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Gondwanan floristic and sedimentological trends during the Permian–Triassic transition: new evidence from the Amery Group, northern Prince Charles Mountains, East Antarctica

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Abstract: The Permian–Triassic boundary within the Amery Group of the Lambert Graben is placed at the contact between the Bainmedart Coal Measures and overlying Flagstone Bench Formation, based on the first regular occurrence of *Lunatisporites pellucidus* and the first appearance of *Aratrisporites* and *Lepidopteris* species. The Permian–Triassic boundary is marked by the extinction of glossopterid and cordaitalean gymnosperms, and by the disappearance or extreme decline of a range of gymnospermous and pteridophytic palynomorph groups. Earliest Triassic macrofloras and palynofloras of the Flagstone Bench Formation are dominated by peltasperms and lycophytes; corystosperms, conifers, and ferns become increasingly common elements of assemblages through the Lower Triassic part of the formation and dominate floras of the Upper Triassic strata. The sedimentary transition across this boundary is conformable but marked by a termination of coal deposits; overlying lowermost Triassic sediments contain only carbonaceous siltstones. Typical red-bed facies are not developed until at least 100 m above the base of the Flagstone Bench Formation, in strata containing ?Middle Triassic palynofloras. Across Gondwana the diachronous disappearance of coal deposits and appearance of red-beds is suggestive of a response to shifting climatic belts, resulting in progressively drier seasonal conditions at successively higher palaeolatitudes during the Late Permian to Middle Triassic. The abrupt and approximately synchronous replacement of plant groups at the Permian–Triassic boundary suggests that factors independent of, or additional to, climate change were responsible for the turnover in terrestrial floras.

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Key words: *Dicroidium*, extinctions, *Glossopteris*, *Lepidopteris*, palynofloras, Permian, Triassic

Introduction

The Permian–Triassic boundary is marked by the largest extinction "event" of the Phanerozoic Eon. Dramatic extinctions were experienced by a broad range of marine invertebrates, terrestrial vertebrates and terrestrial plants. Some estimates suggest a loss of up to 77% of terrestrial tetrapod families (Maxwell & Benton 1987) and 96% of marine invertebrate species (Raup 1979), although Raup (1991) noted that at least the latter figure (based on the reverse rarefaction calculation method) is probably exaggerated. Stanley & Yang (1994) suggested that the end-Permian biotic turnovers may actually represent two closely spaced but distinct extinction events, successively eliminating around 71% and 80% of marine species. Insufficiently precise sampling, the occurrence of "Lazarus taxa" in higher successions, differential preservation of various animal groups, differences in the methods used for calculating percentages of extinct taxa, and the few available continuous marine sequences spanning the Permian–Triassic boundary all contribute to considerable uncertainty about the magnitude of the extinction event (or events) with respect to marine biotas. Numerous mechanisms have been proposed to account for the high levels of extinction at the end of the Permian but as yet no definitive causal factor is widely accepted.

Knoll (1984) noted that the Permian–Triassic interval represented one of the three significant phases of floristic turnover among vascular plants during the Phanerozoic, although few estimates are available for the percentage of species-level extinction. He noted that the changes at this time were most evident in the decline of family-level diversity but that the floristic changes took place over a much longer interval than the invertebrate turnovers and that the changes occurred at different times in different parts of the world. Several investigators (Rocha-Campos 1971, Foster 1982, Wright & Askin 1987, Collinson *et al.* 1994, Veevers *et al.* 1994a, Retallack 1995, Morante 1996) have now analysed sedimentological, macrofloral, palynological, and isotopic changes across the Permian–Triassic boundary in different parts of Gondwana but unanimous agreement on the timing and causes of these changes has not been achieved.

At the close of the Palaeozoic the Lambert Graben of East Antarctica was probably structurally continuous with the Son-Mahanadi Graben of India (Fedorov *et al.* 1982). Its central location within Gondwana endows a critical importance to the Lambert Graben succession and its fossil biota in correlating between the now disparate remnants of the supercontinent and in understanding the timing of key geological events. This paper describes the nature of the Permian–Triassic transition within the non-marine Amery Group in the Lambert Graben and compares the changes in floras and sedimentation to other Gondwanan basins.

Stratigraphy and sedimentology

Recent field studies have completed the mapping, stratigraphic logging, and sedimentological analysis of the entire Permian–Triassic Amery Group exposures in the Beaver Lake region and have resulted in revision of the formal stratigraphic nomenclature (McKelvey & Stephenson 1990, Webb & Fielding 1993a, 1993b, Fielding & Webb 1995, 1996, McLoughlin & Drinnan 1997, in press). The Amery Group is divided into three formations (Fig. 1): the Radok Conglomerate (mid-Permian), Bainmedart Coal Measures (Upper Permian), and Flagstone Bench Formation (lowermost Triassic to Norian). Six members have been recognized within the Bainmedart Coal Measures: Dart Fields Conglomerate Member, Toploje Member, Dragons Teeth Member, Glossopteris Gully Member, Grainger Member, and McKinnon Member, in ascending stratigraphic order. Three subunits have been recognized within the Flagstone Bench Formation: Ritchie Member (earliest Triassic to ?Anisian), Jetty Member (?Anisian to ?Carnian), and

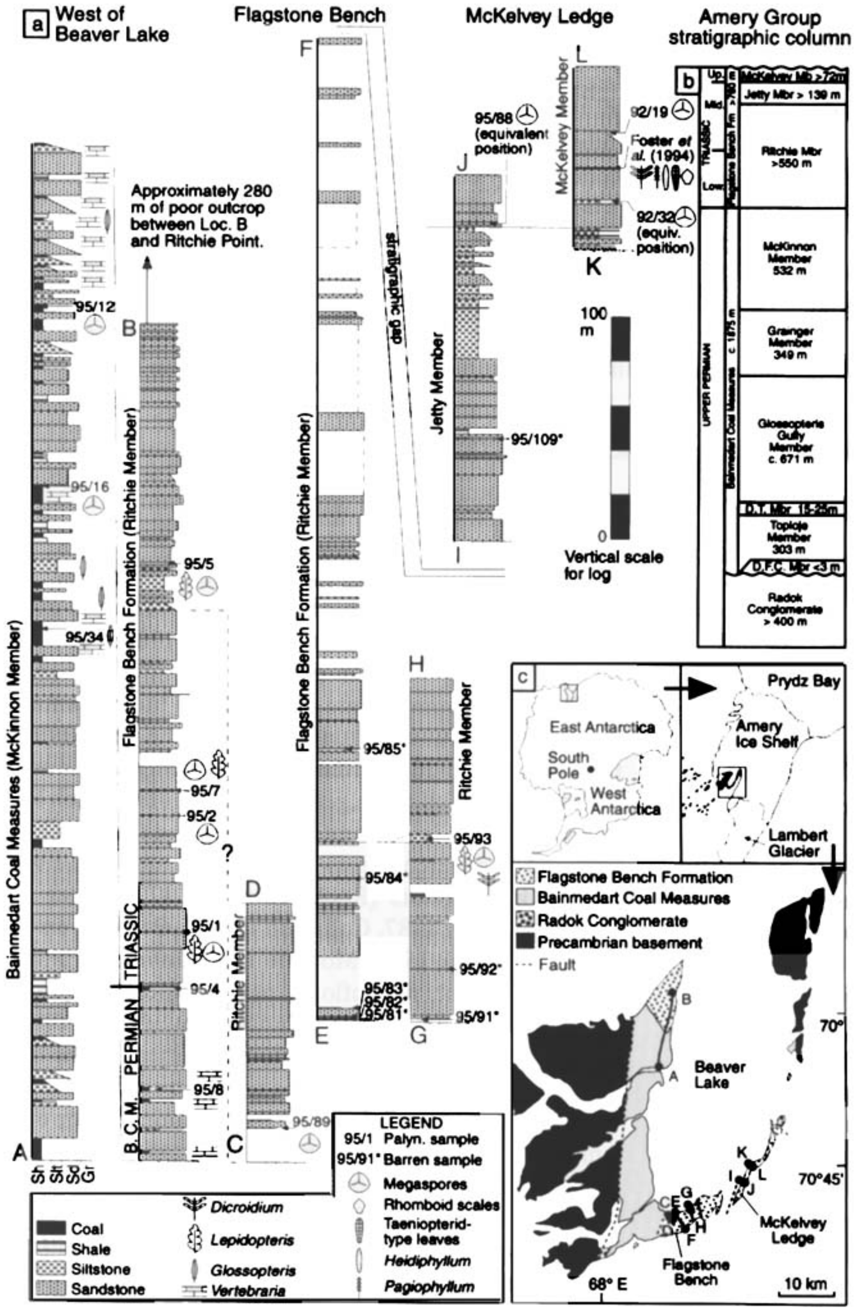


Fig. 1. Geological details of the study area: **a.** geological log of the uppermost Bainmedart Coal Measures (McKinnon Member) and Flagstone Bench Formation; **b.** Amery Group stratigraphic column; **c.** geological map of the Beaver Lake region, northern Prince Charles Mountains showing the distribution of Amery Group exposures and the location of studied sections.

McKelvey Member (Norian). This study focuses on the changes in sedimentology and fossil biota of the uppermost Permian to Upper Triassic succession.

The lower part of the succession (Radok Conglomerate) is characterized by discontinuous beds of pebble to boulder conglomerate interbedded with sandstones, minor siltstones and coal. Palaeocurrents are predominantly directed towards the east and the unit is an alluvial fan deposit derived from the basin margins during the early stages of basin fill (Fielding & Webb 1995).

The succeeding Bainmedart Coal Measures comprise repetitive fining-upward cycles of coarse-grained, prominently cross-bedded, subarkosic sandstones, carbonaceous siltstones, and coals. Palaeocurrents are predominantly directed towards the north or north-east and the sequence is interpreted as high-energy, braided, fluvial channel deposits alternating with widespread, low-energy, flood basin and forest mire environments. A minor lacustrine interval (Dragons Teeth Member) of coarsening-upward, siltstone-dominated packages occurs in the lower part of the coal measures. The proportion of coal to sandstone and the average thickness of coal seams fluctuate throughout the sequence and are useful parameters for the stratigraphical subdivision of the coal measures (Fielding & Webb 1996, McLoughlin & Drinnan 1997).

The cessation of coal beds is a conspicuous geological feature within the Amery Group and marks the boundary between the Bainmedart Coal Measures and the overlying Flagstone Bench Formation (Figs 1 & 2). Strata above and below the boundary are conformable. The Ritchie Member (lower Flagstone Bench Formation) consists of coarse-grained, prominently cross-bedded, subarkosic sandstones interbedded with thin, dark grey, carbonaceous siltstones (in the lower part) and red to green mottled siltstones (in the middle and upper parts). The unit was deposited in northerly directed, braided fluvial systems under a climatic regime that was shifting from consistently wet to more seasonally dry conditions. The Jetty Member (middle Flagstone Bench Formation) comprises interdigitating sheets of coarse-grained sandstones, pebble conglomerates, and ferruginous siltstones at the base, and ferruginous, siltstone-rich, rock packages with prominent desiccation marks towards the top. This unit represents sedimentation by sporadically active, easterly directed alluvial fans under dry, seasonal climates with fluctuating groundwater conditions. The McKelvey Member (upper Flagstone Bench Formation) consists of subarkosic to quartzose sandstones interbedded with minor carbonaceous siltstones yielding rich macro- and palynofloras (Fig. 1), and reflects a return to more consistently wet conditions and northerly directed sediment transport in braided fluvial tracts along the graben axis.

The most notable sedimentological change at the Permian–Triassic boundary is the cessation of coal accumulation. Although the termination of coals appears to be relatively abrupt in the field, the proportion of coal within the sequence and the average thickness of coal seams declines over the uppermost several hundred metres of the Permian succession (McLoughlin & Drinnan 1997).

Although coals do not occur in the Flagstone Bench Formation, carbonaceous siltstones, yielding fossil plant foliage and palynomorphs, persist for several hundred metres above the base of the unit. Thin sandstones with desiccation marks and red, white, and green mottled siltstones and palaeosols of typical "red-bed" aspect are not encountered until *c.* 100–140 m above the top of the coal measures (Fig. 2). The initial development of strongly reddened siltstone layers corresponds to the appearance of spore-pollen assemblages with ?Anisian signatures (Fig. 7). Maximum development of red-beds occurs in the upper Jetty Member of probable Middle Triassic to early Late Triassic age. The Jetty Member red-beds show calcrete development in the form of a range of calcareous nodules and crusts (some infilling desiccation

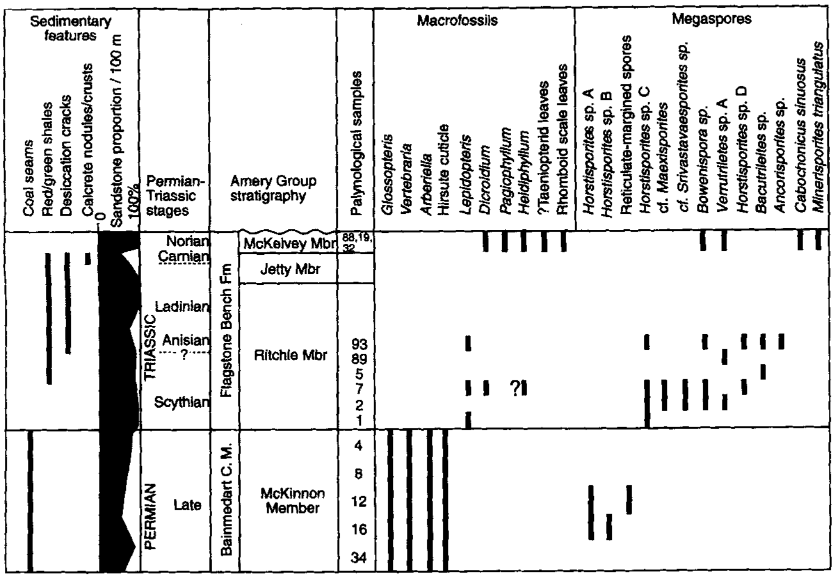


Fig. 2. Distribution of selected sedimentological features, plant macrofossil taxa and megaspores within the uppermost Bainmedart Coal Measures (McKinnon Member) and Flagstone Bench Formation.

cracks, others accreting around root traces, others developed along bedding planes and laminae). Red-bed and calcrete development in the Middle Triassic is suggestive of strongly fluctuating groundwater levels under a semi-arid climate (Van Houten 1973, Reeves 1976, Hubert 1977).

The average thickness of discrete sediment packages (generally fining upward cycles) declines slightly from the Upper Permian (*c.* 7.2 m) through to the Early Triassic (*c.* 5.6 m), although this is largely attributable to the drop in the proportion of mudrock facies within the succession. Sandstone package thicknesses remain fairly constant and typically average *c.* 4 m thick on either side of the boundary. Palaeocurrent directions obtained from major cross-bed orientations do not shift significantly across the boundary between these formations. They maintain a predominantly north-easterly to north-westerly orientation throughout the Upper Permian and Lower Triassic successions.

Permian–Triassic biotic turnover

Fossil flora of the Bainmedart Coal Measures

Although coal seams are abundant in the McKinnon Member, the uppermost unit of the Bainmedart Coal Measures, few beds contain well preserved plant macrofossils. Plant remains within the coal seams have been largely homogenized during humification and coalification processes, and in most cases are taxonomically unidentifiable. A few siltstone and shale intervals within this unit contain fragmentary glossopterid sporangial, leaf, and cuticle remains (Fig. 3j & k), but these are generally not identifiable to species level. Glossopterid root impressions (*Vertebraria indica* Royle, Fig. 3f) commonly underlie coal seams and show variable orientations, either transecting strata or following bedding planes, suggesting that the coals are chiefly derived from autochthonous and quasi-autochthonous plant remains from glossopterid-dominated forest mires. Several lycophyte megaspores (Fig. 3a–c) and marginally hirsute, possibly coniferous, scale leaves (Fig. 3e & g) also occur in assemblages macerated from siltstone intervals. Unidentifiable gymnosperm log impressions up to 60 cm diameter are commonly preserved near the bases of channel-sand packages throughout the Bainmedart Coal Measures.

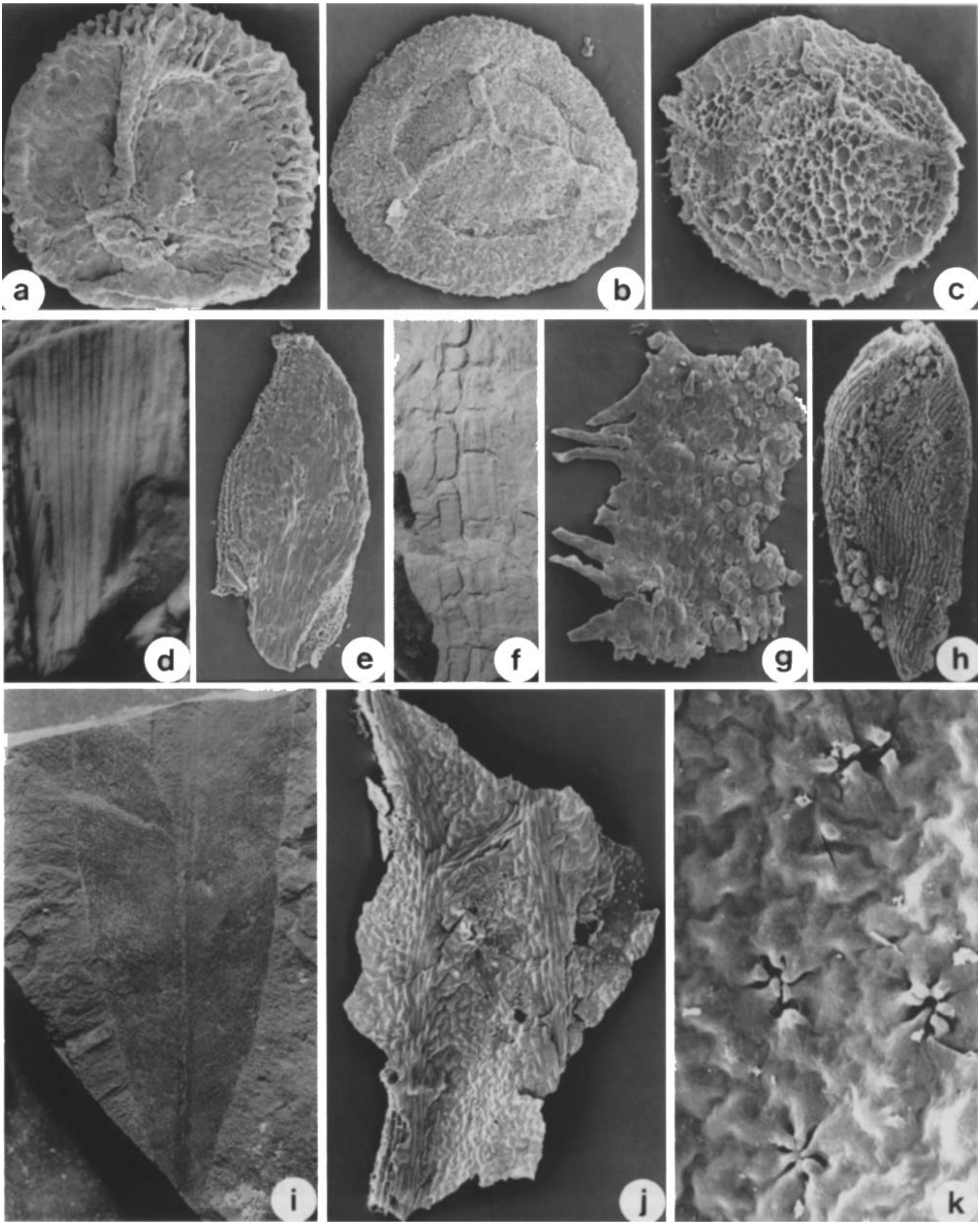
A siliceous permineralized peat layer at the top of the Toploje Member and overlying limonitic/sideritic shales at the base of the Dragons Teeth Member, both *c.* 1570 m below the top of the Permian succession, contain a range of well-preserved macroscopic plant remains. Assemblages are typically low in diversity and dominated by the remains of glossopterid gymnosperms. At least three species of *Glossopteris* Brongniart leaves (Fig. 3i), abundant *Vertebraria* roots, and sporadic glossopterid ovulate fruits (*Plumsteadia* Rigby) and sporangia (*Arberiella* Arber, Fig. 3h) are present. *Noeggerathiopsis* Feistmantel (Cordaitales) leaves (Fig. 3d) are sub-dominant elements within the peat flora. Dispersed and *in situ* permineralized wood assigned to two species of *Australoxylon* Marguerier (Weaver *et al.* 1997) may be derived from glossopterid and/or cordaitalean plants, and is a prominent constituent of the peat profile. Minor plant remains preserved in the peat and associated shales include sphenophyte axes (*Paracalamites* Rigby) and foliage (*Lelstotheca* Maheshwari), fern pinnules (?*Neomariopteris* Maithy), and herbaceous lycophyte axes and megaspores.

Fungal remains, represented by hyphae, fruiting bodies, and pocket-rot cavities in wood, are relatively common within the permineralized peat. In most cases fungal activity was probably centred on decomposition of plant remains in the forest leaf litter, but in the case of wood-decomposition some of the fungal attack probably occurred during growth of the tree. There is often seasonal regularity in the distribution of pocket rot, and some wood cells show the development of wall appositions as a response to pathogen attack (Weaver *et al.* 1997).

There is little evidence for animal life in the Permian succession. Sinuous to irregular invertebrate trails of *Planolites*-type and short vertical burrows occur sporadically through the lower and middle parts of the Amery Group, but no body fossils of macroscopic animals or vertebrate trackways have been found. However, probable insect coprolites, some incorporating recognizable pollen grains, are widely dispersed within the permineralized peat layer at the top of the Toploje Member and in various samples from the remainder of the coal measures. Some wood in the peat layer also shows evidence of invertebrate attack in the form of regular, sharp-walled, frass-filled cavities in the latewood of growth rings. These are suggested to have been caused by the actions of beetle larvae or mites overwintering within the wood of seasonally dormant glossopterid or cordaitalean trees, and there feeding on the wood itself and/or upon fungal agents attacking the wood (Weaver *et al.* 1997).

The palynofloras from the McKinnon Member are generally

Fig. 3. Lycophyte megaspores (a–c) and gymnospermous plant macrofossils (d–k) from the Upper Permian Bainmedart Coal Measures (McKinnon Member, a–c, e–g, j, k; Toploje Member, d, h; Dragons Teeth Member, i). **a.** megaspore with reticulate margin (n. gen.), proximal view, x70, PCM95/12; **b.** *Horstisporites* sp. A, proximal view, x100, PCM95/16; **c.** *Horstisporites* sp. B, equatorial view, x115, PCM95/16; **d.** *Noeggerathiopsis* sp., x2.2, PCM92/3E; **e.** minute papillate scale, x120, PCM95/12; **f.** *Vertebraria indica* Royle, x0.7, 235 m above base of McKinnon Member, Skua Ledge; **g.** hirsute cuticle, x160, PCM95/4; **h.** *Arberiella* sp. cf. *A. africana* Pant & Nautiyal, x70, PCM92/14; **i.** *Glossopteris* sp., x1.5, 2 km northeast of Panorama Point; **j.** charcoalified *Glossopteris* leaf, abaxial surface, x65, PCM92/2C; details of leaf surface (Fig. 3j) showing stomata protected by epidermal papillae, x400.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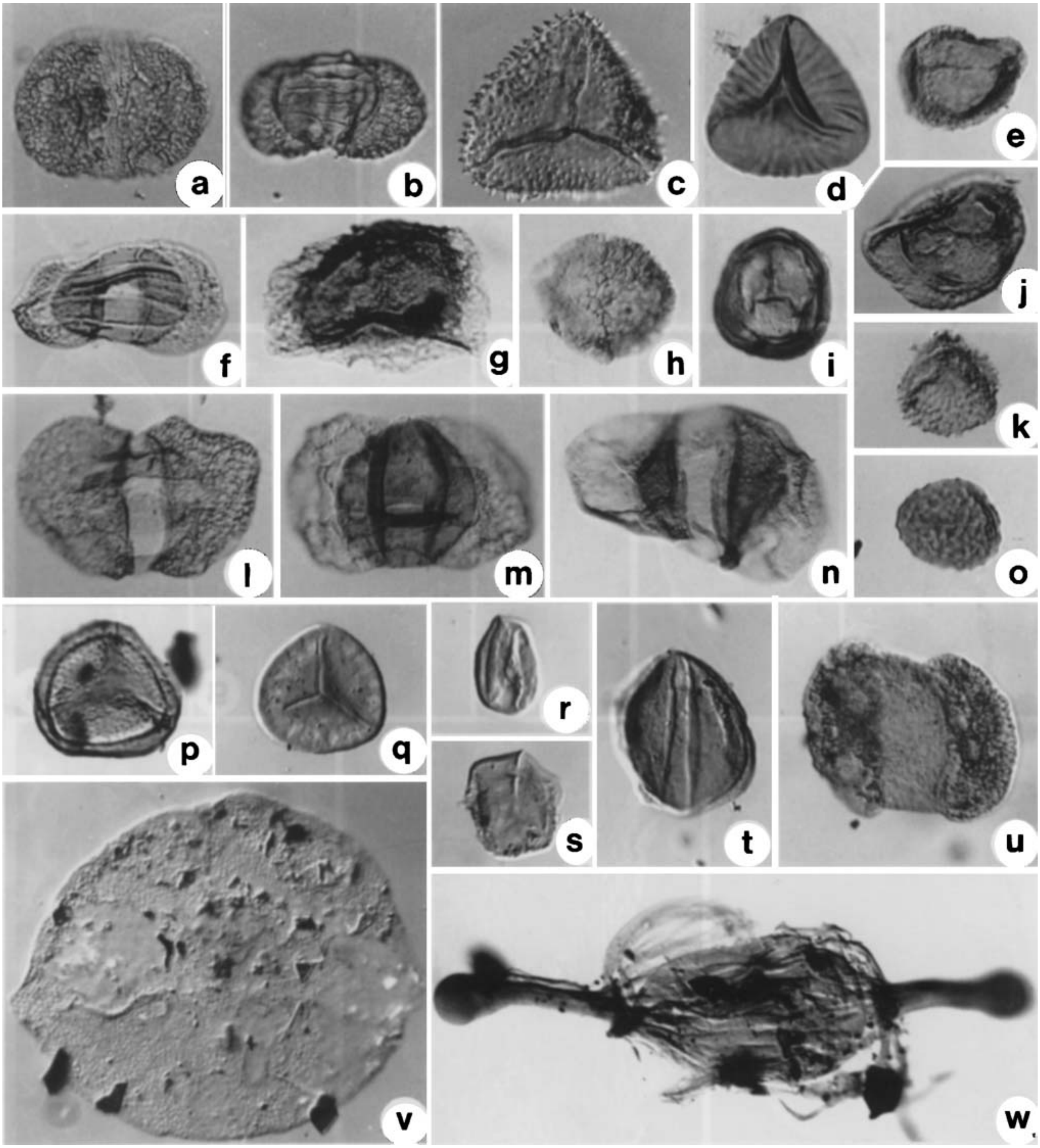


Fig. 4. Upper Permian and Triassic miospores, pollen and algal cysts from the Bainmedart Coal Measures (a–c), and the Ritchie Member (d–o) and McKelvey Member (p–w) of the Flagstone Bench Formation (all x500). Species name followed by sample number and slide number with England-finder coordinates. **a.** *Scheuringipollenites ovatus* (Balme & Hennelly) Foster, PCM92/9:2, K52/2; **b.** *Protohaploxypinus limpidus* (Balme & Hennelly) Balme & Playford, PCM92/9:2, E47/2; **c.** *Didecitriletes ericianus* (Balme & Hennelly) Venkatachala & Kar, PCM92/2b:6 (top of Toploje Member), J19/1; **d.** *Triplexisporites playfordii* (de Jersey & Hamilton) Foster, PCM95/93:21, R48/3; **e.** *Aratrisporites wollariensis* Helby, PCM95/93:16, F43/4; **f.** *Protohaploxypinus samoilovichii* (Jansonius) Hart, PCM95/2:3, O38/3; **g.** *Indotriradites saeptatus* (Balme), PCM95/93:18, F43/4; **h.** *Enzonalasporites* sp., PCM95/93:13, Z39/2; **i.** *Densoisporites playfordii* (Balme) Dettmann, PCM95/2:4, E39/1;

poorly preserved and low in diversity. They are otherwise typical of southern Gondwanan Late Permian assemblages dominated by bisaccate taeniate glossopterid pollen assigned to *Protohaploxypinus* Samoilovich emend. Morbey (Fig. 4b) and *Striatopodocarpidites* Zoricheva & Sedova ex Sedova emend. Hart, together with *Scheuringipollenites* Tiwari (Fig. 4a) a non-taeniate bisaccate gymnosperm pollen. Other gymnospermous pollen grains include *Guttulapollenites hannonicus* Goubin, *Densipollenites indicus* Bharadwaj, *Marsupipollenites triradiatus* Balme & Hennelly (Fig. 5f–h), and *Praecolpatites sinuosus* (Balme & Hennelly) Bharadwaj & Srivastava. Filicalean spores are represented by *Didecitriletes ericianus* (Balme & Hennelly) Venkatachala & Kar (Fig. 4c), *D. uncinatus* (Balme & Hennelly) Venkatachala & Kar, *Indospora clara* Bharadwaj, *Horriditriletes filiformis* (Balme & Henelly) Backhouse, *H. tereteangulatus* (Balme & Henelly) Backhouse, *Leiotriletes directus* Balme & Hennelly, *Brevitriletes levis* (Balme & Hennelly) Bharadwaj & Srivastava, *Lophotriletes novicus* Singh, *Microbaculispora tentula* Tiwari, *M. trisina* (Balme & Hennelly) Anderson and *Osmundacidites wellmanii* Couper. The most well-preserved and diverse palynoflora of the Bainmedart Coal Measures is found in a siliceous permineralized peat bed at the top of the Toploje Member and it contains all of the above mentioned taxa. The majority of these taxa have also been recorded previously in various samples from the lower parts of the Bainmedart Coal Measures (Toploje and Glossopteris Gully Members of McLoughlin & Drinnan 1997) by Balme & Playford (1967), Kemp (1973), Dibner (1976, 1978) and Playford (1990). Many of the dispersed palynomorphs belong to plants that are not represented by macrofossils, suggesting that some plants in the regional biota were composed of delicate, readily destroyed tissues or were living in local habitats not conducive to fossilization of their macroscopic parts.

The absence of members of the *Dulhuntyispora*-complex in assemblages from the Bainmedart Coal Measures hinders correlation with the Australian palynostratigraphic zones, but provides further evidence of floristic provincialism previously noted in the Late Permian (Truswell 1985). The presence in the Bainmedart Coal Measures of *Didecitriletes ericianus*, the index taxon for the base of Australian Lower Stage 5b and other equivalent palynofloras of southern Gondwana (Price 1983, Tiwari & Tripathi 1992), points to an age no older than Ufimian (Roberts *et al.* 1996). Assemblages from the Bainmedart Coal Measures also contain *Guttulapollenites hannonicus* which first appears in late Early Permian assemblages in South Africa (Anderson 1977), Pakistan (Balme 1970) and India (Tiwari & Tripathi 1992). In the Late Permian this taxon is a common and characteristic component of assemblages from these areas together with Zimbabwe (Falcon 1975), Zambia (Utting 1979), Tanzania (Hankel 1987) and Madagascar (Wright & Askin 1987). It has also been recorded from the Late Permian of Dronning Maud Land in Antarctica (Lindström 1996), the southern Perth Basin in Western Australia (Backhouse 1993) and the Bowen Basin in eastern Australia (Foster 1979). The presence of this taxon favours an age younger than Lower Stage 5b for the Bainmedart Coal Measures (i.e., equivalent to Australian Upper Stage 5), as its geographic distribution expands towards the latest Permian.

Fossil flora of the lower Flagstone Bench Formation (Ritchie Member)

With the cessation of coal development at the top of the Bainmedart Coal Measures, fossiliferous strata become scarce. Within the lower part of the Ritchie Member (the basal unit of the Flagstone Bench Formation), thin carbonaceous siltstones and shales yield assemblages containing fragmentary pinnae of the peltasperm *Lepidopteris* Schimper (Fig. 6h). Several types of megaspores (Figs 2, 6a–f) are also preserved and probably belong to a range of pleuromeian, isoetalean, or selaginellalean lycophytes. No glossopterid macrofossils have been found in these strata. Red and green mudrocks located higher in the Ritchie Member (e.g., sample 95/93) contain abundant lycophytic megaspores and microsporangia (Fig. 6n), a few *Lepidopteris* pinnule fragments (Fig. 6i), and possible *Dicroidium* Gothan cuticle (Fig. 2).

The palynofloras from the Ritchie Member on the western side of Beaver Lake (samples PCM95/1, 95/2, 95/7, 95/5) are generally much better preserved and more diverse than those from the McKinnon Member. They are dominated by non-taeniate corystospermous and peltaspermous bisaccate pollen assigned to *Falcisporites australis* (de Jersey) Stevens (Fig. 4n), *Chordasporites australiensis* de Jersey, *Alisporites tenuicorpus* Balme and *Vitreisporites pallidus* (Reissinger) Nilsson, all of which sporadically occur in the McKinnon Member. Taeniate bisaccates include *Lunatisporites pellucidus* (Goubin) Helby ex de Jersey (Fig. 4l), *Protohaploxypinus microcorpus* (Schaarschmidt) Clarke

Fig. 4. (cont.) **j.** *Aratrisporites wollariensis* Helby, PCM95/1:8, T44/3; **k.** *Apiculatisporis clematisi* de Jersey, PCM95/93:18, W44/3; **l.** *Lunatisporites pellucidus* (Goubin) Helby ex de Jersey, PCM95/2:10, H41/1; **m.** *Lunatisporites noviaulensis* (Leschik) Foster, PCM95/2:3, F50/3; **n.** *Falcisporites australis* (de Jersey) Stevens, PCM95/93:13, M47/2; **o.** *Thymospora ipsviciensis* (de Jersey) Jain, PCM95/93:19, V36/3; **p.** *Limatulasporites limatulus* (Playford) Helby & Foster, PCM92/19:8, M48/4; **q.** *Rogalskaisporites cicatricosus* (Rogalska) Danzé-Corsin & Laveine, PCM92/19:3, Q37/3; **r.** *Bartenia communis* Helby, PCM92/19:5, K38-4; **s.** *Bartenia communis* Helby, PCM92/19:4, J27/1; **t.** *Ashmoripollis reducta* Helby, PCM92/19:4, G43/3; **u.** cf. *Samaropollenites speciosus* Goubin, PCM92/19:2, X37/3; **v.** *Playfordiaspora cancellosa* (Playford & Dettmann) Maheshwari & Banerji, outer wall of pollen grain with corpus removed, PCM92/19:2, U38/2; **w.** *Steevesisporites claviger* de Jersey & Raine, PCM95/88:9, K26/3.

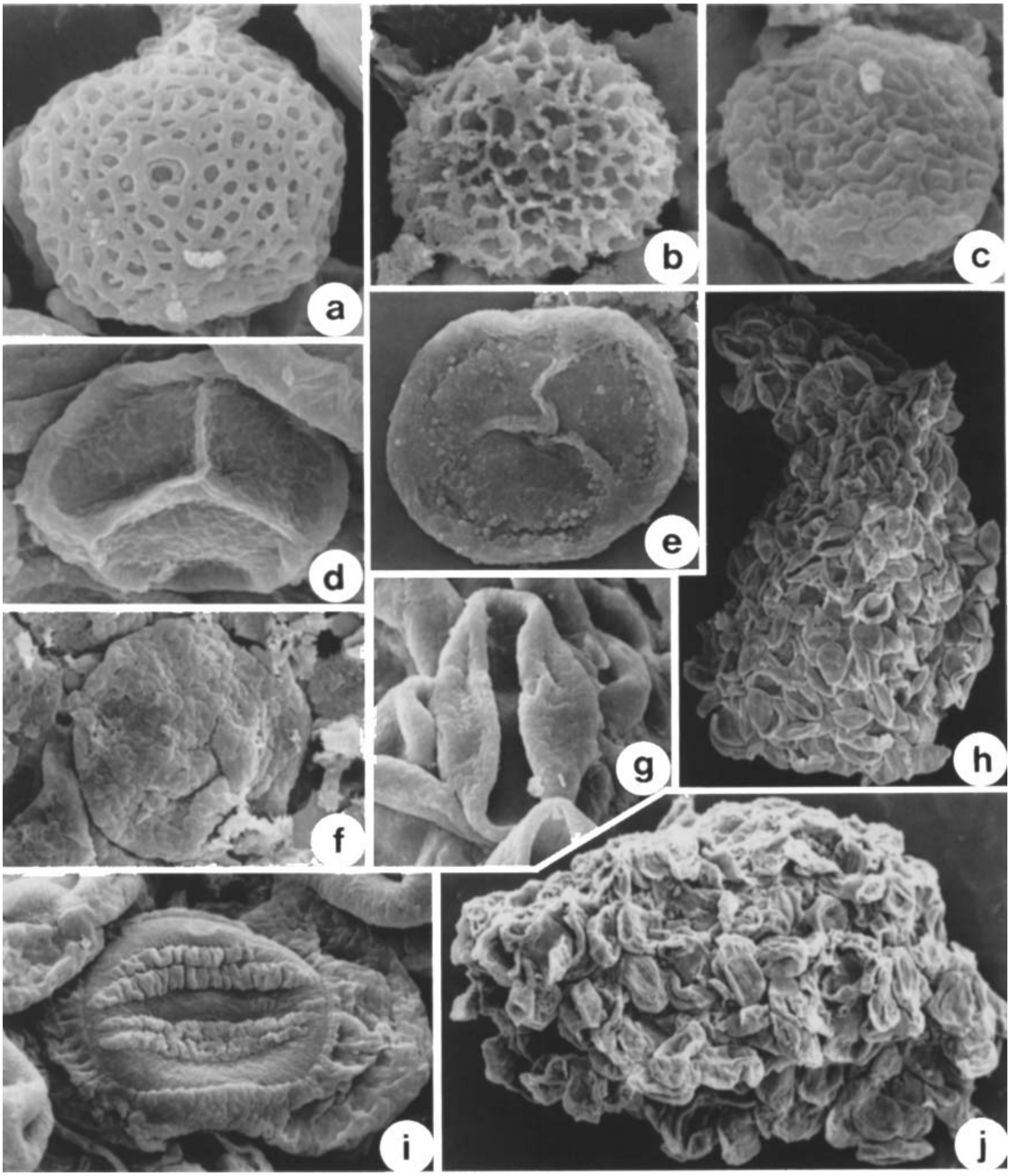


Fig. 5. Scanning-electron micrographs of Permian and Triassic miospores, pollen and algal cysts from the Bainmedart Coal Measures and Flagstone Bench Formation. **a.** *Maculatasporites* sp., note pore in centre of cyst, x1500, PCM95/2; **b.** *Dictyotidium* sp., x1000, PCM95/2; **c.** rugulate algal cyst with sculpture forming an incomplete reticulum, x2000, PCM95/2; **d.** *Limatulasporites* sp. with wrinkled proximal surface, x2000, PCM95/93; **e.** *Limatulasporites* sp. with partially granulate proximal surface, x1200, PCM95/7; **f.** *Marsupipollenites triradiatus* Balme & Hennelly, proximal view, x1000, PCM95/26A; **g.** *Marsupipollenites triradiatus*, distal view, x1000, PCM95/4; **h.** Sporangial mass of *Marsupipollenites triradiatus* pollen, x170, PCM95/4; **i.** *Lunatisporites* sp. with wrinkled/subdivided taeniae, proximal view, x1200, PCM95/93; Sporangial mass of *Lunatisporites* pollen, x200, PCM95/93.

and *P. samoilovichii* (Jansonius) Hart (Fig. 4f). Other bisaccates present are *Klausipollenites schaubergerii* (Potonié & Klaus) Jansonius and *Guttulapollenites hannonicus*. Lycophyte spores include *Densoisporites playfordii*(Balme) Dettmann (Fig. 4i),*Rewanispora foveolata* de Jersey, *Lundbladispora* Balme emend. Playford, rare inconspicuous members of *Aratrisporites* Leschik emend. Playford & Dettmann (Fig. 4e & j) and species of *Uvaesporites* Döring. Bryophytes are represented by spores assigned to *Limatulasporites* Helby & Foster in Foster

(Fig. 4p). Prominent fern spores present in these assemblages are *Brevitriletes hennellyi* Foster, *Dictyophyllidites mortonii* (de Jersey) Playford & Dettmann and *Triplexisporites playfordii* (de Jersey & Hamilton) Foster (Fig. 4d). Algal cysts belonging to a range of taxa (Fig. 5a–c) form a minor but consistent component of the Ritchie Member palynoassemblages (Fig. 7) implying persistence of at least seasonally wet conditions during deposition of the lower part of this unit.

A range of filicalean and sphenophyte spores such as *Brevitriletes levis, Leiotriletes directus, Lophotriletes novicus, Osmundacidites wellmanii, Microbaculispora trisina* and *Laevigatosporites colliensis* (Balme & Hennelly) Venkatachala & Kar found in the Bainmedart Coal Measures persist into the Ritchie Member. Rare examples of taeniate glossopterid pollen (*Protohaploxypinus* and *Striatopodocarpidites*) and sulcate/plicate gymnosperm pollen including *Marsupipollenites triradiatus* Balme & Hennelly (Fig. 5f–h) and *Weylandites lucifer* (Bharadwaj & Salujha) Foster also cross the boundary horizon (Fig. 7). However, it is not clear whether the sparse presence of these typical Permian elements in the lower Ritchie Member represents persistence of the parent plants into Ritchie Member times or whether they represent palynomorphs reworked from underlying sediments. *Guttulapollenites hannonicus* is also present in samples PCM95/2, 95/7 and 95/5 (Figs 1 & 7) from the Ritchie Member, which all contain typical Early Triassic assemblages. The only other areas where *G. hannonicus* has been recorded in the Early Triassic are the Salt Range in Pakistan (Balme 1970) and the southern Morondava Basin in Madagascar (Wright & Askin 1987).

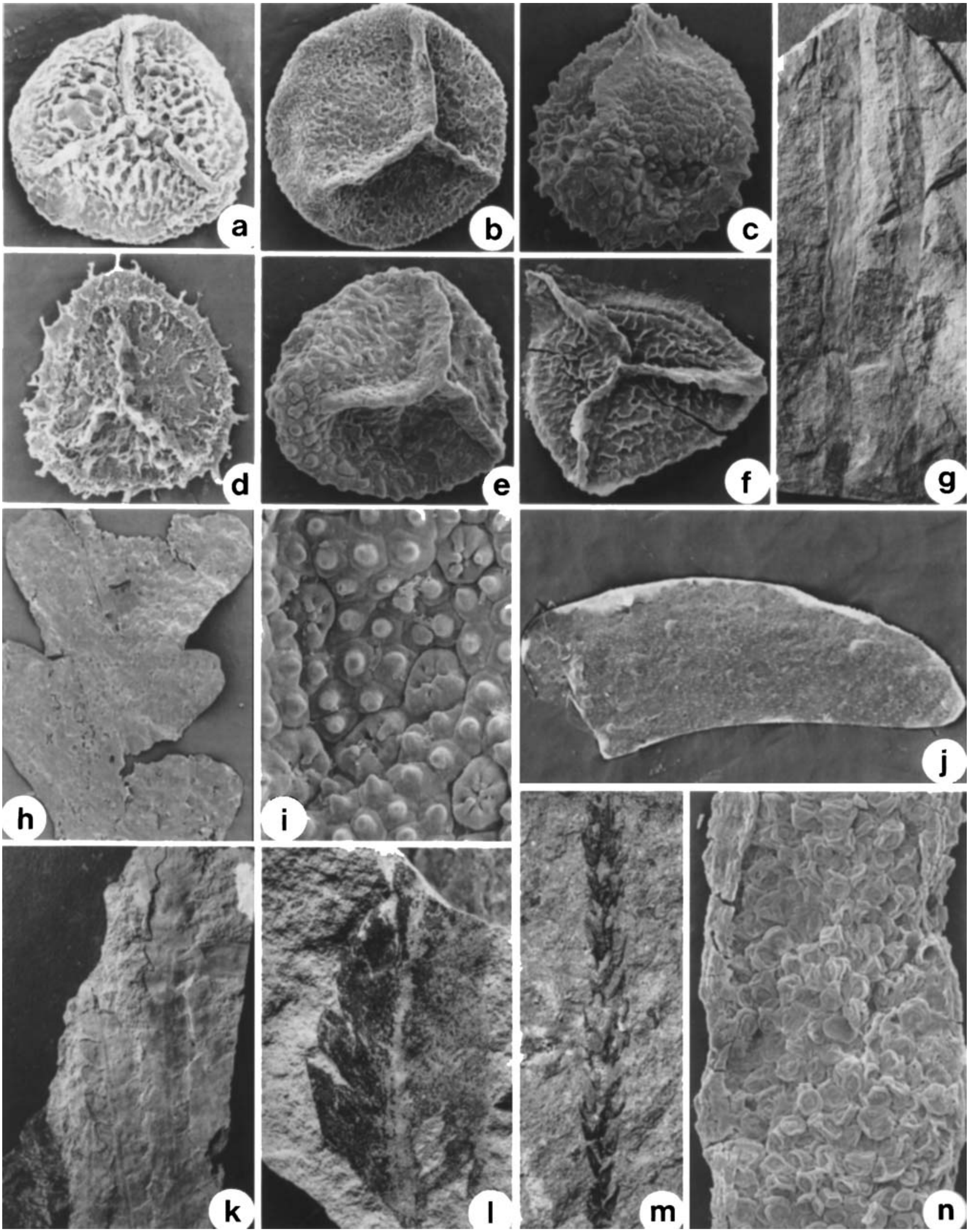
The contact between the Bainmedart Coal Measures and the Ritchie Member on the western side of Flagstone Bench is represented by a fault, and it is probable that part of the section is missing. Assemblages from the two productive samples (PCM95/89 and PCM95/93) from the Ritchie Member on Flagstone Bench differ somewhat in general composition from those recovered from Ritchie Member exposures west of Beaver Lake. *Lunatisporites noviaulensis* (Leschik) Foster and *L. obex* (Balme) de Jersey are the most common taeniate bisaccates in the Flagstone Bench assemblages. The palynoflora from the lower sample (PCM95/89) is poorly preserved, but it is the one most similar to the assemblages from west of Beaver Lake. The assemblage from the upper sample (PCM95/93) is characterized by the common presence of *Goubinispora morondavensis* (Goubin) Tiwari & Rana, the conspicuous lycophyte spores *Kraeuselisporites cuspidus* Balme and *K. saeptatus* Balme, along with the probable marattialean monolete spore *Thymospora ipsviciensis* (de Jersey) Jain.

The two Ritchie Member sections are difficult to correlate. The presence of rare specimens of *Limbosporites* Nilsson in the topmost samples from both sections (i.e. samples PCM95/5 and PCM95/93), and rare members of *Enzonalasporites* Leschik in samples PCM95/5, PCM95/89 and PCM95/93 may indicate that the assemblages from the Flagstone Bench section are equivalent to or somewhat younger than the topmost sample from the section west of Beaver Lake. *Enzonalasporites* is a coniferalean pollen grain, which first appears in Anisian strata in Australia (Helby *et al.* 1987).

Based on the common presence of *Lunatisporites pellucidus* and rare inconspicuous members of *Aratrisporites* the palynomorph associations from the lowermost Ritchie Member (samples PCM95/1, PCM95/2 to PCM95/7) are correlated with Early Triassic palynofloras of the *Lunatisporites pellucidus* and *Protohaploxypinus samoilovichii* Zones of eastern Australia (Foster 1982, Helby *et al.* 1987), and the *Kraeuselisporites saeptatus* Zone of Western Australia (Dolby & Balme 1976, Helby *et al.* 1987). The latter zone is regarded as equivalent to the upper part of the *L. pellucidus* Zone and almost the entire *P. samoilovichii* Zone (see Helby *et al.* 1987; fig. 3). Other assemblages of similar composition and age have been reported from the Mittiwali member in Pakistan (Balme 1970), the Panchet Formation in India (Tiwari & Tripathi 1992), the middle to upper Sakamena Group of Madagascar (Wright & Askin 1987, Hankel 1993), the Lower Mariakani Formation in Kenya (Hankel 1991) and palynological subzone A in Antarctica (Kyle 1977, Kyle & Schopf 1982), whereas the South American Early Triassic palynoflora reported from the Puesto Viejo Formation in Argentina by Ottone & Garcia (1991) is compositionally different.

The assemblages from samples PCM95/5, PCM95/89 and PCM95/93 are considered to be somewhat younger than those from the lowermost Ritchie Member, but because *Aratrisporites* has not been found in abundance in these samples, they are difficult to correlate with the eastern Australian *A. tenuispinosus* Zone of Helby *et al.* (1987) and the Western Australian *Triplexisporites playfordii* Zone of Dolby & Balme (1976). A similar palynoflora has been reported from the Supra-Panchet Formation of India (Tiwari & Tripathi 1992), and this was suggested to be of early Middle Triassic age.

The Australian latest Permian to Early Triassic palynostratigraphic zonations revised by Foster (1982) and Helby *et al.* (1987) include the *Protohaploxypinus microcorpus*, *Lunatisporites pellucidus*, and *Protohaploxypinus samoilovichii* Zones, which are all similar in general appearance and composition (Foster 1982). Distinctions of these zones are mainly based on common associations of key species or quantitative relationships of certain taxa. The base of the *P. microcorpus* Zone is defined by the oldest relatively common occurrence of *Falcisporites australis* and *P. microcorpus* with *P. cancellosa* and *T. playfordii*, and by the virtual absence of *Scheuringipollenites*. The base of the *Lunatisporites pellucidus* Zone is defined by the oldest regular occurrence of the key-taxon, while the upper boundary of the zone is characterized by the first appearance of *Aratrisporites* and a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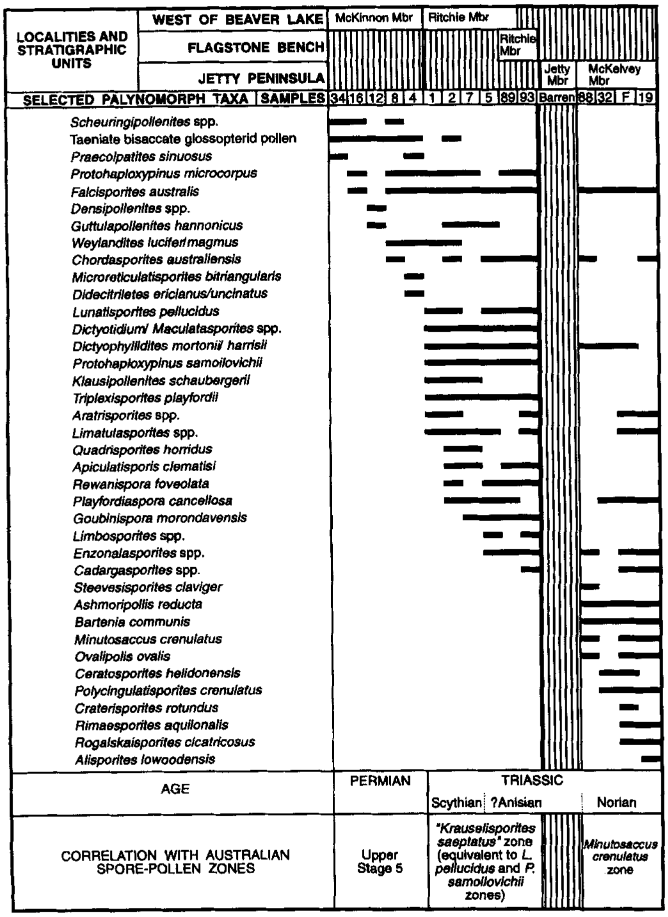

Fig. 7. Stratigraphical ranges of selected spore, pollen, and algal taxa in the upper part of the Amery Group. F = Sample of Foster *et al.* (1994). Sample numbers are abbreviated from Fig. 1.

marked decline of *Falcisporites* (Helby *et al.* 1987). Although the first regular occurrence of *L. pellucidus* has been used by some workers (Helby 1973, de Jersey 1979, Helby *et al.* 1987, Hankel 1991, 1992) to define the Permian–Triassic boundary, currently it is the first appearance of *Aratrisporites* at the base of the *P. samoilovichii* Zone which is considered to be coincident with the base of the Triassic (Foster (1982 and personal communication 1996). However, it is noteworthy that inconsistent occurrences of *Aratrisporites* have been reported from older Australian assemblages attributed to the *L. pellucidus* and *P. microcorpus* zones (Helby *et al.* 1987). Significantly, these earliest inconsistent occurrences of *Aratrisporites* around the base of the *P. microcorpus* zone in Australia also correspond to a sharp shift in $^{13}C/^{12}C$ ratios of fossil organic matter correlative with the Permian–Triassic boundary in Europe (Morante 1996). Helby (1973) suggested that the *P. microcorpus* Zone extends into Lower Triassic strata as a lateral facies equivalent of the *L. pellucidus,* and *P. samoilovichii* Zones. According to Helby *et al.* (1987) the *P. microcorpus* Zone is not readily recognizable in the western and northern parts of Australia. The quantitative differences between Early Triassic assemblage zones may in part reflect local macrofloristic successional states influenced by environmental changes taking place at different times in separate parts of Gondwana. Additionally, all Amery Group samples examined contained numerous whole or fragmentary lycophyte, pteridophyte and gymnosperm sporangia (Figs 3h, 5h & j, 6n), and it is possible that individual assemblages become quantitatively skewed towards any one of these groups when sporangia are disaggregated during the maceration process. If these zones are indeed facies controlled, it is quite possible that they are diachronous across Gondwana. Despite possible facies controls and diachroneity in inception of index taxa like *Aratrisporites* and the zones that they characterize, we consider that the first regular occurrence of *L. pellucidus* and/or the first appearance of *Aratrisporites* to be the best available approximation of the Permian–Triassic boundary. In the Prince Charles Mountains this horizon is at the top of the Bainmedart Coal Measures or within the lowermost 25 m of the Flagstone Bench Formation.

Fossil flora of the upper Flagstone Bench Formation (McKelvey Member)

Abundant remains of Corystosperms (*Dicroidium*, Fig. 6k), conifers (*Pagiophyllum* Heer, Fig. 6m, *Heidiphyllum* Retallack, Fig. 6g) and other gymnosperms or ferns (Fig. 6l) appear in the succession around the base of the Norian McKelvey Member (Cantrill *et al.* 1994, Fig. 2). Hirsute scales (Fig. 6j) recovered by bulk maceration of a siltstone layer (sample 92/19) from the McKelvey Member possibly represent chitinous components of an arthropod exoskeleton, and are the only evidence of animal fossils in the Triassic succession.

Foster *et al.* (1994) reported a Late Triassic (Norian) palynoflora from the McKelvey Member, dominated by

Fig. 6. Scythian to Norian lycophyte megaspores and plant macrofossils from the Flagstone Bench Formation (Ritchie Member, a–e, h, I, n; McKelvey Member, f, g, j–m). **a.** *Horstisporites* sp. C, proximal view, x120, PCM95/93; **b.** Weakly reticulate/scabrate megaspore (n. gen.), proximal view, x125, PCM95/2; **c.** *Bacutrileites* sp., equatorial view, x135, PCM95/5; **d.** *Ancorisporites* sp., proximal view, x145, PCM95/93; **e.** *Verrutriletes* sp. A, proximal view, x95, PCM95/93; **f.** *Minerisporites triangulatus* Cantrill & Drinnan, proximal view, x80, PCM92/19; **g.** *Heidiphyllum elongatum* (Morris) Retallack, x0.7, PCM92/19; **h.** *Lepidopteris* sp., pinna fragment, x12, PCM95/1; **i.** *Lepidopteris* cuticle enlarged to show stomata strongly protected by epidermal papillae, x250, PCM95/93; **j.** hirsute scale from ?arthropod, x110, PCM92/19; **k.** *Dicroidium zuberi* (Scajnocha) Archangelsky, x0.7, PCM92/19; **l.** unidentified gymnosperm leaf or fern pinnule, x2, PCM92/19; **m.** *Pagiophyllum papillatus* Cantrill & Drinnan, x1.6, PCM92/19; **n.** lycophyte microsporangium containing *Limatulasporites*/*Densoisporites*-type spores, x200, PCM95/93.

Falcisporites. Three samples from this unit were examined in this study, none of which are stratigraphically equivalent to the sample of Foster *et al.* (1994, fig. 1). The assemblage examined by Foster *et al.* (1994) and all three samples studied here are referable to the Australian *Minutosaccus crenulatus* zone (Fig. 7), based on the co-occurrence of *Ceratosporites helidonensis* de Jersey, *Polycingulatisporites crenulatus* Playford & Dettmann, *Bartenia communis* Helby (Fig. 4r & s), *Ashmoripollis reducta* Helby (Fig. 4t), *Craterisporites rotundus* de Jersey and *Minutosaccus crenulatus* Dolby in Dolby & Balme. Important associated forms include *Enzonalasporites vigens* Leschik, *Samaropollenites speciosus* Goubin (Fig. 4u) and abundant *Falcisporites australis*.

In this study additional support for a Late Triassic age comes from the presence of rare examples of *Steevesisporites claviger* de Jersey & Raine (Fig. 4w), which has a Carnian to Early Jurassic range in eastern Australia and New Zealand (de Jersey 1970, de Jersey & Raine 1990), and which has also been identified in the Carnian of Argentina (Zavattieri & Batten 1996). The McKelvey Member assemblages are dominated by non-taeniate bisaccate pollen, especially *Falcisporites australis*. In the uppermost sample, however, *Ashmoripollis reducta* and *Alisporites lowoodensis* de Jersey are prominent constituents of the palynoflora. Lycophyte/bryophyte spores (e.g. *Limatulasporites* spp. Figs 4p, 5d & e) show a decline in abundance compared to assemblages from the lower Flagstone Bench Formation and are replaced by spores of probable filicalean alliance. Except for the absence of *Craterisporites rotundus* and dinoflagellates, the three McKelvey Member samples studied herein are otherwise comparable to that of Foster *et al.* (1994) and support a Norian age assignment for the McKelvey Member.

Diachroneity of the change from coal measure to red-bed sedimentation

Part of the difficulty in defining the position of the Permian–Triassic boundary in Gondwanan successions is due to the dearth of marine successions of this age and the strong provinciality of the global terrestrial floras of that time, providing few widespread species for intercontinental correlations. However, part of the difficulty in positioning the boundary may flow from the correlation of diachronous units and fossil assemblages that accumulated under similar climatic conditions in different parts of the supercontinent.

In the palaeotropical belt of Euramerica, the transition from coal deposition to red-bed and evaporite sedimentation took place in latest Carboniferous to earliest Permian times (Fig. 8), and may have been largely synchronous with the peak of Gondwanan glaciation (Bissell 1973, A. Ziegler 1990, P. Ziegler 1990). However, this sedimentological change was not instantaneous and appears to have occurred at slightly different times within different basins. A gradual shift from "palaeophytic" to "mesophytic" floristic signatures corresponds to the sedimentological transition (Meyen 1987, Di Michele & Mamay 1996).

In the higher latitudes of Gondwana a similar sedimentological transition may have occurred throughout the Late Permian to Middle Triassic interval (Veevers *et al.* 1994a, 1994b). On a broad scale it is clear that the transition from coal-bearing strata to red-bed and evaporitic deposits occurred relatively early (around early Late Permian times) in the westernmost portion of Gondwana (Parana Basin, South America), which was then located at relative low latitudes (*c.* 20°S, Rocha-Campos 1971, Soares *et al.* 1978, López-Gamundí *et al.* 1992). In the low to mid-latitude (30°–40°S) basins of Tanzania and Madagascar, red-beds also initiated around Artinskian-Kungurian times (Wopfner 1992, Hankel 1994). Red-beds constituting parts of the Lower Beaufort Group in the Karoo Basin of southern Africa at palaeolatitudes of *c.* 50°–60°S were not deposited until the Late Permian (Kent 1980, Anderson & Anderson 1985).

India lay at latitudes of *c.* 30°–60° during the Late Permian to Late Triassic (Smith *et al.* 1981, Wilson *et al.* 1994). Although some Upper Permian units (e.g. Kulti, Motur, and Kamthi Formations) of peninsular India are deficient in coals and locally contain reddened sideritic or haematitic shales, typical red-beds consisting of greenish white sandstones alternating with red, haematitic mudstones are best developed in the Lower Triassic Panchet Formation and its equivalents (Lele 1969, Casshyap 1979, Fig. 8). Red-bed sedimentation continued in most peninsular India basins throughout the Middle Triassic (Pachmarhi and Denwa Formations and lateral equivalents) and persisted, albeit with lesser expression, into the Late Triassic (Tiki and Parsora Formations and equivalents; Lele 1969, Sastry *et al.* 1979). Dutta & Laha (1979) interpreted the shift from Late Permian coal sedimentation to Early Triassic red-bed development to be a consequence of a change from humid to semi-arid conditions.

In eastern Australia (located at palaeolatitudes of *c.* 60°–75°S), the cessation of coal deposition appears to be close to or slightly below the base of the Triassic as defined by palynological and radiometric data (Foster 1982, Retallack 1995, Roberts *et al.* 1996). Several workers (Morante 1993, 1996, Morante *et al.* 1994, Retallack 1995) have also noted evidence of a sharp drop in $^{13}C/^{12}C$ ratios of kerogen immediately above the highest coal seams within Australian basins, comparable to that found in studies of the Permian–Triassic boundary sequence in other parts of the world. In eastern Australia cessation of coal accumulation generally corresponds to the last appearance of glossopterid macrofossils, although *Glossopteris* has occasionally been reported from strata up to 20 m above the highest coal in the Sydney Basin (Morante 1996). Strata immediately overlying the coals are also marked by the first appearance of *Dicroidium* and/or *Lepidopteris*, typically in association with voltzialean conifers and pleuromeian lycophytes. Gondwanan taeniate bisaccate pollen, traditionally attributed to glossopterids, persists into coal-free Lower Triassic strata. However, some

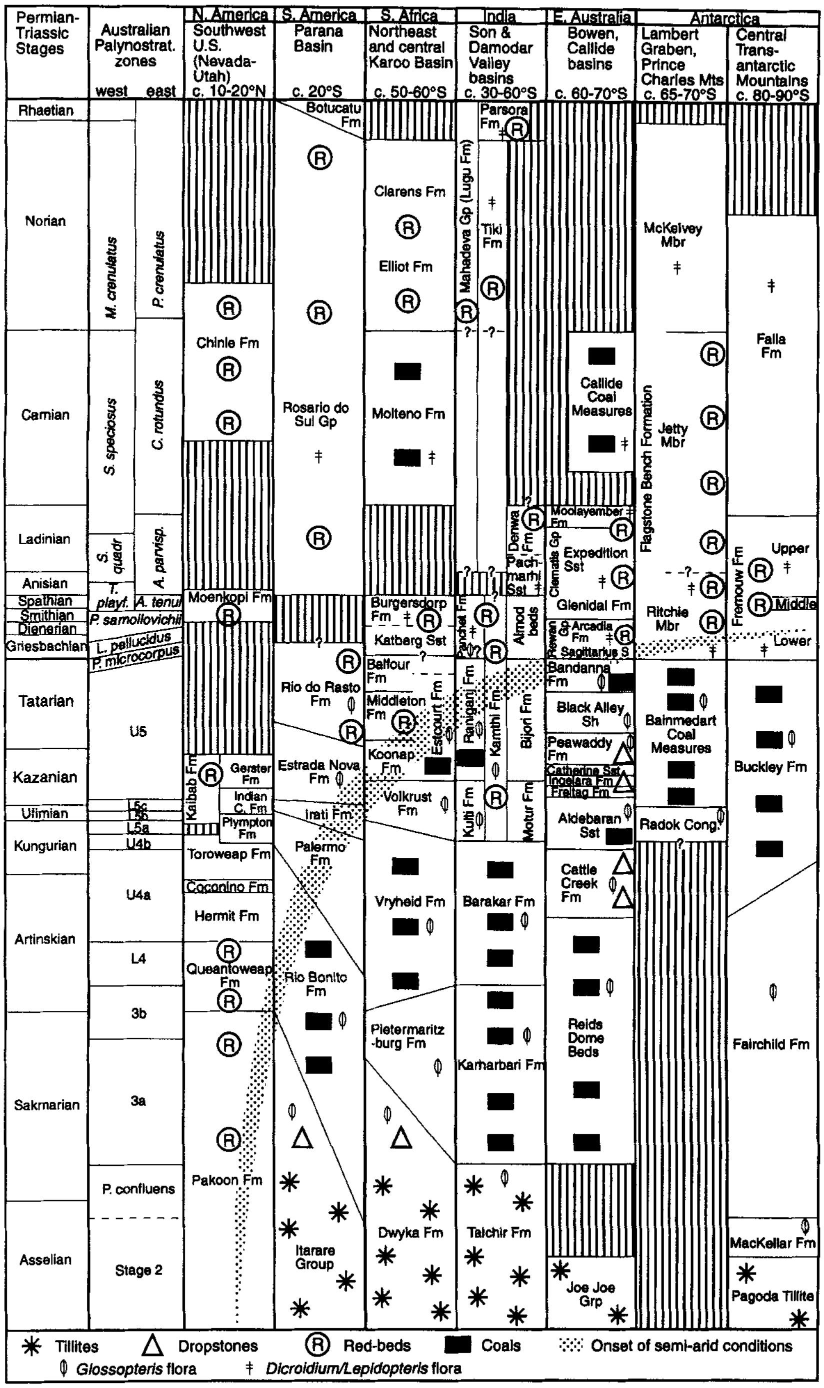

Fig. 8. Correlation chart for Permian–Triassic units in selected Gondwanan and North American basins showing diachronous termination of coals and inception of red-beds from the Early Permian to Middle Triassic between different palaeolatitudes. Stages after Harland *et al.* (1990), palynostratigraphic zones modified from Price (1983) and Helby *et al.* (1987), stratigraphy after Bissell (1973), Dickins & Malone (1973), Rocha-Campos (1971), Sastry *et al.* (1979), Dutta & Laha, (1979), Kent (1980), Zalán *et al.* (1987), Hintze (1988), Collinson *et al.* (1994) and McLoughlin & Drinnan (in press).

of these pollen types may have been produced by non-glossopterid gymnosperms, as similar pollen is abundant in Permian–Triassic rocks of the Northern Hemisphere where glossopterids are unknown. Basal Triassic sequences in eastern Australia are dominated by prominent fluvial sandstone packages, before development of terrestrial red-beds slightly higher in the Lower Triassic (Jensen 1975, Retallack 1977, Tadros 1995, Fig. 8). In most Western Australian basins a prominent hiatus typifies the uppermost Permian (Archbold 1992), before deposition of ammonoid-bearing ferruginous marine sediments in the Early Triassic (Balme 1963, 1989).

The Prince Charles Mountains were centrally located in Gondwana and at palaeolatitudes of *c.* 65°–70°S during the Late Permian and Early Triassic. The major floristic turnover, both in terms of quantitative representation of plant groups and in terms of the peak in extinctions and first appearances, coincides with the termination of coal sedimentation at the Permian–Triassic boundary. Deposition of typical red-beds did not commence until around the late Early Triassic and may not have reached full development until the Middle Triassic or Carnian (Fig. 8). At even higher palaeolatitudes (*c.* 80°–90°) in the Transantarctic Mountains, red-beds and green siltstone facies are represented in Early to Middle Triassic units (Collinson *et al.* 1981, Collinson *et al.* 1994), but are less well developed than in lower palaeolatitude Gondwanan basins.

A general trend in time of initiation of red-bed sedimentation is apparent from Late Carboniferous times at low latitudes in Europe–North America, the mid-Permian in western Gondwana, the close of the Permian or Early Triassic in the India–Australia region, and the late Early to Middle Triassic at the higher latitudes occupied by Antarctica (Fig. 8). This striking sedimentological transition may have been associated with long-term poleward shift of climatic belts subsequent to the decline of Gondwanan glaciation around the beginning of the Permian. The large size of the Gondwanan landmass, spanning polar to near-equatorial latitudes, probably interrupted the normal Equator to Pole zonal atmospheric and oceanic circulation cells, and differential heating and humidity between the coasts and continental interior probably led to strongly seasonal climates over extensive areas after the decline of Permian glaciation (Parrish 1990). Progressive global warming through the remainder of the Permian may have favoured the poleward shift of the "Gondwanan monsoon" conditions described by Parrish (1990, 1995), resulting in a global peak in red-bed development around mid-Triassic times.

Controls on sedimentation and floristic change across the Permian–Triassic boundary

The evidence of sedimentological change in Gondwanan basins favours a gradual climatic change (involving warming and development of seasonally dry climates) from the Early Permian to Middle Triassic (Fig. 8). Sea levels generally fell throughout the Permian following the maximum post-glacial transgressions of the Artinskian, although the general trend may have been punctuated by several marine incursions in the mid- to late Permian (Ross & Ross 1987, Briggs 1989, Erwin 1995). A sharp marine transgression characterized the Early Triassic in many marginal Pangean basins (Balme & Helby 1973), but it is not recognizable in interior Gondwanan rift basins like the Lambert-Mahanadi grabens.

Gondwanan Permian glossopterid-dominated floras were mostly adapted to seasonally cool, consistently moist, mire environments. These floras show gradual taxonomic turnover during the Permian with a notable increase in diversity of glossopterids, other gymnosperms, and herbaceous sphenophytes towards the end of the period (Retallack 1980, McLoughlin 1992). It is clear that some glossopterids produced polymorphic pollen (Lindström *et al.* in press) and that in the dispersed state such pollen would be assigned to several different genera and species. The apparent species-level magnitude of the end-Permian extinctions might be artificially exaggerated if counts of palynomorph species numbers are the only criteria used to assess floristic turnover. Nevertheless, dramatic extinction of glossopterids appears to roughly correspond to the cessation of coal sedimentation around the Permian–Triassic boundary in Australia and Antarctica, although they appear to have persisted, albeit in low numbers, into fluvial successions barren of coal in the Late Permian of western Gondwana (Rohn & Rösler 1989a, 1989b) and may have even persisted within wetter refugia into the earliest Triassic in India (Pant & Pant 1987). Reports of glossopterids from much younger successions are probably misidentifications of typical Mesozoic gymnosperms such as *Gontriglossa* Anderson & Anderson, *Mexiglossa* Delevoryas & Person, *Anthrophyopsis* Nathorst and *Sagenopteris* Presl.

Early Triassic Gondwanan floras were typically also of low-diversity but characterized by herbaceous to shrub-like heterosporous lycophytes probably dominating the understorey and coastal vegetation, and *Lepidopteris* (Peltaspermales), multiforked *Dicroidium* (Corystospermales), and scale-leafed *Voltziopsis* Potonié (Coniferales) dominating the overstorey vegetation of distinct environments or regions (Retallack 1980). In both India and East Antarctica *Lepidopteris*-dominated floras appear immediately after the end-Permian extinctions, and these floras are gradually replaced by *Dicroidium*-dominated floras later in the Triassic (Sastry *et al.* 1979, this study). The Middle and Late Triassic saw diversification of the gymnosperm floras and gradual replacement of lycophytes by ferns as the major understorey plants.

Floristic turnovers around the end of the Permian involving disjunct first appearances of peltasperms, ginkgophytes, ferns, and conifers, and last appearances of cordaitaleans, dicranophyllaleans, cardiolepidaceans, and arborescent lycophytes also occur in the northern high latitude floras (Meyen 1987). However, in most cases the floristic changes appear to initiate earlier in the lower palaeolatitude (*c.* 30°–45°) Sub-angaran and Russian Platform successions than in the higher (*c.* 50°–70°) palaeolatitude central Siberian (Angaran) successions (Meyen 1987). While climate change like the poleward shift of monsoonal conditions during the Permo-Triassic may have been a factor in the turnover of some plant groups in specific regions, a simple climatic explanation may not be applicable to all floristic changes across the globe.

As some components of the *Glossopteris* flora persisted into Late Permian red-bed sequences developed in western parts of Gondwana (Fig. 8), the sharp changes in the floras at the Permian–Triassic boundary do not appear to be entirely a response to climatic warming and drying. Extinctions in the terrestrial realm may have been a response to a combination of factors including: climate change, sea level fluctuation and changes in the proportions of atmospheric gases (Renne *et al.* 1995, Morante 1996). Canyonization of coastal plains during maximum Late Permian regression (during the formation of lowstand systems tracts) probably enhanced the drainage of lowland mires and continental interior lakes (environments favoured by glossopterid communities). Subsequent rapid inundation of coastal habitats during the Early Triassic (forming transgressive systems tracts) probably reduced the area available for coastal lowland mire communities. Although Amery Group sediments were deposited in alluvial valleys away from coastal environments, the substantial fluctuations in sea level around the Permian–Triassic boundary may have affected the dynamics of entire fluvial systems and promoted the demise of glossopterid-dominated swamp vegetation even in areas relatively remote from the coasts.

The presence of diverse palynofloras but low diversity macrofloras in the Late Permian suggests that a number of plant groups that appeared at that time were occupying habitats located away from the major sites of deposition so that their remains are rarely preserved in macrofossil assemblages. Some palynomorph groups (e.g. *Falcisporites* spp.) first appeared in the Late Permian but only rose to prominence in the Early Triassic. Some of the gymnosperm groups that came to dominate the Triassic floras may have established adaptations to well-drained Permian "upland" habitats and following the end-Permian extinctions may have required considerable time to re-diversify and favourably adapt to coastal plain wetland environments and to re-develop coal-forming forest-mire communities with the return of humid conditions in the Late Triassic.

Conclusions

The first abundant occurrence of *Lunatisporites pellucidus* together with the first appearance of *Aratrisporites* spores and *Lepidopteris* foliage is considered to correspond approximately with the base of the Triassic System within the Amery Group succession, although we note several problems involving floristic provincialism and potential diachroneity of first appearances of taxa associated with the recognition of established Early Triassic palynological assemblage zones. These index taxa first occur within the lowest 25 m of the Flagstone Bench Formation and the Permian–Triassic boundary may be coincident with the top of the Bainmedart Coal Measures. The Amery Group Permian–Triassic transition is thus marked by a sharp change from coal-bearing sediments to sandstone-dominated successions lacking coals. The boundary also marks the greatest macro- and palynofloristic turnover within the Amery Group. Glossopterid and cordaitalean gymnosperms that dominated the Permian floras were replaced initially (in the Early Triassic) by peltasperm- and lycophyte-dominated floras, followed (in the Norian) by more diverse corystosperm-, conifer-, and fern-dominated floras. Whereas coals disappear at the end of the Permian, red-beds are not well-developed until the late Early Triassic and may not have reached maximum expression until the Middle Triassic or Carnian (within the upper Jetty Member). The sedimentological and palaeobotanical changes evident at the boundary suggest a transition from consistently wet conditions in the Late Permian to more seasonally dry climates in the Triassic. The demise of glossopterid-dominated vegetation and its replacement by peltasperm-, lycophyte-, and corystosperm-dominated floras appears to be essentially synchronous across Gondwana. This contrasts somewhat with the apparent diachronous demise of coal sedimentation and inception of red-bed development across Gondwana from mid-Permian to mid-Triassic times. The synchroneity of the major floristic change suggests that factors other than, or additional to, simple climatic change may have contributed to the Permian–Triassic terrestrial extinctions.

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