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A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica

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ABSTRACT

The Toploje Member chert is a Roadian to Wordian autochthonous–parautochthonous silicified peat preserved within the Lambert Graben, East Antarctica. It preserves a remarkable sample of terrestrial life from high-latitude central Gondwana prior to the Capitanian mass extinction event from both mega- and microfossil evidence that includes cryptic components rarely seen in other fossil assemblages. The peat layer is dominated by glossopterid and cordaitalean gymnosperms and contains 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.

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

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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, 2013; 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

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