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

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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.

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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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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)

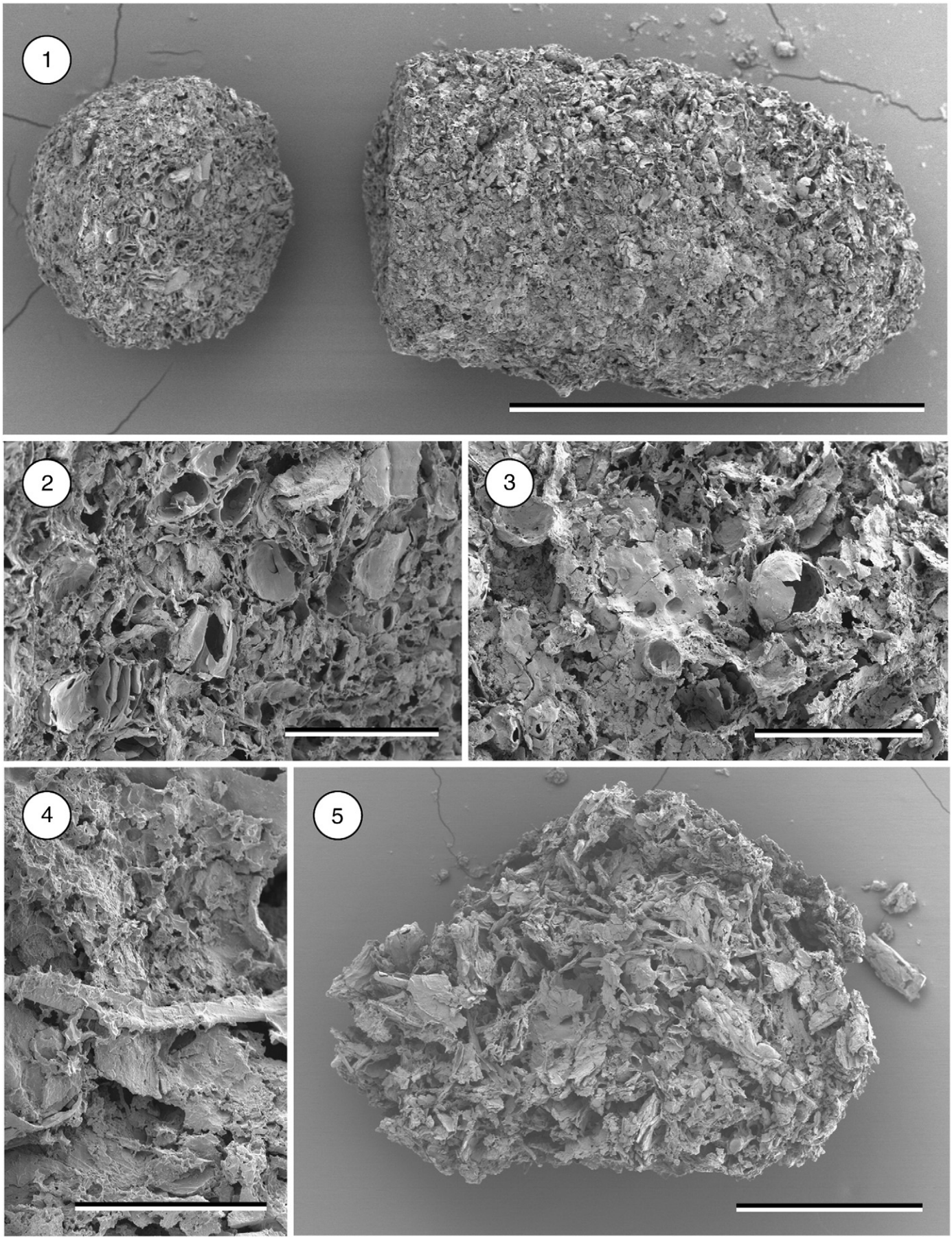


Plate I

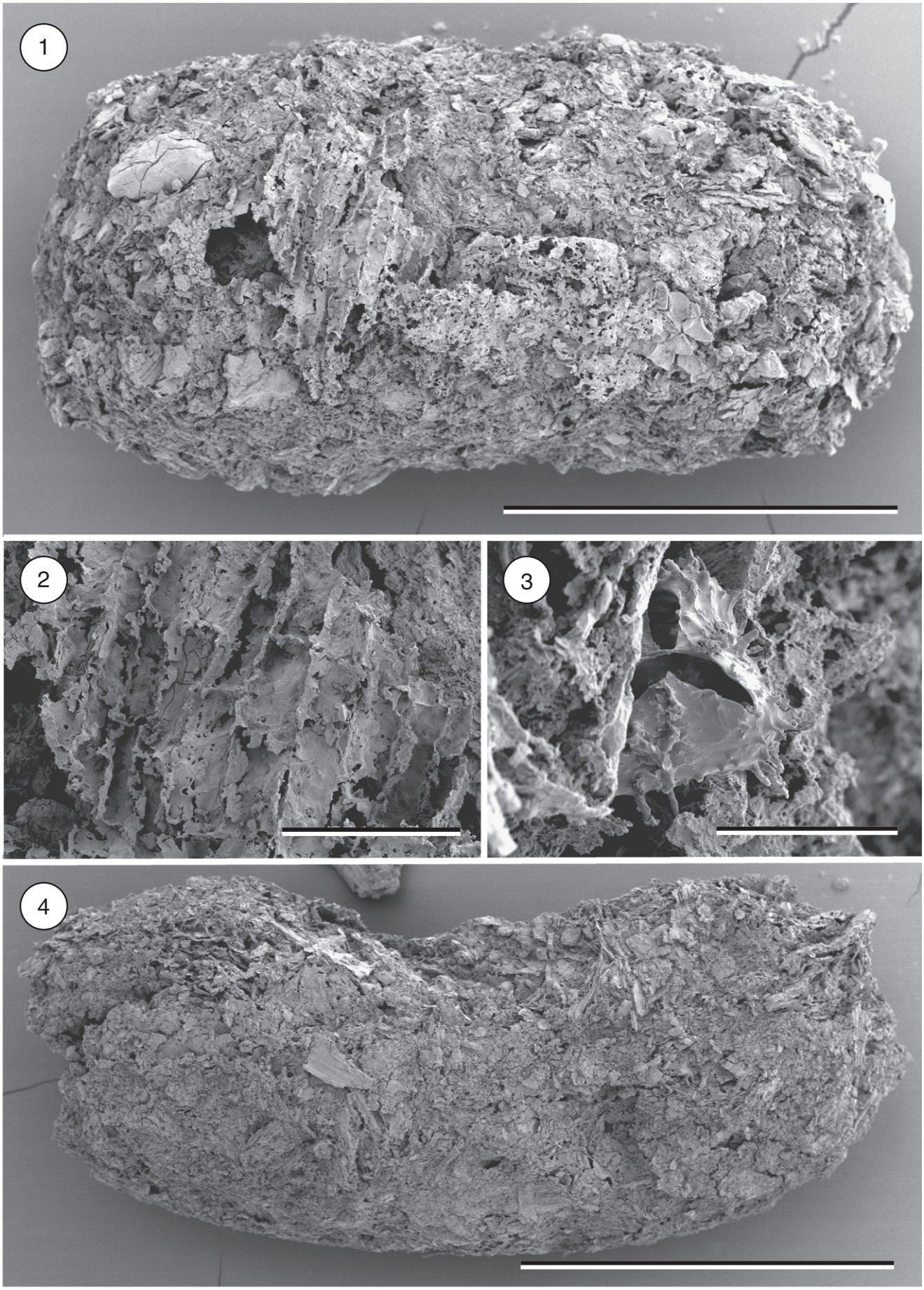


Plate II (*caption on page 112*).

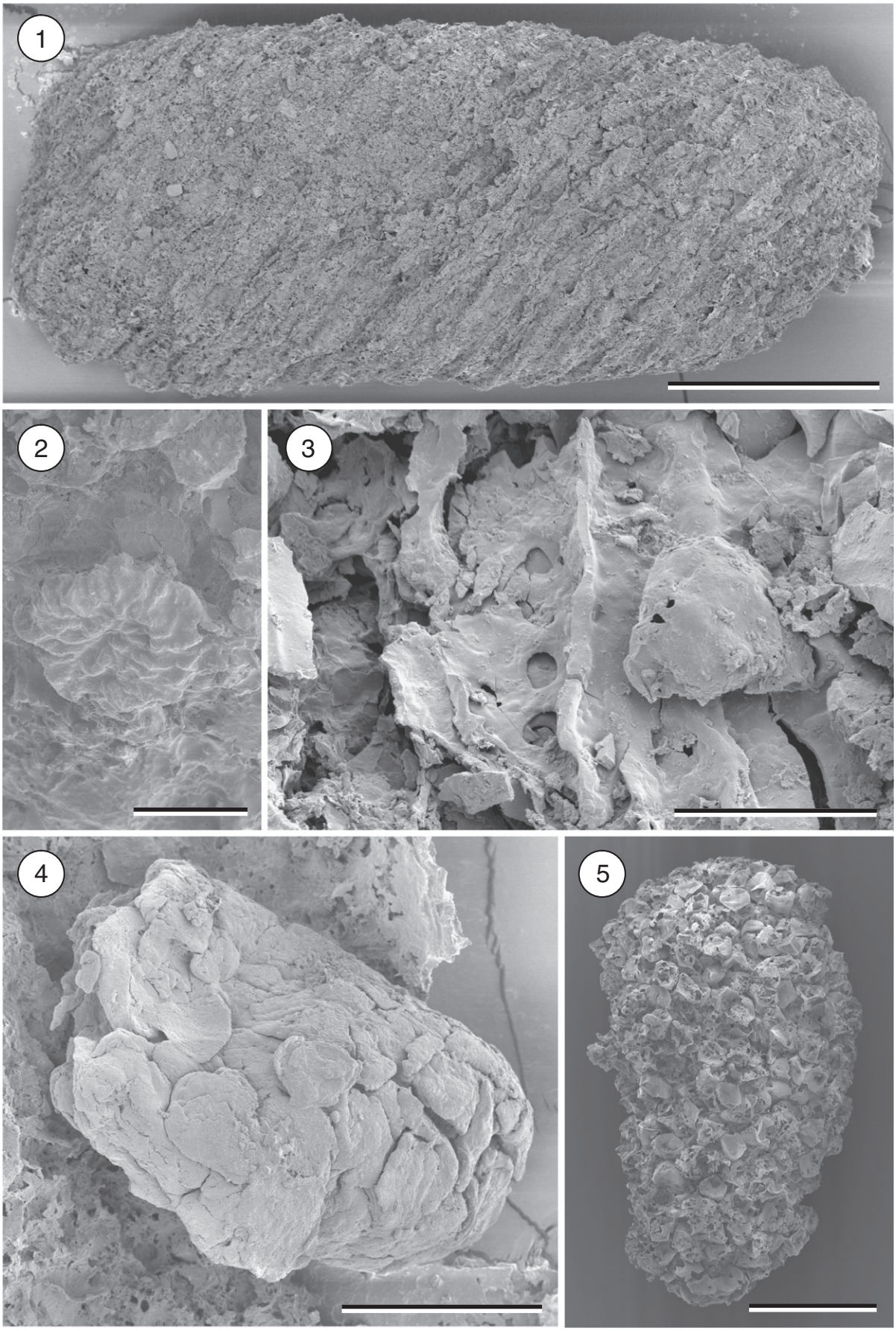


Plate III (*caption on page 112*).

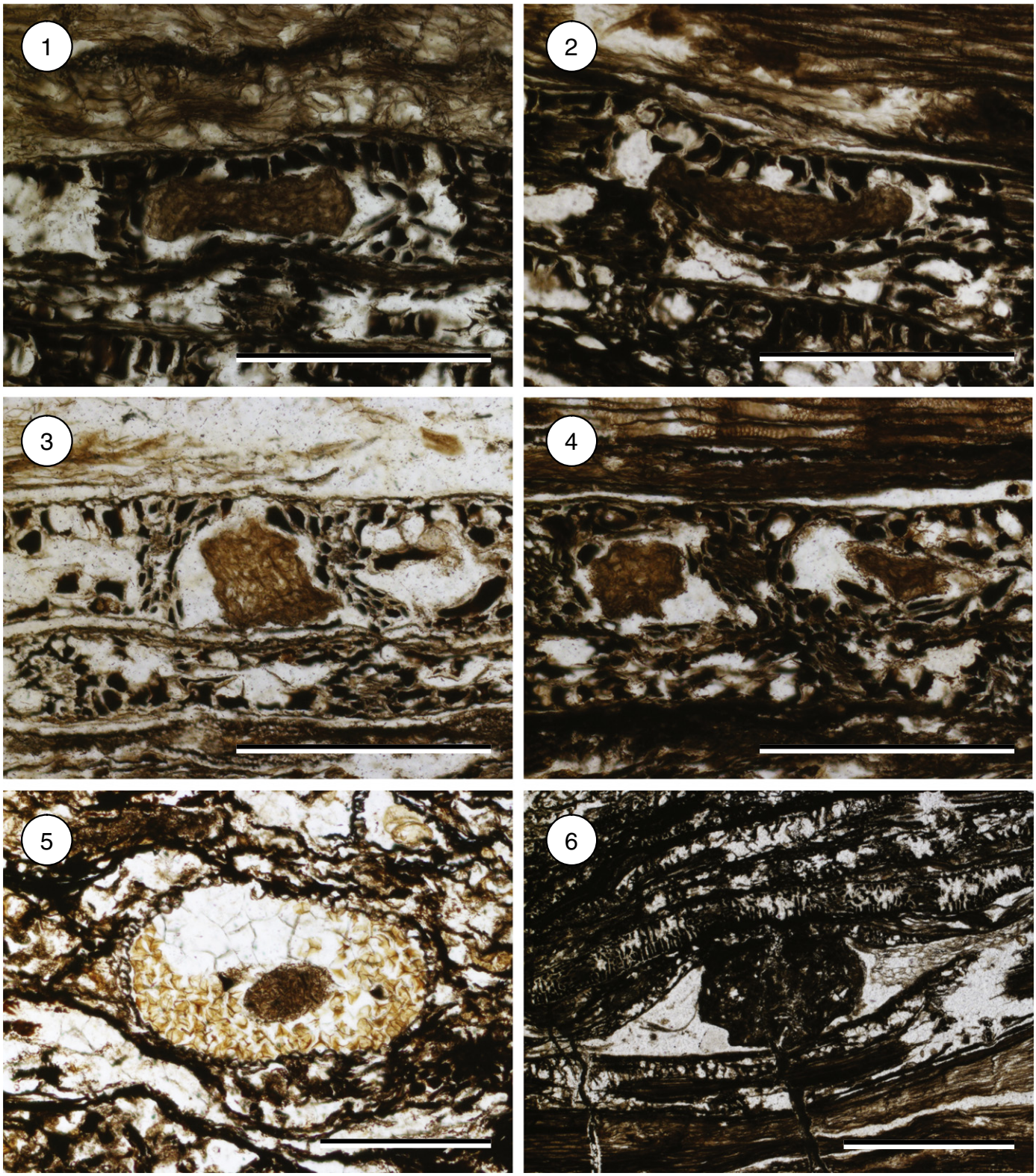


Plate 4. Coprolites preserved within *Glossopteris* leaves (1–4), within sporangia and between matted leaves. 1–4; coprolites with a fine platy texture preserved within cavities excavated between anastomosing veins of *Glossopteris* leaves, scale bars = 500 μm. 5; coprolite inside a partially excavated 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.

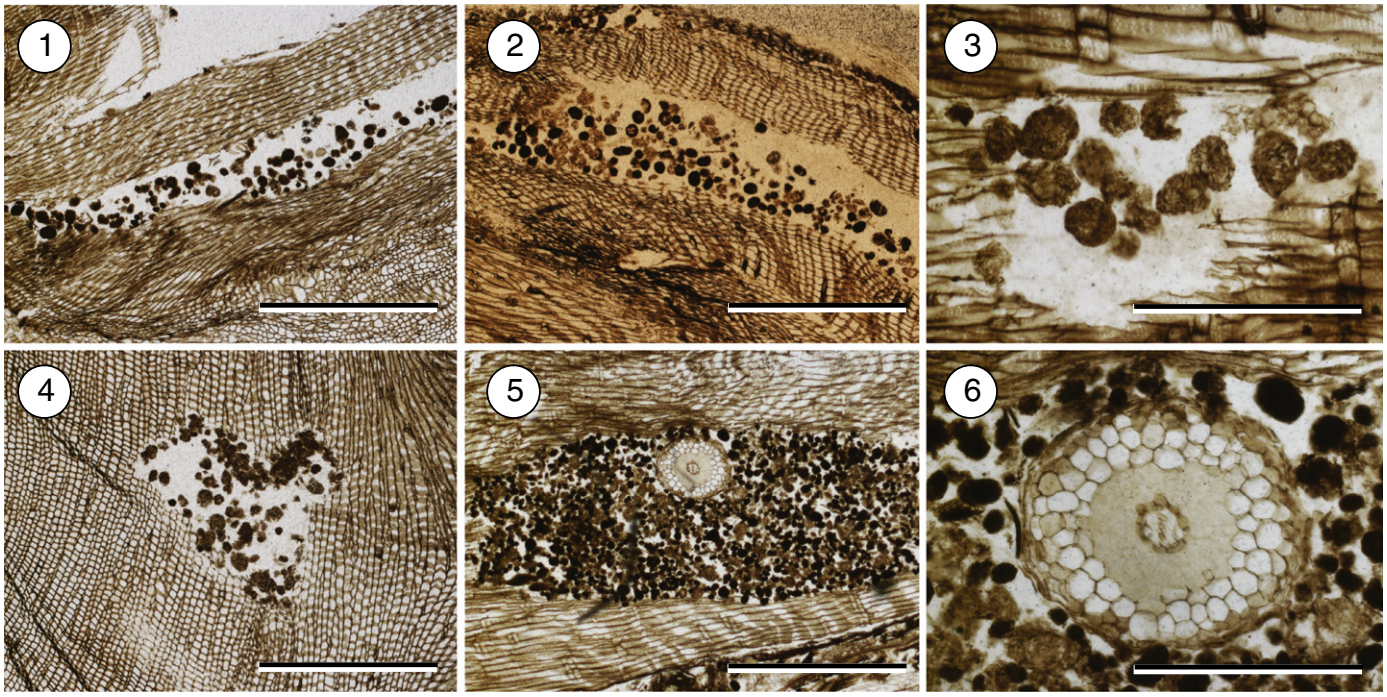


Plate 5. Coprolites preserved within secondary wood of *Vertebraria*. 1–2; small coprolites clustered within excavated galleries inside *Vertebraria* secondary xylem, scale bars = 1 mm. 3; coprolites within excavation containing internal granular fragments of xylem tissues, scale bar = 500 μm. 4; excavation 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.

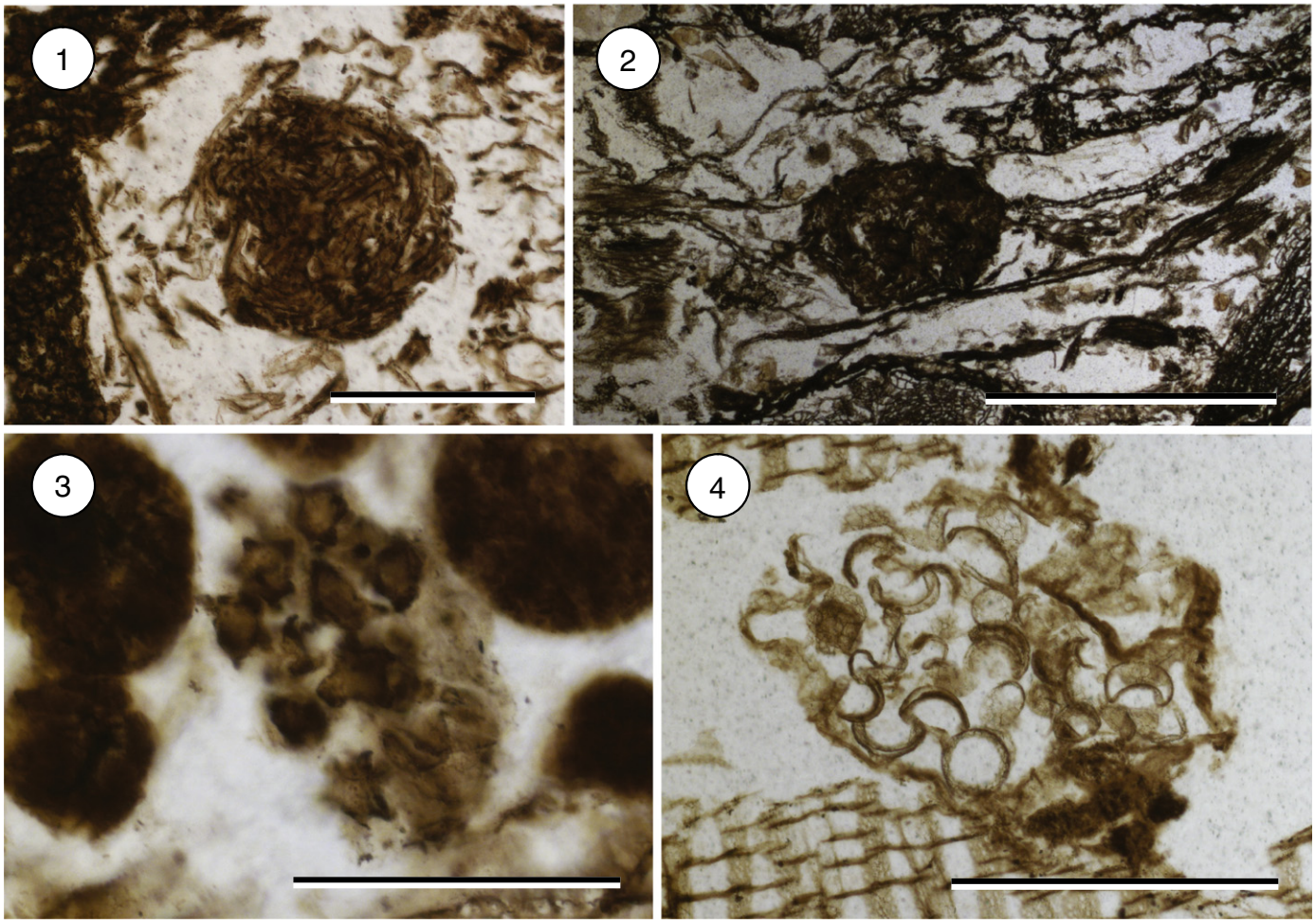


Plate 6. Platy coprolites isolated within the peat matrix (1–2) and fungi-filled coprolites (3–4). 1; coprolite composed of platy plant cell material, scale bar = 1 mm. 2; coprolite composed of platy plant material, scale bar = 1 mm. 3; small coprolite composed of crushed spinose fungal spores within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

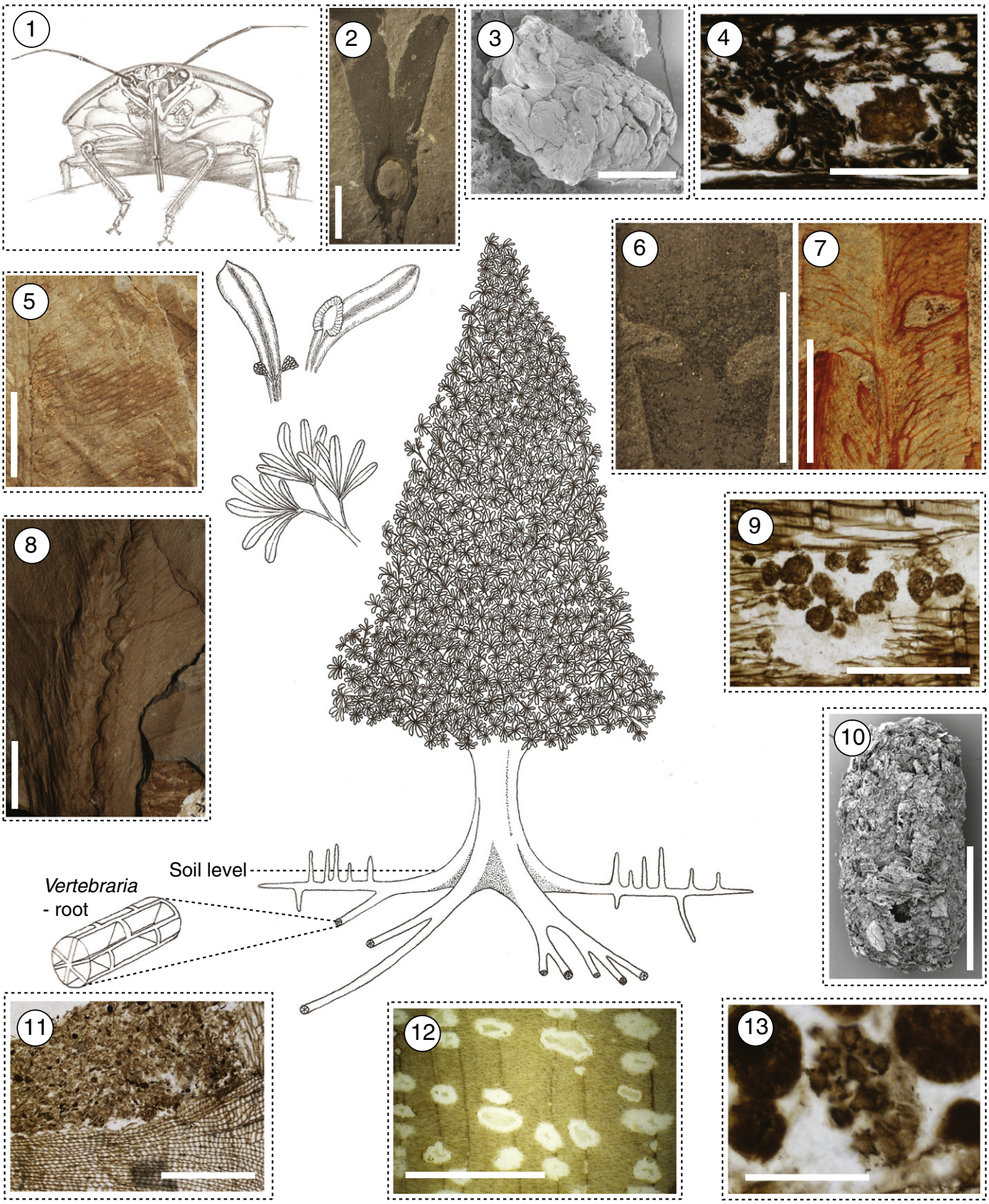
Fungal spores within the coprolites are commonly split and fragmented so were likely part of the diet of an invertebrate (true mycophagy) rather than being the fertile organs of fungi that colonised the coprolites after deposition (Plate 6; 4). However, some fungal hyphae evident in the coprolites possibly 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
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Soil level
Vertebraria
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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.

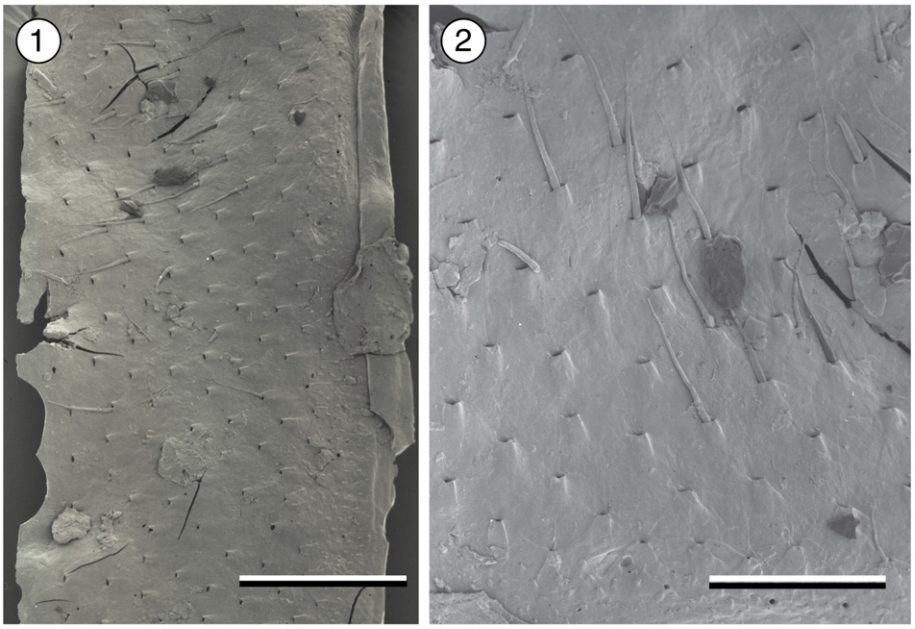

Fig. 2. A fragment of arthropod carapace recovered from the acid maceration of the silicified peat in the Prince Charles Mountains. 1; exoskeleton fragment, scale bar = 100 μm. 2; enlargement of setae, scale bar = 50 μm.

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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