A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the 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 Paleobiology, Swedish Museum of Natural History, Stockholm, Sweden

A B S T R A C T

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 moderately common herbaceous lycophytes, together with a broad array of dispersed organs of ferns and other gymnosperms. Rare arthropod–plant and fungal–plant interactions are preserved in detail, together with a plethora of fungal morphotypes, Peronosporomycetes, arthropod remains and a diverse coprolite assemblage. Comparisons to other Palaeozoic ecosystems show that the macroflora is of low diversity. The fungal and invertebrate–plant associations demonstrate that a multitude of ecological interactions were well developed by the Middle Permian in high-latitude forest mires that contributed to the dominant coal deposits of the Southern Hemisphere. Quantitative analysis of the constituents of the silicified peat and of macerals within adjacent coal seams reveals that whilst silicified peats provide an unparalleled sample of the organisms forming Permian coals, they do not necessarily reflect the volumetric proportions of constituents within the derived coal. The Toploje Member chert Lagerstätte provides a snapshot of a rapidly entombed mire climax ecosystem in the closing stages of the Palaeozoic, but prior to the onset of the protracted crisis that engulfed and overthrew these ecosystems at the close of the Permian.

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1. Introduction

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 (sites of exceptional preservation of organisms) 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 all life (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 terrestrial biotic turnover at the end of the Palaeozoic 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

and include diverse triggers and mechanisms for biotic turnover, such as the massive outpourings of flood basalts, which now form the Siberian Traps, climatic warming, increased aridity, loss of coastal habitats, ocean anoxia or a combination of these mechanisms (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; Benton and Newell, 2014; Retallack, 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 transition (Retallack et al., 2006; Yin et al., 2007; Bond et al., 2010; de la Horra et al., 2012; Retallack, 2013). 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* mire 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. 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; Osório et al., 2006; Kalkreuth et al., 2010; 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 due to differential compaction of plant parts 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. The Skaar Ridge and Collinson Ridge silicified peats of the Transantarctic Mountains appear to be derived from small lenses or possibly fluvially rafted mats of peat associated with volcaniclastic sediments (Taylor et al., 1989; McManus et al., 2002), in contrast to the laterally extensive Toploje Member chert representing a large autochthonous mire community preserved in a succession lacking volcanogenic sediments.

We employ a battery of techniques to elucidate the biotic constituents of a typical peat-forming mire community in Gondwanan high latitudes during the Middle Permian. Further, we assess the taphonomy, quantitative representation of components, and evidence of biotic and other physical interactions to elucidate the depositional setting and palaeoecology of the coal-forming mires of the Lambert Graben. We also survey the fossil record of plant–arthropod interactions across Gondwana to assess the diversity and importance of disparate herbivory strategies in high-latitude glossopterid-dominated communities prior to the end-Permian biotic crisis. Finally, we contrast these findings with the results of a maceral analysis of associated coals to assess whether the petrography of the coals provides a meaningful representation of the original peat community structure.

2. Material and methods

Samples of a range of sizes were collected from multiple localities along a low ridgeline exposing the Toploje Member chert (Fig. 1). 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 s 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 at the Swedish Museum of Natural History (Naturhistoriska riksmuseet). Several elements of the flora 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). Illustrated material is registered in the palaeobotany collections of the Swedish Museum of Natural History, Stockholm (prefixed NRM) and Geoscience Australia (prefixed CPC).

Quantitative analysis of the silicified peat was made by point counting across 20 randomly selected thin sections at 200 μm increments for 4000 points. In addition, four thin sections made from charcoal-rich samples were selected for point counting to analyse variation in peat composition between regular and wildfire-affected microfacies within 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.

3. Geological setting and palaeogeography

Antarctica occupied a central position within Gondwana through the late Palaeozoic and early Mesozoic (McLoughlin, 2001; Fig. 1). 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. The Lambert Graben has been interpreted to represent the southern extension of the Mahanadi Graben in India in pre-breakup palaeogeographic reconstructions of Gondwana (Fedorov et al., 1982; Stagg, 1985; Veevers, 2004; Harrowfield et al., 2005; Boger, 2011; Slater et al., 2011), although alternative alignments with the Godavari Graben have also been mooted (Holdgate et al., 2005). Throughout the Early and Middle Permian, the
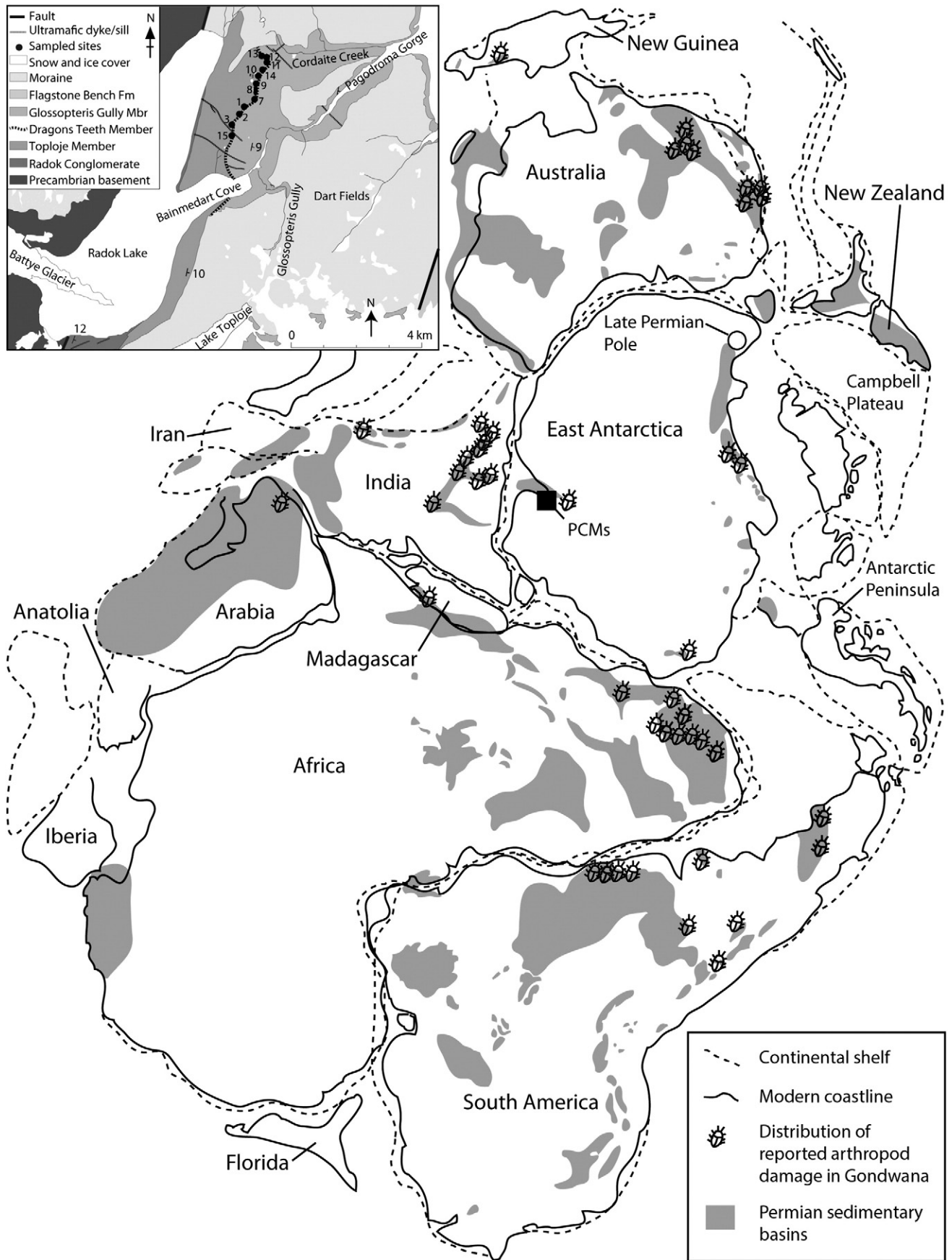
Fig. 1. Map of Gondwana for the Permian showing the distribution of sedimentary basins of that age (grey) and sites yielding evidence of plant–herbivore interactions (see Appendix 1); base map from McLoughlin (2001). Inset map shows the geology of the Radok Lake area, Prince Charles Mountains, with the sites sampled for permineralized peat at the top of the Tolpoje Member.

northern Prince Charles Mountains (Fig. 1) occupied a palaeolatitude of ~65–70°S (McLoughlin et al., 1997), similar to its modern position.

The studied chert constitutes the silicified uncompressed upper portion of a coal seam, which forms the uppermost bed of the 303 m thick Toploje Member (Fig. 2) of the lower Bainmedart Coal Measures in the northern Prince Charles Mountains, East Antarctica (McLoughlin and Drinnan, 1997a). The chert bed is locally up to 40 cm thick and is exposed over a strike length of 3 km (Fig. 1). The Bainmedart Coal

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
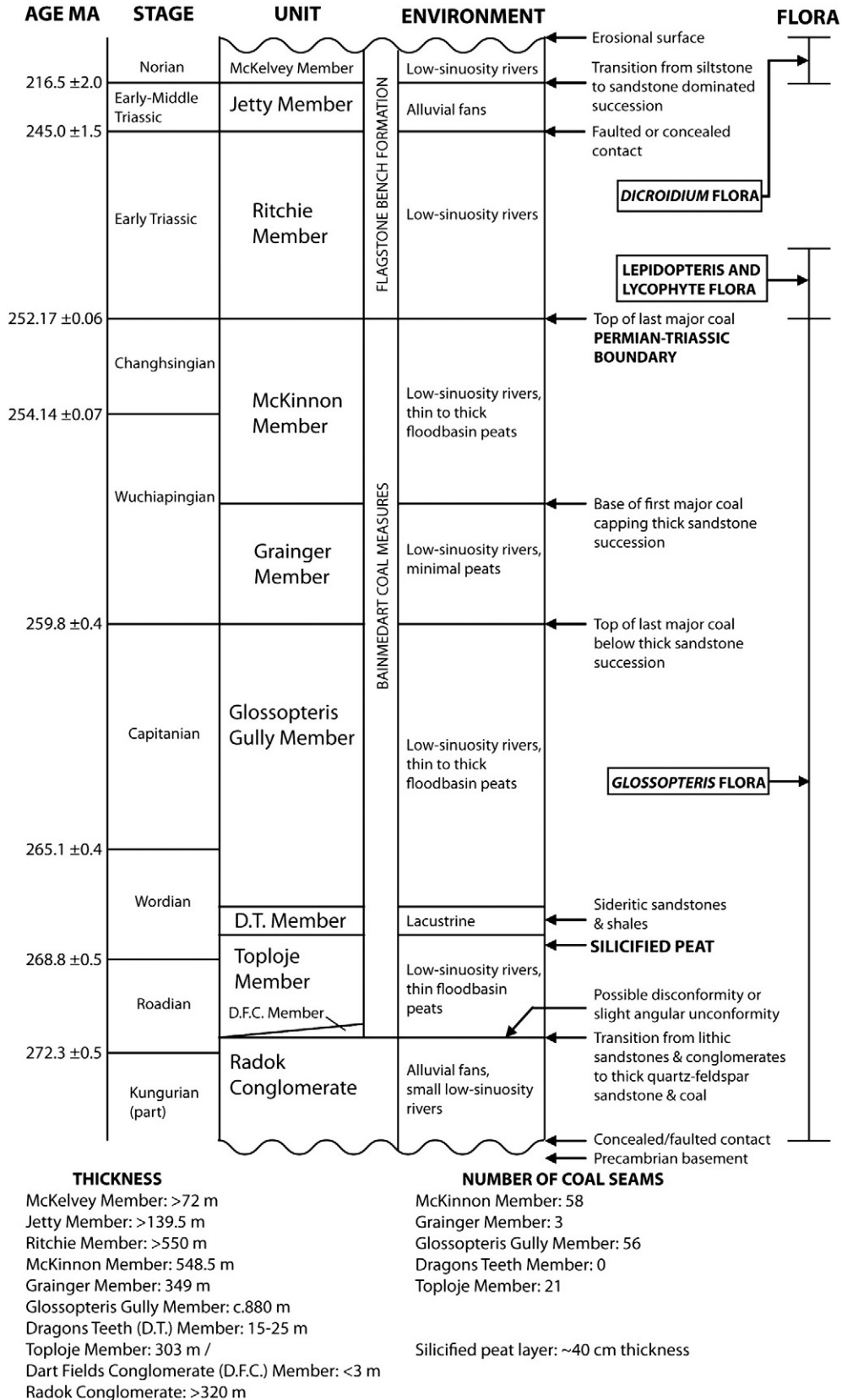
Silicified peat layer: ~40 cm thickness

Fig. 2. Stratigraphic column of the Permian and Triassic strata in the Prince Charles Mountains (Lambert Graben) showing the position of the Toploje Member chert lagerstätten.

Measures represent the middle unit of the Permian–Triassic Amery Group (see Fielding and Webb, 1996; McLoughlin and Drinnan, 1997a, for detailed stratigraphic sections of this unit). The coal measures rest disconformably or partially unconformably on the Radok Conglomerate of Kungurian to early Roadian age, and are in turn conformably overlain by the Flagstone Bench Formation of Triassic age (McLoughlin and Drinnan, 1997b). The Bainmedart Coal Measures are dominated by thick cross-bedded sandstones, siltstones and coals deposited in a cyclic pattern, which has been attributed to the action of Milankovitch-induced changes to sediment supply (Fielding and Webb, 1996).

The chert bed represents the upper part of a peat profile that was impregnated with silica prior to any significant sedimentary loading or compression, hence the entombed plant remains have avoided coalification (Slater et al., 2011). Palynological correlation to the Australian *Didecitriletes ericianus* Zone gives a Roadian–Wordian age for the Toploje Member chert (Lindström and McLoughlin, 2007). Flooding with mineral-rich lake waters and then permineralisation terminated the peat-forming process. The conformably overlying Dragons Teeth Member consists of a series of sideritic shales and minor sandstones deposited in a lacustrine setting (Fielding and Webb, 1996).

Data and findings of this study of the Toploje Member chert will now be presented and discussed.

4. Biota

4.1. 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 (McLoughlin and Drinnan, 1996; Holdgate et al., 2005). 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 (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 1 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 and Taylor, 2011; 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., 2010). 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 based on dispersed pollen floras 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).

Analysis of the relative abundance of the various organisms and their constituent organs/tissues contributing to the peat was carried out by Holdgate et al. (2005) and again in this study using a different set of thin sections of the Toploje Member chert (Fig. 3A). 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 profiles that will require further investigation to delineate their composition and genesis. Our preliminary assessment of compositional variation in the Toploje Member peats via a series of point counts on thin sections of specimens rich in charcoal (Fig. 3B) reveals 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.

4.2. 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 analysed 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: see Holdgate et al., 2005, fig. 3). Trace and major element results, vitrinite reflectance values and some petrological data from these samples were presented by Holdgate et al. (2005). Petrological and coal maturity data were published for a few additional samples from the lower part of the Bainmedart Coal Measures by Bennett and Taylor (1972). Here we elaborate on the organic petrology of the coal and compare the compositions of the coals and silicified peat. The ~40 cm of silicified peat is chosen for comparison with the coals since it represents a snapshot of the peat before compaction, diagenesis and coalification.

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 (Fig. 4). 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 (oxidised 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 (Fig. 4). 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.

Table 1
Summary of the biota preserved in the Toploje Member silicified peat.

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 (~1 mm) 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

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 (Fig. 4). 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
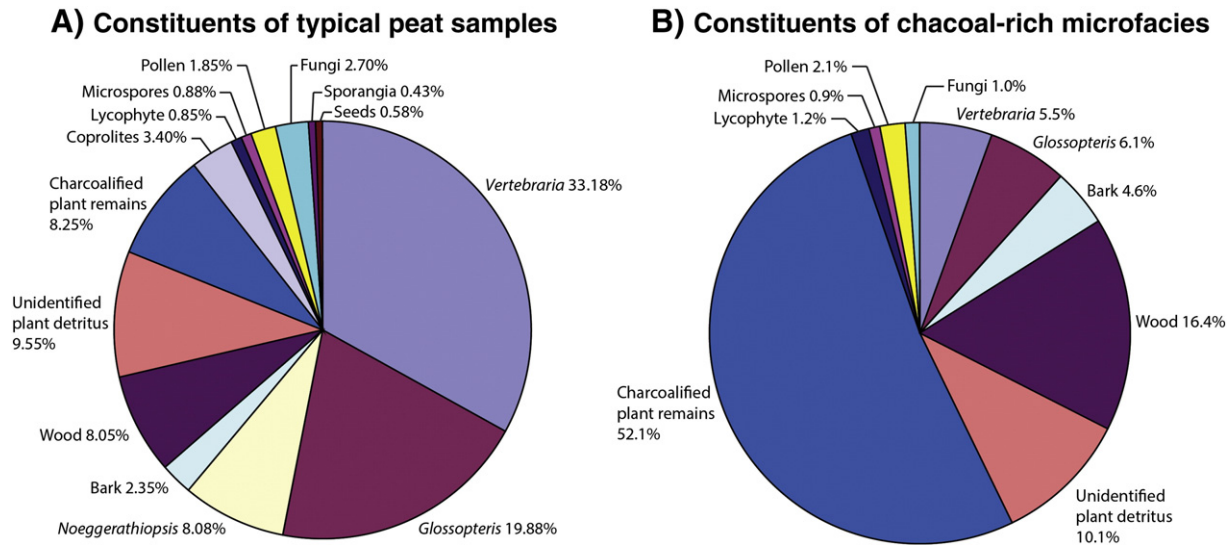
A) Constituents of typical peat samples

Pollen 1.85%
Microspores 0.88%
Lycophyte 0.85%
Coprolites 3.40%
Fungi 2.70%
Sporangia 0.43%
Seeds 0.58%
Charcoalified plant remains 8.25%
Vertebraria 33.18%
Unidentified plant detritus 9.55%
Wood 8.05%
Bark 2.35%
Noeggerathiopsis 8.08%
Glossopteris 19.88%

B) Constituents of chacoal-rich microfacies

Pollen 2.1%
Microspores 0.9%
Lycophyte 1.2%
Fungi 1.0%
Vertebraria 5.5%
Glossopteris 6.1%
Bark 4.6%
Wood 16.4%
Charcoalified plant remains 52.1%
Unidentified plant detritus 10.1%

Fig. 3. 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.

with a corresponding decline in vitrinite (Fig. 4). 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.

5. Palaeoecology

5.1. 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). These stumps and stems attest to the presence of abundant arborescent gymnosperms. Two stem wood morphospecies, *Australoxylon bainii* and *Australoxylon mondii*, were recognised by Weaver et al. (1997) and clearly correspond to two similar gymnosperms; the most likely affiliations being with glossopterids or cordaitaleans based on the co-preserved leaf genera (*Glossopteris* and *Noeggerathiopsis*). *Australoxylon mondii* stem wood cannot be distinguished anatomically from *Vertebraria* (glossopterid) root wood, apart from the absence of
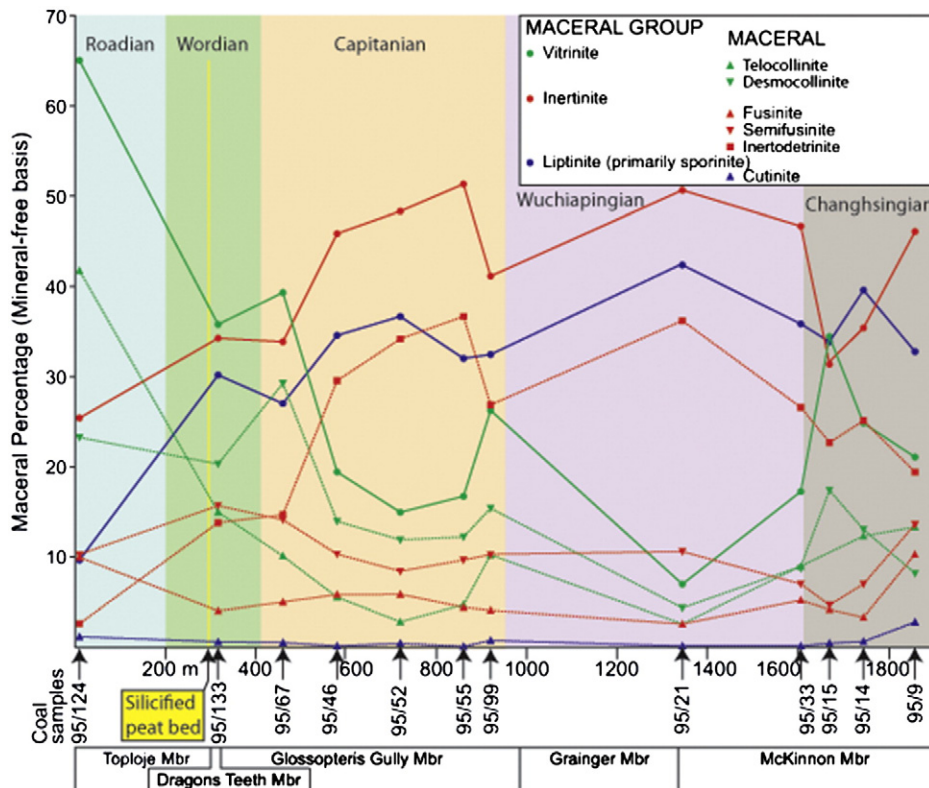

Fig. 4. Plot of the variation in percentages of major macerals in coals from the Bainmedart Coal Measures, Lambert Graben, Antarctica. Detailed stratigraphic positions of coal samples are given by Holdgate et al. (2005).
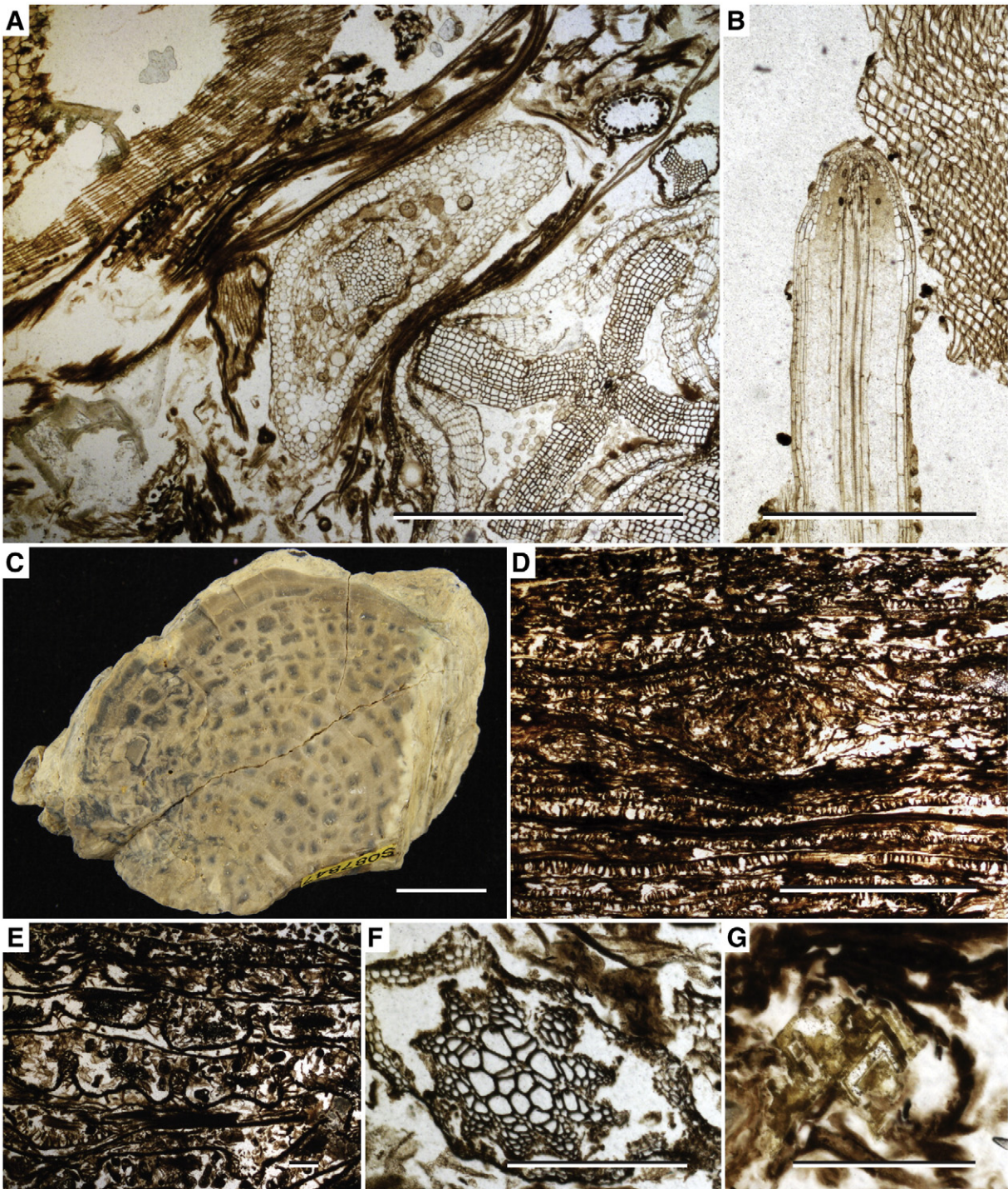
Fig. 5. Range of biota found in thin sections of the Toploje Member silicified peat. A. NRM S087800, *Vertebraria* solid-stele and polyarch roots colonised by fungal spores and hyphae in the peat matrix, scale = 1 mm. B. NRM S088061, young *Vertebraria* root tip in longitudinal section, scale = 1 mm. 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), plate 65, figure 8] 'type B' coprolites from Pennsylvanian coal balls, 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.

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 (Fig. 5A). The polyarch and solid cylinder roots may correspond to two distinct plant species or may be functionally different roots belonging to the same parent glossopterid plant (Neish et al.,

1993). A broad range of dispersed bisaccate, monosaccate, monosulcate and polyplicate pollen within the peat denotes an additional range of shrub- to tree-sized gymnosperms 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 (Slater et al., 2011). These appear to have been centimetre-scale *Paurodendron*-like heterosporous lycophytes that grew on the consistently moist peat surface (Fig. 5F). Roots of these plants occur sporadically within the leaf debris microfacies of 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 fern vegetative remains 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 common feature of most modern moist forest communities (Bartels and Chen, 2012).

Adaptations for the high-palaeolatitude environment 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 (Retallack et al., 1995; Krull, 1999; Retallack, 1999; Holdgate et al., 2005; McLoughlin, 2011b). Such mats of apparently monospecific glossopterid leaves are common features of the Toploje Member chert (Fig. 5D). *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), 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 (Figs. 5A, B, 6B, 7C–E) that possibly functioned to aid respiration in the anoxic or dysoxic 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 poorly cohesive waterlogged soils by intermeshing with the roots of neighbouring trees, as occurs in extant plants that inhabit boggy soils, e.g. 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* (Figs. 6I, 7H, 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 *S. hystrix* can be seen to interlock with the complex ornamentation of the megaspore in X-ray synchrotron tomographic images (Slater et al., 2011). Lycopsids were typical of wetland habitats or riparian areas from the Devonian to present (Falcon-Lang, 2003).

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.

5.2. 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 Toploje Member silicified peat (Figs. 5A, C, 6D–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 nonseptate hyphae, a range of fungal spores, saprotrophic chytrid fungi, fungal sclerotia, and possible mycorrhizal associations (Figs. 5A, 6D, E, F). Regularly (seasonally) distributed pocket rot (Weaver et al., 1997) occurs within the *Australoxylon* wood (Fig. 5C). 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).

5.3. 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 undertaken (McLoughlin et al., 2011; Slater et al., 2012) and one of only a small number of assemblages across Gondwana for which multiple forms of herbivory on Permian plants has been documented (Fig. 1; Appendix 1). The majority of past records are examples of folivory traces on the margins of *Glossopteris* leaves but a few records reveal attack on other parts of the *Glossopteris* plant and on other gymnosperms and pteridophytes in the flora (Appendix 1). Most of these plant–animal interactions have been documented from compression-impression floras (Appendix 1). 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

Fig. 6. Range of biota found in thin sections and bulk-macerations of the Toploje Member silicified peat. A. NRM S087932, Small seed, scale=500μm. B. NRM S089550, phytodebris within a schizogenous cavity of a *Vertebraria* root, scale=500μm. C. NRM S088040, charcoalified wood and root fragments surrounded by mite coprolites, scale=1mm. D. NRM S088051-01, small smooth fungal spores, scale=500μm. E. NRM S087932-01-02, mass of fungal reproductive bodies and hyphae set amongst phytodebris, scale=500μm. F; CPC34952, septate fungal hyphae penetrating *Vertebraria* root cells, scale=100μm. G. NRM S089630, SEM image of arthropod cuticle with hollow setae, scale=50μm. H. NRM S089629, SEM image of an unidentified but distinctive leaf cuticle bearing prominent marginal trichomes, scale=100μm. I. NRM S089540, SEM image of megaspore *Singhisporites hystrix* — the most common megaspore found in the peat, scale=100μm.

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, 2011b), and the Upper Triassic permineralised peat 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*)
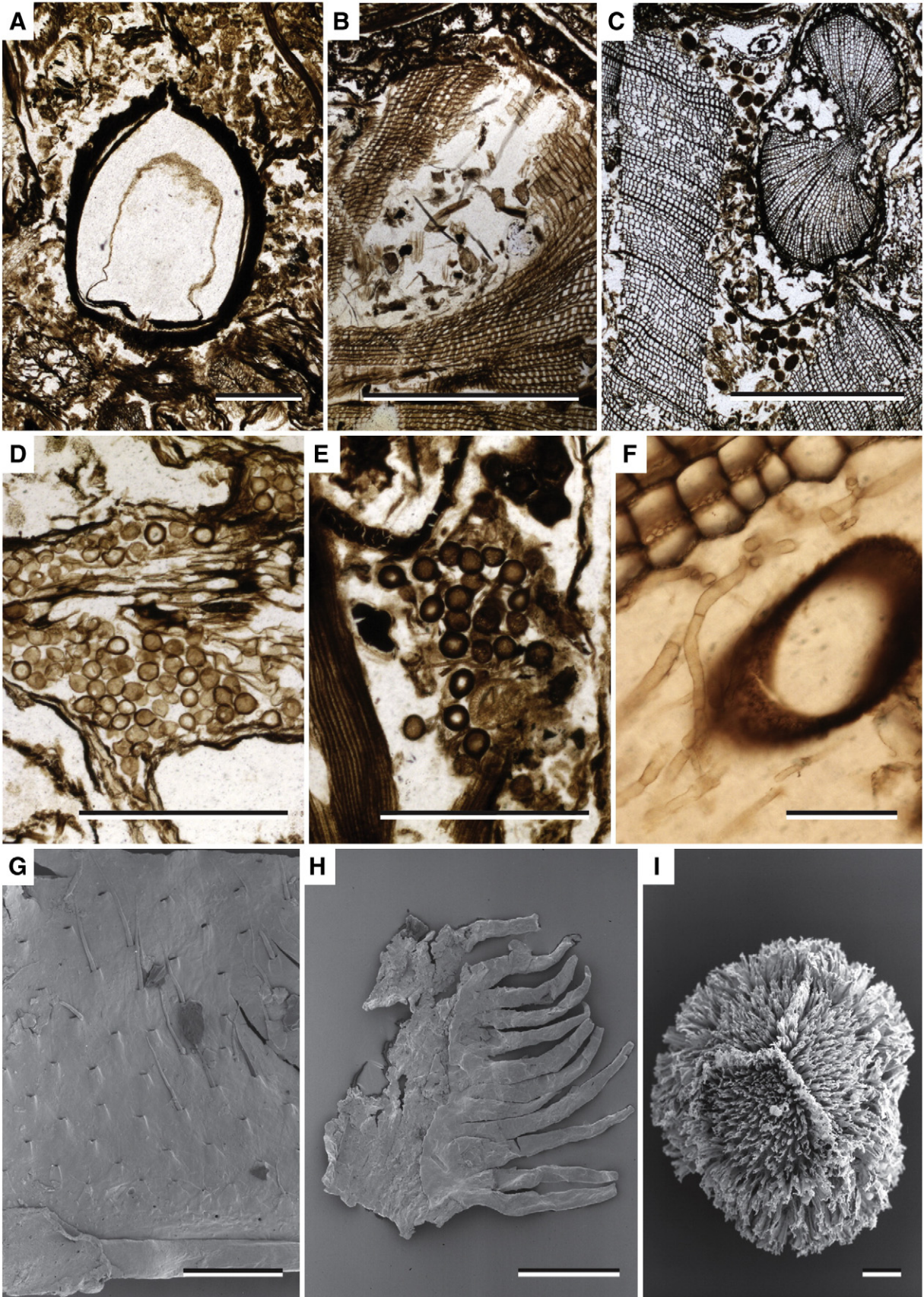
of the arborescent Antarctic glossopterid whole-plant, integrated with records of feeding traces from other assemblages (see Appendix 1 and references therein), illustrates that all major organs of the glossopterid plant were attacked by a community of invertebrates (Slater et al., 2012). Arthropod coprolites 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 (Fig. 6C). 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 within the soil via 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 terrestrial invertebrate biota (Anderson et al., 1999; Labandeira, 2005; 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 cuticles 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 recognisable 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) that attest to the presence of vermiform invertebrates. Permian–Triassic strata elsewhere in Antarctica host a variety of non-marine arthropod ichnogenera giving clues to the stream and soil entomofauna; e.g., 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 made conditions unfavourable for large populations of herbivores without special physiological adaptations or the capacity to migrate long distances (Collinson and Hammer, 2007).

5.4. Energy pathways

Based on the composition of, and interactions between, the fossil biota, we reconstruct the energy pathways in this Middle Permian mire ecosystem (Fig. 8). In the absence of tetrapods, we interpret the high-latitude mire community 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 tree-sized glossopterid gymnosperms together with a significant proportion of Noeggerathiopsis (Cordaitales) of similar stature. Less abundant understorey elements of the flora included ferns and herbaceous lycophytes (Fig. 8). Detritivores were dominantly oribatid mites, but other larger forms of generalist- and specialist-feeding arthropods are evidenced by the diverse range of 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 consistently saturated substrates (either high rainfall or groundwater supply) and regular fire events as evidenced by significant quantities of charcoal commonly occurring in distinct bands within the peats (Fig. 8).

6. Taphonomy

6.1. Accumulation model

The plant organs found in the peat 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 (Fig. 5E), hirsute leaf margins (Fig. 6H), stomatal guard cells (Fig. 7F), and spines on lycophyte megaspores and on the oogonia of Peronosporomycetes (McLoughlin and Drinnan, 1996; 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
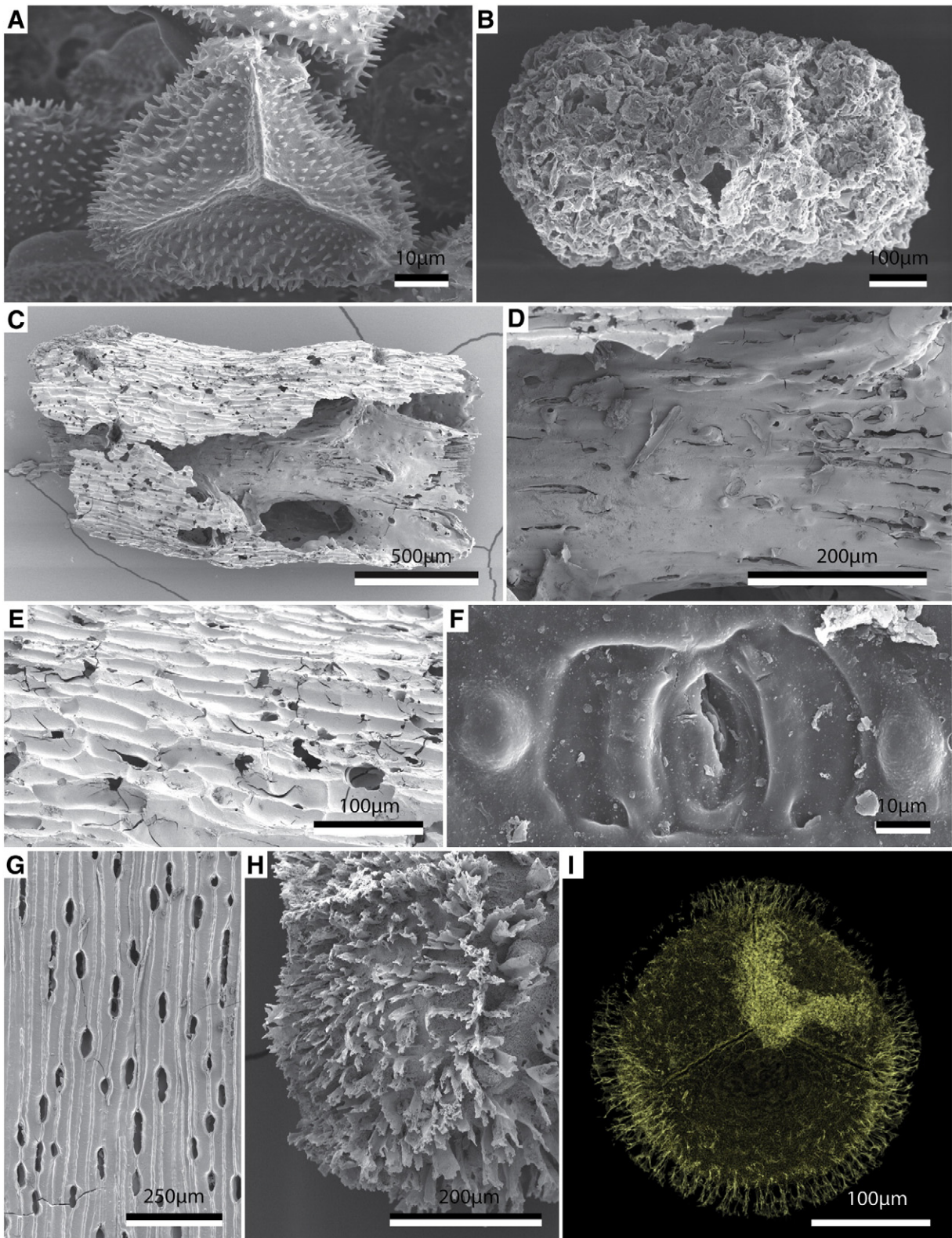
Fig. 7. Scanning electron microscopy images of a range of biota recovered from bulk macerated samples of the Toploje Member silicified peat. A; NRM S089555, fern spores attributable to *Didecitriletes ericianus* within a sporangium. B; NRM S089603, arthropod coprolite containing mixed plant vegetative 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.

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
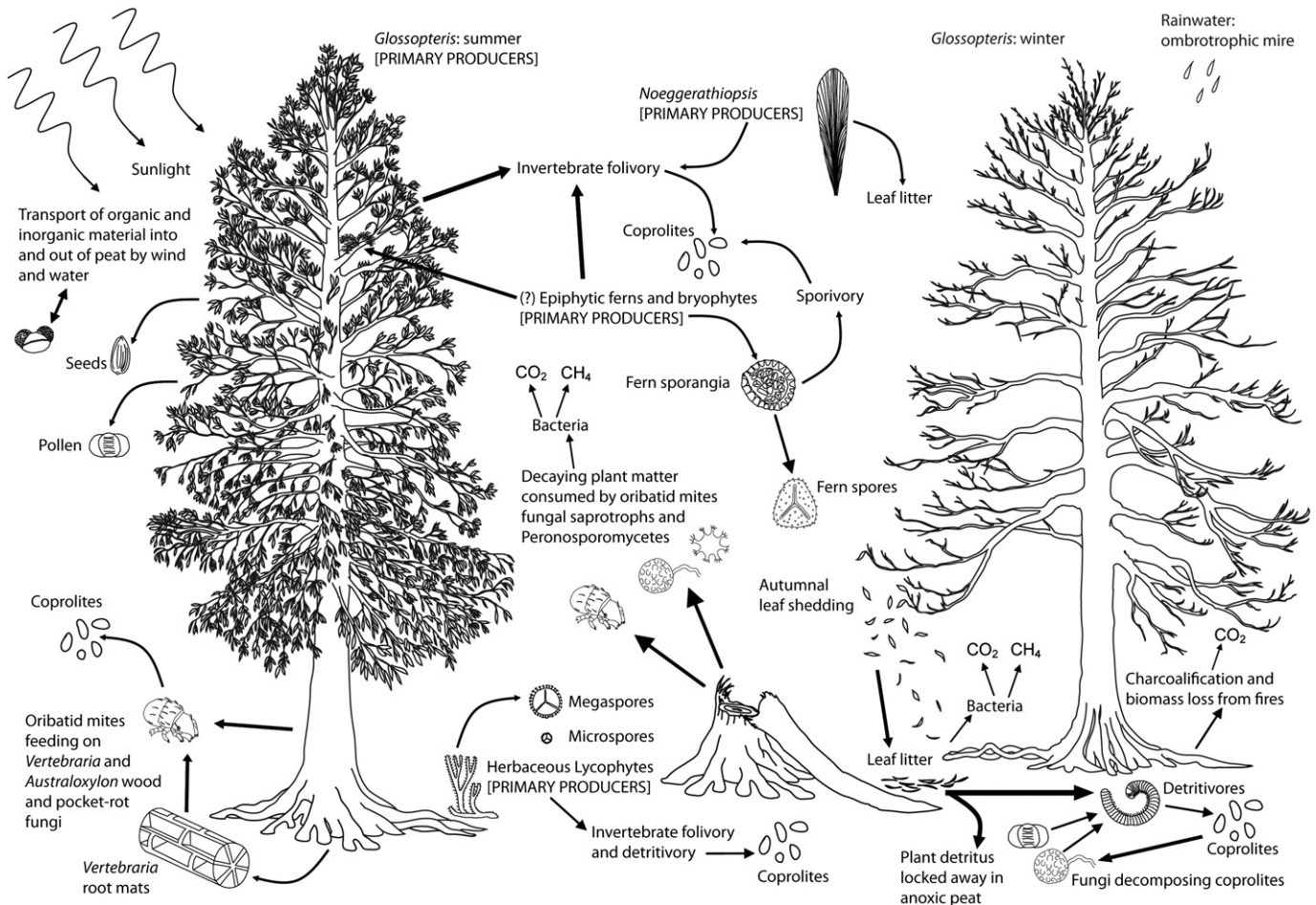
Fig. 8. Schematic representation of energy pathways and nutrient cycling in the Toploje Member chert palaeoecosystem.

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 even 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; Slater et al., 2012).

6.2. 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 (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 (Fig. 5G). 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 these chalcedony/moganite 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 volcanogenic sediments are preserved in the Bainmedart Coal Measures, in contrast to silicified peat occurrences in other Permian strata of eastern Australia and the Transantarctic Mountains (Gould and Delevoryas, 1977; Taylor et al., 1989; McLoughlin, 1992; Pigg and McLoughlin, 1997). Further, no evidence of strong lateral or vertical textural or vegetational gradients within the silicified ecosystem is evident in contrast to typical sinter deposits (Trewin, 1994, 1996; Walter et al., 1998; Trewin et al., 2003; Channing and Edwards, 2004; 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
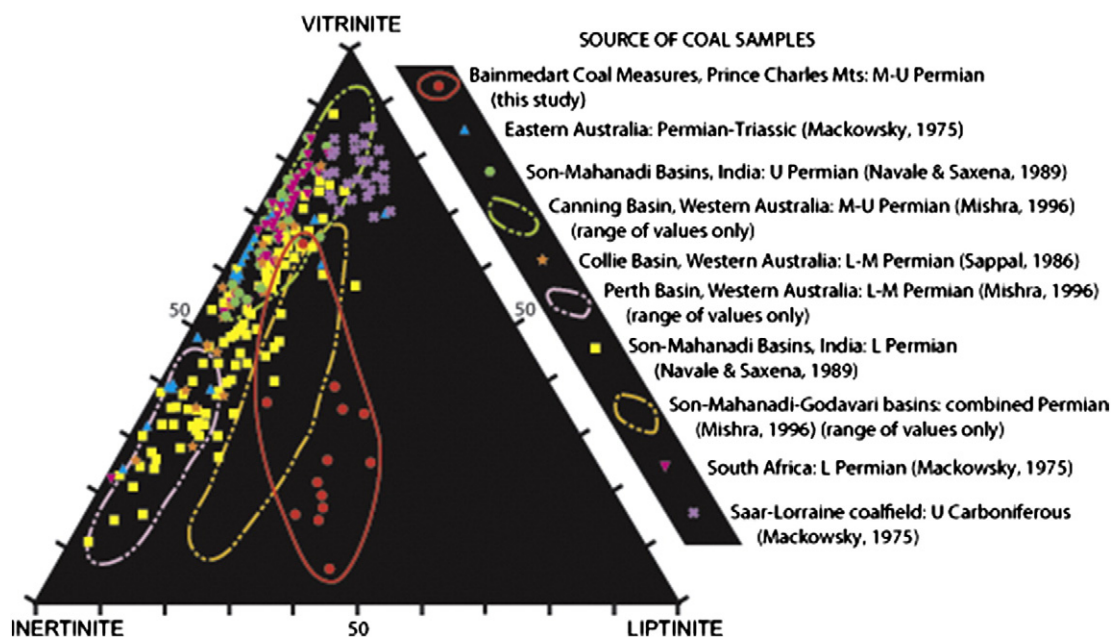
Fig. 9. Ternary diagram showing the range of variation in vitrinite:inertinite:liptinite ratios in coals of the Bainmedart Coal Measures, Antarctica, versus equivalent ratios in typical coals from other parts of Gondwana and from the Saar-Lorraine Coalfield of the Carboniferous Euramerican province (sources indicated on diagram).

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; Wheeler and Textoris, 1978; Wells, 1983). 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 precipitates out of solution when the pH drops sharply due to increased acidity because of the decay of plant matter in the lake (Hesse, 1989).

6.3. Wildfire

Abundant micro- and macro-charcoal is evident in some hand specimens and bulk-macerate residues of the Toploje Member chert (Fig. 3). 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. (2013) argued 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 much higher proportions in this study: Fig. 3B) means that wildfires

were a frequent feature of the Middle Permian high-latitude mire environment.

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 (Fig. 6A), *Glossopteris* leaf midribs, *Vertebraria* axes (Fig. 7C–E), lycophyte axis fragments and microphylls, coprolites (Fig. 5D) and arthropod cuticle (Fig. 6G; 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 wildfire charring. 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 (Figs. 3B, 7G) may be related to aqueous sorting of particles or accumulation of charcoal in 'fire-pockets' on the peat surface in the aftermath of burning events (Staub and Cohen, 1979).

7. Mire type

7.1. Depositional setting

Glossopterid gymnosperms have been documented from a wide range of terrestrial settings (Cúneo et al., 1993; McLoughlin, 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 (Cúneo et al., 1993; McLoughlin, 1993; Rigby, 1993; Guerra-Sommer et al., 2008). Indeed the ubiquitous occurrence of *Glossopteris* leaves in Permian continental deposits of Gondwana suggests that 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 of Gondwana 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 (Fielding and Webb, 1996; Holdgate et al., 2005).

7.2. 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 (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 (Slater et al., 2012), since such deposits are raised above the regional 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 some seams reaching 11 m thick within the Bainmedart Coal Measures (McLoughlin and Drinnan, 1997a). Alternatively, there is the possibility that some of the thicker coal seams may be the product of stacked mires containing several episodes of peat formation. Stacked mires could potentially be identified through the recognition of vertical changes in palynological content and coal petrography of individual seams (Jerrett et al., 2011).

Euramerican late Palaeozoic coals that developed under palaeotropical climates tend to contain high percentages of vitrinite macerals (Mackowsky, 1975; Fig. 9) — 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 (Moore, 1989; Teichmüller, 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 (Fig. 9). Further, the low sulphur content (0.38 to 0.81 wt.%: 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 (Tie and Esterle, 1991) and experiencing fine degradation and oxidation of plant components.

7.3. 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 (Habgood et al., 2004; Adl et al.,

2010). Our reconstruction of the *Glossopteris*-dominated forest mire within the Lambert Graben valley system (Fig. 10) features the dominance of hygrophilous arborescent glossopterid gymnosperms and subsidiary cordaitaleans. Understorey vegetation within the glossopterid forests is represented by herbaceous lycophytes and ferns (Fig. 7A). 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 maximise the collection of light for photosynthesis from low-angle solar radiation (Creber and Chaloner, 1985; McLoughlin, 2011b); thus we reconstruct the dominant trees to have a conical canopy shape (Fig. 10). 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 glossopterid communities to represent open deciduous forests and woodlands sensu many Carboniferous T[0] assemblages (fossil assemblages representing a geological instant), 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 (Fig. 10) 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 (Fig. 10) 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).

7.4. Implications for coal geology

There is a notable contrast between some of the coal petrographic results (Fig. 4) and the composition of the silicified peat obtained via point counts of transects through various permineralised blocks (Fig. 3A). In general, the peat appears to contain much lower 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 permineralized peat show comparable levels of >50% charcoal (Fig. 3B). 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 mound may not have developed to typical maturity or have been subjected to the prolonged oxidation and degradation by fungi, microbes and fires that was experienced by other raised peat (coal-

Fig. 10. 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.

forming) deposits in this formation. We consider that this hypothesis best explains the differential representation of oxidised components.

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 compaction, loss of volatiles and mobilisation of organic gels from unoxidised wood and leaf 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 Measure 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 unrecognised sporopollenin or degraded cuticle material.

Cameron et al. (1989) noted that the proportion of liptinite commonly increases upwards in domed (ombrogenous) peats together with oxidised detrital matter. As per the explanation for depleted oxidised components, 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; Fig. 9).

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 permineralization of silicified peats versus non-mineralised peats, significant losses of pore space, volatile components and mobilisation of organic gels during the peatification and coalification processes may markedly modify the volumetric proportions of some phytoclasts. 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).

8. Integrated 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 permineralized floras of the Transantarctic Mountains include the presence of herbaceous lycophytes in the Permian (Schwendemann et al., 2010; Ryberg et al., 2012b) and diverse fungal elements in both the Permian and Triassic peats (Stubblefield and Taylor, 1986; Krings et al., 2012).

Vertebraria roots were found to be the dominant component of the Toploje Member peats alongside significant quantities of matted *Glossopteris* and *Noeggerathiopsis* leaves (Fig. 3A), whilst charcoalified wood is locally dominant in particular peat microfacies (Fig. 3B). 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 Late Carboniferous wetland floras of 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, 1998, 2013; Rößler, 2000).

Beyond the Permian, Triassic silicified peat 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 (Figs. 5D, 6C, 7B) indicating a rich soil entomofauna and a range of fungal morphotypes and interactions (Figs. 5A, 6D–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., 2012).

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, 1998), the earliest Permian Chemnitz fossil forest (Rößler, 2000), and the 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 (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 at generic level 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, 1994b; Cúneo et al., 1993). The more pronounced seasonal light regime and presumably colder winters may have inhibited many (especially Euramerican) taxa from colonising 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 (Anderson and Trewin, 2003; Fayers 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), and harvestmen documented from the Rhynie Chert (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 might 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 were recovered by bulk maceration of the Toploje Member chert (Holdgate et al., 2005; Slater et al., 2012) and are also known from overlying Triassic sediments (McLoughlin et al., 1997). These fragments likely represent arthropod cuticle because the setae are hollow and 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 the exoskeletons of that group are covered in distinctive granule structures of anti-adhesive function (Nickerl et al., 2013). 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 these sediments are generally studied for their palaeobotanical content. 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; Appendix 2). 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). Records of such arthropod cuticle and other invertebrate remains have been recovered from acid maceration of various sediments, primarily coals, clays, siltstones and cherts (Appendix 2). 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 highlighted by employing a long-used palaeobotanical technique to extract animal fossils from Cambrian marine sediments (Butterfield and Harvey, 2012; Harvey et al., 2012a, 2012b) and this strategy might offer comparable results in unveiling cryptic arthropod diversity in late Palaeozoic terrestrial ecosystems.

9. Conclusions

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. 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. Diverse fossil micro-organisms and coprolites, together with feeding traces and sparse exoskeleton fragments attest to a complex biota of primary producers, arthropod herbivores and saprotrophs inhabiting the peat-forming ecosystem. 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. 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, elucidates 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.

Appendix 1. 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, 1953b (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, 1962, 1963; Melville, 1983a, 1983b (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, 1966; Stephenson and Scott, 1992; Scott et al., 1992; Labandeira, 2002, 2006(C)	late Sakmarian–late Artinskian	Vryheid Formation; Vereeniging, Karoo Basin, Gauteng, South Africa	Scalloped and continuous margin feeding on *Glossopteris*
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., 1978, 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

Appendix 1 (continued)

Study	Age	Formation and locality	Damage type
Chauhan et al., 1985 (C)	Lopingian	Raniganj Formation, Raniganj Coalfield, West Bengal, India	Margin-feeding on *Glossopteris* and *Belemnopteris* leaves; Coprolites 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 Tewari, 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; Labandeira, 2006 (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, 1990b; McLoughlin, 2011a (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 and 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, 1994a, 1994b (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	Possible embayed margin feeding on *Glossopteris*
Rohn et al., 1997 (C)	Lopingian	Teresina Formation, Prudentópolis area, Paraná Basin, Paraná, Brazil	Hole feeding in *Glossopteris*
Weaver et al., 1997; Labandeira, 2002 (AP)	Wordian	Topmost Toploje Member, Bainmedart Coal Measures, Lambert Graben, East Antarctica	Coprolites containing tracheid fragments in ? glossopterid stem wood (attributable to oribatid mites)

Appendix 1 (*continued*)

Study	Age	Formation and locality	Damage type
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-Rodrigues et al., 2004a, 2004b (C)	[1]Artinskian; [2]Late Artinskian–Kungurian or Guadalupian	[1]Rio Bonito and [2]Irati/Serra Alta Formations, Paraná 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*
Kellogg and Taylor, 2004 (AP)	Changhsingian	Buckley Formation; Skaar Ridge, central Transantarctic Mountains, Antarctica	Coprolites containing tracheid fragments within borings in ?glossopterid stem wood (attributed to oribatid mites)
Bolzon et al., 2004 (AP)	Late Artinskian–Kungurian or Guadalupian	Serra Alta Formation; Paraná Basin, Rio Grande do Sul, Brazil	Borings (or possibly fungal pocket rot) in gymnosperm wood
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 Gutiérrez, 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
Césari et al., 2012 (C)	Late Pennsylvanian–Cisuralian	San Ignacio Formation, San Juan, western Argentina	Coprolites within borings (attributed to mites) in gymnosperm (*Cuyoxylon*: possible cordaitalean) roots and stem wood
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, 2012b (C)	[1]Late Artinskian–early Kungurian, possibly Guadalupian; [2,3]Sakmarian–Artinskian; [4]early Sakmarian	[1]Irati/Serra Alta formations; [2]Siderópolis Member, Rio Bonito Formation; [3]Paraguaçu Member, Rio Bonito Formation; [4]Taciba Formation, Itararé Group, southern Paraná Basin, southern, Santa Catarina and Rio Grande do Sul, Brazil	[1]Margin feeding on *Glossopteris*; [2]Hole, slot and margin feeding, surficial feeding, skeletonization, possible mining 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);

Appendix 1 (continued)

Study	Age	Formation and locality	Damage type
Slater et al., 2012 (AP)			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
Labandeira and Currano, 2013 (C)	Artinskian	Rio Bonito Formation, Bainha, Parana Basin, Santa Catarina, Brazil	Oviposition scars on glossopterid or *Noeggerathiopsis* leaf
Labandeira and Prevec, in press (C)	[1]Changhsingian; [2]Changhsingian	[1]Elandsberg Member, Balfour Formation, Wapadsberg Pass, southern Karoo Basin, Eastern Cape Province, South Africa; [2]Emakwezini Formation, Kwa Yaya, Lebombo Basin, KwaZulu-Natal, South Africa	[1]Oviposition scars or surface feeding on *Glossopteris* with associated pathogen infection; [2]Apical damage, margin feeding, hole feeding, oviposition scars and galls on *Glossopteris* spp., all associated with fungal/bacterial damage
Gallego et al., in press (C)	Cisuralian	Rio Genoa Formation, Tepuel-Genoa Basin, Chubut, Argentina	Scalloped and narrowly embayed margin feeding, on *Glossopteris* spp.; Hole feeding on *Ginkgoites*, *Glossopteris* spp.; Circular surface feeding in *Ginkgoites*, *Glossopteris* and *Noeggerathiopsis* spp.; Strip-like surface feeding in *Glossopteris*; Oviposition scars (at least 3 types) on *Gangamopteris* and *Glossopteris* spp.

Appendix 2. 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 and Butterfield, 2008	Early Cambrian; Mount Cap Formation, Northwest Territories, Canada	Crustacean feeding apparatus
Harvey and Butterfield, 2011	Early-Middle Cambrian; Mount Cap Formation, Northwest Territories, Canada	Crustacean cuticles, sclerites, radulae
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

Appendix 2 (continued)

Publication	Age/locality	Description
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, 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., 2014	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, UK	Scorpion fragments extracted from coals
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., 1989a	Middle Devonian; Gilboa, New York State, USA	Spider spinneret
Shear et al., 1989b	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

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