CRYPTIC DIVERSITY OF A GLOSSOPTERIS FOREST: THE PERMIAN PRINCE CHARLES MOUNTAINS FLORAS, ANTARCTICA

by

Ben James Slater

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School of Geography, Earth and
Environmental Sciences
College of Life and Environmental Sciences
University of Birmingham
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ABSTRACT

The Toploje Member chert is a Roadian to Wordian autochthonous–parautochthonous silicified peat preserved within the Lambert Graben, East Antarctica. It preserves a remarkable sample of terrestrial life from high-latitude central Gondwana prior to the Capitanian mass extinction event from both mega- and microfossil evidence that includes cryptic components rarely seen in other fossil assemblages. The peat layer is dominated by glossopterid and cordaitalean gymnosperms and contains sparse herbaceous lycophytes, together with a broad array of dispersed organs of ferns and other gymnosperms. The peat also hosts a wide range of fungal morphotypes, Peronosporomycetes, rare arthropod remains and a diverse coprolite assemblage. The fungal and invertebrate-plant interactions associated with various organs of the *Glossopteris* plant reveal the cryptic presence of a 'component community' of invertebrate herbivores and fungal saprotrophs centred around the *Glossopteris* organism, and demonstrate that a multitude of ecological interactions were well developed by the Middle Permian in high-latitude forest mires. Comparisons of coal maceral data from co-occurring coal seams with quantitative analyses of the silicified peat constituents reveals that while silicified peats provide an unparalleled sample of the organisms forming these coal deposits, they do not necessarily reflect the constituents that ultimately dominate the coal maceral volume.

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CHAPTER 1: INTRODUCTION

1.1 Terrestrial ecosystems of Permian Gondwana

1.1.1 Gondwana and the Glossopteris flora

Gondwana (also widely referred to as Gondwanaland) was the Southern Hemisphere supercontinent that consisted of the modern landmasses of South America, Africa, Arabia, Madagascar, India, Australia, New Guinea, New Zealand and Antarctica (du Toit, 1937; Torsvik and Cocks, 2013). The makeup of Palaeozoic Gondwana is relatively well understood through palaeogeographic and palaeobiogeographic reconstructions that are well supported by palaeomagnetic data and multiple other lines of evidence (Lawver and Scotese, 1987; Archangelsky, 1990; Torsvik and Cocks, 2013).

During the Permian period, large areas of Gondwana played host to terrestrial communities dominated by the glossopterids, a group of gymnospermous plants of unclear affinity that were endemic to Gondwana (Pigg and Trivett, 1994; Retallack and Dilcher, 1981; McLoughlin, 2001; Ryberg, 2009; Gulbranson et al., 2012). *Glossopteris*, the distinctive leaf morphogenus of the glossopterids is synonymous with Permian terrestrial sediments of the now dispersed former Gondwanan continents (Archangelsky, 1990; McLoughlin, 2001). The iconic *Glossopteris* flora is well known for its key role as early supporting evidence to the theory of continental drift (Wegener, 1924; du Toit, 1937); the distribution of *Glossopteris* fossils across the widely separated southern continents puzzled palaeontologists and geologists until the advent of the understanding of plate tectonics set the distribution in a new light (Archangelsky, 1990; McLoughlin, 2001). The circumpolar distribution of the *Glossopteris* phytogeographic realm encompassed all land areas of the

Gondwanan continent between 40° and 90° palaeolatitude (McLoughlin, 2001), the southernmost extent being limited by glacial extent and/or frigidity barriers whilst palaeoequatorial and Northern Hemisphere regions of Gondwana and Pangaea were dominated by other plant groups (McLoughlin, 2001; Berthelin et al., 2006).

The multiphase extinctions that mark the end of the Palaeozoic, culminating in the end-Permian extinction sealed the fate of the *Glossopteris* flora; palynomorph and macrofossil studies show the demise and extinction of glossopterid and cordaitalean gymnosperms at the Permian-Triassic boundary, followed by their replacement by peltasperms, lycophytes and increasing proportions of corystosperms such as *Dicroidium* through the earliest Triassic (McLoughlin et al., 1997; Retallack and Krull, 1999; Lindström and McLoughlin, 2007). Assessments of global palaeodiversity have indicated a protracted decline in some marine organisms and plant groups beginning in the mid-Capitanian (Bond et al., 2010). To understand the impact of this massive restructuring of the terrestrial biosphere it is important to obtain a more complete picture of the pre-extinction Middle Permian palaeoecosystems prior to the onset of biotic decline and extinction. Lagerstätten and T^0 fossil assemblages provide a vital window into the complex web of interactions that had developed in terrestrial ecosystems by the Permian, which permits a deeper understanding of how abiotic factors may have affected late Palaeozoic ecosystems.

1.1.2 Preservation of Gondwanan Permian terrestrial ecosystems

The loss of peat forming ecosystems that occurred at the end of the Permian was a result of conditions that persisted well into the Triassic, marked by the Early Triassic 'coal-gap' so named because no coal beds are recorded from sediments of this age anywhere on Earth, signifying a paucity of heterogeneity in ecosystems, which hindered a rapid recovery of communities in the Early Triassic (Veevers et al., 1994; Retallack et al., 1996, 2011; Retallack, 2012). Prior to this, the wetland habitat to which glossopterid plants were adapted endowed them with being the primary contributors of biomass to the thick deposits of peats which eventually became the economically exploited Permian coals of the Southern Hemisphere (Kershaw and Taylor, 1992; Van Niekerk et al., 2008). In terms of the terrestrial biosphere of Permian Gondwana, our greatest knowledge is of wetland areas (Anderson et al., 1999; Greb et al., 2006). A preservational megabias towards wetland floras is an intrinsic property of the continental fossil record and this factor became well known through comparing the detailed work on Northern Hemisphere Carboniferous coal ball wetland floras of Europe and North America that dominated 19th century and 20th century palaeobotany and the relative dearth of information on the composition of their coeval drier environment floras (Greb et al., 2006; Falcon-Lang et al., 2011b). Gondwanan wetland ecosystems of Permian age have since come to be studied in comparable detail, again through their association with economically important coal deposits. The detail of our knowledge of these palaeoecosystems is, however, not spatially or temporally even. Our picture of terrestrial Gondwanan Permian ecosystems is largely based on remains found in the strata of Australia, the Indian subcontinent and southern Africa. The Antarctic continent is inherently under-sampled due to the smaller proportion of potential outcrop area and its inaccessibility. This is unfortunate since palaeobiogeographic reconstructions place Antarctica at a key crossroads between the various phytogeographic provinces of Gondwana (McLoughlin, 2001; Ryberg, 2009). Antarctica would have acted as a biotic dispersal interchange between the provinces of Gondwana over geological time by virtue of its connection to Africa, India, Australia, New Zealand, and through the Antarctic Peninsula to South America (Figure 1.1).

One region of Antarctica that has permineralised floras that have been well studied to date is the Transantarctic Mountains (e.g. Taylor et al., 1989; Kellogg and Taylor, 2004; Schwendemann et al., 2009; Schwendemann et al., 2010; Ryberg et al., 2012a; Ryberg et al., 2012b). The permineralised floras preserve Permian organisms at Skaar Ridge and Triassic biota at Fremouw Peak localities (Taylor et al., 1989). A range of studies of these well-preserved biotas reveal a picture of these high-palaeolatitude forests as being lower in diversity than the more intensively sampled lower-palaeolatitude regions of Gondwana elsewhere in Australia, Southern Africa and parts of South America. This is to be expected based on typical latitudinal diversity gradients and allows us to further complete the picture of the range of terrestrial ecosystems that existed across Gondwana during the Permian and how they varied geographically. The permineralised biotas of the Transantarctic Mountains however, are preserved as blocks overlying a fluvial sandstone and are interpreted as rafted allochthonous peat wedges that were originally deposited in flood plain swamps (Taylor et al., 1989). The permineralisation is associated with siliceous volcanogenic material (Taylor et al., 1989). The majority of permineralised biotas known from the rock record are associated with hydrothermal activity (Channing and Edwards, 2013), for example the famous Early Devonian Rhynie chert and Windyfield chert from Aberdeenshire, Scotland (Trewin, 2003). Modern biotas that exist around hydrothermally-influenced wetlands are known to include many specialised and restricted elements adapted to the atypical conditions (Stout and Al-Niemi, 2002; Channing and Edwards, 2013). Conversely fossil hot spring biotas may preserve a subset sample of more widespread plant assemblages at large that are pre-adapted to tolerate mineral-charged waters or flooding (Channing and Edwards, 2013).

The Toploje Member chert of the Prince Charles Mountains is another site on the Antarctic continent where an extensive wetland ecosystem has been preserved in exceptional detail. Significantly, the Toploje Member chert appears to preserve a large area of high-latitude *Glossopteris* mire in a hypautochthonous *in situ* manner in contrast to that of the Transantarctic Mountains. Unlike the Skaar Ridge palaeoflora, the Toploje Member chert preserves the remains of an ecosystem that existed in the continental interior of Gondwana (Figure 1.1). In addition, there appears to be no associated volcanogenic or hydrothermal activity involved in the preservation of the peats. The Toploje Member chert therefore provides a chance to sample and reconstruct a more typical and more widespread ecosystem of Permian Gondwana, rather than the perhaps atypical environments sampled in other such deposits.

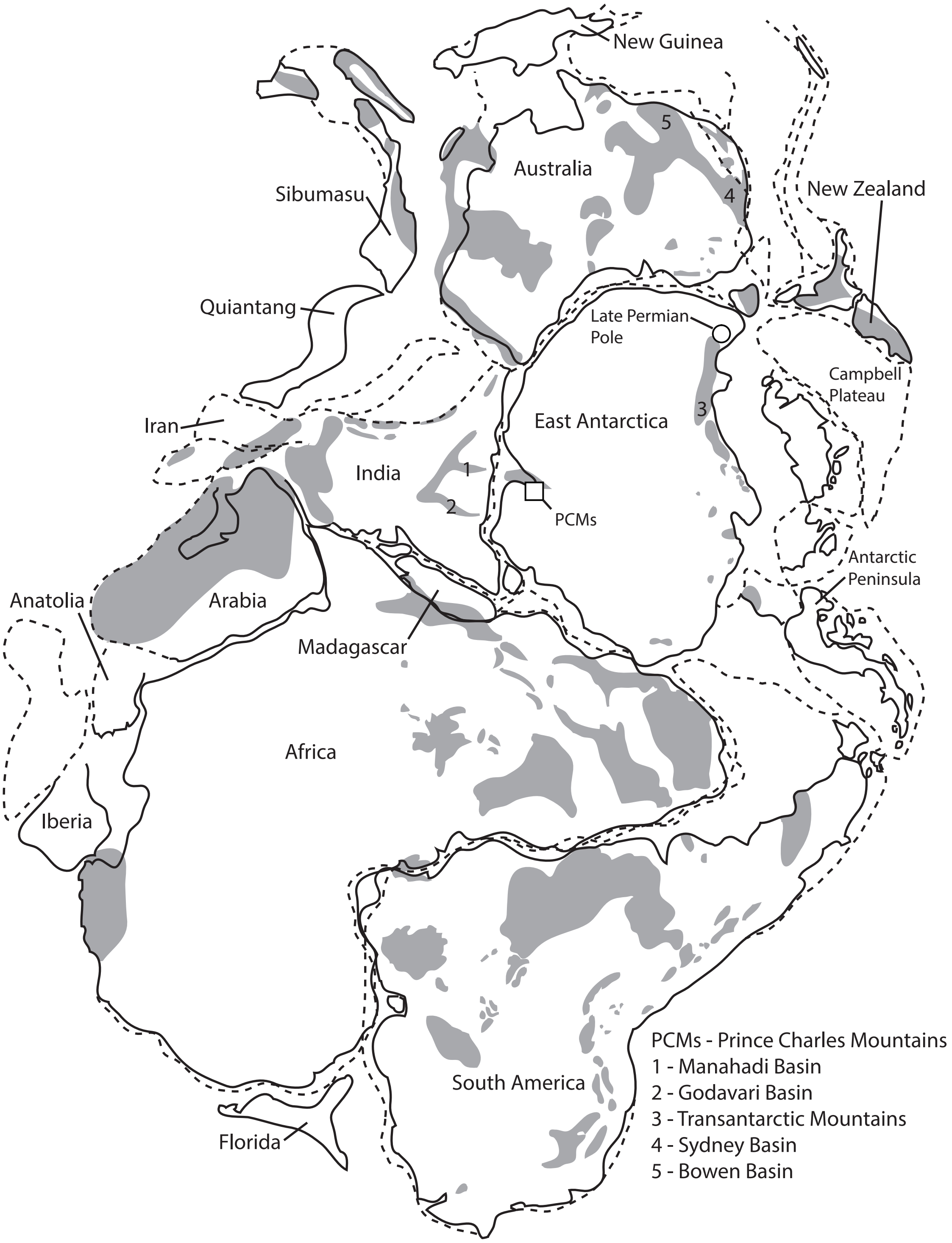


Figure 1.1: Palaeogeographic map of Gondwana in the Middle Permian detailing the position of the Prince Charles Mountains and other sites hosting Permian floras. Grey shading represents Permian sedimentary basins. Base map after McLoughlin (2001).

1.1.3 Contents of the peats

Reconnaissance studies of the floral composition of the peats preserved in the Toploje Member chert show they are chiefly composed of glossopterid gymnosperms (Holdgate et al., 2005). This includes various organ morphotaxa components of the *Glossopteris* whole organism, including the leaves (Figure 1.2, A–B), pollen (Figure 1.2, C), some seeds which were possibly derived from glossopterids or other gymnosperms (Figure 1.2, D), the *Australoxylon* stem wood (Figure 1.2, E–F) and *Vertebraria* root tissues (Figure 1.2, F–H), (McLoughlin and Drinnan, 1996; Holdgate et al., 2005). Other elements include *Noeggerathiopsis* leaves, herbaceous lycophytes and ferns (McLoughlin and Drinnan, 1996; Holdgate et al., 2005). Other components of the peats are less well known, and will be subject to enquiry in the present study.

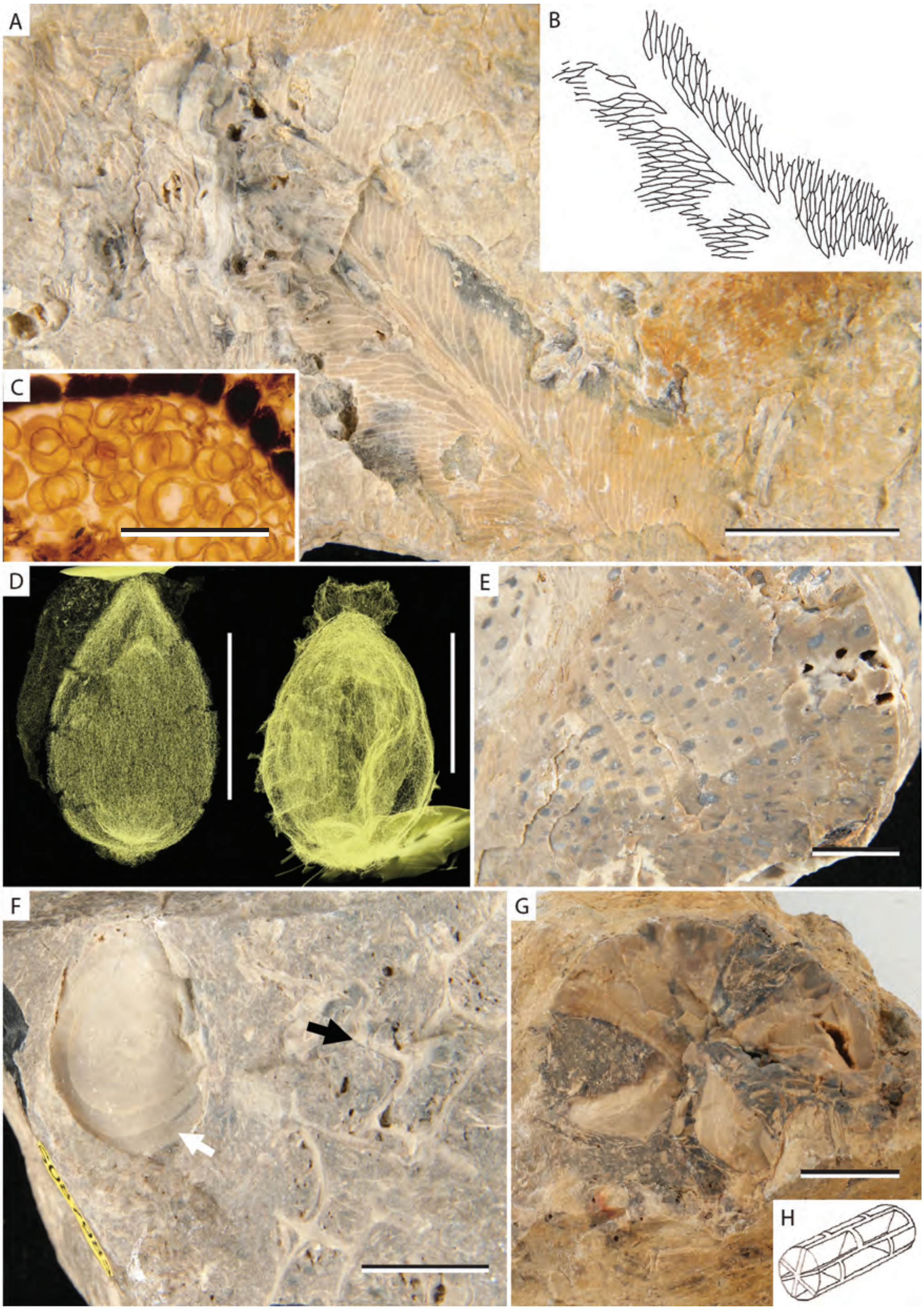


Figure 1.2

Figure 1.2 (previous page): Various isolated elements of the *Glossopteris* whole-plant found in the Toploje Member chert.
A. *Glossopteris* leaf morphogenus on surface of chert block (scale = 1 cm).
B. Anastomosing venation of leaf surface illustrated in 1.2, A, typical of *Glossopteris*.
C. Pollen within a glossopterid sporangia; glossopterid pollen has high intraspecific variation, image courtesy of Stephen McLoughlin (see Lindström et al., 1997; scale = 0.1 mm).
D. Computed tomographic images of two seed morphotypes found in the peats, generated from attenuation-based synchrotron-radiation X-ray tomographic microscopy (SRXTM), (scale bars = 1 mm for left and right seed respectively).
E. *Australoxylon* wood morphogenus showing growth rings and signs of fungal pocket rot, attributable to the stems of the *Glossopteris* whole-plant (scale = 1 cm).
F. Surface of a chert block showing a transverse section through *Australoxylon* wood (white arrow) and a longitudinal section through the distinctive *Vertebraria* (black arrow) chambered roots of the *Glossopteris* plant (scale = 1 cm).
G. Transverse view through a *Vertebraria* root visible at the surface of a chert block (scale = 1 cm).
H. Inset detailing structure of the *Vertebraria* roots.

1.2 Aims of Thesis

1. **To document the diminutive and rarer elements of the palaeoecosystem and describe any new taxa.**
2. **To assess the palaeoecology of the peats focusing in particular on any invertebrate-plant interactions.**
3. **To investigate the taphonomy of the peats and propose a mechanism of silicification.**
4. **To use the Toploje Member chert to better understand the relationship between the organisms of peat forming communities and the constituents which ultimately go on to form coal.**

1.3 Structure of thesis

This thesis has been written as a series of publishable papers, each of which deals with a particular aspect of the biota of the Toploje Member Chert. Chapters 3, 4 and 5 have already been published (Slater et al., 2011, Slater et al., 2012 and Slater et al., 2013 respectively). Chapter 6 includes information that is intended for publication subsequently. Where it has been possible, the chapters have been retained as they were written prior to submission as papers so that each can function as a stand alone study. However, to avoid repetition the geological settings sections have been amalgamated into Chapter 2, and the cited literature compiled into a single reference list. Where work has had significant contributions by co-authors this is clarified below.

The remaining sections of the thesis are organised in the following manner:

Chapter 2 – Geological setting

Chapter 3 – Guadalupian (Middle Permian) megaspores and sporangia from the Toploje Member chert, Bainmedart Coal Measures, Prince Charles Mountains, Antarctica – An analysis and description of the megaspore species present in the Toploje Member chert. Chapter published as a paper; Slater, B.J., McLoughlin, S., Hilton, J., 2011. Guadalupian (Middle Permian) megaspores from a permineralised peat in the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Review of Palaeobotany and Palynology 167, 140–155 (see Appendix 2). Additional analysis and description of isolated fern sporangia is also presented.

Chapter 4 – Animal-plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica – Evidence for a diverse array of invertebrate–plant interactions within the Toploje Member Chert palaeoecosystem is described and discussed. Chapter published as a paper; Slater, B.J., McLoughlin, S., Hilton, J., 2012. Animal–plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology 363–364, 109–126 (see Appendix 2).

Chapter 5 – Peronosporomycetes (Oomycota) from a Middle Permian permineralised peat within the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica – An analysis and description of the fungal-like peronosporomycetes microorganisms found in the Toploje Member chert. A new order and family of extinct peronosporomycetes is established. Chapter published as a paper; Slater, B.J., McLoughlin, S., Hilton, J., 2013.

Peronosporomycetes (Oomycota) from a Middle Permian permineralised peat within the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. PLoS ONE 8(8): e70707. doi:10.1371/journal.pone.0070707 (see Appendix 2).

Chapter 6 – A high latitude Gondwanan lagerstätte: the Permian permineralised biota of the Prince Charles Mountains, Antarctica – An investigation of the palaeoecology, the different interrelationships and trophic levels preserved in the peats, fire ecology, taphonomy and the wider significance of the Toploje Member chert lagerstätten. Analysis of the organic petrology of a selected set of Middle–Upper Permian coal samples from the Bainmedart Coal Measures was undertaken by commercial contractors (Keiraville Konsultants Pty Ltd., Wollongong, Australia), and the data produced on maceral proportions is used in this chapter for comparative studies. Comparative coal maceral data and table of invertebrate herbivory papers were compiled by Stephen McLoughlin. Chapter intended for publication.

Chapter 7 – Conclusions

Appendix 1 – Specimens used in this study – Refer here for a complete list of museum numbers for the specimens described in the thesis.

Appendix 2 – Collection of published papers – Refer here for publications resulting from this thesis.

References – Complete list of all the literature cited in the thesis.

CHAPTER 2: GEOLOGICAL SETTING

2.1 Palaeogeography

Antarctica occupied a central position within Gondwana through the late Palaeozoic and early Mesozoic (McLoughlin, 2001). This location endowed Antarctica with a key role in floristic interchange between the various peripheral regions of the supercontinent (McLoughlin, 2001; Ryberg, 2010). Outside the Transantarctic Mountains, the only Permo-Triassic sedimentary succession in East Antarctica is preserved in the Lambert Graben within the Prince Charles Mountains region. Throughout the Early and Middle Permian, the northern Prince Charles Mountains (Figure 1.1) occupied a palaeolatitude of c. 65–70°S (McLoughlin et al., 1997), similar to their modern day position, and were situated in the central part of the Gondwanan supercontinent (Scotese, 1997). Gondwana was composed of Antarctica, Australia, New Zealand, Africa, Madagascar, India, Arabia, South America and a series of smaller peripheral terranes at this time (Lottes and Rowley, 1990). The central position of landmass that now constitutes modern day Antarctica endows the Antarctic continent with a key role in understanding the history and distribution of the Gondwanan biota. It provides evidence of the highest-latitude southern forests of the Permian and its location may have enhanced its role as a dispersal corridor between the various middle-latitude Gondwanan phytogeographic subprovinces (Ryberg, 2010).

The Amery Group was deposited in the Lambert Graben; sedimentological data and palaeogeographical reconstructions of pre-breakup Gondwana suggest that this basin formed the southern (up-slope) extension of the Mahanadi Graben in eastern India (Fedorov et al., 1982; Stagg, 1985; McLoughlin, 2001; Veevers, 2004; Harrowfield et al., 2005; Boger, 2011; Slater et al., 2011), although alternative alignments of the Lambert Graben with the

Indian Godavari Graben have also been proposed based primarily on coal maceral data (Holdgate et al., 2005). Sediments of the Amery Group were largely sourced from central Antarctica (Veevers, 2004). Furthermore, this basin system was part of an extensive rift system through central Gondwana that was a precursor to eventual continental breakup in the Jurassic (Lottes and Rowley, 1990; Harrowfield et al., 2005).

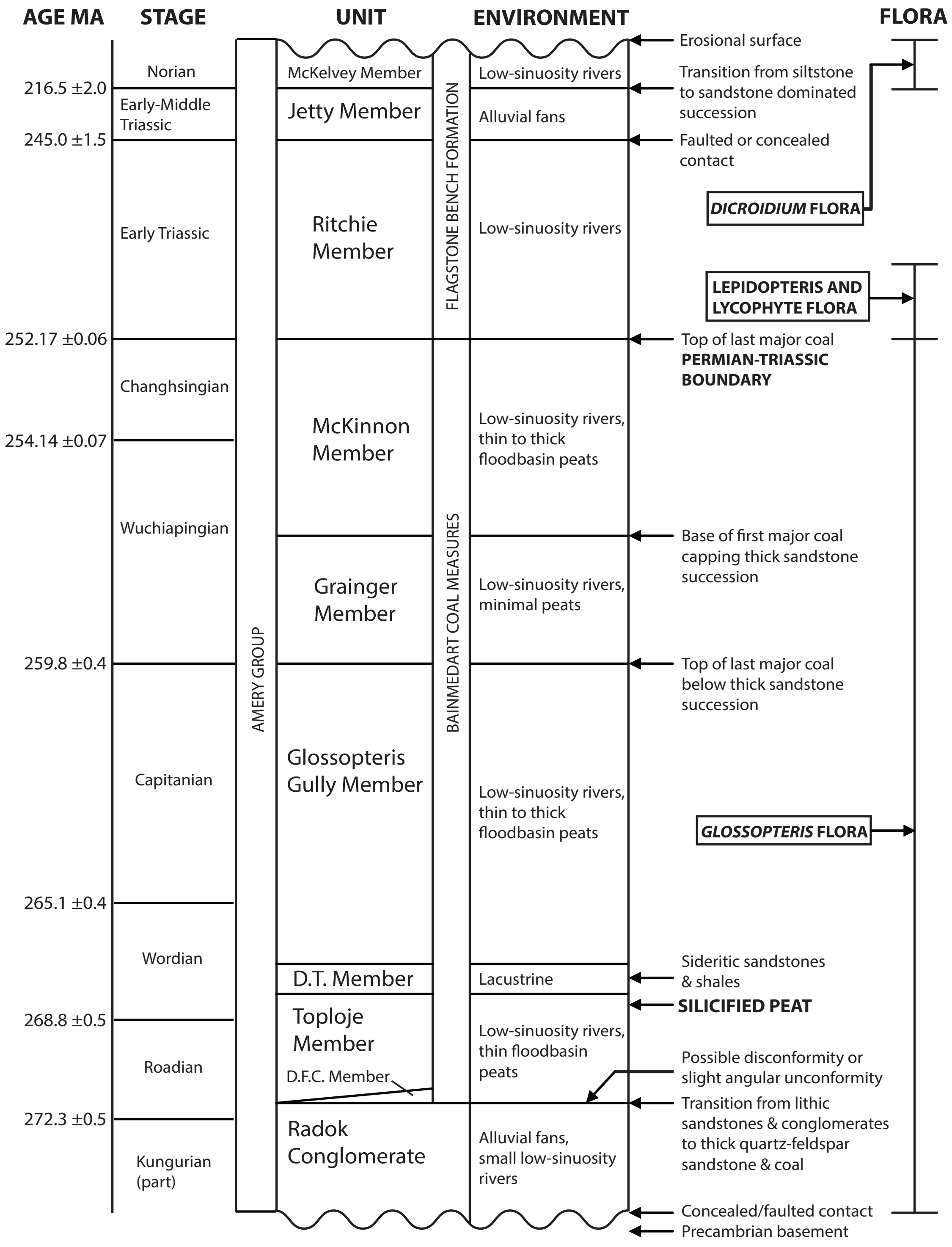
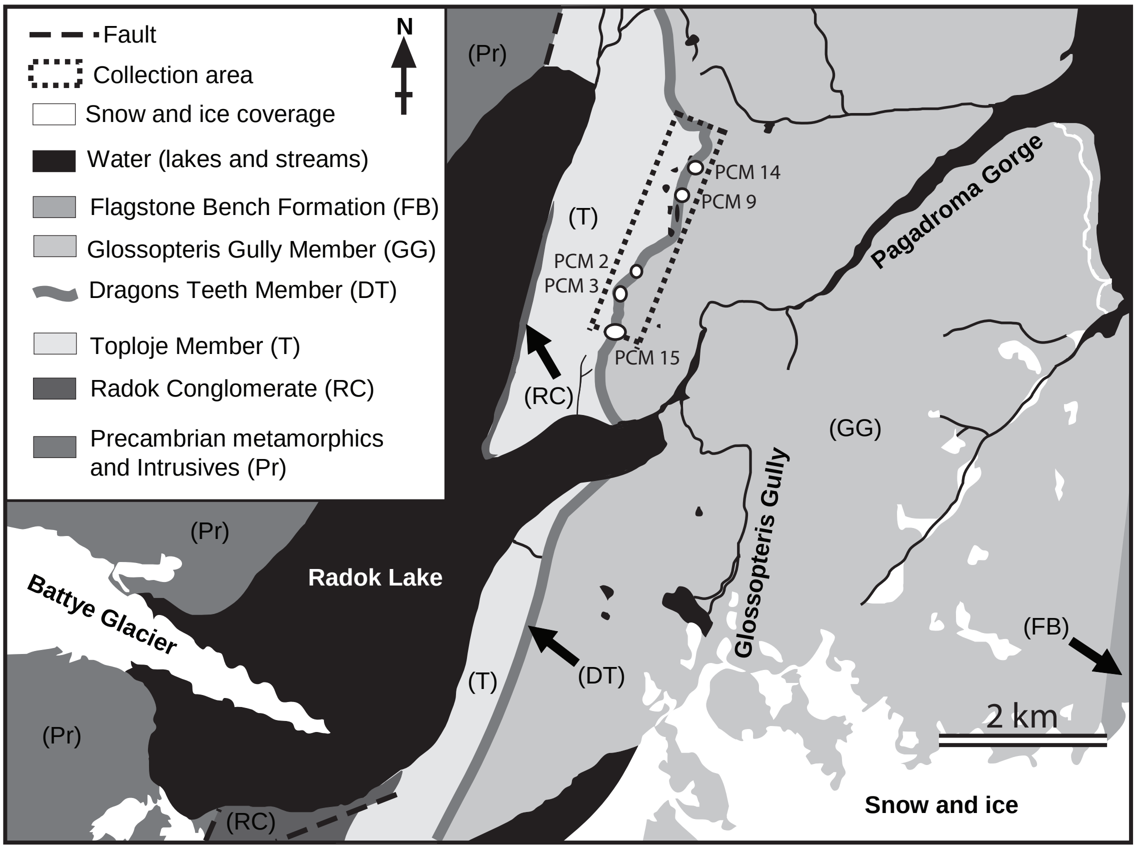


Figure 2.1: Stratigraphic column of the Permian and Triassic strata in the Prince Charles Mountains (Lambert Graben) showing the position of the Toploje Member chert lagerstätten.

2.2 Lithostratigraphy and the Toploje Member chert

The Toploje Member chert is a silicified peat layer which forms the upper portion (~40 cm) of a coal seam (Figure 2.1). This locality of exceptional preservation is situated in the northern Prince Charles Mountains in East Antarctica near to the Lambert Glacier. The silicified peat bed itself crops out along a ~3 km long exposure (Figure 2.2) and constitutes the uppermost part of the 303 m thick Toploje Member of the Bainmedart Coal Measures, the middle unit of the Permian-Triassic Amery Group (Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a; Holdgate et al., 2005; Slater et al., 2011). The Bainmedart Coal Measures were deposited disconformably or slightly unconformably on the Lower to lower-Middle Permian Radok Conglomerate, and are overlain conformably by the Triassic-aged Flagstone Bench Formation forming a rare continuous Permian-Triassic transition sequence (McLoughlin et al., 1997). Palynofloristic dating places the age of the silicified peat as late Roadian to Wordian in the *Didecitriletes ericianus* Palynozone. This is based on first occurrence datum of the nominal index species near the base of the Toploje Member and first occurrence of *Camptotriletes warchianus* in immediately overlying sideritic/limonitic lacustrine sediments of the Dragons Teeth Member (Lindström and McLoughlin, 2007). The lower Bainmedart Coal Measures is dominated by pronounced cyclic sedimentation of subfeldspathic sandstones, siltstones and coal seams deposited in alternating low-energy forest-mire settings and higher-energy braided-channel environments, where the strong cyclicity in the sedimentary sequence is attributed to Milankovic-induced environmental change affecting sediment supply (Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a, 1997b; McLoughlin et al., 1997; Lindström and McLoughlin, 2007).



THICKNESS

McKelvey Member: >72 m
Jetty Member: >139.5 m
Ritchie Member: >550 m
McKinnon Member: 548.5 m
Grainger Member: 349 m
Glossopteris Gully Member: c.880 m
Dragons Teeth (D.T.) Member: 15-25 m
Toploje Member: 303 m /
Dart Fields Conglomerate (D.F.C.) Member: <3 m
Radok Conglomerate: >320 m

NUMBER OF COAL SEAMS

McKinnon Member: 58
Grainger Member: 3
Glossopteris Gully Member: 56
Dragons Teeth Member: 0
Toploje Member: 21

Silicified peat layer: ~40 cm thickness

Figure 2.2: Geological map of the Radok Lake area, Prince Charles Mountains, Antarctica. Modified from Anderson (1977), Lawver and Scotese (1987) and McKelvey and Stephenson (1990). Thickness of geological members and number of coal seams after Holdgate et al. (2005). Sites prefixed PCM represent sampling localities.

2.3 Preservation

The taphonomy of the Toploje Member chert is subject to discussion in several papers (Holdgate et al., 2005; Slater et al., 2011) and is assessed in further detail in Chapter 6, section 6.5. The preservation of the majority of silicified plant lagerstätten including the Rhynie Chert and other localities appears to be related to inundation of peats or riparian vegetation with mineral-rich hydrothermal spring waters (Trewin 1994, 1996; Trewin et al., 2003; Channing and Edwards, 2004, 2009a, 2009b; Stevens, et al., 2010; Strullu-Derrien et al., 2012; Taylor et al., 1989; Womack et al., 2012). The Toploje Member chert, however, has no related hydrothermal or volcanic deposits and silicification appears to be related to inundation by a mineral-charged lake evidenced by the immediately overlying siderite-rich lacustrine sediments of the Dragons Teeth Member (Figure 2.1), silica-precipitation perhaps being driven by seasonal alkalinity fluctuation of the high latitude lake waters (Slater et al., 2011). Silica gels are known in association with several lake deposits in the geological record and in several modern saline or playa lakes and lagoons (Peterson and Von Der Borch, 1965; Colinvaux and Goodman, 1971; Wells, 1983; Wheeler and Textoris, 1978). Lacustrine cherts are formed in modern lake environments where quartz-derived silica is dissolved in alkaline lake waters, alkalinity usually being induced by seasonal fluctuations in the lake volume (Hesse, 1989). Inorganic silica gel is then precipitated from the lake water solution when the pH falls because of acidification related to decaying plant material, in this case peats on the lake bed (Hesse, 1989; Slater et al., 2011). The Toploje Member chert therefore preserves a different taphonomic assemblage to the cherts of sinter/hydrothermal origin. In particular, the sedimentology of the Bainmedart Coal Measures resembles some of the sequences in recent Quaternary sediments where lacustrine cherts are known; peat forming ecosystems from environments in the last interglacial which were then replaced with brackish lakes that had playa-type margins that precipitated silicates, and are now characterised by dry semi-arid environments occur in modern day central Anatolia, Turkey (Kuzucuoğlu et al., 1999). These facies are reminiscent of the possibly Milankovic-induced sedimentation changes seen in the Bainmedart Coal Measures.

CHAPTER 3: GUADALUPIAN (MIDDLE PERMIAN) MEGASPORES AND SPORANGIA FROM THE TOPLOJE MEMBER CHERT, BAINMEDART COAL MEASURES, PRINCE CHARLES MOUNTAINS, ANTARCTICA

3.1 Background

The macrofossil record of lycopsids in Antarctica extends back to at least the Middle Devonian (Grindley et al., 1980; McLoughlin and Long, 1994; Xu and Berry, 2008) and continues well into the Cretaceous (Cantrill, 2001) and, on the basis of dispersed microspores, the group probably persisted in Antarctica into the mid-Cenozoic (Truswell and Macphail, 2009). Previous studies have concluded that heterosporous lycopsids constituted a relatively minor component of Gondwanan Permian peat-forming ecosystems (Diessel, 1992; Glasspool, 2000, 2003), although they were locally important in wetland communities in the early part of the period (Anderson et al., 1999). This is in marked contrast to their great abundance in peat-forming communities in the Carboniferous of Europe and North America (Bateman et al., 1992) and the Permian of China (Wang and Chen, 2001). Although lycopsid macrofossils are relatively rare in Middle to Late Permian Gondwanan peats, especially those in eastern Gondwana, research on Triassic strata from the Prince Charles Mountains (PCMs) demonstrates a resurgence in the abundance of lycopsids following the P-Tr boundary based on microspore, megaspore and macrofossil remains (McLoughlin et al., 1997; Vajda and McLoughlin, 2007; Lindström and McLoughlin, 2007).

The study of fossil megaspores from Gondwana began tentatively in the 1860’s (Carruthers, 1869), but remained confined to a few isolated studies until the first detailed account by Surange et al. (1953), which documented mounted Indian megaspores using reflected light microscopy (Pant and Mishra, 1986). Although lycopsid microspores have been widely employed in Permian biogeography and biostratigraphy (e.g. Foster, 1982; Césari and Gutiérrez, 2000), megaspores have remained a somewhat under-utilized tool but they are likely to have equivalent palaeo-biogeographical and stratigraphical significance and they have found application for local stratigraphic correlation in some Indian basins (Maheshwari & Tewari 1987; Tewari et al., 2004, 2007, 2009; Tewari, 2008). Furthermore, their diversity and abundance offer clues to lycopsid diversity in the source palaeovegetation even in the absence of macrofossil and microspore evidence (e.g. Bateman and Hilton, 2009).

This study investigates megaspores preserved in silicified peats from the Bainmedart Coal Measures in the PCMs, East Antarctica. Earlier studies have investigated the palynology and palaeobotany of the Bainmedart Coal Measures, from which megaspores from siltstones that alternate with coal seams in the Toploje Member were illustrated but not systematically described by McLoughlin et al. (1997). Megaspores have also been recovered from the overlying Lower Triassic Ritchie Member (lower Flagstone Bench Formation) by McLoughlin et al. (1997) and from the Upper Triassic McKelvey Member (upper Flagstone Bench Formation) by Cantrill and Drinnan (1994). The megaspores documented here represent the oldest megaspores systematically described from Antarctica to date, and their significance lies in their exceptional uncompressed preservation within a permineralised peat. Exquisite preservation of the mire-dwelling plants in this deposit reveals cryptic elements of the flora that are not preserved elsewhere in the Lambert Graben succession, including numerous fern microsporangia which allude to the cryptic presence of ferns in the palaeoecosystem and are further discussed here.

3.2 Materials and methods

Samples from several localities exposing the silicified peat layer (Figure 2.2) were bulk-macerated in cold 30% HF for two weeks. The released debris was separated from the HF solution using a 150 micron nylon sieve. The macerated material was then retained in a petri dish with distilled water for examination with a binocular microscope using incident and transmitted light. Megaspores, sporangia and other phytodebris were picked with a fine camel hair brush then mounted on SEM stubs, coated with gold and studied using a Hitachi S-4300 field emission scanning electron microscope at the Swedish Museum of Natural History. Spore morphological terminology used in this study is that of Playford and Dettmann (1996). All measurements and dimensions provided are taken from dried specimens illustrated with SEM. Individual megaspores shrink to c. 80% of their original (wet) size when dehydrated. Some additional megaspore cross-sections were recorded in thin-sections of the permineralised peat (see Holdgate et al., 2005, fig. 14K). Microsporangia were also recorded in thin-sections prepared either with the acetate peel technique (Galtier and Philips, 1999) or ground thin-sectioning (Hass and Rowe, 1999).

The ornamentation, microspores and internal structures of one megaspore species were also studied using synchrotron-based X-ray tomographic microscopy (SRXMT) at the TOMCAT beamline of the Swiss Light Source at the Paul Scherrer Institute, Switzerland. Specimens were mounted on 3 mm diameter brass stubs and examined using the technique outlined by Donoghue et al. (2006). Slice data derived from the scans (Hintermüller et al., 2010) were then analyzed and manipulated using Avizo software for computed tomography. This is the most detailed study of megaspores using synchrotron X-ray tomography to date, and the first such investigation of post-Carboniferous megaspores, thus building on the work of Glasspool et al. (2009).

Illustrated specimens are prefixed NRMS or CPC and are stored in the palaeobotanical collections of the Swedish Museum of Natural History, Stockholm, and the Commonwealth Palaeontological Collection, Geoscience Australia, Canberra, respectively. Figures were prepared using Adobe Photoshop and Illustrator graphics packages.

3.3 Systematic palaeobotany

3.3.1 Duosporites lambertensis

Genus *Duosporites* Høeg et al., 1955, emend. Glasspool (2003)

Duosporites lambertensis B. J. Slater, S. McLoughlin *et* J. Hilton sp. nov. (Figure 3.1, A–B)

Specific diagnosis: Amb subtriangular, laesurae slightly sinuous and extending almost to megaspore margin. Labrae broad and rounded, broadening towards the equator. Curvaturae ridges delimiting contact areas are marked by short spines or grana. Curvaturae ridges bounded proximally by a wide, shallow furrow surrounding the domed polar region of contact faces. Both hemispheres almost laevigate but bearing irregularly spaced, very fine grana and spinula.

Holotype: NRMS089517.

Location, unit and age: Site PCM 15, 1.8 km east of Radok Lake (Figure 2.2), Northern PCMs, East Antarctica; uppermost Toploje Member (Roadian–Wordian), Bainmedart Coal Measures, Amery Group, Lambert Graben.

Etymology: Named after the Lambert Graben, Antarctica.

Abundance and distribution: Rare (n = 2) in the uppermost Toploje Member.

Description: The description is based on two specimens recovered from one locality (PCM 15) exposing the silicified peat layer. The megaspores are trilete, with a convexly subtriangular amb (Figure 3.1, A–B). The equatorial diameter is 400–500 µm. The labrae exhibit one or two slight folds near the pole (Figure 3.1, C) but are otherwise straight, extending to the equator or locally projecting as a weak marginal extension (Figure 3.1, A–B). Labrae are laevigate–microfoveolate, 20–30 µm wide for most of their length but broadening to 60 µm equatorially, c. 20–30 µm high, and of consistent height across most of the proximal surface, but tapering abruptly near the margin of the contact areas (Figure 3.1, A–B). The curvaturae ridges are distinct and marked by a low file of spinula or grana (<1.5 µm high; Figure 3.1, D). Each curvaturae ridge is flanked on the proximal side by a shallow but wide (50–80 µm wide) furrow, which surrounds the domed (convex) polar region of the contact area. Proximal and distal ornamentation of the megaspore is undifferentiated, consisting of irregular, sparse grana and spinula typically <0.5 µm wide and <1 µm high. The spore wall is a dense, porous network of sporopollenin threads (Figure 3.1, D). The inner spore body is subtriangular and 230–325 µm in equatorial diameter and may possess proximal papillae based on the presence of several weak swellings expressed on the contact faces of the outer spore wall (Figure 3.1, B).

Remarks and comparisons: The megaspores are assigned to *Duosporites* (Høeg et al., 1955 emend. Glasspool, 2003) on the basis of their subtriangular amb, the extension of the trilete rays to the megaspore margin and the mostly laevigate nature of the spore wall; features that are distinctive of this genus. Although only represented by two specimens, the new taxon can be distinguished from all other species of *Duosporites* by its possession of sparsely spinulose ornament across the entire surface of the megaspore and by the ridge of short grana and spinula surrounding the contact face and demarcating the curvaturae ridges. These features are considered autapomorphic to the species resulting in the erection of *D. lambertensis* sp. nov.

Duosporites lambertensis sp. nov. differs from *D. congoensis* Høeg et al., 1955, emend. Glasspool, (Glasspool, 2003) in the distribution of very short spines across the entire exine surface endowing it with an almost felt-like texture. In addition, the furrow surrounding the contact faces is proportionally wider, which gives the polar regions of the contact faces a more pronounced domed appearance. The trilete rays are less sinuous than those of *D. congoensis*, being straighter near the equator and only having one or two folds near the pole. The spinulose ornament is similar to that of *D. trivedii* (Dijkstra, 1955) Piérart, 1959, emend Glasspool, 2003. However the ornament of *D. lambertensis* (<0.5 μm wide and <1 μm high) is much smaller than that of *D. trivedii* (with verrucae 10–20 μm in basal diameter). Considering their morphology, size and age, the megaspores are most likely derived from a lycopsid (e.g. Glasspool, 2003).

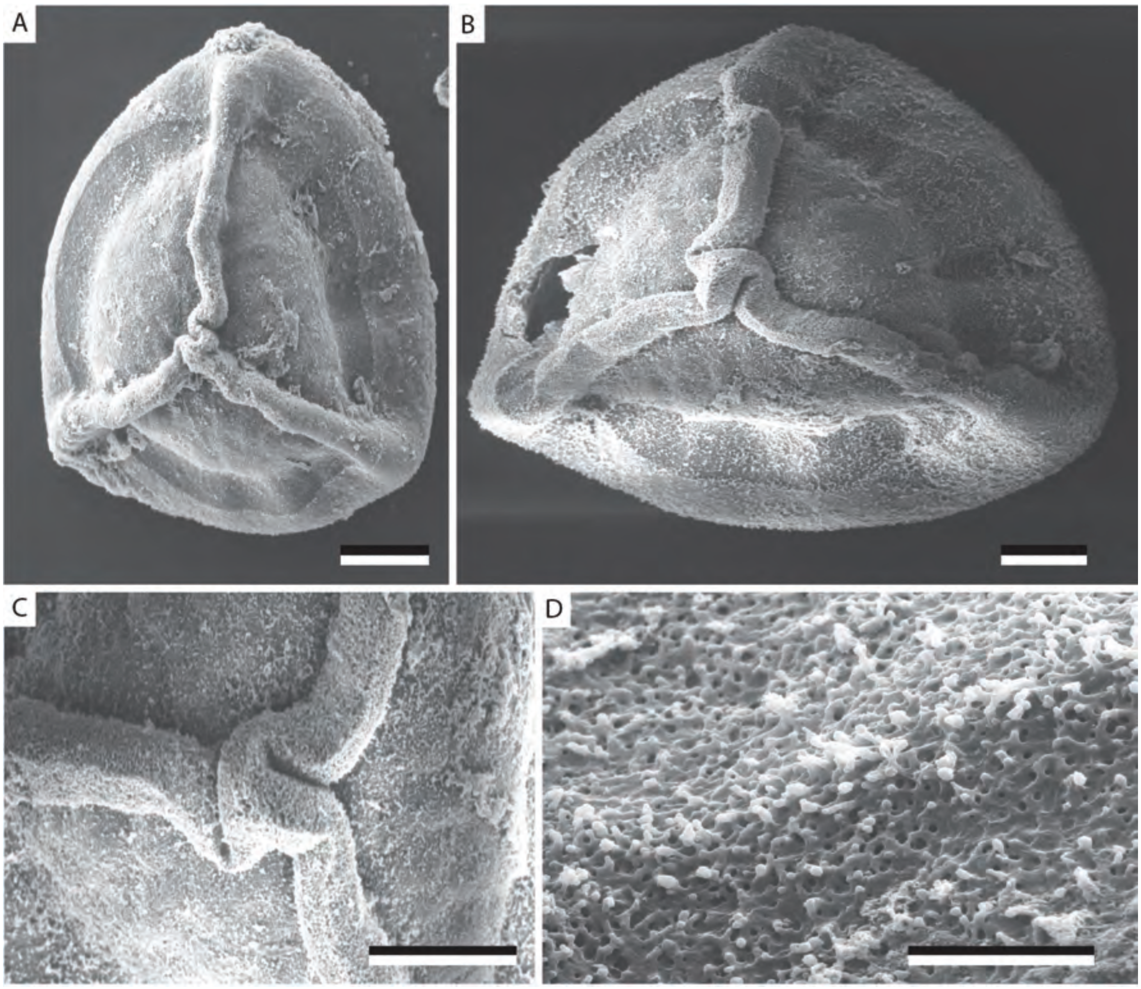


Figure 3.1: Scanning electron micrographs of *Duosporites lambertensis* sp. nov. All from site PCM 15. Scale bars=100 µm for A–C; 10 µm for D.

A. Proximal view of megaspore (NRMS089516) showing notably sunken margin of contact areas.

B. Proximal view of holotype (NRMS089517) showing very fine felt-like ornament, and subtle swellings on the polar regions of the contact faces that may correspond to papillae on a concealed inner body.

C. Enlargement of labrae from 3.1, B, showing sinuosity at the pole.

D. Enlargement from 3.1, B, showing fine ornament and a weak ridge at perimeter of contact surface.

3.3.2 Banksisporites antarcticus

Genus *Banksisporites* Dettmann, 1961, emend. Glasspool, 2003

Banksisporites antarcticus B. J. Slater, S. McLoughlin *et* J. Hilton sp. nov.

Specific diagnosis: Amb subcircular; laesurae straight to slightly sinuous, extending to the equator, which is marked by the curvaturae ridges. Labrae consistent in width throughout their length. Curvaturae ridges distinct to faint. Exine mostly smooth but with sparse short grana across the entire megaspore.

Holotype. NRMS089515.

Location, unit and age: Site PCM 15, 1.8 km east of Radok Lake (Figure 2.2), Northern PCMs, Antarctica; uppermost Toploje Member (Roadian–Wordian), Bainmedart Coal Measures, Amery Group, Lambert Graben.

Etymology: Named after the Antarctic continent where the specimens were found.

Abundance and distribution: Common in the uppermost Toploje Member.

Description: The description is based on >10 specimens. The megaspores are trilete with a circular to subcircular amb (Figure 3.2, A–B) and broadly elliptical polar outline. The equatorial diameter range is 400–600 µm and the polar diameter is c. 500 µm. The contact areas form a broad smooth dome. The laesurae are slightly sinuous near the pole, but are otherwise straight, extending to the equator (Figure 3.2, A–B). The labrae are laevigate–

microfoveolate, <25 μm wide and <50 μm high; their height is consistent apart from their abrupt truncation at the equator (Figure 3.2, A–B). The contact areas are normally delimited by a low curvaturae ridge <10 μm high and <10 μm wide (Figure 3.2, A–B) but in a few cases this feature is not developed (Figure 3.2, C). Both proximal and distal (Figure 3.2, C) surfaces are essentially laevigate but very sparse sculptural elements on both surfaces include <1 μm diameter, <1 μm high grana or spinula emerging from a microfoveolate exine (Figure 3.2, D).

Remarks and comparisons: The megaspores are assigned to *Banksisporites* as they exhibit the diagnostic features of this genus including a subcircular amb, straight–sinuous trilete rays that do not extend beyond the contact area, and more or less smooth proximal and distal surfaces (see discussion and emendation of this genus by Glasspool, 2003). The present species differs from other members of the genus by possessing very sparse short grana across the entire surface and laesurae that are more or less uniform in width and height extending to the margins of the megaspore.

Banksisporites antarcticus sp. nov. differs from *B. endosporitiferus* (Singh, 1953) Tewari and Maheshwari, 1992, emend. Glasspool 2003 in the dimensions of labrae, which widen peripherally in *B. endosporitiferus* but remain more or less of uniform width in *B. antarcticus*. *Banksisporites antarcticus* is distinct from *B. indicus* (Singh, 1953) Glasspool, 2003, since the former lacks verrucae. Laesurae of *B. antarcticus* are also proportionally longer, extending to the equator, whereas in *B. indicus* the laesurae reach a maximum of 80% of the megaspore radius. The labrae of *B. indicus* also taper in height and width with distance from the pole, a feature that is not evident in *B. antarcticus*. The curvaturae ridges of *B. antarcticus* are also much lower (<10 μm high) and less consistently developed than those of

B. indicus (up to 40 µm high). In this respect *B. antarcticus* shares similarities with *B. rotundus* (Singh, 1953) Glasspool, 2003 in its possession of a low arcuate ridge (which is even less well defined in *B. rotundus*). *Banksisporites antarcticus* differs from *B. rotundus* in the possession of sparse grana on both the proximal and distal surfaces, which are absent in *B. rotundus*. A wide range of Gondwanan Mesozoic megaspores has been assigned to *Banksisporites* (Batten and Kovach, 1990; Tosolini et al., 2002) but these can be distinguished from *B. antarcticus* by the character of their labrae, curvaturae ridges, micro-ornament and dimensions.

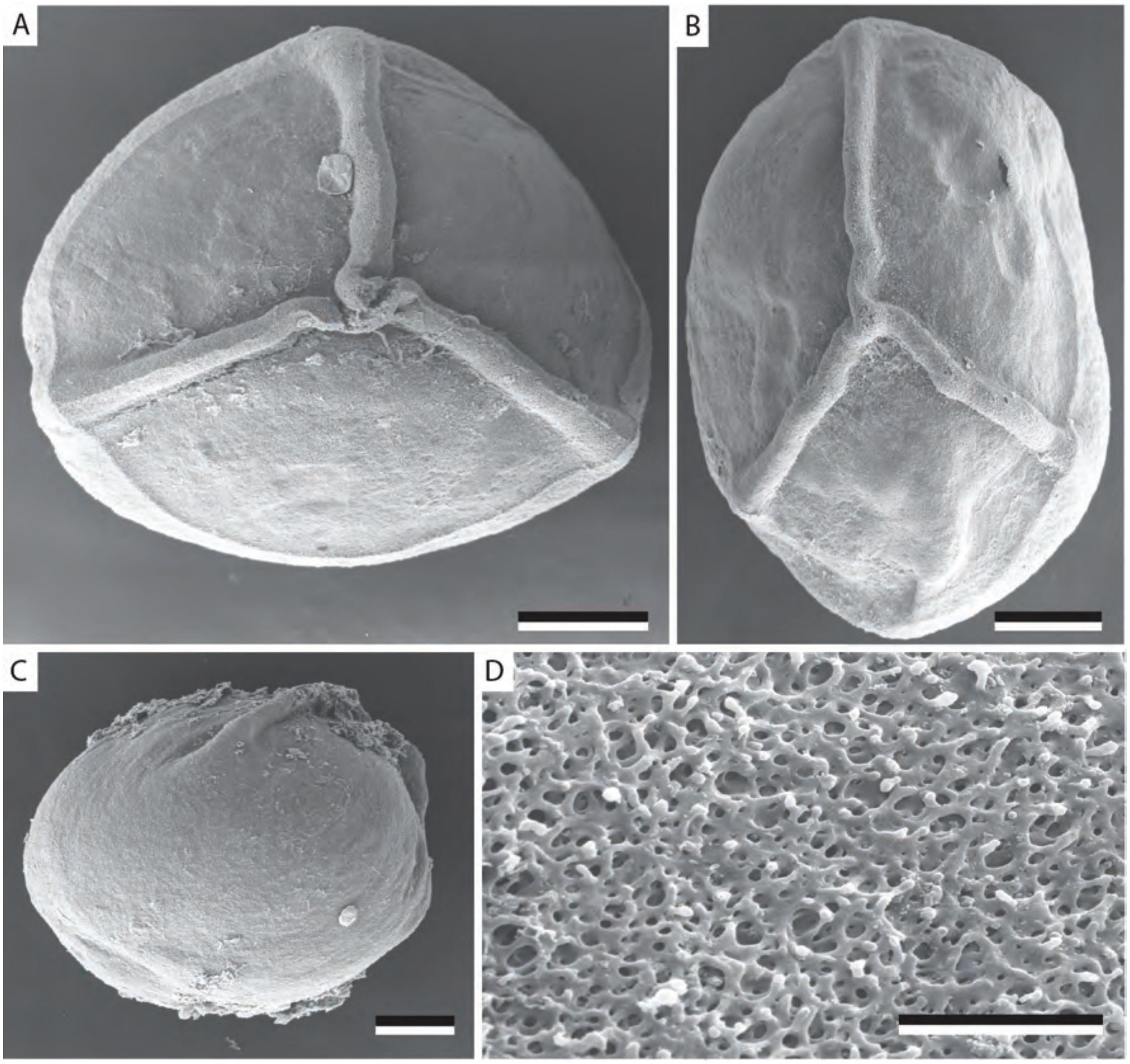


Figure 3.2: Scanning electron micrographs of *Banksisporites antarcticus* sp. nov. Scale bars=100 μm for A–C; 10 μm for D.
A. Proximal view of holotype (NRMS089515; site PCM 15) showing laevigate contact.
B. Proximal view of megaspore (NRMS089527; site PCM2) showing incomplete development of ridge bounding contact areas.
C. Oblique view of megaspore (NRMS089518; site PCM 15) showing distal surface (bottom) and lack of curvaturae ridges connecting labrae.
D. Microfoveolate outer wall of the holotype.

3.3.3 Singhisporites hystrix

Genus *Singhisporites* Potonié, 1956, emend. Glasspool, 2000

Singhisporites hystrix B. J. Slater, S. McLoughlin *et* J. Hilton sp. nov.

Specific diagnosis. Amb circular to subcircular. Laesurae straight, extending 60–80% distance to equator. Contact areas sunken, delimited by sharply defined change in ornamentation along the arcuate rim connecting the equatorial ends of labrae. Contact areas bearing branched or reticulate, slender, sinuous, ribbon-like or bush-like sculptural elements, which branch to mostly pointed tips. Distal surface bearing complex ribbon-like or flared, multiple-branched or reticulate sculptural elements connected to the exine by a spongy pedestal structure. Distal ornament of uniform height but sculptural elements are more than twice the height of those on the contact faces. Outer spore wall coarsely spongeous.

Holotype. CPC34312.

Location, unit and age: Found in samples from all exposures of the silicified peat bed listed herein, 1.8 km east of Radok Lake (Figure 2.2), Northern PCMs, Antarctica; uppermost Toploje Member (Roadian–Wordian), Bainmedart Coal Measures, Amery Group, Lambert Graben.

Etymology: Derived from the Latin for porcupine due to its spiny appearance.

Abundance and distribution: Abundant (>50 specimens) in the Toploje Member permineralised peat layer. Similar megaspores, but assigned to other species of

Singhisporites (Potonié, 1956, emend. Glasspool, 2000) have been found in the Permian of India, Australia and South Africa (Glasspool, 2003). This is the first record of the genus in Antarctica.

Description: The trilete megaspores have a circular amb (Figure 3.3, A–B; Figure 3.4, A–B). The equatorial diameter is 600–800 µm and the polar diameter is approximately 500 µm (Figure 3.3, A–B). The polar outline is broadly elliptical, with contact areas forming a low pyramid (Figure 3.3, C). The laesurae are straight and extend 60–80% of the distance to the equator. The labrae are <15 µm wide, <20 µm high, and are commonly surmounted by flared, multiple-branched, sculptural elements <35 µm in height. The contact areas are sunken, and are delimited by a sharply defined change in ornamentation along the arcuate rim connecting the equatorial ends of the labrae (Figure 3.3, C, E). The contact areas bear solitary, clustered, branched or reticulate, slender, sinuous, sculptural elements 1–3 µm wide, <33 µm high and spaced 10–25 µm apart (Figure 3.3, D). The distal surface of the megaspore bears complex, multiple-branched or reticulate flared, ribbon-like or cylindrical sculptural elements (Figure 3.3, E). These sculptural elements are 10–20 µm wide, 20–70 µm long at the base, flaring to 80 µm wide apically, 60–100 µm high and are spaced 10–30 µm apart (Figure 3.3, E–F; Figure 3.4, A–B). The outer spore wall is typically 25–35 µm thick and coarsely spongeous (Figure 3.3, F; Figure 3.4, C–D). The inner spore wall is apparently closely adpressed to the outer wall and is densely structured, being 1–3 µm thick and forming a sheet fused to the inner surface of the exine (Figure 3.4, C–D). Tomographic imaging reveals that the sculptural ornament is of a uniform maximum height above the surface of the megaspore wall in areas other than the contact faces (Figure 3.6, A–D).

Microspores: A single type of microspore occurs locally trapped between the megaspore sculptural elements of this kind of megaspore (Figure 3.4, A, D; Figure 3.5, A; Figure 3.6, E, F; Figure 3.7, E). Trapped microspores are trilete and 45–50 µm in equatorial diameter (Figure 3.5, B). The laesurae are straight to slightly sinuous, extending around 60 % of the distance to the equator and are flanked by labrae (Figure 3.7, C). The proximal ornamentation is sparsely spinose and proximal spines are <1 µm wide and <1.5 µm high (Figure 3.5, B). The distal surfaces of the microspores are densely ornamented with spines, bacula, or elongate, branched, ribbon-like sculptural elements, typically <5 µm wide and <2.5 µm high (Figure 3.5, C–D). A prominent cingulum extends from the margins of the contact area and is 20–50 µm wide, and commonly has spinose extensions 1–2 µm long (Figure 3.5, B–D). The spore wall is finely spongeous.

Remarks and comparison: These trilete megaspores are assigned to *Singhisporites* Potonié emend. Glasspool (2000) on the basis that their laesurae do not extend beyond the contact areas, the limits of which are defined by a change in the height and complexity of ornamentation along the arcuate rim (Figure 3.6, H). The new species differs from other *Singhisporites* in the evenly distributed and uniform height (apart from the contrast between the contact areas and the rest of the exine) of dense, elaborate ornament on all specimens. The ornament differs from other species of *Singhisporites* in the marked difference between the ornament of the contact face and distal surface; the processes of the contact face are flattened, shorter and always ribbon-like, whereas the larger distal processes are wider, more three-dimensionally branched or cylindrical, commonly forming tubes, with each process mounted on a pedestal structure. The ornament along the arcuate rim is commonly fused to varying degrees to form a curtain, although this feature demonstrates considerable intraspecific variation. It is clear from the x-ray tomographic images that flanking the labrae there are two consistently thick pads of tissue overlain by sculptural elements (Figure 3.7, A, H). The sunken bases of these thickened pads are not clear in the SEM images. The x-ray tomographic images also reveal the presence of a potential inner body (Figure 3.6, A–C; Figure 3.7, D). However this feature is granular in nature rather than smooth and is eccentrically positioned and of irregular shape, and so may represent an aggregation of fine organic debris that has entered the spore via the laesurae. Following Glasspool (2000), the inner body is disregarded as a useful taxonomic character.

Singhisporites hystrix differs from *S. surangei* (Singh, 1953) Potonié, 1956 emend. Glasspool, 2000 in several aspects. In *S. hystrix*, the labrae are more pronounced and are never undulate as in some *S. surangei* specimens. Labrae in *S. hystrix* are similar to those of *S. tubbus* Glasspool, 2000 in being distinct, high and narrow but the ornament of the latter is distinct in consisting of short, flattened processes with ragged margins. The contact faces and all other surfaces in *S. hystrix* are ornamentated in all cases, and this differs from many *S. surangei* specimens, which lack areas of ornament. The ornament of *S. hystrix* is also stouter and has branched, pointed tips (Figure 3.4, D), compared to the more rounded tips evident in *S. surangei*. The latter also lacks the pedestal attachment bases of the sculptural elements (Figure 3.4, A–B). The ornament forms a uniform height around *S. hystrix* and is denser than that of *Singhisporites radialis* (Bharadwaj and Tiwari, 1970), a megaspore that also displays uniform ornament distribution. The ornament also differs from the thick fleshy processes of *Singhisporites radialis* (Bharadwaj and Tiwari, 1970) in being ribbon like. *Singhisporites hystrix* differs from all other *Singhisporites* in the difference between ornament on the contact faces and the distal surface. In *S. hystrix*, the processes covering the contact faces are shorter than the distal ornament and always ribbon-like in structure (Figure 3.3, D; Figure

3.4, C), whereas the larger distal processes are attached to the exine by a pedestal-like structure, are cylindrical (or otherwise three-dimensionally branched) and commonly form hollow tubular structures (Figure 3.3, C; Figure 3.4, D; Figure 3.6, D–G; Figure 3.7, B, F, G). The ribbon-like ornament on the contact faces can appear as spinule-like hollow tubes in degraded (Figure 3.3, B) or over-macerated specimens.

Singhisporites was established by Potonié (1956), and later, Glasspool (2000, 2003) designated the genera *Mammilaespora* (Pant and Srivastava, 1961), *Triapipellitis* (Kar, 1968), *Singraulispora* (Pant and Mishra, 1986), *Ancorisporites* (Pant and Mishra, 1986) and *Ramispinatispora* (Pant and Mishra, 1986) to be junior synonyms of *Singhisporites*. We also consider that *Ramispinatispora mahanadiensis* Tewari et al. (2009) should be reassigned to *Singhisporites* Potonié emend. Glasspool (2000), on the basis that Glasspool (2003) showed that all members of *Ramispinatispora* have equivalent ornamental characters to *Singhisporites*. The specimen assigned to *R. mahanadiensis* by Tewari et al. (2009), however, does display characteristic features, such as entangled web-like ornamentation, to warrant its distinction at the specific level from other representatives of the genus. The other two species referred to *Ramispinatispora* from the Ib-River Coalfield by Tewari et al. (2009), namely *R. indica* and *R. nautiyalii,* were previously transferred to *Singhisporites indica* and *Singhisporites nautiyalii* respectively by Glasspool (2003) and we agree with these reassignments. Furthermore, the specimen identified as *Singhisporites baculatus* (Kar) by Tewari et al. (2009, figure 4.3) should be considered a junior synonym of *Singhisporites surangei* since *S. baculatus* was only separated on the basis of possession of a dark inner body, a feature that Glasspool (2000) concluded is not specifically diagnostic since it is variable between specimens and can be affected by taphonomic processes and the degree of oxidation during preparation. Here *Ramispinatispora mahanadiensis* Tewari, Mehrotra, Meena et Pillai (Tewari et al., 2009) is formally transferred to *Singhisporites* in accordance with the conclusions of Glasspool (2000, 2003).

Microspores adhering to the ornament of *S. hystrix* sp. nov. are similar to dispersed examples of *Lundbladispora* sp. (Visscher et al., 2004) in their sub-rounded shape, possession of a granular to spinose or baculate ornamented distal surface and narrow cingulum. They most likely represent the microspores of the same parent plant as *S. hystrix*. Other species of *Singhisporites*, including *S. grandis* and *S. nautiyalii*, have also been reported to have microspores adhering to their surface ornament. Entrapment of microspores in the elaborate ornament of the megaspores may have been part of their reproductive strategy.

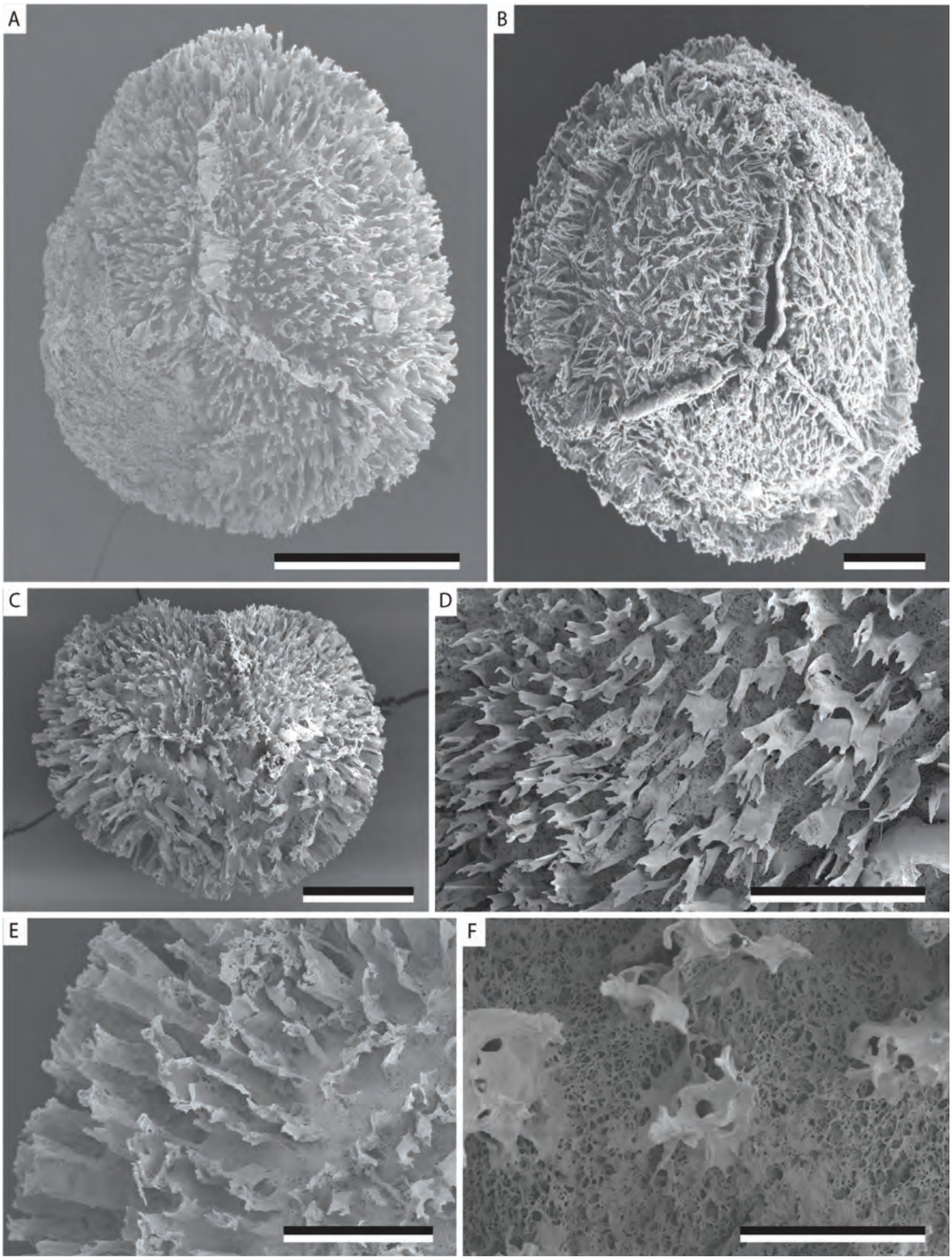


Figure 3.3

Figure 3.3 (previous page): Scanning electron microscope images of *Singhisporites hystrix* sp. nov. Scale bars=250 µm for A and C; 100 µm for B, D, E; 50 µm for F).
A. Proximal view of megaspore: NRMS089368, site PCM 3 (scale bar=250 µm).
B. Proximal view of holotype (CPC34312; site PCM 14) showing slight compression of proximal ornament (scale bar=100 µm).
C. Detail of the contact areas, laesurae and arcuate rim; NRMS089391, site PCM 9 (scale bar=250 µm).
D. Ornamentation on contact surface; NRMS089404, site PCM 9 (scale bar=100 µm).
E. Sharply defined change in ornamentation height and structure along arcuate rim connecting equatorial ends of labrae; NRMS089383, site PCM 9 (scale bar=100 µm).
F. Coarsely spongeous outer spore wall and complex sculptural elements of the proximal surface; NRMS089429, site PCM 2 (scale bar=50 µm).

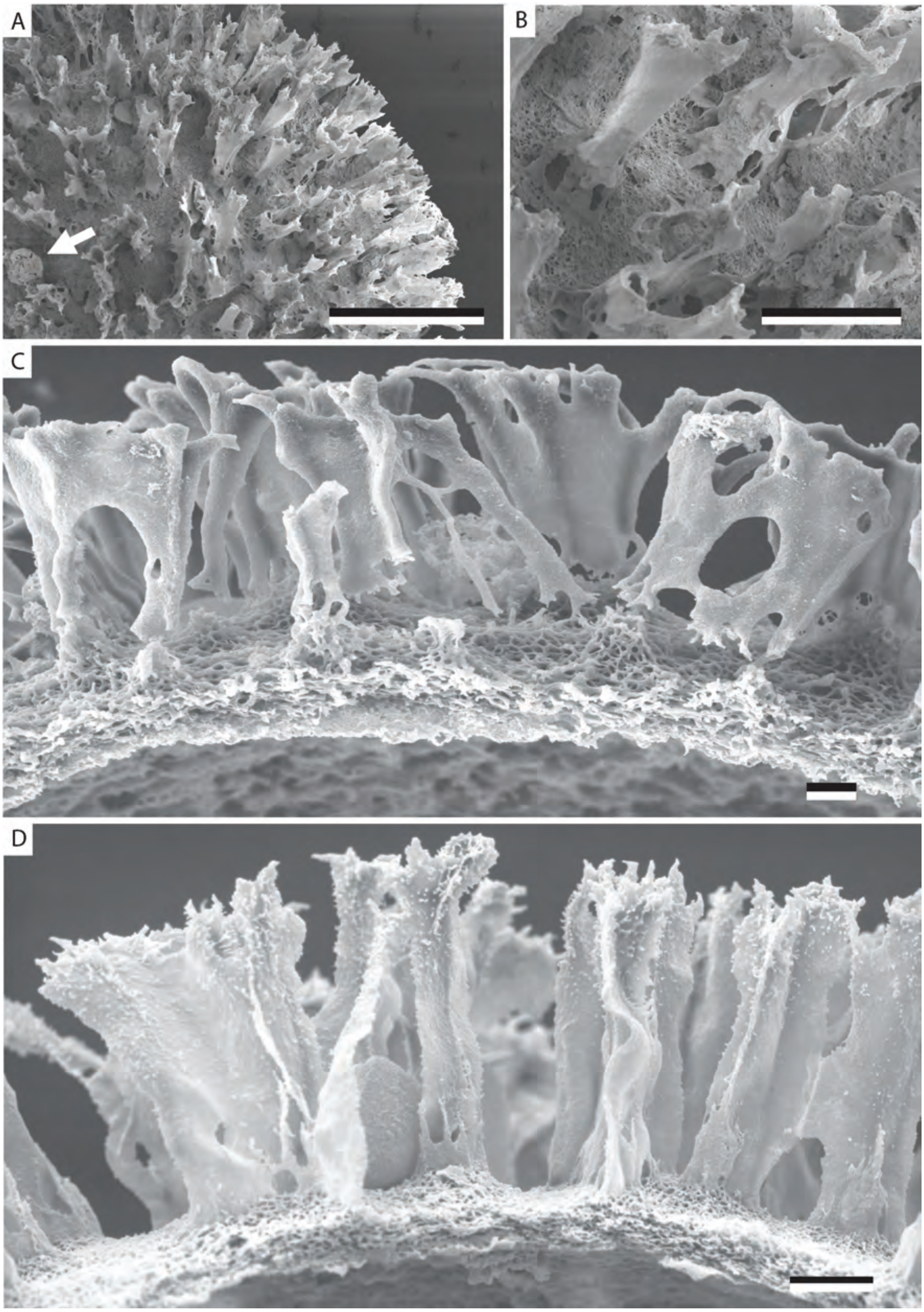


Figure 3.4

Figure 3.4 (previous page): Scanning electron microscope images of the ornament of *Singhisporites hystrix* sp. nov. Scale bars=200 µm for A; 50 µm for B; 10 µm for C; 20 µm for D.
A. Distal sculptural elements with arrow indicating adhering microspore; NRMS089428, site PCM 2 (scale bar=200 µm).
B. Enlargement of ornamentation showing stilt-like basal attachment of the flared sculptural elements to the outer spore wall from 3.4, A (scale bar=50 µm).
C. Section through spore wall across the contact face showing ribbon-like and branched/reticulate sculptural elements; CPC34314, site PCM 14 (scale bar=10 µm).
D. Section through the distal surface spore wall showing taller, stouter, longitudinally ribbed ornamentation; NRMS089541, site PCM 2 (scale bar=20 µm).

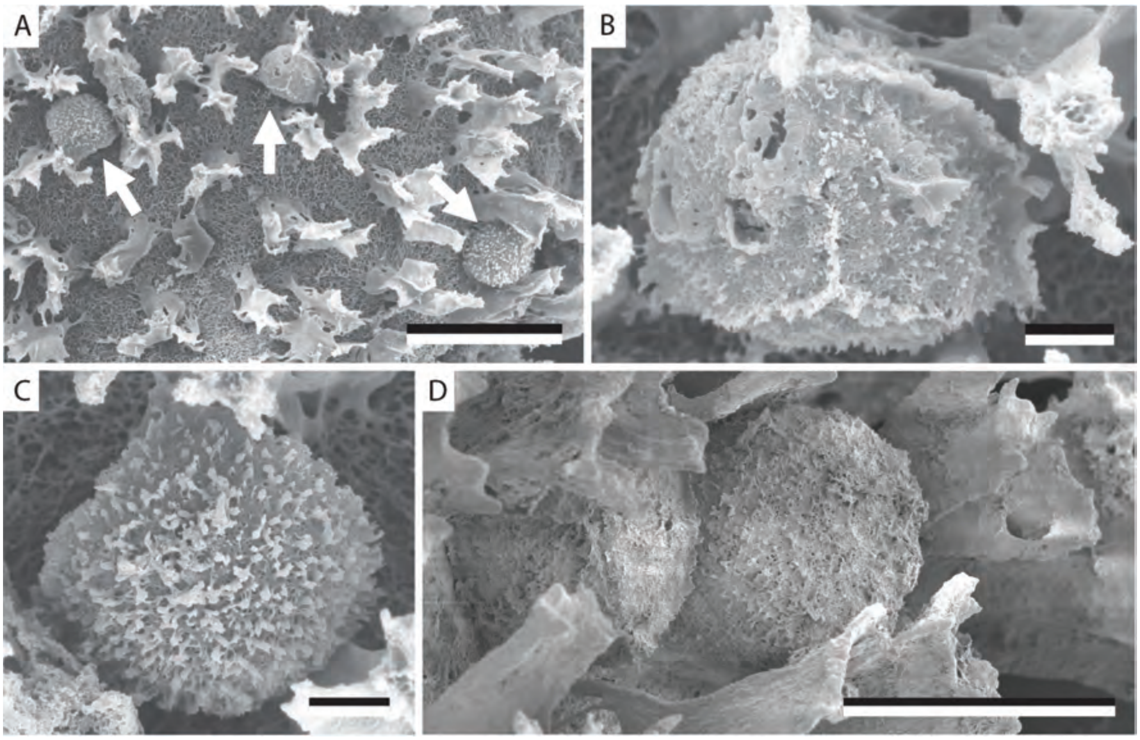


Figure 3.5: Scanning electron microscope images of microspores adhering to the surface of *Singhisporites hystrix*. Scale bars=100 µm for A; 10 µm for B, C; 50 µm for D.
A. Enlargement of megaspore’s proximal ornamentation with attached microspores indicated by arrows; NRMS089538, site PCM 2.
B. Enlargement from 3.5, A, showing proximal face and contact surfaces of microspore.
C. Enlargement from 3.5, A, showing distal surface of microspore.
D. Microspores entrapped within the ornamentation of *Singhisporites hystrix*; NRMS089413.

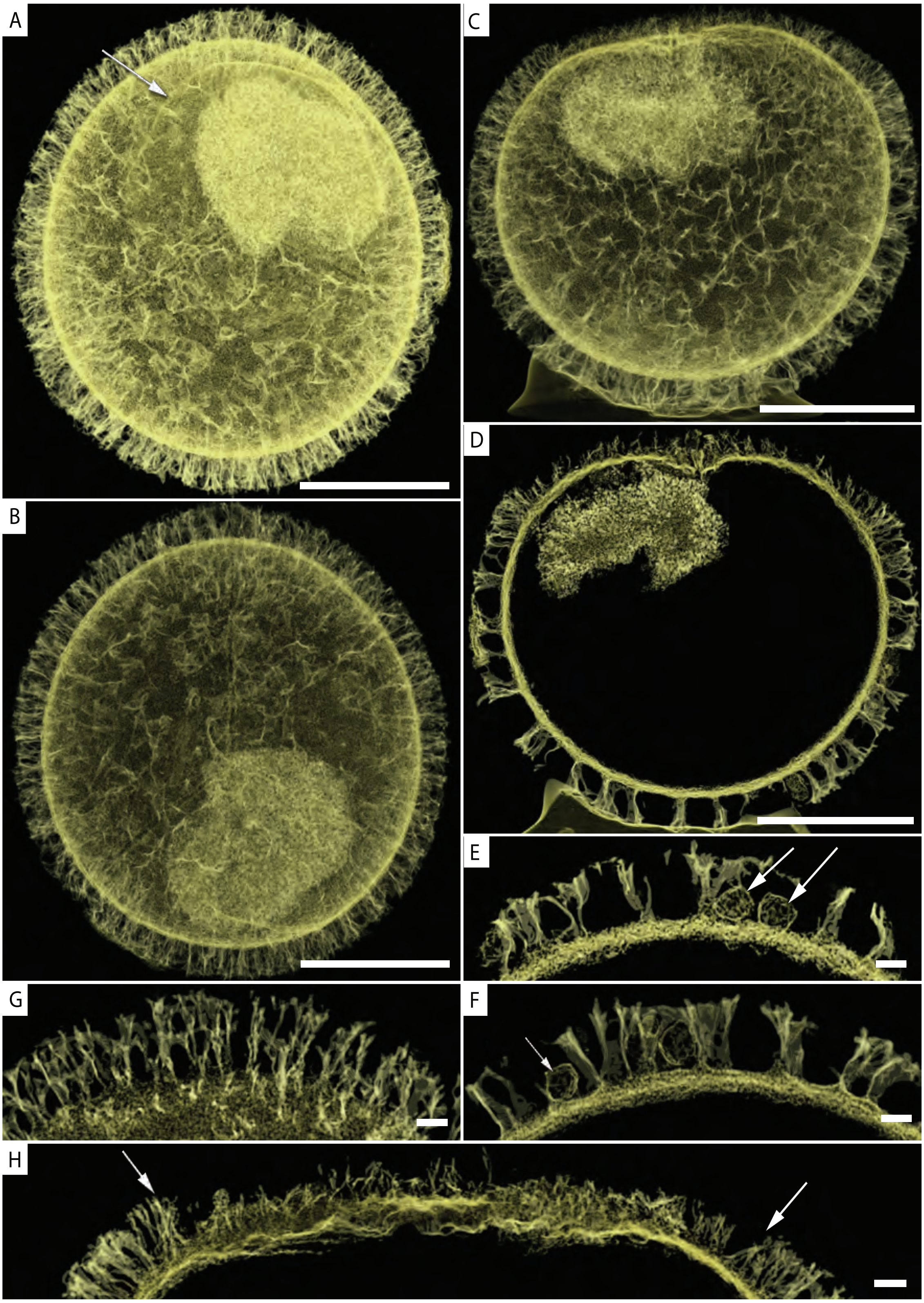


Figure 3.6

Figure 3.6 (previous page): Computed tomographic images of *Singhisporites hystrix* sp. nov., NRMS089351, site PCM 15, generated from attenuation-based synchrotron-radiation X-ray tomographic microscopy (SRXTM). (Scale bars=100 µm for A–D; 10 µm for E–H).
A. Polar view showing thick elaborate ornament and dense internal body. Pale line denoted by arrow indicates outline of underlying mounting medium.
B. Polar view image compiled from fewer tomographic sections than 3.6, A, and showing granular texture of inner body.
C. Equatorial view showing inner body positioned near proximal pole.
D. Equatorial view (polar section) compiled of a small number of tomographic sections showing the contrast in stature between proximal and distal ornament.
E. Enlargement of distal ornament showing sections of two adhering microspores (arrowed).
F. Enlargement of complex distal ornament and an adhering microspore (arrowed).
G. Enlargement of complex distal ornament.
H. Enlargement of the relatively flat proximal surface of megaspore in polar section. Arrows indicate margins of contact areas defined by marked changes in ornament stature.

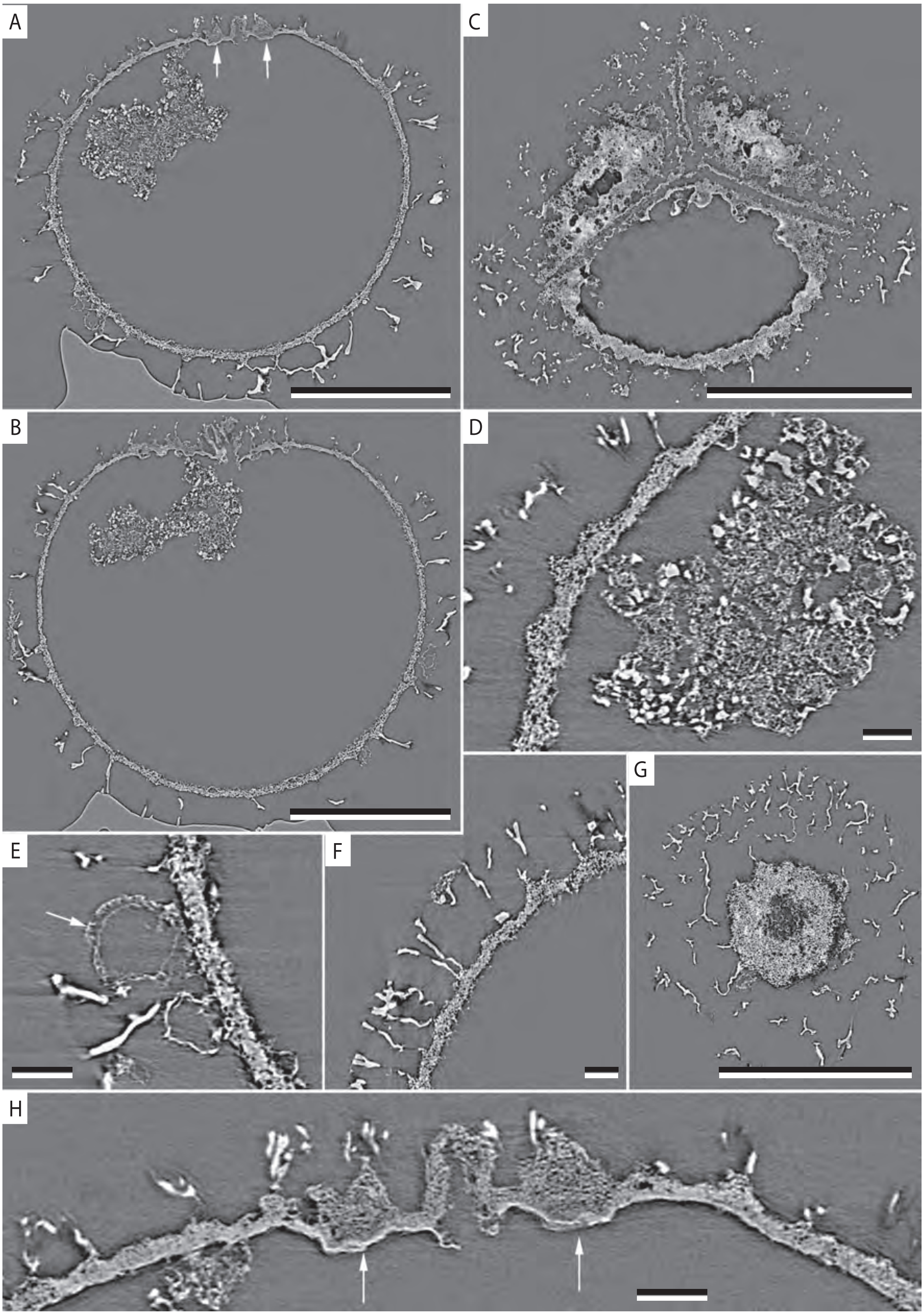


Figure 3.7

Figure 3.7 (previous page): Attenuation-based synchrotron-radiation X-ray tomographic microscopy (SRXTM) images (single sections) of *Singhisporites hystrix* sp. nov., NRMS089351. (Scale bars=100 µm for A–C, G; 10 µm for D–F, H).
A. Polar section showing small sunken pads of wall tissue supporting ornament that flank the labrae.
B. Polar section showing contrast in size of proximal (upper) versus distal (lower) ornament.
C. Transverse section roughly through the proximal surface showing well-defined labrae flanking the laesurae.
D. Polar section showing enlargement of internal granular body.
E. Enlargement of microspore (arrowed) entrapped by ornament of the distal surface.
F. Enlargement of distal spore wall showing robust branching sculptural elements.
G. Tangential section through portion of distal spore wall (central fibrous feature) surrounded by transverse sections of complex-branched distal ornament.
H. Enlargement of polar section through proximal surface showing thickened pads (supporting sculpture) immediately flanking the labrae.

3.3.4 Singhisporites mahanadiensis

Singhisporites mahanadiensis (Tewari, Mehrotra, Meena *et* Pillai) B. J. Slater, S. McLoughlin *et* J. Hilton comb. nov.

Basionym: *Ramispinatispora mahanadiensis*, Tewari, R., Mehrotra, N.C., Meena, K.L. and Pillai, S.S.K. 2009. Permian Megaspores from Kuraloi Area, Ib-River Coalfield, Mahanadi Basin, Orissa. Journal of the Geological Society of India, 74, p. 673, figure 3 (18–19).

Location, unit and age: Permian of Kuraloi area, Ib-River Coalfield, Mahanadi Basin, Orissa, India.

Remarks: It has been deemed necessary to transfer *Ramispinatispora mahanadiensis* to *Singhisporites* on the basis of Glasspool's (2003) assertion that *Ramispinatispora* is a junior synonym of *Singhisporites* based on the characters of its ornamentation.

3.3.5 Isolated fern sporangia

Alongside the megaspores recovered through bulk maceration are numerous microsporangia, these are also common in thin sections of the silicified peat material. Three distinct spore species are found occurring in situ as sporangial masses often with sporangial wall tissues preserved in varying degrees of degradation;

Horriditriletes tereteangulatus spores in situ (Figure 3.8, A–B)
Didecitriletes ericianus spores in situ (Figure 3.8, C–F)
Leiotriletes directus spores in situ (Figures 3.9, D–E; 3.10, A–E)

Remarks: While hydrated in distilled water the spore masses have an orange appearance wheras the sporangial wall has a brown colour. Some samples are relatively barren in sporangial remains whilst others are locally abundant.

Cells of the annulus are preserved in several specimens (Figures 3.8, A; 3.9, F–G), this is an adaptation developed by leptosporangiate ferns to disperse the spores through dehiscence. The orientation of the annulus cannot be conclusively identified in the specimens available, since the precise position of the stalk relative to the stomium is not visible.

Some of the sporangia are preserved in chains or clusters (Figure 3.10), and may have been borne in sori on the abaxial surface of the pinnules in life.

Several specimens exhibit signs of consumption by arthropod herbivores and also fungal saprotrophy. Thin sections show an arthropod coprolite inside a partially excavated *Leiotriletes directus* sporangium (see Chapter 4) showing the direct targeting of *L. directus* spores as a food source. In addition, many detritivore-produced coprolites in the assemblage include *Didecitriletes ericianus* and *Horriditriletes tereteangulatus* spores as a minor component (see Chapter 4).

Several sporangia also show signs of fungal attack with an abundance of fungal spores and hyphae amongst the in situ fern spores (Figures 3.9, D; 3.10, C–E). The fungal spores are 10–20 μm in diameter and dark brown in thin section.

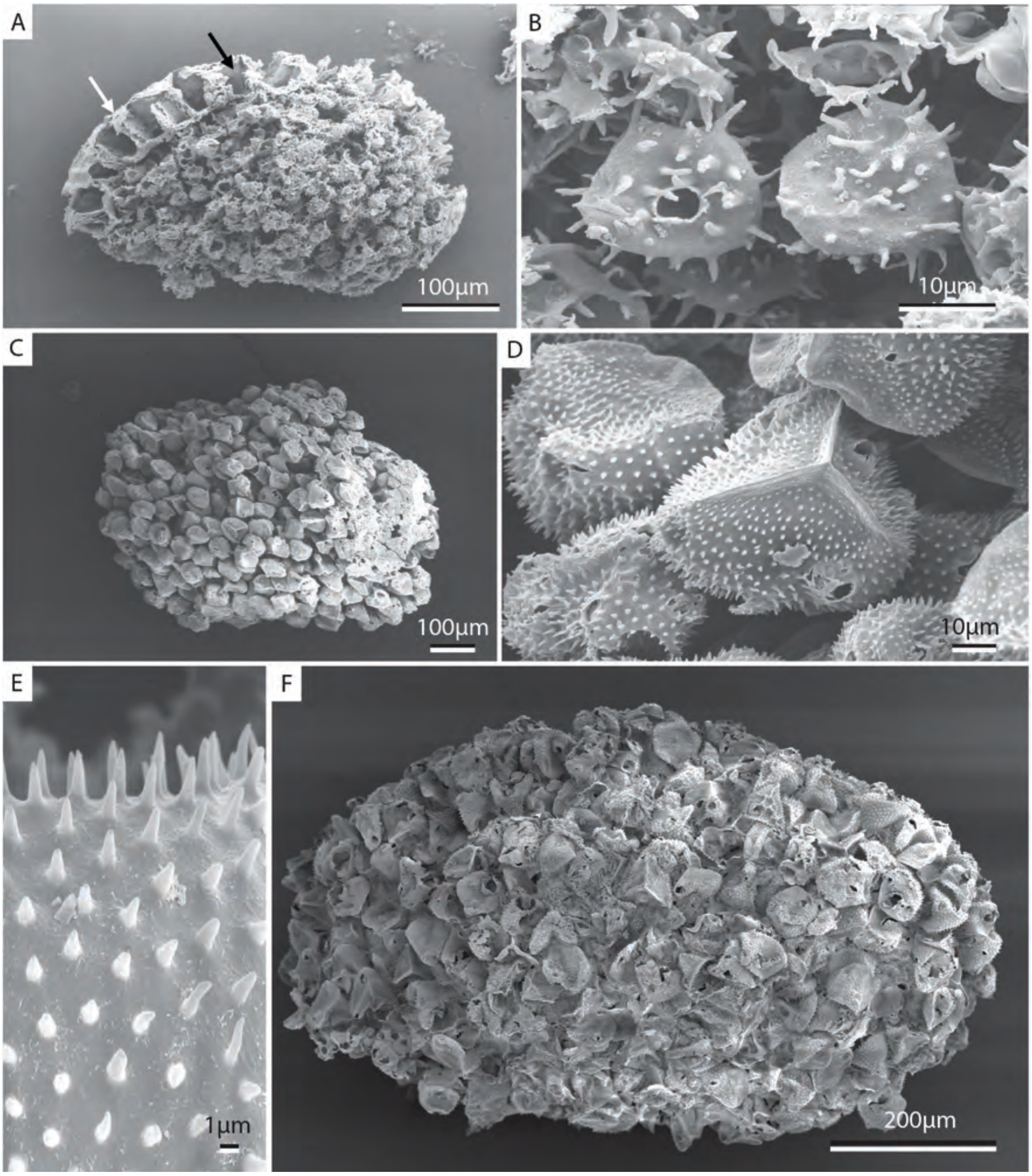


Figure 3.8: Scanning electron microscopy images of isolated fern sporangia and spores.
A. *Horriditriletes tereteangulatus* sporangium with annulus cells (white arrow) and their radial walls (black arrow) preserved, locality 8A, specimen 8A-6, film 18A-0927.
B. *Horriditriletes tereteangulatus* spores in situ, locality 8A, specimen 8A-6, film 18A-0928.
C. *Didecitriletes ericianus* sporangium, locality 9A, specimen 9A-1, film 15B-0902.
D. *Didecitriletes ericianus* spores in situ, locality 9A, specimen 9A-1, film 15B-0903.
E. Close up of densely echinate ornament of *Didecitriletes ericianus* spore, locality 9A, specimen 9A-1, film, 16A-0904.
F. *Didecitriletes ericianus* sporangium.

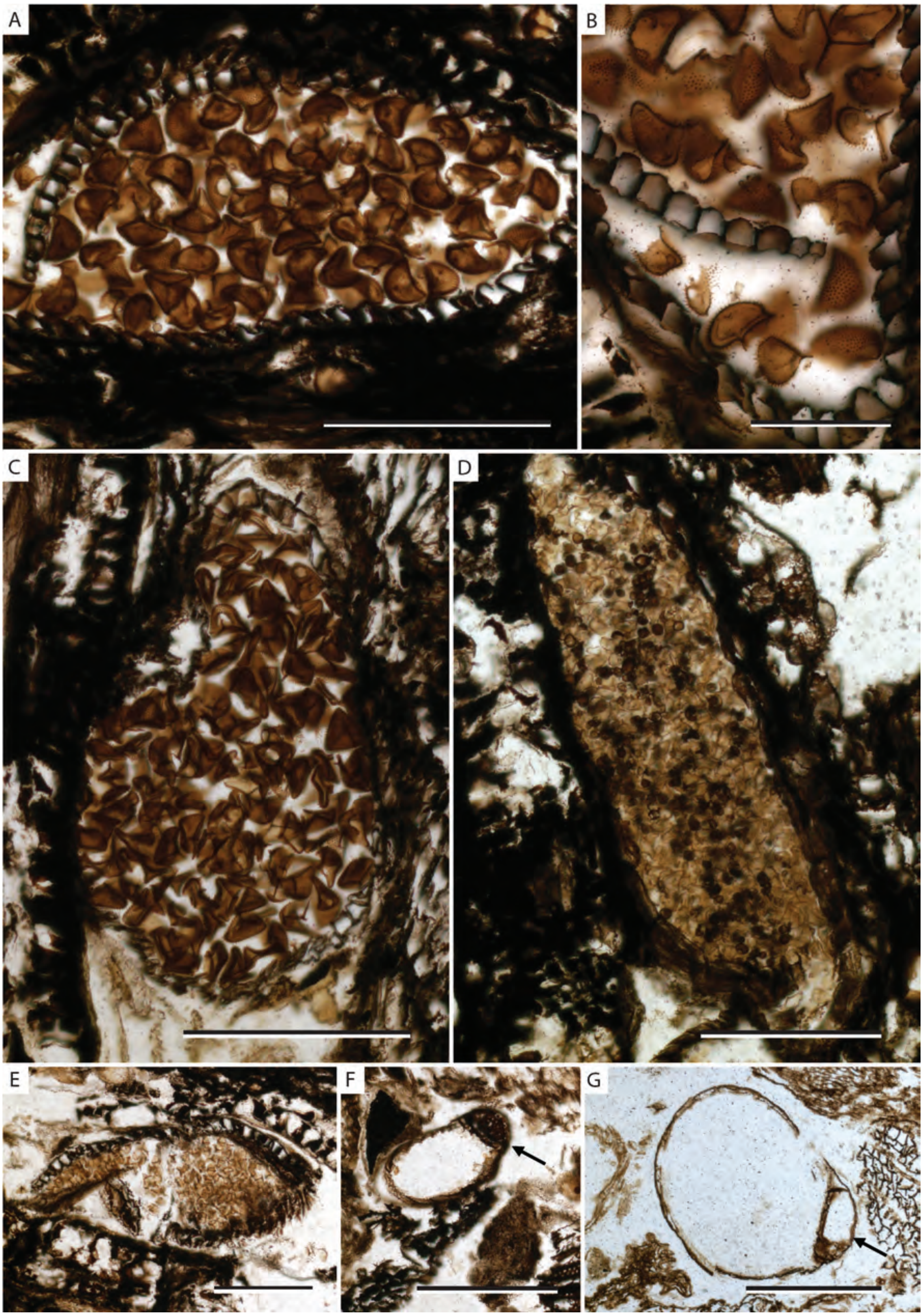


Figure 3.9

Figure 3.9 (previous page): Thin-section images of fern sporangia from the Toploje Member chert.
A. Sporangia containing *Didecitriletes ericianus* spores, scale = 250 µm.
B. Close-up of *Didecitriletes ericianus* spores shown in 3.9, A, scale = 100 µm.
C. Sporangia containing *Didecitriletes ericianus* spores, scale = 250 µm.
D. Sporangia containing *Leiotriletes directus* spores and small saprotrophic fungal spores, scale = 250 µm.
E. Sporangia containing *Leiotriletes directus* spores, scale = 250 µm.
F. Empty sporangium, black arrow indicates position of annulus in section view, scale = 250 µm.
G. Empty sporangium, black arrow indicates position of annulus in section view, scale = 250 µm.

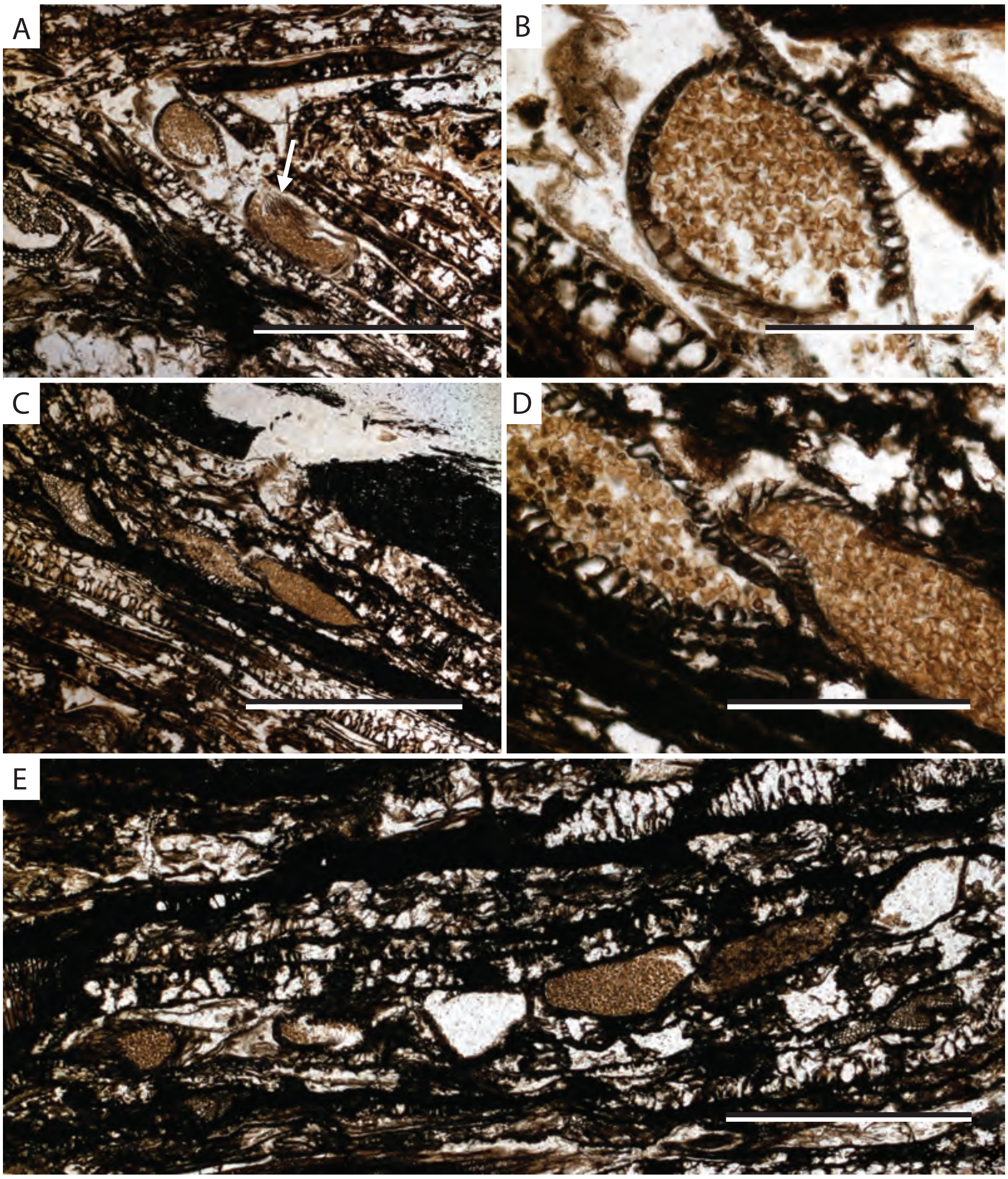
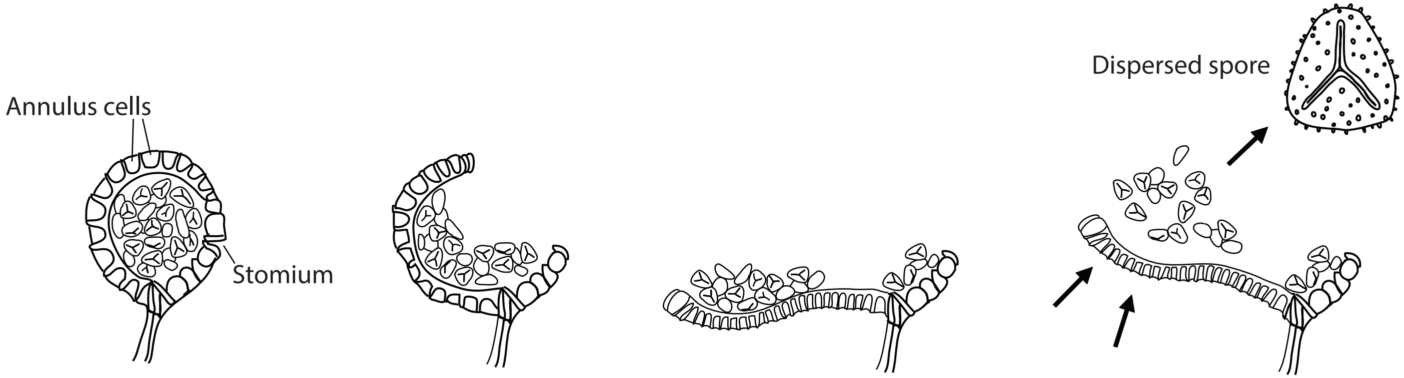


Figure 3.10: Thin-section images of fern sporangia from the Toploje Member chert.
A. Two sporangia containing *Leiotriletes directus* spores, white arrow indicates surface reticulum of capsule cells, scale = 1 mm.
B. Close-up of sporangia depicted in 3.10, A, scale = 250 µm.
C. Two sporangia containing *Leiotriletes directus* spores amongst matted *Glossopteris* leaves and charcoalified plant remains in the peat, scale = 1 mm.
D. Close-up of the two sporangia shown in 3.10, C, the sporangia on the left houses numerous fungal spores, scale = 250 µm.
E. Chain of sporangia, possibly a compressed sorus, containing *Leiotriletes directus* spores between matted leaf remains in the peat, scale = 1 mm.



In situ fern sporangium.

As water content of the annulus cells evaporates negative pressure draws radial walls closer together.

Sporangium is opened exposing the spore contents.

Cavitation bubbles formed, annulus cells expand rapidly catapulting fern spores.

Figure 3.11: Diagram showing stages of sporangial discharge of spores. Based on Noblin et al., 2012.

3.4 Discussion

Three species of lycopsid megaspore have been identified from the genera *Duosporites*, *Banksisporites* and *Singhisporites* within a single layer of Permian permineralised peat from the PCMs, Antarctica. This indicates the presence of at least three whole-plant lycopsids in the source flora (for recent synthesis see Bateman and Hilton, 2009). No previously reconstructed whole-plant lycopsids have megaspores belonging to these morphogenera so it is difficult to further evaluate their systematic position within the Lycopsida or the growth architecture of the plants that produced these megaspores (see Bateman, 1994; Bateman et al., 1992; Bateman and Hilton, 2009). The lycopsid affinity of these megaspores is based on the sculptural spines on the surfaces of the megaspores (known only from lycopsids), the wall ultrastructure and the widespread development of heterospory in this group (Pant and Mishra, 1986; Jha and Tewari, 2003; Jha et al. 2006; Tewari and Jha, 2007; Tewari et al. 2007). The lycopsids that contributed to the peats of the Bainmedart Coal Measures were probably herbaceous, since large arborescent lycopsids have not been recorded after extensive sectioning of the peats. The upper tier vegetation of the mire community was apparently dominated by glossopterid and cordaitalean gymnosperms (Holdgate et al., 2005). Apart from South Africa and South America, where some arborescent forms are known in moderate abundance in the Early Permian (Anderson and Anderson, 1985; Guerra-Sommer and Cazzulo-Klepzig, 2000), lycopsids have been considered relatively insignificant components of the high-latitude Gondwanan Permian floras (Shi et al., 2010). The apparent dearth of lycopsid macrofossils may be due to the diminutive size and fragile architecture of many lycopsids in high-latitude Gondwanan peat-forming communities. Axes and leaves of one such herbaceous lycopsid have been identified in the silicified peat of the Toploje Member (Holdgate et al., 2005) but will be more fully described elsewhere. Schwendemann et al. (2010) described another herbaceous lycopsid from Upper Permian strata of the central Transantarctic Mountains, and Townrow (1968) described a small selaginellalean plant from the Late Permian of eastern Australia. Dispersed lycopsid megaspores have been widely reported from Permian Gondwanan strata and assigned to several dozen species. Collectively, these data suggest that heterosporous lycopsids were widespread but cryptic and not necessarily uncommon ground-storey elements of the Permian vegetation of Gondwana in some habitats.

Synchrotron-based x-ray tomography currently reveals architectural features with a resolution similar to or slightly lower than that obtainable from SEM. The shape and distribution of sculptural elements are well resolved. Details of the spore wall structure (Figure 3.6, E, F, H; Figure 3.7, D–H) are slightly less clear than achievable with TEM. The advantage of the former technique is that internal architecture is discernable without the need to break or section the specimen. Further, SEM can later be undertaken on the same specimen to obtain high resolution images of the outer surface morphology if necessary. With anticipated improvements in resolution to nanometre range, x-ray tomography is likely to become an increasingly valuable analytical tool for precision palyno-taxonomic studies.

3.4.1 Reproductive biology

Megaspores are generally considered to have lesser dispersive potential in comparison to microspores due to their larger size and production in smaller numbers (Bateman and DiMichele, 1994; Playford and Dettmann, 1996). The branched ornamentation of *Singhisporites hystrix*, apart from facilitating entrapment of microspores, might also have aided hydrochory (flotation in water), thus promoting wider dispersal (Tewari et al., 2009). This might explain the higher abundance of *S. hystrix* within the peat layer in comparison to other megaspore taxa. The trilete microspores found adhering sporadically to the *S. hystrix* ornamentation are all of one kind and are likely to be biologically affiliated with the megaspore since they were found attached only to that species. Pant and Mishra (1986) noted microspores entrapped within the extended ornamentation of specimens of '*Mammilaespora grandis*' (now *Singhisporites grandis;* see Glasspool, 2000, 2003) and '*Ramispinatispora nautiyalii*' (now *Singhisporites nautiyalii;* see Glasspool, 2000, 2003), and concluded that long elaborate sculptural elements may serve to trap affiliated microspores, improving the chances of fertilisation. The ornamentation of *S. grandis* and *S. nautiyalii* is similar to that of *S. hystrix*, indicating this strategy of microspore entrapment to be common within the genus where it presumably reflects a selective advantage for reproduction in water and retention of the microspore on the megaspore.

3.4.2 Fern sporangia

Three different morphotypes of sporangia containing three different sporomorph species appear in the peats, which in life would have related to three distinct parent plants. Due to the varying states of degradation of the sporangia it is difficult to confidently ascribe an affinity to these specimens. The sporangia containing *Leiotriletes* spores are pear-shaped to teardrop-shaped, whereas those bearing *Horriditriletes* or *Didecitriletes* are ovoid. In terms of functional morphology, both thin sections and SEM images of the sporangia reveal a row of specialised cells, which are larger than the rest of the sporangial wall cells (Figures 3.8, A; 3.9, F–G). These make up the annulus of the sporangium, which is a biomechanical adaptation developed by leptosporangiate ferns to disperse the spores (Noblin et al., 2012). The annulus functions as a desiccation and cavitation activated mechanism where drying out of the sporangia would have resulted in the annulus cells deforming the overall shape of the sporangia before bursting open at the stomium and exposing the spores (Figure 3.11). The increased pressure that builds up in the annulus cells as they compress then produces cavitation bubbles, which at a certain pressure induce a catapulting effect in the sporangium, which consequently discharges the contents of the sporangia away from the parent plant for subsequent dispersal by wind and water (Noblin et al., 2012). The overall morphology of the sporangia most closely resembles those of the Botryopteridaceae, a widespread Palaeozoic group of filicalean ferns known largely from Mississipian, Pennsylvanian and Permian sediments of Laurasia but also from the Permian of Gondwana including the genus *Botryopteris* (Barthel, 1976; Rothwell, 1991; Rothwell and Good, 2000; Rößler and Galtier, 2003). *Botryopteris* possesses similar teardrop-shaped annulate sporangia that are borne in sori on the abaxial surface of the pinnule as appears to be the case with the sporangia seen in thin sections of the Toploje Member chert (Scott, 1910; Good, 1979, 1981; Rothwell, 1991; Rothwell and Good, 2000; Rößler and Galtier, 2003). In addition, *Botryopteris* sporangia are known to contain *Leiotriletes* type and spinose to verrucate tetrahedral spores in common with the sporangia preserved in the Toploje Member chert (Good, 1979; Thomas and Taylor, 1993).

The lack of foliage or stems is puzzling considering the preservation of abundant pteridophyte spores and entire sporangia. A similar pattern is known from other deposits such as the Permian permineralised peats of the Bowen Basin in Australia where fern spores are common even in the absence of the rest of the plant (McLoughlin, 1993). *Neomariopteris* and *Dichotomopteris* occur in the Permian macroflora of the Bowen Basin in Australia but aside from these forms there are very few other macrofloral remains known despite the high diversity of dispersed spores (Balme and Hennelly, 1956; Gould, 1970; Foster, 1979; Gilby and Foster, 1988; McLoughlin 1993). It has been suggested that the ferns in those palaeocommunities were either growing in erosional environments not conducive to the preservation of their delicate tissues or that an epiphytic habit was common, which prevented many of the fern components from being incorporated into the macrofossil assemblage (McLoughlin, 1993), since epiphytic ferns have a poor fossilisation potential (Dubuisson et al., 2009). It is plausible that a similar situation may be responsible for the pattern seen in the Toploje Member chert. The best known phorophyte from the Palaeozoic is the Pennsylvanian and Permian *Psaronius* tree-fern (Rößler, 2000; Rößler and Galtier, 2003). A range of plants were shown to grow amongst the large root-mantles of the Late Pennsylvanian and Permian *Psaronius*, including small epiphytic ferns (*Tubicaulis* sp.) and the axes of climbing ferns (*Ankyropteris brongniartii*), which used the trunk for support (Rößler, 2000). A similar pattern is seen in association with modern tree-fern species such as *Dicksonia squarrosa* and *Dicksonia antarctica* where other tree species, epiphytic and primary hemiepiphytic seedlings establish in the root mantles or fallen trunks, which offer protection (Gaxiola et al., 2008). Several species of Carboniferous and Permian *Botryopteris* are known to be epiphytes that rooted within the trunks of *Psaronius*, and also *Grammatopteris* tree ferns in the Permian of Gondwana (Rothwell, 1991; Rößler and Galtier, 2003). *Sonapteris* from the Pennsylvanian of the Czech Republic is another fern of the Botryopteridaceae that is thought to have been a trunk epiphyte of *Psaronius* (Pšenička et al., 2005). The sporangia of the Toploje Member chert closely resemble those borne by the *Botryopteris* whole-plant, therefore there is the possibility of the *Glossopteris* tree acting as a phorophyte in an analogous situation to the *Psaronius* tree-fern. Epiphytic and hemiepiphytic ferns are common in modern environments with low disturbance levels (Watkins Jr. et al., 2007) and in the tropics up to two thirds of the fern species may be epiphytes in a given area

(Kress, 1986; Schuettpelz, 2007). Leptosporangiate ferns are by far the most diverse extant fern group, nearly a third of which are obligate or habitual epiphytes (Schuettpelz, 2007).

When the constituents of the peat of the Toploje Member chert are considered, it is primarily the ground-level and soil profile elements that are being preserved alongside whatever plant elements have rained down from the arboreal environment such as the matted leaf deposits of *Glossopteris* and *Noeggerathiopsis* (Holdgate et al., 2005; Slater et al., 2012; see Chapter 6). When compared to the Homevale silicified peats of the Bowen Basin in Australia it is clear that a much higher proportion of the peat preserved in the Toploje Member chert consists of the *Vertebraria* root tissues of the *Glossopteris* plant. The *Vertebraria* rooting systems are proportionally rarer in the Homevale silicified peats but form the highest proportion of the Toploje Member chert constituents (Gould and Delevoryas, 1977; Nishida et al., 2007; Holdgate et al., 2005; see Chapter 6), this may go some way to explaining an organographic bias against canopy elements such as epiphytes. Epiphytes usually require moist environments and are today most speciose in the tropics (Dubuisson et al., 2009; Schuettpelz, 2007) and abundant in temperate rainforests where rainfall levels are high or around the margins of waterfalls (strictly: epipetric) where a permanent spray of moisture is maintained (Dubuisson et al., 2003). Epiphytic ferns appear to have undergone a large radiation during the Cretaceous in association with angiosperms (Schneider et al., 2004; Shuettpelz and Pryer, 2009; Schneider and Kenrick, 2001; Watkins Jr. and Cardelús, 2012) and this continued into the Cenozoic, the majority of fern biomass in modern tropical forests can be locked in the diverse array of canopy-dwelling epiphytes (Benzing, 1990; Watkins Jr. and Cardelús, 2012). This radiation associated with angiosperms may have been driven by the moist environments created by high levels of evapotranspiration in angiosperm forests alongside new shade-tolerance adaptations in ferns (Schneider et al., 2004; Shuettpelz and Pryer, 2009).

Alternatively the apparent dearth of foliage or stem tissue of ferns in the Toploje Member peats may be attributable to other forms of taphonomic bias; it is possible the ferns were growing in an adjacent environment where larger vegetation sheltered the understory vegetation from the wind which could conceivably prevent much of the foliage and stems from being blown into waterlogged areas where it would preserve, whereas the spores and sporangia would still disperse following dehiscence (Collinson, 1978). The durability of the foliage may also be an issue for preservation, however many other delicate plant remains are well represented in the peats. A single fern can also produce many sporangia and spores which are naturally shed in contrast to the other elements of the parent plant, so it should be expected to find these elements in greater abundance. Another possible taphonomic filter would be the preferential removal of the foliage and other tissues by invertebrate herbivory and/or fungal decomposition before incorporation into the peat profile. This is a possibility considering that arthropod grazing was intense in this palaeoecosystem (McLoughlin et al., 2011; Slater et al., 2012; see Chapter 4), and evidence of arthropod exploitation of the fern sporangia (see Chapter 4) and fungal attack (Figures 3.9, D; 3.10, C–E) is also preserved.

3.4.3 Taphonomy

Whereas Late Permian peats from the central Transantarctic Mountains appear to represent small lenses or rafted (allochthonous) wedges of peat (Taylor et al., 1989), the Middle Permian example in the PCMs represents a peat mire community preserved *in situ* that extends as a single layer exposed over several kilometres along strike (Fielding and Webb, 1996). Beyond this, little detailed work has yet been undertaken on the floristic composition or taphonomic history of the Toploje Member silicified peat. The silicified peat layer represents the autochthonous and hypautochthonous remains of a Permian glossopterid-dominated mire flora, from which Holdgate et al. (2005) illustrated its major biotic components and outlined the relative proportions of plant organs within the deposit. Lycopsids represented <0.1% of the peat constituents by volume. Understanding the formation of this organic deposit has importance since it provides an *in situ* window into the ecology of these southern high latitude mire communities and permits confident biological attribution and quantification of isolated remains in the widespread and economically important Permian Gondwanan coals that are otherwise interpreted from strongly altered (chemically and structurally) coal macerals.

The megaspores described here are very well preserved. The apparently rapid silicification process has largely prevented compression of the megaspores so they retain their original three-dimensional structure. There is also little evident damage to the megaspore structure through pyrite crystal growth that commonly reduces the quality of preservation. Many similar deposits of silicified plant remains are associated with hydrothermal activity (surficial hot springs) where organic remains are permineralised through silica ions attaching to free hydrogen bonds in the partially degraded plant tissues and thence via infilling of pore spaces by additional precipitation of silica from solution (Jefferson, 1987; Channing and Edwards, 2009). Examples of this include the Devonian Rhynie Chert in Aberdeenshire, Scotland (Trewin, 2003), the yet to be located lagerstätte of Early Mississippian to Middle Pennsylvanian age that has yielded *ex situ* chert nodules on the Yorkshire coastline (Stevens et al., 2010; Womack et al., 2012), and from the Late Jurassic San Agustín Farm Lagerstätten from the Deseado Massif in Patagonia, Argentina (Guido et al., 2010). The formation of algal mats and resultant changes in in pH conditions of lacustrine or lagoonal environments has also been highlighted as a potential mechanism for silicification (Falcon-lang et al., 2011a; Francis, 1984). However, substantial quantities of algal palynomorphs have not yet been identified in the PCM deposits (McLoughlin et al., 1997; Lindström and McLoughlin, 2007). Other sites preserve permineralised plant remains in volcaniclastic sediments where abundant silica is available from the breakdown of volcanic glass and unstable silicates. Examples of this type of silicification include the Cerro Cuadrado fossil forest in Patagonia (Stockey, 1975), the *Glossopteris*-bearing permineralised peat of the Fort Cooper Coal Measures, northeastern Australia (Gould and Delevoryas, 1977) and the Grand-Croix permineralised plants from central France (Galtier, 2008). Since no volcanigenic sediments are associated with the silicified peat deposit in the PCMs, an alternative mechanism must explain their preservation. The overlying lacustrine sediments of the Dragons Teeth Member (Fielding and Webb, 1996), which cap the silicified peats, indicate the presence of a persistent lake environment that may have experienced fluctuating alkalinity due to strong seasonality at high latitudes during the Permian. This could have created conditions of varying silica solubility within the lake waters, and resulted in siliceous envelopment of the detritus on the lake floor (Stigall et al., 2008), although such radical seasonal swings in alkalinity are typically associated with semi-arid environments, both modern (Hesse, 1989) and ancient (Wheeler and Textoris, 1978). Fluctuating alkalinity has been shown to be an important factor in modern siliceous preservation of marsh plants surrounding hot springs at Yellowstone National Park in Wyoming, USA (Channing and Edwards, 2009). The silicification evident in Jurassic high-latitude lacustrine sediments of Antarctica from the Kirkpatric Basalt has been attributed to microbial mat induced silicification (Stigall et al., 2008), and may have parallels to the conditions operating in the PCMs, although microbial laminae have not been detected in the latter deposits.

3.4.4 Palaeobiogeography

The central position of Antarctica within Gondwana during the Permian endows it with a pivotal role in understanding the relationships between the dispersed Gondwanan biotas (Ryberg, 2010). The PCM permineralised peat represents the remains of southern high-latitude forest mires. Palaeogeographic reconstructions place the Lambert Graben (in which the Bainmedart Coal Measures were deposited) adjacent to the Mahanadi Graben in India prior to the breakup of Gondwana (Fedorov et al., 1982; Stagg, 1985; Veevers, 2004; Bogor, 2011), although there is also an alternative case for the Godavari Graben being positioned adjacent to the Lambert Graben based on similarities in coal deposits (Holdgate et al., 2005). Previous studies of the Permian megaspore assemblages from the Mahanadi Graben have uncovered the genera *Singhisporites* and *Banksisporites* in common with the PCM silicified peat, suggesting a strong phytogeographic link. However, both of these genera are also reported from sediments of the Godavari Graben (Tewari and Jha, 2007).

3.5 Summary of findings

1. Three species of dispersed megaspore have been identified from the Permian flora of the PCMs (*Singhisporites hystrix* sp. nov., *Duosporites lambertensis* sp. nov. and *Banksisporites antarcticus* sp. nov.). These indicate the presence of at least three whole-plant species of presumably herbaceous heterosporous lycopsid.
2. Microspores of *Lundbladispora* sp. adhering to the ornament of *Singhisporites hystrix* are interpreted as the microspores of the same whole-plant species, with this tendency for entrapped microspores within the ornament of the megaspore being common within the genus and presumably part of its reproductive strategy.

3. This pioneering attempt at x-ray tomography of megaspores has demonstrated that internal features such as sunken exinal thickenings flanking the labrae can be observed that would otherwise be missed in SEM images of the external surface. Another advantage of using synchrotron tomography is that the specimens can be removed following the procedure and then be studied using SEM at a later time.

4. Dispersed microsporangia disclose the presence of at least three distinct fern taxa within the immediate/local palaeoecosystem. The discrepancy between the relative abundance of isolated sporangia and the dearth of preserved stem or foliage tissues of any associated fern producers implies the action of a taphonomic filter controlling which constituents were finally incorporated into the peats. This may infer that the ferns were growing in an adjacent coeval environment, the plants themselves were rarely incorporated into the peats perhaps by virtue of an epiphytic habit or they were subject to intense herbivory or degradation.

5. The unusual taphonomic conditions resulting in early silicification of this *in situ* peat layer in the PCMs has preserved the megaspores in an excellent condition, devoid of compression and free from pyritisation. The absence of volcanogenic features lends support to a model of silicification based on seasonal fluctuations in the alkalinity of lake waters that subsequently covered the peats.

6. Previous palaeogeographic reconstructions that place the Indian Mahanadi Graben adjacent to the Lambert Graben of Antarctica during the Middle Permian are here supported by the identification of shared megaspore genera.

CHAPTER 4: ANIMAL-PLANT INTERACTIONS IN A MIDDLE PERMIAN PERMINERALISED PEAT OF THE BAINMEDART COAL MEASURES, PRINCE CHARLES MOUNTAINS, ANTARCTICA

4.1 Background

The first terrestrial arthropods of the early to mid-Palaeozoic appear to have been mostly predators and detritivores based on mouthpart morphology and early coprolite evidence (Jeram et al., 1990; Labandeira and Beall, 1990) although recent evidence suggests the targeting of nutritious sporangial contents by the late Silurian (Edwards et al., 1995; Hagström and Mehlqvist, 2012). However, it is not until the accumulation of silicified wetland deposits of the Rhynie Chert in the Early Devonian that a more detailed picture of early invertebrate-plant interactions can be gathered (Labandeira, 2007) based upon multiple forms of coprolites, plant tissue damage and animal body fossils. Assessment of various categories of herbivory in the fossil record via plant tissue damage, coprolites or gut contents is an important tool for understanding the evolution of feeding traits, trophic complexity and the evolution of the terrestrial biosphere in general (Habgood et al., 2004). Further, fossil evidence of diagnostic plant-animal interactions can reveal the presence of animal groups that are not preserved as body fossils. Where preserved, coprolites can be used to identify the range of feeding guilds represented in a palaeoecosystem, and although many examples cannot be matched conclusively to a producer, they betray the presence of particular guilds of herbivores and selective tissue consumption in the community (Chaloner et al., 1991; Habgood et al., 2004; Labandeira, 2007).

This study focuses on an exceptionally well preserved silicified peat from the Middle Permian of the Prince Charles Mountains (PCMs) in East Antarctica. The community that formed the peats is a low-diversity wetland ecosystem dominated by woody glossopterid and cordaitalean gymnosperms, with lesser proportions of herbaceous lycopsids and ferns (McLoughlin and Drinnan, 1996; Holdgate et al., 2005; Slater et al., 2011). Little information is currently available on the entomofauna associated with the Permian vegetation of the PCMs. Previous work on the silicified peat deposit in the PCMs has identified coprolites within *Australoxylon* (glossopterid or cordaitalean) wood (Weaver et al., 1997) and sparse invertebrate exoskeleton fragments have been recovered from bulk maceration of Permian and Triassic sediments overlying the silicified peat (McLoughlin et al., 1997; Holdgate et al., 2005). Glossopterid or cordaitalean wood from the silicified peats commonly displays signs of intense attack from phytophagous invertebrates in the form of spindle-shaped excavations in the latewood of successive growth rings. Coprolites found within these regular cavities attest to their excavation by arthropods rather than pocket-rot fungi (Weaver et al., 1997). Cavities generated by pocket rot are also present within the woods but are less regularly constrained to the latewood and are more variable in size and shape. Similar cavities in trunk wood from the Permian and Triassic of the Central Transantarctic Mountains are interpreted to have been produced by oribatid mites (Kellogg and Taylor, 2004). Weaver et al. (1997) suggested that the seasonal cyclicity evident in the pattern of attack on the PCM trunk wood was attributable to either mites or the overwintering larvae of coleopterans that fed either directly on the wood or on fungi that was in turn feeding upon the wood in a possible arthropod-fungal symbiotic relationship (the arthropod obtaining food and in turn dispersing the fungi between plants). A three-way (plant-fungal-arthropod) symbiosis, whereby the fungus returned essential micronutrients and other compounds to the host plant also cannot be excluded, though the similarity of fungal-induced cavities in *Australoxylon* to modern white pocket rot suggests that the fungi's relationship to the host plant was primarily saprotrophic.

Coprolites dispersed within the peat matrix contain identifiable pollen and represent the earliest examples of arthropod pollenivory from Antarctica (Holdgate et al., 2005). Pollenivory has been reported from other deposits of Permian age, such as the Lower Permian of the Ural Mountains, Russia (Krassilov and Rasnitsyn, 1996; Novokshonov, 1998; Labandeira, 2000), and evidence for related sporivory extends back to the rise of the vascular plants in the late Silurian (Habgood et al., 2004; Labandeira, 2007; Hagström and Mehlqvist, 2012). Late Palaeozoic coprolite evidence for the consumption of entire sporangia by arthropods has also been reported from the Northern Hemisphere (Meyen, 1984; Rothwell and Scott, 1988).

Elsewhere in Gondwana there is a broad range of evidence for arthropod attack upon Permian plants (McLoughlin, 1994a, 1994b, 2011a). *Glossopteris* floras of the same age as this study (Guadalupian) from the La Golondrina Formation, Santa Cruz province, Argentina, have been shown to contain a diverse array of arthropod-plant interactions (Cariglino and Gutiérrez, 2011). Localities such as Clouston Farm and Wapadsberg Pass in the Karoo Basin, South Africa (Prevec et al., 2009, 2010), the Newcastle Coal Measure insect beds at Belmont, Sydney Basin, Australia (Beattie, 2007), the Rangal Coal Measures and stratigraphic equivalents of the Bowen Basin, Australia (McLoughlin, 1994a, 1994b, 2011), the Damodar Valley basins and Rajmahal Basin, India (Banerji and Bera, 1998; Banerji, 2004; Srivastava and Agnihotri, 2011), the San Ignacio Formation of the Andean Cordillera, Argentina (Césari et al., 2012), and the Rio Bonito Formation, Parana Basin, Brazil (Adami-Rodriguez et al., 2004a, 2004b; Pinheiro et al., 2012a, 2012b), all preserve diverse traces of phytophagous arthropod behaviour in their fossil floras. Thus far, most evidence of arthropod-plant interactions in the Gondwanan Permian has been associated with the dominant plant group (glossopterids), although a few studies have reported oviposition scars on equisetaleans (Beattie, 2007), and borings within the wood and surface and margin feeding traces on the leaves of cordaitaleans (*Noeggerathiopsis*: Adami-Rodriguez et al., 2004a, 2004b; Srivastava and Agnihotri, 2011, Pinheiro et al., 2012a, 2012b; Césari et al., 2012).

Despite the records listed above, relatively little is known about arthropod-plant interactions in the Permian compared to the Cretaceous and Cenozoic. Coprolites containing histologically identifiable plant tissues have been found within permineralised stems of *Psaronius housuoensis* from the Late Permian of southwest China (D'Rozario et al., 2011a) and coprolites were also reported to occur in Permian gymnospermous wood (Feng et al., 2010), stems and rachises (Seyfullah et al., 2009) and ovules (Hilton et al., 2002) from North China. Coprolites have also been documented in root mantles of Early Permian *Psaronius* and their associated fern and pteridosperm epiphytes from Germany, in the same assemblage as *Arthropitys*-type calamitalean wood with arthropod borings (Rössler, 2000, 2006).

Insects such as archostematan Coleoptera, or their immediate precursors, were likely interacting with wood in a variety of states of decay by Permian times, including as endophytic cambial feeders (Weaver et al., 1997; Ponomarenko and Mostovski, 2005). Another group of insects that may have significantly interacted with plants, the Mecoptera (or Scorpionflies), appear in the fossil record at the start of the Permian (Novokshonov, 1997, 2004). Although modern Scorpionflies are predominantly predators and scavengers, the group was much more diverse in the past and recent studies have suggested that some early Mecoptera with long-proboscid mouthparts may have been active in the pollination of gymnosperms prior to the appearance of other insect groups (Labandeira and Sepkoski Jr., 1993; Labandeira, 1994; Ollerton and Coulthard, 2009; Ren et al., 2009). Primitive Mecoptera are well represented in the Belmont insect beds of the Newcastle Coal Measures (Lopingian), Australia (Shi et al., 2010), and may have been pollenivorous, feeding upon microsporangiate *Glossopteris* reproductive structures, with which they co-occur (Tillyard, 1922; Beattie, 2007). Protomecopterids, which are an early group of caddisflies that closely resemble Scorpionflies, are also common in Permian deposits and have been reported from Lopingian *Glossopteris*-rich deposits of South Africa, although this lineage possessed mandibulate mouthparts so would likely have fed on particulate matter rather than nectar (Sukatsheva et al., 2007). Such potential relationships between early Mecoptera and glossopterids within Labandeira's (2006a) Herbivore Expansion Phase 2 may have been the precursors to more complex interactions between arthropods and plants in the early Mesozoic (Herbivore Expansion Phase 3), which highlights the importance of investigations into the entomofauna of glossopterid-bearing deposits such as those of the PCM silicified peats.

4.2 Materials and methods

A range of techniques were employed to study the coprolite content of the PCM permineralised peats. Serial cellulose acetate peels were prepared from the cut silica-permineralised peat blocks following the technique described by Galtier and Phillips (1999). Around 50 silicified peat blocks were cut using a fine bladed Buehler Isomet 5000 linear precision saw then the cut surface was polished and etched in a shallow bath of cold 30% hydrofluoric acid for around 90 seconds so that the organic contents stand above the surface. The acid-etched blocks were then rinsed in water, dried and bonded to cellulose acetate sheets of 50 μm thickness using acetone as a solvent. After drying, the acetate sheets were peeled from the surface of the blocks and portions of the sheets were removed for examination with a transmitted light microscope. Blocks that were discovered to contain coprolites and other evidence of animal-plant interactions were then thin-sectioned to extract better quality anatomical details via light microscopy. An arbitrary selection of 24 additional samples of silicified peat from a series of localities along the exposure were bulk macerated in cold 30% HF solution for two weeks and the residue was then recovered from the HF solution using a 150 micron sieve. The recovered organic debris was then placed in distilled water in a petri dish for examination using an optical stereomicroscope; individual coprolites were picked with a fine artist's brush while hydrated. Individual coprolites were then mounted on aluminium stubs, coated with gold and imaged with the use of a Hitachi S-4300 field emission scanning electron microscope at the Swedish Museum of Natural History. Images were processed and plates compiled using Adobe Photoshop and Illustrator CS4 graphics packages. Terminology used to describe the coprolites follows that of Habgood et al. (2004) where possible.

4.3 Results

Nine distinct coprolite morphotypes are recognized within the silicified peat bed at the top of the Toploje Member on the basis of shape, size, texture and contents. Coprolites occur both isolated within the peat matix and clustered within excavations in a range of plant tissues. Bulk maceration of the peat revealed two size categories [small (Figure 4.1, A–D; Figure 4.2, A–C) and large (Figure 4.2, D)] of isolated coprolites with variable contents. Other forms recovered from bulk macerations included coprolites with coarse plant contents (Figure 4.1, E), spirally ornamented coprolites (Figure 4.3, A), and coprolites containing specifically identifiable contents including leaf trichomes (Figure 4.3, B), leaf cuticle fragments (Figure 4.3, C), pollen remains (Figure 4.3, D) and fern sporangia (Figure 4.3, E). Further categories of coprolites recognized in thin-sections of the peats, include irregular forms containing platy cell wall fragments inside *Glossopteris* leaves (Figure 4.4, A–D), an ellipsoidal morphotype within a fern sporangium (Figure 4.4, E), large isolated coprolites between matted leaves (Figure 4.4, F), clustered forms filling excavations inside *Vertebraria* and *Australoxylon* wood (Figure 4.5, A–F), forms with coarse indeterminate constituents (Figure 4.6, A–B) and others with fungal contents (Figure 4.6, C–D).

4.3.1 Coprolites in Vertebraria and Australoxylon

Description

The coprolites occurring within the secondary wood of *Vertebraria* and *Australoxylon* fall within the smaller size range of the PCM morphotypes. Two sub-categories are recognized: a darker brown form averaging 120 µm long and 115 µm wide (50 specimens measured); and a lighter brown form averaging 150 µm long and 125 µm wide (50 specimens measured). The individual coprolites are ovoid, conoid or equant in shape, the long axis never reaching twice the length of the shortest axis. The termini are typically broadly rounded in both sub-categories. The margins of each coprolite are smooth; the surface consisting of densely compacted fine lignified debris. One sub-category has contents that are a darker brown than the surrounding plant tissues, and the second has a light brown colour roughly equivalent to that of the surrounding wood.

The coprolites are relatively homogeneous, being composed primarily of small angular tracheid wall fragments that have a platy appearance in less densely compacted forms. A minority of coprolites within the excavations are composed entirely of broken fungal sporangia but these are described as a separate category (see section 4.6).

The coprolites in *Vertebraria* and *Australoxylon* occur in clusters of variable numbers (Figure 4.5, A–F). The clusters can be spread diffusely or grouped densely. They are found in a range of short, discontinuous galleries within the secondary xylem and within chambers excavated within the parenchyma of young roots. The same coprolite morphotype also occurs dispersed between matted leaves of the peat profile in some samples. This category of coprolite is by far the most abundant in the peat, with some thin-sections containing >1000 examples.

Remarks

These are the first coprolites to be recorded in the root system of glossopterids. No differences are evident between the coprolites in *Australoxylon* (trunk wood) and *Vertebraria* (root wood). The colour difference evident within the assemblage may simply relate to the density of the compacted contents because other morphological and compositional characters are identical. The excavations and coprolites collectively fall within Zherikhin's (2003) ichnofossil category xylichnia. The morphology of these coprolites suggests production by oribatid mites (Labandeira et al., 1997). This coprolite morphotype has sharper margins and occurs in less continuous excavations than those attributed to *Anobium* sp. (common name 'death-watch beetles': Coleoptera) in Neogene angiosperm wood (Selmeier, 2005). They are slightly smaller, more regularly shaped and occur in narrower, less continuous excavations than pellets attributed to Cerambycidae (Coleoptera) from the Middle Jurassic of Argentina (García-Massini et al., 2012a). The producers and palaeoecological significance of these coprolites are considered in more detail below (section 4.4.3).

4.3.2 Coprolites in leaves

Description

These coprolites are 200–550 μm long and 120–250 μm wide. The length exceeds the width in most cases although some are equidimensional. The majority of the coprolites are elongate and flattened, although a small proportion (ca 20%) are equidimensional. The termini of the coprolites are sub-rounded to angular. The margins of the coprolite are more or less smooth when observed in thin-section, although angular corners and extensions are locally developed (possibly as a post-depositional, compactional, artefact). In thin-section, the coprolites are light brown. They consist entirely of densely packed fragments of leaf mesophyll cell walls.

This coprolite morphotype occurs only within chambers excavated between the anastomosing veins of *Glossopteris* leaves (Figure 4.4, A–D). In slides that are rich in leaf remains, these coprolites are relatively common, but they have not been recognized dispersed within the peat matrix.

Remarks

The occurrence of this morphotype is consistent with either detritivory or arthropod leaf mining. The cavities are positioned where leaf mining would be expected (consistently between the leaf secondary veins), however, it is inherently difficult to recognize bona fide leaf mining within permineralised material as opposed to leaf compressions where features such as an oviposition site, frass trail, and reaction tissue lining the excavation can be detected. The earliest confirmed record of leaf mining in the fossil record appears at the P-Tr boundary (Krassilov and Karasev, 2008). If the cavities and coprolites within the Antarctic leaves are a result of leaf mining, they would represent the first confident example of this feeding strategy within *Glossopteris* leaves and one of the oldest records of leaf mining in the fossil record (Chaloner et al., 1991). A few putative cases of leaf mining have previously been illustrated in *Glossopteris* (Gallego et al., 2003; Prevec et al., 2009; Pinheiro et al., 2012a, 2012b) but incontrovertible examples are lacking thus far.

4.3.3 Coprolite within sporangium

Description

A single identified example of a coprolite within a fern sporangium is 500 µm long and 300 µm wide (Figure 4.4, E). The coprolite is ovoid with broadly rounded termini. The margins (surface) of the coprolite are slightly uneven. The coprolite is dark brown in thin-section. It consists of coarse fragments of degraded spores. The coprolite occurs within the cavity of a partially excavated fern sporangium (Figure 4.4, E). The sporangium still retains some intact fern spores attributable to *Leiotriletes directus* Balme and Hennelly.

Remarks

This rare morphotype constitutes direct evidence of arthropods targeting sporangia as a food source. Although this feeding strategy has not been recorded previously from Gondwanan Permian floras, the record of palynophagy in general extends back to at least the late Silurian (Labandeira, 2007; Hagström and Mehlqvist, 2012). Trigonotarbid remains found within sporangia in the Lower Devonian Rhynie Chert have been suggested to be either feeding on the spores themselves or preying upon mites that also lived within the sporangia (Kevan et al., 1975; Rolfe, 1980; Habgood et al., 2004). We have found no arthropod body fossils associated with this PCM coprolite morphotype.

4.3.4 Isolated large coprolites

Description

These isolated coprolites are 1000–2500 µm long and 500–1300 µm wide. They have variable shapes; the majority possess one longer axis but some are spherical. Both termini are usually subrounded but some have one tapered end (Figure 4.2, D). The margins of such coprolites are either irregular or smooth. The smooth-margined coprolites appear to be bound with some form of amorphous agglutinating material (Figure 4.2, D) or possibly a net-like peritrophic membrane. In thin-section, the largest of the coprolites vary markedly in colour, ranging from black in charcoalified specimens (Figure 4.4, F) to light brown in those with finer constituents.

The isolated large coprolites are composed primarily of fine to coarse unidentifiable plant debris, but also contain some isolated spores and pollen grains. The large coprolites occur in isolation exclusively between matted leaves (Figure 4.4, F). They were markedly resistant to compaction based on their maintenance of a spherical to broadly elliptical form and the deformation of leaf laminae around them. The resistance to compaction could be the result of the coprolite consisting of compact and resistant tissues but in some cases is due to charcoalification. We see no evidence of hardening and cracking of the coprolites through subaerial exposure and dessication. This morphotype is relatively common (>10 specimens).

Remarks

Such coprolites may have been produced by various arthropod herbivores or detritivores, since their contents and shape are variable – some possessing tapered ends and smooth margins, whilst others are sub-rounded and have irregular margins. These large coprolites are grouped here on the basis of their size and contents, which are distinct from other coprolites in the peat. It is likely that the producers of these coprolites were detritivore generalists – feeding on forest floor litter because of their variable content and all examples occuring amongst matted leaf remains (autumnal leaf fall deposits). Constituents such as spores and pollen are common but never make up the bulk of the coprolite mass so it is likely that these were consumed passively as a consequence of indiscriminate feeding on plant detritus.

4.3.5 Isolated small coprolites

Description

These coprolites are 500–750 µm long and 300–350 µm wide, oblong to cylindrical (Figure 4.1, A) with rounded termini. The margins (surface) of the coprolites are either irregular or smooth depending on their contents. The coprolites appear light yellow-brown in thin-section.

Pollen grains, fern spores (Figure 4.2, C) and fragments of sporangia are evident within the coprolites (Figure 4.1, B), together with masses of cell wall detritus (Figure 4.2, B) and broken spinose fungal spores (Figure 4.1, C). The majority of these small- to medium-sized isolated coprolites contain mixed plant remains. The fern spores in these coprolites are corroded and split. Fungal hyphae are also evident within the coprolites although it is unclear whether these were consumed by the producer or infiltrated the coprolite post-deposition (Figure 4.1, D). Small coprolites of this category occur isolated in the peat matrix between various plant tissues.

Remarks

These coprolites have more variable contents than others of similar size and shape found within glossopterid wood galleries. This morphotype is relatively common in the peats (>10 specimens), although it varies significantly in abundance between peat samples based on material recovered from bulk macerations. Some samples lack any examples of this type. Samples that are richer in this morphotype also appear to include a higher proportion of root (*Vertebraria*) tissues. Some examples of this coprolite morphotype are similar in shape and size to Australian Cretaceous forms illustrated by Tosolini and Pole (2010), but the Antarctic Permian examples consistently incorporate coarser (identifiable) plant debris.

4.3.6 Fungi-rich Coprolites

Description

This category of coprolites is defined by its composition, being composed entirely of broken fungal spores. This morphotype is 180–220 μm long and 120–200 μm wide. Some larger coprolites (see sections 4.3.4. and 4.3.5) also contain fungi but as a minor component. A few of the small coprolites contained within galleries excavated in *Australoxylon* or *Vertebraria* are composed entirely of broken fungal spores (Figure 4.6, C). These are identical in shape to the surrounding frass-filled conoid and ovoid coprolites with smooth margins suggesting an origin via a common producer. Other fungi-filled coprolites are equidimensional (Figure 4.6, D). Fungi-filled coprolites vary from smooth to irregularly textured. In thin-section, the fungi-rich coprolites appear light brown.

Remarks

These coprolites occur as a minor component of the small abundant coprolites that fill galleries throughout *Araucarioxylon* (stem wood) and *Vertebraria* (root wood).

Coprolites composed exclusively of fungal remains are relatively rare within the peat (<10 specimens). Forms that are rich in fungal spores and crushed hyphae are slightly larger, though similar in shape and content to food boli produced by the modern oribatid mites *Scheloribates laevigatus* and *Archegozetes longisetosus* (Hubert et al., 2000; Smrž and Norton, 2004).

4.3.7 Coprolites containing pollen

Description

Coprolites composed entirely of compressed and broken pollen grains are small (100–150 μm long and 70–150 μm wide). The coprolites are squat ellipsoidal to spherical with rounded termini. The margins of the coprolites are relatively smooth, the pollen constituents being densely compacted (Figure 4.3, D). These coprolites are light brown in thin-section.

This category of coprolites is composed entirely of densely packed, broken to entire bisaccate pollen referable to *Protohaploxipinus* Samoilovich emend. Morbey. These coprolites occur isolated within the peat amongst a mixture of glossopterid-dominated plant debris. They are uncommon (<10 specimens).

Remarks

Protohaploxypinus pollen is typical of glossopterids (Gould and Delevoryas, 1977), although this plant group also produced various other pollen morphotypes (Lindström et al., 1997), and unrelated plant groups of other floristic provinces also produced similar taeniate pollen (Balme, 1995). These coprolites provide evidence of obligate palynophagy in the biota. The producers are unknown but there is a range of possible palynivores in the

Gondwanan Permian insect fauna including coleopterans (Ponomarenko and Mostovski, 2005). These mesofossils are not considered to be sporangia due to their lack of a distinctive sporangial wall composed of elongate inflated cells typical of glossopterids (Lindström et al., 1997).

4.3.8 Coprolites with coarse constituents

Description

Coprolites of this morphotype are 0.8–1.3 mm long and between 0.5–1 mm wide. They are equidimensional to broadly ellipsoidal, the long axis never reaching more than twice the length of the short axis. The margins of these coprolites are rough and uneven. In thin-section these coprolites appear dark brown.

This morphotype is distinguished primarily on its content of coarse platy materials, including tracheid fragments and leaf mesophyll cell walls and cuticle. These coprolites lack the fine-grained constituents evident in the other morphotypes. The coprolites with coarse constituents occur isolated in the peat matrix, among matted leaves and woody remains. They are uncommon (<10 specimens).

Remarks

These coprolites appear to be the product of feeding on coarse plant materials such as leaf mesophyll and woody tissues (tracheids). Components within the coprolite show only weak degradation and in some cases retain cellular features. The tracheids may derive simply from veins within leaves rather than from axial parts of the plant. We cannot determine whether the contents of these coprolites was consumed by detritivory (via feeding on leaf litter), or by true folivory.

4.3.9 Isolated spiral-ornamented coprolite

Description

This morphotype is represented by a single specimen that is approximately 800 μm long and 300 μm wide. The coprolite is elongate cylindrical with sub-rounded termini. The surface of the coprolite is marked by a series of grooves/ridges that are ca 25 μm wide, spaced at regular (ca 25 μm) intervals, and arranged spirally around the pellet.

The coprolite is composed of finely granular to platy indeterminate tissues. A single example of this morphotype was found in the bulk macerated residues of the peats.

Remarks

This coprolite morphotype is distinguished by its characteristic ornament. We are unaware of modern arthropods that produce faecal pellets with this morphology, although Edwards et al. (1995) and Edwards (1996) report spiral-shaped coprolites from the uppermost Silurian and Lower Devonian of the Welsh Borderlands, though the morphology of those older examples differs from that of the PCMs spirally ornamented coprolite, since the spirals are fewer and much more pronounced. In addition, Lupia et al. (2002) reported more coarsely spiral coprolites from the Upper Cretaceous containing pollen and coarse plant debris and Scott and Taylor (1983) reported grooved coprolites from the Upper Carboniferous.

4.3.10 Other evidence of animals

Arthropod remains (Figure 4.8)

Isolated plates of arthropod exoskeleton were recovered from bulk macerated samples of the peat (Figure 4.8; A, B). The segments of chitinous exoskeleton are covered with acuminate simple setae ca 35–50 µm long and ca 5–7 µm wide. The affinity of such fragments can not be determined accurately. The spines are narrower and much more elongate than those of the arthropod fragment previously illustrated from the upper part (Norian) of the Amery Group in the PCMs (McLoughlin et al., 1997). Such isolated arthropod fragments are minor components of many Palaeozoic and Mesozoic continental deposits (Bartram et al., 1987; Batten, 1998). Insect remains have been reported from a few other Permian deposits of Antarctica but are mostly assigned to unresolved homopterous hemipteran and coleopteran groups (Plumstead, 1962a; Carpenter, 1969; Tasch and Riek, 1969; Tasch, 1971).

Fine detritus patches

Regions of loosely consolidated fine detritus of variable shape are also found amongst the plant materials of the peats. These detritus patches consist of largely unidentifiable fine plant fragments with sparse fungal spores and hyphae. They are of variable shades of brown depending on their density, vary in size (ca 2–3 mm long and 1–3 mm wide) and have an irregular or diffuse surface.

Attributing these patches of frass to a producer organism is difficult because the variably shaped unconsolidated material lacks a clear indication of the size of the organism. It is a possibility that the patches were formed by the pre-burial weathering and dissociation of a coprolite or, alternatively, that they are the accumulated by-products of plant debris that was not consumed during detritivore feeding.

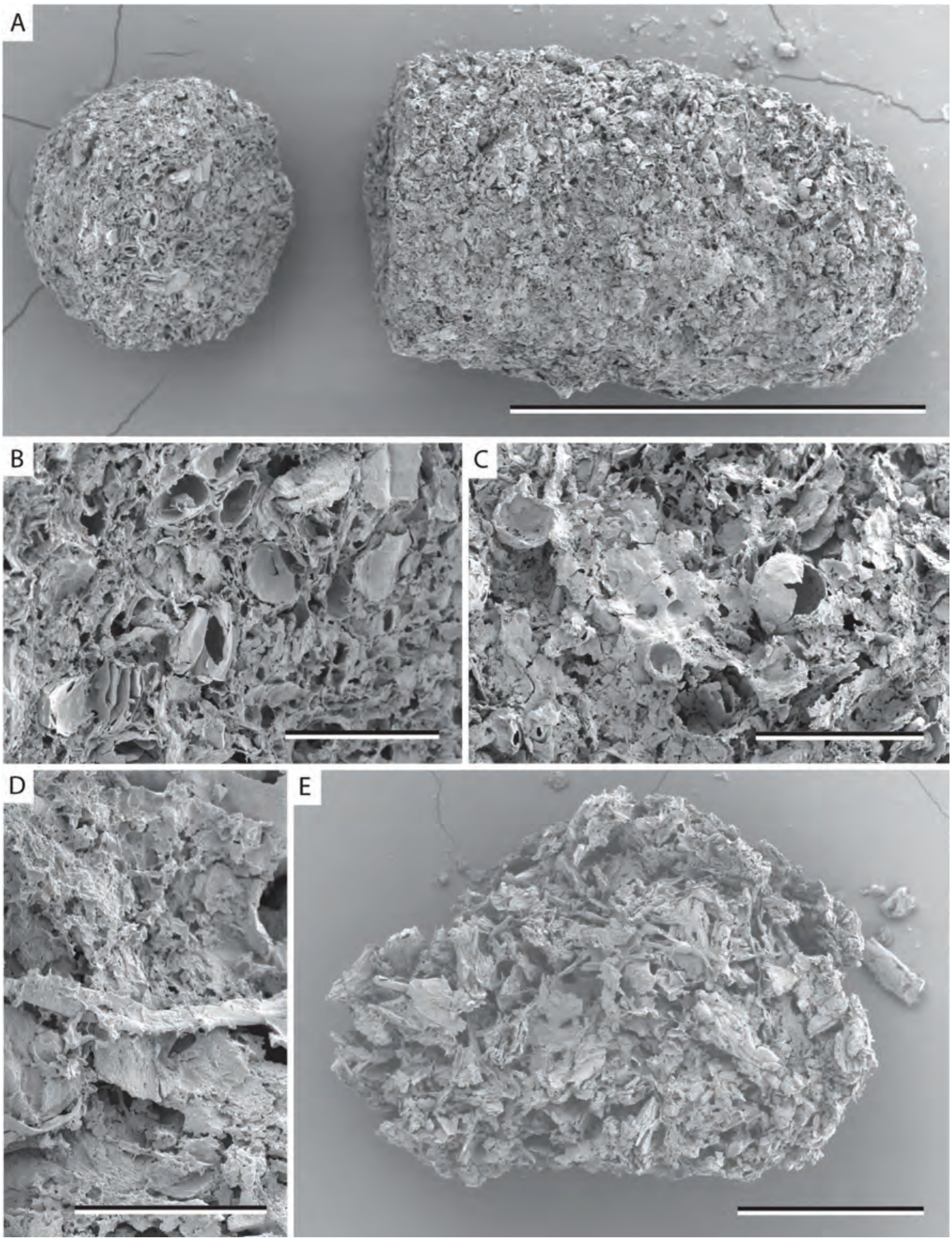


Figure 4.1

Figure 4.1 (previous page): Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat.
A. Coprolite rich in leaf fragments, fern spores and fungal spores, scale bar = 1 mm.
B. Enlargement of fractured surface of coprolite in image A, showing contents of broken fern spores and leaf fragments, scale bar = 100 µm.
C. Enlargement of external surface of coprolite in image A, showing broken fungal bodies and leaf fragments, scale bar = 100 µm.
D. Fugal hyphae in coprolite from image A, degraded state of hyphae suggests it was consumed rather than colonising the coprolite post deposition, scale bar = 20 µm.
E. Coprolite composed entirely of leaf tissues, scale bar=500 µm.

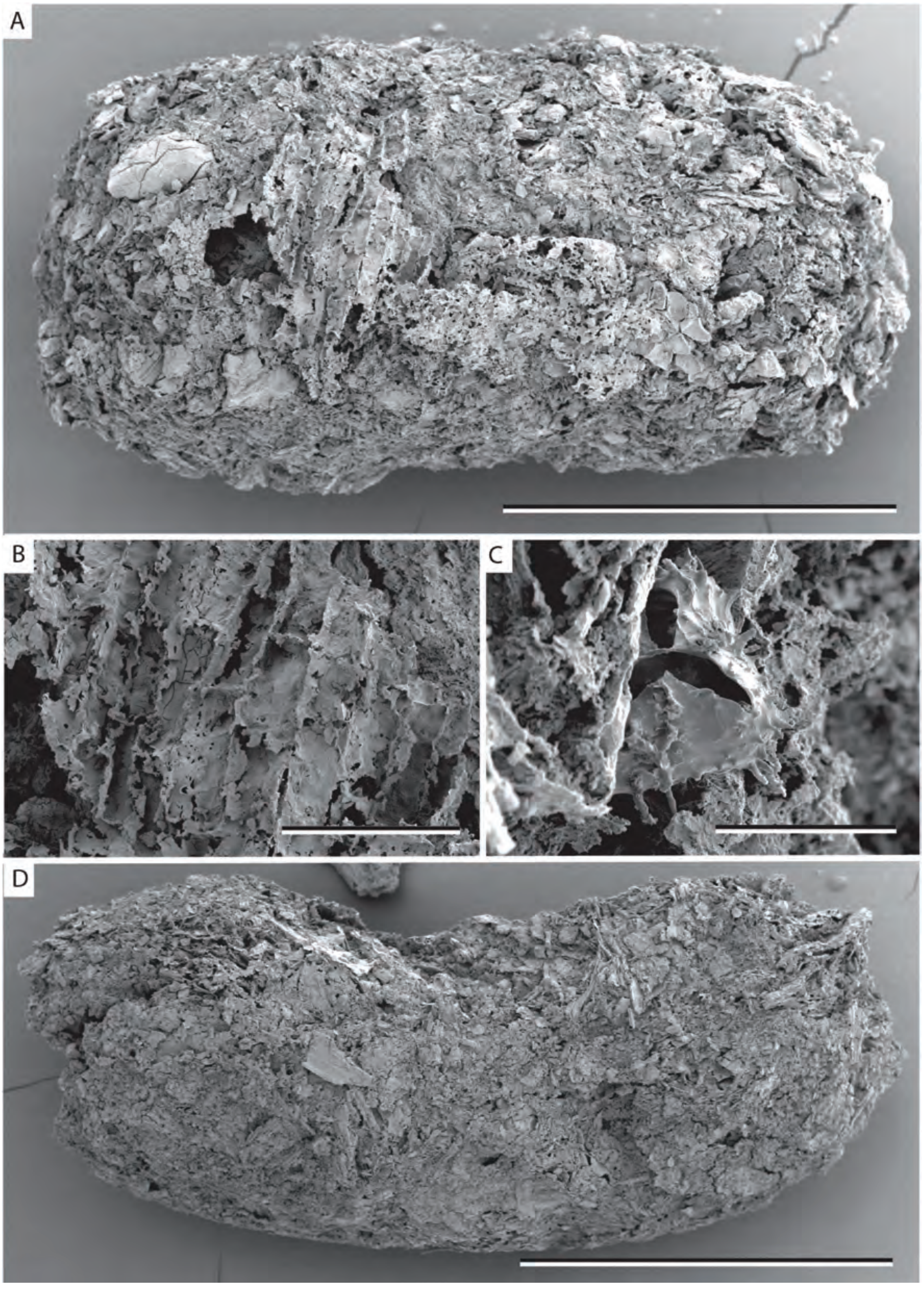


Figure 4.2

Figure 4.2 (previous page): Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat.
A. Coprolite containing mixture of plant remains including leaf tissue fragments and fungal spores, scale bar = 500 µm.
B. Enlargement of plant material on external surface of coprolite in image A, showing large degraded leaf cuticle sheets with epidermal cell markings, scale bar = 100 µm.
C. Enlargement of fern spore [*Horriditriletes tereteangulatus* (Balme and Hennelly) Backhouse] included in coprolite in image A, scale bar = 20 µm.
D. Large coprolite with tapered terminus, containing plant tissue fragments and agglutinated external surface, scale bar = 1 mm.

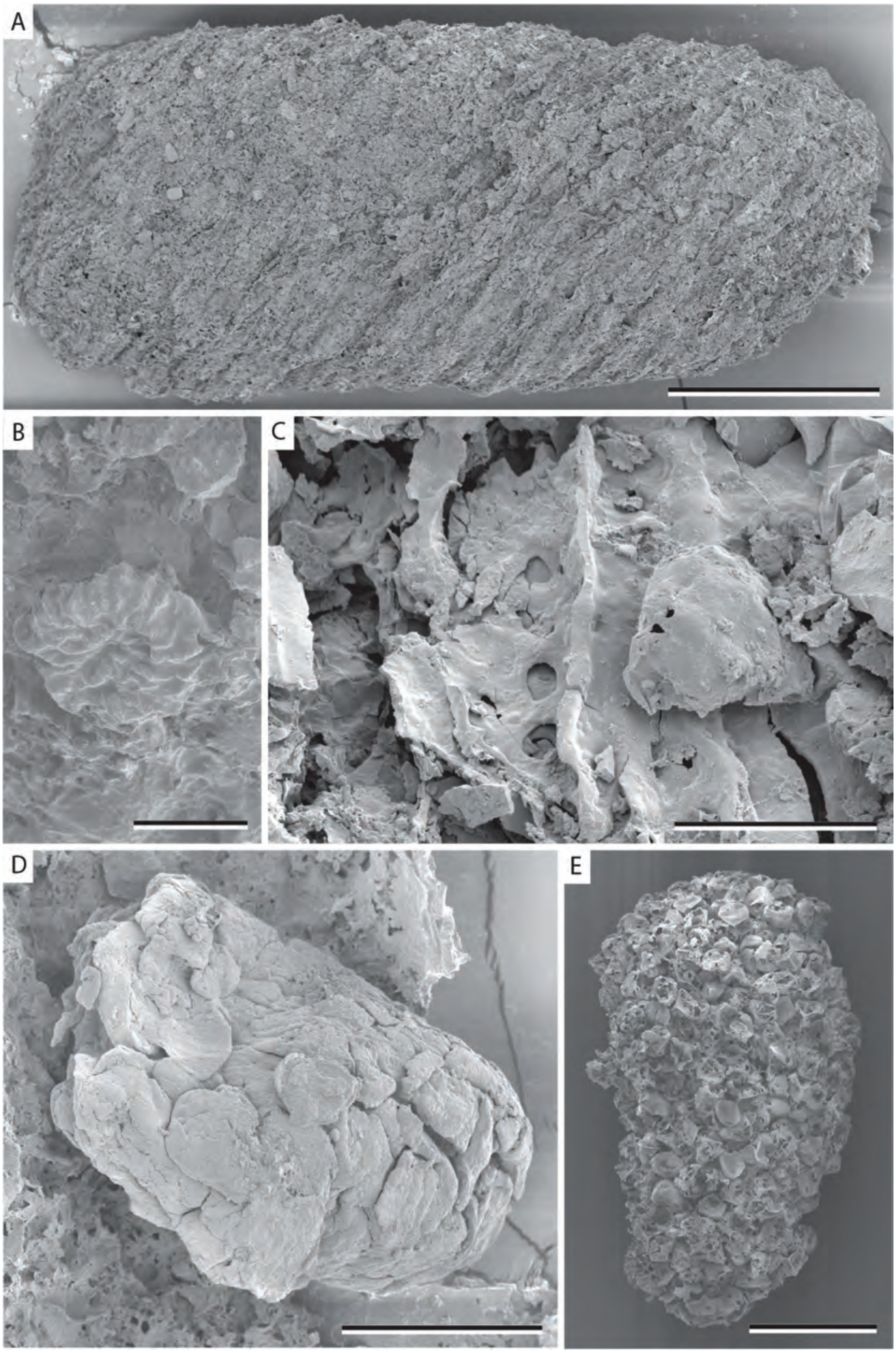


Figure 4.3

Figure 4.3 (previous page): Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat.
A. Spiral-ornamented coprolite, scale bar = 250 µm.
B. Glandular leaf trichome in leaf-rich coprolite, scale bar = 25 µm.
C. Tracheids in leaf-rich coprolite, scale bar = 20 µm.
D. Coprolite composed of pollen, scale bar = 50 µm.
E. Coprolite composed of a consumed fern sporangium—*Leiotriletes directus* Balme and Hennelly spores showing burst and degraded walls, scale bar = 200 µm.

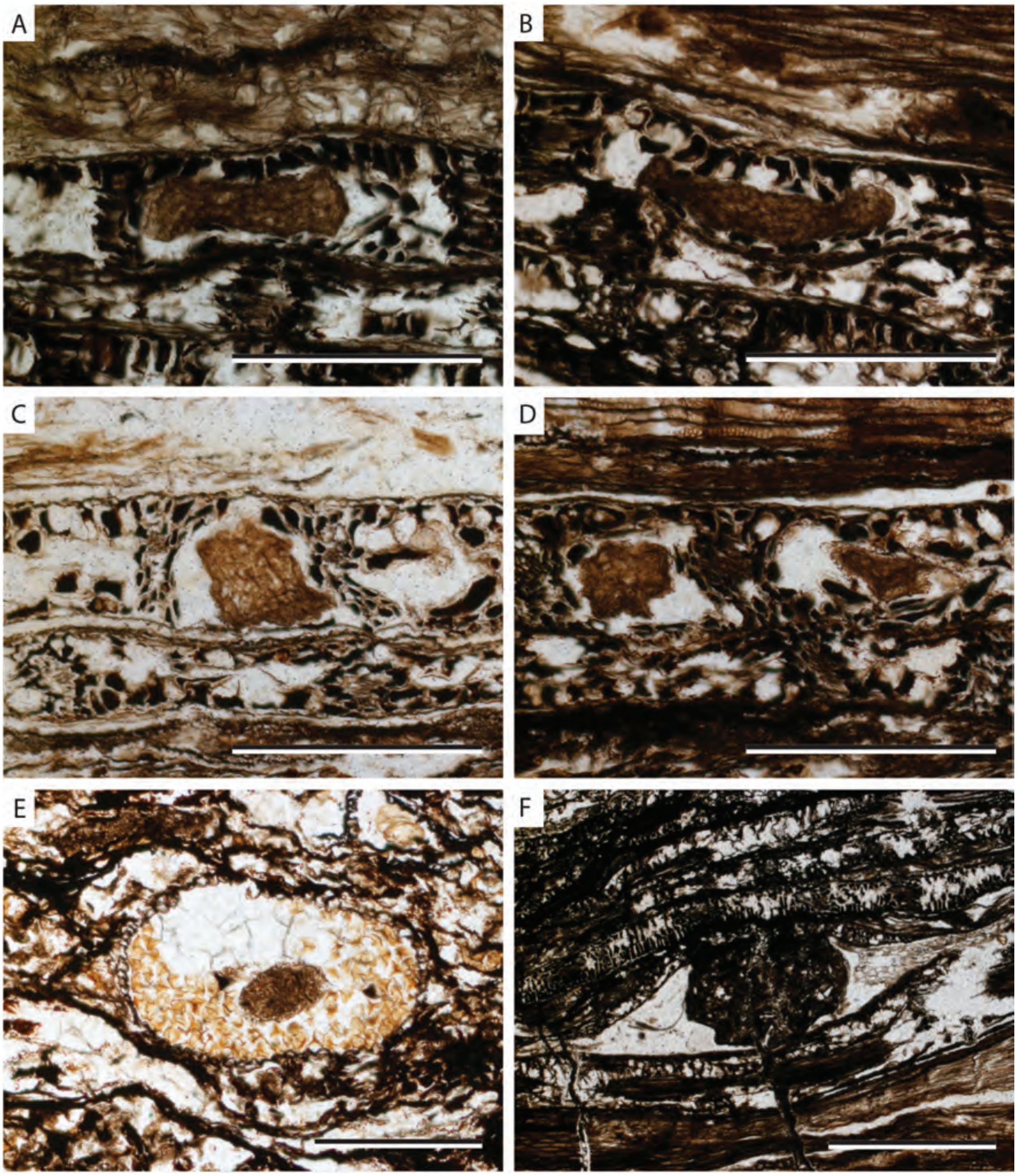


Figure 4.4: Coprolites preserved within *Glossopteris* leaves (A–D), within sporangia and between matted leaves.

A–D. Coprolites with a fine platy texture preserved within cavities excavated between anastomosing veins of *Glossopteris* leaves, scale bars = 500 µm.

E. Coprolite inside a partially excavated fern sporangium, scale bar = 1 mm.

F. Large compaction-resistant and apparently charcoalified coprolite positioned between matted *Glossopteris* leaves, scale bar = 1 mm.

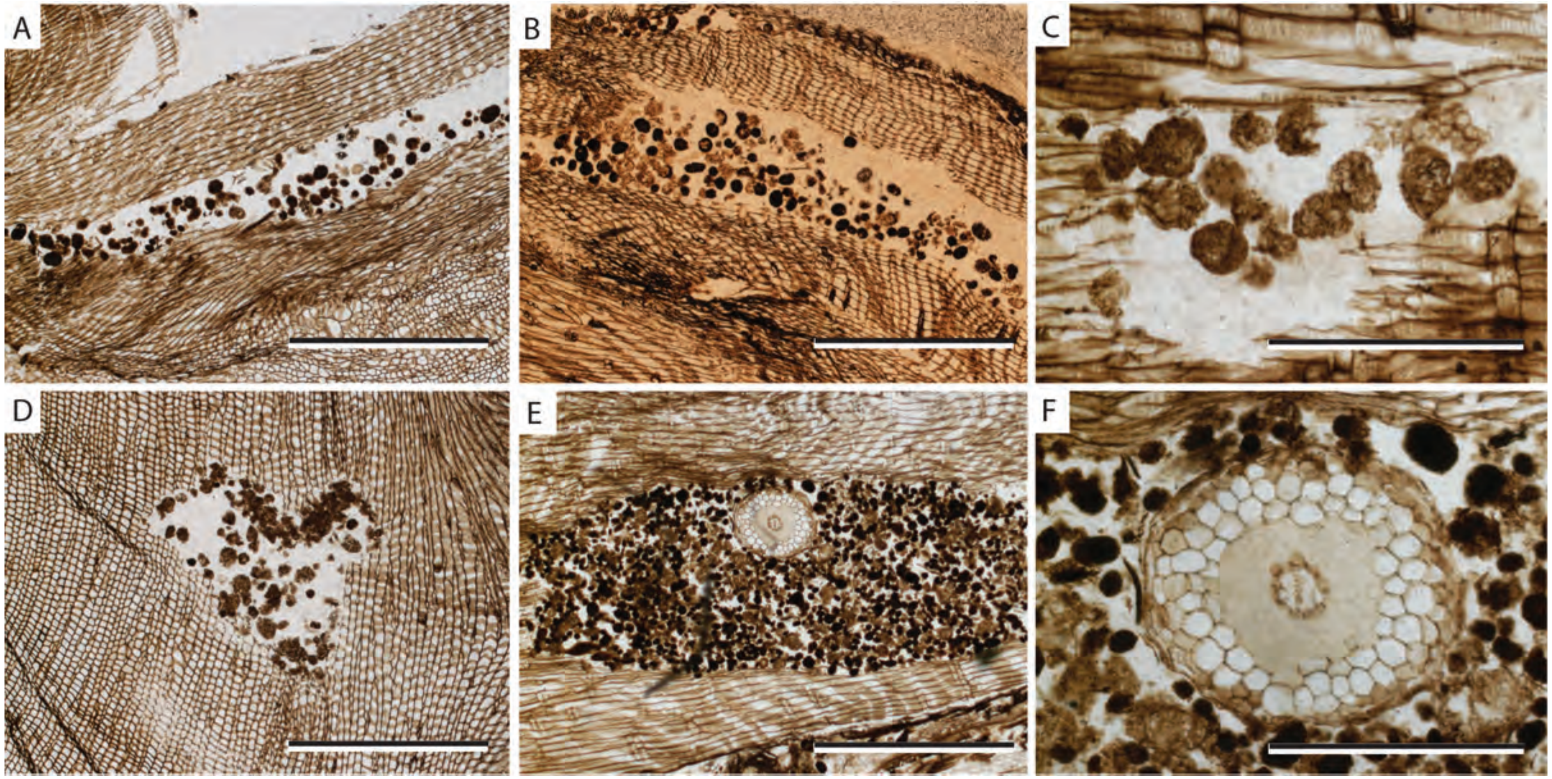


Figure 4.5: Coprolites preserved within secondary wood of *Vertebraria*.
A–B. Small coprolites clustered within excavated galleries inside *Vertebraria* secondary xylem, scale bars = 1 mm.
C. Coprolites within excavation containing internal granular fragments of xylem tissues, scale bar = 500 µm.
D. Excavation through *Vertebraria* containing coprolies, scale bar = 1 mm.
E. Mass of coprolites within an excavation in *Australoxylon* wood, scale bar = 1 mm.
F. Enlargement of young undamaged *Vertebraria* rootlet that apparently penetrated the wood cavity subsequent to emplacement of the coprolite mass, scale bar = 500 µm.

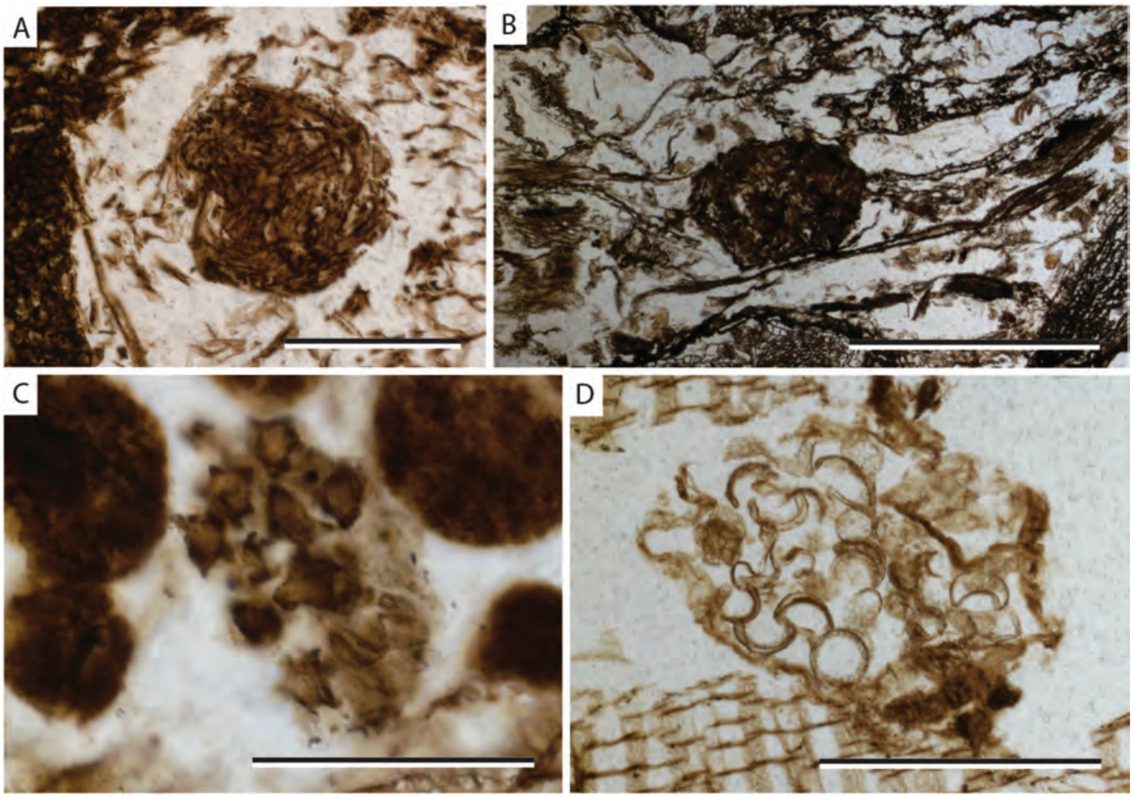


Figure 4.6: Platy coprolites isolated within the peat matrix (A–B) and fungi-filled coprolites (C–D).

A. Coprolite composed of platy plant cell material, scale bar = 1 mm.

B. Coprolite composed of platy plant material, scale bar = 1 mm.

C. Small coprolite composed of crushed spinose fungal spores within a gallery of small coprolites composed of granular plant matter, scale bar = 200 µm.

D. Coprolite composed primarily of fragmented fungal spores, scale bar = 200 µm.

4.4 Discussion

We diagrammatically reconstruct the key interactions between the glossopterid plant and invertebrates based on examples from Antarctica and Australia (Figure 4.7). The range of interactions evident is greater than previous investigations have reported for the Gondwanan Permian flora. New evidence from the PCM peat layer indicates that all parts of the *Glossopteris* plant experienced herbivory.

4.4.1 Feeding guilds

The absence of an extensive body fossil fauna means that trace fossils in sediments and plant-animal-fungal interactions provide the primary means of evaluating invertebrate faunal diversity and trophic levels in Antarctic Permian terrestrial communities. Determining these parameters is important for evaluating the scale of faunal turnover in high-latitude communities at the close of the Palaeozoic (Labandeira, 2005a), at which time Gondwanan plant communities were fundamentally readjusted (Anderson et al., 1999; Vajda and McLoughlin, 2007). Several damage types are distinguishable on plants in the PCM peat (Figure 4.7) attesting to a hidden diversity of terrestrial invertebrates and these feeding strategies are summarized below (see also Table 1):

(A) Xylophagy is represented by gallery and chamber feeders (borers) that targeted specific tissues (xylem and parenchyma and possibly cambial tissues) in the stem and root wood. Given that some coprolites occur within the soft parenchymatous tissues of young roots, at least some of the damage is likely attributable to true xylophagy rather than saproxylophagy.

(B) True folivory (feeding on living leaves) is represented by coprolites preserved within interveinal chambers in glossopterid leaves, and probably by the presence of dispersed coprolites consisting primarily of leaf tissue fragments, although we cannot exclude a detritivorous origin for the latter.

(C) Detritivorous feeding behaviour was characteristic of the producers of the medium and large spherical–oblong coprolites that contain a broad mixture of cell fragments, spores, pollen and fungal hyphae.

(D) Sporangial feeding (sporivory) is evidenced by the presence of coprolites within partially consumed fern sporangia, and dispersed faecal pellets composed entirely of spores (*Leiotriletes directus*) recovered from bulk maceration of the peat matrix. Pollenivory, specifically targeting the microsporangial contents of glossopterid gymnosperms, is evidenced by dispersed coprolites containing exclusively taeniate bisaccate pollen (*Protohaploxypinus* sp.).

(E) Mycophagy is evidenced by coprolites composed exclusively of fungal spores/sporangial fragments.

The range of feeding strategies employed differs sufficiently, in food materials and the occurrence and size of the faecal pellets produced, to have originated from several invertebrate producers. The isolated small- to medium-sized and larger coprolites can be differentiated by size and morphology but in terms of a producer it is possible that they derive from different metamorphic instars rather than different taxa of arthropods. As a 150 µm sieve was used to collect acid-liberated debris from the peats (initially intended for the recovery of lycophyte megaspores: see Chapter 3 and Slater et al., 2011), many smaller coprolite types may have been lost from the bulk macerations. These may be the target of future investigations.

Evidence for selective feeding behaviour amongst the producers of the largest coprolites is equivocal. Although some of these coprolites are very rich in spores, this is not necessarily evidence for obligate sporangial feeding. It is possible that such spore-filled coprolites were produced by opportunistic or indiscriminate feeding by the same invertebrate that excreted coprolites rich in mixed cell debris. Nevertheless, coprolites within fern sporangia, and others containing primarily bisaccate pollen demonstrate that specific targeting of microsporangiate organs did occur within the community – presumably different palynovores targeting the pteridophytes and glossopterid gymnosperms. Spores and pollen represent rich nutrient sources (Willmer, 2011), so specific targeting of these materials for food is to be expected. Sporivory is amongst the first invertebrate-plant interaction to appear in the fossil record with occurrences in the Upper Silurian and Late Devonian (Labandeira, 2007; Hagström and Mehlqvist, 2012; Habgood, 2000; Habgood et al., 2004). Sporangia are also known to be utilised by arthropods such as Trigonotarbids as either a food source or as a site to hunt microarthropod prey that was in turn feeding on spores, since Trigonotarbid remains are known from inside the sporangia of *Rhynia major* in the Early Devonian Rhynie Chert lagerstätten (Kevan et al., 1975; Rolfe, 1980; Habgood et al., 2004). The value of fern spores as a food source is questionable in some cases since the sporopollenin wall of spores is almost nutritionally worthless, and often spores pass through the digestive tract intact as a by-product of detritivory (Habgood, 2000). However, if the sporopollenin wall is breached then the internal spore contents are rich in lipids and proteins (Kevan et al., 1975). Experimental work involving feeding millipedes with spore-containing detritus was shown to result in spore-rich faecal pellets, however, the spores were unbroken and lacked signs of digestion suggesting that spore ingestion in the fossil record may often be a by-product of detritivory (Chaloner et al., 1991; Habgood, 2000). The specific targeting of a sporangium seen in the example in the Toploje Member chert suggests that the producer organism was utilising the spores as a food source. Modern fern sporangia are targeted by a variety of invertebrates including hymenopteran (sawflies, wasps, bees and ants) and lepidopteran (butterflies and moths) larvae (Srivastava et al., 1997; Sawamura et al., 2009). Unlike the case in angiosperms, host-specificity or a 'component-community' is uncommon in ferns, with fern spore-feeders targeting a wide variety of host ferns regardless of taxonomic affinity (Sawamura et al., 2009), alluding that coevolution between insect herbivores and their fern hosts does not occur to the extent seen in gymnosperms and angiosperms. Despite the lack of identification of host-specific component communities in association with ferns, some tropical epiphytic ferns are known to host a greater diversity of arthropod species on a single plant than is found amongst the whole canopy of the inhabited tree (Ellwood and Foster, 2004). A component-community of invertebrates has, however, been identified to occur in association with the Late Pennsylvanian and Permian *Psaronius* tree-fern which was a palaeogeographically widespread and temporally dominant member of the wetland plant vegetation in the Laurentian and Cathaysian tropics during these times (Labandeira, 1998a; Rößler, 2000, 2006; He et al., 2008; D'Rozario et al., 2011a, 2011b). Baxendale (1979) figures a section of fern sporangium annulus inside coprolitic frass material from Pennsylvanian coal balls of North America (plate 65; figure 12 of that paper), an assemblage which contains many similar coprolite morphotypes to those seen in the Toploje Member chert material. A wide range of arthropods feed on modern ferns (Lawton, 1976; Lawton and MacGarvin, 1985), and experimental studies have shown that a significant proportion of ingested fern spores remain viable post-digestion (Chaloner et al., 1991) and therefore sporivory may have been co-opted by early plants as a dispersal mechanism. Sporangia with specialised trichomes that appear to have functioned as faunal-triggered dehiscence mechanisms have been recovered from Pennsylvanian sediments of the Czech Republic, demonstrating that complex fern-animal interactions had already developed by the late

Carboniferous (Pšenička and Bek, 2009). Many Palaeozoic spores also feature elaborately barbed projections which may have served to anchor the spore amongst arthropod setae thereby facilitating dispersal (Kurmann and Hemsley, 1999).

Fungal spores within the coprolites are commonly split and fragmented so were likely part of the diet of an invertebrate (true mycophagy) rather than being the fertile organs of fungi that colonised the coprolites after deposition (Figure 4.6, D). However, some fungal hyphae evident in the coprolites possibly colonised the pellets post-deposition. In these cases, hyphae form long unbroken threads that permeate the coprolite.

Coprolites occurring in excavated cavities between *Glossopteris* leaf veins suggest specialist feeding on the leaf mesophyll of the dominant group of gymnosperms in this palaeoecosystem. Mine-like features on glossopterid leaf impressions have been illustrated previously (Gallego et al., 2003; Prevec et al., 2009; Pinheiro et al., 2012a, 2012b) but their representation of true leaf mining is equivocal and the earliest confident examples of this feeding strategy are documented from the late Middle to early Late Triassic (Rozefelds and Sobbe, 1987; Anderson and Anderson, 1989, p. 231, 265, 439). Although the areal extent of the excavations in the PCM leaves is unresolved, they appear to be restricted to interveinal mesophyll and it is possible that they represent the first examples of leaf mining in *Glossopteris*. Alternatively, such features may represent selective targeting of softer mesophyll tissues in shed leaves by a small detritivore.

Body fossils or traces of vertebrates and other non-marine invertebrates (e.g. molluscs and annelids) are currently unknown from the PCM Permian deposits (McLoughlin et al., 1997). Indeed, vertebrate remains are extremely sparse in Gondwanan Permian non-marine deposits outside of the Karoo Basin, South Africa. A few reptiles and amphibians are known from the Southern Hemisphere Permian (Rubidge, 1995; Warren, 1997; Modesto,

2006) and a slightly broader range of fish and aquatic invertebrate body fossils and locomotion trails have been recorded (Anderson, 1976; Aceñolaza and Buatois, 1993; Shi et al., 2010; Bordy et al., 2011) but evidence of an extensive guild of terrestrial tetrapod herbivores in high-latitude parts of Gondwana is lacking thus far. Terrestrial invertebrate traces are also relatively sparse. No acid-resistant egg cases (e.g. *Dictyothylakos* or *Burejospermum* spp.) of clitellate annelids were recorded from bulk macerations of the peat matrix, and it is possible that these waxy proteinaceous structures only developed within this group after the mid-Triassic (Mannum et al., 1991; Jansson et al., 2008). However, various vermiform traces, vertical tubes, and punctate trackways in floodbasin and fluvial channel sediments of Antarctica attest to a varied soil and surface invertebrate biota in Permian high latitudes that is not yet represented by body fossils (Tasch, 1968a, 1968b; Fitzgerald and Barrett, 1986; Miller and Collinson, 1994; Briggs et al., 2010). In the absence of an extensive record of vertebrates, it is likely that arthropods, fungi and bacteria were overwhelmingly the dominant herbivores, detritivores and saprotrophs in the PCM mid--Permian forest mire community.

Table 1. Summary of coprolite traits in the Toploje Member chert.

Damage/Coprolite Type	**Size range**	**Shape**	**Colour**	**Contents**	**Occurrence**	**Relative abundance**	**Host specificity: 1 (host specific); 2 (intermediate); 3 (host generalized)**
Coprolites in *Vertebraria* and *Australoxylon* (dark)	120 µm long and 115 µm wide	Ovoid, conoid or equant	Dark brown	Small angular fragments of tracheid wall	Roots, wood	High; >1000 in some slides	**1**; Occurs solely in *Vertebraria* and *Australoxylon* wood of the *Glossopteris* plant
Coprolites in *Vertebraria* and *Australoxylon* (light)	150 µm long and 125 µm wide	Ovoid, conoid or equant	Light brown	Small angular fragments of tracheid wall	Roots, wood	High; >1000 in some slides	**1**; Occurs solely in *Vertebraria* and *Australoxylon* wood of the *Glossopteris* plant
Coprolites in leaves	200–550 µm long and 120–250 µm wide	Elongate and flattened, some are equidimensional	Light brown	Fragments of leaf mesophyll cell walls	Between anastomosing veins of *Glossopteris* leaves	Relatively common; >10 specimens	**1**; Occurs solely in *Glossopteris* leaves
Coprolite within fern sporangium	500 µm long and	Ovoid	Dark brown	Fern spores	Inside fern sporangium	Single occurrence	**1**; Occurs solely in fern sporangia

	300 µm wide						
Isolated large coprolites	1000–2500 µm long and 500–1300 µm wide	Elongate, some spherical	Light brown, black in charcoalified specimens	Fine to coarse unidentifiable plant debris, some spores and pollen grains	Amongst matted leaf remains	Relatively common; >10 specimens	**3**; Coprolites contain diverse range of contents
Isolated small coprolites	500–750 µm long and 300–350 µm wide	Oblong to cylindrical	Light yellow-brown	Mixed plant remains, pollen grains, fungal spores	Isolated in peat matrix, amongst matted leaf remains	Relatively common; >10 specimens	**3**; Coprolites contain diverse range of contents
Coprolites containing fungi	180–220 µm long and 120–200 µm wide	Conoid to ovoid or equidimensional	Light brown	Broken fungal spores	Roots, wood and isolated in the peat matrix	Relatively uncommon; <10 specimens	**2**; Coprolites contain solely fungal remains although fungal type appears indiscriminate
Coprolites containing pollen	100–150 µm long and 70–150 µm wide	Squat ellipsoidal to spherical	Light brown	Pollen grains	Isolated in the peat amongst *Glossopteris*-dominated debris	Relatively uncommon; <10 specimens	**1**; Coprolites contain solely *Glossopteris* pollen
Coprolites with coarse constituents	0.8–1.3 mm long and between	Equidimensional to ellipsoidal	Dark brown	Coarse fragments of leaf mesophyll and woody	Isolated in the peat matrix	Relatively uncommon; <10 specimens	**3**; Coarse contents derived from dead wood tissues

	0.5–1 mm wide			tissues			
Spirally ornamented coprolite	800 µm long and 300 µm wide	Elongate cylindrical	Macerated specimen dark brown	Finely granular to platy indeterminate tissues	Macerated from leaf-rich sample	Single occurrence	**?**; Difficult to determine host specificity as only a single specimen recovered from peats

4.4.2 Root feeding

Evidence of a previously unknown feeding behaviour targeting glossopterid roots (*Vertebraria*) (Gould, 1975) is identified from thin-sections of the silicified peats (Figure 4.5, A–F). This root-feeding activity shows preferential targeting of the softer and likely more nutritious parenchymatous tissues, employing a strategy similar to aerenchyma-feeding arthropods in Late Pennsylvanian *Psaronius* roots (Labandeira, 2001). This behavioural pattern may also have facilitated a more energy-efficient method of tunnelling. Root feeding is known elsewhere in the fossil record from several assemblages. Cichan and Taylor (1982) reported anastomosing burrows of 0.3–0.6 mm in diameter in cordaitalean *Premnoxylon* wood from the lower–middle Pennsylvanian of Kentucky. Borings into the cortical tissues of lycopsid roots are known from the Pennsylvanian-Permian boundary in Germany (Geinitz, 1855; Labandeira, 1998b). Cortical borings are also abundant in young roots of *Protojuniperoxylon arcticum* (probable Bennettitales) from the Upper Triassic of Hopen, Svalbard Archipelago (Strullu-Derrien et al., 2012), although these excavations may represent examples of saproxylophagy. In each case, the host plants were mire-dwelling dominant tree species indicating a consistent life environment and feeding strategy of a guild of small arthropod borers (likely oribatid mites in the case of the smaller borings and insects in the case of larger ones) through the late Palaeozoic and Triassic.

The pattern thus far uncovered from the fossil record indicates that feeding on true roots began in the late Pennsylvanian (Labandeira, 2001), which is rather late when compared to the earliest evidence of feeding on other plant organs (Labandeira, 1998b, 2006a). Evidence for arthropod herbivory in stem tissues and sporangia appears much earlier: during the latest Silurian and Early Devonian (Labandeira, 2006b, 2007). This may be due to the inherent inaccessibility of root tissues when compared to subaerial plant organs, especially given that most three-dimensionally fossilized roots were preserved in waterlogged dysaerobic substrates in special environments such as mineral-charged springs and acidic mires.

We illustrate the first examples of root feeding in *Vertebraria*. Boring into these organs raises the question whether some glossopterid roots were aerial in nature, and similar to the pneumatophores of extant *Taxodium distichum* (Briand, 2000–2001). Exposure of the roots above the waterlogged substrate would certainly have provided easier access to terrestrial herbiviores. Cichan and Taylor (1982) proposed that the cordaitean root *Premnoxylon* was an aerial organ based on similar evidence of root boring. *Vertebraria* has traditionally been considered a root characteristic of water-saturated or submerged soils based on its predominantly shallow (horizontal) distribution (Schopf, 1982), position within "seat-earths" underlying coal deposits (Retallack, 1980), and the presence of abundant schizogenous chambers in the secondary xylem that likely acted to facilitate aeration of the living root tissues in dysaerobic conditions (Retallack and Dilcher, 1988; Neish et al., 1993). A possible aerial nature for *Vertebraria* was proposed recently by Decombeix et al. (2009). *Vertebraria* roots are commonly found as dense, ramifying mats within permineralised peat organic debris (organosols: McLoughlin, 1993; Neish et al., 1993), seat earths (Retallack, 1980; Shi and McLoughlin, 1997), and water-saturated floodplain and deltaic palaeosols (hydrosols: Schopf, 1982). Thus, they occupied habitats similar to plants such as semi-aquatic Cupressaceae (e.g., *Taxodium distichum* and *Glyptostrobus pensilis*), red maple (*Acer rubrum*) and water tupelo (*Nyssa aquatica*), which produce pneumatophores to gain access to oxygen for tissue respiration or looping roots, for which a clear function is equivocal (Briand, 2000–2001). Extensive lenticel clusters have not yet been documented in permineralised *Veterbraria*, and discovery of these features would lend support to the hypothesis that pneumatophores were present in glossopterids. A new reconstruction of the *Glossopteris* plant is proposed here with subaerial extensions of *Vertebraria* (Figure 4.7).

The evidence of root boring now complements a broad range of other ichnological evidence indicating that all major organs of the *Glossopteris* plant were subject to arthropod attack (Figure 4.7). This dominant Gondwanan gymnosperm supported a diverse community of invertebrates and feeding strategies similar to the late Palaeozoic tree fern *Psaronius* of the palaeotropics (Rößler, 2000). Seed-herbivory and nectivory are the only major functional feeding strategies outlined by Labandeira (1998b, 2006a) that have not yet been recognized within glossopterid-dominated communities (although evidence of leaf-mining also remains equivocal).

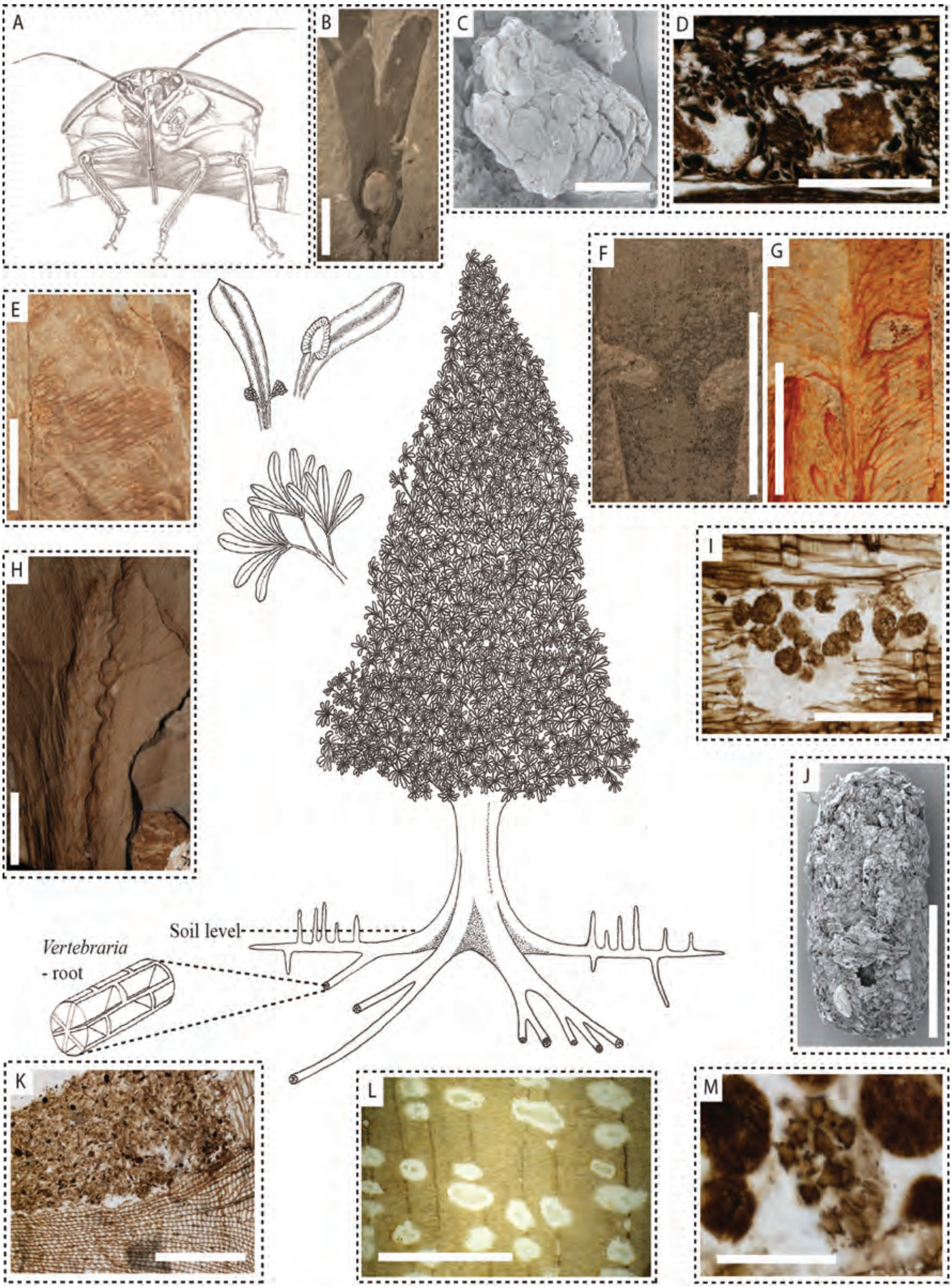


Figure 4.7

Figure 4.7 (previous page): Reconstruction of the *Glossopteris* tree with subaerial extensions of *Vertebraria* roots. The reconstruction is annotated with examples of arthropod damage types (referred to functional feeding groups) on the different organs of the *Glossopteris* plant preserved in the Prince Charles Mountains silicified peat and from Permian deposits elsewhere in Gondwana, demonstrating the suite of invertebrate herbivory acting upon the *Glossopteris* plant.

A. Reconstruction of hemipteran sap-sucking insect feeding on *Glossopteris* (piercing and sucking attack).

B. Galling on a *Glossopteris* leaf, after McLoughlin (2011), scale bar = 10 mm.

C. Coprolite containing consumed *Glossopteris* pollen (palynivory), scale bar = 50 µm.

D. Coprolites in cavities between anastomosing *Glossopteris* leaf veins (selective detritivory or possible leaf mining), scale bar = 500 µm.

E. Fungal damage to a *Glossopteris* leaf, after McLoughlin (1994a, 1994b), scale bar = 10 mm.

F–G. Examples of leaf margin feeding on *Glossopteris* leaves (external foliage feeding), after Beattie (2007), scale bar = 10 mm.

H. Oviposition scars along *Glossopteris bucklandensis* midrib (oviposition), after McLoughlin (1990) and McLoughlin (2011), scale bar = 10 mm.

I. Feeding gallery inside *Australoxylon* wood containing numerous small coprolites attributed to oribatid mites (wood boring: xylophagy or saproxylophagy), scale bar = 500 µm.

J. Coprolite produced by a detritivore likely feeding on shed plant organs (leaf litter detritivory), scale bar = 500 µm.

K. Arthropod feeding damage in *Vertebraria* root tissues showing compressed mass of fine frass and coprolites within a *Vertebraria* internal air chamber (wood boring: xylophagy or saproxylophagy), scale bar = 1 mm.

L. Pocket rot within *Australoxylon* wood (fungal damage), after Weaver et al. (1997), scale bar = 1 mm.

M. Coprolite containing fungi within a *Vertebraria* root (mycophagy), scale bar = 200 µm.

4.4.3 Possible producers

Matching isolated coprolites to a producer is inherently difficult because many invertebrates that are separated widely in terms of phylogeny can produce coprolites that are morphologically very similar (Hantzschel et al., 1968). The main hindrance to the identification of Permian coprolite producers, and animal-plant interactions in general, is the lack of a database or atlas illustrating the morphology of faecal pellets produced by extant arthropods and other terrestrial invertebrates. Galleries in *Vertebraria indica* that are less than 1 mm in diameter and filled with small clusters of spherical coprolites are here interpreted to derive from oribatid mites. This is based on strong similarities to coprolites attributed to oribatid mites from numerous other assemblages throughout the late Palaeozoic and early Mesozoic fossil record (Labandeira et al., 1997; Ash, 2002; Habgood et al., 2004; Kellogg and Taylor, 2004; Labandeira, 2007; Feng et al., 2010; Osborn and Taylor, 2010). Although several extant invertebrate groups bore into woods, pre-Mesozoic examples are predominantly attributed to oribatid mites, although it is noteworthy that few of these records are associated with body fossils of the producer (Labandeira et al., 1997). Characteristics that particularly favour oribatid mites as the originators of the small PCM coprolites include their clustered distribution, uniform size and smoother texture (compared to the rough faecal pellets of collembolans or ridged oblong pellets of termites) without components projecting beyond the surface (Rusek, 1975; Vegter, 1983). Extant oribatid mites are common microherbivores and detritivores in modern soils and plant detritus (Habgood et al., 2004). In some examples from the PCMs, root feeding has left no obvious response tissue around the excavation areas (cf. Jud et al., 2010), highlighting that consumption of dead xylem tissues was present alongside true herbivory on living cells.

Essentially identical spindle-shaped borings containing coprolites in *Australoxylon mondii* wood from the same silicified peat layer have previously been interpreted as being produced by beetle larvae (Weaver et al., 1997). However, derivation of these traces from oribatid mites appears more likely based on the characteristics outlined above and because wood-boring cerambycid beetles appear to have diverged in post-Triassic times and experienced their major expansion in the Cenozoic (Grimaldi and Engel, 2005). Structurally, these cavities are axially elongate spindle-shaped excavations that extend through the outer portion of the earlywood and through almost all of the latewood. Each of the elongate cavities is isolated, 0.45–3.0 mm in radial diameter and 3.5–13.5 mm in length making them slightly larger than the oribatid mite-produced cavities reported from Permian-Triassic woods from the Permian and Triassic of the Central Transantarctic Mountains (Kellogg and Taylor, 2004) and some modern forms (Wallwork, 1976). Cell walls along the margins of the cavities are sharply truncated and the contained pellets consist entirely of cell wall fragments. No exit/entrance holes are evident for these excavations, although they typically extend to the growth ring margin, which would have represented the exterior surface of the secondary xylem at the end of each growth season (Weaver et al., 1997). Emergence of the arthropods may have been through the bark at the end of winter; the cambial activity in the succeeding spring growth spurt then re-sealing the cavity leaving no signs of reaction tissue.

Root boring is a common trait amongst several invertebrate lineages in modern ecosystems. Modern borings are produced by moths (Cuthrell, 1999), beetles (Soltani et al., 2008), mites (Fan and Zhang, 2003), termites [Isoptera (Spragg and Paton, 1980)], ants [Hymenoptera (Vörös and Gallé, 2002)], Diptera (Finch and Ackley, 1977) and cicadas [Hemiptera (Hunter, 2008)]. Some extant taxa, such as *Oryctes agamemnon*, specifically target aerating tissues and feed on the respiratory roots of the date palm (Soltani et al., 2008). Determination of the producers of the *Vertebraria*-hosted coprolites is largely speculative, because none is associated with body fossils, and isolated fragments of exoskeleton recovered by bulk maceration have unresolved affinities. The waterlogged conditions occupied by the *Glossopteris* plant would have potentially left them vulnerable to feeding by aquatic arthropods such as ostracods, cladocerans and copepods (e.g. Womack et al., 2012). Extant forms of these groups are known to feed upon plant matter that is submerged in water although they generally target loose detritus and algae (Anderson and Trewin, 2003).

The isolated larger coprolites found in the bulk macerated materials match the morphology and contents of those produced myriapod detritivores (Scott and Taylor, 1983). It is noteworthy that predatory arthropods commonly switch diet to spore feeding when prey is unavailable, so this adds another group of potential candidates to the producers of the spore-filled coprolites (Kevan et al., 1975).

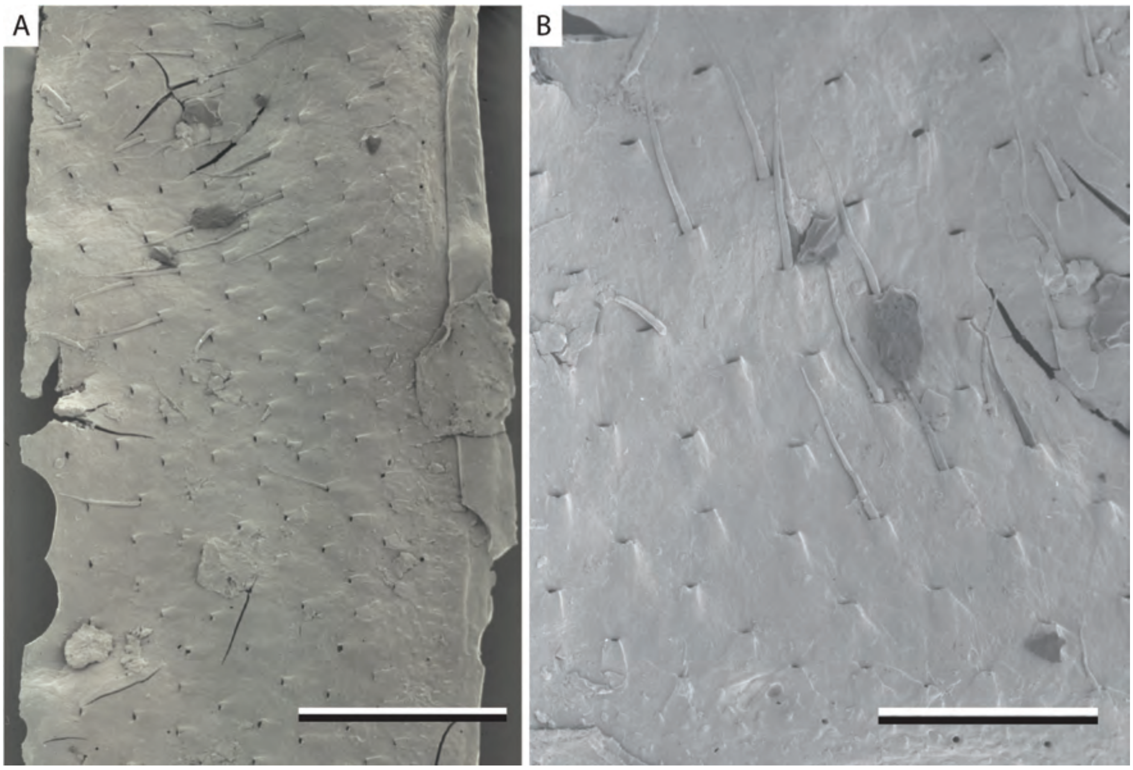


Figure 4.8: A fragment of arthropod carapace recovered from the acid maceration of the silicified peat in the Prince Charles Mountains.
A. Exoskeleton fragment, scale bar = 100 μm.
B. Enlargement of setae, scale bar = 50 μm.

4.4.4 Comparison with Late Pennsylvanian Psaronius communities

Perhaps the most studied Palaeozoic plant-insect association is that of the Late Pennsylvanian *Psaronius* tree fern from the Calhoun Coal (Labandeira, 1998a), the Lower Permian of Germany (Rößler, 2000) and the Upper Permian of Yunnan Province, southwest China (D'Rozario et al., 2011a). The *Psaronius* tree fern formed a plant-arthropod-fungi component community which persisted from the Late Pennsylvanian of Euramerica to the Permian wetlands of Cathaysia as wetland plant communities migrated through the Late Palaeozoic (Hilton and Cleal, 2007; D'Rozario et al., 2011a). Like the early Late Pennsylvanian *Psaronius* communities of the Illinois Basin (Labandeira, 1998a) and northern Germany (Rößler, 2000; Rössler, 2006), the range of functional feeding groups preserved in the *Glossopteris* community represented in the PCMs silicified peats appears to constitute a component community (Root, 1973). A component community (or source community) consists of the source plant, in this case *Glossopteris*, and all herbivores consuming this plant and nutritionally derivative feeding guilds (Root, 1973; Lawton, 1976; D'Rozario et al., 2011b). The finer features of coprolites and feeding traces are different between the *Psaronius* and glossopterid communities indicating that separate species of invertebrates were involved, but the general similarities in herbivory and detrivory between these assemblages indicates that a similar ecological structure was established in both high-latitude and palaeotropical mire systems (Table 2). Studying component communities in the fossil record could provide insights into long-term evolutionary trends such as whether plant-animal associations persist through time, as appears to be the case in the *Psaronius* community, or if host switching is common (Labandeira, 1998a).

Table 2. Comparison of the major feeding traits and herbivore/detritivore invertebrates and their damage associated with late Palaeozoic palaeoequatorial *Psaronius* and high southern latitude glossopterid component communities (with reference to D'Rozario et al., 2011b).

Feeding trait	***Psaronius* component community**	**PCM glossopterid component community**
Root-boring	Feeding on aerenchymatous root tissue	Feeding on *Vertebraria* root tissues
Stem-boring	Boring in *Psaronius* trunk ground parenchyma	Boring in *Australoxylon* stem wood
Folivory	Surface abrasion of *Pecopteris* pinnules	Known on *Glossopteris* from elsewhere in Gondwana. Possible leaf mining, though likely represents selective detritivory
Detritivory	Detritivore pith-boring in Psaronius stem parenchyma; probable myriapod or insect producer	Leaf litter detritivory on shed plant organs; probable myriapod or insect producer
Palynivory/ Sporivory	Palynivory of *Scolecopteris* sporangial tissue and *Punctatisporites* spores	Coprolites composed entirely of *Glossopteris* pollen. Excavations and coprolites from obligate herbivores of fern and glossopterid microsporangia; possibly coleopterans
Galling	Galling of inner parenchyma of *Stipitopteris rachis* demonstrating insect holometaboly	Known on *Glossopteris* from elsewhere in Gondwana
Piercing and sucking	Piercing and sucking damage in xylary tissue of *Stipitopteris rachis*	Known on *Glossopteris* from elsewhere in Gondwana
Coprophagy	Mite feeding on larger, probable insect coprolites	Presently unknown/unrecognised in *Glossopteris* community
Mycophagy	Coprolites containing fungal remains as part of a range of contents	Coprolites composed entirely of fungal remains inside *Vertebraria* and *Australoxylon* woods

4.5 Summary of findings

(1) The Permian swamp-forest biotas of Gondwana reveal a diverse array of plant-arthropod-fungal interactions; several of these categories (root boring, trunk wood boring, pollenivory, sporivory, folivory, fungivory) are represented in the siliceous permineralised glossopterid-dominated plant assemblages from the lower Bainmedart Coal Measures in the Prince Charles Mountains.

(2) Coprolites preserved within plant tissues and dispersed within the silicified peat matrix reveal, by way of transmitted light and scanning electron microscopy, producer organisms with variable feeding strategies – some feeding on specific plant tissues, others adopting generalist feeding behaviours. These feeding strategies include xylophagy, saproxylophagy, folivory, detrivory, microsporangial feeding and mycophagy.

(3) The first evidence of putative oribatid mite feeding on *Vertebraria* root tissues of the *Glossopteris* plant has been found, providing feedback on the biology of the root organs. It suggests that at least some roots were accessible to borer organisms in surficial or shallow soil conditions lending support to the hypothesis that some roots of this type may have been aerial in nature (pneumatophores).

(4) The diversity of plant organs being exploited by arthropod herbivores reveals that like the tree fern *Psaronius* in the late Palaeozoic tropics, the *Glossopteris* tree formed the basis for a complex ecosystem of herbivores, detritivores, saprotrophs and mycophagous organisms in Permian high southern latitudes.

CHAPTER 5: PERONOSPOROMYCETES (OOMYCOTA) FROM A MIDDLE PERMIAN PERMINERALISED PEAT WITHIN THE BAINMEDART COAL MEASURES, PRINCE CHARLES MOUNTAINS, ANTARCTICA

5.1 Background

The Peronosporomycetes (also known as Oomycota or water moulds) are a class of organisms belonging to the phylum Heterokontophyta, which also includes autotrophs such as diatoms and brown algae (David, 2002; Petersen and Rosendahl, 2000; Krings et al., 2010a). Due to superficial similarities in their filamentous morphology, spore-like oogonia (egg-containing sacs) and life habits, the Peronosporomycetes have in the past been grouped with the true fungi (Dick, 2001a). However, they can be distinguished by the morphology of the motile stage of their life cycle, in which the zoospores possess two differently shaped flagella used for propulsion; a lateral whip flagellum and a one-haired tinsel flagellum (Krings et al., 2011a). Peronosporomycetes differ fundamentally from true fungi on a cellular level since their cell walls are composed of cellulose and hydroxyproline as opposed to chitin (Dick, 2001a; Krings et al., 2011a), and the cell nuclei contained in the hyphae-like filaments are diploid as opposed to haploid in true fungi (Dick, 2001a).

Peronosporomycetes are saprotrophs or parasites (Phillips et al., 2008). Some are major plant and animal pathogens in modern ecosystems that are responsible for well-known plant diseases, such as potato blight (*Phytophthora infestans*), sudden oak death (*Phytophthora ramorum*), blister rusts and downy mildews (Dick, 2001a). They are currently responsible for the widespread larch dieback seen in *Larix decidua* in the UK and northern Europe (Dick, 2001a; Christensen, 1951; Spring and Thines, 2004; Grünwald et al., 2008; Grünwald, 2012), major damage to tropical commercial plant species (Erwin and Ribiero, 1996), and extensive death of selected plants in temperate forests and heathlands in the Southern Hemisphere (Von Broembsen and Kruger, 1985; Dell et al., 2005). Peronosporomycetes are capable of reproducing both asexually and sexually (Dick, 2001a; Dick, 1995). Asexual reproduction initiates with the formation of a zoosporangium, from which primary and secondary bi-flagellated motile zoospores are released. When reproducing sexually, the male nuclei are injected directly into the oogonium (Dick, 1995; Bhattacharya et al., 1991). Zoospores achieve dispersal by means of flagellar propulsion through water films either in soil pore water or on the surface of plants and can also spread through overland flow into fluvial and lacustrine environments. Dispersal is, therefore, favoured in moist, damp environments where the zoospores gravitate towards chemical attractants released by plants such as amino acids, sugars, ethanol and acetaldehyde (Heungens and Parke, 2000).

Krings et al. (2011a) reviewed the fossil record of the Peronosporomycetes and concluded that all the reported occurrences of this group older than Devonian are dubious or inconclusive. Confident Palaeozoic and early Mesozoic records are restricted to a small number of occurrences in Devonian, Carboniferous and Triassic permineralised peats and sinter deposits (Dick, 2001a; Schwendemann et al. 2009). These include the Devonian Rhynie Chert (Taylor et al., 2006; Krings et al., 2012b), Carboniferous coal balls from the lower coal measures of the UK (Williamson, 1878, 1880, 1883), Upper Mississippian cherts from France (Krings et al., 2010b), the Upper Pennsylvanian Grand-Croix cherts of France (Krings et al., 2009), and Middle Triassic silicified peats from the Fremouw Peak locality in the Transantarctic Mountains of central Antarctica (Schwendemann et al., 2009). Similar unpublished spinose spore-like bodies are also known from the Upper Triassic of Hopen, Svalbard Archipelago, but are attributed to Ascomycetes (C. Strullu and S. McLoughlin unpublished data). Multilayered oogonium-like structures possibly attributable to Peronosporomycetes have also been reported from a Jurassic hot spring deposit in Patagonia, Argentina (García-Massini et al., 2012b). Other possible examples of Peronosporomycetes have been documented from amber (Poinar, 1992; Schmidt et al., 2004; Schmidt et al., 2008; Adl et al., 2011). However, it is difficult to confidently resolve the affinity of those examples. It has been suggested that outgrowths from a Lower Pennsylvanian fungal sporocarp from Great Britain could represent an example of saprotrophic Peronosporomycetes (Krings et al., 2011b). A possible peronosporomycete affinity has been suggested for some acritarchs (Krings et al., 2011a; Pirozynski, 1976a) based on similarities in their morphology to oogonia of some extant water moulds.

Their sparse fossil record is unfortunate for understanding the evolution of feeding guilds and energy flow within terrestrial communities, since the Peronosporomycetes are important decomposers and parasites in modern ecosystems, particularly in damp soils and freshwater habitats (Jobard et al., 2010), and are also present in the marine realm (Cook et al., 2001). Peronosporomycetes are also significant in a broader evolutionary context since they are possibly among the earliest differentiated lineages of eukaryotes based on phylogenetic analyses of molecular data (e.g. Pirozynski, 1976a, 1976b; Porter, 2006; Bhattacharya et al., 2009).

The Permian cherts (silicified peats) of the Prince Charles Mountains contain a range of microbial elements within a glossopterid- and cordaitalean- (gymnosperm) dominated mire palaeoecosystem (McLoughlin and Drinnan, 1996; Holdgate et al., 2005). The microbial remains are preserved in exquisite cellular detail and retain morphological characters that are not preserved outside of Konservat-Lagerstätten, fossil-bearing deposits with exceptional fidelity of preservation (Briggs and Gall, 1990). Microscopic remains within the permineralised peat include delicate organs such as fungal hyphae, spores, and invertebrate exoskeleton parts (Holdgate et al., 2005; McLoughlin et al., 1997; Slater et al., 2011). Some of these fragile organs are even found within invertebrate coprolites preserved within the peat matrix or inside plant tissues (Slater et al., 2012). Two new forms of peronosporomycete oogonia are here described from the Toploje Member chert of the Prince Charles Mountains that are distinguished from each other primarily by differences in the length and density of the branched external spines. The addition of Peronosporomycetes to the inventory of preserved elements in the fossil community from the Prince Charles Mountains expands the known biodiversity and trophic guilds of the high-latitude peat-forming forests of the Permian.

5.2 Materials and methods

Specimens are held in the palaeobotannical collections at the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Frescativägen 40, 114 18, Stockholm. Specimen numbers of the material described in this study are; NRM S097800-01, NRM S087932-01, NRM S087932-01-02, NRM S088053-01, NRM S088061-01, NRM S088072-01.

Thirty-five thin sections of the chert were prepared for the analysis of diminutive components of the peats because this method has been shown to reveal greater optical detail of many microbial components than obtainable using the acetate peel technique (see Taylor et al., 2011). Images were processed and figures compiled using Adobe Photoshop and Illustrator CS4 graphics packages. Peronosporomycetes was reclassified by Dick et al. (1999), however it is important to note that the alternative names for this clade (Oomycetes and Oomycota) are in common circulation in the scientific literature (David, 2002; Schwendemann et al., 2009). Although these organisms are not true fungi, their morphological features are still described using mycological terminology. Therefore, this chapter will describe the hyphae-like filaments as hyphae for consistency with other current literature.

5.3 Systematic palaeontology

5.3.1 Order and family

Kingdom Straminipila M.W. Dick, 2001(a)
Phylum Heterokonta Cavalier-Smith, 1986
Subphylum Peronosporomycotina M.W. Dick, 2001(a)
Class Peronosporomycetes M.W. Dick, 2001(a)
Order Combresomycetales order nov. B. J. Slater, S. McLoughlin et J. Hilton, 2013

MycoBank number: 804720

Diagnosis

Peronosporomycetes with oogonia having robust ancyrate sculptural elements.

Remarks

The new order differs from other groups of equivalent rank in the Peronosporomycetes by the thick wall and robust ancyrate sculptural elements on the oogonia. Oogonia of the Peronosporales and Pythiales may have punctate, papillate, verrucate or simple spinose ornamentation, but none is known to have complex branched sculptural elements (Dick, 2001b). The new order contains a single extinct family diagnosed below.

Family Combresomycetaceae fam. nov. B. J. Slater, S. McLoughlin et J. Hilton, 2013

MycoBank number: 804721

Diagnosis

Combresomycetales with oogonia having one to two orders of terminal branching on the conical sculptural elements.

Etymology for order and family

Derived from the type genus *Combresomyces*.

Genus *Combresomyces* Dotzler N, Krings M, Agerer R, Galtier J et Taylor TN 2008.

> *Type species*
>
> *Combresomyces cornifer* Dotzler N, Krings M, Agerer R, Galtier J et Taylor TN 2008; upper Viséan; central France.

5.3.2 Combresomyces caespitosus

Combresomyces caespitosus sp. nov. B. J. Slater, S. McLoughlin et J. Hilton

> *Holotype*

NRM S087800-01 (Figure 5.1, image H)

Type locality, stratum and age

Grid reference 70˚49′19″S, 68˚03′54″E (elevation 162 m), 1.4 km east of Radok Lake (Figure 2.2), northern Prince Charles Mountains, Antarctica; uppermost Toploje Member, Bainmedart Coal Measures; Middle Permian (Roadian to Wordian).

Etymology

Latin – tufted or clumped; referring to the tufted branches that cap papillae.

MycoBank number: 803924

Diagnosis

Spherical oogonia having a main body <95 μm in diameter, bearing 6–20 μm long, hollow, slender, conical papillae with at least two orders of strongly divergent, sharply pointed, apical branches. Oogonium attached via a short stalk with single septum to parent hypha 21 μm wide. Papillae spaced 10–20 μm apart.

Description

The oogonia are spherical with a surface ornamentation consisting of hollow, regularly and densely spaced papillae, which bifurcate at least twice to form a multi-branched terminal crown (Figure 5.1; Images A–L). This ornamentation interlocks to give the impression of a reticulum in light microscopic examination of some specimens (Figure 5.1; Images A–C, G).

The main body of the oogonium is 40–95 µm in diameter. The wall is 4–15 µm thick. Sculptural elements (papillae and their crowns) are 5–7 µm in basal width and 6–20 µm tall, of which 3–10 µm is the branched crown. The papillae apices bifurcate twice typically and have sharp tips. Papillae are spaced 10–20 µm apart.

None of the specimens demonstrates a connection to a widespread network of aseptate hyphae that is present in the peat, although one specimen is connected to a 32 µm long solitary parental hypha. This parental hypha is 21 µm wide and attaches via a septum to a truncate basal extension of the main oogonium body (Figure 5.1; Image H). Other oogonia have truncate extensions or breaks in the ornament where the parental hypha presumably attached. It is difficult to discern whether the oogonia have any preserved contents; some specimens house indistinct structures that may represent degraded oospores (Figure 5.1; Image J) but their identity is inconclusive. Antheridia have not been conclusively identified.

Remarks

This form occurs dispersed throughout the silicified peat matrix in approximately 50% of the studied thin-sections. It is particularly found in association with accumulations of plant debris around *Vertebraria* (glossopterid roots) and matted leaf deposits of *Glossopteris* and *Noeggerathiopsis*.

Although known to have a conservative morphology spanning the Pennsylvanian to Middle Triassic (Schwendemann et al., 2009), *Combresomyces* oogonia show subtle differences in size and ornamentation between assemblages of different stratigraphic age. *Combresomyces caespitosus* sp. nov. differs from *Combresomyces cornifer* (Dotzler et al., 2008) and *Combresomyces williamsonii* (Strullu-Derrien et al., 2011) in several respects including slightly denser ornamentation, which abuts or interlocks to form a pseudo reticulum. This feature is not seen in either *C. cornifer* (Dotzler et al., 2008) or *C. williamsonii* (Strullu-Derrien et al., 2011), in which the tips of the ornament remain widely spaced. The oogonia of *C. caespitosus* are larger than specimens of *C. cornifer* from the Pennsylvanian (<40 μm in diameter: Dotzler et al., 2008) but smaller than the large oogonia of *C. cornifer* known from the Middle Triassic (up to 110 μm in diameter: Schwendemann et al., 2009). The wall of the oogonium in *C. caespitosus* is generally thicker (4–15 μm) than that of both *C. cornifer* (described as *ca* 1 μm by Dotzler et al., 2008) or *C. williamsonii* (described as thin-walled by Strullu-Derrien et al., 2011), and the truncate attachment to the parental hypha in *Combresomyces caespitosus* sp. nov. protrudes further from the main body of the oogonium.

The dense multi-branched spines of *Combresomyces caespitosus* oogonia, though markedly smaller, show remarkable similarities in basic morphology to the branched ornamentation of some lycophyte megaspores found in the same beds (see *Singhisporites hystrix* in Chapter 3 and Slater et al. 2011). These similarities might be due functional parallels between these organs as biological dispersive units. The increased surface area generated by densely ramified appendages might have conferred improved buoyancy for dispersal of both megaspores and oogonia in Permian wetland settings (Schwendemann et al., 2009), or have provided a favourable mechanism for attachment of these structures to other materials (e.g., plant debris in the case of the peronosporomycete saprotroph, or conspecific microspores in the case of the lycophyte megaspores, or even attachment to arthropod distributers). Surface sculptures of a broadly similar morphology occur in many unrelated groups and likely performed an important biological function in life (e.g. Hemsley et al., 2004).

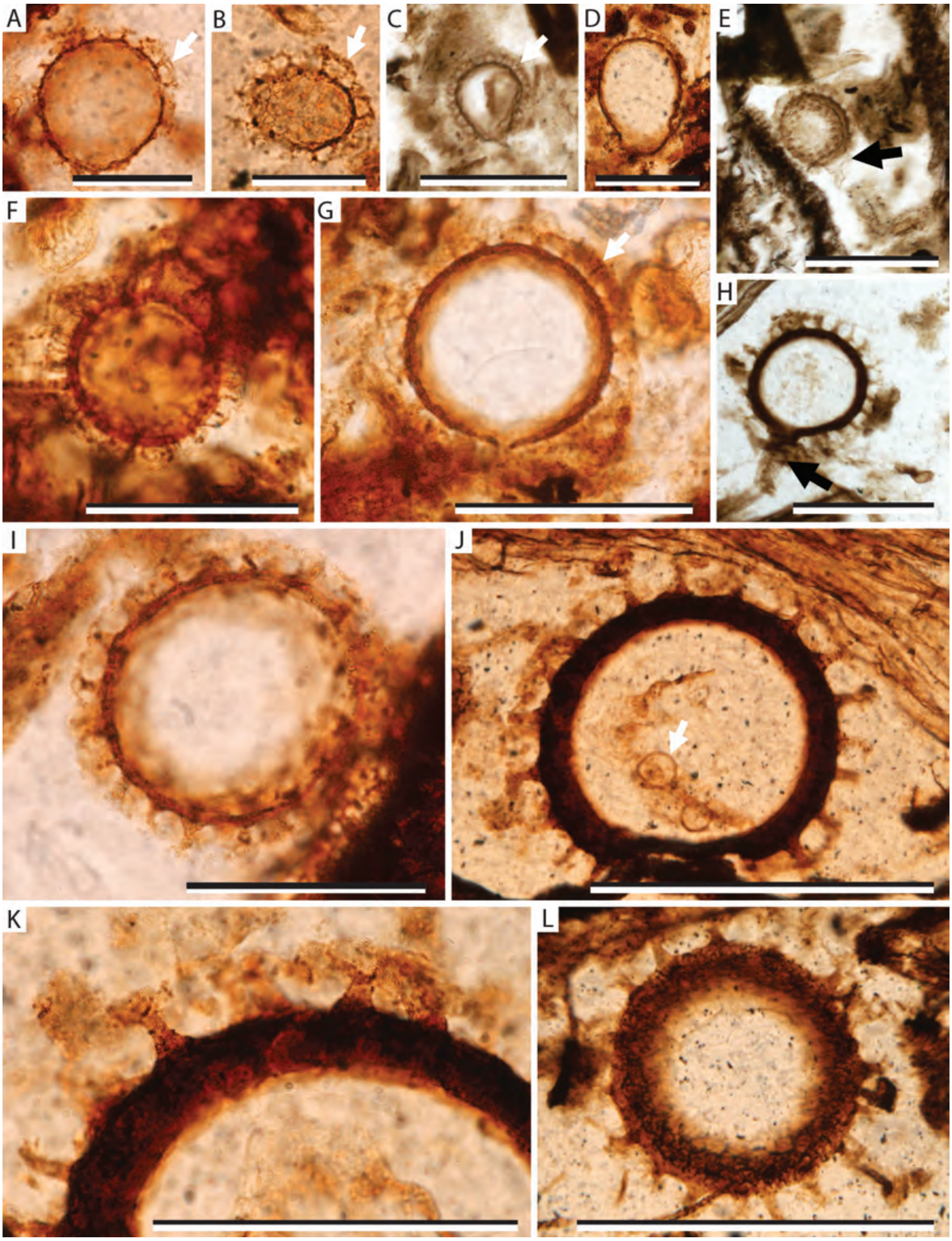


Figure 5.1

Figure 5.1 (previous page): *Combresomyces caespitosus* sp. nov. (Peronosporomycetes: Combresomycetales); Oogonium morphotype with dense coverage of spines.
A. NRM S087932-01-02, scale = 50 µm.
B. NRM S087800-01, scale = 50 µm.
C. NRM S088061-01 oogonium lies within a large coprolitic mass, scale = 100 µm.
D. S087800-01, scale = 50 µm.
E. NRM S088072-01, arrow indicates position of a possible fragment of hypha extending from oogonium, scale = 100 µm.
F. S087800-01, scale = 50 µm.
G. S087800-01, scale = 50 µm.
H. NRM S087800-01 (holotype specimen), arrow indicates truncate extension with attached subtending hyphae, scale = 100 µm.
I. NRM S087932-01-02, scale = 50 µm.
J. NRM S087800-01, arrow indicates indeterminate spherical internal contents of oogonium, scale = 100 µm.
K. NRM S087800-01, enlargement of wall and ornament of oogonium in image J, scale = 50 µm.
L. NRM S087800-01, scale = 100 µm.
Arrows in images A–C and G indicate interlocking ornamentation.

5.3.3 Combresomyces rarus

Combresomyces rarus sp. nov. B. J. Slater, S. McLoughlin et J. Hilton

Holotype

NRM S087932-01-02 (Figure 5.2, image F)

Type locality, stratum and age

Grid reference 70˚49′54″S, 68˚03′05″E (elevation 166 m), 1.25 km east of Radok Lake (Figure 2.2), northern Prince Charles Mountains, Antarctica; uppermost Toploje Member, Bainmedart Coal Measures; Middle Permian (Roadian to Wordian).

Etymology

Latin – sparse; referring to the widely spaced papillae.

MycoBank number: 803925

Diagnosis

Spherical oogonia having a main body <65 μm in diameter, bearing 12–20 μm long, hollow, broad, conical papillae that terminate in at least one bifurcation producing a pair of, generally acutely divergent, sharply pointed branches. Oogonium wall locally bearing a short truncate extension marking attachment point to parent hypha. Papillae spaced 15–20 μm apart.

Description

The oogonia are spherical with sparsely ornamented surfaces. The ornamentation consists of widely spaced, robust, hollow papillae with elongate extensions that bifurcate at least once (Figure 5.2). The oogonium has a central body 38–65 µm in diameter with a wall 2–5 µm thick. The sculptural elements (papillae and apical spines) are 12–20 µm in total length, of which 5–8 µm represents the apical branches. Branch apices are sharply pointed. Papillae are 5–8 µm in basal width and spaced 15–20 µm apart – their bases being confluent to produce intervening broad U-shaped transverse sections of the oogonial wall.

None of the specimens demonstrates a connection to a widespread network of aseptate hyphae found within the peat matrix although some were found connected to short lengths of solitary parental hypha (Figure 5.2; Images C, F, K). The oogonia of the holotype specimen is connected to a 22 µm long length of solitary parental hypha. The parental hypha is 35 µm wide and attaches via a septum to a truncate basal extension of the main oogonium body (Figure 5.2; Image F). A truncate extension marked by a break in ornamentation is evident on some specimens (Figure 5.2; Images B and H) and is interpreted to be the attachment point between the oogonium and the parent hypha. The contents of the oogonia are difficult to elucidate. Antheridia have not been identified although it is notable that the length of hypha in one specimen (Figure 5.2; Image K) is somewhat morphologically similar to the outline expected if the antheridium was formed as a collar-like structure at the base of the oogonium in an amphigynous arrangement. However, the preservation is insufficient to confirm or refute this and the structure is here interpreted as a length of parental hypha.

Remarks

This species is less abundant than *Combresomyces caespitosus* in the Toploje Member chert fossil ecosystem, occurring in approximately 25% of the thin sections prepared from the peats. This form occurs primarily in association with *Vertebraria* and *Australoxylon* (respectively, the root and stem wood of glossopterids). Although of equivalent absolute length, the sculptural elements in *Combresomyces rarus* sp. nov. are proportionally longer in relation to the central body of the oogonium than in *C. caespitosus*, and the ornament does not appear to interlink to form a pseudoreticulum.

The ornament of *C. rarus* is more akin to that of *C. williamsonii* (Strullu-Derrien et al., 2011) than *C. caespitosus*, although the papillae are much more widely spaced with the bases merging to form broad U-shaped transverse sections of the oogonial wall, a feature not seen in *C. williamsonii* (Strullu-Derrien et al., 2011). The ornament of *Combresomyces rarus* is also proportionally larger and less densely distributed than in *C. williamsonii* (Strullu-Derrien et al., 2011).

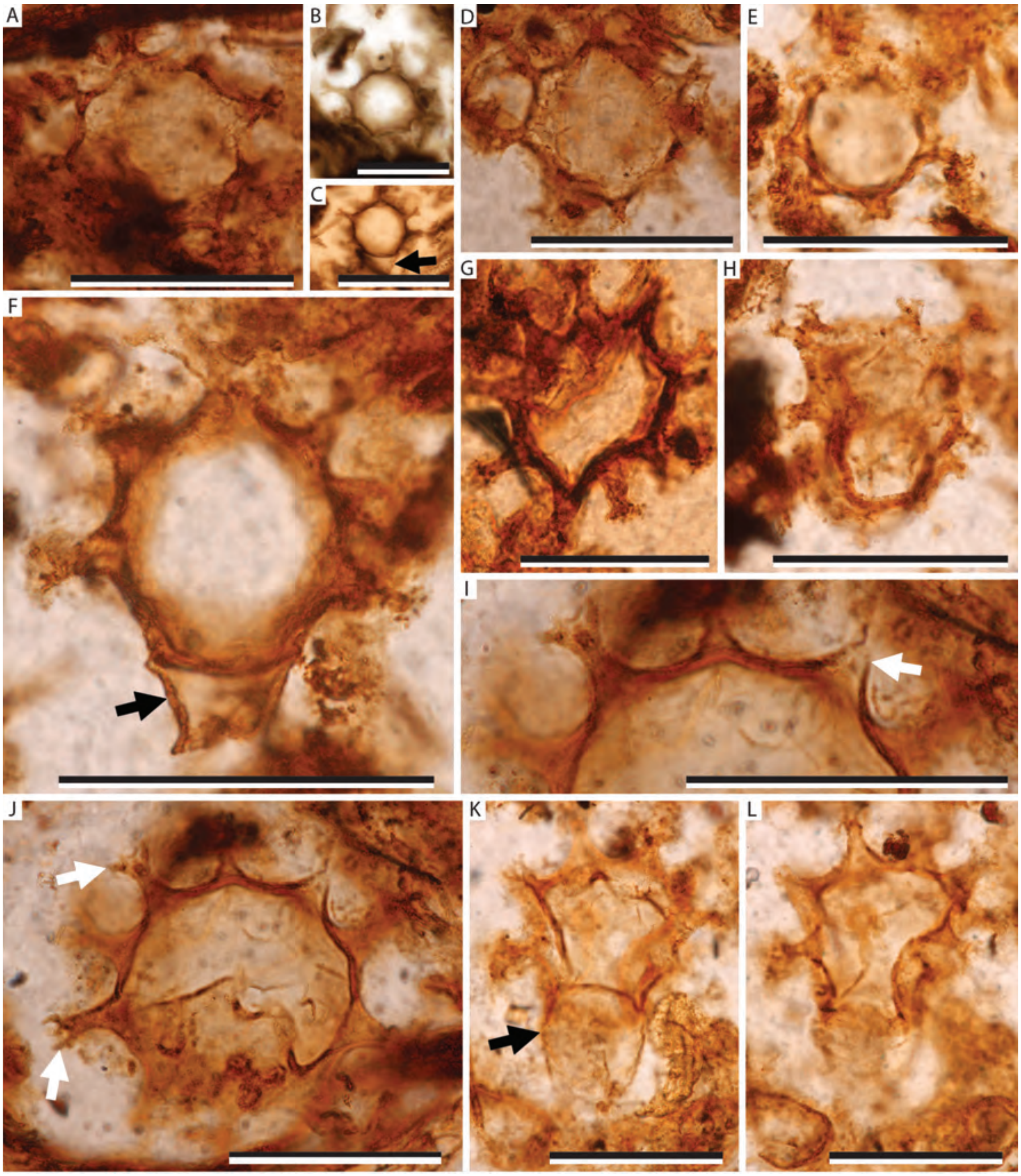


Figure 5.2

Figure 5.2 (previous page): *Combresomyces rarus* sp. nov. (Peronosporomycetes: Combresomycetales); scale bars = 100 µm unless stated otherwise. Oogonium morphotype with sparse coverage of spines; some oogonia contain indeterminate contents.
A. NRM S087932-01-02.
B. NRM S087932-01.
C. NRM S088053-01 arrow indicates attachment point to hyphae.
D. S087932-01-02.
E. S087932-01-02.
F. NRM S087932-01-02 (holotype specimen) arrow indicates attached subtending hypha.
G. NRM S087800-01.
H. NRM S087932-01-02.
I. NRM S087932-01-02 enlargement of oogonia wall and ornamentation, arrow indicates the hollow nature of the papillae, scale = 50 µm.
J. NRM S087932-01-02 arrows indicate branched crown of ornamentation, enlargement shown in image I, scale = 50 µm.
K. NRM S087932-01-02 arrow indicates attached subtending hypha.
L. NRM S087932-01-02 oogonium in image K in different focal plane highlighting the nature of the ornamentation covering the oogonium surface.

5.4 Discussion

We refer these fossils to the Peronosporomycetes based on their morphological similarity to examples of this biological class known from other late Palaeozoic and early Mesozoic assemblages, in which oogonia are more confidently associated with hyphae, e.g., *Combresomyces cornifer* (Schwendemann et al., 2009) and *C. williamsonii* (Strullu-Derrien et al., 2011). Similar isolated oogonia attributed to this group are also known from the Pennsylvanian of France (Krings et al., 2010a). Our confidence in attributing the fossils to the Peronosporomycetes is enhanced by several specimens (Figure 5.1; Image H, Figure 5.2; Images C, F, K) possessing a distinctly truncated extension from the main body of the oogonium that attaches to the parent hypha in the same way as specimens of *Combresomyces cornifer* (Schwendemann et al., 2009). This truncated extension is present in some fossil examples of Peronosporomycetes and in most extant forms, although it is absent in some (Krings et al., 2012b).

Acyrate-conate fossil oogonia attributable to Peronosporomycetes vary significantly over their stratigraphic range. Earlier forms, e.g., from the Pennsylvanian (Dotzler et al., 2008) are generally <40 μm in diameter, whereas Middle Triassic forms reach 110 μm in diameter (Schwendemann et al., 2009). The Prince Charles Mountains examples appear to be the first recorded Permian representatives of this group of Peronosporomycetes and possess distinctive ancyrate-conate oogonia of an intermediate size range (38–95 μm). Schopf (1970) figured what was described as; "the spiny spore with septate germinal tube, possibly fungal zygospore" illustrated in figure J of the Schopf (1970) paper, which may be a Permian peronosporomycete, though branched ornamentation is not visible on the original illustration. The apparently sparse fossil record of this group may in part be attributable to the past prevalence of the acetate peel technique in studying permineralised plant assemblages. Acetate peels have been shown to be inferior to thin sections in revealing the microorganisms preserved in silicified deposits (Taylor et al., 2011). Thin sections provide a greater depth of section (30–50 μm) and reveal greater clarity of characters in a range of fungi, fungi-like organisms and diminutive arthropods with thin-walled tissues than is obtainable with mounted acetate peels of ca 10 μm thickness (Taylor et al., 2011; Womack et al., 2012).

Ovoid structures possibly also representing oogonia have been reported attached to specimens of *Galtierella biscalithecae* from the Upper Pennsylvanian Grand-Croix Cherts from France (Krings et al., 2010a). These are also interpreted to be terminally inserted on the hyphae and but are typically oblong and longer than the oogonia described herein. Possible oogonia have also been reported from the Jurassic San Augustín hot spring deposit from Patagonia, Argentina (García-Massini et al., 2012b) although they lack the forked spines seen in the Prince Charles Mountains examples.

The oogonia of extant Peronosporomycetes, such as *Phytophthora* (de Bary, 1863), form terminally and have a range of morphologies from obpyriform to ellipsoid to ovoid (Mostowfizadeh-Ghalamfarsa et al., 2010). The two morphologies of peronosporomycetes evident in the Toploje Member peat are both covered in ancyrate conate/spinose ornamentation. Fossil examples of this style of ornamentation are numerous (Krings et al., 2011a; Schwendemann et al., 2009; Krings et al., 2010b; Strullu-Derrien et al., 2011). However, the order/family-level affinity of these bodies remains poorly resolved. Although extant Peronosporomycetes oogonia bear ornamentation, none appears to have complex branched crowns on the sculptural elements, a character which is used to distinguish the new order. Some modern *Pythium* oogonia have robust spinose ornamentation (Beakes et al., 1995; Baptista et al., 2004), especially those of *P. oligandrum* Drechsler (1946), (Brozova, 2002), and *P. prolatum* Hendrix and Campbell (Paul et al., 1999), but the extant forms typically lack forked apices on the spines. Other extant forms that exhibit broadly similar robust spinose/conate ornamentation include *Aphanomyces stellatus* de Bary, (1860), (Hallett and Dick, 1986; Diéguez-Uribeondo et al., 2009). Among extant forms, *Pythium prolatum* demonstrates particular similarities with those forms from the Toploje Member peat since it possesses the most heavily ornamented oogonia and has a similar truncate extension adjoining the parental hyphae (Paul et al., 1999). It seems likely that the various fossil forms represented by oogonia with truncate or branched papillae (including *Combresomyces, Frankbaronia* and perhaps *Hassiella*, *Galtierella* and some members of *Zygosporites*) represent a widely distributed extinct late Palaeozoic to early Mesozoic clade within the Peronosporomycetes and are here placed in the new order Combresomycetales. This group is distinguished by its apically branched conate to spinose ornamentation on the surface of the oogonia, but known morphological characters are as yet insufficient to infer close a phylogenetic relationship with any one of the extant orders of Peronosporomycetes.

Despite the poor fossil record of this extremely diverse class (attribution of several fossil examples being equivocal due to the difficulty in identifying diagnostic characters), the documentation of the group's occurrence in palaeocommunities is significant since they are important shapers of modern ecosystems. Ancient Peronosporomycetes, like their modern counterparts, probably played a significant role in recycling organic matter, via saprotrophy, and potentially in parasitizing plants and animals in the Permian high-latitude mire ecosystems. In terms of life habit and ecology, both *Combresomyces caespitosus* sp. nov. and *Combresomyces rarus* sp. nov. appear likely to have occupied a saprotrophic lifestyle. This is based on the association of the oogonia of both species with a broad range of adjacent plant tissues. Neither *C. caespitosus* nor *C. rarus* are consistently associated with any one plant type in the permineralised peats, which suggests they did not have a well-developed parasitic relationship with a particular host species.

The recognition of robustly ancyrate-conate Peronosporomycetes oogonia in Middle Permian silicified peats helps bridge the large (latest Carboniferous to Middle Triassic) gap in the group's fossil record noted by Schwendemann et al. (2009) and attests to the broad climatic tolerance of this group, spanning the palaeotropics to cool palaeotemperate belt; fossil Peronosporomycetes oogonia are known from palaeolatitudes as divergent as the palaeotropics of the Viséan of central France (Dotzler et al., 2008; Krings et al., 2007) to the high palaeolatitudes (ca 65°–70° S) of the Prince Charles Mountains (this study) based on broadly accepted continental reconstructions (Scotese, 1997; Blakey, 2012). Their broad stratigraphic and palaeoclimatic distribution also suggests that the group as a whole was not tied to particular plant hosts; the host floras from the Carboniferous to Triassic variably being dominated by arborescent lycophytes, glossopterids, corystosperms and conifers (Krings et al., 2011a; Schwendemann et al., 2009; Dotzler et al., 2008). This versatility with respect to plant hosts and their distribution through the late Palaeozoic and into the Triassic indicates that Combresomycetales were generalist or opportunistic organisms that were little affected by the end-Permian biotic crisis (Erwin, 2006) and the disappearance of peat-forming ecosystems for over 5 million years during the Early Triassic (Retallack et al., 1996; Vajda and McLoughlin, 2007).

5.5 Concluding remarks

Oogonia with multi-branched sculptural elements do not appear to be represented amongst modern Peronosporomycetes based on our survey of the literature, although published details of oogonia and oospore morphology are admittedly sparse. Nevertheless, the obvious similarities in oogonium shape, size, process morphology and hyphal attachment between the Permian Antarctic forms reported here and fossils documented from the Devonian to Triassic elsewhere in the world suggest that these forms represent an extinct but once widespread Palaeozoic to early Mesozoic branch of the peronosporomycete clade. A new order and family of fossil Peronosporomycetes, Combresomycetales B. J. Slater, S. McLoughlin et J. Hilton and Combresomycetaceae B. J. Slater, S. McLoughlin et J. Hilton, are established on this basis. Two new species of *Combresomyces* are distinguished primarily on subtle differences in oogonium size and ornamentation. These represent the first examples of this group documented from the Permian of Antarctica and add to the biodiversity and trophic levels recognised in high-latitude Permian mire ecosystems of Gondwana. The lack of a consistent association between the oogonia and any particular plant fossils in the permineralised peat or of any reaction tissue in adjacent plant remains suggests that these *Combresomyces* species were saprotrophs rather than parasites. Their complex ornamentation may have been an adaptation for aquatic dispersal or adhesion to host materials in the extensive wetlands of the Gondwanan Permian, yet this group of elaborately sculptured Peronosporomycetes as a whole were sufficiently generalist in their ecology to survive the demise of peat-forming ecosystems during the first five million years of the Triassic.

CHAPTER 6: A HIGH-LATITUDE GONDWANAN LAGERSTÄTTE: THE PERMIAN PERMINERALISED BIOTA OF THE PRINCE CHARLES MOUNTAINS, ANTARCTICA

6.1 Background

The Permian was a crucial period in the history of terrestrial life; the Cisuralian (Early Permian) saw the diachronous demise of the Carboniferous-style wetland floras that had dominated equatorial Euramerica during the Carboniferous and Cathaysia during the Asselian–Kungurian (Knoll, 1984; Hilton et al., 2002; Hilton and Cleal, 2007). In the Southern Hemisphere, the Permian witnessed the flourishing of glossopterid cool-temperate swamp forests, which dominated southern Gondwana until their extinction at the end of the period (e.g. White, 1998; McLoughlin, 2011b). Our knowledge of the diversity, vegetation structure, ecology, biotic interactions, and trophic links within these ecosystems is unfortunately limited by a paucity of konservat lagerstätten in comparison to other time periods in Earth history (e.g. Briggs and Gall, 1990; Selden and Nudds, 2004; Cascales-Miñana, 2011). This preservational bias has hindered our understanding of the developments in austral terrestrial ecosystems during the Permian. A more detailed picture of the trophic complexity and inter-relationships between plants, insects and soil microorganisms would enhance our understanding of how terrestrial communities evolved in the wake of the Gondwanan glaciations up to the end-Permian biotic crisis. The end-Permian mass extinction, which purportedly eradicated up to 95% of marine species (Raup, 1979; Benton and Twitchett, 2003), marks the most significant reduction of diversity in the Phanerozoic. Unlike the Cretaceous/Palaeogene (K/Pg) extinction event 66 Ma, which was likely precipitated by an instantaneous impact mechanism (Alvarez et al., 1980; Vajda and McLoughlin, 2007), the extinction marking the end of the Palaeozoic world appears to have developed as a multiphase series of extinctions (Racki and Wignall, 2005; Yin et al., 2007; de la Horra et al., 2012) that were not necessarily synchronous between disparate regions (Rees, 2002). Evidence from several sources including brachiopod, bivalve, foraminiferal and plant extinctions, shows that major biotic disruptions began in the Capitanian (although often erroneously referred to as the ‘end-Guadalupian extinction’) and this was followed by a protracted diachronous decline in Palaeozoic life throughout the rest of the Permian (Yin et al., 2007; Bond et al., 2010). Discussion of the timing and proposed causes of the extinction(s) beginning in the Capitanian can be found in several sources (Racki and Wignall, 2005; Retallack et al., 2006; Yin et al., 2007; Clapham et al., 2009; Isozaki, 2009, 2010; Ali, 2010; Bond et al., 2010; de la Horra et al., 2012; Retallack, 2012; Benton and Newell, 2013).

The Roadian–Wordian-aged Toploje Member chert of the Prince Charles Mountains (PCMs) preserves, in exceptional three-dimensional detail, the permineralised remains of a terrestrial mire ecosystem prior to the biotic decline that began in the Capitanian and continued through the Lopingian until the Permo-Triassic boundary (Yin et al., 2007; Retallack et al., 2006; Bond et al., 2010; de la Horra et al., 2012; Retallack, 2012). The Toploje Member chert offers a snapshot of the final phases of ‘stable’ terrestrial life before the crisis that engulfed and overthrew these ecosystems.

Aside from its significance in recording a key episode in terrestrial life, the Toploje Member chert also preserves an important *in situ* community of macro- and micro-organisms that constituted part of the high-latitude *Glossopteris* flora that typified vast expanses of southern Gondwana during the Permian (e.g. Anderson et al., 1999; Pigg and Nishida, 2006;

McLoughlin, 2011b) and contributed to the Southern Hemisphere's major economic coal resources. Organs of the *Glossopteris* plant constitute the bulk of the peats, and are co-preserved with significant quantities of *Noeggerathiopsis* leaves and a range of less abundant herbaceous plants (McLoughlin and Drinnan, 1996; Holdgate et al., 2005). The structure of Gondwanan coal is relatively well understood in terms of maceral content and distribution (e.g. Navale and Saxena, 1989; Diessel and Smyth, 1995; Van de Wetering et al., 2013), but how this relates to the taxonomic representation of plant constituents and their component parts is less well resolved, since the transition from peat to coal involves significant volumetric and compositional changes in coal due to differential compaction and diagenetic loss of volatiles. Quantitative comparison of the constituents of the Toploje Member permineralised peat and coals from the same stratigraphic unit provide a means of evaluating the original composition of the coal-forming biota and the changes in coal composition with diagenesis.

The diversity of species in ancient terrestrial ecosystems is inherently difficult to assess. Although not without taphonomic filtering, marine deposits tend to offer a much richer sampling of the shelly biota in the environment as a consequence of bioclast persistence and sedimentary sorting (see Cleal et al., 2012). Therefore, it falls to the patchy occurrences of terrestrial konservat lagerstätten to provide a more accurate picture of what life was like at any one place in time on land. Exceptional preservation occurs elsewhere in Antarctica during the Late Permian with silicified plant remains known from two main deposits in the central Transantarctic Mountains (Taylor et al., 1989). The Skaar Ridge silicified peat of the Transantarctic Mountains appears to derived from small lenses or possibly fluvially rafted mats of peat associated with volcaniclastic sediments, in contrast to the laterally extensive

Toploje Member chert representing a large autochthonous mire community preserved in a succession lacking volcanigenic sediments.

6.2 Material and methods

Samples of a range of sizes were collected from multiple localities along a low ridgeline where the Toploje Member chert is exposed (see Figure 2.2 in Chapter 2 for a map of the chert exposure). A variety of palaeobotanical techniques were then used to investigate the contents of the peats; blocks of the chert were sectioned using a Buehler Isomet 5000 linear precision saw. Following sectioning, acetate peels were produced from the blocks using the technique outlined by Galtier and Phillips (1999). The surface of each block was polished and then submerged in a shallow bath of cold 30% hydrofluoric acid solution for approximately 90 seconds in order to etch away the silica matrix and leave a thin layer of organic matter standing proud of the surface. Each block was then rinsed with distilled water, dried, then covered with acetone before laying a cellulose acetate sheet on the surface to create a peel that was then studied using a transmitted light microscope. Peels were found to be inferior to thin sections for the study of fungi, Peronosporomycetes and coprolites in accordance with the findings of Taylor et al. (2011) and where possible thin sections were preferentially produced for the study of these elements. Several samples from a range of localities across the peat outcrop were selected for bulk maceration in a cold 30% hydrofluoric acid solution. Samples were left in the solution for two weeks and then the remaining organic debris was extracted using a 150 micron nylon sieve. Sieved organic remains were then placed into a petri dish of distilled water and studied using an optical stereomicroscope. Plant, arthropod and fungal remains were then picked while hydrated using a fine art brush. Elements of interest were then mounted on aluminium stubs and sputter-coated with gold to enhance conductivity for imaging with a Hitachi S-4300 field emission scanning electron microscope. Scanning electron microscopy was conducted at the Swedish Museum of Natural History (Naturhistoriska riksmuseet). Several elements of the flora that were extracted via bulk maceration were also analysed using synchrotron X-ray tomographic microscopy. X-ray microtomography was conducted at the TOMCAT beamline of the Swiss Light Source, Paul Scherrer Institute, Switzerland (Slater et al., 2011) using the techniques described by Donoghue et al. (2006).

Quantitative analysis of the peat composition was made by point counting across 20 randomly selected thin sections at 200 μm increments for 4000 points. In addition 4 thin sections made from hand specimens containing abundant charcoal were selected for point counting to analyse variation in peat composition within microfacies affected by wildfire the Toploje Member chert.

The organic petrology of a selected set of Middle to Upper Permian coal samples from the Bainmedart Coal Measures was carried out by a commercial coal analytical contractor (Keiraville Konsultants Pty Ltd, Wollongong, Australia). Results from proximate analyses of these samples were presented by Holdgate et al. (2005); only the data on maceral proportions in the coals are presented here.

6.3 Biota

6.3.1 Composition of the silicified peat

The macrofloral diversity within the silicified peats is relatively low, being dominated by the constituent dispersed organs of arborescent glossopterid and cordaitalean gymnosperms.

Matted leaves of both *Glossopteris* (Glossopteridales) and *Noeggerathiopsis* (Cordaitales), together with roots (*Vertebraria*) and stem wood (*Australoxylon*) are the most prominent constituents of the peat (Holdgate et al., 2005; McLoughlin and Drinnan, 1996). However, the cryptic micro- and meso-fossil components of the peat reveal a much greater biotic diversity in the mire ecosystem than is evident from the macroscopic remains. The fossil micro-organism assemblage includes a broad range of fungal hyphae and reproductive structures together with superficially similar organisms such as Peronosporomycetes (Chapter 5 and Slater et al., 2013). Although arthropod exoskeleton fragments are sparse, disarticulated and fragmentary, a rich entomofauna is indicated by the wealth and diversity of invertebrate feeding traces and coprolite morphotypes, both dispersed in the peat matrix and preserved within specific plant organs (Weaver et al., 1997; Holdgate et al., 2005; Slater et al., 2012; see Table 3 for a list of the biota found to date in the peats). The preservation of groups such as saprotrophic Peronosporomycetes (Oomycota) adds to the sparse, but growing fossil record of these important elements of terrestrial ecosystems (Schwendemann et al., 2009; Krings et al., 2011a; Slater et al., 2013). These, together with a broad diversity of fungal interactions, show that the glossopterid plant was the primary host of a ‘component community’ of saprotrophs, herbivores and detritivores at high latitudes until the end-Permian extinction of this plant group. The roles of soil-inhabiting microorganisms in modern high-latitude peats are still poorly understood (Tveit et al., 2012), so additional investigation of fossil occurrences will improve our knowledge of the evolution of such ecosystems (Adl et al., 2011). The dispersed palynoflora in the silicified peat has not yet been fully documented but includes a broad range of fern, sphenophyte, and lycophyte spores and cycadophyte and pteridosperm pollen that attest to a much higher floristic diversity in the immediate vicinity of the mire ecosystem. Diverse glossopterid pollen morphotypes are also evident within the peat but significant intraspecific variation of the grains has been recorded within *Arberiella* (glossopterid) sporangia from the peat layer (Lindström et al., 1997) suggesting that apparent levels of glossopterid diversity in the ecosystem are inflated. Although *Paracalamites australis* (sphenophyte) axes occur sparsely as impressions in sediments of the Dragons Teeth Member overlying the Toploje Member, macrofossils of this group have not yet been identified in the silicified assemblage. A single undescribed herbaceous lycophyte taxon has been recorded from the permineralised peat (Holdgate et al., 2005).

Quantitative analysis of the relative abundance of the various organisms and their constituent organs/tissues contributing to the peat was undertaken by point counting across thin sections of the Toploje Member chert (Figure 6.1, A). The same method was used by Holdgate et al. (2005) on a different set of thin sections of the Toploje Member chert, although coprolites were not considered as a separate category in that study. The new results largely confirm the gross composition of the peat identified by Holdgate et al. (2005), although some differences were noted. *Vertebraria* roots form an even larger proportion of the total peat composition than was found in the previous study. Further, charcoal was found to be proportionally more abundant in this study. It is clear that the peats of the Toploje Member chert contain a higher proportion of subterranean components, such as roots, compared to subautochthonous canopy elements, such as leaves and seeds, than is evident in other Permian silicified peats, such as those of the Bowen Basin, Australia (McLoughlin, 1992). These differences attest to subtle variations in microfacies within the peat profile that will require further investigation to delineate their composition and genesis. Our preliminary assessment of this intra-peat compositional variation via a series of point counts on thin sections of specimens rich in charcoal (Figure 6.1, B) revealed plant assemblages dominated by charcoalified wood. In general these charcoal-rich microfacies contained much more woody material (both charcoalified and non-charcoalified) than is evident in the typical composition of the peat.

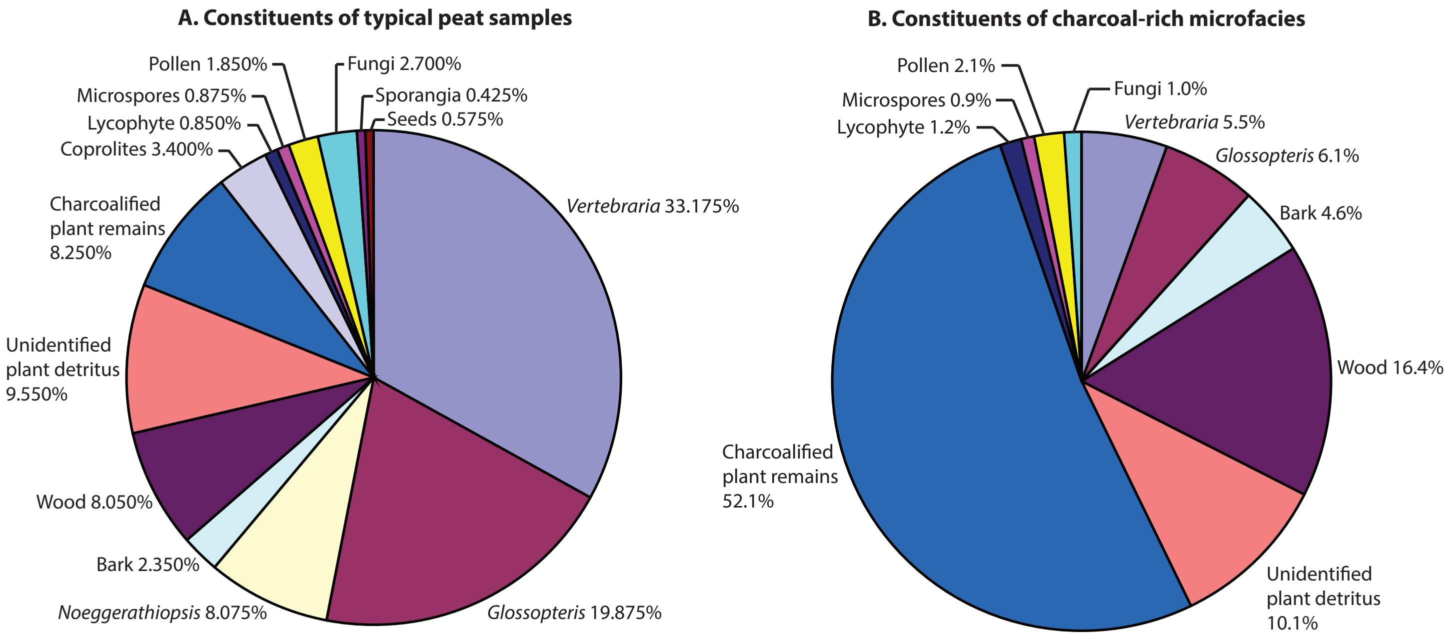


Figure 6.1: Pie charts detailing the relative proportions of organic constituents in:
A. Typical permineralised peat of the Toploje Member chert taken from 4000 point counts at 200 µm increments from 20 thin sections.
B. Charcoal-rich microfacies of the permineralised peat taken from 1000 point counts at 200 µm increments from 4 thin sections.
Small quantities of pyrite crystals, and the silica matrix that occur in the Toploje Member chert were excluded from the counts.

Table 3. Summary of the biota found in the Toploje Member chert to date.

Species/ Organism/ Organ/ Trace	**Affinity**	**Occurrence**	**Relative abundance**
Singhisporites hystrix	Megaspore (heterosporous Lycophyta)	Dispersed throughout peat matrix	Common; >50 specimens
Duosporites lambertensis	Megaspore (heterosporous Lycophyta)	Within peat matrix	Rare; 2 specimens
Banksisporites antarcticus	Megaspore (heterosporous Lycophyta)	Within peat matrix	Rare; 2 specimens
Herbaceous lycophyte	Heterosporous Lycophyta	Dispersed throughout peat matrix	Common; >40 specimens
Fern sporangia	Ferns (several taxa)	Dispersed throughout peat matrix	Relatively abundant; present in ~50% of samples
Vertebraria (at least two anatomical types)	Roots of the *Glossopteris* plant	Occurs throughout the peat matrix, commonly in dense ramifying mats	Abundant; present in almost all samples
Australoxylon (two species)	Wood of the *Glossopteris* (and possibly *Noeggerathiopsis*) plant	Occurs throughout the peat matrix, some microfacies are clearly rich in wood	Common; present in almost all samples
Glossopteris (possibly several species)	Leaves of the *Glossopteris* plant	Occurs throughout the peat matrix, commonly as thick deposits of matted leaves	Abundant; present in almost all samples
Noeggerathiopsis sp.	Leaves of Cordaitales	Occurs throughout the peat matrix, commonly as thick deposits of matted leaves	Common; present in almost all samples
Trichome-fringed cuticle	Gymnosperm with brachyparacytic stomata	Occurs sparsely dispersed throughout the peat matrix	Rare
Seed morphotype 1	Small (~1 mm) spinose seed: indeterminate gymnosperm	Occurs throughout the peat matrix, commonly in deposits rich in matted leaves	Relatively abundant; present in ~40% of samples
Seed morphotype 2	Small (~1 mm) smooth seed: indeterminate gymnosperm	Occurs throughout the peat matrix, commonly in deposits rich in matted leaves	Relatively uncommon; <10 specimens
Seed morphotype 3	Small (~1mm) winged seed: indeterminate gymnosperm	Occurs throughout the peat matrix, commonly in deposits rich in matted leaves	Relatively uncommon; <10 specimens

Fungal morphotype 1: non-septate/aseptate hyphae	Zygomycota	Dispersed throughout peat matrix	Common; present in almost all samples
Fungal morphotype 2: septate hyphae	Basidiomycota and Ascomycota	Dispersed throughout peat matrix	Common; present in almost all samples
Fungal morphotype 3: hyphae with swellings	Glomeromycota?	Occur dispersed throughout peat matrix	Common; present in almost all samples
Fungal morphotype 4: smooth-weakly ornamented spores	Smallest, smooth forms are probably chytrid zoosporangia	Occur dispersed throughout peat matrix	Common; present in almost all samples
Fungal morphotype 5: large smooth-weakly ornamented spores	Glomeromycota? Commonly have small chytrid fungi adhering to the external surface	Occur dispersed throughout peat matrix in samples rich in *Vertebraria* roots	Common; present in almost all samples
Fungal morphotype 6: spinose oblong spores	Ascospores (Ascomycota)	Occur dispersed throughout peat matrix commonly in clusters	Relatively abundant; present in ~50% of samples
Fungal morphotype 7: fungi within pollen	Chytrid? Saprotrophic fungi (Chytridiomycota?)	Occur within or on the surface of bisaccate pollen	Relatively abundant; present in ~50% of samples
Fungal morphotype 8: disc-like clusters of small fungal cells	Chytrid? Saprotrophic fungi (Chytridiomycota?)	Occur dispersed throughout peat matrix	Relatively uncommon; <10 specimens
Fungal morphotype 9: complex fruiting bodies	*Sclerocystis* sporocarp?	Occur dispersed throughout peat matrix in samples rich in *Vertebraria* roots	Relatively uncommon; <10 specimens
Fungal morphotype 10: sclerotia	Fungal resting body	Occur in isolation and in rows where the peat is layered	Relatively uncommon; <10 specimens
Combresomyces caespitosus	Peronosporomycetes (water moulds)	Occurs throughout the peat matrix in association with a wide range of plant tissues and organic debris	Common; >50 specimens
Combresomyces rarus	Peronosporomycetes (water moulds)	Occurs throughout the peat matrix in association with a wide range of plant tissues and organic debris	Common; >40 specimens

Fragment of exoskeleton	Indeterminate arthropod	Within peat matrix	Rare; 2 specimens
Coprolites in *Vertebraria* and *Australoxylon* (dark)	Wood-boring arthropod	Roots, wood	High; >1000 in some slides
Coprolites in *Vertebraria* and *Australoxylon* (light)	Probably oribatid mites	Roots, wood	High; >1000 in some slides
Coprolites in leaves	Possible leaf-mining or detritivorous arthropod	Between anastomosing veins of *Glossopteris* leaves	Relatively common; >10 specimens
Coprolite within fern sporangium	Small palynophagous arthropod	Inside fern sporangium	Single occurrence
Isolated large coprolites	Indeterminate arthropod	Amongst matted leaf remains	Relatively common; >10 specimens
Isolated small coprolites	Indeterminate arthropod	Isolated in peat matrix, amongst matted leaf remains	Relatively common; >10 specimens
Coprolites containing fungi	Fungivorous arthropod	Roots, wood and isolated in the peat matrix	Relatively uncommon; <10 specimens
Coprolites containing pollen	Palynophagous arthropod	Isolated in the peat amongst *Glossopteris*-dominated debris	Relatively uncommon; <10 specimens
Coprolites with coarse contents	Probably generalist detrivorous arthropod	Isolated in the peat matrix	Relatively uncommon; <10 specimens
Spirally ornamented coprolite	Indeterminate arthropod	Isolated in the peat matrix	Rare; single specimen

6.3.2 Composition of associated coals

In order to assess whether the Toploje Member's silicified peat bed is representative of organic accumulations throughout the Middle and Late Permian of the Lambert Graben, 13 coal samples from the major coal-bearing intervals of the Bainmedart Coal Measures were analyzed for their maceral content. One of these samples from outcrop near Soyuz Station on the eastern side of Beaver Lake is not constrained stratigraphically and is only included for maceral ratio comparisons to coals of other regions. The other 12 samples derive from reconnaissance-scale sampling of coals throughout the Bainmedart Coal Measures (generally only 1 sample per 100–150 m of stratigraphic section). Trace and major element results, vitrinite reflectance values and some petrological data from these samples were presented by Holdgate et al. (2005). Further petrological and coal maturity data were presented for a few additional samples from the lower part of the Bainmedart Coal Measures by Bennett & Taylor (1972). The following elaborates on the organic petrology of the coal and compares the compositions of the coals and silicified peat.

Vitrinite (humified plant remains) constitutes 5.65–(22.75)–61.44% of the coal [7.04–(26.89)–65% on a mineral free basis]. This is almost entirely in the form of telocollinite & desmocollinite (Figure 6.2). Desmocollinite (precipitated humic gels) is generally slightly more abundant than telocollinite (gelified woody and mesophyll tissues). In broad terms these macerals track the total representation of vitrinite in similar proportions stratigraphically.

Inertinite (oxidized plant remains) forms 19.63–(31.78)–40.49% of the coal [25.4–(40.79)–50.47% on a mineral free basis]. The three dominant inertinite macerals are inertodetrinite (detrital oxidised components), semifusinite (partially oxidised woody tissues) and fusinite (oxidised woody tissues retaining cellular structure); with inertodetrinite being strongly dominant in the middle and upper Bainmedart Coal Measures reaching maximum levels of 36.54% on a mineral-free basis (Figure 6.2). Fusinite and semifusinite levels are high in the lowest two samples (from beds below and just above the silicified peat bed). Funginite (=sclerotinite; fungal remains) is very sparse.

Liptinite (waxy and resinous plant components) makes up 9.07–(23.97)–34.09% of the coal [9.6–(32.32)–42.49% on a mineral free basis]. The great majority of this is represented by sporinite (5.8–42.25% on a mineral free basis), with consistently low levels of cutinite (Figure 6.2). Suberinite, resinite, alginite and liptodetrinite are represented only in trace amounts.

Inertinite and liptinite broadly increase through the Roadian–mid-Wuchiapingian interval (Toploje Member–Grainger Member) associated with a corresponding decline in vitrinite (Figure 6.2). No clear trend is evident amongst maceral groups for the uppermost Permian (mid-Wuchiapingian–Changhsingian: McKinnon Member), although both inertinite and liptinite levels remain high.

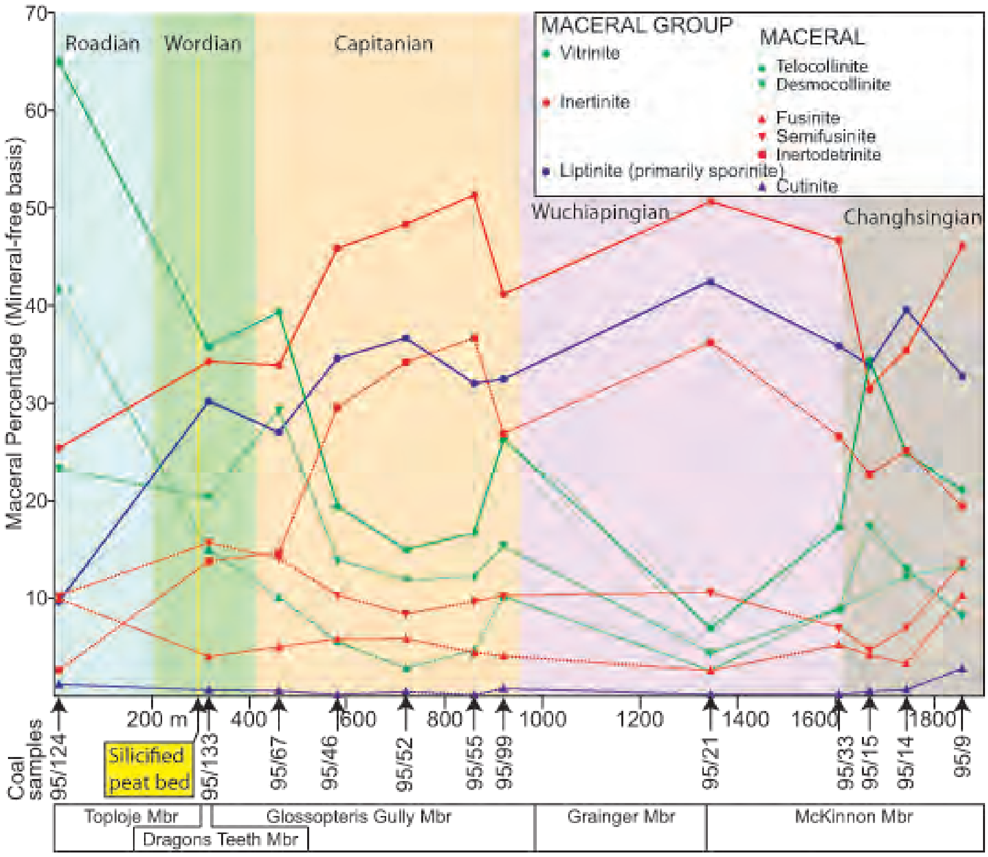


Figure 6.2: Plot of the variation in percentages of major macerals in coals from the Bainmedart Coal Measures, Lambert Graben, Antarctica. Detailed positions of coal samples are given by Holdgate et al. (2005).

6.4 Palaeoecology

6.4.1 Vegetation structure

Vegetation stratification is evident in the assemblage of plants preserved in the Toploje Member chert. Autochthonous upright stumps with a height of 30 cm and diameter of up to 20 cm are locally preserved in the chert together with more abundant parautochthonous axes generally <20 cm in diameter preserved parallel to bedding (Holdgate et al., 2005). Two stem wood morphospecies, *Australoxylon bainii* and *Australoxylon mondii*, were recognised by Weaver et al. (1997) and clearly correspond to two similar arborescent plants; the most likely affiliations being with glossopterids or cordaitaleans based on the co-preserved leaf forms (*Glossopteris* and *Noeggerathiopsis*). *Australoxylon mondii* stem wood cannot be distinguished anatomically from *Vertebraria* (glossopterid) root wood, apart from the absence of schizogenous cavities, suggesting that they likely originated from the same glossopterid plant (Weaver et al., 1997; McLoughlin, 2011b; see Bateman and Hilton, 2009). Two morphotypes of *Vertebraria* roots were recognised and described from the peats by Neish et al. (1993), categorised as ‘polyarch’ and ‘solid cylinder’ based on their ontogeny and architecture (Figure 6.3, A). The polyarch and solid cylinder roots may correspond to two distinct plant species or may be functionally different roots belonging to the same parent *Glossopteris* plant (Neish et al., 1993). A range of dispersed bisaccate, monosaccate, monosulcate and polyplicate pollen within the peat denotes an additional range of shrub- to tree-sized gymnospermous plants in the vicinity of the mire.

Stems and microphylls of diminutive herbaceous lycophytes are moderately common within the peat and are co-preserved with three genera and species of megaspore (Chapter 3; Slater et al., 2011). These appear to have been centimetre-scale *Paurodendron*-like heterosporous lycophytes that grew on the consistently moist peat surface (Figure 6.3, F). Roots of these plants occur sporadically amongst the leaf debris in the peat.

Fern sporangia with intact contents are relatively common in both thin sections and bulk macerations of the Toploje Member chert, though no leaves or stems of these plants have yet been discovered. The abundance of sporangia and paucity of the rest of the fern plants may be the result of: (1) an extremely delicate nature of the plants resulting in their low preservational potential; (2) an epiphytic habit, with ferns residing high on the stems of *Glossopteris* trees and retaining their foliage there until decay; or (3) transport of sporangia and spores into the mire via wind or water from hinterland plant communities. Small epiphytic ferns of *Tubicaulis* sp. are known from Early Permian deposits from Chemnitz in Saxony, Germany (Rößler, 2000). These epiphytes occur among the assemblage of plants that grew in close association with a mantle of adventitious roots of the well studied tree-fern *Psaronius* (Rößler, 2000). No direct evidence of epiphytes has yet been found associated with glossopterid remains, though they are a feature of most modern moist forest communities (Bartels and Chen, 2012), see Chapter 3 for further details.

Adaptations to a high-latitude habitat include a deciduous habit for glossopterids based on the numerous thick mats of leaves that occur as compression fossils and in the silicified peat representing seasonal leaf-shedding events (Krull, 1999; Retallack et al., 1995; Retallack, 1999; Holdgate et al., 2005; McLoughlin, 2011b). Such mats of apparently monospecific glossopterid leaves are common features of the Toploje Member chert (Figure 6.3, D). *Australoxylon bainii* and *A. mondii* woods found in the peats also have distinct growth rings that terminate abruptly, indicating a swift transition to winter dormancy (Weaver et al., 1997; Gulbranson et al., 2012) or seasonal water regimes (Francis, 1986), or both.

Special anatomical adaptations to a waterlogged environment are expressed in the architecture of the preserved gymnosperm axes. *Vertebraria* roots contain large schizogenous chambers (Figures 6.3, A,B; 6.4, B; 6.5, C–E) that possibly functioned to aid respiration in the anoxic or dysoxic waterlogged peat environment (Retallack and Dilcher, 1988; Neish et al., 1993; Decombeix et al., 2009). *Vertebraria* is very characteristic of pallid to dark palaeosols immediately underlying coal seams throughout Gondwana. These soils developed in dysoxic waterlogged environments and commonly host great densities of horizontal and low-angle root (*Vertebraria*) systems (Schopf, 1982; McLoughlin, 1993; Slater et al., 2012). *Australoxylon mondii* also has notable gaps between the ray cells that may have functioned as an aeration system in the lower stem wood of the glossopterid plant (Weaver et al., 1997). Dense horizontally extensive *Vertebraria* root mats may also have helped to stabilise the glossopterid trees in unstable waterlogged soils by intermeshing with the roots of neighbouring trees, as occurs in extant trees that inhabit boggy soils such as Kahikatea (*Dacrycarpus dacrydioides*) of New Zealand (Wardle, 1974; Wardle, 1991).

Other adaptations to moist or semi-aquatic environments amongst the PCM plants include the elaborately ornamented surface of the most abundant megaspore species, *Singhisporites hystrix* (Figures 6.4, I; 6.5, H,I). Its furcate spines may have functioned to aid dispersal through hydrochory in saturated environments and to facilitate entrapment of conspecific microspores in water (Tewari et al., 2009; Slater et al., 2011). The weakly spinose microspores associated with *Singhisporites hystrix* can be seen to interlock with the complex ornamentation of the megaspore in X-ray synchrotron tomographic images (Figure 6.5, I and Chapter 3). The presence of lycopsids is typical of moist terrestrial environments, lycopsids generally being restricted to wetland habitats or riparian areas (Falcon-Lang, 2003).

Recent peats deposited in the cold temperate climatic regions of Canada have been proposed as a suitable analogue for understanding the deposition of Permian high-latitude coals of Australia (Martini and Glooschenko, 1985). Modern high-latitude forests occupying the Boreal biome are limited in their distribution primarily by temperature and the proximity of permafrost to the surface, which hampers water and nutrient uptake (Sayre, 1994). The *Glossopteris* forests of the mid-Permian would have been subject to similar light regimes, but ambient temperatures were probably much higher than at their equivalent modern latitudes (Angiolini et al., 2009). Hence, permafrost development was unlikely to have limited water supply for plant growth.

6.4.2 Fungi and fungi-like organisms

In contrast to the low-diversity macroflora there is a notably high diversity of fungi and fungi-like organisms in the Tobloje Member silicified peat (Figures 6.3, A,C; 6.4, D–F). This is consistent with models of modern high-latitude forests dominated by deciduous trees (Wu et al., 2011), where the soil can be rich in leaf litter and other plant detritus exploitable by fungi. Examples of fungi in the peat matrix and within dispersed plant organs within the Toploje Member chert include septate and non-septate hyphae, a range of fungal spores, saprotrophic chytrid fungi, fungal sclerotia, and possible mycorrhizal associations (Figures 6.3, A; 6.4, D,E,F). Regularly (seasonally) distriubuted pocket rot (Weaver et al., 1997) occurs within the *Australoxylon* wood (Figure 6.3, C). Appositions are evident in secondary xylem cells of subaerial axes, presumably representing a plant response to fungal invasion (Bhuiyan et al., 2009). Other fungi-like microorganisms include two species of Peronosporomycetes or ‘water moulds’ represented by distinctive furcate spinose oogonia, *Combresomyces caespitosus* and *Combresomyces rarus* (Slater et al., 2013). These were likely saprotrophic rather than parasitic forms, and such organisms are very common in modern moist terrestrial habitats (Jobard et al., 2010).

Table 4. List of published records of probable arthropod damage on Gondwanan Permian plants. Publications marked with (C) document arthropod damage from compression/impression fossils, those marked with (AP) document arthropod damage from anatomically preserved specimens.

STUDY	**AGE**	**FORMATION AND LOCALITY**	**DAMAGE TYPE**
Brongniart, 1830 (C)	Kungurian – Wordian or Lopingian	Barakar or Raniganj Formation, Raniganj Coalfield	Possible hole feeding or oviposition scars on *Glossopteris indica* holotype (although this is not clear from the illustrations provided by Chandra and Surange, 1979 or Rigby et al., 1980)
Bunbury, 1861 (C)	Permian	Unit uncertain; Satpura Basin, Nagpur, Maharashtra, India	Oviposition scars or small hole-feeding scars on *Glossopteris*
Tate, 1867 (C)	Permian	Ecca Group or Adelaide Subgroup	Probable oviposition scars on *Rubidgea*/*Gangamopteris*
Carruthers, 1872 (C)	Permian	Probably Bowen Basin, Queensland, Australia	Possible interveinal slot feeding
Mitchell, 1872 (C)	Changhsingian	Newcastle Coal Measures, northern Sydney Basin, New South Wales, Australia	Possible oviposition scars on *Glossopteris*
Feistmantel, 1880a (C)	[1]Lopingian [2]Kungurian–Wordian	[1]Raniganj Formation, Raniganj Coalfield, West Bengal, India; [2]Barakar Formation, Talchir Coalfield, Mahanadi Basin, Orissa, India	[1]Possible scalloped margin feeding and deep longitudinal embayed feeding traces in leaves of *Schizoneura gondwanaensis*; [2]Possible scalloped apical feeding on leaves of *Trizygia speciosa*
Feistmantel, 1880b (C)	Permian	Nagpur, Satpura Basin, Maharashtra, India	Possible oviposition scars on *Glossopteris*
Feistmantel, 1882 (C)	?Kungurian–Wordian	?Barakar Formation, Sohagpur Coalfield, Son Basin, Madhya Pradesh, India	Possible oviposition scars on *Glossopteris*
David, 1891 (C)	Artinskian	Greta Coal Measures, northern Sydney Basin, New South Wales, Australia	Possible oviposition scars on *Gangamopteris*
Zeiller, 1896 (C)	?late Sakmarian– late Artinskian	Probably Vryheid Formation, northern Karoo Basin, Gauteng, South Africa	Oviposition scars on *Glossopteris*
Dolianiti, 1953a, b (C)	Artinskian	Rio Bonito Formation, Bainha, Parana Basin, Santa Catarina, Brazil	Possible apical and hole feeding on *Glossopteris*; possible deeply embayed margin feeding on *Glossopteris* or *Rhabdotaenia*;
Sen, 1955 (C)	Kungurian–Wordian	Barakar Formation, Sohagpur Coalfield, Son Basin, Madhya Pradesh, India	Possible piercing and sucking damage, galls or mineral staining on *Glossopteris*
Plumstead, 1962b, 1963; Melville 1983a, b (C)	late Sakmarian– late Artinskian	Vryheid Formation; Breyton Colliery, Karoo Basin, Mpumalanga, South Africa	Possible isolated gall (*Breytenia plumsteadiae*)
Menendez, 1962 (C)	Cisuralian	Bonete Series, Buenos Aires Province, Argentina	Possible oviposition scars or sporangial impressions on glossopterid scale leaf (=*Lanceolatus bonairensis*)
Plumstead, 1963; Van Amerom,	late Sakmarian– late Artinskian	Vryheid Formation; Vereeniging, Karoo Basin,	Scalloped and continuous margin feeding on *Glossopteris*

1966; Stephenson and Scott, 1992; Scott et al., 1992 (C)		Gauteng, South Africa	
Sen, 1963 (C)	?Kungurian	Lower Barakar Formation; Pachwara Coalfield, Bihar, India	Possible gall on *Glossopteris* midrib
Cridland, 1963 (C)	Lopingian	Mount Glossopteris Formation; Ohio Range, Antarctica	Possible hole feeding in glosopterid scale leaf
Maheshwari and Prakash, 1965 (C)	Lopingian	Permian exposures along Bansloi River, Rajmahal Hills, Bihar, India	Scalloped leaf-margin feeding on *Glossopteris*
Maithy, 1965, 1977 (C)	Artinskian	Karharbari Formation, Giridh Coalfield, Damodar Basin, Bihar, India	Possible galls, piercement scars or oviposition scars on indeterminate axis previously assigned to *Buriadia* and cf. *Cyclodendron*
Plumstead, 1970; Bordy and Prevec, 2008 (C)	Lopingian	Emakwezini Formation, Lebombo Basin, KwaZulu-Natal, South Africa	Scalloped marginal feeding traces and oviposition scars on *Glossopteris*
Bernardes de Oliveira and Pons, 1975 (C)	Sakmarian–Artinskian	Ecca Group equivalents, Zambezi Basin, Mozambique	Possible deeply embayed margin feeding on *Glossopteris*
Appert, 1977 (C)	Sakmarian–Artinskian	Sakoa Series, Sakoa Basin, Madagascar	Possible apical feeding on *Sphenophyllum*; possible scalloped margin feeding, hole feeding and oviposition scars on *Glossopteris*
Bernardes de Oliveira and Pons, 1977 (C)	Artinskian	Rio Bonito Formation, Bainha, Parana Basin, Santa Catarina, Brazil	Scalloped apical or marginal feeding on *Noeggerathiopsis*
Bose et al., 1977 (C)	Changsingian	?lowermost Panchet Group, Ramkola-Tatapani Coalfield, Madhya Pradesh, India	Possible leaf-margin feeding on *Glossopteris*
Kovács-Endrödy, 1977 (C)	late Sakmarian–late Artinskian	Vryheid Formation, Vereeniging, Karoo Basin, Gauteng, South Africa	Scalloped margin feeding on *Glossopteris* and associated leaf arching
Srivastava, 1979 (C)	Lopingian	Raniganj Formation, Auranga Coalfield, Damodar Basin, Bihar, India	Possible apical feeding on glossopterid scale leaf
Van Dijk et al., 1979; Van Dijk, 1981 (C)	Lopingian	Normandien/Estcourt Formation (Beaufort Group); Karoo Basin, KwaZulu-Natal, South Africa	Scalloped leaf-margin feeding and interveinal surface feeding? on *Glossopteris*; possible hole feeding on *Lidgettonia* sporophylls; leaf crypsis (?homopteran wings)
Kovács-Endrödy, 1981 (C)	late Sakmarian–late Artinskian	Vryheid Formation equivalent, Hammanskraal, outlier of northern Karoo Basin, Gauteng, South Africa	Possible oviposition scars flanking midrib of *Glossopteris angustifolia*
Millan and Dolianiti, 1982 (C)	Sakmarian	Itararé Group, Itapema, Paraná Basin, São Paulo, Brazil	Scalloped apical feeding on *Rubidgea* species
Rohn, 1984 (C)	?Changhsingian	Serrinha Member, Rio do Rasto Formation, Dorizon, Paraná Basin, Paraná, Brazil	Scalloped margin feeding, apical feeding on several *Glossopteris* species
Chauhan et al., 1985 (C)	Lopingian	Raniganj Formation, Raniganj	Margin-feeding on *Glossopteris* and *Belemnopteris* leaves; Coprolites

		Coalfield, West Bengal, India	containing leaf cuticle
Anderson and Anderson, 1985 (C)	^{1}late Sakmarian–late Artinskian; ^{2}Lopingian	^{1}Vryheid Formation, Vereeniging, Karoo Basin, Gauteng, South Africa; ^{2}Normandien/Estcourt Formation and equivalents (Beaufort Group); Karoo Basin, KwaZulu-Natal, South Africa	^{1}Possible oviposition scar on *Noeggerathiopsis elongata*; Possible apical feeding on *Ottokaria ferrugistratum*; scalloped, notched and continuous margin feeding on several *Glossopteris* species; ^{2}Scalloped, notched and continuous margin feeding on several *Glossopteris* species
Cúneo, 1986 (C)	Permian	Argentina	Leaf crypsis, potential arthropod pollination vector for conifers
Maheshwari and Tiwari, 1986 (C)	Artinskian	Karharbari Formation, Shahdol district, Madhya Pradesh, India	*Maheshwariella spinicornuta* seeds (6 × 2.5 mm) with 0.75 mm long micropylar horns bearing reverse-orientated epidermal barbs: possible seed transport
Cúneo, 1987 (C)	Cisuralian	Rio Genoa Formation; Tepuel-Genoa Basin, Chubut, Argentina	Oviposition or hole feeding on *Ginkgoites* leaves
Pant and Singh, 1987 (AP)	Lopingian	Raniganj Coalfield, West Bengal, India	Possible arthropod borings (or fungal pocket rot) in latewood of *Catervoxylon*
Archangelsky and Cúneo, 1987 (C)	Cisuralian	Arroyo Totoral Formation, La Rioja Province, Argentina.	Potential insect-mediated pollination mechanism in *Ferugliocladus*
Rohn and Rösler 1989 (C)	Lopingian	Rio do Rasto Formation, Reserva-Cândido de Abreu, Paraná Basin, Brazil	Scalloped marginal or apical feeding on *Ilexoidephyllum* leaves
Srivastava, 1988, 1996, 2008; Srivastava and Agnihotri, 2011 (C)	?Kungurian	Lower Barakar Formation; Raniganj Coalfield, West Bengal, India	Continuous and isolated scalloped and notched margin-feeding, hole feeding, vein-parallel surface feeding, possible galls and/or piercing and sucking scars, and oviposition scars in various arrangements on several *Glossopteris* species; Apical margin feeding embayments between veins in *Noeggerathiopsis*
Maheshwari and Bajpai, 1990 (C)	Permian	Siltstone overlying Lalmatia bottom coal seam, Hura Coalfield, Rajmahal Basin, Bihar, India	Inferred leaf mines on *Saportaea* leaf [probably imprints of burrows in underlying sediment]
McLoughlin, 1990a, b, 2011 (C)	^{1}late Sakmarian–late Artinskian; ^{2}Wordian–Capitanian; ^{3}Wuchiapingian	^{1}Vryheid Formation, Vereeniging, Karoo Basin, Gauteng, South Africa; ^{2}Ulan coal mine, Cullen Bullen Subgroup, Illawarra Coal Measures, northwestern Sydney Basin, New South Wales, Australia; ^{3}Black Alley Shale, southwestern Bowen Basin, Queensland, Australia	^{1}Galling on *Palaeovittaria*; ^{2}Galling on *Glossopteris*; ^{3}Gall or solitary oviposition scar on *Glossopteris* midrib; paired oviposition scars adjacent to midrib of *Glossopteris*
Chaloner et al., 1991; Scott et al., 1992 (C)	Permian (probably Changhsingian)	Australia (probably Illawarra Coal Measures, western Sydney Basin)	Continuous scalloped margin and apical feeding
Zavada & Mentis, 1992 (AP)	late Sakmarian–Changhsingian	Vryheid – Normandien/Estcourt formations, Karoo Basin, South Africa	Arthropod borings in late-season wood of *Agathoxylon* (=*Dadoxylon*). Inferred increase in vertebrate herbivory towards end of Permian based on reduced size and increased lignin content (vein

			concentrations) of *Glossopteris* leaves [may alternatively have been climatically influenced]
Chandra and Singh, 1992 (C)	Changhsingian	Kamthi Formation, Mahanadi Graben, Dhenkanal, Orissa, India	Oviposition scars flanking midrib, and possible scalloped margin-feeding and hole feeding on *Glossopteris*
McLoughlin, 1992 (AP)	Capitanian–Wuchiapingian	McMillan Formation, central Bowen Basin, Queensland, Australia	Arthropod borings or fungal pocket rot in both early- and late-season wood of *Agathoxylon* (=*Araucarioxylon*)
McLoughlin, 1994 a, b (C)	^{1}Wuchiapingian – Changhsingian; ^{2}Wuchiapingian; ^{3}Capitanian–Changhsingian ^{4}Wuchiapingian	Central Bowen Basin, Queensland, Australia: ^{1}Burngrove Formation, Rangal Coal Measures, Bandanna Formation; ^{2}Black Alley Shale, ^{3}McMillan Formation, Burngrove Formation, Rangal Coal Measures, ^{4}Gyranda Formation, Black Alley Shale, Burngrove Formation equivalents	Several *Glossopteris* species with: ^{1}Notched, scalloped, deeply or narrowly embayed margin feeding, ^{2}Oviposition scars, ^{3}Possible apex-feeding, ^{4}Possible surface interveinal feeding
Guerra-Sommer, 1995 (C)	Artinskian	Rio Bonito Formation, Parana Basin, Rio Grande do Sul, Brazil	Scalloped and deeply embayed margin- and ?apical-feeding on *Glossopteris* and *Rubidgea* leaves
Pant and Srivastava, 1995 (C)	?Kungurian	Mamal Formation, Mamal Nala Section, Pahalgam, Kashmir Himalaya, India	Pouch-like galls on *Glossopteris* leaves
Holmes, 1995 (C)	Changhsingian	Illawarra Coal Measures; Western Sydney Basin, New South Wales, Australia	Deeply embayed margin feeding and possible galls on *Glossopteris*
Chandra and Singh, 1996 (C)	Asselian–Sakmarian	Talchir Formation, Talchir Coalfield, Mahanadi Basin, Orissa, India	Apical feeding and oviposition scars on *Gangamopteris*; Possible see predation on *Cordaicarpus*
Rigby, 1996 (C)	Kungurian–Roadian	Aifam Group, Irian Jaya	Scalloped and deeply embayed margin feeding on *Glossopteris*
Srivastava and Tewari, 1996 (C)	Kungurian–Wordian	Barakar Formation, Auranga Coalfield, Bihar, India	Possible apical feeding on several *Glossopteris*/*Gangamopteris* species
Melchor and Césari, 1997(C)	Lopingian	Carapacha Formation, Carapacha Basin, La Pampa, Argentina	Deeply embayed margin feeding on *Glossopteris*
Rohn et al., 1997 (C)	Lopingian	Teresina Formation, Prudentopólis area, Paraná Basin, Paraná, Brazil	Hole feeding in *Glossopteris*
Weaver et al., 1997 (AP)	Wordian	Topmost Toploje Member, Bainmedart Coal Measures, Lambert Graben, East Antarctica	Coprolites containing tracheid fragments in ?glossopterid stem wood (attributable to oribatid mites)
Banerjee and Bera 1998 (C)	Lopingian	Raniganj Formation, Jharia Coalfield, Mohuda Basin, West Bengal, India	Crater-like galls on *Glossopteris*
Adami-Rodrigues and Ianuzzi, 2001, Adami-Rodriguez et al., 2004a, b (C)	^{1}Artinskian; ^{2}Kungurian–Guadalupian	^{1}Rio Bonito and ^{2}Irati/Serra Alta Formations, Parana Basin, Rio Grande do Sul, Brazil	^{1}Continuous irregular margin feeding, deep embayments, and interveinal hole feeding in *Glossopteris* (and possibly *Gangamopteris*); Possible leaf mining in *Glossopteris*; Oviposition scars on *Glossopteris*; Possible piercing and sucking damage on *Glossopteris*; Possible skeletonization of *Glossopteris* lamina; Possible galls on *Glossopteris*; Hole and

			discontinuous margin feeding on *Noeggerathiopsis* ^{2}Irregular margin and apical feeding on *Glossopteris*
Singh, 2002 (C)	Kungurian–Wordian	Barakar Formation, West Bokaro Coalfield, Damodar Valley, Jharkhand, India	Possible oviposition scars or galls (*Bokarospermum maheshwari*) on *Glossopteris*
Berthelin et al., 2003 (C)	late Roadian or early Wordian	Gharif Formation; Huqf area, Oman	Scalloped margin feeding and probable oviposition scars on *Glossopteris*
Bolzon et al., 2004 (AP)	Lopingian	Serra Alta Formation, Paraná Basin, Rio Grande do Sul State, Brazil	Borings and galleries in gymnosperm stem wood
Kellogg and Taylor, 2004 (AP)	Changhsingian	Buckley Formation; Skaar Ridge, central Transantarctic Mountains, Antarctica	Coprolites containing tracheid fragments in ?glossopterid stem wood (attributed to oribatid mites)
McLoughlin et al., 2005 (C)	Guadalupian	Undefined shale unit at Fossilryggen, Vestfjella, Dronning Maud Land, Antarctica	Possible notched margin feeding on *Glossopteris* sp. cf. *G. spatulata*
Beattie, 2007 (C)	Changhsingian	Upper Newcastle Coal Measures, Belmont, New South Wales, Australia	Notched, scalloped and deeply embayed isolated and continuous margin feeding on *Glossopteris*; Oviposition scars on *Paracalamites* axis
Prevec et al., 2009 (C)	Lopingian	Clouston Farm, Normandien Formation, northeastern Karoo Basin, KwaZulu-Natal, South Africa	22 distinctive damage types on 137 plant organs. Scalloped margin feeding on *Glossopteris*, scale leaves, lycophyte axis, sphenophyte roots; Apical feeding on *Glossopteris*; Hole feeding on *Glossopteris*, scale leaves, sphenophyte roots, unidentified axes; Mine-like strip-feeding on *Glossopteris*; Skeletonization of *Glossopteris* leaves; Surface feeding on *Glossopteris*, scale leaves; Galling on *Glossopteris*; Piercing and sucking scars on *Glossopteris*; Oviposition on *Glossopteris*, scale leaves and sphenophyte axes
Pal et al., 2010 (C)	Changhsingian	Maitur Formation (lowermost Panchet Group), Raniganj Coalfield, Damodar Basin, West Bengal, India	Possible leaf apex and margin feeding on *Glossopteris retifera*
Prevec et al. 2010; Prevec 2012 (C)	Changhsingian	Elandsberg Member, Balfour Formation, Wapadsberg Pass, southern Karoo Basin, Eastern Cape Province, South Africa	Rectangular marginal feeding traces and various oviposition scars on *Glossopteris*
Cariglino and Gutiérez, 2011 (C)	Wordian-Wuchiapingian	Laguna Polina Member, La Golondrina Formation, La Golondrina Basin, Santa Cruz, Argentina	Scalloped, deeply embayed and continuous margin-feeding; hole feeding, oviposition scars on several *Glossopteris* species
McLoughlin, 2012 (C)	Mid-Sakmarian–late Artinskian	Reids Dome beds, GSQ Taroom 11 stratigraphic bore, south-western Bowen Basin, Queensland, Australia	Broad area of pitted damage to *Glossopteris* leaf (possible arthropod, fungal, physical, or diagenetic damage)
Pinheiro et al., 2012a, b (C)	^{1}Late Artinskian–early Kungurian;	^{1}Irati/Serra Alta formations; ^{2}Siderópolis Member, Rio Bonito Formation;	^{1}Margin feeding on *Glossopteris*; ^{2}Hole, slot and margin feeding, surficial feeding, skeletonization, possible mining

	[2,3]Sakmarian–Artinskian; [4]early Sakmarian	[3]Paraguaçu Member, Rio Bonito Formation; [4]Taciba Formation, Itararé Group, southern Paraná Basin, southern, Santa Catarina and Rio Grande do Sul, Brazil	on *Glossopteris*; slot feeding, galls, oviposition scars on *Gangamopteris*; Hole feeding on *Noeggerathiopsis*; [3]Scalloped, continuous and deeply embayed margin feeding, hole and slot/trench feeding on *Glossopteris*; margin feeding on *Noeggerathiopsis*; [4]Margin, hole, slot and surficial feeding on *Glossopteris*; margin and slot feeding on *Gangamopteris*
Slater et al., 2012 (AP)	Wordian	Upper Toploje Member, Bainmedart Coal Measures, Lambert Graben, Prince Charles Mountains, East Antarctica	Coprolites with tracheid fragments in *Vertebraria* and *Australoxylon* (boring and/or saproxylophagy); Sub-rounded to angular coprolites containing densely packed mesophyll cell wall fragments in cavities within *Glossopteris* mesophyll (leaf mining or detritivory); Ovoid coprolite in fern sporangium (palynivory); Isolated large ellipsoid to spherical coprolites with amorphous contents in leaf debris (?detritivory); Isolated small oblong or cylindrical coprolites containing pollen and spore fragments, cell walls, fungi in peat matrix (generalist ?detritivory); Spherical to ovoid coprolites containing fungal spores (fungivory); Squat ellipsoidal to spherical coprolites containing glossopterid pollen (palynivory); Spherical to ellipsoidal coprolites containing coarse constituents (folivory or detritivory); Oblong spiral ornamented coprolite with amorphous contents

6.4.3 Plant-animal-fungal interactions

The Toploje Member chert is one of only a few Palaeozoic–Mesozoic deposits from which a detailed survey of the arthropod-plant interactions has been described (McLoughlin et al., 2011; Slater et al., 2012) and one of only a small number of assemblages across Gondwana for which herbivory on glossopterid gymnosperms has been documented (Figure 6.6; Table 4). The majority of past records are examples of folivory traces on the margins of *Glossopteris* leaves from compression-impression floras (Table 4). Other Palaeozoic and Mesozoic assemblages from which invertebrate-plant relationships and coprolite suites have been extensively documented include those from the Silurian and Lower Devonian deposits in the Welsh Borderland (Edwards, 1996; Edwards et al., 2012), the Rhynie Chert (Habgood et al., 2004), the Pennsylvanian coal balls of the United States (Baxendale, 1979), the ‘component community’ of invertebrate feeders on the Palaeozoic tree fern *Psaronius* (Rößler, 2000; D’Rozario et al., 2011a, b), and the Upper Triassic permineralised peats of Hopen in the Svalbard archipelago (Strullu-Derrien et al., 2012). The identification of feeding traces in the roots (*Vertebraria*), stems (*Australoxylon*) and leaves (*Glossopteris*) of the arborescent Antarctic glossopterid whole-plant, integrated with records of feeding traces from other assemblages (McLoughlin, 1994a, 1994b, 2011a; Banerji and Bera, 1998; Adami-Rodrigues et al., 2004b; Beattie, 2007; Prevec et al., 2009, 2010; Srivastava and Agnihotri, 2011; Cariglino and Gutiérrez, 2011), illustrates that all major organs of the glossopterid plant were attacked by a community of invertebrates (Slater et al., 2012). Arthropod coprolites inside fern sporangia show that exploitation of plant food sources was not limited to glossopterids. The herbaceous lycophytes of the understorey (Slater et al., 2011) may have also provided an important source of food or egg-hosting sites for invertebrates based on the extra-Gondwanan occurrence of Triassic *Isoetites* bearing oviposition scars on their leaves (Moisan et al., 2012).

Small faecal pellets attributed to oribatid mites are the most abundant coprolites in the Toploje Member silicified peat (Figure 6.4, C). These small coprolites commonly occur in dense clusters and are dimensionally and morphologically identical to those of extant oribatid mites (Rusek, 1975; Vegter, 1983; Slater et al., 2012). Molecular dating has placed the origin of the oribatid mites at 571 ± 37 million years ago (Schaefer et al., 2010). This predates their first occurrence in the fossil record by a large ‘mite gap’ of ~130–90 ± ~40 million years (Schaefer et al., 2010). There must have been significant pre-Devonian radiation and adaptation of oribatid mites since the group was already moderately diverse by the Devonian (Norton et al., 1988) and complex land based food webs already existed in the Silurian (Edwards, 1996), including some mite-like microarthropod coprolites (Hagström and Mehlqvist, 2012). Hence, microcoprolite studies offer the potential to not only track the early history of some arthropod clades in the absence of body fossils, but also to assess patterns of food consumption and guild/trophic complexity.

Alongside being potential early colonisers of the terrestrial environment, oribatid mites and other soil-dwelling microarthropods were likely important drivers in the development of the soil-based ecosystems in which Palaeozoic vascular plants thrived. A diverse and abundant invertebrate soil fauna including oribatid mites is known to be important for macro-vegetation in the recycling of nutrients from decaying plant matter, and for enhancing soil aeration and water retention through increased porosity (Bardgett, 2005). Recent studies of extant oribatid mites have revealed that they play a role in dispersing the spores of ectomycorrhizal fungi throughout the soil through their faeces and through entrapment of spores in the hairs of their exoskeleton (Lilleskov and Bruns, 2005). The presence of oribatid mites likely also supported a community of soil micro-predators such as pseudoscorpions, which prey upon extant mites and also have a fossil record extending to the Devonian (Shear et al., 1989b). The abundance of oribatid mite coprolites in the Toploje Member chert attests to their key role in recycling organic matter and opening up pathways for fungal decomposers in the plant litter and dead wood of high-latitude Gondwanan coal-forming mires. Modern boreal forests that include a significant proportion of deciduous trees have been shown to house a high diversity of soil organisms comparable even to that of tropical rainforests (Wu et al., 2011). The exceptional preservation in the Toploje Member chert provides an opportunity to assess the invertebrate diversity and trophic guilds in these mires prior to the onset of ecosystem decline that began in the Capitanian, and could aid our understanding of the impact of the end-Palaeozoic floral turnover on the associated invertebrate biota (Anderson et al., 1999; Labandeira, 2005a, 2005b; Slater et al., 2012).

The remains of animals are probably more common in silicified plant-bearing deposits than has been generally documented (Smoot and Taylor, 1985), since it is inherently difficult to identify an arthropod body fossil in thin section amongst densely packed plant remains, particularly since plant and arthropod cuticle look similar in thin section (Bartram et al., 1987). Further, distinctive waxy clitellate annelid egg cases have not yet been recorded from any Palaeozoic peats, which is surprising given that these remains are readily recognizable and common in Mesozoic to modern floodbasin deposits (Manum et al., 1991; Jansson et al., 2008; Tosolini and Pole, 2010; Bomfleur et al., 2012). More extensive use of the bulk maceration technique on silicified peats and other organic-rich sediments offers the potential to extract more taxonomically informative components of arthropod exoskeletons (e.g., wings) and annelid egg capsules.

Sparse trace fossils occur in the Permian-Triassic Amery group fluvial sediments of the Prince Charles Mountains including *Planolites* trails and short vertical burrows (McLoughlin et al., 1997). Permian-Triassic strata elsewhere in Antarctica host a variety of arthropod ichnogenera giving clues to the stream, soil and entomofauna; *Diplopodichnus* and *Diplichnites* myriapod traces were reported from the Permian-Triassic sediments of the central Transantarctic Mountains, together with an interpreted resting trace of a jumping insect (Briggs et al., 2010).

Tetrapods are currently unknown from Permian strata of the Prince Charles Mountains as either body fossils or ichnofossils (McLoughlin et al., 1997). The fossil record of Gondwanan Permian terrestrial vertebrates is poor beyond the confines of the Karoo Basin in South Africa (Rubidge et al., 1995; Lucas, 2004). It is possible that macro-herbivores were relatively sparse in southern high latitudes during the Permian, particularly in forest mire communities. The deciduous habit of the dominant woody plants, coupled with strongly seasonal climatic fluctuations at high latitudes, probably provided unfavourable conditions for large populations of herbivores without special physiological adaptations or the capacity to migrate long distances (Collinson and Hammer, 2007).

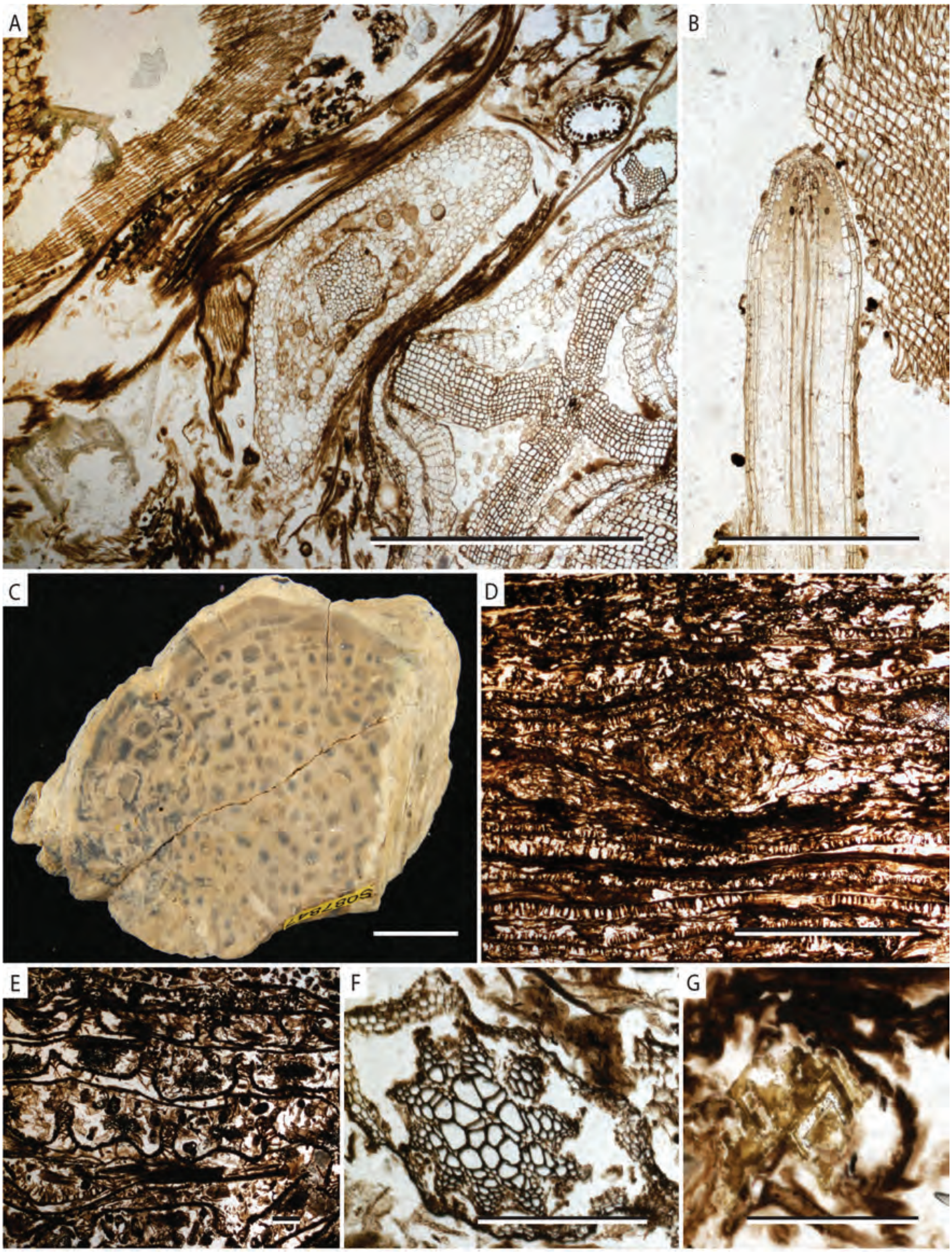


Figure 6.3

Figure 6.3 (previous page): Range of biota found in thin sections of the Toploje Member silicified peat.
A. NRM S087800, *Vertebraria* solid-stele and polyarch roots colonised by fungal spores and hyphae in the peat matrix, scale = 1 mm.
B. NRM S088061, Young *Vertebraria* root tip in longitudinal section, scale = 1 mm.
C. NRM S087847, Transverse section through a silicified gymnosperm stem with fungal pocket rot, scale = 1 cm.
D. NRM S089551, Large coprolite between matted *Glossopteris* leaves [similar to that figured by Baxendale (1979) plate 65, figure 1 and akin to Baxendale's (1979) 'type B' coprolites from Pennsylvanian coal balls, plate 65, figure 8], scale = 1 mm.
E. NRM S089553, Matted *Noeggerathiopsis* leaves with prominent abaxial trichome-bearing furrows, scale = 500 μm.
F. CPC34952, Transverse section through the axis of a herbaceous lycophyte, scale = 500 μm.
G. NRM S087932-01-03, Pyrite crystals amongst plant debris embedded in silica matrix, scale = 500 μm.

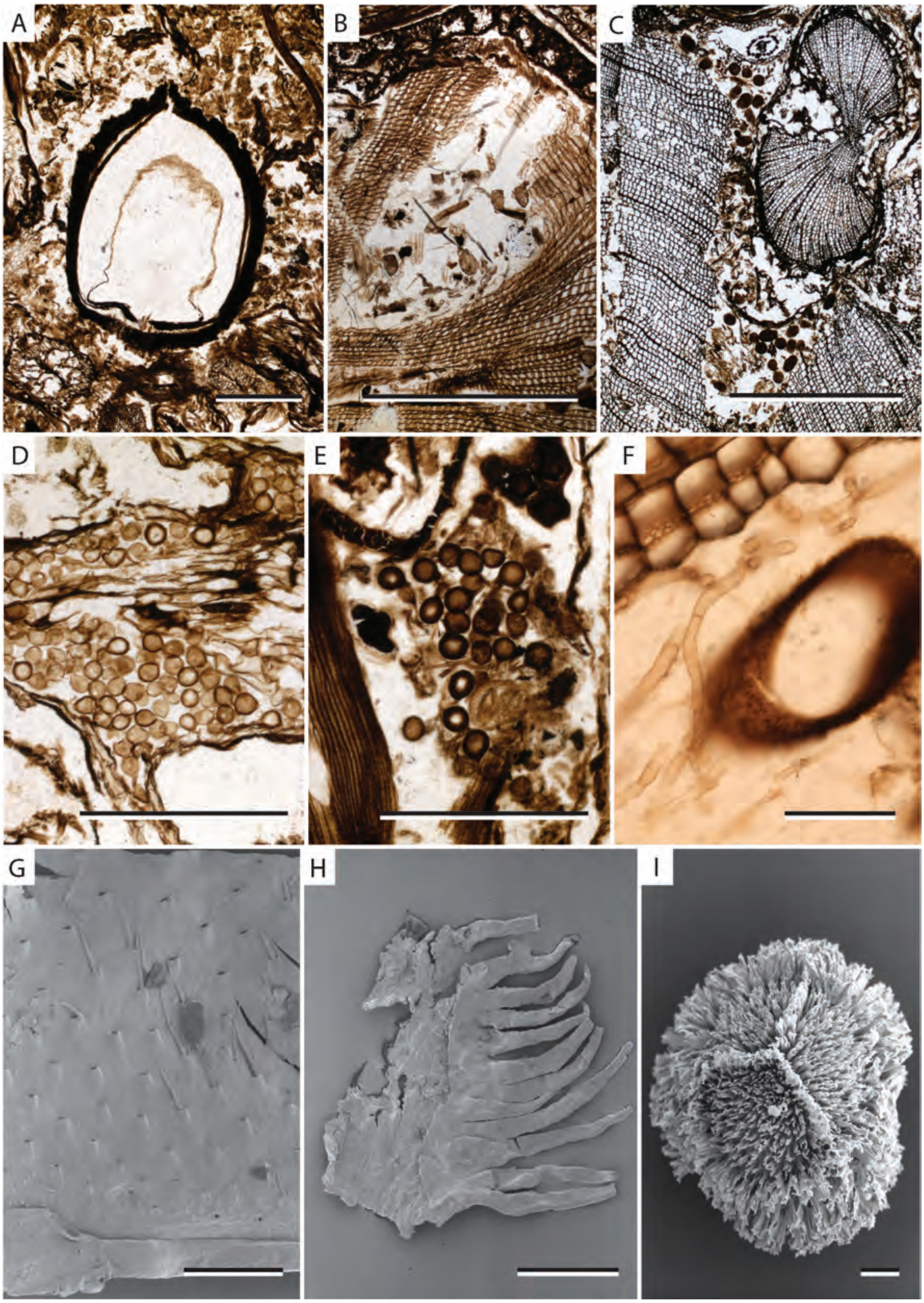


Figure 6.4

Figure 6.4 (previous page): Range of biota found in thin sections and bulk-macerations of the Toploje Member silicified peat.
A. NRM S087932, Small seed, scale = 500 µm.
B. NRM S089550, Phytodebris within a schizogenous cavity of a *Vertebraria* root, scale = 500 µm.
C. NRM S088040, Charcoalified wood and root fragments surrounded by mite coprolites, scale = 1 mm.
D. NRM S088051-01, Small smooth fungal spores, scale = 500 µm.
E. NRM S087932-01-02, Mass of fungal reproductive bodies and hyphae set amongst phytodebris, scale = 500 µm.
F; CPC34952, Septate fungal hyphae penetrating *Vertebraria* root cells, scale = 100 µm.
G. NRM S089630, SEM image of arthropod cuticle with hollow setae, scale = 50 µm.
H. NRM S089629, SEM image of an unidentified but distinctive leaf cuticle bearing prominent marginal trichomes, scale = 100 µm.
I. NRM S089540, SEM image of megaspore *Singhisporites hystrix* – the most common megaspore found in the peat, scale = 100 µm.

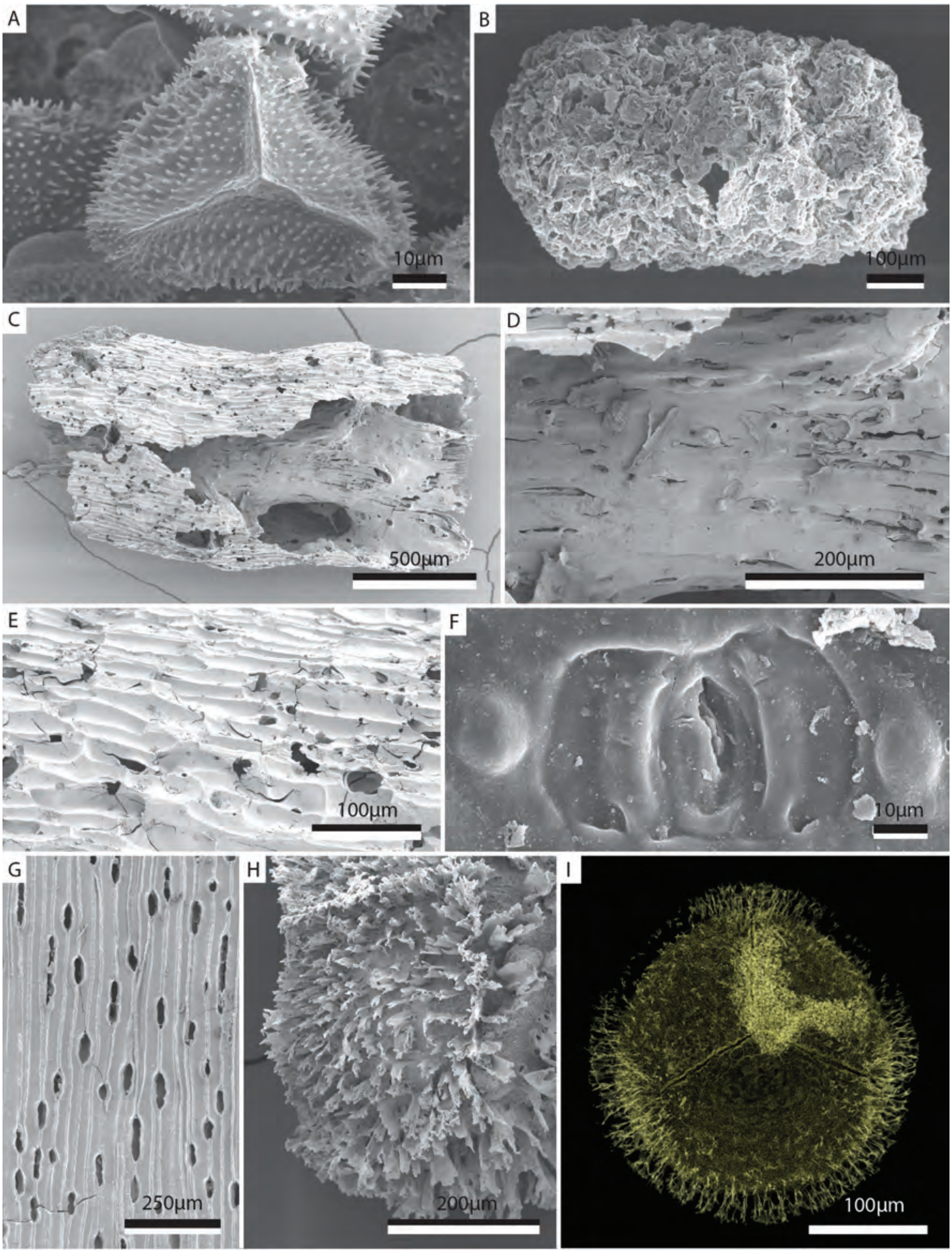

A
10µm
B
100µm
C
500µm
D
200µm
E
100µm
F
10µm
G
250µm
H
200µm
I
100µm

Figure 6.5

Figure 6.5 (previous page): Scanning electron microscopy images of a range of biota recovered from bulk macerated samples of the Toploje Member silicified peat.
A. NRM S089555, Fern spores attributable to *Didecitriletes ericianus* within a sporangium.
B. NRM S089603, Arthropod coprolite containing mixed plant vegetative remains and spores.
C. NRM S088043, Broken, uncompressed *Vertebraria* rootlet showing internal air chambers.
D. NRM S088043, Enlargement of the central column of a *Vertebraria* rootlet.
E. NRM S088043, Enlargement of external surface of young *Vertebraria* rootlet.
F. NRM S089574, Apparently brachyparacytic stoma on the surface of an unidentified trichome-fringed gymnosperm leaf.
G. NRM S088062-A, Tangential longitudinal sectional of charcoalified wood showing longitudinal tracheids and sections of rays 1–3 cells high.
H. NRM S087801-A, Elaborately ornamented surface of a *Singhisporites hystrix* megaspore.
I. NRM S089351, X-ray synchrotron tomographic image of an elaborately ornamented *Singhisporites hystrix* megaspore with an apparently shrivelled (pale) inner body.

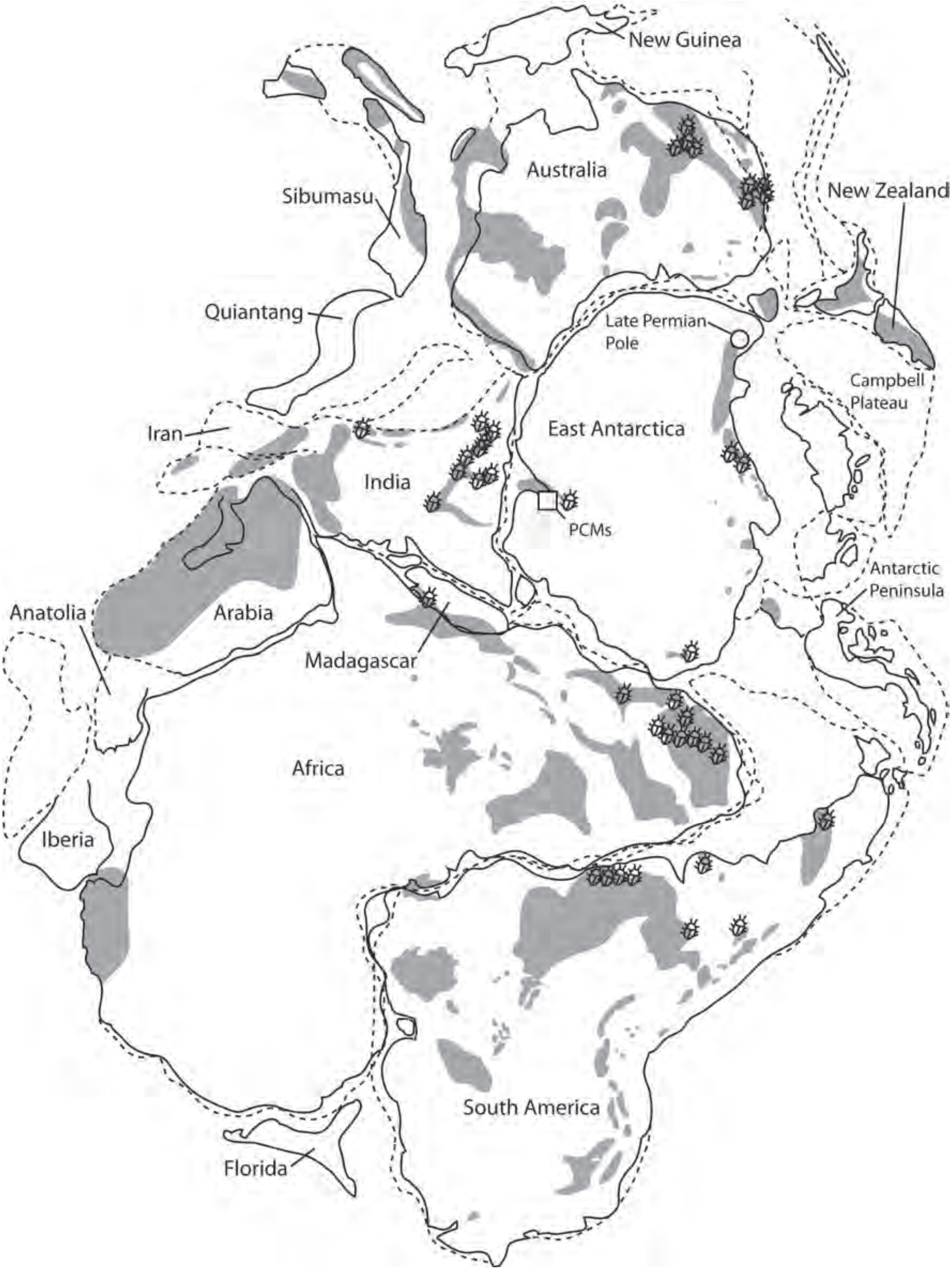


Figure 6.6: Map of Gondwana for the Permian showing the distribution of sedimentary basins of that age (grey) and sites yielding evidence of plant–herbivore interactions (see Table 4), bug symbols mark position of sites where plant–herbivore interactions have been described; base map from McLoughlin (2001).

6.4.4 Energy pathways

Based on the composition of, and interactions between, the fossil biota, a reconstruction of the energy pathways in this Middle Permian mire ecosystem is presented (Figure 6.7). In the absence of tetrapods, the high-latitude mire community is interpreted to have been dominated by a low diversity of woody gymnosperms and sparse understory ferns and lycophytes that supported a broad range of invertebrate herbivores and detritivores. The primary producers were dominantly glossopterid gymnosperms along with a significant proportion of *Noeggerathiopsis*, as well as smaller elements of the flora in the form of ferns and herbaceous lycophytes (Figure 6.7). Detritivores were dominantly oribatid mites, but other larger forms are evidenced by coprolites. Fungi and fungi-like organisms appear to have played key roles in nutrient cycling through saprotrophy, and possibly via mycorrhizal interactions with the plants. The *Glossopteris* trees themselves appear to have been the keystone species within the ecosystem, since many groups of arthropods and fungal saprotrophs fed directly or indirectly on both the living and decaying tissues of the *Glossopteris* plant. Based on the high-latitude setting and evidence of pronounced annual growth increments in the gymnosperms, the energy flux and consumer activity in this ecosystem likely varied greatly on a seasonal basis. Abiotic factors that influenced this ecosystem included rainfall and also fires as evidenced by significant quantities of locally abundant charcoal representing localised burning events within the peats (Figure 6.7).

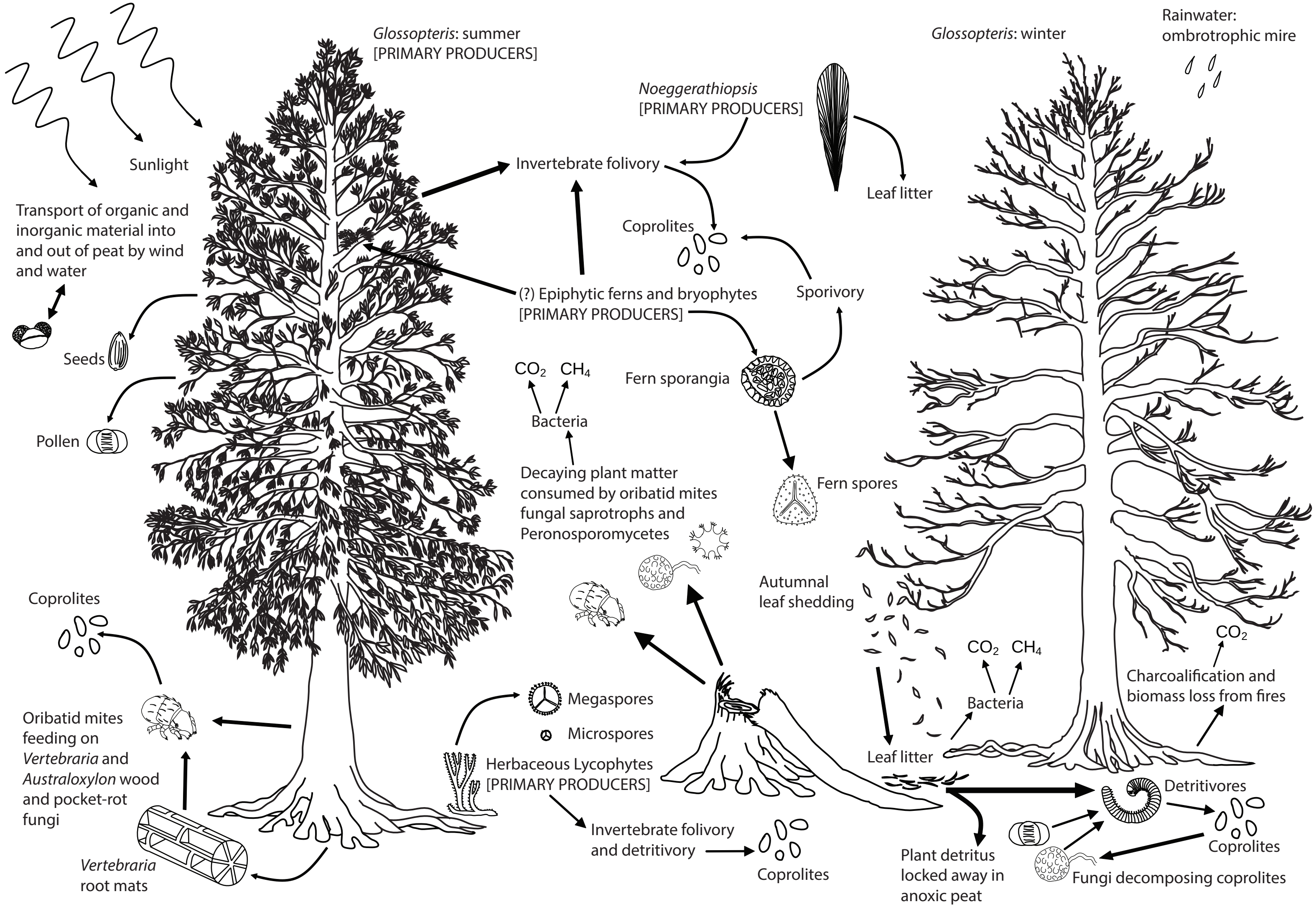


Figure 6.7: Schematic representation of energy pathways and nutrient cycling in the Topolje Member chert palaeoecosystem.

6.5 Accumulation and early diagenesis

6.5.1 Accumulation model

The plant organs found in the peats lack signs of regular abrasion and are preserved relatively intact. The organic components of the peat also lack either imbrication or systematic sorting with the exception of a few discontinuous centimetre-scale bands that are enriched in macroscopic charcoal. The delicate structures preserved on some organs, such as fine trichomes in the stomatal grooves of *Noeggerathiopsis* leaves (Figure 6.3, E), hirsute leaf margins (Figure 6.4, H), stomatal guard cells (Figure 6.5, F) and spines on lycophyte megaspores and on the oogonia of Peronosporomycetes (McLoughlin and Drinnan, 1996; Chapter 3 and Slater et al., 2013) suggest that the bulk of the detached plant remains had not been transported any significant distance before incorporation into the peat. Some upright stumps and intertwined *Vertebraria* roots in the peat profile denote that at least some glossopterid remains were preserved in growth position. This contrasts with some Late Permian silicified peats from the central Transantarctic Mountains that may represent rafted peat mats preserved out of context of the original depositional environment (Taylor et al., 1989). Rafting of peat loads by rivers and in lakes and by the action of ice is well known in modern environments (Argow et al., 2011), some organic mats, tussocks and floating islands of vegetation even being rafted across large marine water bodies (Houle, 1998). Floatation of peats has been proposed as a mechanism for the accumulation of organic matter forming the lower Maastrichtian coals of the eastern Pyrenees of Catalonia, Spain (Villalba-Breva et al., 2012). The peats preserved in the Toploje Member chert are the silicified remains of an *in situ* mire, since they are laterally extensive (persisting over 3 km of outcrop) and preserve few siliciclastic grains (Holdgate et al., 2005).

6.5.2 Silicification and compaction

The silicification process in the uppermost Toploje Member appears to have occurred before any significant compression of the peats, since delicate and even hollow structures, such as small seeds and megaspores, are preserved in their original three-dimensional form (see Chapter 3 and Slater et al., 2011). Soft tissues such as phloem are locally preserved, which suggests a rapid silicification process and inhibition of bacterial degradation. The strongly acidic nature of the original waterlogged peat profile probably suppressed decay prior to silicification. Pyrite is common through the peat matrix and occurs primarily as small crystals that appear to have developed contemporaneously with silicification (Figure 6.3, G). For the most part, these crystals do not impact on the quality of preservation of the organic matter and do not show preferential nucleation on any particular plant tissues. Some larger cavities within the peat (e.g., voids within *Vertebraria* roots) show weakly defined concentric infilling by cryptocrystalline silica but little textural or compositional differences between layers is apparent. Hand specimens of the chert show very few cross-cutting mineral veins. These factors suggest that the bulk of the chert's silica was introduced and precipitated in a short interval rather than in multiple phases over a longer time period, during which a greater range of textural and compositional variation would be expected in the precipitates.

The primary source of silica in the chert remains unresolved. No volcanic ash beds or other volcanigenic sediments are preserved in the Bainmedart Coal Measures, in contrast to silicified peat occurrences in other Permian strata of Australia and the Transantarctic Mountains (Gould and Delevoryas, 1977; Taylor et al., 1989; McLoughlin, 1992; Pigg & McLoughlin, 1997). Further, no evidence of strong lateral or vertical textural or vegetational gradients within the silicified ecosystem are evident in contrast to typical sinter deposits

(Walter et al., 1998; Guido et al., 2010). The stratigraphic position of the chert bed immediately below the lacustrine sideritic shales of the Dragons Teeth Member, suggests that drowning of the peat surface by mineral-charged lake waters was key to the entombment process. Mineral-charged springs emanating from basin-margin faults offer one potential source of silica, with precipitation around the organic matter of the drowned peat potentially being facilitated by strongly alkaline conditions in the high palaeolatitude lake. The precursor to chert-formation, silica gels, have been reported from some modern lacustrine settings, particularly in brine rich/saline playa lakes and also lagoonal environments (Peterson and Von Der Borch, 1965; Colinvaux and Goodman, 1971; Wells, 1983; Wheeler and Textoris, 1978). Such silica gels form in the sediments of modern lake beds when silica, derived from quartz or other sources, is dissolved into the lake water due to highly alkaline conditions and then falls out of solution when the pH drops sharply due to increased acidity because of the decay of plant matter in the lake (Hesse, 1989).

6.5.3 Wildfire

Some hand specimens of the Toploje Member chert are relatively rich in charcoalified plant tissues and the abundance of micro- and macro-charcoal in bulk-macerated sediment samples is commonly high. Fire plays a significant role in shaping the structure, diversity and ecological succession of many modern plant communities (Crutzen and Goldammer, 1993). Wildfire has been a major factor in the environment since land vegetation produced a highly oxygenated atmosphere in the Carboniferous (Scott, 1989, 2000). Even earlier evidence of fire in the form of sparse but dispersed fusain and a few identifiable charcoalified plant organs extends back to the dawn of terrestrial vascular plant communities (Scott and Glasspool, 2006). Jasper et al. (2012) showed that fire was a consistent feature of the Gondwanan Permian landscape and may have played an important role in vegetation overturn across the supercontinent.

Besides preserving a record of the distribution of wildfires through time, charcoalification can aid plant preservation by transforming the cell walls of the plant material into almost pure carbon, which hinders the decay process and retains anatomical detail. Such charcoalification of plant tissues occurs in wildfires with a specific temperature range (240–370°C), providing insights into the style of wildfire propagation in palaeoecosystems (Scott and Jones, 1991; Collinson et al., 2007). The common presence of charcoal in the silicified peats of the PCMs (measured at 1.2% organic volume by Holdgate et al., 2005, but locally in higher proportions in this study: Figure 6.1, B) means that wildfires were a frequent feature of the Middle Permian high-latitude mire landscape.

The charcoalification of the PCMs plant material is also of importance taphonomically (Scott, 2000). Organic remains that have been charcoalified in the Toploje Member chert include macroscopic fragments of *Australoxlyon* wood, gymnosperm seeds (Figure 6.4, A), *Glossopteris* leaf midribs, *Vertebraria* axes (Figure 6.5, C–E), lycophyte axis fragments and microphylls, coprolites (Figure 6.3, D) and arthropod cuticle (Figure 6.4, G), (Weaver et al., 1997; Holdgate et al., 2005). Some of these organs (e.g. seeds and lycophyte microphylls) are otherwise ill-preserved in the peats suggesting a taphonomic bias against their preservation in the absence of wildfires. The greater cohesion and particle strength endowed by the charcoalification process aids the recovery of anatomical information from delicate plant tissues. Remains of charcoalified *Australoxlyon* wood locally exceed 5 cm in diameter (Holdgate et al., 2005). The concentration of charcoal in bands within some chert samples (Figures 6.1, B; 6.5, G) may be related to subaqueous sorting of particles or through accumulation of charcoal in fire-pockets on the peat surface in the aftermath of burning events.

6.6 Mire type

6.6.1 Depositional setting

Glossopterid gymnosperms have been documented from a wide range of terrestrial settings (McLoughlin, 1993; Cúneo et al., 1993). They ranged from periglacial to warm and intermittently dry temperate climates (Chandra, 1992), and are preserved in a diverse array of deltaic, alluvial valley, lake- and lagoon-margin, and potentially even upland settings (McLoughlin, 1993; Rigby, 1993; Cúneo et al, 1993; Guerra-Sommer et al., 2008). Indeed the ubiquitous occurrence of Glossopteris leaves in Permian continental deposits of Gondwana suggests they occupied most parts of the fluvial and deltaic landscapes from levees to floodbasin mires and well-drained valley fringes, but detailed quantitative studies of the partitioning of plants within alluvial systems have yet to be undertaken.

In the context of the Permian deposits of the Prince Charles Mountains, the Toploje Member was deposited in a narrow but very long (>1000 km) graben complex (the Lambert Graben) that developed as part of an incipient rifting phase in central Gondwana (Harrowfield et al., 2005). Deposition of basin-wide peats occurred in alternation with pluvial pulses depositing extensive blankets of channel sandstones within braided river systems (Fielding and Webb, 1996). We envisage glossopterids occupying predominantly fluvial levees and raised floobasin mires, but also extending onto wetter parts of the valley flanks.

6.6.2 Rheotrophic vs. ombrotrophic mire

The peats preserved in the Toploje Member chert are interpreted to represent the product of an ombrotrophic mire as opposed to a rheotrophic mire (Martini and Glooschenko, 1985; Slater et al., 2012). Ombrotrophic mires obtain their water and nutrient supply through high levels of precipitation, whereas rheotrophic (or minerotrophic) mires are supplied with water by streams or springs (Diessel, 1992). Rheotrophic mires receive a higher nutrient supply and are characteristically richer in inorganic content than ombrotrophic mires (Diessel, 1992). The paucity of siliciclastic grains coupled with the abundance of fungi and charcoal (and especially of charcoalified roots) suggests the peat layer was the product of an ombrotrophic mire (Martini and Glooschenko, 1985; Slater et al., 2012), since such deposits are raised above the water table and are subject to greater aerobic decay and sporadic burning than rheotrophic systems. Ombrotrophic mires generally also produce thicker organic accumulations than rheotrophic systems and this is consistent with the presence of seams reaching 11 m thick within the Bainmedart Coal Measures (McLoughlin and Drinnan, 1997a).

Euramerican late Palaeozoic coals that developed under palaeotropical climates tend to contain high percentages of vitrinite macerals (Mackowsky, 1975; Figure 6.8) – a consequence of enhanced gelification of organic constituents. High-palaeolatitude Gondwanan coals, especially those of Permian age, are renowned for their high inertinite content (Mackowsky, 1975), although this is not always the case (Diessel and Smyth, 1995). High inertinite concentrations are considered characteristic of ombrogenous peats, in which the upper part of the organic profile is subject to oxidation and regular burning due to a fluctuating water table (Teichmüller, 1989; Moore, 1989). The high inertinite levels in most coal samples from the Bainmedart Coal Measures are consistent with proportions represented in other Gondwanan Permian (glossopterid-derived) coals (Figure 6.8). Further, the low sulphur content (0.38 to 0.81 weight percent: Holdgate et al., 2005) and dominance of inertodetrinite amongst the inertinite maceral component is consistent with the interpretation of the Lambert Graben Permian peat-forming environments as raised forest mires of alluvial valley settings subject to strongly fluctuating water tables and experiencing fine degradation and oxidation of plant components.

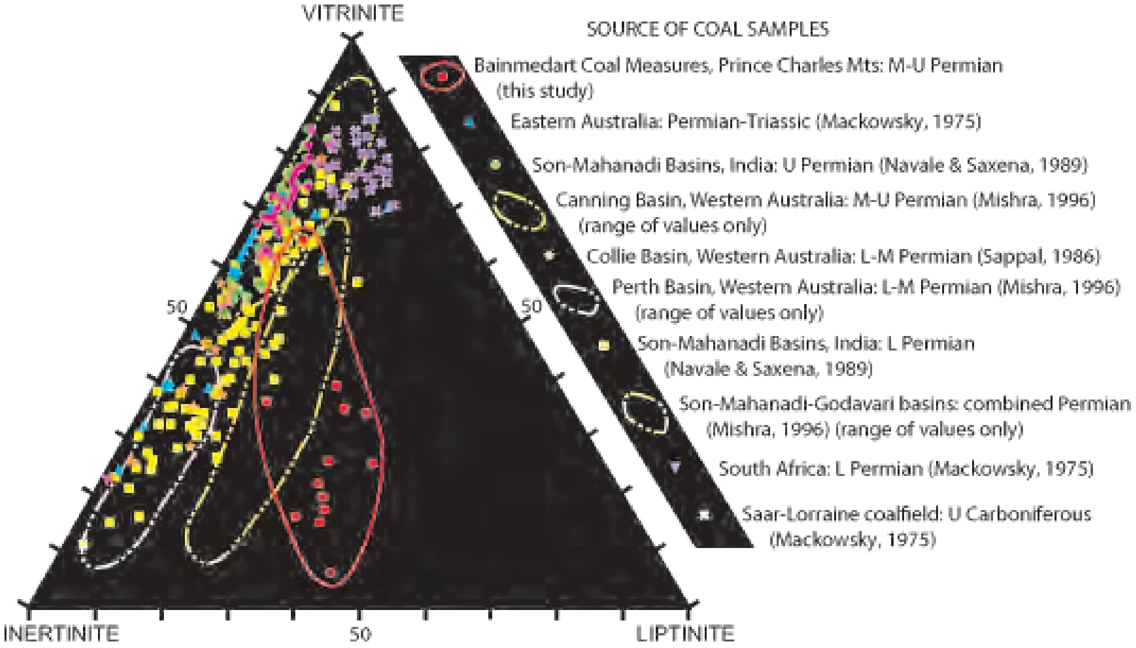


Figure 6.8: Ternary diagram showing the range of variation in vitrinite:inertinite:liptinite ratios in coals of the Bainmedart Coal Measures, Antarctica, versus equivalent ratios in typical coals from other parts of Gondwana and from the Saar-Lorraine Coalfield of the Carboniferous Euramerican province (sources indicated on diagram).

6.6.3 Structure (and reconstruction) of a glossopterid mire

Reconstructions of the food web, trophic levels and soil ecology of ancient forest ecosystems have been attempted in several studies of exceptionally preserved fossil assemblages of (Adl et al., 2011; Habgood et al., 2004). The reconstruction of the *Glossopteris*-dominated forest mire within the Lambert Graben valley system presented here (Figure 6.9) features the dominance of hygrophilous arborescent glossopterid gymnosperms and subsidiary cordaitaleans. Lower storey vegetation within the glossopterid forests is represented by herbaceous lycophytes and ferns (Figure 6.5, A). Sphenophytes, more typical of the lacustrine deposits of the Dragons Teeth Member, are envisaged to have occupied more open, lake-margin or disturbed settings similar to the habitats occupied by modern *Equisetum*. Abundant deadwood, hosting a range of fungal saprotrophs, and widespread waterlogged soil habitats would have characterised the landscape.

The topology of arborescent plants at higher latitudes tends towards tall tapered forms in order to maximize the collection of light for photosynthesis from low-angle solar radiation (Creber and Chaloner, 1985; McLoughlin, 2011b); thus the dominant trees are here reconstructed to have a conical canopy shape (Figure 6.9). Relatively open woodlands also characterise modern high-latitude woody vegetation, especially those areas close to the temperature-controlled tree-line (Doležal et al., 2006). Hence, we interpret these glosopterid communities to represent open deciduous forests and woodlands *sensu* many Carboniferous T^0 assemblages, which reveal an open canopy distribution of large plants (Gastaldo et al., 2004; DiMichele et al., 2009; DiMichele and Falcon-Lang, 2011) rather than the closed canopy system seen in many angiosperm forests.

The extensive portrayal of wetlands in the reconstruction highlights year-round high moisture levels and is consistent with the broad representation of hygrophilous elements in the flora and the abundance of moisture-loving micro-organisms (e.g., Peronosporomycetes). The distal part of the reconstruction (Figure 6.9) portrays features representative of the sedimentology of the lower Bainmedart Coal Measures. Sedimentary facies associations of the Toploje Member are represented by thick sandstone packages deposited in braided river channels, alternating with extensive floobasin mudrocks and coals (Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a) within an alluvial valley setting flanked by fault-delineated valley margins of considerable relief that were developed in Precambrian crystalline rocks (Boger, 2011).

Figure 6.9: Reconstruction of the Lambert Graben Middle Permian Alluvial valley palaeoecosystem based on fossil and sedimentological data from the Toploje Member chert and stratigraphically adjacent strata of the Bainmedart Coal Measures in the Prince Charles Mountains. Artwork by Pollyanna von Knorring.

6.6.4 Implications for coal geology

There is a notable contrast between some of the coal petrographic results (Figure 6.2) and the composition of the silicified peat obtained via point counts of transects through various permineralised blocks (Figure 6.1, A). In general, the peat appears to contain much lesser proportions of obviously oxidised components (charcoal) and waxy material (spores and cuticle) and higher proportions of non-oxidised woody and leaf mesophyll components than is registered in the coal.

Charcoalified (oxidised) material typically has greater compactional resistance than other plant remains, hence its relative volumetric representation probably increases through the early stages of coalification. However, the very high levels of inertinite (up to 50%) in some coal samples are greater than would be expected from differential compaction alone. It is possible that the small selection of coal samples examined were preferentially enriched in charcoal through local fire events. Such bands in the permineralised peat show levels of >50% charcoal (Figure 6.1, B). Further, the preservation of the silicified peat differs from other organic accumulations in the Bainmedart Coal Measures in that the peat surface was drowned rapidly by lake waters that saw deposition of the overlying Dragons Teeth Member. Hence, the upper part of this peat profile may not have been subjected to the prolonged oxidation and degradation by fungi, microbes and fires that was experienced by other raised peat (coal-forming) deposits in this formation. This may better account for the lesser proportion of oxidised plant material recognised in the silicified peat compared to inertinite in the coals of the same formation.

The organic matter in the silicified peat has undergone relatively little compression before mineral entombment, whereas the associated coals of sub-bituminous to high-volatile bituminous rank (Holdgate et al., 2005) have probably experienced >80% loss of volume through compaction, gelification and diagenesis (Teichmüller and Teichmüller, 1982). Apart from the loss of pore space, much of this volume reduction was probably accommodated by crushing, loss of volatiles and mobilization of organic gels from unoxidised wood and mesophyll cellulosic cell walls. We suspect that this accounts for the high proportion of woody and leafy tissues in the silicified peat compared to the relatively modest levels of vitrinite in the coals.

The high proportion of liptinite macerals in the Bainmedart Coal Measures coals also appears anomalous with respect to the low volumetric proportion of spores, pollen and sporangia (<2%) in the permineralised peat (Holdgate et al., 2005). Low degrees of compaction for these dense waxy materials may account for somewhat higher percentages in the associated coals but it is unlikely to account for the very high levels of liptinite (up to 40%) in some coal samples. Holdgate et al. (2005) suggested several other factors that might account for the anomalously high spore content of the Lambert Graben coals in contrast to the silicified peat. These included potential misidentification of small cutinite fragments in the coal as sporinite, and the possibility that a considerable proportion of the finely dispersed unidentifiable organic matter in the peat represents represents unrecognised sporopollenin material.

Cameron et al. (1989) noted that the proportion of liptinite commonly increases upwards in domed (ombrogenous) peats together with oxidised detrital matter. The abrupt termination of peat development at the top of the Toploje Member via flooding may indicate that the silicified peat capping this unit did not reach the optimal domed stage of other coals in the host formation. In general, high liptinite contents, in the absence of alginite, might also be diagnostic of coals derived from high-latitude alluvial valley forest mires dominated by low-diversity deciduous gymnosperm vegetation with high pollen production. In this respect, it is notable that Permian coals from the continental-interior, alluvial valley deposits of the Godavari-Son-Mahanadi Graben system in India also have relatively high liptinite contents and have the most similar proportions of maceral groups to the Lambert Graben coals (Navale and Saxena, 1989; Mishra, 1996).

Quantitative analyses of the permineralised and coalified organic accumulations in the Bainmedart Coal Measures indicate that although silicified peats provide excellent details of the botanical constituents of coal-forming deposits, they do not always reflect the ultimate volumetric representation of macerals in the coals. In addition to differences in the oxidation state at the time of permineralisation of silicified peats versus non-mineralised peats, significant losses of pore space, volatile components and mobilization of organic gels during the peatification and coalification processes may markedly modify the volumetric proportions of some macerals. Furthermore, permineralised peats, coal balls, and coal itself may not be fully representative of the standing biomass of the peat-forming community, since peats tend to be enriched in root material compared to subaerial parts of the vegetation (Raymond, 1987; DiMichele and Phillips, 1994).

6.7 Discussion

The permineralised community represented in the Toploje Member chert shares many similarities with the Permian and Triassic peats of the Transantarctic Mountains that occur at marginally higher palaeolatitudes than those of the Prince Charles Mountains. The Permian palaeocommunity in the Transantarctic Mountains is also dominated by glossopterids, evidenced by a range of plant vegetative organs and megasporophyll and microsporophyll genera (Ryberg et al., 2012a), but differs in the absence of *Noeggerathiopsis*, which is common in the Toploje Member peats. Other notable shared features with the permineralised floras of the Transantarctic Mountains include the presence of herbaceous lycophytes in the Permian (Ryberg et al., 2012b; Schwendemann et al., 2010) and diverse fungal elements in the Triassic peats (Krings et al., 2012a).

Vertebraria roots were found to be the dominant component of the peats alongside significant quantities of matted *Glossopteris* and *Noeggerathiopsis* leaves (Figure 6.1, A), whilst charcoalified wood can be locally dominant in particular peat microfacies (Figure 6.1, B). The paucity of arboreal components of the plants such as stem wood and fruiting bodies in comparison to the dominance of root tissues leads us to interpret that there was a taphonomic bias against incorporation of at least some subaerial organs into the peat profile. Similar proportions of floral elements were found in quantitative analysis of coal ball vegetation from Pennsylvanian age wetland floras from Pennsylvania, USA where root tissue was also found to be the dominant component of the preserved assemblage (Feng, 1989).

Lower-latitude Gondwanan permineralised assemblages, such as those from the Late Permian Fort Cooper Coal Measures of the Bowen Basin, Australia (Gould and Delevoryas, 1977; Nishida et al., 2007) are characterised by slightly higher macrofloral diversity, although those floras have yet to be fully described. Outside the Gondwanan phytogeographic province, silicified Permian terrestrial communities differ in their macrofloral composition; however, many of the key microorganism groups are represented and invertebrate-plant interactions appear to have been established in a similar ecological structure throughout the late Palaeozoic world (Baxendale, 1979; Labandeira, 1998a, 2013; Rößler, 2000).

Beyond the Permian, a block of Triassic silicified plant remains collected from Hopen Island in the Svalbard Archipelago and deposited in northern high middle latitudes contains many of the soil microbe groups preserved in the Toploje Member chert (Strullu-Derrien et al., 2012); these include a diverse range of coprolites (Figures 6.3, D; 6.4, C; 6.5, B) indicating an assortment of soil entomofauna and a range of fungal morphotypes and interactions (Figures 6.3, A; 6.4, D–F). Equivalent microbial communities, though associated with a more diverse macroflora are evident in Late Triassic permineralised peats from the Transantarctic Mountains (Schwendemann et al., 2009; Krings et al., 2012a).

Similar communities of microorganisms are also present in the Upper Pennsylvanian Grand-Croix cherts of France, including a diverse fungal inventory and examples of Peronosporomycetes (Krings et al., 2009). The *Glossopteris* component community of the Toploje Member chert also closely resembles the structure and resource partitioning evident in the *Psaronius* component community preserved in the early Late Pennsylvanian coal balls of the Illinois Basin (Labandeira, 1998a), the earliest Permian Chemnitz fossil forest (Rößler, 2000), and the Early Permian Cathaysian coal measures of southwest China (He et al., 2008; D'Rozario et al., 2011a) with exploitation of every part of the dominant host plant by invertebrate herbivores and detritivores (see Chapter 4 and Slater et al., 2012).

The relatively low diversity of the Prince Charles Mountains macroflora compared to palaeotropical Euramerican late Palaeozoic peat assemblages shows that, as is the case today, there was a latitudinal diversity gradient in the Permian. Even within Gondwana, greater floristic diversity is evident in adpression assemblages from lower palaeolatitudes of South America and southern Africa (Archangelsky and Arrondo, 1969; Anderson and Anderson, 1985) compared to higher palaeolatitude regions of eastern Australia and Antarctica (McLoughlin 1992, 1994a, b; Cúneo et al., 1993). The more pronounced seasonal light regime and presumably colder winters may have inhibited many (especially Euramerican) taxa from colonizing the highest latitudes of Gondwana during the Permian.

Cryptic and diminutive faunal elements that occur in similar permineralised assemblages include freshwater crustaceans known from the Rhynie Chert/Windyfield cherts and from an Early Mississippian to Middle Pennsylvanian *ex situ* chert cobble from Yorkshire, UK (Fayers and Trewin, 2003; Anderson and Trewin, 2003; Anderson et al., 2004; Stevens et al., 2010; Haug et al., 2012; Womack et al., 2012), trigonotarbid arachnids known from the Silurian Přídolí Series of Ludford Lane in Shropshire, UK (Dunlop, 1996) and from the Rhynie Chert (Fayers et al., 2005), as well as Rhynie Chert harvestmen (Dunlop et al., 2004).

The absence of complete body fossils of aquatic crustaceans and other arthropods may be due to the speed of silicification and the environment the assemblages accumulated in. Unlike the Rhynie Chert or the *ex situ* Yorkshire cobble, the mode of entombment in the Toploje Member chert does not appear to be related to very rapid hydrothermal precipitation of silica that could have killed and preserved free-moving arthropods in their life positions (Guidry and Chafetz, 2003; Anderson et al., 2004; Womack et al., 2012). Instead, the Toploje Member peat represents a long-lived acidic mire environment, into which silica was subsequently introduced in high concentrations associated with flooding of the mire surface. Any arthropod remains would likely be represented by dissociated exoskeletons and exuviae from the moulting of ecdysozoans that were incorporated into the peat or trapped within excavations inside woody tissues. Fragments of such arthropod cuticle with attached setae from the Toploje Member chert were recovered by bulk maceration of the chert (Holdgate et al., 2005; see Chapter 4 and Slater et al., 2012) and are also known from overlying Triassic sediments (McLoughlin et al., 1997). These fragments likely represent arthropod cuticle since the setae are hollow as they are collapsed or flattened in places, whereas similar setae of annelid origin are solid (Orrhage, 1971). The setae may have served a mechanosensory function in life (Crouau, 1997; Keil, 2012). The cuticles are unlikely to be of collembolan affinity since collembolan exoskeleton is covered in granule structures of anti-adhesive function, which are absent in the Toploje Member chert specimens (Nickerl et al., 2012). Beyond this, the arthropod fragments cannot be identified.

Relatively little attention has been directed towards arthropod cuticles extracted from coals, silicified peats and coal balls (Bartram et al., 1987), perhaps in part because the contents of these sediments are generally studied for their palaeobotanical content, and such remains may benefit from the attention of specialist arthropod workers. The mode of preservation of such arthropod cuticles in silicified deposits and coals has been the subject of some debate (e.g. Stankiewicz et al., 1998; Table 5). Examples of scorpion exoskeleton have been described from Pennsylvanian (Westphalian) coals of Yorkshire, UK (e.g. Bartram et al., 1987) and the Late Triassic Lower Keuper Sandstone of Bromsgrove, Worcestershire, UK (Dunlop et al., 2007). Cuticles of possible eurypterid affinity are also known from the Lower Devonian of Podolia, Ukraine (Filipiak et al., 2012) and the body of a trigonotarbid was also recovered via HF maceration from Přídolí shales of Shropshire, UK (Dunlop, 1996). Arthropod cuticles have also been recovered through HF maceration of early Silurian (Llandovery) terrestrial strata from Pennsylvania, providing some of the earliest direct evidence for land or freshwater animals (Gray and Boucot, 1994). Table 5 lists a compilation of the records of such arthropod cuticle and other invertebrate remains recovered from acid maceration of sediments, primarily coals, clays, siltstones and cherts. Exceptionally preserved Palaeozoic arthropods are also known from siderite concretions, particularly from Carboniferous sites such as Coseley, UK (Garwood and Sutton, 2010), Mazon Creek, Illinois (Carpenter, 1997) and the Montceau Lagerstätte, France (Garwood et al., 2012). Arthropods preserved in siderite concretions have increasingly been studied using X–ray synchrotron microtomography, which unveils exceptional detail in the fossil (Garwood et al., 2012).

However, the maceration of silicified peats and scanning electron microscopy of residues could potentially yield comparable anatomical information and also be used to more accurately assess diversity through the comparison of different cuticle types in coals and other organic-rich lithologies. Several studies have also used the acetate peel technique to study the cuticle of arthropods such as eurypterids and scorpions in detail (Braun, 1999; Tetlie et al., 2008). The potential of such fragmentary arthropod cuticle remains has recently been investigated in detail in Cambrian marine sediments by making use of a long-used palaeobotanical technique to extract animal fossils (Harvey et al., 2012a; Harvey et al., 2012b; Butterfield and Harvey, 2012) and could offer comparable results in unveiling cryptic diversity in Palaeozoic terrestrial ecosystems.

Table 5. List of Palaeozoic and Mesozoic records of arthropod cuticle recovered from bulk maceration of sedimentary rocks.

PUBLICATION	AGE/LOCALITY	DESCRIPTION
Al-Ameri, 1983	Silurian; Ghadames Basin, Tripolitania, Libya	Eurypterid cuticle from borehole macerals
Bartram et al., 1987	Late Carboniferous; Yorkshire.	Scorpion cuticles
Bartram et al., 1987	Pennsylvanian; Ohio, USA	Arthropod cuticle extracted from coal balls
Batten, 1998	Lower Cretaceous; Weald Clay Formation, Surrey, England, UK.	Insect fragments
Braun, 1997	Rhenish Early Devonian and Late Carboniferous of the Ruhr and the Saar Basin. Devonian, early Emsian; Waxweiler, Eifel region. Late Carboniferous; Germany.	Various arthropod cuticle remains from coal, clay and siltstones. Near complete ostracods and mites. Appendages of ostracods, mites and scorpions. Chelicerata (presumed arachnid) cuticle with sensory organs. Slit sensilla. Lyriform organs.
Braun, 2004	Various ages and locations: [1]Earlyr Devonian, early Emsian; Nellenköpfchen Formation, Alken an der Mosel, Germany. [2]Late Carboniferous; Saar, Germany. [3]Late Carboniferous; Piesberg, near Osnabrück, Germany.	[1]Ventral eurypterid appendage, and setae. [2]Near complete mite. [3]Front appendages of freshwater ostracod
Butterfield and Harvey, 2012	Various ages and locations: late early Cambrian, Mount Cap Formation, Northwest Territories, Canada. late early Cambrian Forteau Formation, Newfoundland. late early Cambrian Mahto Formation, Alberta, Canada. early middle Cambrian Hess River Formation, Northwest Territories, Canada. late middle Cambrian Pika Formation, Alberta, Canada. late middle Cambrian Earlie Formation, Saskatchewan, Canada.	*Wiwaxia* sclerites, priapulid-like scalids, mollusc radulae.
Clarke and Ruedemann, 1912	Devonian; New York State, USA	Eurypterid cuticle
Dalingwater, 1973	Silurian; 'Passage Beds' at Ludlow, Shropshire, England, UK	Eurypterid, *Pterygotus (Pterygotus) ludensis,* cuticle ultrastructure.
Dalingwater, 1975	Silurian; Gotland, Sweden.	Eurypterid cuticle
Dalingwater, 1980	Silurian; Gotland, Sweden.	Eurypterid cuticle
Dunlop et al., 2007	Late Triassic; Lower Keuper Sandstone, Bromsgrove, Worcestershire, England, UK.	Scorpion cuticle
Dunlop, 1996	Late Silurian, Přídolí; Welsh borderland, Shropshire, England, UK	Entire Trigonotarbid body extracted from shales.
Filipiak and Zatoń, 2011	Early Devonian; Southern Poland	Arthropod (?eurypterid) cuticle
Filipiak et al., 2012	Early Devonian; Podolia, Ukraine	Eurypterid and possible scorpion

		cuticle.
Goodarzi, 1984	Cretaceous-Palaeocene; Anxiety Butte coal zone, Ravenscrag Formation, Saskatchewan, Canada	Arthropod cuticle extracted from coal.
Gray and Boucot, 1994	Early Silurian, Llandovery; Tuscarora Formation, Pennsylvania, USA.	Terrestrial deposits with fragments of arthropod (?eurypterid);jaw fragment of annelid
Harvey et al., 2012a	Middle Cambrian; Kaili Formation, Guizhou Province, China	Assorted cuticle remains including *Wiwaxia* sclerites, fragments of chancelloriids, brachiopods, hyolithids and a priapulid−like scalidophoran
Harvey et al., 2012b	Middle to late Cambrian; Deadwood Formation, Saskatchewan and Alberta, Canada	Assorted crustacean mandibles and articulated limbs of likely branchiopod, copepod and ostracod affinity
Harvey et al., 2012c	Middle to late Cambrian; Deadwood Formation, Saskatchewan and Alberta, Canada	Range of fragmentary remains of crustaceans, paraconodonts and several other taxa
Holdgate et al., 2005	Permian, Guadalupian; Prince Charles Mountains, East Antarctica	Arthropod fragments
Jaglin and Paris, 2002	Late Silurian; Northwest Libya.	Eurypterid cuticle from borehole macerals.
Jansson et al., 2008;	Early Jurassic, Pliensbachian; Eastern Australia	Annelid cocoons; arthropod fragments
Jeram, 1990	Early Carboniferous, Dinatian; Limestone, East Kirkton Quarry, West Lothian, Scotland, UK	Scorpion cuticle, acid-etched to stand proud of the rock with HCL
Jeram et al., 1990	Late Silurian, Přídolí; Welsh borderland, Shropshire, England, UK	Trigonotarbid, eurypterid, centipedes, scorpions, millipedes
Kethley et al., 1989	Middle Devonian; Gilboa, New York State, USA.	Alicorhagiid mite
Labandeira et al., 1988	Early Devonian, Early Emsian. Battery Point Sandstone, Gaspé Peninsula, Québec, Canada	Head and thorax of a bristletail
Manum et al., 1991	Various post-Triassic strata	Annelid cocoons
Manum, 1996	Various post-Triassic strata	Annelid cocoons
McLoughlin et al., 1997	Triassic; Prince Charles Mountains, East Antarctica	Arthropod fragments
McLoughlin et al., 2002	Early Cretaceous (Valanginian–Hauterivian); lower Strzelecki Group, Gippsland Basin, Victoria, Australia	Arthropod exoskeleton fragments, coleopterans, arthropod head with palps/mandibles
McLoughlin et al., In Press	Early Jurassic, Pliensbachian; Eastern Australia.	Arthropod fragments
Mutvei, 1977	Silurian; Gotland, Sweden.	Eurypterid cuticle
Rolfe, 1962	Middle Silurian; Scotland, UK.	Crustacean cuticle
Scott, 1977	Late Carboniferous, Westphalian B; Swillington Brickpit, Yorkshire, England, UK	Scorpion fragments extracted from coals
Scott, 1978	Late Carboniferous, Westphalian B; Swillington Brickpit, Yorkshire, England,	Scorpion fragments extracted from coals

	UK.	
Scott, 1984	Late Carboniferous, Westphalian B. Swillington Brickpit, Yorkshire, England, UK	Scorpion fragments extracted from coals
Selden, 1981	Silurian, Gotland, Sweden	Eurypterid cuticle
Selden et al., 2008a	Devonian; Gilboa and South Mountain localities, New York State, USA	Arachnid fragments, spider spinnerets, cheliceral fangs, flagellar structure
Selden et al., 2008b	Jurassic, Upper Callovian; Oxford Clay, South Cave Station Quarry, Yorkshire, UK.	Iron Pyrite Replacement specimen, oribatid mite. Not cuticle, but specimen sieved out from sediments
Selden et al., 2010	Late Carboniferous; eastern Oman.	Copepod crustacean fragments
Shear and Bonamo, 1988	Middle Devonian; Gilboa, New York State, USA	Centipedes, fragments and complete specimens
Shear and Bonamo, 1990	Middle Devonian; Gilboa, New York State, USA.	Centipedes, fragments and complete specimens
Shear et al., 1989(a)	Middle Devonian; Gilboa, New York State, USA.	Spider spinneret
Shear et al., 1989(b)	Middle Devonian; Gilboa, New York State, USA.	Pseudoscorpion fragments
Slater, et al., 2012	Permian, Guadalupian; Prince Charles Mountains, East Antarctica	Arthropod fragments
Stankiewicz et al., 1998	Carboniferous; North America.	Discussion of the molecular taphonomy of arthropod cuticles
Taugourdeau, 1967	Silurian–Devonian; Sahara, Africa	Eurypterid cuticle
Tosolini and Pole, 2010	Cretaceous and Cenozoic; Australia and New Zealand	Scale insect shields, annelid cocoons
Wilson and Hoffmeister, 1956	Pennsylvanian (Desmoinesian); Croweburg Coal.	Arthropod fragments
Winslow, 1959	Late Mississippian and Pennsylvanian; Illinois, USA.	Arthropod cuticle extracted from coal
Wellman, 1995	Early Devonian; Old Red Sandstone, Scotland, UK.	Possible eurypterid cuticle fragments

CHAPTER 7: CONCLUSIONS

7.1 Recap of thesis aims

The primary aims of the thesis were;

1. **To document the diminutive and rarer elements of the Prince Charles Mountains Middle Permian palaeoecosystem and describe any new taxa.**
2. **To assess the palaeoecology of the peats focusing in particular on any invertebrate-plant interactions.**
3. **To investigate the taphonomy of the peats and propose a mechanism of silicification.**
4. **To use the Toploje Member chert to better understand the relationship between the organisms of peat-forming communities and the constituents which ultimately go on to form coal.**

7.2 Central findings of the thesis

The Toploje Member chert in the Bainmedart Coal Measures of the Lambert Graben, East Antarctica, contains a low-diversity Middle Permian macroflora dominated by arborescent glossopterids and subordinate cordaitaleans. A substantially greater floristic diversity is evident in meso- and palyno-fossil assemblages from the same bed. Findings from this study show that the chert preserves part of the profile of an ombrotrophic mire that was entombed with moderate rapidity by silica precipitated after flooding of the peat surface by mineral-rich lake waters. Diminutive elements of the palaeoflora have also been documented and described, including three new species of dispersed megaspore (*Duosporites lambertensis* sp.

nov., *Banksisporites antarcticus* sp. nov. and *Singhisporites hystrix* sp. nov.) revealing the presence of at least three species of presumably herbaceous heterosporous lycopsid (Chapter 3). X-ray synchrotron microtomography of the megaspore species *Singhisporites hystrix* sp. nov. demonstrated the relationship of the elaborate ornament to the entrapment of microspores of *Lundbladispora* sp., here interpreted as the corresponding microspores of the same parent plant. This technique also revealed internal morphological features such as sunken exinal thickenings flanking the labrae which would otherwise have been missed if solely relying on SEM images of the megaspores.

Other often overlooked elements of the palaeoecosytem that were described include two new species of Peronosporomycetes, *Combresomyces caespitosus* sp. nov. and *Combresomyces rarus* sp. nov. These are the first examples of this group described from the Permian of Antarctica, adding to our knowledge of the biodiversity and trophic interactions recorded from Permian mire ecosystems of high palaeolatitude Gondwana (Chapter 5). Morphological similarities in the shape of the oogonium, size, ornamentation and hyphal attachment between the two new species and fossil forms reported from Devonian to Triassic deposits elsewhere in the world provide sufficient basis for the establishment of a new order and family of these fossil Peronosporomycetes (Combresomycetales order nov. and Combresomycetaceae fam. nov.). The temporal and spatial distribution of these ornamented fossil forms suggests they represent an extinct but once common and widespread Palaeozoic to early Mesozoic branch of the peronosporomycete clade.

Diverse fossil micro-organisms and coprolites, together with feeding traces and sparse exoskeleton fragments are documented and attest to a complex biota of primary producers, arthropod herbivores and saprotrophs inhabiting the peat-forming ecosystem (Chapter 4). The various plant-arthropod-fungal interactions that can be identified in the

Toploje Member chert are categorised and include root boring, trunk wood boring, pollenivory, sporivory, folivory and fungivory. A variety of evidence recovered from thin-sections and bulk macerations of the chert reveal that the *Glossopteris* tree formed the basis for a complex ecosystem of herbivores, detritivores, saprotrophs and mycophagous organisms, which exploited all available organs of the *Glossopteris* whole-plant.

The peat deposit represents primarily autochthonous to parautochthonous accumulation of plant remains, which due to early silicification, have endured little compression or diagenesis. Fire was a common factor in the Middle Permian high-latitude mire ecosystem, and is locally evidenced by discrete charcoal bands within the peat profile. Comparisons of coal maceral data from co-occurring coal seams with quantitative analyses of the constituents of the Toploje Member chert reveal that whilst silicified peats provide an unparalleled sample of the organisms forming these coal deposits, they are not necessarily representative of the constituents that ultimately dominate the coal maceral volume (Chapter 6). The glossopterid-dominated mire ecosystem of the Prince Charles Mountains is reconstructed to occupy valley flanks and floodbasin settings within a braided river complex in a fault-bound alluvial valley.

The exceptional ultrastructural preservation of the macroflora, the diverse microorganisms and the complex interactions between the invertebrates, plants and fungi make the Prince Charles Mountains silicified peat an important Permian Lagerstätte and a valuable source of information on terrestrial ecosystems in southern high latitudes during the late Palaeozoic. The Toploje Member chert provides a snapshot of a high-latitude Middle Permian terrestrial ecosystem and, thus, yields valuable insights into the composition and ecology of Gondwanan climax mire forests prior to the two major extinctions (Capitanian and end-Permian) at the close of the Palaeozoic (Retallack et al., 2006; Bond et al., 2010).

Since the plants, microorganisms and fauna preserved in the Toploje Member chert inhabited an ombrotrophic mire rather than a sinter-pool habitat or other mineral-charged spring setting, they provide the opportunity to study the ecology of the more widespread peat-forming biotas of the late Palaeozoic in contrast to the specialised thermophilic biotas preserved three-dimensionally in hot spring habitats. In light of the discovery of invertebrate-plant-fungal interactions in the Toploje Member chert, there are significant opportunities for advancing knowledge of ancient terrestrial arthropod and micro-organism occurrences and trophic relationships through studies of other silicified organic deposits and via bulk maceration of organic sediments.

7.2.1 Recommendations for future work

Ongoing research into the fossil biota locked within the Toploje Member Chert has the potential to yield further information on the high-latitude terrestrial wetland ecosytems of the Late Palaeozoic. Areas that could be targeted for further research include;

1. Systematic appraisal and formal description of the morphology and anatomy of the lycophyte vegetative remains associated with the megaspores. This might provide additional insights into the systematic affinities of the megaspores.
2. Investigation of the discrepancy between the number of dispersed seed morphotypes and the comparatively low diversity of leaf morphotypes. This might provide insights into the intra-clade variation in seed morphotypes of glossopterids, and additionally provide evidence of rarer gymnospermous elements in the flora whose foliage may be too rare for recognition or taphonomically excluded from the peats.

3. Further recovery and description of fern sporangia and a systematic search for fern foliage would provide clearer insights into the role of ferns in the understorey of glossopterid mire forests or help explain why the foliage of this group is so rarely preserved.
4. A plethora of undescribed fungal remains occur in the Toploje Member permineralised peat. A targeted study of this group would help identify the diversity of fungi in high-latitude Permian mire ecosystems, the fungal clades represented, and elucidate the range of interactions between fungi, plants and arthropods.
5. A thorough systematic palynological study of the permineralised peat, and the associated sedimentary strata is warranted. This would provide the most accurate appraisal of the diversity of plant groups represented in the catchment system of the Lambert Graben. It would also potentially improve palynostratigraphic dating and correlation of the Middle to Late Permian succession and provide information of phytogeographic links between the now disparate parts of Gondwana.
6. Further geochemical and mineralogical studies are needed to resolve the precise mode of permineralisation of the peat in the absence of any obvious hot-spring system or volcanigenic sediments.
7. Systematic description of the glossopterid leaf types in the permineralised peat would be advantageous. Although glossopterid leaves are clearly the dominant foliage type in the peat, venation and gross morphological parameters of leaves (those typically used for species differentiation) are difficult to obtain from weathered surfaces of peat blocks. Systematic appraisal must, therefore, depend on anatomical differences. A study of glossopterid leaf anatomy would provide insights into the diversity of glossopterids represented in a typical peat mire and possibly shed light on the ecological significance of some anatomical characters such as bundle sheaths and hypodermis layers in some leaves.

8. Since the Dragons Teeth Member overlying the Toploje Member peat is the only significant lacustrine deposit in the Bainmedart Coal Measures, a systematic survey of this unit for insect remains would provide the greatest potential for identifying body fossils of arthropods associated with the wetland systems of the Middle Permian.

9. Vertical and lateral microfacies analyses of the Toploje Member peat would yield valuable information on the spatial distribution of organic remains within the peat body and would potentially identify whether there is any regularity in the distribution of fire horizons and fungal masses that might aid in interpreting larger scale environmental influences on peat accumulation.

10. Finally, some plants preserved in the peat, such as *Noeggerathiopsis*, bear deep trichome-filled stomatal grooves - features that are commonly associated with xerophytes in modern plant communities. More thorough anatomical investigations targeting the ecophysiological traits of such plant fossils would be fruitful in resolving the environmental conditions under which the peat flora developed.

APPENDIX

Specimens used in this study:

Specimens housed in palaeobotanical collections of the Swedish Museum of Natural History, Stockholm. Prefix: NRM	Specimens housed in the Commonwealth Palaeontological Collection, Geoscience Australia, Canberra. Prefix: CPC
S087800	34312
S087800-01	34314
S087801-A	34952
S087847	
S087932	
S087932-01	
S087932-01-02	
S087932-01-03	
S088040	
S088043	
S088051-01	
S088053-01	
S088061	
S088061-01	
S088062-A	
S088072-01	
S089351	
S089368	
S089383	
S089391	
S089404	
S089413	
S089428	
S089429	
S089515	
S089516	
S089517	
S089518	
S089527	
S089538	
S089540	
S089541	
S089550	
S089551	

S089553	
S089555	
S089574	
S089603	
S089629	
S089630	

APPENDIX 2

Collection of published material from thesis

Pages 202–217: Slater, B.J., McLoughlin, S., Hilton, J., 2011. Guadalupian (Middle Permian) megaspores from a permineralised peat in the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Review of Palaeobotany and Palynology 167, 140–155.

Pages 218–236: Slater, B.J., McLoughlin, S., Hilton, J., 2012. Animal-plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Palaeogeography, Palaeoclimatology, Palaeoecology 363–364, 109–126.

Pages 237–245: Slater, B.J., McLoughlin, S., Hilton, J., 2013. Peronosporomycetes (Oomycota) from Middle Permian permineralized peats of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. PLoS ONE 8, e70707. doi:10.1371/journal.pone.0070707.

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Animal–plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica

Ben J. Slater [a,*], Stephen McLoughlin [b], Jason Hilton [a]

[a] *School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, UK*
[b] *Department of Paleobotany, Swedish Museum of Natural History, Stockholm, Sweden*

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ABSTRACT

Evidence for invertebrate feeding on glossopterid gymnosperms is documented from Middle Permian silicified peats of the Prince Charles Mountains, Antarctica, in the form of coprolites occurring both free in the peat matrix and clustered within excavations in roots, aerial wood and leaves. Observations of coprolites in thin-sections of the peats and from scanning electron microscopy of examples extracted via bulk maceration reveal nine morphotypes distinguished by size, shape, surface texture and contents. These include coprolites with coarse plant debris, spirally ornamented coprolites, coprolites containing spore/pollen remains and fern sporangia, coprolites within *Glossopteris* leaves, an ellipsoidal morphotype within a fern sporangium, large isolated coprolites between matted leaves, clustered forms filling galleries inside *Vertebraria* roots and *Australoxylon* wood, forms with coarse indeterminate constituents and others with fungal contents. Other faunal evidence is limited to indeterminate arthropod exoskeleton fragments. Collectively, the coprolites within the permineralised peat from the Prince Charles Mountains document the presence of diverse feeding behaviours including stem feeding, sporangial feeding, palynivory, root feeding and mycophagy. The first evidence of invertebrate feeding traces in *Vertebraria* (glossopterid) roots is identified. These findings indicate that herbivory by invertebrates in the high-latitude Permian forest-mire ecosystems of Antarctica was more intense and diverse than previous studies have reported, and affected all parts of the *Glossopteris* plant, together with components of associated herbaceous taxa.

1. Introduction

The first terrestrial arthropods of the early to mid-Palaeozoic appear to have been mostly predators and detritivores based on mouthpart morphology and early coprolite evidence (Jeram et al., 1990; Labandeira and Beall, 1990) although recent evidence suggests the targeting of nutritious sporangial contents by the late Silurian (Edwards et al., 1995; Hagström and Mehlqvist, 2012). However, it is not until the accumulation of silicified wetland deposits of the Rhynie Chert in the Early Devonian that a more detailed picture of early invertebrate–plant interactions can be gathered (Labandeira, 2007) based upon multiple forms of coprolites, plant tissue damage and animal body fossils. Assessment of various categories of herbivory in the fossil record via plant tissue damage, coprolites or gut contents is an important tool for understanding the evolution of feeding traits, trophic complexity and the evolution of the terrestrial biosphere in general (Habgood et al., 2004). Further, fossil evidence of diagnostic plant–animal interactions can reveal the presence of animal groups that are not preserved as body fossils. Where preserved, coprolites can be used to identify the range of feeding guilds represented in a palaeoecosystem, and although many examples cannot be matched conclusively to a producer, they betray the presence of particular guilds of herbivores and selective tissue consumption in the community (Chaloner et al., 1991; Habgood et al., 2004; Labandeira, 2007).

This study focuses on an exceptionally well preserved silicified peat from the Middle Permian of the Prince Charles Mountains (PCMs) in East Antarctica. The community that formed the peats is a low-diversity wetland ecosystem dominated by woody glossopterid and cordaitalean gymnosperms, with lesser proportions of herbaceous lycopsids and ferns (McLoughlin and Drinnan, 1996; Holdgate et al., 2005; Slater et al., 2011). Little information is currently available on the entomofauna associated with the Permian vegetation of the PCMs. Previous work on the silicified peat deposit in the PCMs has identified coprolites within *Australoxylon* (glossopterid or cordaitalean) wood (Weaver et al., 1997) and sparse invertebrate exoskeleton fragments have been recovered from bulk maceration of Permian and Triassic sediments overlying the silicified peat (McLoughlin et al., 1997; Holdgate et al., 2005). Glossopterid or cordaitalean wood from the silicified peats commonly displays signs of intense attack from phytophagous invertebrates in the form of spindle-shaped excavations in the latewood of successive growth rings. Coprolites found within these regular cavities attest to their excavation by arthropods rather than pocket-rot fungi (Weaver et al., 1997). Cavities

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* Corresponding author. Tel.: +44 121 41 46152; fax: +44 121 41 44942.
E-mail address: bxs574@bham.ac.uk (B.J. Slater).

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generated by pocket rot are also present within the woods but are less regularly constrained to the latewood and are more variable in size and shape. Similar cavities in trunk wood from the Permian and Triassic of the Central Transantarctic Mountains are interpreted to have been produced by oribatid mites (Kellogg and Taylor, 2004). Weaver et al. (1997) suggested that the seasonal cyclicity evident in the pattern of attack on the PCM trunk wood was attributable to either mites or the overwintering larvae of coleopterans that fed either directly on the wood or on fungi that was in turn feeding upon the wood in a possible arthropod–fungal symbiotic relationship (the arthropod obtaining food and in turn dispersing the fungi between plants). A three-way (plant–fungal–arthropod) symbiosis, whereby the fungus returned essential micronutrients and other compounds to the host plant also cannot be excluded, though the similarity of fungal-induced cavities in *Australoxylon* to modern white pocket rot suggests that the fungi's relationship to the host plant was primarily saprotrophic.

Coprolites dispersed within the peat matrix contain identifiable pollen and represent the earliest examples of arthropod pollenivory from Antarctica (Holdgate et al., 2005). Pollenivory has been reported from other deposits of Permian age, such as the Lower Permian of the Ural Mountains, Russia (Krassilov and Rasnitsyn, 1996; Novokshonov, 1998; Labandeira et al., 2000), and evidence for related sporivory extends back to the rise of the vascular plants in the late Silurian (Habgood et al., 2004; Labandeira, 2007; Hagström and Mehlqvist, 2012). Late Palaeozoic coprolite evidence for the consumption of entire sporangia by arthropods has also been reported from the Northern Hemisphere (Meyen, 1984; Rothwell and Scott, 1988).

Elsewhere in Gondwana there is a broad range of evidence for arthropod attack upon Permian plants (McLoughlin, 1994a, 1994b, 2011). *Glossopteris* floras of the same age as this study (Guadalupian) from the La Golondrina Formation, Santa Cruz province, Argentina, have been shown to contain a diverse array of arthropod–plant interactions (Cariglino and Gutiérrez, 2011). Localities such as Clouston Farm and Wapadsberg Pass in the Karoo Basin, South Africa (Prevec et al., 2009, 2010), the Newcastle Coal Measure insect beds at Belmont, Sydney Basin, Australia (Beattie, 2007), the Rangal Coal Measures and stratigraphic equivalents of the Bowen Basin, Australia (McLoughlin, 1994a, 1994b, 2011), the Damodar Valley basins and Rajmahal Basin, India (Banerji and Bera, 1998; Banerji, 2004; Srivastava and Agnihotri, 2011), the San Ignacio Formation of the Andean Cordillera, Argentina (Césari et al., 2012), and the Rio Bonito Formation, Parana Basin, Brazil (Adami-Rodrigues et al., 2004a, 2004b; de Souza Pinheiro et al., 2012), all preserve diverse traces of phytophagous arthropod behaviour in their fossil floras. Thus far, most evidence of arthropod–plant interactions in the Gondwanan Permian has been associated with the dominant plant group (glossopterids), although a few studies have reported oviposition scars on equisetaleans (Beattie, 2007), and borings within the wood and surface and margin feeding traces on the leaves of cordaitaleans (*Noeggerathiopsis*: Adami-Rodrigues et al., 2004a, 2004b; Srivastava and Agnihotri, 2011; Césari et al., 2012; de Souza Pinheiro et al., 2012).

Despite the records listed above, relatively little is known about arthropod–plant interactions in the Permian compared to the Cretaceous and Cenozoic. Coprolites containing histologically identifiable plant tissues have been found within permineralised stems of *Psaronius housuoensis* from the Late Permian of southwest China (D'Rozario et al., 2011a) and coprolites were also reported to occur in Permian gymnospermous wood (Feng et al., 2010), stems and rachises (Seyfulla et al., 2009) and ovules (Hilton et al., 2002) from North China. Coprolites have also been documented in root mantles of Early Permian *Psaronius* and their associated fern and pteridosperm epiphytes from Germany, in the same assemblage as *Arthropitys*-type calamitalean wood with arthropod borings (Rößler 2000, 2006).

Insects such as archostematan Coleoptera, or their immediate precursors, were likely interacting with wood in a variety of states of decay by Permian times, including as endophytic cambial feeders (Weaver et al., 1997; Ponomarenko and Mostovski, 2005). Another group of insects that may have significantly interacted with plants, the Mecoptera (or Scorpionflies), appears in the fossil record at the start of the Permian (Novokshonov, 1997, 2004). Although modern Scorpionflies are predominantly predators and scavengers, the group was much more diverse in the past and recent studies have suggested that some early Mecoptera with long-proboscid mouthparts may have been active in the pollination of gymnosperms prior to the appearance of other insect groups (Labandeira and Sepkoski, 1993; Labandeira, 1994; Ollerton and Coulthard, 2009; Ren et al., 2009). Primitive Mecoptera are well represented in the Belmont insect beds of the Newcastle Coal Measures (Lopingian), Australia (Shi et al., 2010), and may have been pollenivorous, feeding upon microsporangiate *Glossopteris* reproductive structures, with which they co-occur (Tillyard, 1922; Beattie, 2007). Protomecopterids, which are an early group of caddisflies that closely resemble Scorpionflies, are also common in Permian deposits and have been reported from Lopingian *Glossopteris*-rich deposits of South Africa, although this lineage possessed mandibulate mouthparts so would likely have fed on particulate matter rather than nectar (Sukatsheva et al., 2007). Such potential relationships between early Mecoptera and glossopterids within Labandeira's (2006a) Herbivore Expansion Phase 2 may have been the precursors to more complex interactions between arthropods and plants in the early Mesozoic (Herbivore Expansion Phase 3), which highlights the importance of investigations into the entomofauna of glossopterid-bearing deposits such as those of the PCM silicified peats.

2. Geological setting

The silicified peat layer from which the studied samples were obtained is situated in the northern PCMs, East Antarctica, and forms a 3 km long exposure that reaches 40 cm thick and constitutes part of the Bainmedart Coal Measures, the middle unit of the Permo-Triassic Amery Group (Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a; Slater et al., 2011). The Bainmedart Coal Measures rest disconformably or slightly unconformably on the Radok Conglomerate (Lower to lower Middle Permian) and are overlain conformably by the Flagstone Bench Formation (Triassic). The silicified peat layer forms the upper part of a coal seam and marks the top of the 303 m thick Toploje Member of the lower Bainmedart Coal Measures (McLoughlin and Drinnan, 1997a). The peat is attributable to the *Didecitriletes ericianus* Palynozone of late Roadian to Wordian age, based on the first occurrence of the nominal index species near the base of the Toploje Member, and the first occurrence of *Camptotriletes warchianus* in the immediately overlying Dragons Teeth Member (Lindström and McLoughlin, 2007). The Dragons Teeth Member is a lacustrine unit rich in sideritic shales (Fielding and Webb, 1996). The lower Bainmedart Coal Measures are otherwise characterized by strongly cyclic sequences of subfeldspathic sandstones, siltstones and coals deposited in alternating high-energy braided fluvial channel networks and low-energy, basin-wide forest-mire systems (Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a, 1997b; McLoughlin et al., 1997; Lindström and McLoughlin, 2007). The sedimentary cyclicity has been attributed to climate-induced variation in sediment supply controlled by Milankovitch cycles (Fielding and Webb, 1996).

The PCMs were located at 65–70°S in the mid-Permian and positioned in the central part of the Gondwanan supercontinent (Scotese, 1997). The Amery Group was deposited in the Lambert Graben; sedimentological data and palaeogeographical reconstructions suggest that this basin was a southern (up-slope) extension of the Mahanadi Graben in eastern India (Fedorov et al., 1982; Stagg, 1985; Bogor, 2011; Slater et al., 2011), the contained sediments being sourced largely from central Antarctica (Veevers, 2004). Furthermore, this basin system was part of an extensive rift system through central Gondwana that was a precursor to eventual continental breakup in the Jurassic (Lottes and Rowley, 1990; Harrowfield et al., 2005).

3. Materials and methods

A range of techniques was employed to study the coprolite content of the PCM permineralised peats. Serial cellulose acetate peels were prepared from the cut silica-permineralised peat blocks following the technique described by Galtier and Phillips (1999). Around 50 silicified peat blocks were cut using a fine bladed Buehler Isomet 5000 linear precision saw then the cut surface was polished and etched in a shallow bath of cold 30% hydrofluoric acid for around 90 s so that the organic contents stood above the surface. The acid-etched blocks were then rinsed in water, dried and bonded to cellulose acetate sheets of 50 μm thickness using acetone as a solvent. After drying, the acetate sheets were peeled from the surface of the blocks and portions of the sheets were removed for examination with a transmitted light microscope. Blocks that were discovered to contain coprolites and other evidence of animal–plant interactions were then thin-sectioned to extract better quality anatomical details via light microscopy. An arbitrary selection of 24 additional samples of silicified peat from a series of localities along the exposure was bulk macerated in cold 30% HF solution for two weeks and the residue was then recovered from the HF solution using a 150 micron sieve. The recovered organic debris was then placed in distilled water in a petri dish for examination using an optical stereomicroscope; individual coprolites were picked with a fine artist's brush whilst hydrated. Individual coprolites were then mounted on aluminium stubs, coated with gold and imaged with the use of a Hitachi S-4300 field emission scanning electron microscope at the Swedish Museum of Natural History. Images were processed and plates compiled using Adobe Photoshop and Illustrator CS4 graphics packages. Terminology used to describe the coprolites follows that of Habgood et al. (2004) where possible.

4. Results

Nine distinct coprolite morphotypes are recognized within the silicified peat bed at the top of the Toploje Member on the basis of shape, size, texture and contents. Coprolites occur both isolated within the peat matrix and clustered within excavations in a range of plant tissues. Bulk maceration of the peat revealed two size categories [small (Plate 1; 1–4: Plate 2; 1–3) and large (Plate 2; 4)] of isolated coprolites with variable contents. Other forms recovered from bulk macerations included coprolites with coarse plant contents (Plate 1; 5), spirally ornamented coprolites (Plate 3; 1), and coprolites containing specifically identifiable contents including leaf trichomes (Plate 3; 2), leaf cuticle fragments (Plate 3; 3), pollen remains (Plate 3; 4) and fern sporangia (Plate 3; 5). Further categories of coprolites recognized in thin-sections of the peats, include irregular forms containing platy cell wall fragments inside *Glossopteris* leaves (Plate 4; 1–4), an ellipsoidal morphotype within a fern sporangium (Plate 4; 5), large isolated coprolites between matted leaves (Plate 4; 6), clustered forms filling excavations inside *Vertebraria* and *Australoxylon* wood (Plate 5; 1–6), forms with coarse indeterminate constituents (Plate 6; 1–2) and others with fungal contents (Plate 6; 3–4).

4.1. Coprolites in Vertebraria and Australoxylon

4.1.1. Description

The coprolites occurring within the secondary wood of *Vertebraria* and *Australoxylon* fall within the smaller size range of the PCM morphotypes. Two sub-categories are recognized: a darker brown form averaging 120 μm long and 115 μm wide (50 specimens measured); and a lighter brown form averaging 150 μm long and 125 μm wide (50 specimens measured). The individual coprolites are ovoid, conoid or equant in shape, the long axis never reaching twice the length of the shortest axis. The termini are typically broadly rounded in both sub-categories. The margins of each coprolite are smooth; the surface consisting of densely compacted fine lignified debris. One sub-category has contents that are a darker brown than the surrounding plant tissues, and the second has a light brown colour roughly equivalent to that of the surrounding wood.

The coprolites are relatively homogeneous, being composed primarily of small angular tracheid wall fragments that have a platy appearance in less densely compacted forms. A minority of coprolites within the excavations are composed entirely of broken fungal sporangia but these are described as a separate category (see Section 4.6).

The coprolites in *Vertebraria* and *Australoxylon* occur in clusters of variable numbers (Plate 5; 1–6). The clusters can be spread diffusely or grouped densely. They are found in a range of short, discontinuous galleries within the secondary xylem and within chambers excavated within the parenchyma of young roots. The same coprolite morphotype also occurs dispersed between matted leaves of the peat profile in some samples. This category of coprolite is by far the most abundant in the peat, with some thin-sections containing >1000 examples.

4.1.2. Remarks

These are the first coprolites to be recorded in the root system of glossopterids. No differences are evident between the coprolites in *Australoxylon* (trunk wood) and *Vertebraria* (root wood). The colour difference evident within the assemblage may simply relate to the density of the compacted contents because other morphological and compositional characters are identical. The excavations and coprolites collectively fall within Zherikhin's (2003) ichnofossil category xylichnia. The morphology of these coprolites suggests production by oribatid mites (Labandeira et al., 1997). This coprolite morphotype has sharper margins and occurs in less continuous excavations than those attributed to *Anobium* sp. (common name 'death-watch beetles': Coleoptera) in Neogene angiosperm wood (Selmeier, 2005). They are slightly smaller, more regularly shaped and occur in narrower, less continuous excavations than pellets attributed to Cerambycidae (Coleoptera) from the Middle Jurassic of Argentina (García Massini et al., 2012). The producers and palaeoecological significance of these coprolites are considered in more detail below (Section 5).

4.2. Coprolites in leaves

4.2.1. Description

These coprolites are 200–550 μm long and 120–250 μm wide. The length exceeds the width in most cases although some are equidimensional. The majority of the coprolites are elongate and flattened, although a small proportion (ca 20%) are equidimensional. The termini of the coprolites are sub-rounded to angular. The margins of the coprolite are more or less smooth when observed in thin-section, although angular corners and extensions are locally developed (possibly as a post-depositional, compactional, artefact). In thin-section, the coprolites are light brown. They consist entirely of densely packed fragments of leaf mesophyll cell walls.

This coprolite morphotype occurs only within chambers excavated between the anastomosing veins of *Glossopteris* leaves (Plate 4; 1–4). In slides that are rich in leaf remains, these coprolites are relatively common, but they have not been recognized dispersed within the peat matrix.

4.2.2. Remarks

The occurrence of this morphotype is consistent with either detritivory or arthropod leaf mining. The cavities are positioned where leaf mining would be expected (consistently between the leaf secondary veins), however it is inherently difficult to recognize bona fide leaf mining within permineralised material as opposed to leaf compressions where features such as an oviposition site, frass trail, and reaction tissue lining the excavation can be detected. The earliest confirmed record of leaf mining in the fossil record appears at the P–Tr boundary (Krassilov and Karasev, 2008). If the cavities and coprolites within the Antarctic leaves are a result of leaf mining, they would represent the first confident example of this feeding strategy within *Glossopteris* leaves and one of the oldest records of leaf mining in the fossil record (Chaloner et al., 1991). A few putative cases of leaf mining have previously been illustrated in *Glossopteris* (Gallego et al., 2003; Prevec et al., 2009; de Souza Pinheiro et al., 2012) but incontrovertible examples are lacking thus far.

4.3. Coprolite within sporangium

4.3.1. Description

A single identified example of a coprolite within a fern sporangium is 500 μm long and 300 μm wide (Plate 4; 5). The coprolite is ovoid with broadly rounded termini. The margins (surface) of the coprolite are slightly uneven. The coprolite is dark brown in thin-section. It consists of coarse fragments of degraded spores. The coprolite occurs within the cavity of a partially excavated fern sporangium (Plate 4; 5). The sporangium still retains some intact fern spores attributable to *Leiotriletes directus* Balme and Hennelly.

4.3.2. Remarks

This rare morphotype constitutes direct evidence of arthropods targeting sporangia as a food source. Although this feeding strategy has not been recorded previously from Gondwanan Permian floras, the record of palynivory in general extends back to at least the late Silurian (Labandeira, 2007; Hagström and Mehlqvist, 2012). Trigonotarbid remains found within sporangia in the Lower Devonian Rhynie Chert have been suggested to be either feeding on the spores themselves or preying upon mites that also lived within the sporangia (Kevan et al., 1975; Rolfe, 1980; Habgood et al., 2004). We have found no arthropod body fossils associated with this PCM coprolite morphotype.

4.4. Isolated large coprolites

4.4.1. Description

These isolated coprolites are 1000–2500 μm long and 500–1300 μm wide. They have variable shapes; the majority possess one longer axis but some are spherical. Both termini are usually subrounded but some have one tapered end (Plate 2; 4). The margins of such coprolites are either irregular or smooth. The smooth-margined coprolites appear to be bound with some form of amorphous agglutinating material (Plate 2; 4) or possibly a net-like peritrophic membrane. In thin-section, the largest of the coprolites vary markedly in colour, ranging from black in charcoalified specimens (Plate 4; 6) to light brown in those with finer constituents.

The isolated large coprolites are not only composed primarily of fine to coarse unidentifiable plant debris, but also contain some isolated spores and pollen grains. The large coprolites occur in isolation exclusively between matted leaves (Plate 4; 6). They were markedly resistant to compaction based on their maintenance of a spherical to broadly elliptical form and the deformation of leaf laminae around them. The resistance to compaction could be the result of the coprolite consisting of compact and resistant tissues but in some cases is due to charcoalification. We see no evidence of hardening and cracking of the coprolites through subaerial exposure and desiccation. This morphotype is relatively common (>10 specimens).

4.4.2. Remarks

Such coprolites may have been produced by various arthropod herbivores or detritivores, since their contents and shape are variable—some possessing tapered ends and smooth margins, whilst others are subrounded and have irregular margins. These large coprolites are grouped here on the basis of their size and contents, which are distinct from other coprolites in the peat. It is likely that the producers of these coprolites were detritivore generalists—feeding on forest floor litter because of their variable content and all examples occurring amongst matted leaf remains (autumnal leaf fall deposits). Constituents such as spores and pollen are common but never make up the bulk of the coprolite mass so it is likely that these were consumed passively as a consequence of indiscriminate feeding on plant detritus.

4.5. Isolated small coprolites

4.5.1. Description

These coprolites are 500–750 μm long and 300–350 μm wide, oblong to cylindrical (Plate 1; 1) with rounded termini. The margins (surface) of the coprolites are either irregular or smooth depending on their contents. The coprolites appear light yellow–brown in thin-section.

Pollen grains, fern spores (Plate 2; 3) and fragments of sporangia are evident within the coprolites (Plate 1; 2), together with masses of cell wall detritus (Plate 2; 2) and broken spinose fungal spores (Plate 1; 3). The majority of these small- to medium-sized isolated coprolites contain mixed plant remains. The fern spores in these coprolites are corroded and split. Fungal hyphae are also evident within the coprolites although it is unclear whether these were consumed by the producer or infiltrated the coprolite post-deposition (Plate 1; 4). Small coprolites of this category occur isolated in the peat matrix between various plant tissues.

4.5.2. Remarks

These coprolites have more variable contents than others of similar size and shape found within glossopterid wood galleries. This morphotype is relatively common in the peats (>10 specimens), although it varies significantly in abundance between peat samples based on material recovered from bulk macerations. Some samples lack any examples of this type. Samples that are richer in this morphotype also appear to include a higher proportion of root (*Vertebraria*) tissues. Some examples of this coprolite morphotype are similar in shape and size to Australian Cretaceous forms illustrated by Tosolini and Pole (2010), but the Antarctic Permian examples consistently incorporate coarser (identifiable) plant debris.

4.6. Fungi-rich coprolites

4.6.1. Description

This category of coprolites is defined by its composition, being composed entirely of broken fungal spores. This morphotype is 180–220 μm long and 120–200 μm wide. Some larger coprolites (see Sections 4.4. and 4.5) also contain fungi but as a minor component. A few of the small coprolites contained within galleries excavated in *Australoxylon*

Plate 1. Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat. 1; coprolite rich in leaf fragments, fern spores and fungal spores, scale bar = 1 mm. 2; enlargement of fractured surface of coprolite in image 1, showing contents of broken fern spores and leaf fragments, scale bar = 100 μm. 3; enlargement of external surface of coprolite in Fig. 1, showing broken fungal bodies and leaf fragments, scale bar = 100 μm. 4; fugal hyphae in coprolite from image 1, degraded state of hyphae suggests it was consumed rather than colonising the coprolite post deposition, scale bar = 20 μm. 5; coprolite composed entirely of leaf tissues, scale bar = 500 μm.

Plate 2. Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat. 1; coprolite containing mixture of plant remains including leaf tissue fragments and fungal spores, scale bar = 500 μm. 2; enlargement of plant material on external surface of coprolite in image 1, showing large degraded leaf cuticle sheets with epidermal cell markings, scale bar = 100 μm. 3; enlargement of fern spore [*Horriditriletes tereteangulatus* (Balme and Hennelly) Backhouse] included in coprolite in image 1, scale bar = 20 μm. 4; large coprolite with tapered terminus, containing plant tissue fragments and agglutinated external surface, scale bar = 1 mm. (see on page 114)

Plate 3. Scanning electron microscopy images of coprolites from bulk macerations of the Toploje Member permineralised peat. 1; spiral-ornamented coprolite, scale bar = 250 μm. 2; glandular leaf trichome in leaf-rich coprolite, scale bar = 25 μm. 3; tracheids in leaf-rich coprolite, scale bar = 20 μm. 4; coprolite composed of pollen, scale bar = 50 μm. 5; coprolite composed of a consumed fern sporangium—*Leiotriletes directus* Balme and Hennelly spores showing burst and degraded walls, scale bar = 200 μm. (see on page 115)

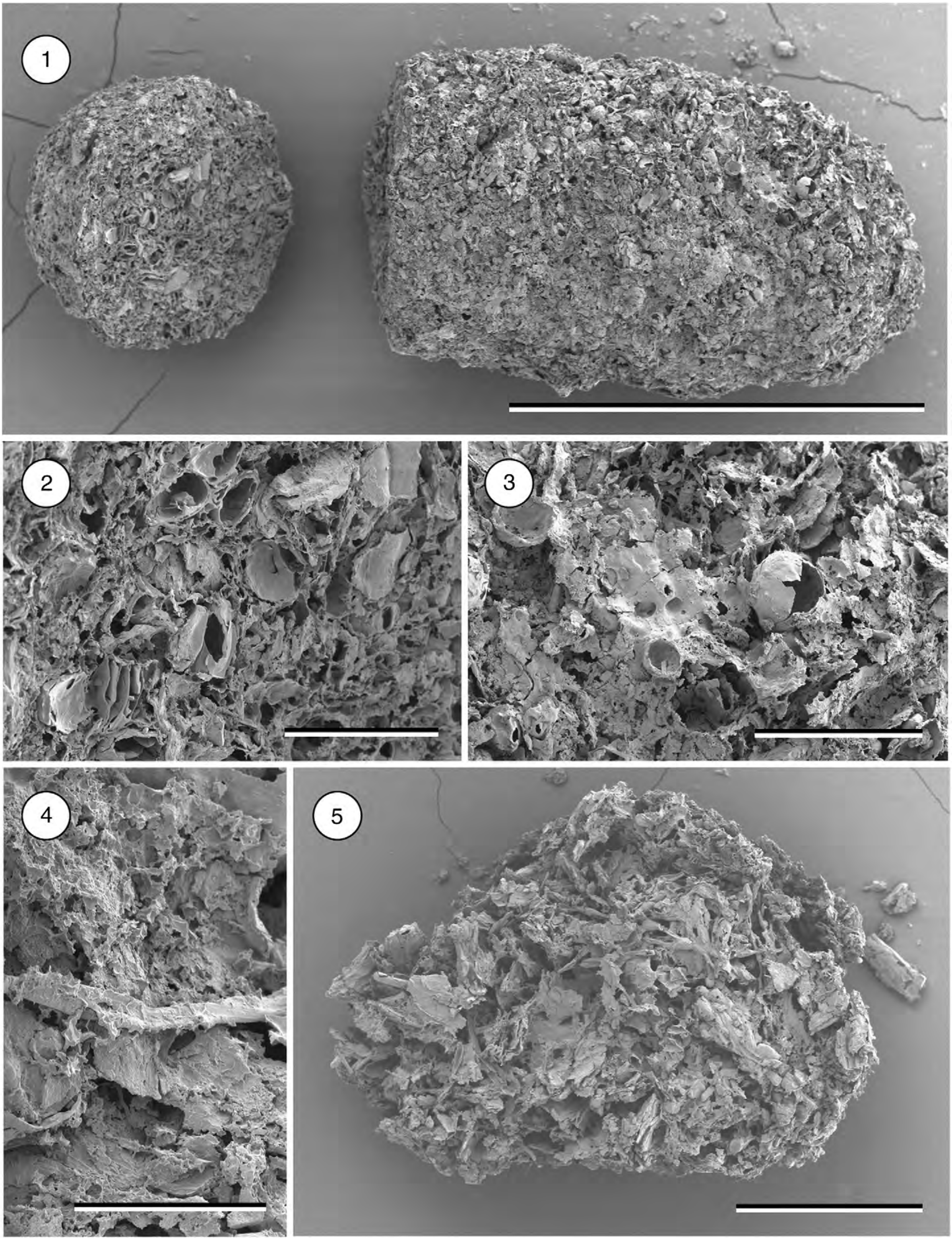


Plate I

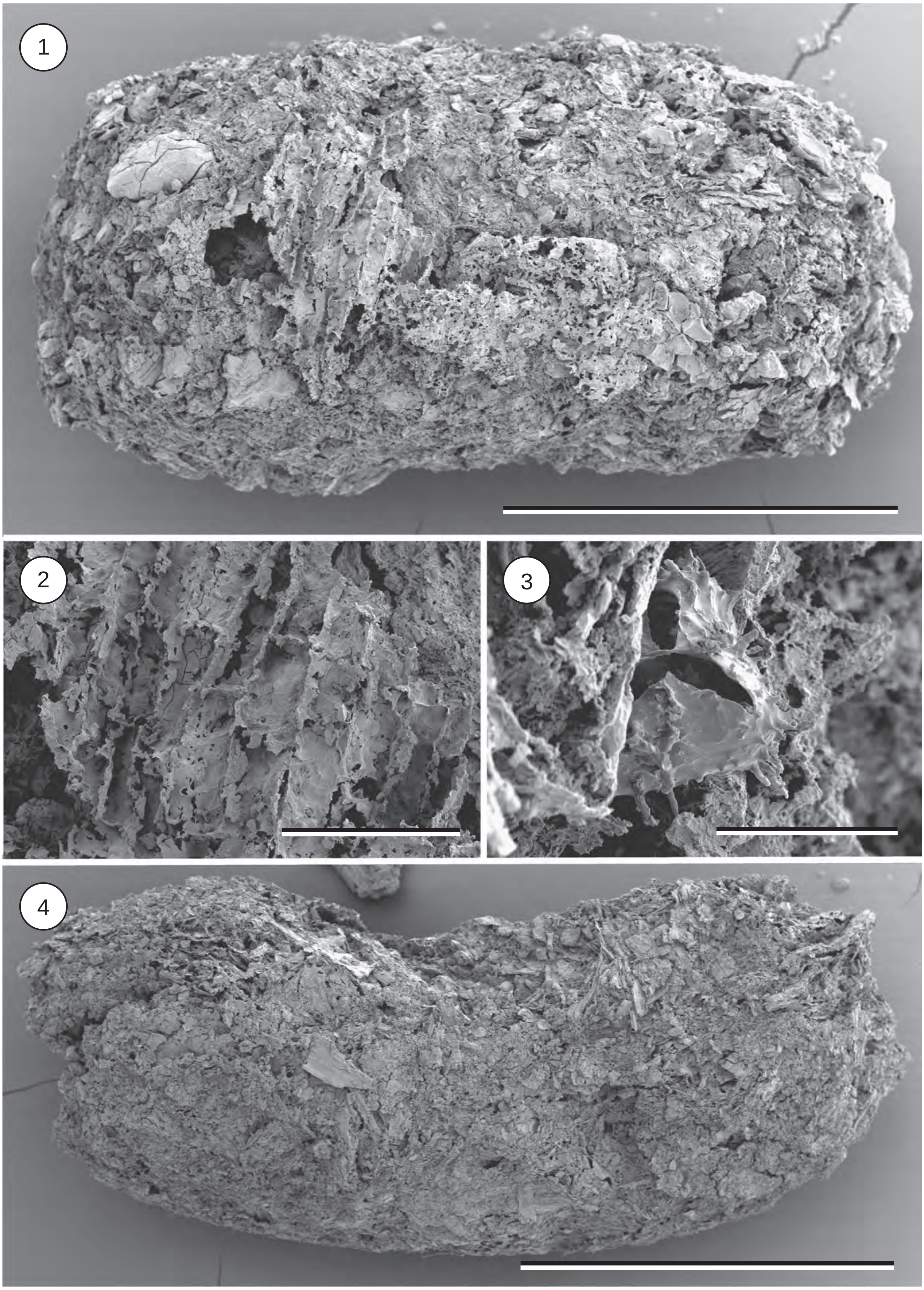


Plate II (*caption on page 112*).

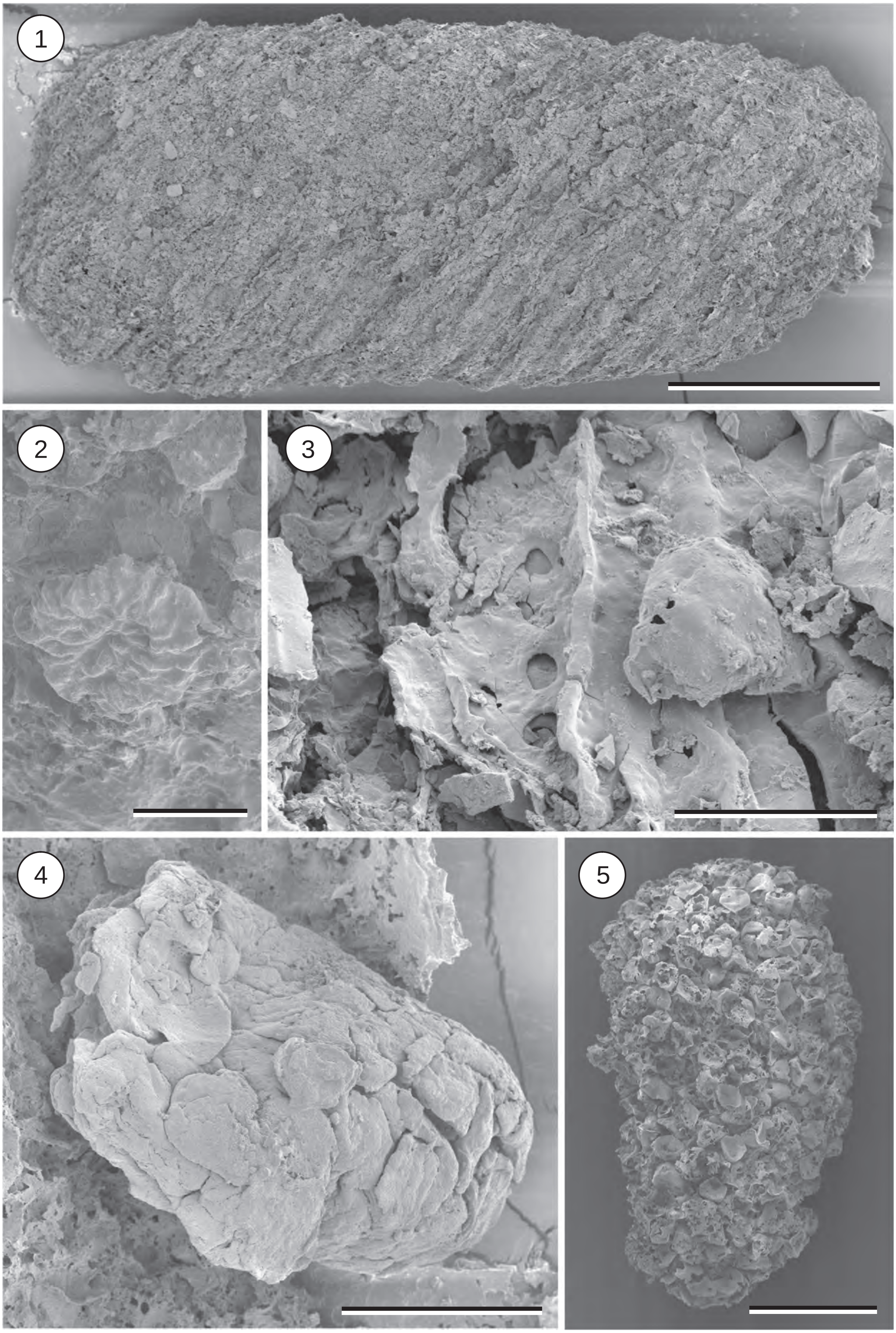


Plate III (*caption on page 112*).

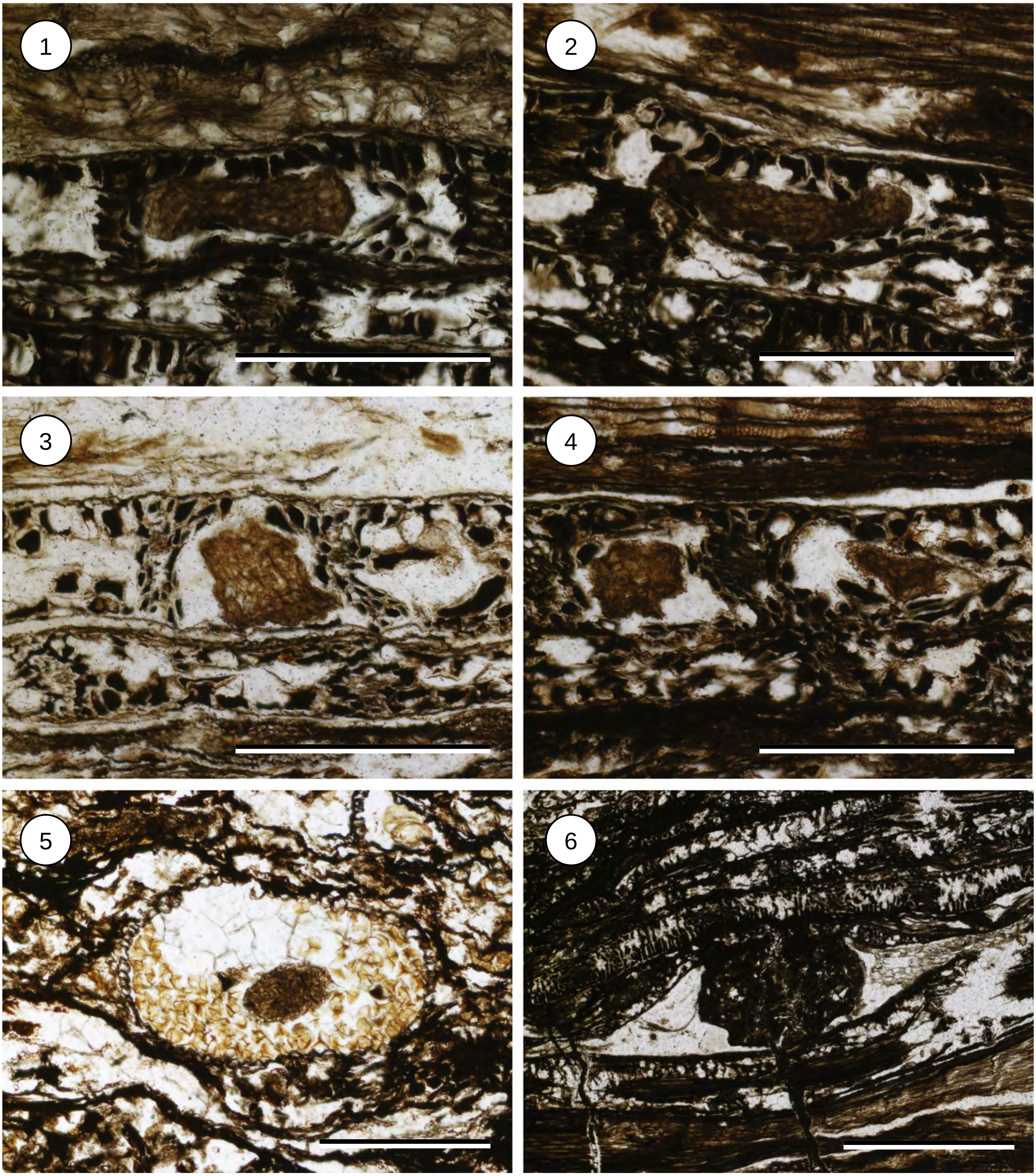


Plate 4. Coprolites preserved within *Glossopteris* leaves (1–4), within sporangia and between matted leaves. 1–4; coprolites with a fine platy texture preserved within cavities excavated between anastomosing veins of *Glossopteris* leaves, scale bars = 500 μm. 5; coprolite inside a partially excavated fern sporangium, scale bar = 1 mm. 6; large compaction-resistant and apparently charcoalified coprolite positioned between matted *Glossopteris* leaves, scale bar = 1 mm.

or *Vertebraria* are composed entirely of broken fungal spores (Plate 6; 3). These are identical in shape to the surrounding frass-filled conoid and ovoid coprolites with smooth margins suggesting an origin via a common producer. Other fungi-filled coprolites are equidimensional (Plate 6; 4). Fungi-filled coprolites vary from smooth to irregularly textured. In thin-section, the fungi-rich coprolites appear light brown.

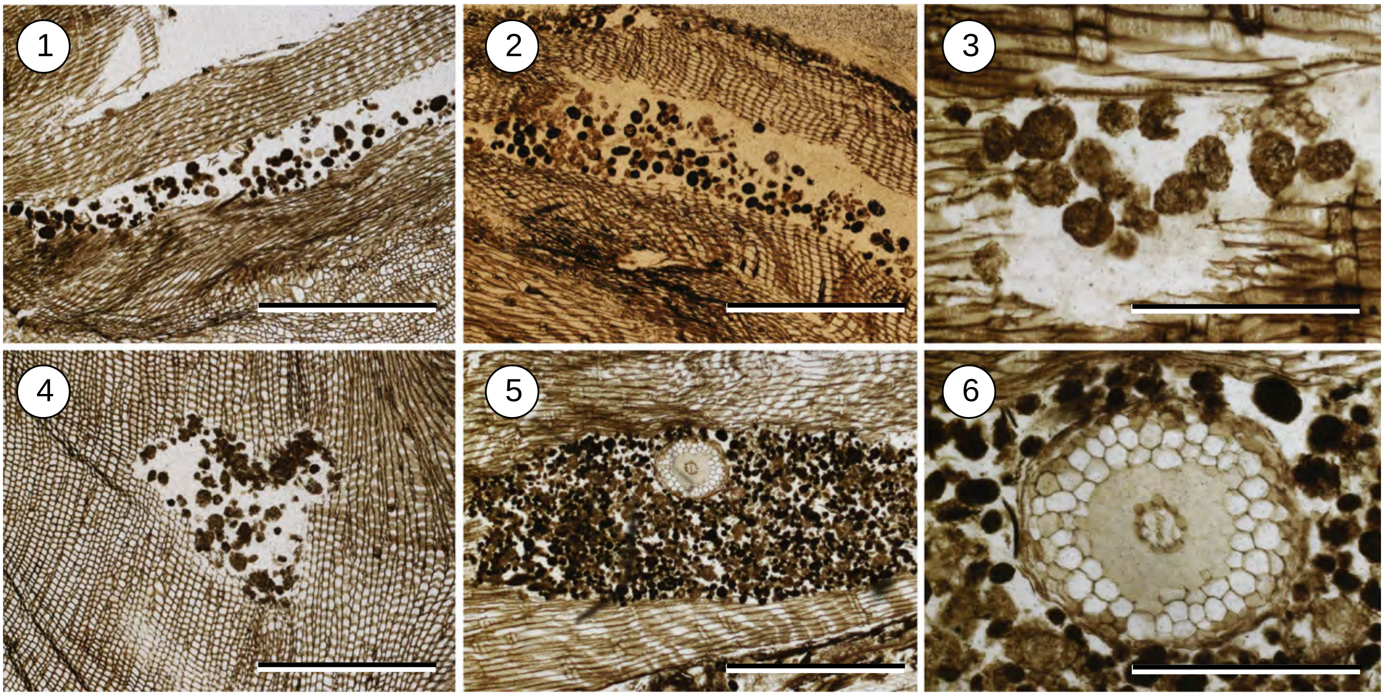


Plate 5. Coprolites preserved within secondary wood of *Vertebraria*. 1–2; small coprolites clustered within excavated galleries inside *Vertebraria* secondary xylem, scale bars = 1 mm. 3; coprolites within excavation containing internal granular fragments of xylem tissues, scale bar = 500 μm. 4; excavation through *Vertebraria* containing coprolites, scale bar = 1 mm. 5; mass of coprolites within an excavation in *Australoxylon* wood, scale bar = 1 mm. 6; enlargement of young undamaged *Vertebraria* rootlet that apparently penetrated the wood cavity subsequent to emplacement of the coprolite mass, scale bar = 500 μm.

4.6.2. Remarks

These coprolites occur as a minor component of the small abundant coprolites that fill galleries throughout *Australoxylon* (stem wood) and *Vertebraria* (root wood). Coprolites composed exclusively of fungal remains are relatively rare within the peat (<10 specimens). Forms that are rich in fungal spores and crushed hyphae are slightly larger, though similar in shape and content to food boli produced by the modern oribatid mites *Scheloribates laevigatus* and *Archegozetes longisetosus* (Hubert et al., 2000; Smrž and Norton, 2004).

4.7. Coprolites containing pollen

4.7.1. Description

Coprolites composed entirely of compressed and broken pollen grains are small (100–150 μm long and 70–150 μm wide). The coprolites are squat ellipsoidal to spherical with rounded termini. The margins of the coprolites are relatively smooth, the pollen constituents being densely compacted (Plate 3; 4). These coprolites are light brown in thin-section.

This category of coprolites is composed entirely of densely packed, broken to entire bisaccate pollen referable to *Protohaploxipinus* Samoilovich emend Morbey. These coprolites occur isolated within the peat amongst a mixture of glossopterid-dominated plant debris. They are uncommon (<10 specimens).

4.7.2. Remarks

Protohaploxypinus pollen is typical of glossopterids (Gould and Delevoryas, 1977), although this plant group also produced various other pollen morphotypes (Lindström et al., 1997), and unrelated plant groups of other floristic provinces also produced similar taeniate pollen (Balme, 1995). These coprolites provide evidence of obligate palynivory in the biota. The producers are unknown but there is a range of possible palynivores in the Gondwanan Permian insect fauna including coleopterans (Ponomarenko and Mostovski, 2005). These mesofossils are not considered to be sporangia due to their lack of a distinctive sporangial wall composed of elongate inflated cells typical of glossopterids (Lindström et al., 1997).

4.8. Coprolites with coarse constituents

4.8.1. Description

Coprolites of this morphotype are 0.8–1.3 mm long and between 0.5 and 1 mm wide. They are equidimensional to broadly ellipsoidal, the long axis never reaching more than twice the length of the short axis. The margins of these coprolites are rough and uneven. In thin-section these coprolites appear dark brown.

This morphotype is distinguished primarily on its content of coarse platy materials, including tracheid fragments and leaf mesophyll cell walls and cuticle. These coprolites lack the fine-grained constituents evident in the other morphotypes. The coprolites with coarse constituents occur isolated in the peat matrix, amongst matted leaves and woody remains. They are uncommon (<10 specimens).

4.8.2. Remarks

These coprolites appear to be the product of feeding on coarse plant materials such as leaf mesophyll and woody tissues (tracheids). Components within the coprolite show only weak degradation and in some cases retain cellular features. The tracheids may derive simply from veins within leaves rather than from axial parts of the plant. We cannot determine whether the contents of these coprolites was consumed by detritivory (via feeding on leaf litter), or by true folivory.

4.9. Isolated spiral-ornamented coprolite

4.9.1. Description

This morphotype is represented by a single specimen that is approximately 800 μm long and 300 μm wide. The coprolite is elongate cylindrical with sub-rounded termini. The surface of the coprolite is marked by a series of grooves/ridges that are ca 25 μm wide, spaced at regular (ca 25 μm) intervals, and arranged spirally around the pellet.

The coprolite is composed of finely granular to platy indeterminate tissues. A single example of this morphotype was found in the bulk macerated residues of the peats.

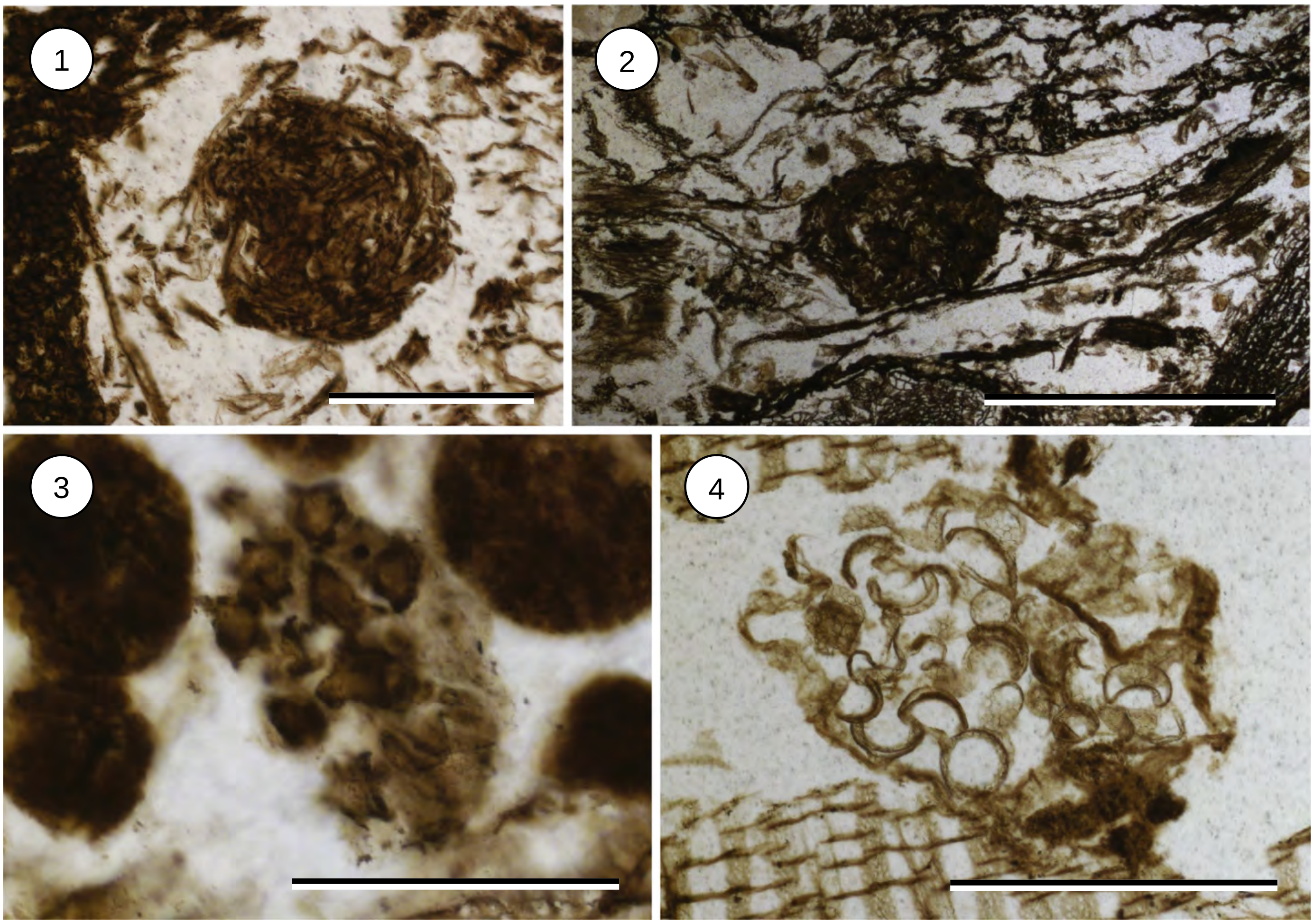


Plate 6. Platy coprolites isolated within the peat matrix (1–2) and fungi-filled coprolites (3–4). 1; coprolite composed of platy plant cell material, scale bar = 1 mm. 2; coprolite composed of platy plant material, scale bar = 1 mm. 3; small coprolite composed of crushed spinose fungal spores within a gallery of small coprolites composed of granular plant matter, scale bar = 200 μm. 4; coprolite composed primarily of fragmented fungal spores, scale bar = 200 μm.

4.9.2. Remarks

This coprolite morphotype is distinguished by its characteristic ornament. We are unaware of modern arthropods that produce faecal pellets with this morphology, although Edwards et al. (1995) reported spiral-shaped coprolites from the latest Silurian and Early Devonian of the Welsh Borderlands, though the morphology of those older examples differs from that of the PCMs spirally ornamented coprolite, since the spirals are fewer and much more pronounced. In addition, Lupia et al. (2002) reported more coarsely spiral coprolites from the Late Cretaceous containing pollen and coarse plant debris and Scott and Taylor (1983) reported grooved coprolites from the Upper Carboniferous.

4.10. Other evidence of animals

4.10.1. Arthropod remains (Fig. 2)

Isolated plates of arthropod exoskeleton were recovered from bulk macerated samples of the peat (Fig. 2; 1, 2). The segments of chitinous exoskeleton are covered with acuminate simple setae ca 35–50 μm long and ca 5–7 μm wide. The affinity of such fragments cannot be determined accurately. The spines are narrower and much more elongate than those of the arthropod fragment previously illustrated from the upper part (Norian) of the Amery Group in the PCMs (McLoughlin et al., 1997). Such isolated arthropod fragments are minor components of many Palaeozoic and Mesozoic continental deposits (Bartram et al., 1987; Batten, 1998). Insect remains have been reported from a few other Permian deposits of Antarctica but are mostly assigned to unresolved homopterous hemipteran and coleopteran groups (Plumstead, 1962; Carpenter, 1969; Tasch and Riek, 1969; Tasch, 1971).

4.10.2. Fine detritus patches

Regions of loosely consolidated fine detritus of variable shape are also found amongst the plant materials of the peats. These detritus patches consist of largely unidentifiable fine plant fragments with sparse fungal spores and hyphae. They are of variable shades of brown depending on their density, vary in size (ca 2–3 mm long and 1–3 mm wide) and have an irregular or diffuse surface.

Attributing these patches of frass to a producer organism is difficult because the variably shaped unconsolidated material lacks a clear indication of the size of the organism. It is a possibility that the patches were formed by the pre-burial weathering and dissociation of a coprolite or, alternatively, that they are the accumulated by-products of plant debris that was not consumed during detritivore feeding.

5. Discussion

We diagrammatically reconstruct the key interactions between the glossopterid plant and invertebrates based on examples from Antarctica and Australia (Fig. 1). The range of interactions evident is greater than previous investigations have reported for the Gondwanan Permian flora. New evidence from the PCM peat layer indicates that all parts of the *Glossopteris* plant experienced herbivory.

5.1. Feeding guilds

The absence of an extensive body fossil fauna means that trace fossils in sediments and plant–animal–fungal interactions provide the primary means of evaluating invertebrate faunal diversity and trophic levels in Antarctic Permian terrestrial communities. Determining these parameters is important for evaluating the scale of faunal turnover in high-latitude communities at the close of the Palaeozoic (Labandeira, 2005), at which time Gondwanan plant communities were fundamentally readjusted (Anderson et al., 1999; Vajda and McLoughlin, 2007). Several damage types are distinguishable on plants in the PCM peat (Fig. 1) attesting to a hidden diversity of terrestrial invertebrates and these feeding strategies are summarized below (see also Table 1):

(A) Xylophagy is represented by gallery and chamber feeders (borers) that targeted specific tissues (xylem and parenchyma and possibly cambial tissues) in the stem and root wood. Given that some coprolites occur within the soft parenchymatous tissues of young roots, at least some of the damage is likely attributable to true xylophagy rather than saproxylophagy.

(B) True folivory (feeding on living leaves) is represented by coprolites preserved within interveinal chambers in glossopterid leaves, and probably by the presence of dispersed coprolites consisting primarily of leaf tissue fragments, although we cannot exclude a detritivorous origin for the latter.

(C) Detritivorous feeding behaviour was characteristic of the producers of the medium and large spherical–oblong coprolites that contain a broad mixture of cell fragments, spores, pollen and fungal hyphae.

(D) Sporangial feeding (sporivory) is evidenced by the presence of coprolites within partially consumed fern sporangia, and dispersed faecal pellets composed entirely of spores (*Leiotriletes directus*) recovered from bulk maceration of the peat matrix. Pollenivory, specifically targeting the microsporangial contents of glossopterid gymnosperms, is evidenced by dispersed coprolites containing exclusively taeniate bisaccate pollen (*Protohaploxypinus* sp.).

(E) Mycophagy is evidenced by coprolites composed exclusively of fungal spores/sporangial fragments.

The range of feeding strategies employed differs sufficiently, in food materials and the occurrence and size of the faecal pellets produced, to have originated from several invertebrate producers. The isolated small- to medium-sized and larger coprolites can be differentiated by size and morphology but in terms of a producer it is possible that they derive from different metamorphic instars rather than different taxa of arthropods. As a 150 μm sieve was used to collect acid-liberated debris from the peats (initially intended for the recovery of lycophyte megaspores: Slater et al., 2011), many smaller coprolite types may have been lost from the bulk macerations. These may be the target of future investigations.

Evidence for selective feeding behaviour amongst the producers of the largest coprolites is equivocal. Although some of these coprolites are very rich in spores, this is not necessarily evidence for obligate sporangial feeding. It is possible that such spore-filled coprolites were produced by opportunistic or indiscriminate feeding by the same invertebrate that excreted coprolites rich in mixed cell debris. Nevertheless, coprolites within fern sporangia, and others containing primarily bisaccate pollen demonstrate that specific targeting of microsporangiate organs did occur within the community—presumably different palynivores targeting the pteridophytes and glossopterid gymnosperms. Spores and pollen represent rich nutrient sources (Willmer, 2011), so specific targeting of these materials for food is to be expected.

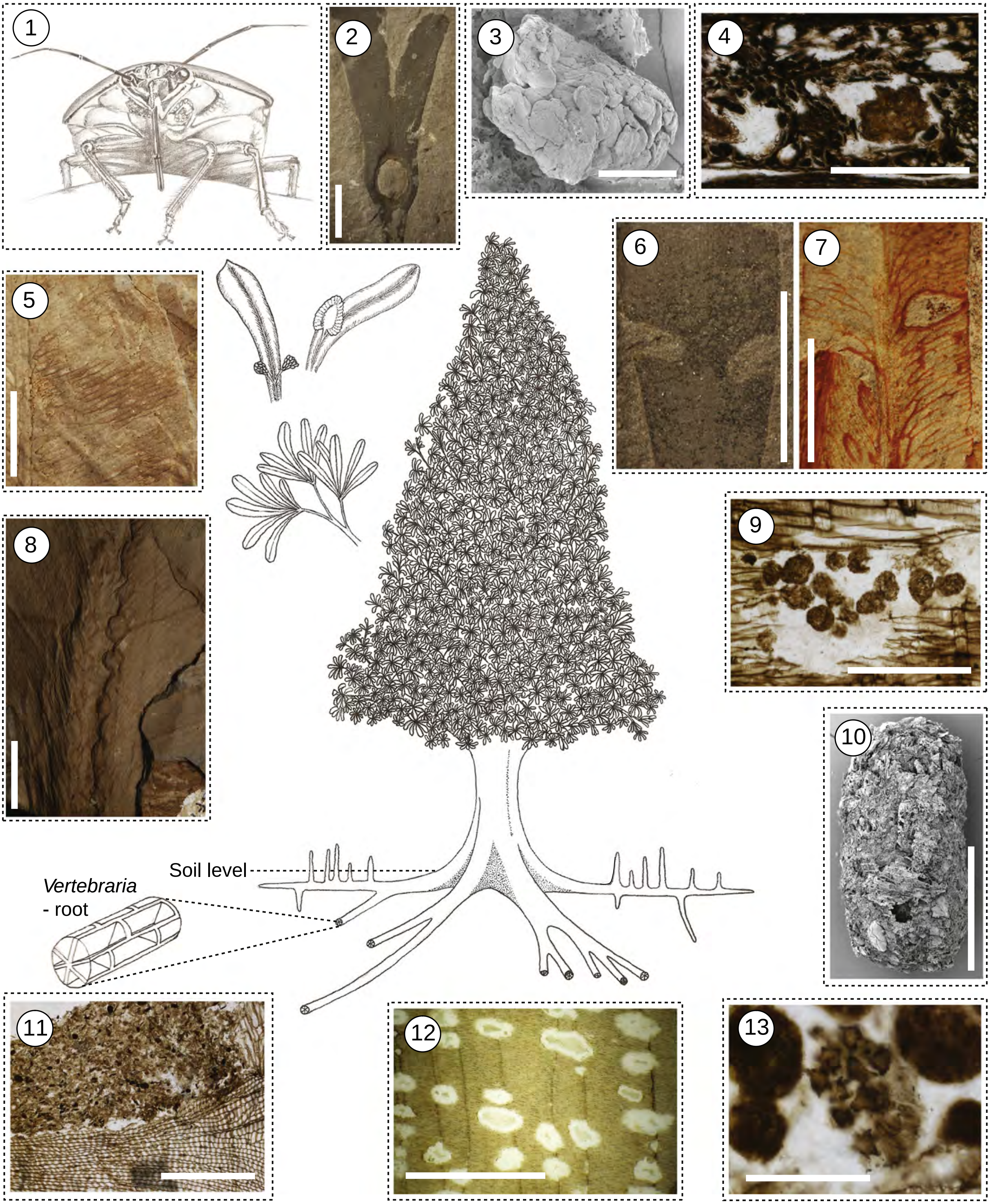
Fungal spores within the coprolites are commonly split and fragmented so were likely part of the diet of an invertebrate (true mycophagy) rather than being the fertile organs of fungi that colonised the coprolites after deposition (Plate 6; 4). However, some fungal hyphae evident in the coprolites possibly colonised the pellets post-deposition. In these cases, hyphae form long unbroken threads that permeate the coprolite.

Coprolites occurring in excavated cavities between *Glossopteris* leaf veins suggest specialist feeding on the leaf mesophyll of the dominant group of gymnosperms in this palaeoecosystem. Mine-like features on glossopterid leaf impressions have been illustrated previously (Gallego et al., 2003; Prevec et al., 2009; de Souza Pinheiro et al., 2012) but their representation of true leaf mining is equivocal and the earliest confident examples of this feeding strategy are documented from the late Middle to early Late Triassic (Rozefelds and Sobbe, 1987; Anderson and Anderson, 1989, p. 231, 265, 439). Although the areal extent of the excavations in the PCM leaves is unresolved, they appear to be restricted to interveinal mesophyll and it is possible that they represent the first examples of leaf mining in *Glossopteris*. Alternatively, such features may represent selective targeting of softer mesophyll tissues in shed leaves by a small detritivore.

Body fossils or traces of vertebrates and other non-marine invertebrates (e.g. molluscs and annelids) are currently unknown from the PCM Permian deposits (McLoughlin et al., 1997). Indeed, vertebrate remains are extremely sparse in Gondwanan Permian non-marine deposits outside of the Karoo Basin, South Africa. A few reptiles and amphibians are known from the Southern Hemisphere Permian (Rubidge, 1995; Warren, 1997; Modesto, 2006) and a slightly broader range of fish and aquatic invertebrate body fossils and locomotion trails has been recorded (Anderson, 1976; Aceñolaza and Buatois, 1993; Shi et al., 2010; Bordy et al., 2011) but evidence of an extensive guild of terrestrial tetrapod herbivores in high-latitude parts of Gondwana is lacking thus far. Terrestrial invertebrate traces are also relatively sparse. No acid-resistant egg cases (e.g. *Dictyothylakos* or *Burejospermum* spp.) of clitellate annelids were recorded from bulk macerations of the peat matrix, and it is possible that these waxy proteinaceous structures only developed within this group after the mid-Triassic (Manum et al., 1991; Jansson et al., 2008). However, various vermiform traces, vertical tubes, and punctate trackways in floodbasin and fluvial channel sediments of Antarctica attest to a varied soil and surface invertebrate biota in Permian high latitudes that is not yet represented by body fossils (Tasch, 1968a, 1968b; Fitzgerald and Barrett, 1986; Miller and Collinson, 1994; Briggs et al., 2010). In the absence of an extensive record of vertebrates, it is likely that arthropods, fungi and bacteria were overwhelmingly the dominant herbivores, detritivores and saprotrophs in the PCM mid-Permian forest mire community.

5.2. Root feeding

Evidence of a previously unknown feeding behaviour targeting glossopterid roots (*Vertebraria*) (Gould, 1975) is identified from thin-sections of the silicified peats (Plate 5; 1–6). This root-feeding activity shows preferential targeting of the softer and likely more nutritious parenchymatous tissues, employing a strategy similar to aerenchyma-feeding arthropods in Late Pennsylvanian *Psaronius* roots (Labandeira, 2001). This behavioural pattern may also have facilitated a more energy-efficient method of tunnelling. Root feeding is known elsewhere in the fossil record from several assemblages. Cichan and Taylor (1982) reported anastomosing burrows of 0.3–0.6 mm in diameter in cordaitalean *Premnoxylon* wood from the lower–middle Pennsylvanian of Kentucky. Borings into the cortical tissues of lycopsid roots are known from the Pennsylvanian–Permian boundary in Germany (Geinitz, 1855; Labandeira, 1998b). Cortical borings are also abundant in young roots of *Protojuniperoxylon arcticum* (probable Bennettitales) from the Upper Triassic of Hopen, Svalbard Archipelago (Strullu-Derrien et al., 2012), although these excavations may represent examples of saproxylophagy. In each case, the host plants were mire-dwelling dominant tree species indicating a consistent life environment and feeding strategy of a guild of small arthropod borers (likely oribatid mites in the


1
2
3
4
5
6
7
8
9
10
Soil level
Vertebraria
- root
11
12
13

case of the smaller borings and insects in the case of larger ones) through the late Palaeozoic and Triassic.

The pattern thus far uncovered from the fossil record indicates that feeding on true roots began in the late Pennsylvanian (Labandeira, 2001), which is rather late when compared to the earliest evidence of feeding on other plant organs (Labandeira, 1998b, 2006a). Evidence for arthropod herbivory in stem tissues and sporangia appears much earlier: during the latest Silurian and Early Devonian (Labandeira, 2006b, 2007). This may be due to the inherent inaccessibility of root tissues when compared to subaerial plant organs, especially given that most three-dimensionally fossilized roots were preserved in waterlogged dysaerobic substrates in special environments such as mineral-charged springs and acidic mires.

We illustrate the first examples of root feeding in *Vertebraria*. Boring into these organs raises the question whether some glossopterid roots were aerial in nature, and similar to the pneumatophores of extant *Taxodium distichum* (Briand, 2000–2001). Exposure of the roots above the waterlogged substrate would certainly have provided easier access to terrestrial herbivores. Cichan and Taylor (1982) proposed that the cordaitean root *Premnoxylon* was an aerial organ based on similar evidence of root boring. *Vertebraria* has traditionally been considered a root characteristic of water-saturated or submerged soils based on its predominantly shallow (horizontal) distribution (Schopf, 1982), position within "seat-earths" underlying coal deposits (Retallack, 1980), and the presence of abundant schizogenous chambers in the secondary xylem that likely acted to facilitate aeration of the living root tissues in dysaerobic conditions (Retallack and Dilcher, 1988; Neish et al., 1993). A possible aerial nature for *Vertebraria* was proposed recently by Decombiex et al. (2009). *Vertebraria* roots are commonly found as dense, ramifying mats within permineralised peat organic debris (organosols: McLoughlin, 1993; Neish et al., 1993), seat earths (Retallack, 1980; Shi and McLoughlin, 1997), and water-saturated floodplain and deltaic palaeosols (hydrosols: Schopf, 1982). Thus, they occupied habitats similar to plants such as semi-aquatic Cupressaceae (e.g., *Taxodium distichum* and *Glyptostrobus pensilis*), red maple (*Acer rubrum*) and water tupelo (*Nyssa aquatica*), which produce pneumatophores to gain access to oxygen for tissue respiration or looping roots, for which a clear function is equivocal (Briand, 2000–2001). Extensive lenticel clusters have not yet been documented in permineralised *Vertebraria*, and discovery of these features would lend support to the hypothesis that pneumatophores were present in glossopterids. A new reconstruction of the *Glossopteris* plant is proposed here with subaerial extensions of *Vertebraria* (Fig. 1).

The evidence of root boring now complements a broad range of other ichnological evidence indicating that all major organs of the *Glossopteris* plant were subject to arthropod attack (Fig. 1). This dominant Gondwanan gymnosperm supported a diverse community of invertebrates and feeding strategies similar to the late Palaeozoic tree fern *Psaronius* of the palaeotropics (Rößler, 2000). Seed-herbivory and nectivory are the only major functional feeding strategies outlined by Labandeira (1998b, 2006a) that have not yet been recognized within glossopterid-dominated communities (although evidence of leaf-mining also remains equivocal).

5.3. Possible producers

Matching isolated coprolites to a producer is inherently difficult because many invertebrates that are separated widely in terms of phylogeny can produce coprolites that are morphologically very similar (Hantzschel et al., 1968). The main hindrance to the identification of Permian coprolite producers, and animal–plant interactions in general, is the lack of a database or atlas illustrating the morphology of faecal pellets produced by extant arthropods and other terrestrial invertebrates. Galleries in *Vertebraria indica* that are less than 1 mm in diameter and filled with small clusters of spherical coprolites are here interpreted to derive from oribatid mites. This is based on strong similarities to coprolites attributed to oribatid mites from numerous other assemblages throughout the late Palaeozoic and early Mesozoic fossil record (Labandeira et al., 1997; Ash, 2002; Habgood et al., 2004; Kellogg and Taylor, 2004; Labandeira, 2007; Feng et al., 2010; Osborn and Taylor, 2010). Although several extant invertebrate groups bore into woods, pre-Mesozoic examples are predominantly attributed to oribatid mites although it is noteworthy that few of these records are associated with body fossils of the producer (Labandeira et al., 1997). Characteristics that particularly favour oribatid mites as the originators of the small PCM coprolites include their clustered distribution, uniform size and smoother texture (compared to the rough faecal pellets of collembolans or ridged oblong pellets of termites) without components projecting beyond the surface (Rusek, 1975; Vegter, 1983). Extant oribatid mites are common microherbivores and detritivores in modern soils and plant detritus (Habgood et al., 2004). In some examples from the PCMs, root feeding has left no obvious response tissue around the excavation areas (cf. Jud et al., 2010), highlighting that consumption of dead xylem tissues was present alongside true herbivory on living cells.

Essentially identical spindle-shaped borings containing coprolites in *Australoxylon mondii* wood from the same silicified peat layer have previously been interpreted as being produced by beetle larvae (Weaver et al., 1997). However, derivation of these traces from oribatid mites appears more likely based on the characteristics outlined above and because wood-boring cerambycid beetles appear to have diverged in post-Triassic times and experienced their major expansion in the Cenozoic (Grimaldi and Engel, 2005). Structurally, these cavities are axially elongate spindle-shaped excavations that extend through the outer portion of the earlywood and through almost all of the latewood. Each of the elongate cavities is isolated, 0.45–3.0 mm in radial diameter and 3.5–13.5 mm in length making them slightly larger than the oribatid mite-produced cavities reported from Permian–Triassic woods from the Permian and Triassic of the Central Transantarctic Mountains (Kellogg and Taylor, 2004) and some modern forms (Wallwork, 1976). Cell walls along the margins of the cavities are sharply truncated and the contained pellets consist entirely of cell wall fragments. No exit/entrance holes are evident for these excavations, although they typically extend to the growth ring margin, which would have represented the exterior surface of the secondary xylem at the end of each growth season (Weaver et al., 1997). Emergence of the arthropods may have been through the bark at the end of winter; the cambial activity in the

Fig. 1. Reconstruction of the *Glossopteris* tree with subaerial extensions of *Vertebraria* roots. The reconstruction is annotated with examples of arthropod damage types (referred to functional feeding groups) on the different organs of the *Glossopteris* plant preserved in the Prince Charles Mountains silicified peat and from Permian deposits elsewhere in Gondwana, demonstrating the suite of invertebrate herbivory acting upon the *Glossopteris* plant. 1; reconstruction of hemipteran sap-sucking insect feeding on *Glossopteris* (piercing and sucking attack). 2; galling on a *Glossopteris* leaf, after McLoughlin (2011), scale bar = 10 mm. 3; coprolite containing consumed *Glossopteris* pollen (pollenivory), scale bar = 50 μm. 4; coprolites in cavities between anastomosing *Glossopteris* leaf veins (selective detritivory or possible leaf mining), scale bar = 500 μm. 5; fungal damage to a *Glossopteris* leaf, after McLoughlin (1994a, 1994b), scale bar = 10 mm. 6–7; examples of leaf margin feeding on *Glossopteris* leaves (external foliage feeding), after Beattie (2007), scale bar = 10 mm. 8; oviposition scars along *Glossopteris bucklandensis* midrib (oviposition), after McLoughlin (1990) and McLoughlin (2011), scale bar = 10 mm. 9; feeding gallery inside *Australoxylon* wood containing numerous small coprolites attributed to oribatid mites (wood boring: xylophagy or saproxylophagy), scale bar = 500 μm. 10; coprolite produced by a detritivore likely feeding on shed plant organs (leaf litter detritivory), scale bar = 500 μm. 11; arthropod feeding damage in *Vertebraria* root tissues showing compressed mass of fine frass and coprolites within a *Vertebraria* internal air chamber (wood boring: xylophagy or saproxylophagy), scale bar = 1 mm. 12; pocket rot within *Australoxylon* wood (fungal damage), after Weaver et al. (1997), scale bar = 1 mm. 13; coprolite containing fungi within a *Vertebraria* root (mycophagy), scale bar = 200 μm.

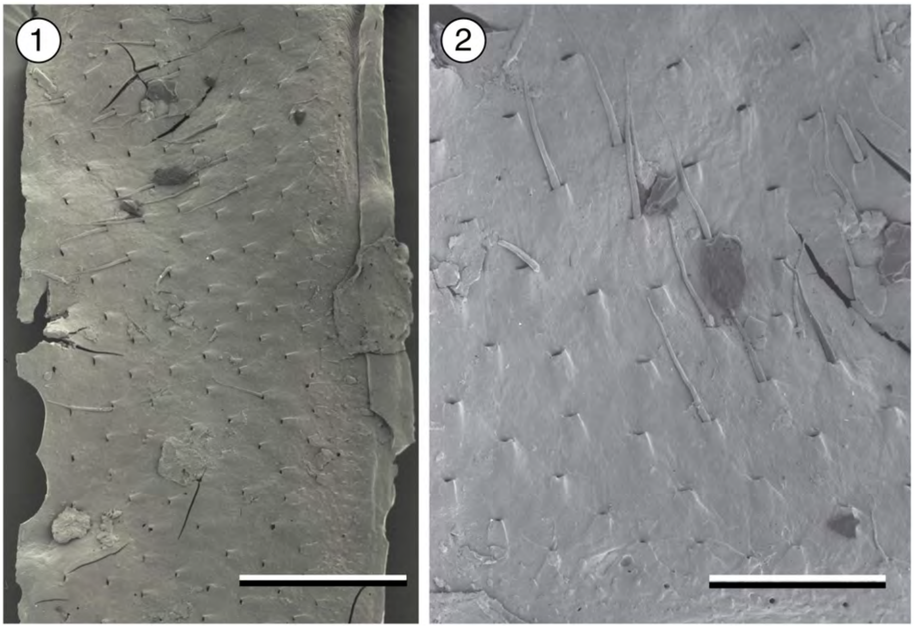


Fig. 2. A fragment of arthropod carapace recovered from the acid maceration of the silicified peat in the Prince Charles Mountains. 1; exoskeleton fragment, scale bar = 100 μm. 2; enlargement of setae, scale bar = 50 μm.

Table 1
Summary of coprolite traits in PCM Middle Permian peat.

Damage/ coprolite type	Size range	Shape	Colour	Contents	Occurrence	Relative abundance	Host specificity: 1 (host specific); 2 (intermediate); 3 (host generalized)
Coprolites in *Vertebraria* and *Australoxylon* (dark)	120 μm long and 115 μm wide	Ovoid, conoid or equant	Dark brown	Small angular fragments of tracheid wall	Roots, wood	High; > 1000 in some slides	1; Occurs solely in *Vertebraria* and *Australoxylon* wood of the *Glossopteris* plant
Coprolites in *Vertebraria* and *Australoxylon* (light)	150 μm long and 125 μm wide	Ovoid, conoid or equant	Light brown	Small angular fragments of tracheid wall	Roots, wood	High; > 1000 in some slides	1; Occurs solely in *Vertebraria* and *Australoxylon* wood of the *Glossopteris* plant
Coprolites in leaves	200–550 μm long and 120–250 μm wide	Elongate and flattened, some are equidimensional	Light brown	Fragments of leaf mesophyll cell walls	Between anastomosing veins of *Glossopteris* leaves	Relatively common; > 10 specimens	1; Occurs solely in *Glossopteris* leaves
Coprolite within fern sporangium	500 μm long and 300 μm wide	Ovoid	Dark brown	Fern spores	Inside fern sporangium	Single occurrence	1; Occurs solely in fern sporangia
Isolated large coprolites	1000–2500 μm long and 500–1300 μm wide	Elongate, some spherical	Light brown, black in charcoalified specimens	Fine to coarse unidentifiable plant debris, some spores and pollen grains	Amongst matted leaf remains	Relatively common; > 10 specimens	3; Coprolites contain diverse range of contents
Isolated small coprolites	500–750 μm long and 300–350 μm wide	Oblong to cylindrical	Light yellow–brown	Mixed plant remains, pollen grains, fungal spores	Isolated in peat matrix, amongst matted leaf remains	Relatively common; > 10 specimens	3; Coprolites contain diverse range of contents
Coprolites containing fungi	180–220 μm long and 120–200 μm wide	Conoid to ovoid or equidimensional	Light brown	Broken fungal spores	Roots, wood and isolated in the peat matrix	Relatively uncommon; < 10 specimens	2; Coprolites contain solely fungal remains although fungal type appears indiscriminate
Coprolites containing pollen	100–150 μm long and 70–150 μm wide	Squat ellipsoidal to spherical	Light brown	Pollen grains	Isolated in the peat amongst *Glossopteris*-dominated debris	Relatively uncommon; < 10 specimens	1; Coprolites contain solely *Glossopteris* pollen
Coprolites with coarse constituents	0.8–1.3 mm long and between 0.5 and 1 mm wide	Equidimensional to ellipsoidal	Dark brown	Coarse fragments of leaf mesophyll and woody tissues	Isolated in the peat matrix	Relatively uncommon; < 10 specimens	3; Coarse contents derived from dead wood tissues
Spirally ornamented coprolite	800 μm long and 300 μm wide	Elongate cylindrical	Macerated specimen dark brown	Finely granular to platy indeterminate tissues	Macerated from leaf-rich sample	Single occurrence	?; Difficult to determine host specificity as only a single specimen recovered from peats

succeeding spring growth spurt then re-sealing the cavity leaving no signs of reaction tissue.

Root boring is a common trait amongst several invertebrate lineages in modern ecosystems. Modern borings are produced by moths (Cuthrell, 1999), beetles (Soltani et al., 2008), mites (Fan and Zhang, 2003), termites [Isoptera (Spragg and Paton, 1980)], ants [Hymenoptera (Vörös and Gallé, 2002)], Diptera (Finch and Ackley, 1977) and cicadas [Hemiptera (Hunter, 2008)]. Some extant taxa, such as *Oryctes agamemnon*, specifically target aerating tissues and feed on the respiratory roots of the date palm (Soltani et al., 2008). Determination of the producers of the *Vertebraria*-hosted coprolites is largely speculative, because none is associated with body fossils, and isolated fragments of exoskeleton recovered by bulk maceration have unresolved affinities. The waterlogged conditions occupied by the *Glossopteris* plant would have potentially left them vulnerable to feeding by aquatic arthropods such as ostracods, cladocerans and copeopods (e.g. Womack et al., 2012). Extant forms of these groups are known to feed upon plant matter that is submerged in water although they generally target loose detritus and algae (Anderson and Trewin, 2003).

The isolated larger coprolites found in the bulk macerated materials match the morphology and contents of those produced myriapod detritivores (Scott and Taylor, 1983). It is noteworthy that predatory arthropods commonly switch diet to spore feeding when prey is unavailable, so this adds another group of potential candidates to the producers of the spore-filled coprolites (Kevan et al., 1975).

5.4. Comparison with Late Pennsylvanian Psaronius communities

Perhaps the most studied Palaeozoic plant–insect association is that of the Late Pennsylvanian *Psaronius* tree fern from the Calhoun Coal (Labandeira, 1998a; Rößler, 2000) and the Upper Permian of Yunnan Province, southwest China (D'Rozario et al., 2011a). The *Psaronius* tree fern formed a plant–arthropod–fungi component community which persisted from the Late Pennsylvanian of Euramerica to the Permian wetlands of Cathaysia as wetland plant communities migrated through the Late Palaeozoic (Hilton and Cleal, 2007; D'Rozario et al., 2011a). Like the early Late Pennsylvanian *Psaronius* communities of the Illinois Basin (Labandeira, 1998a, 1998b) and northern Germany (Rößler, 2000; Rößler, 2006), the range of functional feeding groups preserved in the *Glossopteris* community represented in the PCMs silicified peats appears to constitute a component community (Root, 1973). A component community (or source community) consists of the source plant, in this case *Glossopteris*, and all herbivores consuming this plant and nutritionally derivative feeding guilds (Root, 1973; Lawton, 1976; D'Rozario et al., 2011b). The finer features of coprolites and feeding traces are different between the *Psaronius* and glossopterid communities indicating that separate species of invertebrates were involved, but the general similarities in herbivory and detrivory between these assemblages indicates that a similar ecological structure was established in both high-latitude and palaeotropical mire systems (Table 2). Studying component communities in the fossil record could provide insights into long-term evolutionary trends such as whether plant–animal associations persist through time, as appears to be the case in the *Psaronius* community, or if host switching is common (Labandeira, 1998a).

6. Conclusions

(1) The Permian swamp-forest biotas of Gondwana reveal a diverse array of plant–arthropod–fungal interactions; several of these categories (root boring, trunk wood boring, pollenivory, sporivory, folivory, fungivory) are represented in the siliceous permineralised glossopterid-dominated plant assemblages from the lower Bainmedart Coal Measures in the Prince Charles Mountains.

(2) Coprolites preserved within plant tissues and dispersed within the silicified peat matrix reveal, by way of transmitted light and scanning electron microscopy, producer organisms with variable feeding strategies—some feeding on specific plant tissues, others adopting generalist feeding behaviours. These feeding strategies include xylophagy, saproxylofagy, folivory, detrivory, microsporangial feeding and mycophagy.

(3) The first evidence of putative oribatid mite feeding on *Vertebraria* root tissues of the *Glossopteris* plant has been found, providing feedback on the biology of the root organs. It suggests that at least some roots were accessible to borer organisms in surficial or shallow soil conditions lending support to the hypothesis that some roots of this type may have been aerial in nature (pneumatophores).

(4) The diversity of plant organs being exploited by arthropod herbivores reveals that, like the tree fern *Psaronius* in the late Palaeozoic tropics, the *Glossopteris* tree formed the basis for a complex ecosystem of herbivores, detritivores, saprotrophs and mycophagous organisms in Permian high southern latitudes.

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Table 2
Comparison of the major feeding traits and herbivore/detritivore invertebrates and their damage associated with late Palaeozoic palaeoequatorial *Psaronius* and high southern latitude glossopterid component communities (with reference to D'Rozario et al., 2011b).

Feeding trait	*Psaronius* component community	PCM glossopterid component community
Root-boring	Feeding on aerenchymatous root tissue	Feeding on *Vertebraria* root tissues
Stem-boring	Boring in *Psaronius* trunk ground parenchyma	Boring in *Australoxylon* stem wood
Folivory	Surface abrasion of *Pecopteris* pinnules	Known on *Glossopteris* from elsewhere in Gondwana. Possible leaf mining, though likely represents selective detritivory
Detritivory	Detritivore pith-boring in *Psaronius* stem parenchyma; probable myriapod or insect producer	Leaf litter detritivory on shed plant organs; probable myriapod or insect producer
Palynivory/sporivory	Palynivory of *Scolecopteris* sporangial tissue and *Punctatisporites* spores	Coprolites composed entirely of *Glossopteris* pollen. Excavations and coprolites from obligate herbivores of fern and glossopterid microsporangia; possibly coleopterans
Galling	Galling of inner parenchyma of *Stipitopteris rachis* demonstrating insect holometaboly	Known on *Glossopteris* from elsewhere in Gondwana
Piercing and sucking	Piercing and sucking damage in xylary tissue of *Stipitopteris rachis*	Known on *Glossopteris* from elsewhere in Gondwana
Coprophagy	Mite feeding on larger, probable insect coprolites	Presently unknown/unrecognised in *Glossopteris* community
Mycophagy	Coprolites containing fungal remains as part of a range of contents	Coprolites composed entirely of fungal remains inside *Vertebraria* and *Australoxylon* woods

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Peronosporomycetes (Oomycota) from a Middle Permian Permineralised Peat within the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica

Ben J. Slater[1]*, **Stephen McLoughlin**[2], **Jason Hilton**[1]

1 School of Geography, Earth and Environmental Sciences, University of Birmingham, Edgbaston, Birmingham, United Kingdom, **2** Department of Paleobiology, Swedish Museum of Natural History, Stockholm, Sweden

Abstract

The fossil record of Peronosporomycetes (water moulds) is rather sparse, though their distinctive ornamentation means they are probably better reported than some true fungal groups. Here we describe a rare Palaeozoic occurrence of this group from a Guadalupian (Middle Permian) silicified peat deposit in the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. Specimens are numerous and comprise two morphologically distinct kinds of ornamented oogonia, of which some are attached to hyphae by a septum. *Combresomyces caespitosus* sp. nov. consists of spherical oogonia bearing densely spaced, long, hollow, slender, conical papillae with multiple sharply pointed, strongly divergent, apical branches that commonly form a pseudoreticulate pattern under optical microscopy. The oogonia are attached to a parental hypha by a short truncated stalk with a single septum. *Combresomyces rarus* sp. nov. consists of spherical oogonia bearing widely spaced, hollow, broad, conical papillae that terminate in a single bifurcation producing a pair of acutely divergent sharply pointed branches. The oogonium bears a short truncate extension where it attaches to the parental hypha. We propose that similarities in oogonium shape, size, spine morphology and hyphal attachment between the Permian forms from the Prince Charles Mountains and other reported Peronosporomycetes from Devonian to Triassic strata at widely separated localities elsewhere in the world delimit an extinct but once cosmopolitan Palaeozoic to early Mesozoic branch of the peronosporomycete clade. We name this order Combresomycetales and note that it played an important role in late Palaeozoic and early Mesozoic peatland ecosystems worldwide.

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* E-mail: bxs574@bham.ac.uk

Introduction

The Peronosporomycetes (also known as Oomycota or water moulds) are a class of organisms belonging to the phylum Heterokontophyta, which also includes autotrophs such as diatoms and brown algae [1–3]. Due to superficial similarities in their filamentous morphology, spore-like oogonia (egg-containing sacs) and life habits, the Peronosporomycetes have in the past been grouped with the true fungi [4]. However, they can be distinguished by the morphology of the motile stage of their life cycle, in which the zoospores possess two differently shaped flagella used for propulsion; a lateral whip flagellum and a one-haired tinsel flagellum [5]. Peronosporomycetes differ fundamentally from true fungi on a cellular level since their cell walls are composed of cellulose and hydroxyproline as opposed to chitin [4,5], and the cell nuclei contained in the hyphae-like filaments are diploid as opposed to haploid in true fungi [4].

Peronosporomycetes are saprotrophs or parasites [6]. Some are major plant and animal pathogens in modern ecosystems that are responsible for well-known plant diseases, such as potato blight (*Phytophthora infestans*), sudden oak death (*Phytophthora ramorum*), blister rusts and downy mildews [4]. They are currently responsible for the widespread larch dieback seen in *Larix decidua* in the UK and northern Europe [4,7–10], major damage to tropical commercial plant species [11], and extensive death of selected plants in temperate forests and heathlands in the Southern Hemisphere [12,13]. Peronosporomycetes are capable of reproducing both asexually and sexually [4,14]. Asexual reproduction initiates with the formation of a zoosporangium, from which primary and secondary bi-flagellated motile zoospores are released. When reproducing sexually, the male nuclei are injected directly into the oogonium [14,15]. Zoospores achieve dispersal by means of flagellar propulsion through water films either in soil pore water or on the surface of plants and can also spread through overland flow into fluvial and lacustrine environments. Dispersal is, therefore, favoured in moist, damp environments where the zoospores gravitate towards chemical attractants released by plants such as amino acids, sugars, ethanol and acetaldehyde [16].

Krings et al. [5] reviewed the fossil record of the Peronosporomycetes and concluded that all the reported occurrences of this group older than Devonian are dubious or inconclusive. Confident Palaeozoic and early Mesozoic records are restricted to a small number of occurrences in Devonian, Carboniferous and Triassic permineralised peats and sinter deposits [4,17]. These include the Devonian Rhynie Chert [18,19], Carboniferous coal balls from the lower coal measures of the UK [20–22], Upper Mississippian cherts from France [23], the Upper Pennsylvanian Grand-Croix cherts of France [24], and Middle Triassic silicified peats from the Fremouw Peak locality in the Transantarctic Mountains of central Antarctica [17]. Similar unpublished spinose spore-like bodies are also known from the Upper Triassic of Hopen, Svalbard Archipelago, but are attributed to Ascomycetes (C. Strullu and S. McLoughlin unpublished data). Multilayered oogonium-like structures possibly attributable to Peronosporomycetes have also been reported from a Jurassic hot spring deposit in Patagonia, Argentina [25]. Other possible examples of Peronosporomycetes have been documented from amber [26–29]. However, it is difficult to confidently resolve the affinity of those examples. It has been suggested that outgrowths from a Lower Pennsylvanian fungal sporocarp from Great Britain could represent an example of saprotrophic Peronosporomycetes [30]. A possible peronosporomycete affinity has been suggested for some acritarchs [5,31] based on similarities in their morphology to oogonia of some extant water moulds.

Their sparse fossil record is unfortunate for understanding the evolution of feeding guilds and energy flow within terrestrial communities, since the Peronosporomycetes are important decomposers and parasites in modern ecosystems, particularly in damp soils and freshwater habitats [32], and are also present in the marine realm [33]. Peronosporomycetes are also significant in a broader evolutionary context since they are possibly among the earliest differentiated lineages of eukaryotes based on phylogenetic analyses of molecular data (e.g. [31,34–36]).

The Permian cherts (silicified peats) of the Prince Charles Mountains contain a range of microbial elements within a glossopterid- and cordaitalean- (gymnosperm) dominated mire palaeoecosystem [37,38]. The microbial remains are preserved in exquisite cellular detail and retain morphological characters that are not preserved outside of Konservat-Lagerstätten, fossil-bearing deposits with exceptional fidelity of preservation [39]. Microscopic remains within the permineralised peat include delicate organs such as fungal hyphae, spores, and invertebrate exoskeleton parts [38,40,41]. Some of these fragile organs are even found within invertebrate coprolites preserved within the peat matrix or inside plant tissues [42]. Here we describe two new forms of peronosporomycete oogonia from the Toploje Member chert of the Prince Charles Mountains that are distinguished from each other primarily by differences in the length and density of the branched external spines. The addition of Peronosporomycetes to the inventory of preserved elements in the fossil community from the Prince Charles Mountains expands the known biodiversity and trophic guilds of the high-latitude peat-forming forests of the Permian.

Geological Setting and Stratigraphic Age

Samples of silicified peat were obtained from a 3-km-long outcrop of chert in the northern Prince Charles Mountains, East Antarctica (see Slater et al. [41] fig. 1 for a map of the sampled locality). The silicified interval is ca 40 cm thick and caps a coal seam representing the topmost bed of the Toploje Member within the Bainmedart Coal Measures, the middle unit of the Permo-Triassic Amery Group [43,44]. The Amery Group is characterised by numerous cycles of thickly bedded sandstones, siltstones and coal seams deposited in an alluvial valley dominated by braided rivers [41,43,45]. The cyclicity of the Bainmedart Coal Measures sedimentary facies has been attributed to climatically triggered fluctuations in sediment supply related to Milankovitch cycles [45]. The cause of silicification in the uppermost Toploje Member has not been resolved but appears to be related to geochemical changes in the surface layers of the peat during lacustrine drowning of the mire accompanying deposition of the overlying sideritic–limonitic Dragons Teeth Member [43,45]. Palynostratigraphic evidence indicates the silicified peat bed is of Roadian to Wordian age [46]. The coals of the lower Bainmedart Coal Measures are of sub-bituminous rank but organic remains within the single layer of silicified peat appear to have been entombed rapidly and shielded from significant compression or thermal alteration [38].

The Amery Group was deposited within a series of half-grabens that constitute the Lambert Graben complex [44,47,48], which was a southern extension of the Mahanadi Graben of eastern India before Gondwanan breakup [41,47,49–51]. The Prince Charles Mountains were situated at a palaeolatitude of 65–70°S during the Middle Permian [52]. The silicified peats, therefore, provide a snapshot of a high-latitude mire community that was likely subject to significant seasonal variation in environmental parameters.

The taphonomy of the silicified peat layer was discussed in detail by Slater et al. [41]. The peat includes a range of plant remains dominated by *Glossopteris* and *Noeggerathiopsis* (glossopterid and cordaitalean gymnosperms, respectively), herbaceous lycophytes and ferns. The community likely represents a raised (ombrotrophic) forest-mire ecosystem based on the substantial thickness of individual coal seams in the Bainmedart Coal Measures, together with the occurrence in the coal of significant quantities of charcoal, fungi and coprolites [42] but minimal siliciclastic components [41].

Materials and Methods

Ethics

All necessary permits were obtained for the described study from the Australian Antarctic Division and Australian National Antarctic Research Expeditions program, which complied with all relevant regulations. Specimens are held in the palaeobotannical collections at the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Frescativägen 40, 114 18, Stockholm. Specimen numbers of the material described in this study are; NRM S097800-01, NRM S087932-01, NRM S087932-01-02, NRM S088053-01, NRM S088061-01, NRM S088072-01.

Thirty-five thin sections of the chert were prepared for the analysis of diminutive components of the peats because this method has been shown to reveal greater optical detail of many microbial components than obtainable using the acetate peel technique (see [53]). Images were processed and figures compiled using Adobe Photoshop and Illustrator CS4 graphics packages. Peronosporomycetes was reclassified by Dick et al. [54], however it is important to note that the alternative names for this clade (Oomycetes and Oomycota) are in common circulation in the scientific literature [1,17]. Although these organisms are not true fungi, their morphological features are still described using mycological terminology. Therefore, this report will describe the hyphae-like filaments as hyphae for consistency with other current literature.

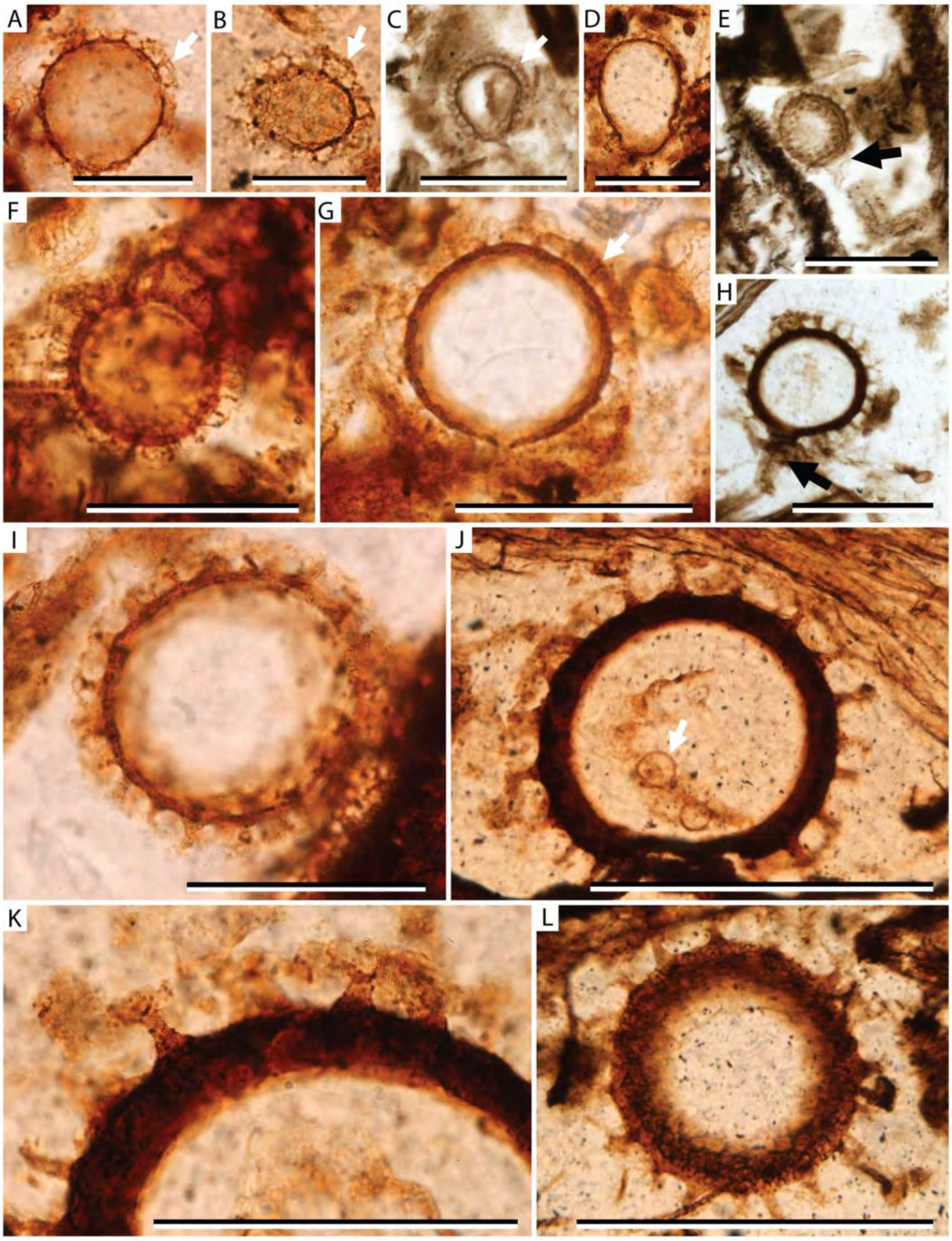

Figure 1. ***Combresomyces caespitosus*** **sp. nov. (Peronosporomycetes: Combresomycetales); Oogonium morphotype with dense coverage of spines.** A. NRM S087932-01-02, scale = 50 µm; B. NRM S087800-01, scale = 50 µm; C. NRM S088061-01 oogonium lies within a large

coprolitic mass, scale = 100 μm; D. S087800-01, scale = 50 μm; E. NRM S088072-01, arrow indicates position of a possible fragment of hypha extending from oogonium, scale = 100 μm; F. S087800-01, scale = 50 μm; G. S087800-01, scale = 50 μm; H. NRM S087800-01 (holotype specimen), arrow indicates truncate extension with attached subtending hyphae, scale = 100 μm; I. NRM S087932-01-02, scale = 50 μm; J. NRM S087800-01, arrow indicates indeterminate spherical internal contents of oogonium, scale = 100 μm; K. NRM S087800-01, enlargement of wall and ornament of oogonium in image J, scale = 50 μm; L. NRM S087800-01, scale = 100 μm; Arrows in images A–C and G indicate interlocking ornamentation.
doi:10.1371/journal.pone.0070707.g001

Nomenclature

The electronic version of this article in Portable Document Format (PDF) in a work with an ISSN or ISBN will represent a published work according to the International Code of Nomenclature for algae, fungi, and plants, and hence the new names contained in the electronic publication of a *PLOS ONE* article are effectively published under that Code from the electronic edition alone, so there is no longer any need to provide printed copies. In addition, new names contained in this work have been submitted to MycoBank from where they will be made available to the Global Names Index. The unique MycoBank number can be resolved and the associated information viewed through any standard web browser by appending the MycoBank number contained in this publication to the prefix http://www.mycobank.org/MycoTaxo.aspx?Link = T&Rec = . The online version of this work is archived and available from the following digital repositories: PubMed Central, LOCKSS.

Results: Systematic Palaeontology

Kingdom Straminipila M.W. Dick, 2001[a] [4]

Phylum Heterokonta Cavalier-Smith, 1986 [55]

Subphylum Peronosporomycotina M.W. Dick, 2001[a] [4]

Class Peronosporomycetes M.W. Dick, 2001[a] [4]

Order Combresomycetales order nov. B. J. Slater, S. McLoughlin et J. Hilton, 2013

MycoBank number: 804720

Diagnosis

Peronosporomycetes with oogonia having robust ancyrate sculptural elements.

Remarks

The new order differs from other groups of equivalent rank in the Peronosporomycetes by the thick wall and robust ancyrate sculptural elements on the oogonia. Oogonia of the Peronosporales and Pythiales may have punctate, papillate, verrucate or simple spinose ornamentation, but none is known to have complex branched sculptural elements [56]. The new order contains a single extinct family diagnosed below.

Family Combresomycetaceae fam. nov. B. J. Slater, S. McLoughlin et J. Hilton, 2013

MycoBank number: 804721.

Diagnosis

Combresomycetales with oogonia having one to two orders of terminal branching on the conical sculptural elements.

Etymology for Order and Family

Derived from the type genus *Combresomyces*.

Genus *Combresomyces* Dotzler N, Krings M, Agerer R, Galtier J et Taylor TN 2008 [57].

Type Species

Combresomyces cornifer Dotzler N, Krings M, Agerer R, Galtier J et Taylor TN 2008 [57]; upper Viséan; central France.

Combresomyces caespitosus sp. nov. B. J. Slater, S. McLoughlin et J. Hilton.

Holotype

NRM S087800-01 (Figure 1, image H).

Type Locality, Stratum and Age

Grid reference 70°49′19″S, 68°03′54″E (elevation 162 m), 1.4 km east of Radok Lake, northern Prince Charles Mountains, Antarctica; uppermost Toploje Member, Bainmedart Coal Measures; Middle Permian (Roadian to Wordian).

Etymology

Latin – tufted or clumped; referring to the tufted branches that cap papillae.

MycoBank number: 803924.

Diagnosis

Spherical oogonia having a main body <95 μm in diameter, bearing 6–20 μm long, hollow, slender, conical papillae with at least two orders of strongly divergent, sharply pointed, apical branches. Oogonium attached via a short stalk with single septum to parent hypha 21 μm wide. Papillae spaced 10–20 μm apart.

Description

The oogonia are spherical with a surface ornamentation consisting of hollow, regularly and densely spaced papillae, which bifurcate at least twice to form a multi-branched terminal crown (Figure 1; Images A–L). This ornamentation interlocks to give the impression of a reticulum in light microscopic examination of some specimens (Figure 1; Images A–C, G). The main body of the oogonium is 40–95 μm in diameter. The wall is 4–15 μm thick. Sculptural elements (papillae and their crowns) are 5–7 μm in basal width and 6–20 μm tall, of which 3–10 μm is the branched crown. The papillae apices bifurcate twice typically and have sharp tips. Papillae are spaced 10–20 μm apart.

None of the specimens demonstrates a connection to a widespread network of aseptate hyphae that is present in the peat, although one specimen is connected to a 32 μm long solitary parental hypha. This parental hypha is 21 μm wide and attaches via a septum to a truncate basal extension of the main oogonium body (Figure 1; Image H). Other oogonia have truncate extensions or breaks in the ornament where the parental hypha presumably attached. It is difficult to discern whether the oogonia have any preserved contents; some specimens house indistinct structures that may represent degraded oospores (Figure 1; Image J) but their identity is inconclusive. Antheridia have not been conclusively identified.

Remarks

This form occurs dispersed throughout the silicified peat matrix in approximately 50% of the studied thin-sections. It is particularly found in association with accumulations of plant debris around *Vertebraria* (glossopterid roots) and matted leaf deposits of *Glossopteris* and *Noeggerathiopsis*.

Although known to have a conservative morphology spanning the Pennsylvanian to Middle Triassic [17], *Combresomyces* oogonia show subtle differences in size and ornamentation between assemblages of different stratigraphic age. *Combresomyces caespitosus* sp. nov. differs from *Combresomyces cornifer* [57] and *Combresomyces williamsonii* [58] in several respects including slightly denser ornamentation, which abuts or interlocks to form a pseudo reticulum. This feature is not seen in either *C. cornifer* [57] or *C. williamsonii* [58], in which the tips of the ornament remain widely spaced. The oogonia of *C. caespitosus* are larger than specimens of *C. cornifer* from the Pennsylvanian (<40 μm in diameter: [57]) but smaller than the large oogonia of *C. cornifer* known from the Middle Triassic (up to 110 μm in diameter: [17]). The wall of the oogonium in *C. caespitosus* is generally thicker (4–15 μm) than that of both *C. cornifer* (described as *ca* 1 μm [57]) or *C. williamsonii* (described as thin-walled [58]), and the truncate attachment to the parental hypha in *Combresomyces caespitosus* sp. nov. protrudes further from the main body of the oogonium.

The dense multi-branched spines of *Combresomyces caespitosus* oogonia, though markedly smaller, show remarkable similarities in basic morphology to the branched ornamentation of some lycophyte megaspores found in the same beds (see *Singhisporites hystrix* [41]). These similarities might be due functional parallels between these organs as biological dispersive units. The increased surface area generated by densely ramified appendages might have conferred improved buoyancy for dispersal of both megaspores and oogonia in Permian wetland settings [17], or have provided a favourable mechanism for attachment of these structures to other materials (e.g., plant debris in the case of the peronosporomycete saprotroph, or conspecific microspores in the case of the lycophyte megaspores, or even attachment to arthropod distributers). Surface sculptures of a broadly similar morphology occur in many unrelated groups and likely performed an important biological function in life (e.g. [59]).

Combresomyces rarus sp. nov. B. J. Slater, S. McLoughlin et J. Hilton.

Holotype

NRM S087932-01-02 (Figure 2, image F).

Type Locality, Stratum and Age

Grid reference 70°49′54″S, 68°03′05″E (elevation 166 m), 1.25 km east of Radok Lake, northern Prince Charles Mountains, Antarctica; uppermost Toploje Member, Bainmedart Coal Measures; Middle Permian (Roadian to Wordian).

Etymology

Latin – sparse; referring to the widely spaced papillae.

MycoBank number: 803925.

Diagnosis

Spherical oogonia having a main body <65 μm in diameter, bearing 12–20 μm long, hollow, broad, conical papillae that terminate in at least one bifurcation producing a pair of, generally acutely divergent, sharply pointed branches. Oogonium wall locally bearing a short truncate extension marking attachment point to parent hypha. Papillae spaced 15–20 μm apart.

Description

The oogonia are spherical with sparsely ornamented surfaces. The ornamentation consists of widely spaced, robust, hollow papillae with elongate extensions that bifurcate at least once (Figure 2). The oogonium has a central body 38–65 μm in diameter with a wall 2–5 μm thick. The sculptural elements (papillae and apical spines) are 12–20 μm in total length, of which 5–8 μm represents the apical branches. Branch apices are sharply pointed. Papillae are 5–8 μm in basal width and spaced 15–20 μm apart – their bases being confluent to produce intervening broad U-shaped transverse sections of the oogonial wall.

None of the specimens demonstrates a connection to a widespread network of aseptate hyphae found within the peat matrix although some were found connected to short lengths of solitary parental hypha (Figure 2; Images C, F, K). The oogonia of the holotype specimen is connected to a 22 μm long length of solitary parental hypha. The parental hypha is 35 μm wide and attaches via a septum to a truncate basal extension of the main oogonium body (Figure 2; Image F). A truncate extension marked by a break in ornamentation is evident on some specimens (Figure 2; Images B and H) and is interpreted to be the attachment point between the oogonium and the parent hypha. The contents of the oogonia are difficult to elucidate. Antheridia have not been identified although it is notable that the length of hypha in one specimen (Figure 2; Image K) is somewhat morphologically similar to the outline expected if the antheridium was formed as a collar-like structure at the base of the oogonium in an amphigynous arrangement. However, the preservation is insufficient to confirm or refute this and we interpret the structure as a length of parental hypha.

Remarks

This species is less abundant than *Combresomyces caespitosus* in the Toploje Member chert fossil ecosystem, occurring in approximately 25% of the thin sections prepared from the peats. This form occurs primarily in association with *Vertebraria* and *Australoxylon* (respectively, the root and stem wood of glossopterids). Although of equivalent absolute length, the sculptural elements in *Combresomyces rarus* sp. nov. are proportionally longer in relation to the central body of the oogonium than in *C. caespitosus*, and the ornament does not appear to interlink to form a pseudoreticulum.

The ornament of *C. rarus* is more akin to that of *C. williamsonii* [58] than *C. caespitosus*, although the papillae are much more widely spaced with the bases merging to form broad U-shaped transverse sections of the oogonial wall, a feature not seen in *C. williamsonii* [58]. The ornament of *Combresomyces rarus* is also proportionally larger and less densely distributed than in *C. williamsonii* [58].

Discussion

We refer these fossils to the Peronosporomycetes based on their morphological similarity to examples of this biological class known from other late Palaeozoic and early Mesozoic assemblages, in which oogonia are more confidently associated with hyphae, e.g., *Combresomyces cornifer* [17] and *C. williamsonii* [58]. Similar isolated oogonia attributed to this group are also known from the Pennsylvanian of France [3]. Our confidence in attributing the fossils to the Peronosporomycetes is enhanced by several specimens (Figure 1; Image H, Figure 2; Images C, F, K) possessing a distinctly truncated extension from the main body of the oogonium that attaches to the parent hypha in the same way as specimens of *Combresomyces cornifer* [17]. This truncated extension is present in some fossil examples of Peronosporomycetes and in most extant forms, although it is absent in some [19].

Acyrate-conate fossil oogonia attributable to Peronosporomycetes vary significantly over their stratigraphic range. Earlier forms, e.g., from the Pennsylvanian [57] are generally <40 μm in diameter, whereas Middle Triassic forms reach 110 μm in

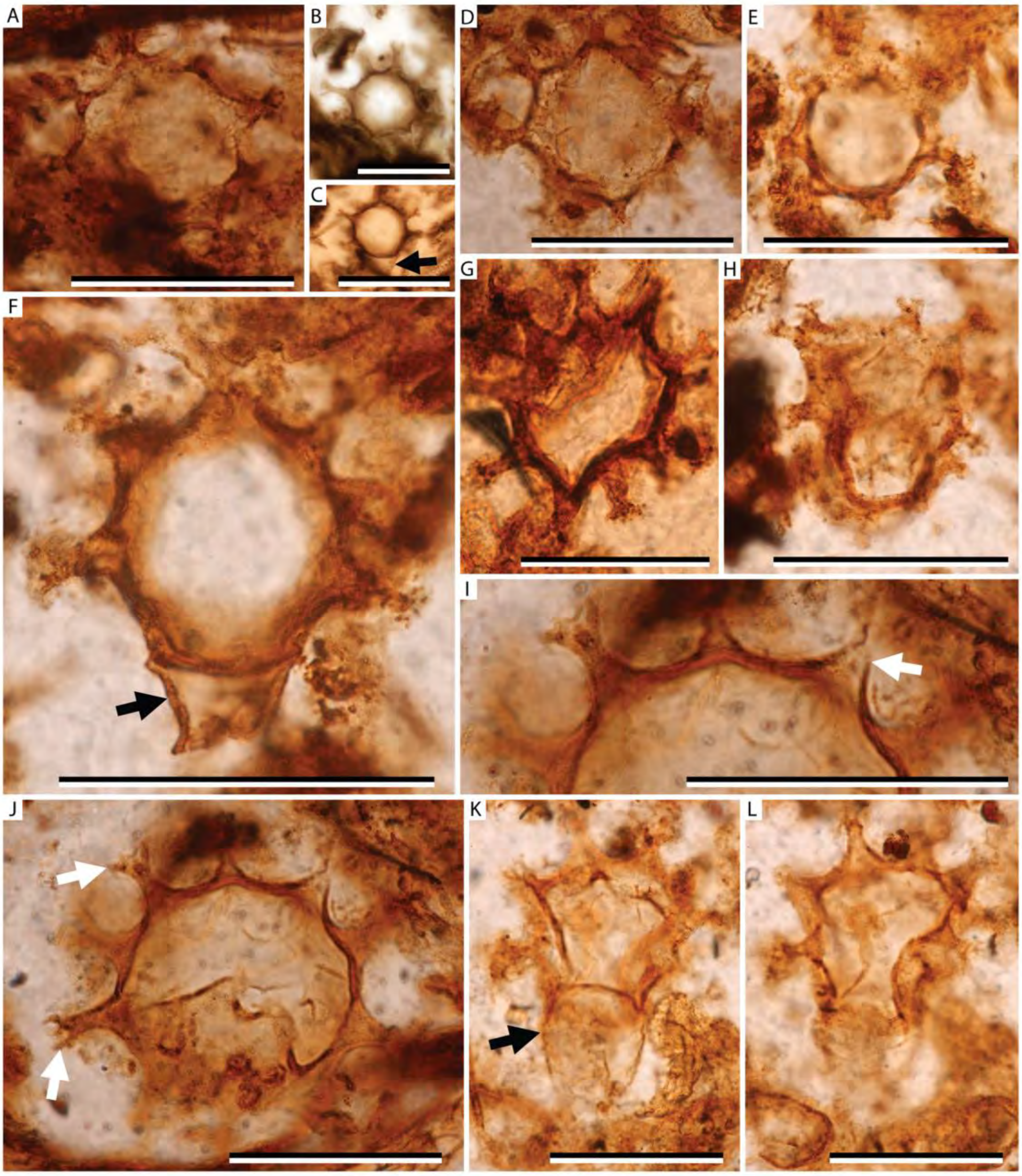

Figure 2. ***Combresomyces rarus*** **sp. nov. (Peronosporomycetes: Combresomycetales); scale bars = 100 µm unless stated otherwise.** Oogonium morphotype with sparse coverage of spines; some oogonia contain indeterminate contents. A. NRM S087932-01-02; B. NRM S087932-01; C. NRM S088053-01 arrow indicates attachment point to hyphae; D. S087932-01-02; E. S087932-01-02; F. NRM S087932-01-02 (holotype specimen) arrow indicates attached subtending hypha; G. NRM S087800-01; H. NRM S087932-01-02; I. NRM S087932-01-02 enlargement of oogonia wall and ornamentation, arrow indicates the hollow nature of the papillae, scale = 50 µm; J. NRM S087932-01-02 arrows indicate branched crown of ornamentation, enlargement shown in image I, scale = 50 µm; K. NRM S087932-01-02 arrow indicates attached subtending hypha; L. NRM S087932-01-02 oogonium in image K in different focal plane highlighting the nature of the ornamentation covering the oogonium surface.
doi:10.1371/journal.pone.0070707.g002

diameter [17]. The Prince Charles Mountains examples appear to be the first recorded Permian representatives of this group of Peronosporomycetes and possess distinctive ancyrate-conate oogonia of an intermediate size range (38–95 μm). Schopf [60] figured what was described as; "the spiny spore with septate germinal tube, possibly fungal zygospore" (illustrated in figure J of the Schopf paper [60]), which may be a Permian peronosporomycete, though branched ornamentation is not visible on the original illustration. The apparently sparse fossil record of this group may in part be attributable to the past prevalence of the acetate peel technique in studying permineralised plant assemblages. Acetate peels have been shown to be inferior to thin sections in revealing the microorganisms preserved in silicified deposits [53]. Thin sections provide a greater depth of section (30–50 μm) and reveal greater clarity of characters in a range of fungi, fungi-like organisms and diminutive arthropods with thin-walled tissues than is obtainable with mounted acetate peels of ca 10 μm thickness [53,61].

Ovoid structures possibly also representing oogonia have been reported attached to specimens of *Galtierella biscalithecae* from the Upper Pennsylvanian Grand-Croix Cherts from France [3]. These are also interpreted to be terminally inserted on the hyphae and but are typically oblong and longer than the oogonia described herein. Possible oogonia have also been reported from the Jurassic San Augustín hot spring deposit from Patagonia, Argentina [25] although they lack the forked spines seen in the Prince Charles Mountains examples.

The oogonia of extant Peronosporomycetes, such as *Phytophthora* [62], form terminally and have a range of morphologies from obpyriform to ellipsoid to ovoid [63]. The two morphologies of peronosporomycetes evident in the Toploje Member peat are both covered in ancyrate conate/spinose ornamentation. Fossil examples of this style of ornamentation are numerous [5,17,23,58]. However, the order/family-level affinity of these bodies remains poorly resolved. Although extant Peronosporomycetes oogonia bear ornamentation, none appears to have complex branched crowns on the sculptural elements, a character which is used to distinguish the new order. Some modern *Pythium* oogonia have robust spinose ornamentation [64,65], especially those of *P. oligandrum* [66], [67], and *P. prolatum* Hendrix and Campbell [68], but the extant forms typically lack forked apices on the spines. Other extant forms that exhibit broadly similar robust spinose/conate ornamentation include *Aphanomyces stellatus* [69], [70,71]. Among extant forms, *Pythium prolatum* demonstrates particular similarities with those forms from the Toploje Member peat since it possesses the most heavily ornamented oogonia and has a similar truncate extension adjoining the parental hyphae [68]. It seems likely that the various fossil forms represented by oogonia with truncate or branched papillae (including *Combresomyces*, *Frankbaronia* and perhaps *Hassiella*, *Galtierella* and some members of *Zygosporites*) represent a widely distributed extinct late Palaeozoic to early Mesozoic clade within the Peronosporomycetes and are here placed in the new order Combresomycetales. This group is distinguished by its apically branched conate to spinose ornamentation on the surface of the oogonia, but known morphological characters are as yet insufficient to infer close a phylogenetic relationship with any one of the extant orders of Peronosporomycetes.

Despite the poor fossil record of this extremely diverse class (attribution of several fossil examples being equivocal due to the difficulty in identifying diagnostic characters), the documentation of the group's occurrence in palaeocommunities is significant since they are important shapers of modern ecosystems. Ancient Peronosporomycetes, like their modern counterparts, probably played a significant role in recycling organic matter, via saprotrophy, and potentially in parasitizing plants and animals in the Permian high-latitude mire ecosystems. In terms of life habit and ecology, both *Combresomyces caespitosus* sp. nov. and *Combresomyces rarus* sp. nov. appear likely to have occupied a saprotrophic lifestyle. This is based on the association of the oogonia of both species with a broad range of adjacent plant tissues. Neither *C. caespitosus* nor *C. rarus* are consistently associated with any one plant type in the permineralised peats, which suggests they did not have a well-developed parasitic relationship with a particular host species.

The recognition of robustly ancyrate-conate Peronosporomycetes oogonia in Middle Permian silicified peats helps bridge the large (latest Carboniferous to Middle Triassic) gap in the group's fossil record noted by Schwendemann et al. [17] and attests to the broad climatic tolerance of this group, spanning the palaeotropics to cool palaeotemperate belt; fossil Peronosporomycetes oogonia are known from palaeolatitudes as divergent as the palaeotropics of the Viséan of central France [57,72] to the high palaeolatitudes (ca 65°–70° S) of the Prince Charles Mountains (this study) based on broadly accepted continental reconstructions [52,73]. Their broad stratigraphic and palaeoclimatic distribution also suggests that the group as a whole was not tied to particular plant hosts; the host floras from the Carboniferous to Triassic variably being dominated by arborescent lycophytes, glossopterids, corystosperms and conifers [5,17,57]. This versatility with respect to plant hosts and their distribution through the late Palaeozoic and into the Triassic indicates that Combresomycetales were generalist or opportunistic organisms that were little affected by the end-Permian biotic crisis [74] and the disappearance of peat-forming ecosystems for over 5 million years during the Early Triassic [75,76].

Conclusions

Oogonia with multi-branched sculptural elements do not appear to be represented amongst modern Peronosporomycetes based on our survey of the literature, although published details of oogonia and oospore morphology are admittedly sparse. Nevertheless, the obvious similarities in oogonium shape, size, process morphology and hyphal attachment between the Permian Antarctic forms reported here and fossils documented from the Devonian to Triassic elsewhere in the world suggest that these forms represent an extinct but once widespread Palaeozoic to early Mesozoic branch of the peronosporomycete clade. A new order and family of fossil Peronosporomycetes, Combresomycetales B. J. Slater, S. McLoughlin et J. Hilton and Combresomycetaceae B. J. Slater, S. McLoughlin et J. Hilton, are established on this basis. Two new species of *Combresomyces* are distinguished primarily on subtle differences in oogonium size and ornamentation. These represent the first examples of this group documented from the Permian of Antarctica and add to the biodiversity and trophic levels recognised in high-latitude Permian mire ecosystems of Gondwana. The lack of a consistent association between the oogonia and any particular plant fossils in the permineralised peat or of any reaction tissue in adjacent plant remains suggests that these *Combresomyces* species were saprotrophs rather than parasites. Their complex ornamentation may have been an adaptation for aquatic dispersal or adhesion to host materials in the extensive wetlands of the Gondwanan Permian, yet this group of elaborately sculptured Peronosporomycetes as a whole were sufficiently generalist in their ecology to survive the demise of peat-forming ecosystems during the first five million years of the Triassic.

Author Contributions

Conceived and designed the experiments: BJS SM JH. Performed the experiments: BJS SM JH. Analyzed the data: BJS SM JH. Contributed reagents/materials/analysis tools: BJS SM JH. Wrote the paper: BJS SM JH.

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