myriamycetes</i> (mycorrhizae in <i>Antarctocyclus schopffii</i>)																Phipps & Taylor 1996					
				<i>Glomites cycestrís</i> (mycorrhizae in <i>Antarctocyclus schopffii</i>)																	Schwendemann <i>et al.</i> 2011				
				Mycorrhizal root nodules in <i>Natophyllum krausei</i>																	Harper <i>et al.</i> 2015a				
Middle to Late Triassic (Anisian)	Fremouw Formation, Victoria Group, Upper Beacon Supergroup	Fremouw Peak, Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains of Antarctica	stems	Mycorrhizae in <i>Natophyllum krausei</i>														Taylor & Stubblefield 1987							
				Chytrid-like structures in <i>Antarctocyclus schopffii</i>	○															Harper 2015					
				Fungi in <i>Ashikuluis schopffii</i>																	Stubblefield & Taylor 1985, 1986				
				Pocket rot in <i>Agarthaoylon</i> wood																	Bergene <i>et al.</i> 2013				
Middle to Late Triassic (Anisian)	Fremouw Formation, Victoria Group, Upper Beacon Supergroup	Fremouw Peak, Beardmore Glacier area, Queen Alexandra Range, central Transantarctic Mountains of Antarctica	reproductive structure	Fungal hyphae in <i>Dorochitrites arcanus</i>															Bergene <i>et al.</i> 2013						
				Fungal "sporecaps" near <i>Rubixylon serbetianum</i>		○															Bonifleur <i>et al.</i> 2013				
				Fungal remains in microbial mats																		Bonifleur <i>et al.</i> 2007			
				Tylosis formation and fungi in wood																		Harper <i>et al.</i> 2012			
Early Jurassic (Toarcian)	Kirkpatrick Basalt Group	Gair Mesa range in northern Victoria Land (west of specimen no. B1-4 W2), Transantarctic Mountains, East Antarctica	stem wood	Fibril structures within tracheids																Jefferson <i>et al.</i> 1983					
				Thick-walled hyphae in vascular bundles of <i>Brachyphyllum</i> -type leaves																	Hieger <i>et al.</i> 2015				
				Wood decay (no fungi) in <i>Podocarpoxylon</i>																		Falcon-Lang <i>et al.</i> 2002			
				Fibril structures within tracheids																		Jefferson 1982, Jefferson 1987			
Early Cretaceous (Aptian)	Triton Point Formation, Fossil Bluff Group	southeastern Alexander Island	stem wood	Wood decay (no fungi) in <i>Podocarpoxylon</i>																	Falcon-Lang <i>et al.</i> 2001				
				Fungal spores in <i>Podocarpoxylon</i>																			Poole <i>et al.</i> 2000		
				Fungal structures in <i>Weinmannioxylon nordenskiöldii</i>																				Cantrill 2000	
				Circular inclusions in <i>Centrifucus antarcticus</i>																				Poole & Francis 2000	
Late Cretaceous (Coniacian-Santonian)	Hidden Lake Formation	Lachman Crags Member of the Santa Marta Formation, Marambio Group	stem	Fungal structures in <i>Winteroxylon jamesrossi</i>																			Poole & Francis 2000		
				Fungal structures in <i>Laureliopsis philippiana</i>																					Poole & Francis 1999

lesser extent, amber (Taylor *et al.* 2009). On the other hand, compression fossils may yield information on the epidermal anatomy if preserved in fine-grained sediment. Petrification occurs when the cell lumina and walls are completely replaced by minerals, possibly as a weathering effect. In contrast, permineralization is a form of preservation in which minerals have replaced the internal contents of the cells, but the cell walls are not completely replaced by minerals (Williams & Crerar 1985, Williams *et al.* 1985). The anatomical details provided by these two modes of preservation provide an unparalleled level of resolution to study fungal interactions in the fossil record.

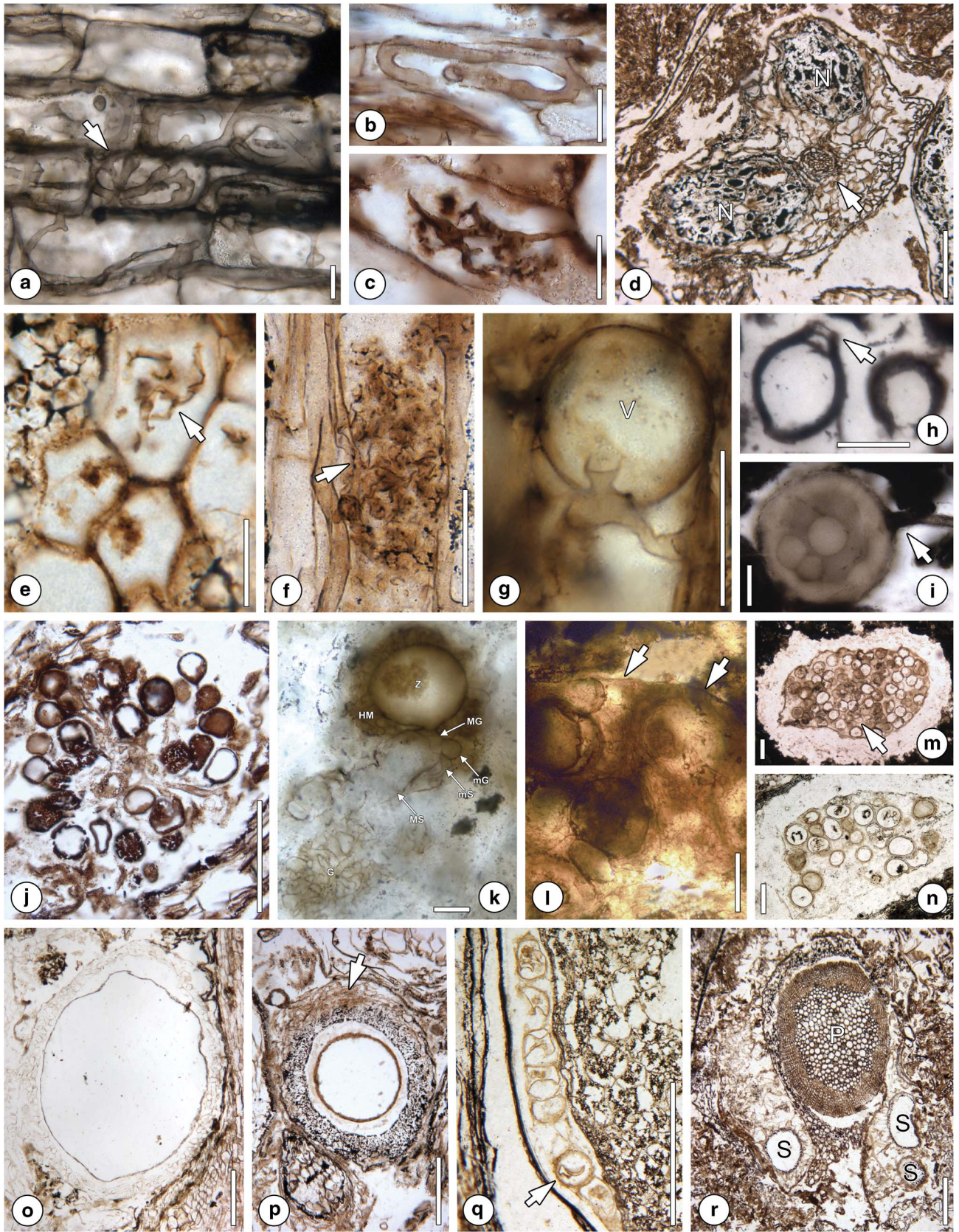
The co-occurrence of permineralized deposits from multiple periods of geologic time in one area is exceptionally rare. Some of the best-known examples come from the Permian, Triassic and Jurassic of the Transantarctic Mountains (Taylor *et al.* 1989, Taylor & Taylor 1990, Bomfleur *et al.* 2014b). In contrast to the harsh environment of Antarctica today, favourable climatic conditions existed during warmer periods of Earth history supporting a rich forest vegetation in South Polar latitudes (e.g. Cantrill & Poole 2013). Middle Permian (Wordian) permineralized peat (i.e. a chert that formed within a peat-forming environment) occur in the Prince Charles Mountains, East Antarctica (Bennett & Taylor 1972, McLoughlin *et al.* 1997), whereas Late Permian and Middle Triassic (Anisian) permineralized peats have been reported from the central Transantarctic Mountains (Barrett 1969, Schopf 1970, Taylor *et al.* 1989). The Transantarctic Mountain deposits have been suggested as peat mire rafts that eroded into river channels, and once entombed in sand, silica-rich water initiated the permineralization process (Taylor *et al.* 1989, Collinson *et al.* 1994), whereas the peats from the Prince Charles Mountains come from outcrops extending for >2 km (e.g. McLoughlin & Drinnan 1996). The Permian–Triassic transition marks the shift from the palaeophytic (e.g. *Glossopteris*-dominated) to more modern and highly diversified vegetation types resulting from the drastic change in physical environment and global temperature (Taylor *et al.* 1986, Iglesias *et al.* 2011). Southern Gondwana experienced a generally warmer and less seasonal climate after the end-Permian event that marked the passage from a global icehouse condition in the Early Permian to the hothouse state of the Early Triassic, and eventually the greenhouse climate, which persisted throughout the Triassic (Kidder & Worsley 2004, Lindström & McLoughlin 2007, Preto *et al.* 2010, Escapa *et al.* 2011). The vast majority of what is known about Triassic fungi and plant–fungal interactions is based on Middle Triassic permineralized peat deposits of Fremouw Peak. The initial fragmentation of Gondwana occurred during the transition from the Triassic to Jurassic, and is characterized by increased

volcanic activity reflected in the geologic record (Hergt & Brauns 2001, Riley *et al.* 2006, Bromfield *et al.* 2007, Elliot & Fleming 2008). Jurassic chert containing plant remains and fungi, as well as silicified wood, come from the Gair Mesa Range, northern Victoria Land, and the Carapace Nunatak, southern Victoria Land (Gunn & Warren 1962, Gair *et al.* 1965, Ballance & Watters 1971, Bomfleur *et al.* 2011, Hieger *et al.* 2015). During the Cretaceous, Antarctica reached the approximate geographical position that it occupies today (Lawver *et al.* 1992), but was still considered a climatic greenhouse. Several sites on the Antarctic Peninsula, including Alexander Island, James Ross Island, Livingston Island, Table Nunatak and Seymour Island have yielded silicified wood (including specimens that contain fungi), as well as foliage fossils, spores and pollen grains, and flowers (Francis *et al.* 2008).

Since the initial review of Antarctic fossil fungi by Taylor (1990) a considerable body of new information has been amassed on the fungi occurring in the plant-bearing cherts and silicified wood from Antarctica. However, this evidence is scattered and often included in works focusing on other aspects of ancient life in Antarctica. This review critically surveys the evidence of fungi extending from the Permian to Cretaceous in chert deposits and silicified wood from Antarctica, as well as reports on certain fungal palynomorphs, dispersed remains and compression-impression fungal fossils, and is intended primarily as a tool to access the primary literature, but may also be used to define future research perspectives. It focuses on the evidence of mutualistic and parasitic plant–fungal interactions, as well as saprotrophism, but also addresses dispersed fungal remains from the matrix and examples of fungi as components of food webs (see Table I).

Mutualistic fungal interactions (mycorrhizas)

Plant growth depends on the availability of a variety of macro- and micronutrients in the rhizosphere, including phosphorous, nitrogen, potassium, copper and zinc (Marschner & Dell 1994, Talbot *et al.* 2008). To increase and facilitate the uptake of some of these nutrients, most extant plants enter into one or several types of mycorrhizal associations with fungi. These associations are generally mutualistic (commonly interpreted to be beneficial for both partners), but in some cases may become weakly parasitic (Johnson *et al.* 1997, Kirk *et al.* 2008). Mycorrhizal associations occur in an estimated 90% of extant plants, including bryophytes, lycophytes, pteridophytes, gymnosperms and angiosperms (Wang & Qiu 2006). Despite the prevalence of mycorrhizal associations today, documented fossil evidence of mycorrhizas is scarce.



Mycorrhizal associations have been described in three seed plant taxa from Antarctica.

Vertebraria spp.

The Glossopteridales, an extinct group of Palaeozoic arborescent seed ferns that dominated the forest ecosystems of Antarctica during the Permian, are characterized by tongue-shaped leaves with a unique pattern of reticulate venation, stems with secondary xylem exhibiting mixed pitting (*Australoxylon* spp.) and an interesting type of rooting structure known as *Vertebraria* (Schopf 1970, Rigby 1972, Mussa 1978). The most distinctive features of older (woody) *Vertebraria* roots are radiating, wedge-shaped lacunae (Neish *et al.* 1993, Decombeix *et al.* 2009). In contrast, young rootlets lack lacunae. They consist of a central vascular strand surrounded by a parenchymatous cortex and the rhizodermis. Evidence of a mycorrhiza involving a glomeromycotan fungus (*Glomites vertebrariae* C.J. Harper, T.N. Taylor, M. Krings *et al.* E.L. Taylor) occurs in small *Vertebraria* rootlets (0.3–1 mm in diameter) from Skaar Ridge in the central Transantarctic Mountains (Fig. 1a). The fungus is characterized by intracellular septate hyphae that extend through a discrete zone of the cortex 2–3 cell layers below the rhizoepidermis. Arbuscules range from serpentine to coiled and are morphologically similar to extant *Paris*-type mycorrhizas (Harper *et al.* 2013). Additional structural

features of the fungal partner occur in the form of globose–ellipsoid vesicles that lack a septum at the hyphal attachment. The *Vertebraria*–*G. vertebrariae* association represents the only example to date of a mycorrhiza in seed ferns, and the oldest fossil evidence of *Paris*-type morphology in mycorrhizal fungi.

Antarcticycas schopfii

Cycads are an ancient group of seed plants that are interpreted to have originated during the late Palaeozoic (Norstog & Nicholls 1997, Pant 2002). From the Middle Triassic Fremouw Peak locality, the cycad *Antarcticycas schopfii* E.L. Smoot, T.N. Taylor *et al.* T. Delevoryas has been reconstructed based on structurally preserved stems (Smoot *et al.* 1985), cataphylls, petiole bases, leaves (*Yelchophyllum omegapetiolaris* E. Hermsen, T.N. Taylor, E.L. Taylor *et al.* D.W. Stevenson), stems, microstrobili (*Delemaya spinulosa* S.D. Klavins, E.L. Taylor, M Krings *et al.* T.N. Taylor) and roots (Stubblefield *et al.* 1987b, 1987c, Phipps & Taylor 1996, Klavins *et al.* 2003, Hermsen *et al.* 2009). Small rootlets of *A. schopfii* are typically radial and diarch; surrounding the vascular cylinder is a band of cells filled with a dark ergastic substance bounded on the outside by the endodermis and at the periphery a parenchymatous cortex (Smoot *et al.* 1985). Many rootlets are colonized by two distinct types of glomeromycotan fungi, *Gigasporites myriamycetes* C.J. Phipps *et al.* T.N. Taylor and *Glomites cycestris*

Fig. 1. Mycorrhizal associations, complementary evidence of mycorrhizal fungi (additional information in the text). **a.** Cortical cells of *Vertebraria* sp. containing *Paris*-type morphology of mycorrhizal hyphae with hyphal knob (arrow). Scale bar = 25 µm. Originally illustrated in Harper *et al.* 2013: Pl. II, 2. **b.** Coiled *Gigasporites myriamycetes* hyphae in *Antarcticycas schopfii*. Scale bar = 25 µm. Originally illustrated in Phipps & Taylor 1996: fig. 3. **c.** *Glomites cycestris* arbuscule. Scale bar = 25 µm. Originally illustrated in Phipps & Taylor 1996: fig. 15. **d.** Two mature root nodules (N) with small vascular cylinder (arrow) of *Notophytum krauselii*. University of Kansas Division of Paleobotany (KUPB) specimen 11277 B2 side bot #18. Scale bar = 200 µm. **e.** Putative arbuscules (arrow) in cortex of *N. krauselii* root nodule. Scale bar = 30 µm. Originally illustrated in Schwendemann *et al.* 2011: fig. 1F. **f.** Arbuscule in cortical cell of non-nodule forming *N. krauselii* rootlet showing attachment to trunk hypha (arrow). Scale bar = 25 µm. Originally illustrated in Harper *et al.* 2015a: Pl. II, 9. **g.** Spherical vesicle (V) in non-nodule forming *N. krauselii* rootlet. Scale bar = 25 µm. Originally illustrated in Harper *et al.* 2015a: Pl. II, 12. **h.** Terminal multi-layered (arrow) chlamydospore in peat matrix. Scale bar = 25 µm. Originally illustrated in García Massini 2007a: fig. 1G. **i.** Asexual spore with subtending hypha (arrow); note internal contents. Scale bar = 25 µm. Originally illustrated in Harper *et al.* 2015b: Pl. I, 13. **j.** *Sclerocystis*-like fungal fossil. Scale bar = 15 µm. Originally illustrated in Stubblefield *et al.* 1987a: fig. 1. **k.** *Jimwhitea circumtecta* (Endogonaceae) holotype. Zygosporangium (Z) surrounded by hyphal mantle (HM). Sporangium arises from megagametangium (MG) subtended by megasuspensor (MS). Laterally attached to megagametangium is microgametangium (mG) subtended by microsuspensor (mS). The entire complex appears to have developed from loose network of hyphae (G). Scale bar = 20 µm. Originally illustrated in Krings *et al.* 2012: figs 1A & 3. **l.** Portion of sporocarp attributed to *J. circumtecta*. Arrows indicate narrow peridium. Scale bar = 50 µm. Originally illustrated in Krings *et al.* 2012: fig. 2A. **m.** ‘Fungus no. 2’. Cluster of spores enveloped in massive peridium. Scale bar = 100 µm. Originally illustrated in White & Taylor 1989: Pl. I, 3. **n.** ‘Fungus no. 3’. Mantled spores surrounded by mycelial peridium. Scale bar = 100 µm. Originally illustrated in White & Taylor 1989: Pl. II, 1. **o.** *Endochaetophora antarctica* showing interwoven hyphal meshwork surrounding central cavity. Scale bar = 250 µm. Originally illustrated in White & Taylor 1989a: Pl. I, 4. **p.** *Mycocarpon asterineum* spheroidal ‘sporocarp’ with empty cavity, acellular investment layer, surrounded by loosely interwoven mycelial investment (arrow). Scale bar = 100 µm. Originally illustrated in White & Taylor 1991: Pl. I, 3. **q.** *Mycocarpon asterineum* (arrow) in *Parasciadopitys aequata*. Scale bar = 100 µm. Originally illustrated in Schwendemann *et al.* 2010a: fig. 4D. **r.** Hyphal network containing what appear to be ‘sporocarps’ (S) enveloping a petriellalean stem (P). Scale bar = 250 µm. Originally illustrated in Bomfleur *et al.* 2014a: fig. 4J.

C.J. Phipps *et al.* T.N. Taylor, that form mycorrhizal associations with *A. schopfii* (Phipps & Taylor 1996). Both fungi produce inter- and intracellular hyphae, arbuscules (one per host cell), and ovoid to ellipsoidal vesicles. However, *G. myriamycetes* is distinguished from *G. cycestris* by hyphal loops and coils that commonly branch dichotomously (Fig. 1b), in some cases trichotomously, and coarse, robust arbuscules that branch twice. Conversely, *G. cycestris* hyphae are typically straight (sporadically sinuous), branch dichotomously and produce delicate arbuscules that terminate in segments < 1 µm in diameter (Fig. 1c). These two distinct mycorrhizas in *A. schopfii* indicate that vesicular arbuscular mycorrhizal associations represent an ancient relationship in the cycad lineage.

Notophytum krauselii

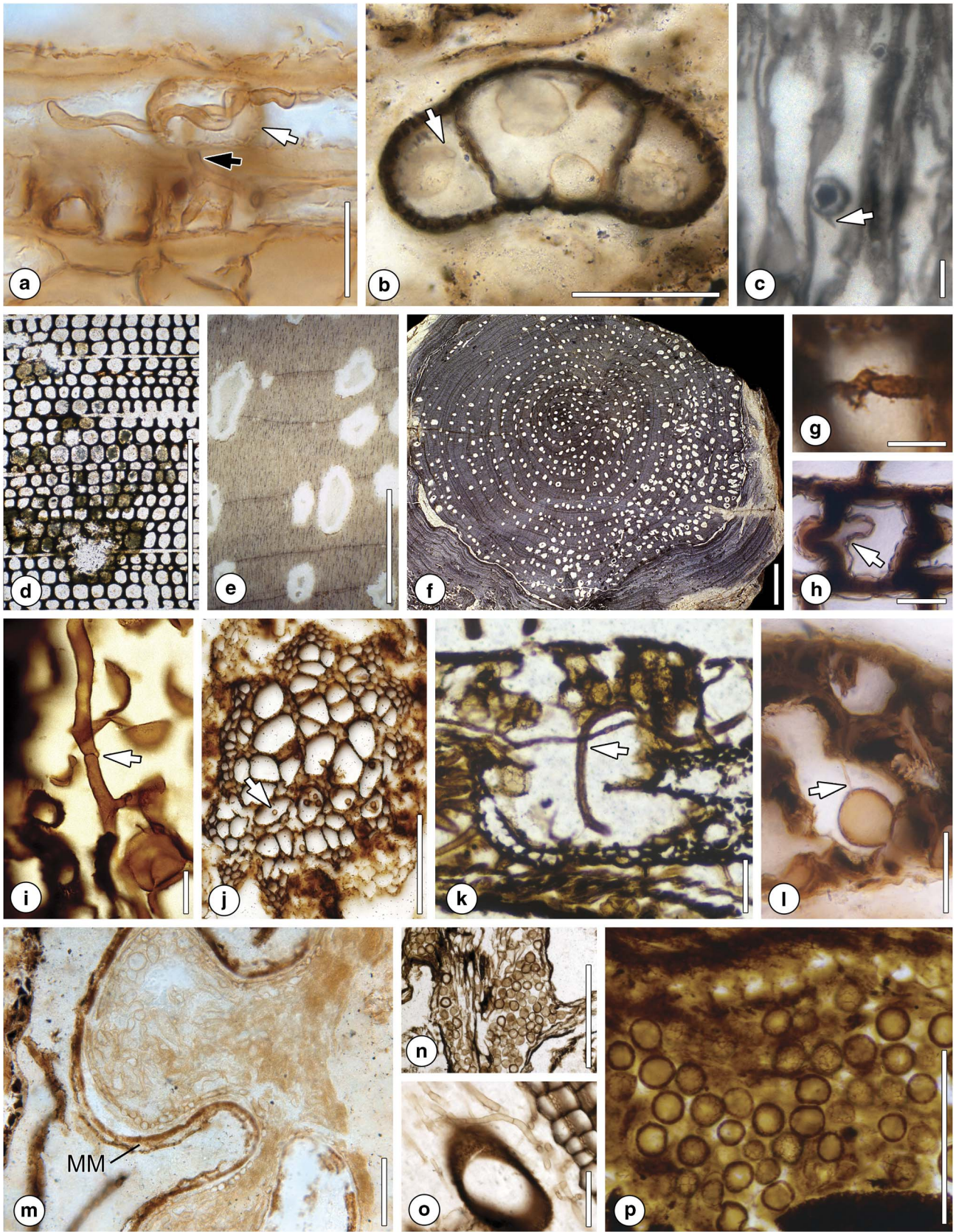
A second example of the co-occurrence of two mycorrhizal fungi in a gymnosperm from the Triassic of Antarctica is *Notophytum krauselii* B. Meyer-Berthaud *et al.* T.N. Taylor, a voltzialean conifer (Meyer-Berthaud & Taylor 1991, Axsmith *et al.* 1998, Bomfleur *et al.* 2013). The Voltziales are a morphologically heterogeneous group of conifers considered to be transitional between the Palaeozoic Cordaitales and the modern conifers (Florin 1951, Hernández-Castillo *et al.* 2001, Rothwell *et al.* 2005). Schwendemann *et al.* (2011) describe rootlets of *N. krauselii* that are characterized by paired prolate spheroidal structures interpreted as root nodules (Fig. 1d). In the cortex of the nodules are mycorrhizal fungi comprised of hyphae, vesicles, intracellular hyphal coils and arbuscules (Fig. 1e). Fungal hyphae are also present on the surface of the nodules, and dispersed

glomoid spores occur scattered throughout the matrix surrounding the nodules. More recently, Harper *et al.* (2015a) reported a different mycorrhiza that also occurs in young *N. krauselii* rootlets. These latter rootlets resemble the nodule-bearing rootlets regarding internal organization but lack nodules. The mycorrhizal fungus is restricted to the outer root cortex and characterized by septate hyphae, multi-branched arbuscules (Fig. 1f) and vesicles (Fig. 1g). The occurrence of mycorrhizal fungi in two different types of *N. krauselii* roots may suggest that this plant entered into several types of mycorrhizal associations simultaneously, perhaps at different soil levels or in different regions of the rooting system, or was able to switch between different mycorrhizal associations, a condition that also occurs in some extant plants (e.g. Demchenko *et al.* 2004). Another report of putative root nodules in fossil gymnosperms from Antarctica comes from the Upper Cretaceous (Albian) of Alexander Island. Compression fossils of small conifer rootlets show numerous swellings that are morphologically similar to extant podocarp root nodules (see Pl. 7, fig. b of Cantrill & Falcon-Lang 2001). Mycorrhizal fungi may have helped the Mesozoic gymnosperms of Antarctica to function in adverse environmental conditions, and it will be interesting to see if other groups of plants growing in the polar forest palaeoecosystems also entered into complex mutualistic associations with fungi.

Complementary evidence of mycorrhizal fungi

Fossil mycorrhizas are ideally documented from evidence showing both partners together. However, most evidence of fossil Glomeromycota and other possibly mycorrhizal

Fig. 2. Parasitic and saprotrophic fungi (additional information in the text). **a.** Hypha (black arrow) penetrating tylosis wall (white arrow). University of Kansas Division of Paleobotany (KUPB) slide TS-GIX-SB-036-01. Scale bar = 25 µm. **b.** Chytrid-like organisms with pore (arrow) in pollen grain corpus and sacci. KUPB slide 26590. Scale bar = 25 µm. **c.** Putative endoparasitic chytrid *Synchytrium permicus*. Arrow indicates possible discharge papilla. Scale bar = 10 µm. Originally illustrated in García Massini 2007b: figs 1–4. **d.** Transverse section of *Australoxylon* wood showing decay cavity surrounded by damaged tracheids. Scale bar = 500 µm. Originally illustrated in Weaver *et al.* 1997: fig. 9A. Courtesy of S. McLoughlin. **e.** Diffuse decay cavities in *Australoxylon*. Scale bar = 5 mm. Originally illustrated in Weaver *et al.* 1997: fig. 11A. Courtesy of S. McLoughlin. **f.** Cross section of *Araucarioxylon* axis showing pockets of decay. Arrow indicates pocket within a single growth ring. Scale bar = 2 cm. Originally illustrated in Stubblefield & Taylor 1986: fig. 1. **g.** Simple-intermediate medallion clamp connection in *Vertebraria* root wood. Scale bar = 10 µm. **h.** Swollen cell wall pinching into cell lumen (arrow) in *Vertebraria* root wood. Scale bar = 10 µm. **i.** Vegetative and reproductive features of *Palaeofibulus antarctica* with partially developed clamp connection (arrow). Scale bar = 20 µm. Originally illustrated in Osborn *et al.* 1989: fig. 5. **j.** Fungal hyphae (arrow) penetrating *Paurodendron* tracheids. Scale bar = 100 µm. Originally illustrated in McLoughlin *et al.* 2015: Pl. II, 7. Courtesy of S. McLoughlin. **k.** Hyphae (arrow) ramifying through mesophyll of *Noeggerathiopsis* leaf. Scale bar = 100 µm. Originally illustrated in Holdgate *et al.* 2005: fig. 14i. Courtesy of S. McLoughlin. **l.** Degraded mesophyll containing chytrid-like organism showing minute hyphal attachment (arrow). Scale bar = 10 µm. Originally illustrated in Harper *et al.* 2015b: Pl. 1, 3. **m.** Fungus in megaspore membrane (MM) of *Dordrechites arcanus*; note hyphae in multiple orientations. Scale bar = 50 µm. Originally illustrated in Bergene *et al.* 2013: fig. 6E. **n.** Small fungal spores. Scale bar = 500 µm. Originally illustrated in Slater *et al.* 2015: fig. 6D. Courtesy of S. McLoughlin and B.J. Slater. **o.** Septate fungal hyphae penetrating *Vertebraria* root cells. Scale bar = 100 µm. Originally illustrated in Slater *et al.* 2015: fig. 6F. Courtesy of S. McLoughlin and B.J. Slater. **p.** Fungal fruiting body containing smooth-walled spores. Scale bar = 100 µm. Originally illustrated in Holdgate *et al.* 2005: fig. 14i. Courtesy of S. McLoughlin.



fungi from Antarctica does not occur *in situ*, but rather dispersed within litter or the peat matrix. For example, a cluster of terminal and intercalary chlamydospores, formally described as *Glomorphites intercalaris* García Mass. (Fig. 1h), occurs within highly degraded plant material from the Permian Skaar Ridge locality (García Massini 2007a). The affinities of these spores with the Glomeromycota were suggested based on morphological similarities to extant *Glomus*. Dispersed (chlamydo-) spores have also been reported (Fig. 1i) from Skaar Ridge (Harper *et al.* 2015b). Many of these spores are close to *Vertebraria* rootlets in the matrix, thus suggesting that they might belong to *G. vertebrariae* (see above). Still other (chlamydo-)spores, some containing evidence of intrusive microfungi, with possible affinities to the Glomeromycota come from the Triassic peat at the Fremouw Peak site (White & Taylor 1989b, 1991). Some of these scattered fungal remains are similar to extant forms and have been directly compared to modern genera. Stubblefield *et al.* (1987a) report one example of a peculiar fossil interpreted as a *Sclerocystis*-like spore cluster (Fig. 1j). However, modern *Sclerocystis* forms spores in sporocarps bounded by a massive peridium (Yao *et al.* 1996). The absence of a peridium argues against affinities of the fossil to *Sclerocystis*. Rather, several extant glomoid species are known to produce spore clusters not enveloped in a peridium, e.g. *Funneliformis badium* (Oehl, D. Redecker *et al.* Sieverd.) C. Walker *et al.* A. Schüßler, *Glomus fuegianum* (Speg.) Trappe & Gerd. and *Glomus rubiforme* (Gerd. & Trappe) R.T. Almeida *et al.* N.C. Schenck (Godfrey 1957, Gerdemann & Trappe 1974, Almeida & Schenck 1990, Oehl *et al.* 2005), that closely resemble the fossil. An alternative hypothesis is that early in the evolution of *Sclerocystis*, spores were produced in clusters that lacked a peridium.

Besides Glomeromycota, it is known that several members of the Endogonales (Mucoromycotina) also enter into mycorrhizal associations with plants (Morton 1990, Walker & Trappe 1993, Read *et al.* 2000). However, compelling evidence of fossil endogonalean mycorrhizas has not been discovered to date (but see Strullu-Derrien *et al.* 2014). Several (putative) endogonalean fungi have been reported from the Triassic peats of Antarctica but none are closely associated with a plant. The most significant of these fossils is perhaps *Jimwhitea circumtecta* M. Krings, T.N. Taylor, N. Dotzler *et al.* G. Persichini (Krings *et al.* 2012), a structure interpreted as a zygosporangium-posed gametangia complex resembling extant *Endogone* (Fig. 1k). Moreover, a sporocarp containing *J. circumtecta*-like structures suggests that the zygosporangia were produced within a sporocarp (Fig. 1l). There are two other examples of sporocarps, informally named fungus no. 2 and fungus no. 3, in the Triassic peats (White & Taylor 1989b). These

sporocarps are bounded by a massive mycelial peridium and contain numerous 'spores'. The spores of fungus no. 2 (Fig. 1m) are thin-walled and some show what appear to be inflated subtending hyphae or gametangia. The spores of fungus no. 3 are characterized by a hyphal mantle and contain opaque matter (Fig. 1n).

Two types of enigmatic fungal fossils, *Endochaetophora antarctica* J.F. White *et al.* T.N. Taylor (White & Taylor 1988, 1989a) and *Mycocarpon asterineum* T.N. Taylor *et al.* J.F. White (Taylor & White 1989), have also been described from the Triassic of Antarctica. Both structures consist of a central cavity enveloped in a hyphal investment, but differ in the organization of the investment. Together with similar structures from the Devonian and Carboniferous (e.g. Krings *et al.* 2014), these two Triassic fossils have collectively been termed fungal 'sporocarps' (see Krings *et al.* 2011). 'Sporocarps' have variously been hypothesized as representing ascomycete cleistothecia, mucoromycotinan zygosporangia or glomeromycotan spores, but structural features that could be used to determine their affinities have not yet been documented (Taylor *et al.* 2015).

Endochaetophora antarctica is characterized by a three-layered investment, with a non-hyphal middle layer that developed secondarily after the outer and inner layers had been established (White & Taylor 1988). In addition, numerous appendages extend from the inner layer to the outside of the structure, and a distinct opening is present in some of the specimens (Fig. 1o). Taylor & White (1989) reconstructed several developmental stages in *E. antarctica*, and discussed the ecological role of this fungus as a saprotrophic organism in the peat. *Mycocarpon asterineum* is morphologically similar to several Carboniferous representatives of *Mycocarpon* (Hutchinson 1955), but differs from the latter regarding the investment, which is composed of an outer hyphal and inner non-hyphal component in *M. asterineum* (Fig. 1p). Other specimens of *M. asterineum* have been described as endophytes in a *Parasciadopitys aequata* X. Yao, T.N. Taylor *et al.* E.L. Taylor (vltzialean conifer) seed (Fig. 1q; Schwendemann *et al.* 2010a).

In another comprehensive study, White & Taylor (1991) describe several examples of what appear to be fungal 'sporocarps' of uncertain systematic affinities, some of which are enveloped in hyphal investments and contain varying numbers of spores. Finally, several specimens of an interesting 'sporocarp' occur embedded in a confluent mycelial meshwork surrounding a specimen of the petriellalean stem *Rudixylon serbetianum* B. Bomfleur, A.-L. Decombeix, A.B. Schwendemann, I.H. Escapa, E.L. Taylor, T.N. Taylor *et al.* S. McLoughlin (see fig. 4J of Bomfleur *et al.* 2014a). Although the authors did not describe the fungus in their study, it appears to be morphologically similar to other Triassic 'sporocarps', especially *Endochaetophora* (Fig. 1r).

Parasitism

Parasitism is a nutritional mode in which one organism derives nutrients from another organism, typically at the other organism's expense (Zelmer 1998). Parasitism in fossils can be recognized through the presence of disease symptoms, some type of host response such as cell and tissue alteration, or local necroses (e.g. Mendgen *et al.* 1996, Pearce 1996). However, not all parasites elicit host responses, and thus it may be difficult to determine the nutritional modes of asymptomatic fossil fungi associated with intact host tissue. Moreover, many of the host responses known in extant plants (e.g. chemical responses; Swain 1977) are not identifiable in fossils or are easily mistaken for natural degradation activities (e.g. necroses; Van Loon *et al.* 2006).

A possible parasitic fungus and host response in the form of tyloses occurs in silicified conifer wood from the Jurassic of Antarctica (Harper *et al.* 2012). Extensive hyphal proliferation is visible throughout the wood, with numerous tyloses that extend into the tracheids (Fig. 2a). Harper *et al.* (2012) demonstrate that the fungus penetrates the tyloses to form coils, and subsequently exits the tyloses to spread out within the tracheid lumen; however, other hyphae do not penetrate but rather grow around the tyloses. Tyloses, some of which are associated with fungi, have also been documented in Permian *Australoxylon mondii* L. Weaver, S. McLoughlin *et al.* A.N. Drinnan wood from the Prince Charles Mountains (see figs 7a–f of Weaver *et al.* 1997). These authors comment that it is not possible to generalize about the cause of tylosis formation, but it is possible to suggest that tylosis formation and fungal decay are related because of the highly degraded nature and reported fungal decay in the wood.

Resting spores, sporangia and rhizoids of what appear to be parasitic chytrid-like organisms have been documented in the stem parenchyma of the Triassic cycad *A. schopfi* (see figs 3 & 4 of Taylor & Stubblefield 1987). Moreover, many sporangia of the fern *Gleichenopteris antarcticus* C.J. Phipps, B.J. Axsmith, T.N. Taylor *et al.* E.L. Taylor from Fremouw Peak contain spherical bodies up to 30 µm in diameter, some of which are characterized by tubular projections extending from the surface, while others show a single orifice or pore in the wall (see Pl. 2, figs 6 & 7 of Phipps *et al.* 2000). These authors suggest that the bodies are morphologically similar to certain extant members in the Chytridiomycota that parasitize spores and pollen grains. In another study, Slater *et al.* (2015) distinguish ten different fungal morphotypes from the Prince Charles Mountains. Among these morphotypes is one that occurs in association with pollen grains and is interpreted as evidence of a parasitic or saprotrophic chytrid. Similar associations of chytrid-like fungi in

pollen grains have been documented from the Triassic Fremouw Peak locality (Fig. 2b; Harper 2015).

Finally, several developmental stages of *Synchytrium permicus* García Mass., interpreted as a *Synchytrium*-like fossil member of the Chytridiomycota, have been reported in plant remains from the Skaar Ridge locality (García Massini 2007b; Fig. 2c). *Synchytrium permicus* is interpreted as a parasite based on what appear to be hypertrophic host responses in plant roots, leaves and stems where the fungus occurs.

Saprotrophism

The most important ecological role of fungi today is the decomposition of organic material (Cooke & Rayner 1984). Saprotrophic fungi are difficult to recognize as fossils, however, because there are no consistent structural features characteristic of this nutritional mode. Silicified wood is probably the only type of plant fossil in which the activities of fungi can be preserved faithfully enough to reveal stages in the degradation process (Stubblefield & Taylor 1985, 1986, Stubblefield *et al.* 1985). Historically, there are three principal types of fungal decay or wood rot: white, brown and soft rot. The delineating structural characteristics of these rot types include the type of wood being degraded, pattern of degradation, presence or absence of certain cell wall components in the degraded wood and the systematic affinities of the fungus involved (Schwarze *et al.* 2000, Stokland *et al.* 2012).

A specimen of *Australoxylon bainii* L. Weaver, S. McLoughlin *et al.* A.N. Drinnan, a wood type attributed to the Glossopteridales (Merlotti & Kurzawe 2006), from the Permian Prince Charles Mountains exhibits irregular cavities that lack definitive margins (Fig. 2d), as well as gradational decay patterns extending into the surrounding xylem, tracheids with small holes in the cell walls near the edges of the cavities, and characteristic cell wall appositions (Weaver *et al.* 1997). The causative agent for these alterations was not determined, but fungal decay was suggested. However, filamentous structures do occur within tracheid lumina and may represent simple hyphae (see fig. 11g & h of Weaver *et al.* 1997). Another specimen of *Australoxylon* from the same locality exhibits decay symptoms in the form of spindle-shaped cavities that occur both within individual growth rings and across growth ring boundaries. The cavities are restricted to specific regions of the wood or randomly dispersed throughout the wood (Fig. 2e; Weaver *et al.* 1997). As in *A. bainii*, appositions may be present. Finally, White (1969) reports axes of silicified Permian wood with lenticular patches (see figs 5 & 6 of White 1969) that superficially resemble the spindle-shaped cavities produced by certain white pocket rot fungi.

White pocket rot and white rot fungi also occur in Triassic *Agathoxylon* (formerly *Araucarioxylon*; see

Rössler *et al.* 2014), a conifer-type stem or branch wood (see Seward & Ford 1906), and Permian *Vertebraria* (Glossopteridales; see above) root wood from Antarctica (Stubblefield & Taylor 1985, 1986). Specimens of *Agathoxylon* display a range of different decay pocket distribution patterns when viewed in transverse section, including pockets restricted to individual growth rings or specific areas of the wood, and others in which the pockets cross growth ring boundaries (Fig. 2f). These distribution patterns can be used to infer details about the types of fungi involved and the timing of fungal colonization (Ander & Eriksson 1977, Blanchette 1984). In contrast to the *Australoxylon* material described by Weaver *et al.* (1997), several of the *Agathoxylon* specimens display not only decay symptoms but also contain remains of the fungi involved in the decay process, including branched septate hyphae in the pockets, tracheids and ray parenchyma (Eriksson *et al.* 1990). Some hyphae possess clamp connections, which are diagnostic of fungi included in the Basidiomycota. Detailed analyses of cell wall layer degradation (Stubblefield & Taylor 1986, Harper 2015) indicate that the secondary walls of the tracheids are first degraded along the long axis resulting in a collenchyma-like pattern, with intact cell walls only remaining in the corner areas between adjacent cells. Subsequently, the cell wall material from the corner areas is also degraded, resulting in only the middle lamella remaining. White pocket rot in woody *Vertebraria* roots has initially been documented based on poorly preserved hyphae that show little detail, and irregularly shaped pockets (Schopf 1970, Stubblefield & Taylor 1985, 1986, Neish *et al.* 1993). However, more recent studies indicate that the hyphae are septate and form multiple types of clamp connections (Fig. 2g); host responses (Fig. 2h) and arthropod coprolites were also documented in this wood (Harper 2015).

Fungal decay has also been reported in Early Jurassic wood from the Kirkpatrick Basalt Group in the Mesa Range area of northern Victoria Land (Jefferson *et al.* 1983). Silica was deposited onto helical fibrillar structures within the cell walls (see fig. 2d of Jefferson *et al.* 1983) and these were interpreted as a result of early fungal delignification. Moreover, Jefferson (1982) reports fungal colonization in a wood specimen from the Lower Cretaceous Fossil Bluff Formation on Alexander Island (see Pl. 67, fig. 6; Pl. 68 all figs of Jefferson 1982). Other examples of fungi in Cretaceous wood from Alexander Island include hyphae and structures interpreted as fungal spores (see Pl. 28, figs 12–13 of Jefferson 1987). In addition, Falcon-Lang *et al.* (2001) found large, spindle-shaped cavities that are restricted to the latewood in several wood specimens from Alexander Island (see fig. 6d of Falcon-Lang *et al.* 2001) and abundant hyphae in tracheids (Falcon-Lang & Cantrill 2001). The specimens also contain oval fungal structures (9–12 by 3–15 µm), which the authors compare to modern

basidiospores or teliospores. They hypothesize that the restricted occurrence of the rot symptoms in latewood might be related to the trees' defence mechanisms being particularly vulnerable during the low light levels of late autumn or dark winter. Another example of fungal rot restricted within tree rings is seen in a *Podocarpoxylon* specimen from the Lower Cretaceous (Aptian) Cerro Negro Formation of Livingston Island (see fig. 5h & i of Falcon-Lang & Cantrill 2002). The wood axial parenchyma is reported to contain abundant fungal hyphae. Similar to the woods from Alexander Island, the presence of rots within growth increments, followed by distorted tissue zones, has been used to imply that rotting occurred during the growing season.

Several specimens of Maastrichtian (Late Cretaceous) silicified sapwood from Vega and Seymour islands in the Antarctic Peninsula area contain abundant fungal hyphae associated with tracheids, vessels and ray parenchyma (Poole & Cantrill 2006). These authors speculate that the prevailing moist conditions may have encouraged fungal growth within the wood debris on the forest floor. Finally, there are several reports of angiosperm wood containing spherical inclusions and filaments that possibly represent fungi, including the xylotaxa *Laureliopsis philippiana* (Looser) Schodde (southern sassafras; see Pl. I, figs 2 & 3 of Poole & Francis 1999), *Winteroxylon jamesrossii* I. Poole *et al.* (see fig. 2 of Poole & Francis 2000) and *Weinmannioxylon nordenskjöldii* I. Poole, D.J. Cantrill, P. Hayes *et al.* (see Pl. I, fig. 1 of Poole *et al.* 2000).

An example of another possible saprotrophic fungus occurs in *Spaciinodum collinsonii* J.M. Osborn *et al.* T.N. Taylor, a Triassic sphenophyte from Fremouw Peak (Osborn *et al.* 1989, 2000). Apices of this plant may contain numerous minute structures that were initially interpreted as spores of *S. collinsonii* (Osborn *et al.* 2000), but later reinterpreted as the spores produced by a saprotrophic or parasitic fungus (Schwendemann *et al.* 2010b). Co-occurring with *S. collinsonii* in some peat blocks is *Palaeofibulus antarctica* J.M. Osborn, T.N. Taylor *et al.* J.F. White, a fungus with probable affinities to the Basidiomycota that produced large spherical spores (Fig. 2i; Osborn *et al.* 1989). However, a physical connection between *P. antarctica* and the fungal spores in *S. collinsonii* has not been demonstrated to date.

Fungal remains of uncertain affinities and nutritional mode

The vast majority of fungal remains in the fossil record occur as dispersed units and fragments lacking definitive features that could be used to determine their systematic affinities and nutritional mode (Taylor *et al.* 2015). For example, axes of the lycophyte *Paurodendron stellatum* S. McLoughlin, A.N. Drinnan, B.J. Slater *et al.* J. Hilton from the Permian Toploje Member peat of the Prince

Charles Mountains contain fragments of hyphae of an unidentified fungus in the metaxylem tracheids (Fig. 2j; McLoughlin *et al.* 2015). These hyphae, together with the widespread absence of thin-walled tissues in the axes, are interpreted as signifying moderate aerobic decay before fossilization. What appear to be thick-walled fungal hyphae also occur in the vascular bundles of Jurassic *Brachyphyllum*-type foliage occurring cheirolepidiacean pollen cones from Carapace Nunatak (see Pl. I, fig. 10 of Hieger *et al.* 2015).

Leaves constitute a harsh habitat for fungi due to temporary nutrient availability and extreme fluctuations in humidity, temperature, gas-exchange gradients and ultraviolet radiation (Goodman & Weisz 2002). Nevertheless, leaf fungi constitute a major component of fungal associations with plants today (Leben 1965, Carroll 1988, Arnold 2007, Rodriguez *et al.* 2009). Fungi associated with Permian leaves from Antarctica have been reported from the Prince Charles Mountains in the form of narrow hyphae ramifying through the mesophyll of a *Noeggerathiopsis* leaf (Fig. 2k; Holdgate *et al.* 2005). There was no discussion of the nature of this fungal association, but it probably represents a saprotroph based on the partially degraded condition of the leaf. Partially degraded *Glossopteris* leaves from Skaar Ridge also contain ramifying hyphae, mycelia, remains suggestive of chytrid-like organisms, mantled spores and globose structures (Fig. 2l), probably belonging to a community of saprotrophs involved in the decomposition of the leaves (Harper *et al.* 2015b). The paucity of documented evidence of leaf fungi in the permineralized peats from Antarctica may be due in part to the mechanical destruction of most leaves prior to fossilization. The possibility also exists that the prevailing climatic conditions during these periods of time and the physiology of the high-palaeolatitude plants did not support extensive growth of fungi on/in leaves.

We are aware of only a single report of fungi associated with adpression foliage fossils from Antarctica. Several hyphae have been documented on a leaf of *Heidiphyllum elongatum* (Morris) Retallack from the Upper Triassic flora of the Allan Hills in southern Victoria Land (see fig. 6c of Bomfleur *et al.* 2013). Reports on Permian adpression fossils suggesting indirect evidence of the presence of fungi include damaged areas on leaves in the form of spots on *Gangamopteris* sp. cf. *G. obovata* (Carruthers) White from Milorgfjella, Dronning Maud Land (see Pl. IXc of Plumstead 1975) and leaves with fungal damage from the Whichaway Nunataks, Coats Land (Plumstead 1962).

Equally rare are reports of fossil fungi associated with plant reproductive structures. Several specimens of the enigmatic gymnosperm ovulate structure *Dordrechtites arcanus* J.A. Bergene, E.L. Taylor *et* T.N. Taylor from the Middle Triassic of Mount Falla in the central Transantarctic Mountains contain abundant fungal

hyphae in the megaspore membrane and transfusion parenchyma (Fig. 2m; Bergene *et al.* 2013). A similar pattern of fungal colonization has also been reported in the conifer ovule *Parasciadopitys aequata* (Schwendemann *et al.* 2010a) from Fremouw Peak. These fungi probably represent saprotrophs based on the poor preservation of most of the specimens and the lack of recognizable host responses. Finally, Perovich & Taylor (1989) report on hyphae of an unidentified fungus that occur in Middle Triassic *Ignotospermum* ovules from the Fremouw Peak permineralized peat.

Fungi constitute a large portion of the total biodiversity within modern soil communities (Baldrian *et al.* 2013, Wardle & Lindahl 2014). It is, therefore, not surprising that the vast majority of fungal remains in the Antarctic permineralized peats occur in the peat matrix. Slater *et al.* (2015) distinguish ten fungal morphotypes, including septate and aseptate (Fig. 2n) hyphae, hyphae with swellings, spores (Fig. 2o), ornamented spores, disc-like structures, possible sclerotia and complex fruiting bodies (Fig. 2p). A fossil closely resembling one of the putative fungal fruiting bodies illustrated by Slater *et al.* (2015) has also been described by Holdgate *et al.* (2005). The systematic affinities and ecological roles of these fungi currently remain unknown.

Reports of fungi from the Cretaceous of Antarctica are primarily from dispersed remains and silicified wood. Some exceptions include circular inclusions (15–20 µm in diameter) within cells of the cycad *Centricycas antarcticus* from James Ross Island (see fig. 3a & b of Cantrill 2000). Cantrill (2000) discusses that the inclusions might represent original cell contents, but it is also possible that they are fungal. Moreover, globular bodies on the surface of the Late Cretaceous lycophyte megaspore *Caboconicus* from the Table Nunatak at the end of Kenyon Peninsula on the eastern margin of the Antarctic Peninsula have been interpreted as a result of fungal attack (see fig. 2a–c of Eklund *et al.* 2004). Cantrill & Drinnan (1994) note that some Antarctic Triassic lycopsid megaspores were previously misinterpreted as fungi.

Fungus-like organisms

One group of fungus-like organisms that appears to have been quite abundant in several peat-forming palaeoenvironments of Antarctica is the Peronosporomycetes (Oomycota). In modern ecosystems, Peronosporomycetes function as saprotrophs and facultative or obligate parasites of plants, animals and other fungi (Padgett *et al.* 1988, Dick 1992, 2001). The fossil record of Peronosporomycetes from Antarctica consists entirely of dispersed microfossils assigned to the fossil genus *Combresomyces* (Schwendemann *et al.* 2009, Slater *et al.* 2013, Harper *et al.* 2015b). *Combresomyces*, first reported from the Carboniferous of France and

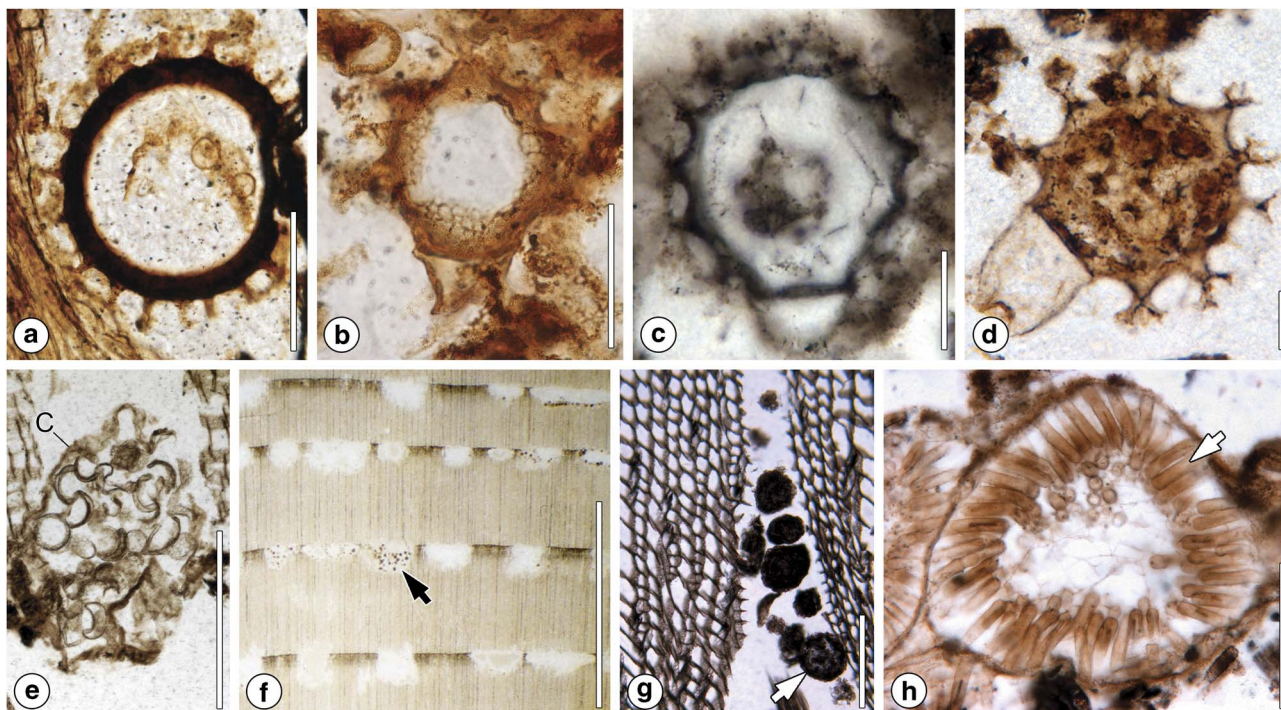


Fig. 3. Fungus-like organisms, animal interactions (additional information in the text). **a.** *Combresomyces caespitosus* oogonium containing indeterminate spherules. Scale bar = 25 μm . Originally illustrated in Slater *et al.* 2013: fig. 1J. Courtesy of S. McLoughlin and B.J. Slater. **b.** *Combresomyces rarus* oogium with attached subtending hypha. Scale bar = 50 μm . Originally illustrated in Slater *et al.* 2013: fig. 2F. Courtesy of S. McLoughlin and B.J. Slater. **c.** *Combresomyces*-like oogonium attached to wide hypha. Scale bar = 25 μm . Originally illustrated in Harper *et al.* 2015a: Pl. 1, fig.17. **d.** *Combresomyces cornifer*. Oogonium with subtending hypha. Scale bar = 20 μm . Originally illustrated in Schwendemann *et al.* 2009: Pl. I, 1. **e.** Coprolite (C) composed of fragmented fungal spores (arrow). Scale bar = 200 μm . Originally illustrated in Slater *et al.* 2012: Pl. 6, 4. Courtesy of S. McLoughlin and B.J. Slater. **f.** Arthropod borings in *Australoxylon*, some containing coprolites (arrow). Scale bar = 5 mm. Originally illustrated in Weaver *et al.* 1997: fig. 10A. Courtesy of S. McLoughlin and B.J. Slater. **g.** Galleries in decayed *Vertebraria* wood filled with coprolites (arrow). Scale bar = 100 μm . Originally illustrated in Harper 2015; pl. 12, fig. 156. **h.** Putative trichomycete. Palisade of thalli (arrow) on possible arthropod cuticle. Scale bar = 100 μm . Originally illustrated in White & Taylor 1989c: fig. 1.

Great Britain (Dotzler *et al.* 2008, Strullu-Derrien *et al.* 2010), consists of spheroidal to pyriform reproductive units located at the tip of broad hyphae. The reproductive units are characterized by a complex surface ornament comprised of ‘antler-like’ extensions positioned on hollow papillations of the wall. Clavate antheridia attached to some of the specimens from France indicate that *Combresomyces* represents a peronosporomycete oogonium (Dotzler *et al.* 2008).

Two species of *Combresomyces* have been described by Slater *et al.* (2013) from the Permian of the Prince Charles Mountains, including *C. caespitosus* B.J. Slater, S. McLoughlin *et J.* Hilton, characterized by long, hollow, slender, conical papillae with at least two orders of apical branches (Fig. 3a). It was noted that *C. caespitosus* occurs close to *Vertebraria* roots and *Glossopteris* and *Noeggerathiopsis* leaves. On the other hand, *C. rarus* B.J. Slater, S. McLoughlin *et J.* Hilton is characterized by broad conical papillae that terminate in

at least one bifurcation producing a pair of generally acutely divergent and sharply pointed branches (Fig. 3b). Slater *et al.* (2013) suggest that *Combresomyces* played a significant role in the decomposition of organic matter or perhaps thrived as a parasite of plants and/or animals. A third *Combresomyces* species comes from the Triassic Fremouw Peak locality (Fig. 3d). This form is morphologically similar to the type species *C. cornifer* from the Carboniferous of France, but is considerably larger (Schwendemann *et al.* 2009, 2010a). *Combresomyces*-like fossils have recently also been discovered in Skaar Ridge peat (Fig. 3c; Harper *et al.* 2015b). Moreover, an enigmatic fossil from Skaar Ridge (Upper Permian) illustrated by Schopf (see fig. J of Schopf 1970) superficially resembles an ornamented oogonium attached to a fragment of a wide parental hypha. The occurrence of *Combresomyces* in the Permian and Triassic of Antarctica has been used to suggest that these organisms were able to recover during times of

global climate change and floral turnover, and perhaps were effective as generalists in the high latitude peat-forming environments (Schwendemann *et al.* 2009).

Fungi in food webs

Co-occurring with the plants and fungal fossils in the Permian and Triassic peats from Antarctica are various animal remains, e.g. arthropod cuticles and coprolites. Slater *et al.* (2012) describe coprolites from the Permian Toploje Member peat of the Prince Charles Mountains. These frass specimens are composed almost exclusively of broken fungal spores and crushed hyphae (Fig. 3e), some within arthropod-excavated galleries of *Australoxylon* or *Vertebraria*. Coprolites of this type attest to the occurrence of fungivory in the palaeoecosystems as represented by these peats. Arthropod borings, typically restricted to the latewood, with coprolites in some of the cavities (Fig. 3f) also occur in *Australoxylon mondii* from the Prince Charles Mountains (Weaver *et al.* 1997). Similar evidence of arthropod–plant interactions has been discovered in white rot-affected *Vertebraria* wood from Skaar Ridge (Fig. 3g).

Direct evidence of an interaction of a fungus-like organism and an animal from the Triassic of Antarctica occurs in the form of hyphal thalli with possible affinities to the Eccrinales (Trichomycetes) that are attached to what was interpreted to represent an insect cuticle (Fig. 3h; White & Taylor 1989c). However, Cafaro (2005) challenged the affinities of the fossil with the Eccrinales since septal plugs are not known in modern members of this group. Moreover, there is no conclusive evidence to suggest that the fossil is in fact attached to the cuticle of an arthropod.

Palynomorphs and the dispersed record

Extensive palynological sampling and analysis have been conducted in several Cretaceous sequences from Antarctica (see Truswell 1989), primarily to reconstruct palaeovegetation and assess palaeoenvironmental and palaeoclimatic conditions. Fungal palynomorphs (e.g. spores, conidia, mycelial fragments) frequently occur in the samples, and some have been used as proxy indicators of several climate parameters. For example, certain fungal palynomorphs have been used to document warm and cold episodes and the occurrence of seasonal sea ice during the Late Cretaceous of Antarctica (Bowman *et al.* 2013).

Among the most abundant fungal palynomorphs during the Cretaceous of Antarctica are representatives of *Pluricellaesporites* sp. from Lower Cretaceous deposits on Byers Peninsula, Livingston Island, and the Upper Cretaceous of Seymour Island, Antarctic Peninsula (see Pl. 8, fig. 7 of Duane 1996, see fig. 4–30 of Bowman *et al.* 2014). Several palynomorph assemblages that include

fungal remains have also been reported from Seymour Island (Cranwell 1959, Askin 1989, Bowman *et al.* 2014). The fungal remains have been interpreted as reflecting saprotrophic degradation of terrestrial biomass in a humid palaeoenvironment. Reports of remains of more complex fungal structures such as microthyriaceous fruiting bodies from the Lower Cretaceous Byers Group on Livingston Island (see Pl. 8, figs 9 & 10 of Duane 1996) and *Asterothyrites* (see fig. 8Y of Di Pasquo & Martin 2013) from James Ross Island are interpreted to reflect low lying, coastal regions that experienced a moist, temperate to tropical climate. Abundant fungal spores in Late Cretaceous (Campanian–Maastrichtian) palynological debris have also been reported from King George Island, Antarctic Peninsula (Song & Cao 1994, Dutra & Batten 2000). Finally, several authors have described *Reticulatisporites pudens* Balme as a fungal spore, suggesting that this taxon could be used to infer that volcanically perturbed post-eruption riparian systems occurred in the upper Cerro Negro Formation from Walker Bay erratics (Lower Cretaceous) on Livingston Island (Chen *et al.* 2015). Although documented evidence of fungi from the Antarctic Cenozoic is beyond the scope of this review, one report of the Palaeocene (Danian) epiphyllous fungus *Trichopeltinites* on cuticles from Seymour Island is particularly interesting because this fungus has been interpreted as becoming at the Cretaceous–Palaeogene boundary in the Western Interior of North America (see fig. 2e of Upchurch & Askin 1989).

The palynomorph *Reduviasporonites* is the focal point of several influential studies suggesting a major accumulation (a so-called ‘fungal spike’, ‘fungal abundance event’ or ‘fungal disaster event’) of this fossil at the end of the Permian. Such evidence has been used to suggest that this accumulation is indicative of the destruction of terrestrial vegetation by fungal pathogens that led to the end-Permian collapse of terrestrial ecosystems (Visscher *et al.* 1996, 2011, Steiner *et al.* 2003, Vajda & McLoughlin 2007). Visscher *et al.* (2011) hypothesize that fungal disease was an essential accessory in the destabilization of the vegetation that accelerated widespread tree mortality during the end-Permian crisis. Moreover, they dismiss results from a study by Foster *et al.* (2002), who, based on geochemical evidence, concluded that *Reduviasporonites* might be of algal origin. *Reduviasporonites chalastus* (Foster) Elsik has been reported from the Prince Charles Mountains and constitutes 24% of the latest Permian palynomorph assemblage at this locality. The taxon is also present but less common (4–10%) in the earliest Triassic (Lindström & McLoughlin 2007). These authors note that several typically Permian taxa have their last occurrences c. 19 and 24 m below the *Reduviasporonites* zone, possibly corresponding to an initial extinction level. Overall, the

occurrence of *Reduviasporonites* in Antarctica demonstrates the worldwide distribution of this taxon near the P-T boundary.

Discussion

Although the Permian, Triassic, Jurassic and Cretaceous permineralized peat and wood from Antarctica are well known as sources of new information on the morphology and internal organization of the plants that occurred on this continent during the late Palaeozoic and Mesozoic, relatively little is known to date about the associations and interactions that these plants formed with other ecosystem constituents in order to exist in the extreme habitats. Future research with Antarctic palaeobiological systems will be directed towards screening the permineralized peats and silicified wood for organisms associated with the plants, especially fungi. It comes as no surprise that a large number of fungi and fungal interactions have been discovered in recent years, some of which are represented by exceptional examples that in turn provide the opportunity for detailed comparisons with modern analogues. The presence of major lineages of fungi, such as the Glomeromycota, is documented by dispersed remains in the matrix, but also by direct evidence of vesicular arbuscular mycorrhizas in three gymnosperm taxa. We are confident that further studies of the wide array of permineralized plants from Antarctica will yield additional examples of mycorrhizal associations in these polar palaeoecosystems. On the other hand, several major fungal lineages have not been recorded from Antarctica to date, including Blastocladiomycota and Ascomycota. One possible reason for the apparent absence of Blastocladiomycota may be the compacted nature and usually highly degraded content of the permineralized peats that may not allow preservation of very delicate fungal structures. Additionally, the environments during the Permian through Cretaceous in Antarctica were perhaps not conducive for members of the Blastocladiomycota. On the other hand, ascomycete fruiting bodies (e.g. cleistothecia and perithecia) are structures that should readily lend themselves to preservation in recognizable form. We speculate that these structures either have not yet been recognized or have simply been neglected in studies focusing on Antarctic plants. Some of the 'sporocarps' from the Triassic (e.g. *Endochaetophora*) were initially considered as members of the Ascomycota. However, new data suggest that these structures may be more closely related to the Mucoromycotina (see Krings *et al.* 2013, 2014).

The vast majority of fungal remains reported from Antarctica to date come from Permian and Triassic peats, as well as from Cretaceous silicified woods. Evidence of fungi in Jurassic sediments are presently limited to a brief note by Bomfleur *et al.* (2007) on fungal remains that appear to occur within a microbial mat from Mount

Carson (northern Victoria Land), they associated with a tylosis-forming conifer wood (Harper *et al.* 2012), and putative hyphae within leaf vascular bundles (Hieger *et al.* 2015). These studies indicate that the Jurassic provides a largely untapped source of information on fungal diversity and plant–fungal interactions in the Mesozoic of Antarctica. There are also several reports of fossil fungi in Cenozoic wood from Antarctica (e.g. Pujana *et al.* 2015), but no systematic studies of these fungi have been conducted. Finally, there is an informative palynological and dispersed record that may be used in palaeoecosystem and palaeoclimatology reconstructions.

Future perspective

This review surveys and briefly characterizes the numerous fungi that have been described from deposits in the Permian to Cretaceous of Antarctica, including well-preserved examples of fungal associations and interactions with land plants. Although the record indicates that fungi were important constituents of the Antarctic polar terrestrial palaeoecosystems, the roles that fungi played in these environments remain incompletely understood. We contend that a concerted research effort that brings together different types of data can eventually answer a series of interesting questions regarding the polar palaeoecosystems. For example, what adaptations were used by plants, especially large trees, to live in environments that, based on environmental considerations today, would be regarded as largely adverse? Together with detailed information on the anatomy and physiology of the host plants, as well as data on the sedimentology and palaeoclimatology, the study of fungi from Antarctica may make it possible to provide a more comprehensive palaeoecological analysis of how fungal relationships may have contributed to the success of plant growth in Gondwanan polar ecosystems.

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Author contributions

All authors contributed equally and declare no conflict of interest.

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