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# Late Permian flora of the Little River Coal Measures, northeastern Australia

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#### ABSTRACT

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A small assemblage of plant macrofossils incorporating representatives of *Glossopteris*, *Vertebraria*, *Dictyopteridium*, *Samaropsis* and *Schizoneura* is described from the Little River Coal Measures in northeast Queensland, Australia. The assemblage is interpreted to be of Lopingian age based on taxa shared with units in the Bowen Basin to the south. The fossil assemblage represents the northernmost late Permian flora yet described from Australia but has a typical representation of Gondwanan taxa and lacks evidence of Cathaysian elements. The only evidence of an associated fossil fauna is in the form of possible oviposition scars on some *Glossopteris* leaves. The assemblage is associated with coal beds and is considered to reflect growth in peat-forming alluvial plain settings under a mid-latitude humid temperate climate.

Keywords: Glossopteris, Schizoneura, Dictyopteridium, Lopingian, end-Permian, Laura Basin, Australia.

#### **INTRODUCTION**

A small collection of fossil plants from the Little River Coal Measures in the Cooktown region of northeastern Australia recovered during a regional geological mapping program was briefly documented in an unpublished Australian Bureau of Mineral Resources record by White (1961b). Morphological details of some of those specimens are difficult to resolve from the halftone images in that report, hence the initial identifications and age of the host unit have remained equivocal. Although Jack (1882) first reported *Glossopteris* leaves and log impressions from this unit, White's (1961b) brief report has provided the only descriptive documentation of the flora of the Little River Coal Measures, which, together with the Normanby Formation and un-named coal-bearing strata hosting plant remains in the adjacent Lakefield and Olive River basins, represent the northernmost Permian continental strata in Australia (Wells 1989a, b, c). Palynological studies have not yielded spore-pollen assemblages from the Little River Coal Measures (Hawkins & Williams 1990), apparently owing to the high thermal maturity of the unit resulting from an elevated geothermal gradient imposed by mid-Triassic orogenic events in the region. In the absence of palynomorphs, marine fossils or datable ash beds, the plant macrofossils provide the primary means for assigning an age to this unit.

This study is part of an ongoing program to document and revise the Permian floras of eastern Australia. Given the limited understanding of the age and fossil content of the Little River Coal Measures, this study aims to describe and illustrate the available fossil flora with modern techniques, and assess the host unit's age based on taxa shared with units in adjacent basins. **GEOLOGICAL SETTING** 

The Little River Coal Measures crop out sporadically in the Little Kennedy River valley, near Fairlight Station located around 150 km west of



Figure 1. Geological setting of the Little River Coal Measures. A, Late Permian palaeogeographic map showing the position of the Little River Coal Measures and the Sydney-Gunnedah-Bowen foreland basin complex in southeastern Gondwana. B, Map of Queensland (northeastern Australia) showing the distribution of Permian basins with exposed strata (blue) and subsurface strata (yellow). C, Geological map of northern Queensland (see area marked in B) showing the distribution of rock units in the area exposing the Little River Coal Measures. D, Geology of the Palmer River–Fairlight Station district (area marked in red box in C). Fossil locality indicated by a star in A, C, D. Geology after Domagala et al. (1997) and Bain & Draper (1997).

Cooktown and 40 km west of Laura in northern Queensland, Australia (Figure 1.A–D). The formation, named by Bryan (1928), occurs in a fault-bound block, c. 2 km wide and >20 km long (Figure 1.D), near the southern flanks of the Laura Basin (Figure 1.C) in a structurally deformed region controlled by strike- and dip-slip movement along the Palmerville Fault (Bultitude 1997, McConachie et al. 1997). The coal measures are steeply dipping (35-70°) and faulted against the Jurassic Dalrymple Sandstone overlying Mesoproterozoic metamorphic rocks to the west and the Silurian-Devonian Chillagoe Formation to the east (Jack 1882, Wells 1989c). The region has a relatively rugged topography, is covered by fairly dense mixed tropical savannah woodland, and lacks extensive infrastructure (Bernal & Osborne 2019). Visiting the fossil locality can be difficult during the wet season owing to periodic flooding of the primarily access via the Palmerville Road (Figure 1.D).

The Little River Coal Measures reach at least 500 m thick and consist primarily of feldspathic and lithic sandstone, siltstone, carbonaceous and ferruginous shale, with lesser proportions of coal and siliceous (?tuffaceous) mudstone (de Keyser & Lucas 1968, Domagala et al. 1997). De Keyser & Lucas (1968) reported lenses of impure limestone within the unit, although this seems to be at odds with the fluvial-lacustrine-paludal depositional setting inferred for the coal measures (McConachie et al. 1997). The formation contains at least five prominent coal seams (Jack 1882).

The presence of coal in this unit has attracted the attention of economic geologists for 150 years. Coal was first discovered in the area by the geologist Norman Taylor on William Hann's exploratory expedition to northern Queensland in 1872; one seam (around the middle of the succession) reportedly reaches 6 m thick (Jack 1882). Several surveys prospecting for economic coal and/or hydrocarbon resources have been carried out around Fairlight Homestead and adjacent areas of the Laura Basin in the past few decades (e.g. Bernal & Osborne 2019). Despite the presence of thick seams, the coal is heavily cleaved, is of anthracitic grade, has a

fairly high ash content, is steeply dipping, and lateral continuity of beds is constrained by extensive faulting and chaotic folding caused by post-Permian movement along the Palmerville Fault (Wells 1989c, Bultitude 1997). Owing to their generally small geographic extent, poor quality and structural complexity, there has been no commercial exploitation of the coals from the Little River Coal Measures to date (Carr 1975, McConachie et al. 1997).

The Little River Coal Measures are probably correlative with the Glossopteris-bearing Normanby Formation (Lucas & de Keyser1965) exposed in small (<2 km wide) fault blocks around 30 km southwest of Cooktown and considered to be of Lopingian age (McConachie et al. 1997). Further, these two units are probably correlative with un-named Permian-?Triassic strata within the Lakefield Basin (McConachie et al. 1997) that are overlain by the extensive Jurassic and Cretaceous strata of the Laura Basin to the north (Wells 1989c). The lateral extent of Permian-Triassic strata beneath the Laura Basin remains poorly resolved, but they possibly range in the subsurface eastwards to the edge of the continental shelf and northwards along the coast to the small Olive River Basin near Cape Grenville (Wells 1989a). The Mount Mulligan Coal Measures, exposed in an outlier around 90 km west of Cairns, are also probably correlative with the Little River Coal Measures but are much less deformed (Wells 1989b) and contain a well-preserved late Permian (Lopingian) flora (White 1961a, Shi et al. 2010).

#### **MATERIAL AND METHODS**

This study is based on a very small number of plant fossils held in the Commonwealth Palaeontological Collections at Geoscience Australia, Canberra (c. 10 slabs prefixed CPC F), the Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm (two slabs prefixed NRM S), and the Geological Survey of Queensland fossil collections (single specimen prefixed GSQ F) housed at the Queensland Museum, Brisbane. These appear to be the only fossil specimens available from the Little River Coal Measures in institutional collections. All specimens are preserved as impressions in grey to reddish (ferruginous) siltstones.

Specimens were photographed using a Canon 40D digital camera with low angle illumination of the specimen from the upper left unless otherwise stated. All specimens are preserved as impressions, hence cuticular analysis was not possible. References for the authorities of extant taxa can be found in the International Plant Names Index (https://www.ipni.org/).

#### SYSTEMATIC PALAEOBOTANY

**Class:** *Polypodiopsida* Cronq., Takht. & W. Zimm.

Order: Equisetales DC. ex Bercht. & J. Presl

Family: *Echinostachyaceae* Grauvogel-Stamm 1978

Genus: Schizoneura Schimp. & A. Moug. 1844

**Type species:** *Schizoneura paradoxa* Schimp. & A. Moug. 1844; Lower Triassic, Mulhouse, Germany.

Schizoneura gondwanensis Feistm. 1876a

Figure 2.A–D

**Material:** CPC F21878, CPC F21879, CPC F21880, CPC F21881, CPC F21885.

**Description:** Paired foliar units, each consisting of up to nine laterally fused linear leaves, arranged oppositely at nodes on a 2–3 mm wide, longitudinally striate stem (Figure 2.B). Internode length >16 mm. Lamina units broadly obovate, elliptical to lanceolate (Figure 2.A, C), up to 18 mm wide and estimated to be c. 60 mm long (all units incomplete). Individual fused leaves typically 2.0–2.5 mm in maximum width, with a prominent midvein (up to 0.5 mm wide), and distinct transverse striae on the lamina (probably denoting epidermal cell orientations: Figure 2.D).

**Remarks:** The paired arrangement of foliar units (sets of fused leaves), imposes bilateral symmetry on the plant and, together with the slender attached axes, suggests that these remains represent distal portions of a small, possibly climbing, sphenopsid. A climbing or scrambling habit has been proposed for Schizoneura species by various authors (Grauvogel-Stamm 1978, McLoughlin 1993a, McLoughlin et al. 2021a). Moreover, Bomfleur et al. (2013) noted that the number of foliar units varies with the diameter of the host axis in Gondwanan schizoneurids and inferred that S. gondwanensis may represent the distal portions of the same plant that bore more robust S. africana-type foliage in its proximal parts. Schizoneura gondwanensis appears to have been a relatively common understorey component of the Lopingian and Early Triassic vegetation across Gondwana, being one of the few plant taxa that persisted through the end-Permian extinction event (Feistmantel 1876a, b, Etheridge 1903, Anderson & Anderson 1985, Rohn & Rösler 1986, Goswami et al. 2006, Prevec et al. 2009). The leaf fragment identified by Vajda et al. (2020) as Ginkgophytopsis sp. probably also represents a portion of a S. gondwanensis foliar unit indicating the presence of this species in beds immediately overlying the end-Permian extinction horizon in the Sydney Basin.

#### Class: Dictyopteridiopsida Doweld 2001

**Order:** *Dictyopteridiales* McLoughlin ex Doweld 2001

Figure 2. Plant macrofossils from the Little River Coal Measures (Lopingian), northeastern Australia. A–D. Schizoneura gondwanensis Feistm. 1876a. A. Lamina segment composed of nine laterally fused univeined leaves, CPC F21878; B. Two overlapping stems with paired lamina units, CPC F21880; C. Matted elliptical lamina units, CPC F21881; D. Enlargement of a fused univeined leaf with transverse striations, CPC F21881. E. Samaropsis sp. with reniform lateral wings, CPC F21877c. F–G. Glossopteris linguiformis McLoughlin 1994b. F. GSQF1840; G, CPC F21883. H–I. Glossopteris sp. cf. G schopfii Pigg 1990, NRM S048220. H. Matted leaves with oviposition scars along midrib (arrows); I. Enlargement of an elliptical oviposition scar. J–M. Glossopteris xiphophyllus McLoughlin 1994b. J. Distal portion of leaf, NRM S048219; K. Lanceolate leaf, CPC F21877b; L. Enlargement of venation, CPC F21877b; M. Proximal portion of leaf, CPC F21877a. N. Vertebraria australis (McCoy1847) emend. J.M. Schopf 1982, segmented root impression, CPC F21882b. O. Dictyopteridium sp. winged glossopterid fructification, CPC F21882a. Scale bars for A–C, F–H, J, K, M, N = 10 mm; D, E, I, L, O = 1 mm.



Family: Uncertain

Genus: Glossopteris Brongn. ex Brongn. 1831

**Type species:** *Glossopteris browniana* Brongn. 1828, by subsequent designation of Brongniart (1831); Permian, New South Wales, Australia.

# *Glossopteris linguiformis* McLoughlin 1994b Figure 2.F–G

#### Material: CPC F21883, GSQ F1840.

**Description:** The two available incomplete fossil leaves are broad (40–49 mm wide), with lengths >50 mm. The midrib is robust (3–4 mm wide), consisting of numerous tightly spaced parallel veins (Figure 2.G). Secondary veins emerge from the midrib at c. 10° and arch consistently across the lamina to intersect the margin at 60–70° (Figure 2.F–G). Veins typically anastomose c. 5–6 times producing long, slender curved meshes. The marginal vein concentration is c. 25 per 10 mm. The lamina margin is entire to slightly wavy.

**Remarks:** These broad leaves with regularly curved dense venation are consistent with the circumscription of *Glossopteris linguiformis*, recorded from several Guadalupian–Lopingian units from the Bowen Basin in central Queensland (McLoughlin 1994b). The specimen assigned to *Glossopteris retusa* H.K. Maheshw. from Lopingian strata (Newcastle Coal Measures) of the Sydney Basin by Rigby et al. (1980, figs 46, 47) appears to belong to the same species. It lacks the marginal notches of *G. retusa* described from India (Maheshwari 1965).

## *Glossopteris* sp. cf. *G. schopfii* Pigg 1990 Figure 2.H–I

**Material:** NRM S048220 (several overlapping specimens).

**Description:** No apical or basal parts of these leaves are preserved, but the mid-lamina fragments have lengths of c. 35 mm and maximum widths of 27–43 mm. Midveins are prominent (up to 2.5 mm wide), longitudinally striate, giving off secondary veins at 10– 20° that arch moderately in the inner lamina then pass relatively straight to intersect the margin at c. 55°(Figure 2.H). The veins anastomose 4–6 times across the lamina to produce relatively coarse (up to 0.8 mm wide) polygonal to oblong meshes.

**Remarks:** These lamina fragments most closely match the morphologies of leaves attributed to *Glossopteris* sp. cf. *G. schopfii* from Guadalupian– Lopingian strata of the Bowen Basin, central Queensland (McLoughlin 1994b), and exposed fragments of permineralized leaves attributed to *G. schopfii* from the Buckley Formation (Lopingian), Transantarctic Mountains (Pigg 1990). The single small slab available bears several fragments of leaves with equivalent morphology preserved within an apparent autumnal leaf-fall assemblage. At least two of these leaves bear elliptical to obovate (2 × 1 mm) damage features flanking the midrib that may represent insect oviposition scars (Figure 2.H–I).

# *Glossopteris xiphophyllus* McLoughlin 1994b Figure 2.J–M

#### Material: CPC F21877a and b, NRM S048219.

**Description:** Oblanceolate leaves c. 60 mm long (estimated) and 11–12 mm wide (L:W ratio c. 5–5.4); base gradually tapered (Figure 2.K, M), apex damaged in all specimens, margin entire. Midrib robust and markedly striate proximally, tapering, persistent. Secondary veins emerge from the midrib at  $10-20^{\circ}$ , arch consistently across the lamina to intersect the margin at  $40-70^{\circ}$ , anastomosing up to four times, forming slender, oblong–falcate meshes (Figure 2.J, L); marginal vein density 25–40 per 10 mm.

**Remarks:** These leaves are incomplete but fall comfortably within the morphological range of leaves attributed to the abundant and widespread eastern Australian species *Glossopteris xiphophyllus* McLoughlin 1994b. Diagnostic features include their slender oblanceolate form, dense secondary venation, and generally strong and consistent vein curvature.

Family: Dictyopteridiaceae Rigby 1978

**Genus:** *Dictyopteridium* Feistm. ex Zeiller 1902 emend. McLoughlin 1990a

**Type species:** *Dictyopteridium sporiferum* Feistm. ex Zeiller 1902; Raniganj Formation (Lopingian), Raniganj Coalfield, India. Figure 2.O

#### Material: CPC F21882a.

**Description:** The single incomplete fructification has a lanceolate receptacle that is15 mm long (base absent), 3 mm wide, and covered by indistinct, c. 0.2 mm diameter, tuberculate seed scars. The receptacle is surrounded by a 3.8 mm broad wing with prominent transverse striae and undulations (Figure 2.O).

**Remarks:** This specimen is clearly referable to *Dictyopteridium*, a genus established for winged, lanceolate, tuberculate, ovuliferous, glossopterid fructifications, but assignment to a particular species is challenging owing to its poor preservation. The notably broad and transversely creased wing suggests that it is probably conspecific with fructifications from the Bowen Basin attributed to *Cyclodendron leslii* by Rigby (1963, p. 341, plate 11, figure 4), *Dictyopteridium sporiferum* by White (1963, p. 2), cf. *Dictyopteridium* sp. by Rigby (1972, p. 9; text-figure G), *Dictyopteridium sporiferum* by Rigby 1978 (p. 13), and possibly the 'fertile structure (?)'illustrated by Rigby (1978, pp. 15–16, figure 24).

**Genus:** *Vertebraria* Royle ex McCoy 1847 emend. J.M. Schopf 1982

**Type species:** Vertebraria australis (McCoy1847) emend. J.M. Schopf 1982; Raniganj Formation (Lopingian), Raniganj Coalfield, India.

Vertebraria australis (McCoy 1847) emend.

#### J.M. Schopf1982

Figure 2.N

#### Material: CPC F21882b.

**Description:** The single available specimen consists of a 50 mm long, 8.5 mm wide, root incorporating four longitudinal rows of rectangular– oblong segments c. 8–13 mm long and 1.5–3 mm wide (Figure 2.N). Segments of adjacent rows are slightly offset from each other. A very slender (1 mm wide) subsidiary (lateral) rootlet appears to depart from one segment junction (Figure 2.N, lower left).

Remarks: Segments in this root represent

indentations generated by the collapse of internal air chambers during compression. A few indeterminate rootlets illustrated by White (1961b, figure 4; CPC F12884) probably represent fine lateral roots of Lithorhiza type (see Pant 1958) emanating from larger Vertebraria australis roots. Vertebraria australis or its synonym, V. indica (see Schopf 1982, Doweld 2012, Joshi et al. 2015, Herendeen 2015 for discussion of the taxonomy and nomenclature of this species), has been recorded widely in Permian strata across Gondwana and is universally accepted to represent the roots of glossopterid gymnosperms (Gould 1975, Schopf 1982, Neish et al. 1993, Decombeix et al. 2009). The uppermost occurrences of Vertebraria australis in eastern Australia are immediately below the end-Permian extinction horizon (Fielding et al. 2019, Mays et al. 2020, McLoughlin et al. 2021a).

#### Genus: Samaropsis Göpp. 1864

**Type species:** *Samaropsis ulmiformis* Göpp. 1864; Permian, Bohemia.

#### Samaropsis sp.

Figure 2.E

#### Material: CPC F21877c.

**Description:** A single seed in the assemblage has a longitudinally elliptical central body 3.8 mm long and 2.5 mm wide, flanked by marginal wings 1.4 mm in maximum width that are contracted at the chalazal and micropylar ends. The seed is otherwise featureless.

**Remarks:** Dispersed winged seeds in Gondwanan Permian fossil assemblages are commonly assigned to *Samaropsis* Göpp., *Cordaicarpus* H.B. Geinitz or various other genera (Maithy 1965, Millan 1981, McLoughlin 1992, Singh 2002, Bernardes-de-Oliveira et al. 2007, Souza & Iannuzzi 2009) but, in many cases, there are few diagnostic characters to facilitate consistent taxonomic differentiation. Moreover, the broader affiliations of such seeds are ambiguous in most cases. Given the absence of any other gymnosperm foliage in the Little River Coal Measures assemblage, it is likely that the seed described here was produced by a glossopterid gymnosperm. Seeds of similar size and morphology recovered from the Bowen Basin to the south have been found attached to, or considered to be affiliated with, various glossopterid fructifications in *Dictyopteridiaceae* (McLoughlin 1992, McLoughlin & Prevec 2019, 2021).

#### **DISCUSSION AND CONCLUSIONS**

The Little River Coal Measures flora is dominated by the remains of glossopterid gymnosperms and schizoneurid sphenopsids, probably representing canopy and understorey plants, respectively, of the original vegetation. Although of low diversity, the content of the small fossil assemblage is similar to floras from various units further south in eastern Australia. In her initial report on the fossil flora, White (1961b) assigned all the glossopterid leaves to two species (Glossopteris indica Schimp. and G. angustifolia Brongn.) following an approach employed extensively by early researchers on this plant group, who recognized only a few broadly defined species to occur across vast regions of Gondwana (e.g. Kovács-Endrödy 1981 for a discussion). More recent detailed studies of glossopterid leaf morphology and anatomy, especially where affiliated with reproductive structures, generally recognize more narrowly defined Glossopteris species (or morphotypes) having more restricted geographic distributions, e.g. constrained to neighbouring basins (Pant & Singh 1971, Anderson & Anderson 1985, Rigby et al. 1988, McLoughlin 1994a 1994b, Prevec et al. 2009, 2010, McLoughlin et al. 2019).

Species identified in the Little River Coal Measures have distributions that are primarily limited to foreland basin systems of eastern Australia and adjacent areas of Antarctica. *Glossopteris linguiformis* and *G. xiphophyllus* are relatively long-ranging species in Guadalupian to uppermost Changhsingian strata of eastern Australian basins, but both are notably more common in Changhsingian formations, e.g. the Burngrove Formation, Rangal Coal Measures and equivalent units (Ball 1912, Lewis 1940, McLoughlin 1994a, b, Fielding et al. 2019, Mays et al. 2020). *Glossopteris* sp. cf. *G. schopfii* is, likewise, longranging, but is most common in the Burngrove Formation (early Changhsingian) and equivalent strata (McLoughlin 1994b). The root taxon Vertebraria australis has a long stratigraphic range in the Permian throughout Gondwana. The glossopterid fructification Dictyopteridium is widespread across Gondwana but has a range restricted to the Lopingian (McLoughlin 1993b) or possibly ranging downwards to the upper Guadalupian (Bordy & Prevec 2008). Broad-winged Dictyopteridium species are especially common in the Black Alley Shale to Bandanna Formation (and equivalent) interval of the Bowen Basin (Rigby 1978, McLoughlin 1990b). Schizoneura gondwanensis has a range in eastern Australia that is restricted to the Lopingian and lowermost Triassic (Blackwater Group of the Bowen Basin and basal Narrabeen Group of the Sydney Basin: Etheridge 1903, McLoughlin et al. 1992). However, if Schizoneura gondwanensis and S. africana represent different portions of the same plant as inferred by Bomfleur et al. (2013), then its range may extend from the Lopingian to Middle or Upper Triassic. Elsewhere in Gondwana, the earliest occurrences of S. gondwanensis, may extend down to the Guadalupian (Singh 2000). Collectively, the fossil data supports a Lopingian (probable Changhsingian) age for the Little River Coal Measures and correlation with the upper part of the Blackwater Group (Rangal Coal Measures and equivalents) in the Bowen Basin to the south.

There is little evidence of animal life in the Little River Coal Measures fossil assemblage. The only indications of animal activity in the studied assemblage are several simple ovate–elliptical indentations flanking the midribs of *Glossopteris* sp. cf. *G. schopfii* leaves (Figure 2.H–I) that are broadly similar in size and position to insect oviposition scars on various other glossopterid leaves across Gondwana (e.g. Prevec et al. 2009, McLoughlin 2011, Srivastava & Agnihotri 2011, Cariglino et al. 2021, McLoughlin et al. 2021b).

The economically important Rangal Coal Measures of the Bowen Basin appear to correlate with various outliers and subsurface coal bearing strata of apparent

Lopingian age distributed across northern Queensland and resting unconformably on older Palaeozoic sedimentary or crystalline rocks (e.g. the Little River Coal Measures, Mount Mulligan Coal Measures, Normanby Formation, and subsurface strata in the Lakefield and Olive River basins). Although these strata are generally interpreted to have been deposited in isolated grabens based on the faulted margins of their exposures (Wells 1989a, b, c), their wide distribution, similar character, and shared fossil flora suggest that alluvial sedimentation incorporating extensive peatland development was much more widespread in the Changhsingian of northeastern Australia than represented by the present distribution of coal-bearing strata. It is possible that the isolated exposures in northeastern Queensland constitute remnants of a formerly extensive sheet of sedimentary strata that represented a northerly extension of the Sydney-Gunnedah-Bowen foreland basin complex that has been largely removed by post-Permian erosion or covered by Jurassic-Cenozoic strata. At least, the commonalities of sedimentary features and fossil content suggest the extension of similar depositional systems and palaeoclimatic conditions from central Queensland (Bowen Basin) to the far north of the state.

Mixing of typical Gondwanan and Cathaysian elements is evident in assemblages from West Papua (Rigby 1996, 2001) dated as Kungurian-Roadian (Playford & Rigby 2008). No data on fossil floras from that region are available for the Lopingian. The Little River Coal Measures host the northernmost documented late Permian plant assemblages from Australia. Yet, despite their location in middle palaeolatitudes (c. 45°S: Figure 1A; Torsvik & Cocks 2013), close to the northern geographic range of Glossopteris (McLoughlin 2001), there is no indication of Cathaysian/Tethyan elements in these deposits at that time. The Cape York Peninsula region appears to have been located in the southern temperate humid climate belt beyond the influence of the warm Tethys Ocean and outside the geographic range of palaeotropical plant groups.

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#### REFERENCES

- Anderson J.M. & Anderson H.M. 1985. Palaeoflora of southern Africa. Prodromus of South African megafloras Devonian to Lower Cretaceous. A.A. Balkema, Rotterdam. 423 pp.
- Bain J.H.C. & Draper J.J. 1997. Atlas of North Queensland Geology
  1:3 Million Scale. Australian Geological Survey Organization,
  Canberra, and Geological Survey of Queensland, Brisbane, 95 pp.
- Ball L.C. 1912. Mount Mulligan Coalfield. Geological Survey of Queensland Publication 237: 1–39.
- Bernal J. & Osborne J. 2019. Fairway Coal EPC 1058 'Fairlight' Final Report to 9 July 2019. http://gsq-prod-ckan-horizonpublic.s3.amazonaws.com/Report/113631/Document/532270/ cr 113631 1.pdf
- Bernardes-de-Oliveira M.E., De Castro-Fernandes M.C., Tewari R. & Ricardi-Branco F. 2007. Platyspermic seeds from the Early Permian of Paraná Basin, Brazil. Palaeobotanist 56: 1–19.
- Bomfleur B., Escapa I.H., Taylor E.L. & Taylor T.N. 2013. A reappraisal of *Neocalamites* and *Schizoneura* (fossil *Equisetales*) based on material from the Triassic of East Antarctica. Alcheringa 37: 1–17. https://doi.org/10.1080/03115518.2013.764693
- Bordy E.M. & Prevec R. 2008. Sedimentology, palaeontology and palaeo-environments of the Middle (?) to Upper Permian Emakwezini Formation (Karoo Supergroup, South Africa). South African Journal of Geology 111: 429–456. https://doi.org/10.2113/ gssajg.111.4.429
- Brongniart A. 1928. Prodrôme d'une Histoire des végétaux fossiles. F.G. Levrault, Paris: 223 pp.
- Brongniart A. 1831. Histoire des Vegetaux fossiles au Recherches botaniques et geologiques sur les Vegetaux renfermes dans les diverses couches du Globe. G. Dufour & E. D'Ocagne, Paris and Amsterdam, Volume 1: 209–248, pls 50, 53, 57, 58, 61 bis, 62, 64, 65, 67, 68, 70, 71, 73, 76.
- Bryan W.H. 1928. A glossary of Queensland stratigraphy. University of Queensland, Brisbane, 69 pp.
- Bultitude R.J., Garrad P.D., Donchak P.J.T., Domagala J., Champion D.C., Rees I.D., Mackenzie D.E., Wellman P., Knutson J., Fanning C.M., Fordham B.G., Grimes K.G., Oversby B.S., Rienks I.P., Stephenson P.J., Chappell B.W., Pain C.F., Wilford J.R., Rigby J.F., Woodbury M.J. 1997. Cairns Region. In: Bain J.H.C. & Draper J.J. (Editors) North Queensland Geology. AGSO Bulletin 240: 225–325.
- Cariglino B., Moisan P. & Lara M.B. 2021. The fossil record of plant-insect interactions and associated entomofaunas in Permian and Triassic floras from southwestern Gondwana: A review and future prospects. Journal of South American Earth Sciences 111: 103512. https://doi.org/10.1016/j.jsames.2021.103512
- Carr A.F. 1975. Little River-Oaky Creek district, Queensland. In: Traves D.M. & King D. (Editors) Economic Geology of Australia and Papua New Guinea, Volume 2, Monograph 6. The Australasian Institute of Mining and Metallurgy, Melbourne, pp. 251–252.
- de Keyser F. & Lucas K.G. 1968. Geology of the Hodgkinson and Laura Basins, North Queensland. Bulletin of the Bureau of Mineral

Resources, Geology and Geophysics, Australia 84: 1–254. https://d28rz98at9flks.cloudfront.net/147/Bull\_084.pdf

- Decombeix A.L. Taylor E.L. & Taylor T.N. 2009. Secondary growth in *Vertebraria* roots from the late Permian of Antarctica: a change in developmental timing. International Journal of Plant Sciences 170: 644–656. https://doi.org/10.1086/597784
- Domagala J., Grimes K.G. & Lane R.P. 1997. Cooktown Sheet SD55-13 Second Edition 1:250 000 Geological Series Map, Queensland. Department of Mines and Energy, Brisbane.
- Doweld A.B. 2001. Prosyllabus Tracheophytorum. Tentamen Systematis Plantarum Vascularium (Tracheophytorum). GEOS, Moscow, 200 pp.
- Doweld A.B. 2012. (2097–2098) Proposals to conserve the name Vertebraria Royle ex McCoy (fossil Gymnospermae, Glossopteridales) against Vertebraria Roussel (Rhodymeniophyta) and Sphenophyllum indicum (V. indica) against V. australis and Clasteria australis. Taxon 61:1129–1131. https://doi.org/10.1002/ tax.615032
- Etheridge R. Jr 1903. The fructification of *Schizoneura australis*, Etheridge fil. Geological Survey of New South Wales Record 7: 234–235.
- Feistmantel O. 1876a. XIX contributions towards the knowledge of fossil flora of India I. On some fossil plants from the Damuda Series in the Raniganj Coalfield, collected by Mr J. Wood-Mason. Journal of the Asiatic Society of Bengal 45(2): 329–382.
- Feistmantel O. 1876b. Notes on the age of some fossil floras of India. Records of the Geological Survey of India 9(3–5): 63–79.
- Fielding C.R., Frank T.D., McLoughlin S., Vajda V., Mays C., Tevyaw A.P., Winguth A., Winguth C., Nicoll R.S., Bocking M. & Crowley J.L. 2019. Age and pattern of the southern high-latitude continental end-Permian extinction constrained by multiproxy analysis. Nature Communications 10:385. https://doi.org/10.1038/s41467-018-07934-z
- Geinitz H.B. 1862. Dyas oder die Zechsteinformation und das Rothliegende. Heft II. Die Pflanzen der Dyas und Geologisches. W. Engelmann, Leipzig, vii +212 pp.
- Göppert H.R. 1864–65. Die fossile flora der ermischen Formation. Palaeontographica 12: 1–224 (1864), 225–316 (1865).
- Goswami S., Singh K.J. & Chandra S. 2006. Palaeobotany of Gondwana basins of Orissa State, India: A bird's eye view. Journal of Asian Earth Sciences 28: 218–233. https://doi:10.1016/ j.jseaes.2005.09.010
- Gould R.E. 1975. A preliminary report on petrified axes of *Vertebraria* from the Permian of eastern Australia. In: Campbell, K.S.W. (Editor) Gondwana Geology. Australian National University Press, Canberra, 109–115.
- Grauvogel-Stamm L. 1978. La flore du Grès a Voltzia (Buntsandstein supérieur) des Vosges du Nord (France). Morphologie, anatomie, interprétations phylogénique et paléogéographique. Sciences Géologiques, Université Louis Pasteur de Strasbourg, Institut de Géologie, Memoir 50: 1–225.
- Hawkins P.J. &Williams L.J. 1990. Review of the geology and economic potential of the Laura Basin. Queensland Resource Industries Record 1990/12: 1–36.
- Herendeen P.S. 2015. Report of the Nomenclature Committee on Fossils: 9. Taxon 64: 1306–1312. https://doi.org/10.12705/646.14
- Jack R.L. 1882. Report on the Little River Coalfield, near Cooktown. Geological Survey of Queensland Publication 11: 1–4.

- Joshi A., Tewari R., Agnihotri D., Pillai S.S.K. & Jain R.K. 2015. Occurrence of Vertebraria indica (Unger) Feistmantel 1877–an evidence for coal-forming vegetation in Kothagudem area, Godavari Graben, Telangana. Current Science 108: 330–333. https:// www.jstor.org/stable/24216559
- Kovács-Endrödy E. 1981. "Broad sense interpretation" of Glossopteris leaves: a critique. Palaeontologia Africana 24: 35– 38.
- Lewis A.N. 1940. Record of *Glossopteris* from Cygnet. Papers and Proceedings of the Royal Society of Tasmania 1939: 95–96. https:/ /eprints.utas.edu.au/13262/
- Lucas K.G. & de Keyser F. 1965. The Geology of Cooktown, Queensland 1:250 000 Sheet SD/55-13 (CD Reprint 2008). Geological Survey of Queensland / Department of Mines & Energy, Brisbane.
- Maheshwari H.K. 1965. Studies in the *Glossopteris* Flora of India 22. On some species of the genus *Glossopteris* from the Raniganj Stage of Raniganj Coalfield, Bengal. Palaeobotanist 13: 129–143.
- Maithy P.K. 1965. Studies in the *Glossopteris* flora of India 18. Gymnospermic seeds and seed-bearing organs from the Karharbari beds of the Giridih Coalfield, Bihar. Palaeobotanist 13: 45–56.
- Mays C., Vajda V., Frank T.D., Fielding C.R., Nicoll R.S., Tevyaw A.P. & McLoughlin S. 2020. Refined Permian–Triassic floristic timeline reveals early collapse and delayed recovery of south polar terrestrial ecosystems. Geological Society of America Bulletin 132: 1489–1513. https://doi.org/10.1130/B35355.1
- McConachie B.A., Wellman P., Dunster J.N., Wiford J.R., Denaro T.J. & Draper J.J. 1997. Quinkan region. In: Bain J.H.C & Draper J.J. (Editors) North Queensland Geology. Australian Geological Survey Organisation Bulletin 240: 399–407.
- McCoy F. 1847. On the fossil botany and zoology of the rocks associated with the coal in Australia. Annals and Magazine of Natural History 20: 145–157.
- McLoughlin S. 1990a. Some Permian glossopterid fructifications and leaves from the Bowen Basin, Queensland, Australia. Review of Palaeobotany and Palynology 62: 11–40.
- McLoughlin S. 1990b. Palaeobotany and palaeoenvironments of Permian strata, Bowen Basin, Queensland. PhD thesis, University of Queensland, Brisbane, 312 pp. (unpublished).
- McLoughlin S. 1992. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 1. Palaeontographica Abt. B 228: 105–149.
- McLoughlin S. 1993a. Plant fossil distributions in some Australian Permian non-marine sediments. Sedimentary Geology 85: 601– 619.
- McLoughlin S. 1993b. Glossopterid megafossils in Permian nonmarine biostratigraphy. In: Findlay R.H., Banks H.R., Veevers J.J. & Unrug R. (Editors) Gondwana 8–Assembly, Evolution, and Dispersal. A.A. Balkema, Rotterdam, 253–264.
- McLoughlin S. 1994a. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 2. Palaeontographica Abt. B 231: 1–29.
- McLoughlin S. 1994b. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 3. Palaeontographica Abt. B 231:31–62.
- McLoughlin S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. Australian Journal of Botany 49: 271–300. https://doi.org/10.1071/BT00023

- McLoughlin S. 2011. New records of leaf galls and arthropod oviposition scars in Permian–Triassic Gondwanan gymnosperms. Australian Journal of Botany 59: 156–169. https://doi.org/10.1071/ BT10297
- McLoughlin S., Maksimenko A. & Mays C. 2019. A new highpaleolatitude permineralized peat flora from the late Permian of the Sydney Basin, Australia. International Journal of Plant Sciences 180: 513–539. https://doi.org/10.1086/702939
- McLoughlin S., Nicoll R.S., Crowley J.L., Vajda V., Mays C., Fielding C.R., Frank T.D., Wheeler A. & Bocking, M. 2021. Age and paleoenvironmental significance of the Frazer Beach Member—a new lithostratigraphic unit overlying the end-Permian extinction horizon in the Sydney Basin, Australia. Frontiers in Earth Sciences 8: 600976. https://doi.org/10.3389/feart.2020.600976
- McLoughlin S. & Prevec R. 2019. The architecture of Permian glossopterid ovuliferous reproductive organs. Alcheringa 43: 480– 510. https://doi.org/10.1080/03115518.2019.1659852
- McLoughlin S. & Prevec R. 2021. The reproductive biology of glossopterid gymnosperms – a review. Review of Palaeobotany and Palynology 295: 104527. https://doi.org/10.1016/ j.revpalbo.2021.104527
- McLoughlin S., Prevec R. & Slater B.J. 2021. Arthropod interactions with the Permian *Glossopteris* flora. Journal of Palaeosciences 70: 43–133. https://www.bsip.res.in/JPS%20Volume%2070compressed.pdf
- Millan J.H. 1981. Distribution of platyspermic gondwanic seeds. Palaeobotanist 28–29: 63–74.
- Neish P.G., Drinnan A.N. & Cantrill D.J. 1993. Structure and ontogeny of *Vertebraria* from silicified Permian sediments in East Antarctica. Review of Palaeobotany and Palynology 79: 221–244. https:// doi.org/10.1016/0034-6667(93)90024-O
- Pant D.D. 1958. Structure of some roots and spores from the lower Gondwana (Permo-Carboniferous) of east Africa. Vijnana Parishad Anushandhan Patrika 1: 231–244.
- Pant D.D. & Singh K.B. 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part 3. Palaeontographica Abt. B 135: 1–40.
- Pigg K.B. 1990. Anatomically preserved *Glossopteris* foliage from the central Transantarctic Mountains. Review of Palaeobotany and Palynology 66: 105–127. https://doi.org/10.1016/0034-6667(90)90030-M
- Playford G. & Rigby J.F. 2008. Permian palynoflora of the Ainim and Aiduna formations, West Papua. Revista Española de Micropaleontología 40: 1–57.
- Prevec R., Gastaldo R.A., Neveling J., Reid S.B. & Looy C.V. 2010. An autochthonous glossopterid flora with latest Permian palynomorphs and its depositional setting in the *Dicynodon* Assemblage Zone of the southern Karoo Basin, South Africa. Palaeogeography, Palaeoclimatology, Palaeoecology 292: 391– 408. https://doi.org/10.1016/j.palaeo.2010.03.052
- Prevec R., Labandeira C.C., Neveling J., Gastaldo R.A., Looy C.V. & Bamford M. 2009. Portrait of a Gondwanan ecosystem: a new Late Permian fossil locality from KwaZulu-Natal, South Africa. Review of Palaeobotany and Palynology 156: 454–493. https:// doi.org/10.1016/j.revpalbo.2009.04.012
- Rigby J.F. 1963. On a collection of plants of Permian age from Baralaba, Queensland. Proceedings of the Linnean Society of New South Wales 87: 341–351.

- Rigby J.F. 1972. The flora of the Kaloola Member of the Baralaba Coal Measures, central Queensland. Geological Survey of Queensland Publication 352, Palaeontological Paper 26: 1–12.
- Rigby J.F. 1978. Permian glossopterid and other cycadopsid fructifications from Queensland. Publications of the Geological Survey of Queensland 367, Palaeontological Paper 41: 1–21.
- Rigby J.F. 1996. The significance of a Permian flora from Irian Jaya (West New Guinea) containing elements related to coeval floras of Gondwanaland and Cathaysialand. Palaeobotanist 45: 295– 302.
- Rigby J.F. 2001. A review of the Early Permian flora from Papua (West New Guinea). In: Metcalfe I., Smith J.M.B., Morwood M. & Davidson I. (Editors) Faunal and Floral Migrations and Evolution in SE Asia–Australasia. Balkema, Lisse, 85–95.
- Rigby J.F., Maheshwari H.K., Schopf J.M. 1980. Revision of the plants collected by J.D. Dana during 1839–1840 in Australia. Geological Survey of Queensland Publication 376, Palaeontological Paper 47: 1–25.
- Rigby J.F., Chandra S. & Surange K.R. 1988. Glossopterid plant remains in the Permian of Western Australia. Association of Australasian Palaeontologists Memoir 5: 73–78.
- Rohn R. & Rösler O. 1986. Schizoneura gondwanensis Feistmantel da Formação Rio do Rasto (Bacia do Paraná, Permiano superior) no estado do Paraná e no norte do estado de Santa Catarina. Boletim IG-USP 17: 27–37.
- Schimper W.P. & Mougeot A. 1844. Monographie des plantes fossiles du gres bigarre de la chaine des Vosges. Leipzig, 83 pp.
- Schopf J.M. 1982. Forms and facies of *Vertebraria* in relation to Gondwana coal. Antarctic Research Series 36: 37–62.
- Shi G.R., Waterhouse J.B. & McLoughlin S. 2010. The Lopingian of Australasia: a review of biostratigraphy, correlations, palaeogeography and palaeobiogeography. Geological Journal 45: 230–263. https://doi.org/10.1002/gj.1213
- Singh K.J. 2000. Plant biodiversity in the Mahanadi Basin, India, during the Gondwana period. Journal of African Earth Sciences 31, 145–155. https://doi.org/10.1016/S0899-5362(00)00079-8
- Singh S.M. 2002. Seeds, fructifications, bracts and calamitalean axes from the Karanpura and Bokaro group of coalfields. Palaeobotanist 51:73–79.
- Souza J.M. de & Iannuzzi R. 2009. The genus *Cordaicarpus* Geinitz in the Lower Permian of the Parana Basin, Rio Grande do Sul, Brazil. Revista Brasileira de Paleontologia 12: 5–16.
- Srivastava A.K. & Agnihotri D. 2011. Insect traces on Early Permian plants of India. Paleontological Journal 45: 200–206.
- Torsvik T.H. & Cocks L.R.M. 2013. Gondwana from top to base in space and time. Gondwana Research 24: 999–1030. https://doi.org/ 10.1016/j.gr.2013.06.012
- Vajda V., McLoughlin S., Mays C., Frank T., Fielding C.R., Tevyaw A. Lehsten V., Bocking M. & Nicoll R.S. 2020. End-Permian (252 Mya) deforestation, wildfires and flooding – An ancient biotic crisis with lessons for the present. Earth and Planetary Science Letters 529: 115875. https://doi.org/10.1016/j.epsl.2019.115875
- Wells A.T. 1989a. Late Permian coal measures beneath the Olive River Basin, Queensland. In: Harrington H.J. (Editor) Permian Coals of Eastern Australia. Bureau of Mineral Resources Bulletin 231: 171–173.
- Wells A.T. 1989b. The Late Permian Mount Mulligan Coal Measures, Queensland. In: Harrington H.J. (Editor) Permian Coals of Eastern

Australia. Bureau of Mineral Resources Bulletin 231: 175–177.

- Wells A.T. 1989c. Permian coal measures in the sub-Laura Basin sequence, Little River – Oakey Creek district, Queensland. In: Harrington H.J. (Editor) Permian Coals of Eastern Australia. Bureau of Mineral Resources Bulletin 231: 179–183.
- White M.E. 1961a. Plant fossils from Mitchell River and Mount Mulligan, north Queensland. Bureau of Mineral Resources, Geology and Geophysics, Australia, Record 1961/16: 1–5. (unpublished). https://ecat.ga.gov.au/geonetwork/srv/api/records/ a05f7892-fefe-7506-e044-00144fdd4fa6

White M.E. 1961b. Fossil plants from the Little River Coal Measures,

in the Cooktown region of north Queensland. Bureau of Mineral Resources, Geology and Geophysics, Australia, Record 1961/ 121: 1–4. (unpublished). https://ecat.ga.gov.au/geonetwork/srv/ api/records/a05f7892-7da7-7506-e044-00144fdd4fa6

- White M.E. 1963. Report on 1962 plant fossil collections. Bureau of Mineral Resources, Geology and Geophysics, Australia, Record 1963/1, 1–9. (unpublished). https://ecat.ga.gov.au/geonetwork/srv/ api/records/a05f7892-fca7-7506-e044-00144fdd4fa6
- Zeiller R. 1902. Observations sur quelques plantes fossiles des Lower Gondwanas. Memoirs of the Geological Survey of India, Palaeontologia Indica. N.S. 2: 1–40.