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Abstract

Wind-blown pollen (pollen rain) is a major contributor to element cycling in modern forests and aquatic ecosystems, particularly in high-latitude and acidic settings where nutrients are a limiting factor. The rich package of proteins, nitrogen and phosphorus residing within pollen is, nonetheless, inaccessible to most organisms, owing to the indigestible sporopollenin walls. Saprotrophic breakdown by fungi, and some non-fungal microorganisms, can make nutrients bioavailable, and represents a key trophic link in element cycling and the transfer of organic carbon. Little is known about when micro-saprotrophs first adapted to exploit pollen, thus establishing this crucial step in the evolution of modern terrestrial ecosystems. One approach is to examine the rich fossil record of palynomorphs. Here we describe translucent bodies referable either to fungi (Chytridiomycota) or water moulds (Oomycetes) within the pollen of glossopterid gymnosperms and cordaitaleans, and fern spores from silicified Permian (Guadalupian–Lopingian) peats of the Toploje Member, Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. These probable holocarpic thalli or oospores exploited the nutrient-rich microgametophyte tissue of dispersed miospores in high-palaeolatitude wetlands. The exceptional preservation of fossil microorganisms in permineralised peats offers insights into the deep-time evolution of intimate ecological relationships, otherwise known only among extant biotas. Permineralisation has preserved sub-micron details of these delicate and cryptic saprotrophs that likely played key roles in cycling nutrients in the acidic forest mires of the Permian. Our study reveals that the extensive recapture of spore/pollen-derived nutrients via saprotrophic digestion was already at play in the high-latitude ecosystems of the late Palaeozoic.

Keywords: *Chytridiomycota, oomycetes, Prince Charles Mountains, Bainmedart Coal Measures, Guadalupian, Lopingian, saprotrophy, permineralised peat, Glossopteridales, nutrient cycling*

Substantial volumes of pollen are shed by many plants during their reproductive cycle, yet only a miniscule fraction of these dispersed grains are ever involved in the fertilisation of ovules and generation of new plant offspring. The remainder either become entrained among the plant litter and soils, or are washed into freshwater aquatic and marine environments. In principle, this 'pollen rain' is a significant resource—especially for nutrients, such as nitrogen and phosphorus—that is available to any heterotrophic organisms able to capture it (Stark 1972; Greenfield 1999). The notoriously recalcitrant sporopollenin walls of pollen grains, however, makes the digestion of pollen a challenge, as attested to by the rich fossil record of intact spores and pollen. Several clades of saprotrophic fungi and fungus-like organisms are, nevertheless, able to degrade and digest pollen and spores, enabling the liberation of

these nutrients into the food web (Hutchison & Barron 1997; Perez-Moreno & Read 2001; Rösel et al. 2012; Magyar et al. 2018; Manirajan et al. 2018). Pollen that enters the soil is unlikely to be involved in reproduction and is essentially 'lost' to the parent plant—yet recapture of these nutrients via mycorrhizal fungal digestion of pollen facilitates the recycling of otherwise lost pollen resources, enabling plants to sustain greater yields of wind-dispersed pollen in the first case (Perez-Moreno & Read 2001). Despite this importance, surprisingly little is known about when these crucial processes first evolved, or how they have changed over macroevolutionary time as terrestrial ecosystems developed. This is in spite of the rich archives of pollen and spores available among the fossil record of palynomorphs.

In this study, we document exceptionally well pre-served remains of silicified Permian (*c.* 260 Ma) pollen and spores that apparently show evidence of saprotrophic attack by microfungi or other microorganisms. Specifically, we document fossilised fungus-like remains that appear to have had a special-ised relationship to pollen of the iconic Permian glos-sopterid seed plants.

Fungi and oomycetes have a surprisingly rich fossil record in Antarctica owing to their representation in an extensive record of fossil leaves, woods and permi-neralised peats preserved in Permian to Paleogene strata (Jefferson 1982; Stubblefield et al. 1987; White & Taylor 1991; Weaver et al. 1997; Cantrill & Falcon-Lang 2001; Falcon-Lang & Cantrill 2002; Garcia Massini 2007a, 2007b; Slater et al. 2013, 2015; Harper 2015; Hieger et al. 2015; Pujana et al. 2015; Harper et al. 2016, 2017; McLoughlin 2020). Antarctic Permian records derive primarily from a single Capitanian–Wuchia-pingian permineralised peat in the Prince Charles Mountains (Slater et al. 2013, 2015) and several Changhsingian silicified peats in the Transantarctic Mountains (Harper 2015; Harper et al. 2016, 2017).

The fossil remains of fungi and fungus-like organ-isms are abundant in a layer of siliceous permineralised peat (chert) exposed near Radok Lake in the Prince Charles Mountains, MacRobertson Land, East Antarctica (Slater et al. 2013, 2015; de Anca Prado & McLoughlin 2020). These are entombed within the chert along with a modest range of three-dimensionally preserved roots, wood and leaves of glossopterid gymnosperms (Neish et al. 1993; Weaver et al. 1997), cordaitaleans (McLoughlin & Drinnan 1996), isoetalean lycopsids (Slater et al. 2011; McLoughlin et al. 2015) and various unde-scribed ferns (McLoughlin et al. 1997; Lindström

& McLoughlin 2007). In addition, coprolites and various fossil herbivory, detritivory and saprotrophy traces record a broad range of ecological interactions in the original mire community (Weaver et al. 1997; Slater et al. 2012). High abundances of charcoalified plant remains within the permineralised peats indi-cate the prevalence of wildfire in these high-latitude Permian glossopterid-dominated forest mires, despite the presumably ever-wet conditions during peat accumulation (Slater et al. 2015; Mays & McLoughlin 2022). This palaeobiota plays an impor-tant role in understanding the structure of high-palaeolatitude mire ecosystems close to the end-Gua-dalupian and end-Permian mass extinction events and can be related to fossil assemblages preserved in similar-aged permineralised peats in eastern Aus-tralia (Gould & Delevoryas 1977; Pigg & McLough-lin 1997; McLoughlin et al. 2018, 2019) and the Transantarcic Mountains (Taylor & Taylor 1989).

Fungi play a primary role in the decomposition of organic remains and the recycling of carbon, nitrogen and other nutrients in both continental and marine ecosystems. Fungi are primarily saprotrophs or para-sites, but many are also involved in symbiotic, mycor-rhizal, associations with plants. Many fungal groups have special mutualistic or parasitic associations with individual plant taxa. Fungi have a patchy fossil record in permineralised deposits (Taylor et al. 2015b), as organic films on plant remains (McLoughlin et al. 2021), and as dispersed acid-resistant hyphae and spores in palynoassemblages (Elsik 1981; Shevchuk 2010; Gibson 2022).

Chytrid fungi (Chitridiomycota) include both saprotrophic and parasitic forms. Parasitic chytrids primarily infect algae, dinoflagellates and other eukaryote and prokaryote microbes, but some are known to target land plants and, particularly, dis-persed pollen and spores (Skvarla & Anderegg 1972; Taylor et al. 2015b). Chytrids are mostly aquatic (both marine and freshwater) or are confined to moist soils and peats. They are considered to play an important role in the ecology of marine settings, lakes, wetland ecosystems, moist soils and temporary forest ponds (Gleason et al. 2008; Davis et al. 2016; Fernández-Valero et al. 2023; Hanrahan-Tan et al. 2023) and range from equatorial to polar regions and oceans to alpine settings (Webster & Weber 2007; Nakanishi et al. 2023). They are able to degrade particularly robust organic materials, such as sporopollenin, keratin, chitin and cellulose.

Oomycetes (Stramenopiles) constitute a distinct lineage of heterotrophic organisms, commonly referred to as water moulds. Although not true fungi, they possess fungus-like hyphae, reproduce

both sexually and asexually, have saprotrophic or parasitic habits, and include forms that are pathogens on many fish, amphibians and crop plants. Like chytrids, some oomycetes are known to target dispersed pollen and are able to penetrate the robust sporopollenin wall (Stoyneva et al. 2013). Both chytrids and oomycetes are candidates for producing the spherical biotic structures found within Permian pollen grains from Antarctica.

This study aims to document the distribution and abundance of enigmatic pollen-hosted fungus-like bodies in the permineralised peat biota of the Amery Group, Prince Charles Mountains. We describe the characters of these fossil microbes and their host pollen and spores, and offer hypotheses as to their taxonomic affinities and ecological roles in the palaeoecosystem.

Geological setting

The studied material derives from multiple sites along the exposure of a 30–40-cm-thick permineralised (silicified) peat layer capping the uppermost coal bed within the middle Permian Toploje Member of the Bainmedart Coal Measures, northern Prince Charles Mountains, Antarctica (Figure 1A–E). The silicified peat is exposed over a strike length of around 3 km and grades laterally into silicified sandy palaeosols (northward) or non-silicified coals (southward). The fossiliferous layer represents an accumulation of autochthonous and parautochthonous organic detritus from a glossopterid-dominated forest-mire community (Slater et al. 2015). The peat bed is sharply, but conformably, overlain by lacustrine sideritic shales and sandstones of the Dragons Teeth Member (Fielding & Webb 1996). The source of the silica involved in the permineralisation process remains ambiguous, since there are no volcanogenic sediments associated with the deposit. Intense silicification might have derived from hydrothermal fluids emerging from nearby graben-margin fault systems (e.g. the Amery Fault) during basin subsidence.

The Toploje Member occurs in the lower part of the roughly 3-km-thick continental sedimentary succession constituting the Amery Group preserved within the Lambert Graben of East Antarctica (Figure 1A: Fielding & Webb 1995, 1996; McLoughlin & Drinnan 1997a, 1997b). During the middle Permian, this basin was located in the central part of Gondwana (McLoughlin 2001) where subsidence was initiated via intracontinental rifting that created crustal weaknesses that were subsequently exploited during the mid-Mesozoic by tectonic forces that led to Gondwanan continental

breakup (Harrowfield et al. 2005). During the middle to late Permian, the Lambert Graben was located at around 65–70 °S (Torsvik & Cocks 2013)—in roughly equivalent palaeolatitudes to its present location.

The upper bed of the Toploje Member was earlier assigned a Roadian–Wordian (middle Permian: early to middle Guadalupian) age via palynostratigraphic correlation to the Australian *Didecitrileles ericianus* Zone, especially based on the presence of the index taxon *Didecitrileles ericianus* (Balme et Hennelly) Venkantachala et Kar, and the occurrence of *Camptotrileles warchianus* Balme, typical of the *Dulhuntyispora parvithola* Zone, in the immediately overlying Dragons Teeth Member (Lindström & McLoughlin 2007). However, recalibration of the palynozonation scheme by high-precision U-Pb CA-IDTIMS dating of zircons from tuff beds in eastern Australian basins (Laurie et al. 2016) now suggests that the upper part of the *Didecitrileles ericianus* Zone may extend up to the Capitanian or Wuchiapingian.

Material and methods

Around 100 thin-sections (ground to thicknesses of 50 μm) and cellulose acetate peels (*c.* 20–30 μm thick) were prepared from the chert (silicified peat) blocks following the procedures of Hass and Rowe (1999) and Galtier and Phillips (1999). Pollen and spores containing fungal bodies were detectable in both the cellulose acetate peels and thin-sections. The pollen and enclosed fungi were generally more distinct in thin sections, but some features of the dark fungal walls were clearer in the thinner acetate peels.

All microscopy slides and parent rock samples are housed in the collections of the Palaeobiology Department, Swedish Museum of Natural History (NRM), Stockholm, Sweden, prefixed S, and the Commonwealth Palaeontological Collections, Geoscience Australia, Canberra, Australia, prefixed CPC. Specimens were photographed with an Olympus BX-51 compound transmitted light microscope equipped with an Olympus DP-71 digital camera. Microscopic features were measured using CellSens© Dimension version 1.6 (Olympus Soft Imaging Systems, Münster, Germany). For enhanced clarity of anatomical features, photomicrographs from multiple focal planes were aligned and stacked into focused composite images using Adobe Photoshop (Adobe Inc.) software.

Results

Numerous dispersed bisaccate pollen from eight sites along the exposure of the permineralised peat bear up
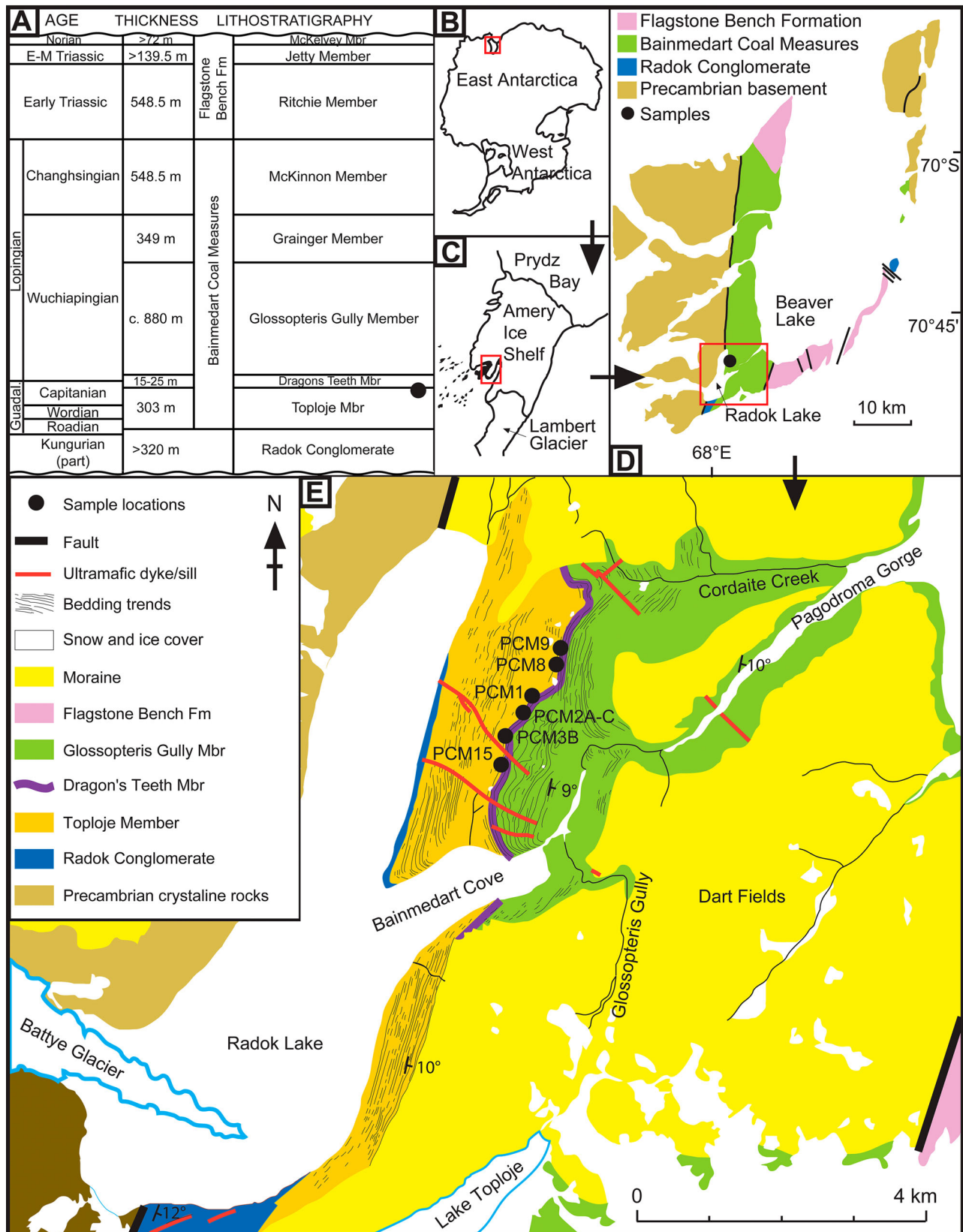
Figure 1. Stratigraphic and geographic sources of the studied material. **A.** Stratigraphy of the Amery Group showing the position of the sampled bed (dot). **B.** Location of the Prince Charles Mountains (box) in east Antarctica. **C.** Location of the Amery Oasis (box) in the Prince Charles Mountains. **D.** Location of the Radok Lake area (box) within the Amery Oasis. **E.** Geological map of the Radok Lake area showing the locations of the studied samples (black dots). Map modified from McLoughlin et al. (2015), and ages of stratigraphic units recalibrated after Laurie et al. (2016).
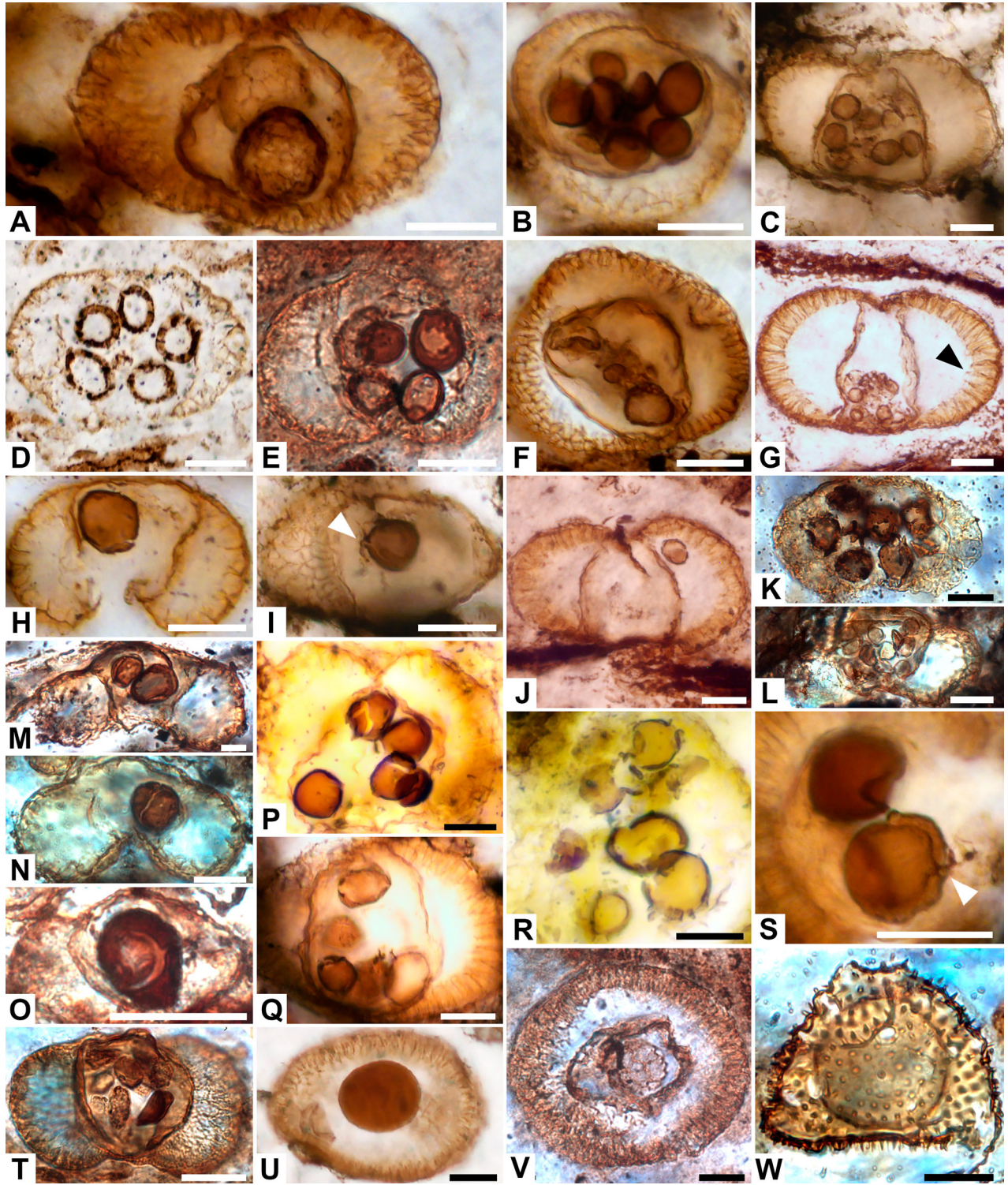
Figure 2. Illustrations of chytrid- or oomycete-like remains within bisaccate glossopterid pollen (**A–T**), monosaccate cordaitalean pollen (**U, V**) and a trilete fern spore (**W**) preserved in permineralised peat from the uppermost bed of the Toploje Member, Bainmedart Coal Measures, Amery Group (Type 1 bodies in **A–T**; Type 2 bodies in **U–W**). **A.** Two spherical bodies with weakly reticulate ornamentation in pollen corpus; PCM2B; S089895-01. **B.** Eight smooth bodies in corpus of obliquely sectioned pollen grain; PCM3; S089923-01. **C.** Eight smooth bodies in pollen corpus; PCM3B; S089909-01. **D.** Bodies with weakly ridged (reticulate?) ornamentation in pollen corpus; PCM8; S088064(A)-02. **E.** Four smooth elliptical bodies in pollen corpus; PCM1; S088061-02. **F.** Bodies of varied size in corpus of pollen in

oblique section; PCM3B; S089909-01. **G.** Aggregation of small bodies on one side of pollen corpus; arrow indicates infraexinal ramifications extending towards, but not filling, saccus chamber; PCM2B; S090342. **H.** Solitary body in pollen corpus; PCM2B; S089895-01. **I.** Solitary body with pore and possible bore and tubular extension in pollen corpus (arrowed); PCM3B; S089909-01. **J.** Elliptical body in pollen saccus; PCM2C; S090344. **K.** Six bodies in corpus of degraded pollen; PCM8; S088064(A)-02. **L.** At least ten small bodies in pollen corpus; PCM3B; S090343. **M.** Two bodies in pollen corpus; PCM1; S089892-02. **N.** Solitary smooth cleft body in pollen corpus; PCM3B; S090343. **O.** Solitary body with crescentic fracture in pollen corpus; PCM1; S124943-02. **P.** Smooth-walled and cleft bodies in pollen corpus; PCM2B; S088072-03. **Q.** Thin-walled bodies in pollen corpus; PCM3B; S089909-01. **R.** Ragged bodies in pollen corpus; PCM2B; S088072-03. **S.** Spherical bodies, one with possible pore and tubular extension (arrowed) in pollen corpus; PCM2B; S088072-03. **T.** Elliptical to irregularly distorted bodies in pollen corpus; PCM2A; S090345. **U.** Large dark body in pollen centre; PCM3; S089923-01. **V.** Thin-walled degraded body in centre of pollen grain; PCM1; S088061(A)-03. **W.** Large spherical body with darkened rim in spinose spore; PCM1; S089892-02. Scale bars – 20 μm. A–C, E–W = thin sections; D = cellulose acetate peel.

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to ten spherical darkened bodies within individual corpi (Figure 2A–I, K–T) and, less commonly, in the sacci (Figure 2J). A few similar bodies were noted in other (e.g. monosaccate: cf. *Cannanoropollis* sp.) pollen grains (Figure 2U, V) and within trilete fern spores (e.g. *Didecitriletes ericianus* [Balme et Hennelly] Venkatachala et Kar: Figure 2W). Rare examples of similar structures also occur around fragmentary organic matter dispersed within the peat matrix.

The most common pollen types hosting these spherical remains in the assemblage are bisaccate, haploxylonoid to weakly diploxylonoid forms referable to the *Protohaploxypinus limpidus – Protohaploxipinus amplus – Striatopodocarpites cancellatus* complex (see Lindström et al. 1997), with corpus and saccus lengths of 19–50 μm, corpus widths of 35–47 μm, saccus widths of 12–40 μm and total widths of 47–107 μm. Infraexinal ramifications extend interiorly from the exine but do not fill the sacci, leaving broad cavities (Figures 2G arrow, H, J, 3D). Taeniate bisaccate pollen grains of this type, lacking any fungal contents, are dispersed extensively within the same peat layer (Figure 3A–E).

Invasive bodies contained within the corpus or sacci of pollen grains appear to belong to at least two forms based on shape, gross dimensions, wall density and number of enclosed bodies. Type 1 bodies are primarily spherical or slightly elliptical, hollow, with diameters of 5–25 μm (average 13 μm), and of variable opacity. In rare cases, these bodies are contracted and oblong or have less regular shapes (Figure 2T). Type 1 bodies have a robust wall *c.* 0.5–1 μm thick with a smooth (Figure 2O–S)
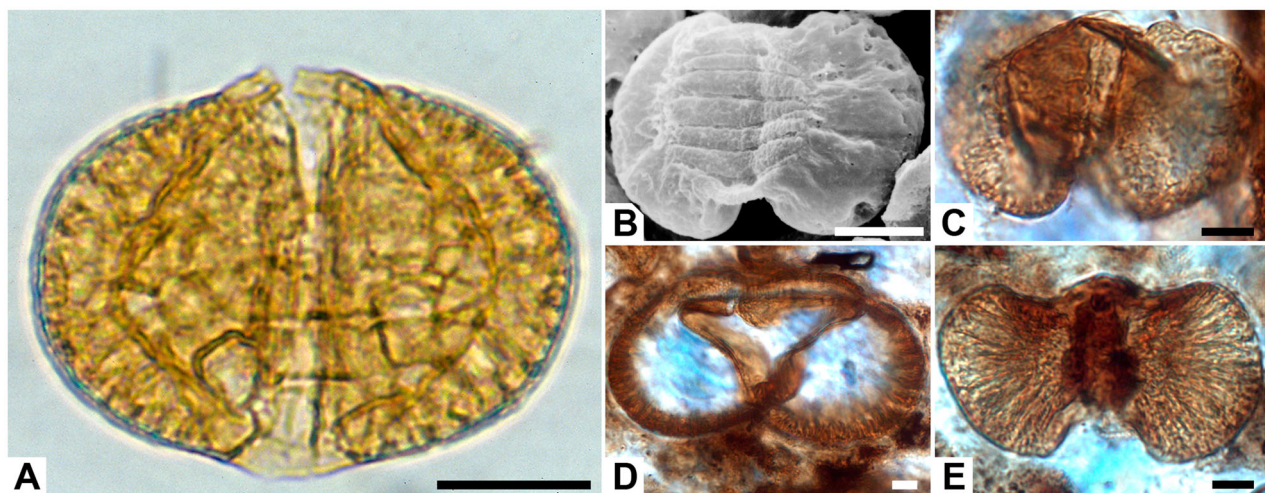

Figure 3. Typical taeniate bisaccate glossopterid pollen (lacking fungus-like inclusions) attributable to the *Protohaploxypinus limpidus–Protohaploxypinus amplus–Striatopodocarpites cancellatus* complex extracted by acid dissolution (Lindström et al. 1997) from the permineralised peat of the uppermost bed of the Toploje Member, Bainmedart Coal Measures, East Antarctica. **A.** Light micrograph of *Protohaploxypinus limpidus*-type pollen in polar view with haploxylonoid amb; PCM3B; CPC34338. **B.** Scanning electron microscopy image of *Striatopodocarpites cancellatus*-type pollen with taeniate corpus; PCM3B; CPC34305-01. **C.** *Striatopodocarpites*-type pollen with darkened corpus; PCM 1; S089892-02. **D.** Section through pollen grain in equatorial view showing hollow sacci; PCM2A; S090345. **E.** *Striatopodocarpites*-type pollen in distal polar view showing dark-rimmed leptoma: PCM1; S088061-02. Scale bars – 10 μm.

to weakly reticulate or ridged (Figure 2A, D) surface. Apart from the weak ornamentation on some specimens, there are no discernible structural components within the fungal body wall. A single pore (1–2 μm diameter) and, in some cases, a narrow (2 μm wide), short (6–15 μm long), hyphal extension is evident in a few specimens (Figure 2I, S arrowed). Several bodies bear desiccation cracks or fractures in the wall (Figure 2N–P). The fungal bodies are commonly clustered within the corpus (Figure 2B) and, in some cases, located close to the corpus wall (Figure 2G). However, they do not occur in a regimented arrangement, and some occur markedly isolated from others (Figure 2P, Q).

Type 2 bodies (Figure 2T–W) occur centrally within both monosaccate pollen (48–72 μm in maximum dimensions) and trilete spores (54–57 μm in equatorial diameter). These fungus-like bodies are circular to elliptical, large (30–40 μm in maximum dimensions), thin- to thick-walled (*c.* 0.3–1.5 μm thick) and strongly (Figure 2V, W) to weakly (Figure 2T) translucent. No pores or hyphal remains were identified in these specimens.

Occurrences of infected pollen among the samples are relatively common. A survey of thin-sectioned peat blocks taken from eight sites along the outcrop of the permineralised peat revealed modest variation (10.4–23.3% based on counts of 30–500 grains per sample) in the proportions of pollen grains hosting fungus-like bodies within the palaeomire complex (Table I). Various other hyphae and reproductive structures of fungi and oomycetes were detected in the silicified peat profiles, but none could be physically linked to those preserved within the pollen and spores.

Table I. Percentage of dispersed pollen/spores in the permineralised peat containing fungus-like bodies in the corpus or sacci segregated by sampling locality (Figure 1E). Total counts represent all available dispersed miospores counted in the representative slide, constituting a total of 1274 grains studied from the peat bed.

Sampling locality	Percentage of pollen/ spores containing fungus-like bodies	Number of dispersed pollen/spores counted
PCM1	22.8	145
PCM2A	14.6	321
PCM2B	10.4	67
PCM2C	19.9	146
PCM3B	14.6	501
PCM8	21.9	32
PCM9	23.3	30
PCM15	12.5	32

Discussion

Affinities of palynomorph inclusions

Fungi and fungus-like organisms have various relationships to spores and pollen, from degradation of sporopollenin walls (a habit that forms characteristic crater-like scarring; Srivastava et al. 1999), to penetration and exploitation of pollen contents as a nutrient source (Perez-Moreno & Read 2001; Marques et al. 2013; Kagami et al. 2017). Some extant ascomycote fungi (e.g. *Retiarius*) have even been documented to produce erect hyphae or conidia specially adapted to capture and parasitise viable wind-borne pollen grains in the phyllosphere (Olivier 1978; Magyar et al. 2017).

Our results show infestation of the corpi of bisaccate pollen to be relatively common in the middle–upper Permian peat deposits of East Antarctica. The great majority of infected palynomorphs are bisaccate pollen of more-or-less identical dimensions and morphology. Although taeniae are rarely evident on those pollen containing inclusions, owing to the plane of section passing through the centre of the corpus, these grains are consistent in all other respects with the *Protohaploxypinus limpidus–Protohaploxipinus amplus–Striatopodocarpites cancellatus* complex (Figure 3A–E; Lindström et al. 1997) produced by glossopterid gymnosperms (McLoughlin & Prevec 2021). Permian pollen from India bearing equivalent dark bodies have been assigned previously to a broad range of taxa including *Striatopodocarpites*, *Faunipollenites*, *Ibisporites*, *Platysaccus* and *Scheuringipollenites* (Tiwari & Kumar 2002; Aggarwal et al. 2015). However, we consider nearly all of those previously illustrated forms to represent variably orientated, folded and compressed specimens consistent with the *Protohaploxypinus limpidus–P. amplus–Striatopodocarpites cancellatus* complex, meaning that the Indian examples also likely represent saprotrophic fungal infestation of glossopterid pollen. The only exception to this is a monosaccate grain figured by Aggarwal et al. (2015, figure 3C) and assigned to *Barakarites* enclosing at least four darkened bodies. We noted two monosaccate (*Cannanoropollis*-type) pollen grains in the Toploje Member peat that contain single large darkened (Type 2) bodies. Permian monosaccate pollen from Gondwana is generally considered to be affiliated with cordaitaleans or conifers (Pant 1982; Archangelsky & Cúneo 1987; Balme 1995). Two examples of possible fungus-like inclusions within spinose fern spores (both *Didecitriletes ericianus*) in the Antarctic material further suggests that microbial saprotrophy may have targeted a broader array of

palynomorphs, though glossopterids represent the overwhelming majority of pollen subject to degradation. The percentage of palynomorphs infected by fungus-like bodies in samples from the Toploje Member peat (*c.* 10–23%) is generally higher than that (2–14%) recorded by Aggarwal et al. (2015), however, the Indian palynoassemblages probably represent pollen and spores derived from a broader fluvial catchment area. Palynoassemblages from the Lopingian of Europe dominated by bisaccate conifer pollen reveal strongly variable infection rates by fungus-like bodies of < 1% to 27.5% (Gibson 2022).

Fungi and bacteria that primarily attack pollen or other plant cell walls typically leave stereotypical crater-, chamber- or tunnel-like damage features that are commonly aggregated (Daniel & Nilsson 1988; Maheshwari & Bajpai 1996; Srivastava et al. 1999; Nilsson & Björdal 2008; Philippe et al. 2022). Given the attached hyphae and substantial size of the spherical bodies preserved inside the pollen grains, we exclude their affiliation with bacteria or other prokaryotes. Nor are the regular spherical shapes of these bodies consistent with the contracted remnants of microgametophyte tissues (Vijaya & Meena 1996). We interpret these bodies to have fungal or fungus-like affinities based on their size, shape, robust walls, and rare pores or emergent hypha-like filaments. In agreement with Aggarwal et al. (2015), we interpret the solitary pores and rare filaments attached to these bodies as pre-formed discharge pores or tubes of some saprotrophic or parasitic fungus, or fungus-like organism. Several similar types of remains have been reported previously from late Permian glossopterid pollen in both dispersed palynological assemblages from India (Vijaya & Meena 1996; Aggarwal et al. 2015) and within permineralised peats from the Transantarctic Mountains (Harper 2015; Harper et al. 2016) and these likely have the same affiliation.

Chytridiomycota represents one of the earliest diverging lineages of fungi (Li et al. 2021) and this group is atypical for fungi in reproducing via flagellate zoospores produced via mitosis. Sparse sexual reproduction generates a zygote that is held in a resting spore or cyst that aids survival through adverse environmental conditions. Given their common association with modern pollen, the Permian fossils are possibly affiliated with Chytridiomycota as suggested by Aggarwal et al. (2015). However, most putative fossil chytrids are interpreted to represent zoospores attached to the outer surface of spores or pollen, or zoosporangia embedded within the spore-pollen wall (Taylor

et al. 2015a) based on comparison with extant Chytridomycota that attack pollen (e.g. Skvarla & Anderegg 1972). Some modern chytrids, particularly those that infect *Pinus* pollen, also produce a globose sporangium within the corpus (Übelmesser 1956). In the fossil record, there is at least one example of chytrid endobiotic sporangia containing zoospores within the corpus of the Pennsylvanian cordaitalean pollen *Sullisaccites* (Millay & Taylor 1978), and similar features have been illustrated in Gondwanan Permian monosaccate pollen (Foster 1979, pl. 22, figure 7). Owing to the morphological simplicity of these structures (Taylor et al. 2015b) and overall paucity of characters, it is inherently difficult to determine the lower-order taxonomic affinities of these organic microfossils with any precision.

Impediments to a confident assignment to Chytridiomycota are also posed by possible affinities to other fungi-like groups, in particular Hyphochytriomycetes and Oomycetes. These groups all have representatives that produce morphologically simple reproductive bodies or resting cysts (Barr 1970; Marano & Steciow 2006; Taylor et al. 2015b). In many cases, where fossil specimens lack diagnostic connections with hyphal, zoospore or oogonia remains, it is currently not possible to distinguish which particular groups the fossils belong to (Taylor et al. 2015b). The dark spherical bodies found inside glossopterid pollen are preserved within the corpus (or more rarely the sacci) and may, plausibly, represent oomycete holocarpic thalli or oospores similar to those of the extant endobiotic parasite *Ducellieria chodatii* (F. Ducell.), which are known to occur in clusters within modern Pinaceae pollen (Hesse et al. 1989; Stoyneva et al. 2013; see also figure 1A of Buaya & Thines 2023). In typical *Ducellieria*, a zoospore bearing two laterally inserted flagella settles on a pollen grain, penetrates the wall layers and develops as an internal spherical to ovoid holocarpic thallus/zoosporangium. After maturation, many new protoplasmatic units are then released through one or more short discharge tubes and go on to form a new *Ducellieria* aggregate that generates new zoospores. It is not uncommon for multiple zoospores to infest a single pollen grain. After many cycles, and where several zoospores penetrate a pollen grain, sexual reproduction may occur, and an oosporangium with a single, smooth, thick-walled resting spore (oospore) is developed (Hesse et al. 1989; Stoyneva et al. 2013). Indeed, a new order of obligate endobiotic pollen-parasitic oomycetes has recently been recognised and established as 'Ducellieriales' (Buaya & Thines 2023), comprising the known species *D. chodatii* (Ducellier)

Teiling, *D. tricuspidata* (Borge) Teiling, and *D. corcontica* Matula. Although we did not detect any contents within the invasive bodies, their spherical shape, thick, smooth or weakly sculptured walls, single aperture with a short extension, and multiple occurrences within the corpus has strong parallels with the holocarpic thalli/oosporangia and/or oospores of *Ducellieria*-type oomycetes. It is worth noting that there is an extensive fossil record of such fungal and oomycete interactions with spores and pollen extending back to the very dawn of land plants (Taylor et al. 2015b).

Saprotrophic digestion of pollen in modern and ancient ecosystems

Pollen accumulations represent a substantial portion of the nutrients potentially available in many terrestrial and aquatic ecosystems (Hutchison & Barron 1997). Nevertheless, the resilient sporopollenin walls of pollen makes these dispersed nutrient-rich grains essentially indigestible or difficult for other organisms to access the contents. However, saprotrophic chytrids degrade pollen, and thereby make the nutrients locked within the microgametophyte bioavailable (Phuphumirat et al. 2011). This is particularly important in modern freshwater aquatic settings (Masclaux et al. 2011; Rösel et al. 2012; Wurzbacher et al. 2014; Kagami et al. 2017; Page & Flannery 2018), where chytrid breakdown of pollen means that the contents become available as a significant food resource for aquatic invertebrates, especially immature crustacean zooplankton (e.g. *Daphnia*), benefiting their growth and eventual reproductive capacity (Gleason et al. 2008). A comparable process with consumption by zooplankton has also been documented where pollen is dispersed into marine habitats (Pawlik & Ficek 2023). Significantly, the higher proportions of saprotroph-like inclusions within bisaccate fossil pollen described here may reflect a trend that has been observed in extant ecosystems: when entrained in water, most pollen sinks rapidly, yet wind-dispersed bisaccate pollen possessing air-sacs tends to float, or sink more slowly, allowing time for exposure to colonisation by fungal pathogens (e.g. chytrid fungi) in the water column (Hopkins 1950; Kagami et al. 2017). It is plausible that a similar process was at play during the Permian, whereby annual shedding of glossopterid pollen in Gondwanan high-latitudes provided an injection of nutrients, organic carbon, and a burst of fungal zoospores that enriched surrounding soils and lacustrine trophic systems. Indeed, the peats of the Bainmedart Coal Measures have been hypothesised to be derived from ombrotrophic Permian mires (Slater

et al. 2015). In recent (Holocene–present) rainwater-fed mires of this kind, pollen has been shown to be an important component of the available nutrient supply (Shumilovskikh et al. 2015).

Oomycetes are also important saprotrophs and parasites in modern marine, freshwater and moist terrestrial environments (Masigol et al. 2019). Aquatic fungi and fungus-like organisms are especially important in regulating nitrogen and phosphorus in modern acidic wetlands (Gulis et al. 2006; Dileo et al. 2010; Krauss et al. 2011). Modern groups of oomycetes and fungi also have mechanisms for metal avoidance and tolerance (Krauss et al. 2011) that, if analogous in their ancient relatives, might provide insights into the chemistry of the ancient mire–lake system that was entombed by silica in the Prince Charles Mountains area.

The fairly common occurrence of chytrid- or oomycete-like remains in the dispersed pollen of the Toploje Member peat, and in non-marine deposits of India, the Transantarctic Mountains, and northwest Europe (Gibson 2022) suggests that these organisms were important contributors to nutrient recycling in middle–late Permian wetland communities across Gondwana and in Northern Hemisphere lowland settings. Tracking the first occurrences of such pollen–fungi/oomycete associations in the fossil record should provide insights into when saprotrophic chytrids/oomycetes evolved to exploit pollen in deep time, and how this impacted nutrient flow in continental ecosystems.

Conclusions

This study builds upon the range of known fossil organisms preserved in the Amery Group permineralised peat, and the interactions represented in the middle to late Permian high-palaeolatitude mire community. Significantly, this study highlights the importance of permineralised peats in preserving very small and delicate saprotrophic/parasitic organisms that provide a window into the composition of the cryptic components of ancient terrestrial ecosystems. The ancient chytrid- or oomycete-like organisms documented here were clearly important decomposers of robust glossopterid pollen grains, along with cordaitalean pollen and the spores of some ferns. This saprotrophic relationship, common in modern high-latitude forests where pollen production is high, appears to have already evolved by the late Paleozoic, and was likely a key part of the trophic structure within the consistently moist high-latitude mires that once covered much of Gondwana. Regardless of the affinities of these

saprotrophs (fungal or fungus-like oomycetes), they clearly represent organisms that fed on the nutrient-rich contents of the plant microgametophyte and were important for recycling organic nutrients in the acidic forest-mire ecosystem.

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