

# The first record of the Permian *Glossopteris* flora from Sri Lanka: implications for hydrocarbon source rocks in the Mannar Basin

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**Abstract** – Strata exposed near Tabbowa Tank, Tabbowa Basin, western Sri Lanka have yielded the first representatives of the distinctive Permian *Glossopteris* flora from that country. The assemblage includes gymnosperm foliage attributable to *Glossopteris raniganjensis*, roots referable to *Vertebraria australis*, seeds assigned to *Samaropsis* sp., sphenophyte axes (*Paracalamites australis*) and foliage (*Sphenophyllum emarginatum*), and fern foliage (*Dichotomopteris lindleyi*). This small macroflora is interpreted to be of probable Lopingian (late Permian) age based on comparisons with the fossil floras of Peninsula India. Several *Glossopteris* leaves in the assemblage bear evidence of terrestrial arthropod interactions including hole feeding, margin feeding, possible lamina skeletonization, piercing-and-sucking damage and oviposition scarring. The newly identified onshore Permian strata necessitate re-evaluation of current models explaining the evolution of the adjacent offshore Mannar Basin. Previously considered to have begun subsiding and accumulating sediment during Jurassic time, we propose that the Mannar Basin may have initiated as part of a pan-Gondwanan extensional phase during late Palaeozoic – Triassic time. We interpret the basal, as yet unsampled, seismically reflective strata of this basin to be probable organic-rich continental strata of Lopingian age, equivalent to those recorded in the Tabbowa Basin, and similar to the Permian coal-bearing successions in the rift basins of eastern India and Antarctica. Such continental fossiliferous strata are particularly significant as potential source rocks for recently identified natural gas resources in the Mannar Basin.

Keywords: Glossopterids, plant–insect interactions, petroleum systems, Gondwana, continental break-up.

## 1. Introduction

*Glossopteris* was formally defined by Brongniart (1828), and the genus has been emended subsequently by several workers. This fossil-genus of tongue-shaped leaves with reticulate venation characterizes continental strata throughout the middle- to high-latitude regions of the Gondwanan Permian (McLoughlin, 2001, 2011). Indeed, the distribution of the genus was central to early arguments that the Southern Hemisphere continents were formerly united into a supercontinent (Gondwana) during late Palaeozoic time (du Toit, 1937). *Glossopteris* has so far been recorded throughout the core regions of Gondwana (India, Africa, Arabia, Madagascar, South America, Australia, Antarctica and New Zealand) with the notable exception of Sri Lanka (McLoughlin, 2001). In addition, a few leaves in peri-Gondwanan terranes, for example Thailand (Asama, 1966), Turkey (Archangelsky & Wagner, 1983), Laos (Bercovici *et al.* 2012) and in

isolated parts of low-palaeolatitude Gondwana (e.g. Morocco; Broutin *et al.* 1998) have been assigned to *Glossopteris*, but these records need thorough taxonomic re-appraisal. Leaves attributed to *Glossopteris* in areas remote from Gondwana, for example the Russian Far East (Zimina, 1967), together with examples from much younger strata, such as Triassic (Johnston, 1886) or Jurassic (Harris, 1932; Delevoryas, 1969), undoubtedly belong to other plant groups that evolved morphologically similar leaves (Harris, 1937; Delevoryas & Person, 1975; Anderson & Anderson, 2003).

Apart from its palaeobiogeographic importance, the *Glossopteris* flora contributed to the accumulation of vast economic coal resources across the Southern Hemisphere that are exploited and distributed globally for the generation of electricity, metal refining and other industrial purposes (Balme, Kershaw & Webb, 1995; Maher *et al.* 1995; Rana & Al Humaidan, 2016). Buried Permian plant remains (principally wood, spore/pollen and leaf material converted to type II and III kerogens) also constitute a major source

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of both conventional and coal-seam gas (McCarthy *et al.* 2011), which are exploited widely in nations occupying the ancient Gondwanan landmass (Flores, 2014).

Records of plant macrofossils from Sri Lanka are sparse. Previous studies have identified only Jurassic plants (Sitholey, 1944; Edirisooriya & Dharmagunawardhane, 2013a, b), and these have been recovered from outcrops in small isolated graben systems in the northwestern part of the island. No Permian fossils or strata have been reported from Sri Lanka so far, although Katupotha (2013) speculated that some topographic planation features and isolated erratic boulders might date back to an ancient glacial episode, the last of which affected this region during early Permian time (Fielding, Frank & Isbell, 2008).

Here we describe the first assemblage of the *Glossopteris* flora from Sri Lanka derived from the first documented exposures of Permian strata in the Tabbowa Basin. In addition to *Glossopteris*, the flora contains the remains of ferns and sphenophytes that help constrain the age of the deposit. We also highlight the potential significance of this discovery for hydrocarbon source rocks in the adjacent (offshore) Mannar Basin.

## 2. Geological setting

Around 90% of the bedrock in Sri Lanka consists of Precambrian crystalline rocks. Jurassic, Miocene and Quaternary strata are largely confined to a thin belt of exposures in the north and northwest of the island (Herath, 1986; Fig. 1a). The fossiliferous strata sampled in this study are exposed close to the spillway of an irrigation reservoir – the Tabbowa Tank (8° 04' 21" N, 79° 56' E) – within the Tabbowa Basin (Fig. 1a, b). The Tabbowa Basin is a small graben previously considered to host only Jurassic strata. The basin extends over an area of only a few square kilometres in the Northwestern Province of Sri Lanka (Wayland, 1925; Cooray, 1984) and has a surface topography of slightly elevated but flat terrain. The graben developed in a crystalline basement terrane and hosts nearly 1000 m of strata consisting mostly of grey to reddish shales, mudstones, siltstones and arkosic sandstones (Cooray, 1984). A similar succession is developed 30 km to the south of Tabbowa in the Andigama–Pallama Basin, which hosts at least 350 m of strata (Herath, 1986). The surrounding Precambrian basement rocks comprise mainly granitic gneisses with extensive jointing and faulting (Wayland, 1925; Cooray, 1984).

In the offshore region between northwestern Sri Lanka and southern India (Tamil Nadu) lies the Mannar Basin (Fig. 1a), covering an area of about

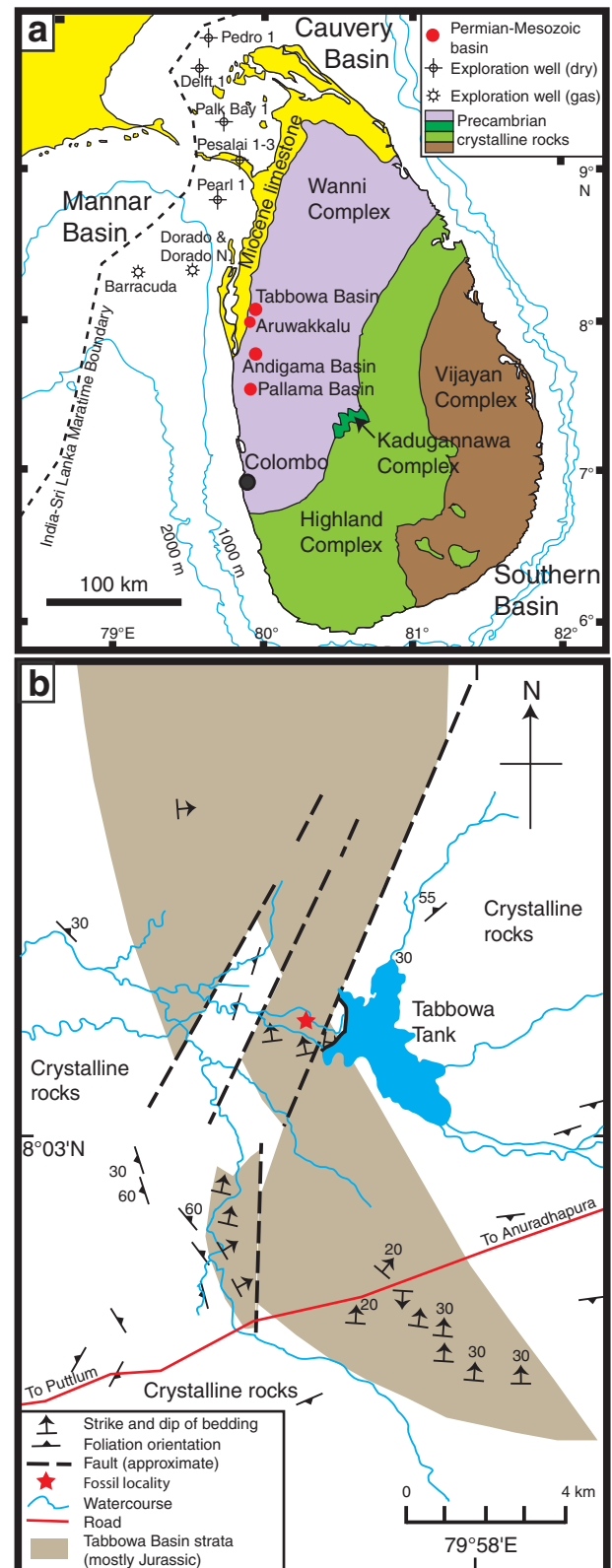


Figure 1. (Colour online) Maps showing: (a) the major geological provinces of Sri Lanka and (b) the sample location (indicated by a star) adjacent to Tabbowa Tank (modified after Wayland, 1925 and Ratnayake & Sampei, 2015).

45 000 km<sup>2</sup>. This basin contains >6000 m of strata and is covered by water to depths generally greater than 1000 m (Premarathne *et al.* 2013). The sedimentary development of this basin is poorly understood since

there have been relatively few seismic surveys and no hydrocarbon exploration wells have penetrated the full stratigraphic succession. To date, the succession has been subdivided into four informally defined allostratigraphic megasequences. The oldest, ‘megasequence IV’, has been assumed to represent mostly continental strata of Late Jurassic – early Albian age (Baillie *et al.* 2004), based mainly on a model of basin initiation during middle Mesozoic continental break-up and by correlation with Jurassic strata in the on-shore grabens of northwestern Sri Lanka (Premarathne *et al.* 2016). Significantly, Cairn Lanka Private Limited drilled several exploration wells in the Mannar Basin in 2011; two of these, CLPL-Dorado-91H/1z (Dorado) and CLPL-Barracuda-1G/1 (Barracuda), were the first to yield hydrocarbons (mostly gas) in Sri Lankan territory (Fig. 1a). The hydrocarbons were trapped in Campanian–Maastrichtian sandstones that are underlain by a substantial stratigraphic section of uncertain age, since no well in the basin has yet penetrated below Lower Cretaceous strata (Premarathne *et al.* 2013).

### 3. Materials and methods

More than 20 rock slabs bearing numerous *Glossopteris* leaves were recovered during this study from an outcrop c. 1 km west of Tabbowa Tank spillway (8° 04' 22.59" N, 79° 56' 29.32" E; Fig. 1b). Exposures in the area are poor and discontinuous due to deep weathering and soil cover; the sampled strata therefore cannot be placed in a continuous stratigraphic section. Several specimens of *Sphenophyllum*, sphenophyte ribbed axes and fertile fern foliage are co-preserved on the studied slabs. The plant macrofossils are preserved predominantly as impressions within grey shale. The fossils are typically a slightly darker shade of grey or are pinkish compared with the matrix, due to minor mineral staining or clay coatings. Some shales are strongly ferruginous with leaf impressions stained by iron oxides. No organic matter is preserved in the fossils, but venation details are well defined. Plant mesofossils, pollen and spores could not be extracted from these sediments due to deep weathering of the strata.

Fossils were photographed with an Optika vision Pro dissecting microscope and camera attachment under low-angle incident light from the upper left. Line drawings were produced by tracing venation details from images imported into Adobe Illustrator CS5. Leaf shape terminology follows that of Dilcher (1974), venation angle measurements follow the convention of McLoughlin (1994a) and leaf size categories are those of Webb (1959). All fossiliferous rock slabs are housed at the National Museum, Colombo, Sri Lanka and have been assigned registration numbers of that institution (CNM SA.1–SA.20); individual specimens on those slabs are designated with letter suffixes (a, b, c, etc.).

### 4. Systematic palaeobotany

Order Equisetales Dumortier, 1829

Family uncertain

Genus *Paracalamites* Zalesky, 1932

*Type species.* *Paracalamites striatus* (Schmalhausen) Zalesky, 1927; by subsequent designation of Boureau (1964); Jurassic, Russia.

*Paracalamites australis* Rigby, 1966 (Fig. 2m)

*Material.* Seven axes on CNM SA.7 and SA.8 (illustrated specimen: CNM SA.7b).

*Description.* Articulate ribbed stems preserved as external impressions in grey and reddish shales and siltstones (Fig. 2m). Fragmentary, longitudinally ribbed, linear axes, exceeding 80 mm long, 21 to >79 mm wide, with indistinct nodes. Ribs straight to flexuous, each with a central slender groove; ribs and intervening troughs smooth or with fine longitudinal striae. Ribs opposite at nodes or alternate only where new ribs are added. Ribs commonly bear fine longitudinal striae. There are 15–20 ribs visible across the stem. Ribs 0.5–5 mm apart depending on size of axis; density higher in small compared with large axes.

*Remarks.* None of the several fragmentary axes available retains attached foliage or fructifications. Moreover, the axes are too large to have accommodated co-preserved *Sphenophyllum* leaf whorls. They might have borne some other type of equisetalean foliage, such as *Phyllothea*, which is common in Permian floras elsewhere in Gondwanan and typically co-preserved with *Paracalamites* axes (Prevec *et al.* 2009), but such foliage has not yet been recorded from Tabbowa. The studied axes can be readily accommodated within *Paracalamites australis* based on their dimensions and coarse ribbing (Rigby, 1966; McLoughlin, 1992a, b).

Order Sphenophyllales Campbell, 1905

Family Sphenophyllaceae Potonié, 1893

Genus *Sphenophyllum* Koenig, 1825

*Type species.* *Sphenophyllum emarginatum* (Brongniart) Koenig, 1825; ?Carboniferous, Gotha, Thuringia, Germany.

*Sphenophyllum churulianum* Srivastava & Rigby, 1983 (Fig. 2a, b)

*Material.* More than 10 leaf whorls on rock slabs CNM SA.2, SA.7 and SA.9 (illustrated specimens: CNM SA.7a and SA.9a).

*Description.* Slender, striate, segmented axes 1–1.5 mm wide, expanded slightly near nodes, bearing radially arranged whorls of six leaves at nodes (Fig. 2a, b); internodes 25–28 mm long. Leaves not forming a basal sheath, generally equal in size, but varying in degree of apical dissection. A few whorls appear to have leaves of variable size (Fig. 2b), but this may be a consequence of oblique compression. Leaves wide



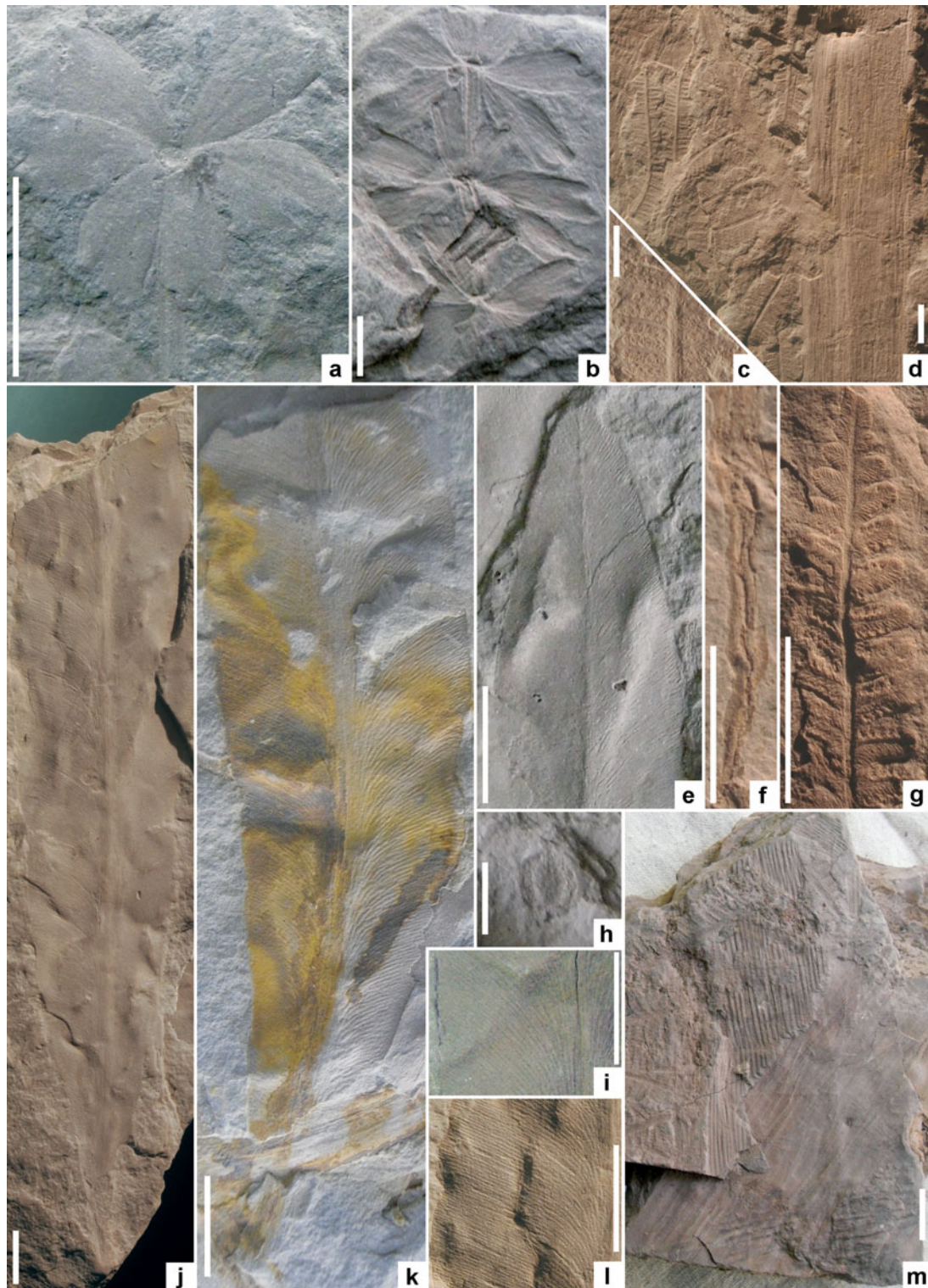


Figure 2. (Colour online) Permian plant fossils from the Tabbowa Basin. (a, b) *Sphenophyllum churulianum* Srivastava & Rigby, 1983, slender axes with leaf whorls (Reg. numbers CNM SA.7a and CNM SA.9a respectively). (c, d, g) *Dichotomopteris lindleyi* (Royle) Maithy, 1974; (c) enlargement of fertile pinna (CNM SA.8a); (d) rachis with attached subsidiary pinnae (CNM SA.8a); and (g) pinna showing variation of fertile and sterile pinnules (CNM SA.3a). (e, i–l) *Glossopteris raniganjensis* Chandra & Surange, 1979, details of (e) leaf apex (CNM SA.9b); (j) base (CNM SA.5a); (k) mid-region (CNM SA.2a); and (i, l) venation CNM SA.2b and SA.5a, respectively. (f) *Vertebraria australis* (McCoy, 1847) emend Schopf, 1982, segmented glossopterid root (CNM SA.3b). (h) *Samaropsis* sp., winged seed (CNM SA.4a). (m) *Paracalamites australis* Rigby, 1966, ribbed axes (CNM SA.7b). Scale bars: (a–f, i–m) 10 mm and (g, h) 5 mm.

obovate to narrow obovate or oblanceolate, 25–27 mm long, up to 18 mm wide, base cuneate, apex gently to moderately dissected by one or more notches up to *c.* 5 mm deep, rarely entire. Single vein enters the leaf and bifurcates regularly to maintain vein concentrations of 7–8 per centimetre. Veins straight to gently arched and mostly terminating at apical margin.

*Remarks.* The more-or-less equal-sized and symmetrically arranged leaves of this taxon favour its assignment to *Sphenophyllum* rather than the superficially similar but bilaterally symmetrical *Trizygia* within the Sphenophyllales. *Sphenophyllum* has a long range through the Permian of Gondwana, whereas *Trizygia* is more typical of Upper Permian assemblages (McLoughlin, 1992a; Goswami, Das & Guru, 2006). McLoughlin (1992b, table 1) summarized the general morphological characters of Permian Gondwanan *Sphenophyllum* leaves. Most taxa can be differentiated using a combination of characters related to leaf shape, size and the degree of apical dissection. The Sri Lankan forms are similar to *Sphenophyllum archangelskii* Srivastava & Rigby, 1983 from the Laguna Polina Member, La Golondrina Formation (Guadalupian) of Argentina in leaf dimensions and their depth of dissection, but the latter have more numerous apical incisions. Although Srivastava & Rigby (1983) described *Sphenophyllum churulianum* (from the Guadalupian Barakar Formation of India) as being entire, most of the apices on the holotype are damaged, and specimens attributed to this species subsequently (Srivastava & Tewari, 1996) have a subtle central apical notch a few millimetres deep. The species has also been reported from the Kamthi Formation (Lopingian) of India (Goswami, Das & Guru, 2006), indicating a long stratigraphic range in that region. We tentatively ascribe the Sri Lankan specimens to *S. churulianum* with the qualification that cuticles and fructifications of this taxon, which would enhance confidence in identification, remain unknown from India or Sri Lanka.

Order ?Osmundales Link, 1833

Genus *Dichotopteris* Maithy, 1974

*Type species.* *Dichotopteris major* (Feistmantel) Maithy, 1974; Raniganj Formation (Late Permian), Damuda Group, Raniganj Coalfield, India.

*Dichotopteris lindleyi* (Royle) Maithy, 1974  
(Fig. 2c, d, g)

*Material.* Around 20 frond fragments on rock slabs CNM SA.3, SA.7 and SA.8 (illustrated specimens: CNM SA.3a, SA.8a).

*Description.* Fronds tripinnate. Rachis longitudinally striate, reaching 25.0 mm wide (Fig. 2d). Primary pinnae robust, alternate, orientated at 30–90° to rachis, longitudinally striate, up to 8.0 mm wide. Secondary pinnae linear to lanceolate, alternate; inserted on primary pinna rachilla at *c.* 90° proximally, *c.* 45° distally; apex with terminal rounded pinnule; rachilla

1 mm wide. Sterile ultimate pinnules oblong, entire, alternate, up to 8 mm long and 5 mm wide, inserted at 60–90° to parent rachilla (Fig. 2g). Pinnules appear to have full basal attachment and a decurrent basisopic margin; apices rounded. Midvein prominent; lateral veins undivided or once-forked, typically at around 60° to midvein. Fertile pinnules with entire to slightly undulate margins, bearing circular sori, *c.* 1 mm in diameter, aligned through the mid-lamina region along each side of the midvein (Fig. 2c, g).

*Remarks.* These specimens match the characters of *Dichotopteris lindleyi* Maithy, 1974, originally described from India, but widely reported across eastern Gondwana (Royle, 1833–1840; Maithy, 1975; Rigby, 1993; McLoughlin, 1993). This species differs from the other widely reported eastern Gondwanan ferns attributed to *Neomariopteris* species by their oblong, generally entire-margined pinnules and prominent row of mid-lamina sori. This type of foliage is considered to have probable osmundacean affinities based on the presence of *Osmundacidites*-like *in situ* spores in fertile specimens, and its occurrence in association with *Palaeosmunda* axes elsewhere in Gondwana (Gould, 1970; Maithy, 1974; McLoughlin, 1992a). Based on the >20 mm width of the rachis in some specimens, these fronds derive from a fern of substantial size; it may have attained an erect (tree-fern) habit.

Order Glossopteridales *sensu* Pant (1982)

Genus *Glossopteris* Brongniart, 1828 ex Brongniart, 1831

*Type species.* *Glossopteris browniana* Brongniart, 1828, by subsequent designation of Brongniart (1831); ?Newcastle or Tomago Coal Measures (Guadalupian or Lopingian), Sydney Basin, Australia.

*Glossopteris raniganjensis* Chandra & Surange, 1979  
(Figs 2e, i, j–l; 3; 4a–i)

*Material.* More than 85 leaves on rock slabs CNM SA.1–SA.20 (illustrated leaves: CNM SA.2a, SA.2b, SA.2c, SA.2d, SA.2e, SA.2f, SA.2g, SA.5a, SA.9b, SA.9c, SA.9d, SA.10a, SA.10b, SA.10c).

*Description.* All leaves are incomplete, 55 to >150 mm long, 10–46 mm wide (notophyll–mesophyll), narrowly elliptical, narrowly obovate, oblanceolate or narrowly oblanceolate. Base cuneate–acute (Fig. 2j, k); apex generally pointed acute (Fig. 2e), in a few cases obtuse. Position of the widest point at one-half to four-fifths lamina length. Margin entire. Midrib 0.5–1.5 mm wide at base of lamina, tapering distally but persisting to apex. Secondary veins emerge from midrib at *c.* 5–20°, arch moderately to sharply near midrib, then pass with gentle curvature across the lamina to intersect the margin at typically 60–80°; degree of arching *c.* 10–20° (Figs 2i, l; 3). Secondary veins dichotomize and anastomose 2–7 times across the lamina generating short triangular,



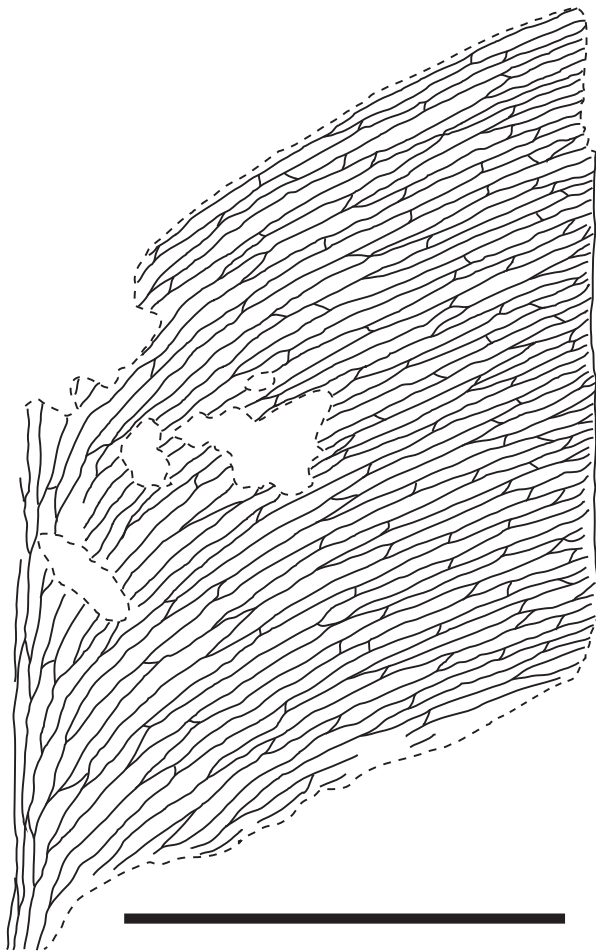


Figure 3. Line drawing of venation details of *Glossopteris raniganjensis* Chandra & Surange, 1979 (CNM SA.2c). Scale bar: 10 mm.

semicircular and rhombic areolae near the midrib, becoming elongate polygonal, narrowly linear and falcate towards the margin (Fig. 3). Vein density near the midrib is typically 6–10 per centimetre, increasing to 15–30 per centimetre near the margin.

*Remarks.* Although there is modest variation in the size, venation angles and degree of anastomoses among *Glossopteris* leaves in the Tabbowa assemblage, the continuum in preserved forms suggests that these all belong to a single natural species. Over 100 species of *Glossopteris* have been established since the genus was defined by Brongniart (1828), and many species names have been applied in a broad sense to encompass diverse leaf morphotypes. We favour the more restrictive definitions of species applied by Chandra & Surange (1979) in their review of the Indian species of the genus, since that scheme employs more rigorous morphological criteria and has biostratigraphic utility.

Several established species, especially *G. indica* Schimper, 1869, *G. communis* Feistmantel, 1879, *G. decipiens* Feistmantel, 1879, *G. arberi* Srivastava, 1956, *G. spatulata* Pant & Singh, 1971, *G. tenuinervis* Pant & Gupta, 1971, *G. nimishea* Chandra & Surange,

1979 and *G. raniganjensis* Chandra & Surange, 1979, bear marked similarities in size, shape, vein density and narrow areolae to the *Glossopteris* leaves described here. Of these, *G. arberi* and *G. communis* differ from the Tabbowa specimens by having an obtuse apex and relatively few secondary vein anastomoses. *Glossopteris decipiens*, *G. indica*, *G. nimishea* and *G. spatulata* have less strongly arched veins in either the inner or outer portions of the lamina and consequently tend to have lesser marginal venation angles than the Tabbowa specimens. *Glossopteris tenuinervis* has generally straighter secondary veins and a greater marginal venation angle. *Glossopteris raniganjensis* was one of several species that Chandra & Surange (1979) segregated from the broadly defined ‘*G. communis*-type’ complex of leaves. The similarities between *G. raniganjensis* specimens from the Kamthi Formation of India and the Tabbowa specimens is especially notable in their dimensions, acute apices, vein density and secondary veins that are inserted at low angles to the midrib in the inner lamina but pass outwards in sweeping arcs to the margin. We, therefore, confidently assign the Sri Lankan specimens to that species.

Genus *Samaropsis* Goeppert, 1864

*Type species.* *Samaropsis ulmiformis* Goeppert, 1864. Permian, Braunau, Bohemia.

*Samaropsis* sp. (Fig. 2h)

*Material.* Two poorly preserved small seeds are available on sample CNB SA.4 of which one (CNB SA.4a) is illustrated (Fig. 2h).

*Description.* The seeds are roughly circular, c. 1–2 mm in diameter with a longitudinally elliptical inner body flanked by a pair of <0.5 mm wings. A short micropylar extension is present but the details are ill-defined.

*Remarks.* Similar small winged seeds have been recorded extensively from Permian strata across Gondwana (Maithy, 1965; Millan, 1981; Anderson & Anderson, 1985; McLoughlin, 1992a; Bordy & Prevec, 2008). When preserved as impressions they offer few characters for consistent taxonomic differentiation or affiliation. Only when attached to fructifications (e.g. Pant & Nautiyal, 1984; Anderson & Anderson, 1985; Prevec, 2011, 2014) or preserved as permineralizations with pollen in the micropyle (Gould & Delevoryas, 1977; Ryberg, 2010) can such seeds be confidently affiliated with glossopterids. Nevertheless, the absence of any gymnosperm foliage other than *Glossopteris* in the Tabbowa Basin macrofossil assemblage makes a strong case for the studied seeds having affinities to *G. raniganjensis*.

Genus *Vertebraria* Royle ex McCoy, 1847 emend. Schopf, 1982

*Type species.* *Vertebraria australis* (McCoy, 1847) emend Schopf, 1982; Raniganj Formation (upper Permian), Ranigani Coalfield, India.

*Vertebraria australis* (McCoy, 1847) emend Schopf, 1982 (Fig. 2f)

**Material.** Two roots on sample CNM SA.3, of which one (CNM SA.3b) is illustrated (Fig. 2f).

**Description.** These roots are preserved as impressions along bedding planes hosting fern foliage and sphenophyte axes (Fig. 2f). The roots exceed 100 mm long but are less than 10 mm wide and bear irregular longitudinal and transverse creases.

**Remarks.** Schopf (1982), Doweld (2012), Joshi *et al.* (2015) and Herendeen (2015) have discussed at length the complex nomenclatural history of glossopterid root fossils attributed to *Vertebraria*. Here we follow the recent decision of the Nomenclature Committee on Fossil Plants (Herendeen, 2015) in retaining *Vertebraria australis* (McCoy, 1847) emend Schopf, 1982 as the type of this genus. Moreover, since there are no meaningful morphological or anatomical differences between *V. australis* (originally described from Australia) and *V. indica* (Unger) Feistmantel, 1876 (originally described from India), we apply the former name to the Sri Lankan Permian roots.

The Sri Lankan specimens are irregularly segmented roots typical of *V. australis*, the root form universally linked to glossopterids (Gould, 1975; McLoughlin, Larsson & Lindström, 2005; Decombeix, Taylor & Taylor, 2009). The Tabbowa Basin specimens are small and probably represent distal rootlets with few internal compartments. They approach the size and morphology of terminal rootlets that Pant (1958) assigned to *Lithozhiza tenuirama* but possess some segmentation. No additional characters are available from the studied specimens that add to the extensive descriptions of *V. australis* from other parts of Gondwana.

## 5. Arthropod–plant interactions

Various forms of damage are evident on the *Glossopteris* leaves from Tabbowa. Some represent physical attrition features, but others were evidently produced by arthropod herbivory or egg-laying habits based on their distinctive shapes, distributions, necrotic rims or similarity to modern forms of insect/mite-induced damage. Five moderately common types of arthropod-induced damage on *Glossopteris* leaves identified in the Tabbowa assemblage are outlined in the following sections. This diversity is consistent with the range of feeding strategies registered previously for Gondwanan glossopterids (McLoughlin, 1990, 2011; Adami-Rodriguez, Iannuzzi & Pinto, 2004; Beattie, 2007; Prevec *et al.* 2009, 2010; Srivastava & Agnihotri, 2011; Cariglino & Gutiérrez, 2011; Slater, McLoughlin & Hilton, 2012). No unequivocal arthropod damage was detected on any of the non-glossopterid elements of the flora.

### 5.a. Hole feeding

Several leaves have large elliptical to linear incisions in the middle to outer parts of the lamina that broadly fol-

low the course of the veins (Fig. 4a, c). Each incision removes tissue spanning several secondary veins and interveinal areas. The margins of the damaged areas vary from smooth to somewhat irregular and are surrounded by a very narrow reaction rim.

Similar hole-feeding damage has been recorded on Permian *Glossopteris* leaves from India (Srivastava & Agnihotri, 2011, fig. 2f) and in similar-aged gigantopterid foliage from China (Glasspool *et al.* 2003). Such external foliage feeding might have been produced by protorthopteroids or coleopterans (Labandeira, 2006) during Permian time, but a specific causal agent cannot be identified in this instance.

### 5.b. Margin feeding

At least one clear example of margin feeding is represented in the small assemblage of leaves from Tabbowa (Fig. 4b). It is expressed by a deep (6 mm long, 2.5 mm wide) U-shaped incision in the margin of the mid-region of a *Glossopteris* leaf. The scallop terminus is rounded and the margin is relatively smooth with a minimally developed reaction rim. A second specimen bears tapering clefts on either side of the lamina in the apical half of the leaf (Fig. 4f). The clefts penetrate about half the width of the lamina.

Similar U-shaped margin-feeding damage has been reported on *Glossopteris* leaves from Australia (Beattie, 2007), South Africa (Prevec *et al.* 2009), Brazil (Adami-Rodriguez, Iannuzzi & Pinto, 2004) and India (Srivastava & Agnihotri, 2011). This U-shaped damage may have been caused by the feeding habits of protorthopteroids or coleopterans.

Based on their rounded shoulders, the clefts in specimen CNM SA.2g (Fig. 4f) also appear to represent faunal rather than abiological (e.g. wind) damage. They may represent examples of margin feeding during the early stages of leaf development before the lamina had fully expanded. Examples of *Glossopteris retusa* (Maheshwari, 1965) and *Glossopteris major* (Pant & Singh, 1971) from India, and *Glossopteris truncata* (McLoughlin, 1994b) from Australia bear similar notched margins in the apical half of the leaves that may derive from an equivalent process.

Other leaves in the Tabbowa assemblage have sharp clefts (lacking rounded shoulders) that penetrate all the way to the midrib following the course of the secondary venation (Fig. 4i). These are more likely to represent physical attrition features (simple tears along secondary veins) through wind or aqueous transport rather than arthropod feeding damage.

### 5.c. Oviposition scars

A single *Glossopteris* leaf in the assemblage bears two possible arthropod oviposition scars (Fig. 4d). Two elliptical scars of similar dimensions (1 × 2 mm) and with depressed margins are positioned along the flank and on top of the leaf midrib.



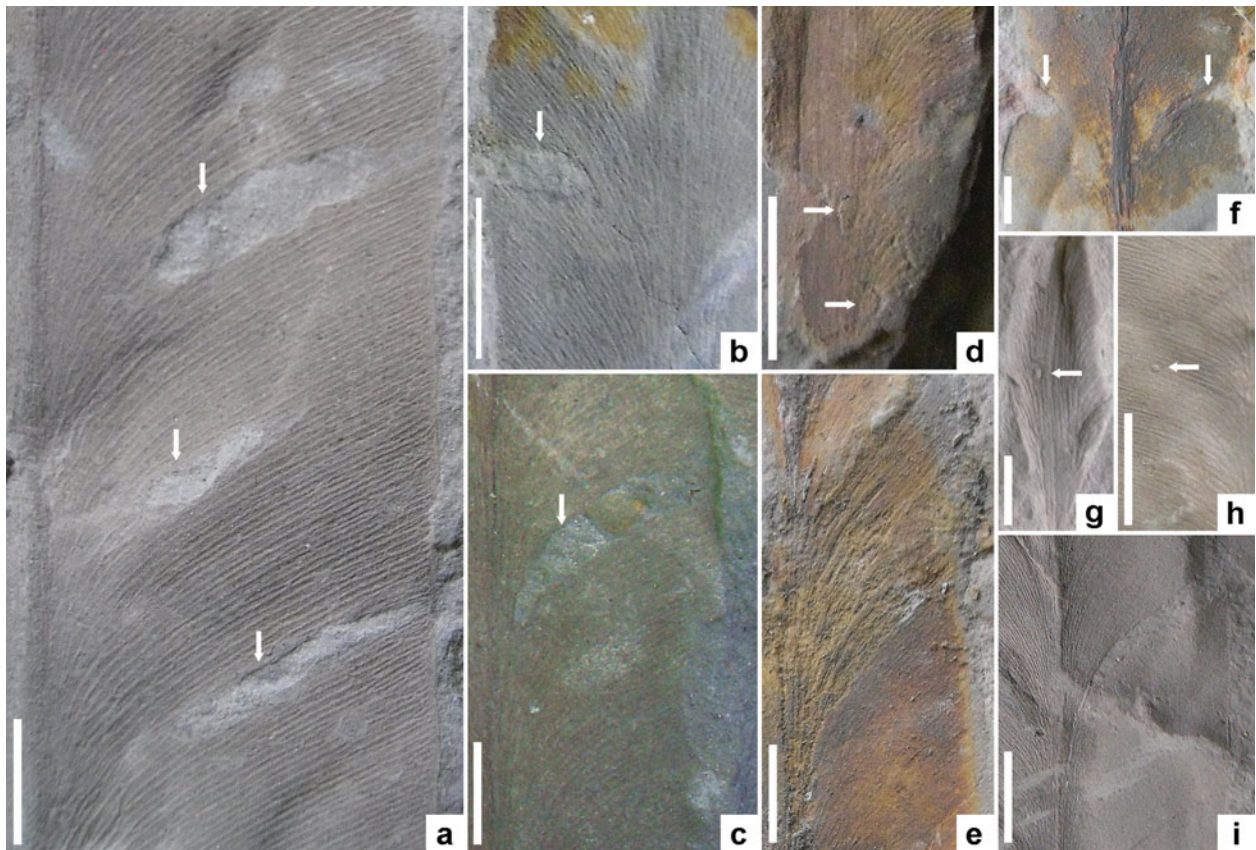


Figure 4. (Colour online) Arthropod (a–h) interactions and (i) physical attrition on *Glossopteris raniganjensis* Chandra & Surange, 1979 leaves. (a, c) Elliptical hole feeding traces with slender reaction rims (arrowed) (CNM SA10a and CNM SA.2d, respectively). (b) Deep, U-shaped, margin-feeding damage (arrowed) (CNM SA.2e). (d) Oviposition scars flanking and overlying the leaf midrib (arrowed) (CNM SA.2f). (e) Possible skeletonization damage through a portion of the lamina (CNM SA.10b). (f) Possible early-stage margin feeding damage represented by tapering clefts (arrowed) on either side of the lamina in the apical half of the leaf (CNM SA.2g). (g, h) Possible piercing-and-sucking scars situated over secondary veins (Reg. numbers CNM SA.9c and CNM SA.10c respectively). (i) Lamina tearing along secondary veins (CNM SA.9d). All scale bars: 10 mm.

These traces are considered probable insect (odonatan?) oviposition scars based on their similarity in size, shape and position against the midrib to several previous examples noted on *Glossopteris* leaves from Australia (McLoughlin, 1990, 2011), South Africa (Prevec *et al.* 2009, 2010), South America (Adami-Rodriguez, Iannuzzi & Pinto, 2004; Cariglino & Gutiérrez, 2011) and India (Srivastava & Agnihotri, 2011).

#### 5.d. Skeletonization

A single example of possible partial leaf skeletonization is present in the assemblage (Fig. 4e). A significant segment of the mid-portion of this *Glossopteris raniganjensis* leaf has inter-secondary vein degradation. This zone tracks the orientation of the secondary veins and the leaf shows no differential staining in this area, so the damage does not appear to be an effect of weathering.

Examples of skeletonization in *Glossopteris* leaves are scarce and equivocal, although Adami-Rodriguez, Iannuzzi & Pinto (2004, fig. 6E, F) illustrated one putative example from Permian strata of Brazil that

is similar to the example documented here. A causal agent cannot be ascertained.

#### 5.e. Piercing-and-sucking damage

Several leaves bear small (<1 mm diameter) circular scars over the midrib (Fig. 4g) or secondary veins (Fig. 4h). These are similar to piercing-and-sucking damage on a broad range of leaves in the Mesozoic (McLoughlin, Martin & Beattie, 2015). Labandeira (2006) noted that piercing-and-sucking damage was already widely developed on fern and gymnosperm leaves by late Palaeozoic time and might have been produced by various groups, such as palaeodictyopteroid or early hemipteroid insects (Labandeira & Phillips, 1996).

## 6. Discussion and conclusions

### 6.a. Plant taphonomy

The plant fossils are generally well preserved and variably orientated. The assemblage is dominated by *Glossopteris* leaves and associated organs, with lesser



proportions (<5% each) of *Sphenophyllum* leaf whorls, large longitudinally ribbed *Paracalamites* (sphenophyte) axes and *Dichotomopteris* (fern) fronds. No complete plants or foliage-bearing woody axes were identified. The dominant leaves in the assemblage fall into the notophyll–mesophyll size range of Webb (1959). A few leaves are partially torn along the venation (Fig. 4i), and many are dissected by fracturing of the bedding planes. The leaves are otherwise relatively complete which, together with the fine-grained, fissile lithology, suggests deposition within relatively quiet-water (lacustrine) settings. Their dense association is consistent with preservation as an autumnal leaf accumulation, a taphonomic feature typical of glossopterid foliar fossil assemblages (Plumstead, 1969; McLoughlin, 1993; McLoughlin, Larsson & Lindström, 2005; Slater, McLoughlin & Hilton, 2015).

#### 6.b. Age of the fossil assemblage

Deep Cenozoic weathering has eliminated any opportunity to undertake palynostratigraphic analysis of the exposed strata at Tabbowa, although coring of deep subsurface strata may yield spore-pollen assemblages in the future. Currently, plant macrofossils provide the only means of dating these strata. Most of the plant genera recorded in the new fossil assemblage (i.e. *Paracalamites*, *Sphenophyllum*, *Glossopteris*, *Vertebraria* and *Samaropsis*) have long ranges in the Permian strata of Gondwana. However, *Dichotomopteris lindleyi*, and indeed other members of this genus, are most common in Lopingian strata (Raniganj Formation and equivalents) in the rift basins of Peninsula India (Chandra, 1974; Maithy, 1975; Pant & Misra, 1977; Goswami, Das & Guru, 2006) and the foreland basins of eastern Australia (Burngrove Formation and equivalents: McLoughlin, 1992a). Similarly, *Glossopteris raniganjensis* is most common in the Lopingian Raniganj and Kamthi formations of eastern India, although a few examples from the underlying Barakar and Kulti formations (Guadalupian–Lopingian) have also been attributed to this species (Chandra & Surange, 1979). *Sphenophyllum churulianum*, initially described from the Barakar Formation of India (Srivastava & Rigby, 1983) and tentatively dated as Guadalupian on the basis of palynostratigraphic correlations proposed by Veevers & Tewari (1995) and revised dating of those palynozones by Nicoll *et al.* (2015), has subsequently been identified in Lopingian strata in India (Goswami, Das & Guru, 2006). Although high-resolution biostratigraphic indices are lacking, the limited macrofloral data outlined above broadly favour a Lopingian (late Permian) age for the *Glossopteris*-bearing beds near Tabbowa Tank.

#### 6.c. Significance for hydrocarbon exploration

Sri Lanka currently imports all of its hydrocarbon requirements, imposing considerable constraints on the national economy (Singh, 2009). The recent discov-

ery of natural gas reservoirs in the offshore Mannar Basin has led to some hope of developing a domestic hydrocarbon energy source (Premarathne *et al.* 2016). Nevertheless, the source(s) and generation history of gas in the Mannar Basin remain poorly resolved. Current models have tied the evolution of the basin to mid-Mesozoic continental rifting associated with the break-up of Gondwana, but we hypothesize that the basin may have initiated during late Palaeozoic time with intra-rift continental sedimentation, and only later accumulated a thick blanket of Jurassic–Cretaceous strata linked to continental separation.

Seismic profiles through the offshore Mannar Basin reveal a thick sedimentary succession transected by normal faulting below the mid-Cretaceous–Cenozoic interval (Premarathne *et al.* 2016, fig. 4). Hydrocarbon exploration wells have so far penetrated the succession only down to strata of mid-Cretaceous age. Past geological modelling has generally inferred a Jurassic–Early Cretaceous age for the basin's lowermost (unexplored) strata (Baillie *et al.* 2004; Premarathne *et al.* 2013). However, prominent and laterally continuous seismic reflectors within the lower part of this succession (Premarathne *et al.* 2016, fig. 4) may represent Permian coals or organic-rich lacustrine mudrocks. Such strata are known to have developed extensively within the Permian–Triassic pan-Gondwanan rift system prior to continental break-up, which developed along the same structural domain during middle Mesozoic time (Boast & Nairn, 1982; Casshyap & Tewari, 1984; Kreuser, 1987; Cockbain, 1990; Smith, 1990; McLoughlin & Drinnan, 1997a, b; Delvaux, 2001; Holdgate *et al.* 2005; Harrowfield *et al.* 2005). Notably, Permian strata are also present in the subsurface of the Indian sector of the Cauvery Basin (Basavaraju & Govindan, 1997), which represents a northerly extension of the Mannar Basin failed rift system (Premarathne, 2015). The discovery of strata hosting a glossopterid-dominated macroflora in the parallel onshore Tabbowa Basin now lends support to the development of Permian subsidence and sedimentation within the whole northwestern Sri Lankan sector as part of the late Palaeozoic pan-Gondwanan rifting event (Harrowfield *et al.* 2005). We hypothesize that this event may have left remnants of a Permo-Triassic, predominantly continental, stratigraphic succession not only in the Mannar Basin, but throughout the pan-Gondwanan rift corridor. This intra-rift succession constitutes a potentially important hydrocarbon (especially gas) target for future exploration (Fig. 5).

Permian continental strata, particularly those rich in coals (dominated by type II and III kerogens), represent important natural gas source rocks in various sectors of the pan-Gondwanan rift corridor (Kantsler & Cook, 1979; Kreuser, Schramedei & Rullkotter, 1988; Clark, 1998; Raza Khan *et al.* 2000; Ghori, Mory & Iasky, 2005; L. Dresy, unpubl. MSc thesis, University of Stavanger, 2009; Farhaduzzamana, Abdullaha & Islam, 2012). Should the basal strata of the

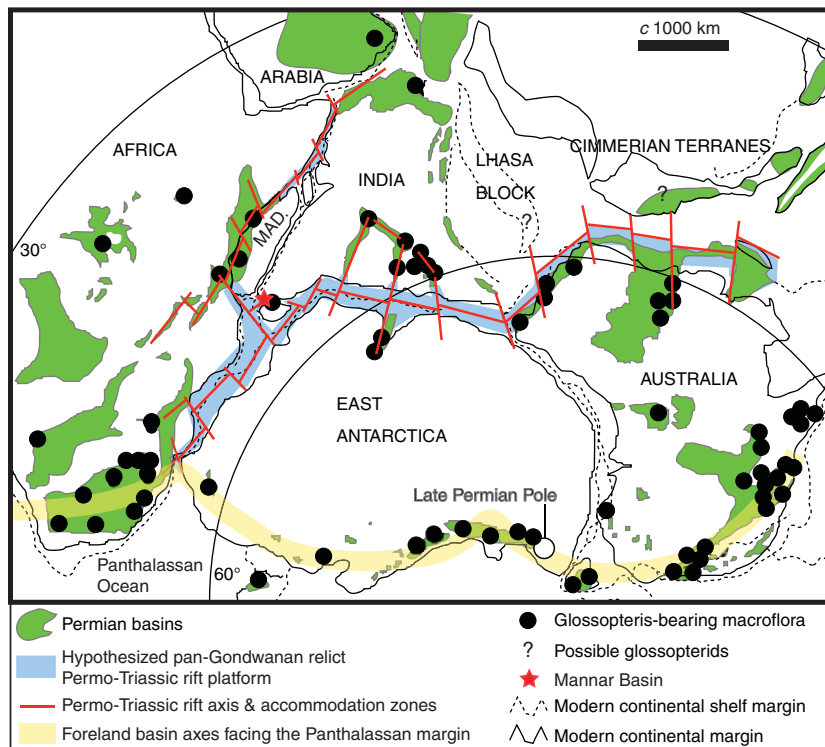


Figure 5. (Colour online) Map of central Gondwana at the end of Palaeozoic time showing the distribution of Permian basins, deposits hosting *Glossopteris* macrofloras, the location of the Mannar Basin, and the hypothesized relict pan-Gondwanan Permo-Triassic rift-fill system (modified from Harrowfield *et al.* 2005).

Mannar Basin be confirmed to host Permian plant-rich sediments, as in the adjacent Tabbowa Basin, this will enhance the hydrocarbon prospectivity of the region. This is especially the case since the basal succession of the Mannar Basin has been modelled to lie within the oil- to gas-generating windows (Ratnayake & Sampei, 2015; Premarathne *et al.* 2016).

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## References

- ADAMI-RODRIGUES, K., IANNUZZI, R. & PINTO, I. D. 2004. Permian plant–insect interactions from a Gondwana flora of southern Brazil. *Fossils and Strata* **51**, 106–25.
- ANDERSON, J. M. & ANDERSON, H. M. 1985. *Palaeoflora of Southern Africa. Prodrum of South African megaflores, Devonian to Lower Cretaceous*. Rotterdam: A.A. Balkema, 416 pp.
- ANDERSON, J. M. & ANDERSON, H. M. 2003. *Heyday of the Gymnosperms: Systematics and Biodiversity of the Late Triassic Molteno Fructifications*. Pretoria: Strelitzia 15, National Botanical Institute, South Africa, 398 pp.
- ARCHANGELSKY, S. & WAGNER, R. H. 1983. *Glossopteris anatolica* sp. nov. from uppermost Permian strata in south-east Turkey. *Bulletin of the British Museum (Natural History) Geology* **37**, 81–91.
- ASAMA, K. 1966. Permian plants from Phetchabun, Thailand and problems of flora migration from Gondwanaland. *Bulletin of Natural Science Museum, Tokyo* **13**, 291–316.
- BAILLIE, P., BARBER, P. M., DEIGHTON, I., GILLERAN, P. A., JINADASA, W. A. & SHAW, R. D. 2004. Petroleum systems of the deepwater Mannar Basin, offshore Sri Lanka. *Proceedings, Deepwater and Frontier Exploration in Asia & Australasia Symposium, December 2004*. Jakarta: Indonesian Petroleum Association, DFE04-PO-015, 13 pp.
- BALME, B. E., KERSHAW, A. P. & WEBB, J. A. 1995. Floras of Australian coal measures, with notes on their associated Mesozoic faunas. In *Geology of Australian Coal Basins* (eds C. R. Ward, H. J. Harrington, C. W. Mallett & J. W. Beeston), pp. 41–62. Sydney: Geological Society of Australia, Coal Geology Group, Special Publication no. 1.
- BASAVARAJU, M. H. & GOVINDAN, A. 1997. First record of Permian palynofossils in sub-surface sediments of Cauvery Basin, India. *Journal of the Geological Society of India* **50**, 571–6.
- BEATTIE, R. 2007. The geological setting and palaeoenvironmental and palaeoecological reconstructions of the Upper Permian insect beds at Belmont, New South Wales, Australia. *African Invertebrates* **48**, 41–57.
- BERCOVICI, A., BOURQUIN, S., BROUTIN, J., STEYER, J.-S., BATAILL, B., VERAN, M., VACANT, R., KHENTHAYONG, B. & VONGPHAMANY, S. 2012. Permian continental paleoenvironments in southeastern Asia: new insights from the Luang Prabang Basin (Laos). *Journal of Asian Earth Sciences* **60**, 197–211.
- BOAST, J. & NAIRN, A. E. M. 1982. An outline of the geology of Madagascar. In *The Ocean Basin and Margins*,



- Vol. 6: *The Indian Ocean* (eds A. E. M. Nairn & F. G. Stehli), pp. 649–96. New York: Plenum Press.
- BORDY, E. M. & PREVEC, R. 2008. Sedimentology, palaeontology and palaeo-environments of the Middle (?) to Upper Permian Emakwenzini Formation (Karoo Supergroup, South Africa). *South African Journal of Geology* **111**, 429–58.
- BOUREAU, E. 1964. *Traité de Paléobotanique. Tome III. Sphenophyta, Noeggerathiophyta*. Paris: Masson et Cie, 544 pp.
- BRONGNIART, A. 1828. *Prodrome d'une Histoire des Végétaux Fossiles*. Paris: F.G. Levrault, VIII+223 pp.
- BRONGNIART, A. 1831. *Histoire des Végétaux Fossiles*. 1 (5–6). Paris: G. Dufour et E. d'Ocagne, pp. 209–64.
- BROUTIN, J., AASSOUMI, H., EL WARTITI, M., FREYET, P., KERP, H., QUESADA, C. & TOUTIN-MORIN, N. 1998. The Permian basins of Tiddas, Bou Achouch and Khenifra (central Morocco). *Biostratigraphic and palaeophytogeographic implications*. In *Peri-Tethys Memoir 4: Epicratonic Basins of Peri-Tethyan Platforms* (eds S. Crasquin-Soleau & E. Barrler), pp. 257–78. Paris: Muséum National d'Histoire Naturelle, Memoir no. 179.
- CAMPBELL, D. H. 1905. *The Structure and Development of the Mosses and Ferns (Archegoniatae)*. 2nd edition. New York, London: Macmillan, 657 pp.
- CARIGLINO, B. & GUTIÉRREZ, P. R. 2011. Plant-insect interactions in a *Glossopteris* flora from the La Golondrina Formation (Guadalupian–Lopingian), Santa Cruz province, Patagonia, Argentina. *Ameghiniana* **48**, 103–12.
- CASSHYAP, S. M. & TEWARI, R. C. 1984. Fluvial models of the Lower Permian coal measures of the Son-Mahandi and Koel-Damodar Valley basins, India. *Coal and Coal bearing Sequences* (eds R. A. Rahmani & R. M. Flores), pp. 121–47. International Association of Sedimentologists, Special Publication no. 7.
- CHANDRA, S. 1974. Ferns and fern-like plants from the Lower Gondwana. In *Aspects and Appraisal of Indian Palaeobotany* (eds K. R. Surange, R. N. Lakhanpal & D. C. Bharadwaj), pp. 62–72. Lucknow: Birbal Sahni Institute of Palaeobotany.
- CHANDRA, S. & SURANGE, K. R. 1979. *Revision of the Indian species of Glossopteris*. Lucknow: Birbal Sahni Institute of Palaeobotany Monograph 2, 291 pp.
- CLARK, D. N. 1998. Review of the exploration potential of Madagascar. *Houston Geological Society Bulletin*, **July 1998**, 23–9.
- COCKBAIN, A. E. 1990. Perth Basin. In *Geology and Mineral Resources of Western Australia* (ed. A. F. Trendall), pp. 495–525. Perth: Western Australian Geological Survey, Memoir no. 3.
- COORAY, P. G. 1984. *An Introduction to the Geology of Sri Lanka (Ceylon)*, 2nd revised edition. Colombo: National Museums of Sri Lanka, xix + 340 pp.
- 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**, 644–56.
- DELEVORYAS, T. 1969. Glossopterid leaves from the Middle Jurassic of Oaxaca, Mexico. *Science* **165**, 895–6.
- DELEVORYAS, T. & PERSON, C. P. 1975. *Mexiglossa varia* gen. et sp. nov., a new genus of glossopteroid leaves from the Jurassic of Oaxaca, Mexico. *Palaeontographica A* **154**, 114–20.
- DELVAUX, D. 2001. Karoo rifting in western Tanzania: precursor of Gondwana break-up? In *Contributions to Geology and Palaeontology of Gondwana in Honour of Helmut Wopfner* (ed. R. H. Weiss), 111–25. Cologne: Geological Institute, University of Cologne.
- DILCHER, D. L. 1974. Approaches to the identification of angiosperm leaf remains. *Botanical Review* **40**, 1–157.
- 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**, 1129–31.
- DUMORTIER, B. C. 1829. *Analyses des Familles des Plantes, avec l'Indication des Principaux Genres qui s'y rattachent*. Tornay: J. Casterman, 49 pp.
- DU TOIT, A. L. 1937. *Our Wandering Continents*. London: Oliver & Boyd, 366 pp.
- EDIRISOORIYA, G. & DHARMAGUNAWARDHANE, H. A. 2013a. Plant insect-interactions in Jurassic fossil flora from Sri Lanka. *International Journal of Scientific and Research Publications* **3**(1), 1–12.
- EDIRISOORIYA, G. & DHARMAGUNAWARDHANE, H. A. 2013b. New species of Bennettitales from the Jurassic rocks of Sri Lanka. *International Journal of Scientific and Research Publications* **3**(2), 1–7.
- FARHADUZZAMANA, MD., ABDULLAHA, W. H. & ISLAM, MD. A. 2012. Depositional environment and hydrocarbon source potential of the Permian Gondwana coals from the Barapukuria Basin, Northwest Bangladesh. *International Journal of Coal Geology* **90–91**, 162–79.
- FEISTMANTEL, O. 1876. 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**, 329–80.
- FEISTMANTEL, O. 1879. The fossil flora of the Lower Gondwanas – 1. The flora of the Talchir-Karharbari beds. *Memoirs of the Geological Survey of India, Palaeontologia Indica Series 12* **3**(1), 1–64.
- FIELDING, C. R., FRANK, T. D. & ISBELL, J. L. 2008. Chapter 24: The late Paleozoic ice age—A review of current understanding and synthesis of global climate patterns. In *Resolving the Late Paleozoic Ice Age in Time and Space* (eds C. R. Fielding, T. D. Frank & J. L. Isbell), pp. 343–54. Geological Society of America, Special Paper no. 441.
- FLORES, R. M. 2014. *Coal and Coalbed Gas: Fueling the Future*. Waltham, MA: Elsevier, 697 pp.
- GHORI, K. A. R., MORY, A. J. & IASKY, R. P. 2005. Modeling petroleum generation in the Paleozoic of the Carnarvon Basin, Western Australia: Implications for prospectivity. *AAPG Bulletin* **89**, 27–40.
- GLASSPOOL, I., HILTON, J., COLLINSON, M. & WANG, S.-J. 2003. Foliar herbivory in late Palaeozoic Cathaysian gigantopterids. *Review of Palaeobotany and Palynology* **127**, 125–32.
- GOEPPERT, H. R. 1864. Die fossile flora der ermisschen Formation. *Palaeontographica* **12**, 1–224 (1864), 225–316 (1865).
- GOSWAMI, S., DAS, M. & GURU, B. C. 2006. Permian biodiversity of Mahanadi Master Basin, Orissa, India and their environmental countenance. *Acta Palaeobotanica* **46**, 101–18.
- GOULD, R. E. 1970. *Palaeosmunda*, a new genus of siphonostelic osmundaceous trunks from the Upper Permian of Queensland. *Palaeontology* **13**, 10–28.
- GOULD, R. E. 1975. A preliminary report on petrified axes of *Vertebraria* from the Permian of eastern Australia. In *Gondwana Geology* (ed. K. S. W. Campbell), pp. 109–15. Canberra: Australian National University Press.

- GOULD, R. E. & DELEVORIAS, T. 1977. The biology of *Glossopteris*: evidence from petrified seed-bearing and pollen-bearing organs. *Alcheringa* **1**, 387–99.
- HARRIS, T. M. 1932. The fossil flora of Scoresby Sound East Greenland – Part 2: description of seed plants incertae sedis together with a discussion of certain cycadophyte cuticles. *Meddelelser om Grønland* **85**(3), 1–112.
- HARRIS, T. M. 1937. The fossil flora of Scoresby Sound, East Greenland. Part 5: Stratigraphic relations of the plant beds. *Meddelelser om Grønland* **112**, 1–114.
- HARROWFIELD, M., HOLDGATE, G., WILSON, C. & MCLOUGHLIN, S. 2005. Tectonic significance of the Lambert Graben, East Antarctica: reconstructing the Gondwanan rift. *Geology* **33**, 197–200.
- HERATH, J. W. 1986. *Economic Geology of Sri Lanka*. Colombo: Natural Resources, Energy & Science Authority, 207 pp.
- HERENDEEN, P. S. 2015. Report of the Nomenclature Committee on Fossils: 9. *Taxon* **64**, 1306–12.
- HOLDGATE, G. R., MCLOUGHLIN, S., DRINNAN, A. N., FINKELMAN, R. B., WILLETT, J. C. & CHIEHOWSKY, L. A. 2005. Inorganic chemistry, petrography and palaeobotany of Permian coals in the Prince Charles Mountains, East Antarctica. *International Journal of Coal Geology* **63**, 156–77.
- JOHNSTON, R. M. 1886. Fresh contribution to our knowledge of the character and the relationship of the upper Paleozoic and Mesozoic formations of Tasmania with the associated diabasic rocks. *Papers and Proceedings of the Royal Society of Tasmania* **1885**, 310–11.
- 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**, 330–3.
- KANTSLEER, A. J. & COOK, A. C. 1979. Maturation patterns in the Perth Basin. *Australian Petroleum Exploration Journal* **19**, 94–107.
- KATUPOTHA, J. 2013. Planated surfaces and erratic boulders of Sri Lanka. *Proceedings to 29th Technical Sessions of Geological Society of Sri Lanka, 2013*. Colombo: Geological Society of Sri Lanka, 91–4.
- KOENIG, C. 1825. *Icones Fossilium Sectiles*. London: G.B. Sowerby, 4 pp.
- KREUSER, T. 1987. Late Palaeozoic glacial sediments and transition to coal-bearing Lower Permian sediments in Tanzania. *Facies* **17**, 149–58.
- KREUSER, T., SCHRAMMEDEI, R. & RULLKOTTER, J. 1988. Gas-prone source rocks from cratogene Karoo basins in Tanzania. *Journal of Petroleum Geology* **11**, 169–84.
- LABANDEIRA, C. C. 2006. The four phases of plant–arthropod associations in deep time. *Geologica Acta* **4**, 409–38.
- LABANDEIRA, C. C. & PHILLIPS, T. L. 1996. Insect fluid-feeding on Upper Pennsylvanian tree ferns (Palaeodictyoptera, Marattiales) and the early history of the piercing-and-sucking functional feeding group. *Annals of the Entomological Society of America* **89**, 157–83.
- LINK, J. H. F. 1833. *Hortus Regius Botanicus Berolinensis*, 2. Berlin: G. Reimer, 138 pp.
- MAHER, T. P., BOSIO, M., LINDNER, E. R., BROCKWAY, D. J., GALLIGAN, A. G., MORAN, V. J., PECK, C., WALKER, M. P., BENNETT, P. A. & COXHEAD, B. A. 1995. Coal resources, quality and utilization. In *Geology of Australian Coal Basins* (eds C. R. Ward, H. J. Harrington, C. W. Mallett & J. W. Beeston), 133–59. Sydney: Geological Society of Australia, Coal Geology Group, Special Publication no. 1.
- MAHESHWARI, H. K. 1965. Studies in the *Glossopteris* flora of India—22. On some species of the genus *Glossopteris* from the Raniganj Stage of the Raniganj Coalfield, Bengal. *Palaeobotanist* **13**, 129–43.
- 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.
- MAITHY, P. K. 1974. *Dichotomopteris*, a new type of fern frond from the Lower Gondwana of India. *Palaeobotanist* **21**, 365–7.
- MAITHY, P. K. 1975. Some contributions to the knowledge of Indian Lower Gondwana ferns. *Palaeobotanist* **22**, 29–38.
- MCCARTHY, K., ROJAS, K., NIEMANN, M., PALMOWSKI, D., PETERS, K. & STANKIEWICZ, A. 2011. Basic petroleum geochemistry for source rock evaluation. *Oilfield Review* **23**(2), 32–43.
- 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**, 145–57.
- MCLOUGHLIN, S. 1990. Some Permian glossopterid fructifications and leaves from the Bowen Basin, Queensland, Australia. *Review of Palaeobotany and Palynology* **62**, 11–40.
- MCLOUGHLIN, S. 1992a. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 1. *Palaeontographica B* **228**, 105–49.
- MCLOUGHLIN, S. 1992b. Permian sphenophytes from the Collie and Perth Basins, Western Australia. *Review of Palaeobotany and Palynology* **75**, 153–82.
- MCLOUGHLIN, S. 1993. Plant fossil distributions in some Australian Permian non-marine sediments. *Sedimentary Geology* **85**, 601–19.
- MCLOUGHLIN, S. 1994a. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 2. *Palaeontographica B* **231**, 1–29.
- MCLOUGHLIN, S. 1994b. Late Permian plant megafossils from the Bowen Basin, Queensland, Australia: Part 3. *Palaeontographica 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.
- MCLOUGHLIN, S. 2011. *Glossopteris* – insights into the architecture and relationships of an iconic Permian Gondwanan plant. *Journal of the Botanical Society of Bengal* **65**, 93–106.
- MCLOUGHLIN, S. & DRINNAN, A. N. 1997a. Revised stratigraphy of the Permian Bainmedart Coal Measures, northern Prince Charles Mountains, East Antarctica. *Geological Magazine* **134**, 335–53.
- MCLOUGHLIN, S. & DRINNAN, A. N. 1997b. Fluvial sedimentology and revised stratigraphy of the Triassic Flagstone Bench Formation, northern Prince Charles Mountains, East Antarctica. *Geological Magazine* **134**, 781–806.
- MCLOUGHLIN, S., LARSSON, K. & LINDSTRÖM, S. 2005. Permian plant macrofossils from Fossilryggen, Vestfjella, Dronning Maud Land. *Antarctic Science* **17**, 73–86.
- MCLOUGHLIN, S., MARTIN, S. K. & BEATTIE, R. 2015. The record of Australian Jurassic plant–arthropod interactions. *Gondwana Research* **27**, 940–59.
- MILLAN, J. H. 1981. Distribution of platyspermic gondwanic seeds. *Palaeobotanist* **28–29**, 63–74.
- NICOLL, R. S., MCKELLAR, J., AREEBA AYAZ, S., LAURIE, J., ESTERLE, J., CROWLEY, J., WOOD, G. & BODORKOS, S. 2015. CA-IDTIMS dating of tuffs, calibration of palynostratigraphy and stratigraphy of the Bowen and Galilee



- basins. In: *Bowen Basin Symposium 2015: Bowen Basin and Beyond* (ed. J. W. Beeston), pp. 211–8. Hornsby: Geological Society of Australia, Coal Geology Group.
- PANT, D. D. 1958. Structure of some roots and spores from the lower Gondwana (Permo-Carboniferous) of east Africa. *Vijnana Parishad Anushandhan Patrika* **1**, 231–44.
- PANT, D. D. 1982. The Lower Gondwana gymnosperms and their relationships. *Review of Palaeobotany and Palynology* **37**, 55–70.
- PANT, D. D. & GUPTA, K. L. 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part 2. *Palaeontographica B* **132**, 130–52.
- PANT, D. D. & MISRA, L. 1977. On two genera of pterophylls *Damudosorus* gen. nov. and *Trithecopteris* gen. nov. from the Lower Gondwanas of the Raniganj Coalfield. *Palaeontographica B* **164**, 76–86.
- PANT, D. D. & NAUTIYAL, D. D. 1984. On the morphology and structure of *Ottokaria zeilleri* sp. nov.—a female fructification of *Glossopteris*. *Palaeontographica B* **193**, 127–52.
- PANT, D. D. & SINGH, K. B. 1971. Cuticular structure of some Indian Lower Gondwana species of *Glossopteris* Brongniart. Part 3. *Palaeontographica B* **135**, 1–40.
- PLUMSTEAD, E. P. 1969. *Three Thousand Million Years of Plant Life in Africa. Alex. L. du Toit Memorial Lectures No. 1*. Pretoria: Geological Society of South Africa, 72 pp.
- POTONIÉ, H. 1893. Über die Sphenophyllaceen. *Naturwissenschaften Wochenschriften* **8**, 219–20.
- PREMARATHNE, U. 2015. Petroleum potential of the Cauvery Basin, Sri Lanka: a review. *Journal of Geological Society of Sri Lanka* **17**, 41–52.
- PREMARATHNE, U., SUZUKI, N., RATNAYAKE, N. P. & KULARATHNE, E. K. C. W. 2013. A petroleum system in the Gulf of Mannar Basin, offshore Sri Lanka. *Proceedings to 29th Technical Sessions of Geological Society of Sri Lanka, 2013*. Colombo: Geological Society of Sri Lanka, 9–12.
- PREMARATHNE, U., SUZUKI, N., RATNAYAKE, N. & KULARATHNE, C. 2016. Burial and thermal history modelling of the Mannar Basin, offshore Sri Lanka. *Journal of Petroleum Geology* **39**, 193–214.
- PREVEC, R. 2011. A structural re-interpretation and revision of the type material of the glossopterid ovuliferous fructification *Scutum* from South Africa. *Palaeontologia africana* **46**, 1–19.
- PREVEC, R. 2014. *Elatra*: a glossopterid fructification with a bipartite, hooded wing from the lower Permian of Madagascar and South Africa. *Review of Palaeobotany and Palynology* **210**, 119–39.
- 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.
- 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**, 454–93.
- RANA, M. S. & AL HUMAIDAN, F. S. 2016. Statistical data on worldwide coal reserves, production, consumption, and future demand. In *Coal Production and Processing Technology* (eds M. R. Raisi & R. Gupta), pp. 31–50. Boca Raton, FL: CRC Press.
- RATNAYAKE, A. S. & SAMPEI, Y. 2015. Preliminary prediction of the geothermal activities in the frontier Mannar Basin, Sri Lanka. *Journal of Geological Society of Sri Lanka* **17**, 19–29.
- RAZA KHAN, M. S., SHARMA, A. K., SAHOTA, S. K. & MATHUR, M. 2000. Generation and hydrocarbon entrapment within Gondwanan sediments of the Mandapeta area, Krishna-Godavari Basin, India. *Organic Geochemistry* **31**, 1495–507.
- RIGBY, J. 1993. Plants. In *Palaeontology of the Permian of Western Australia* (ed. S. K. Skwarko), 77–83. Perth: Geological Survey of Western Australia, Bulletin no. 136.
- RIGBY, J. F. 1966. The Lower Gondwana floras of the Perth and Collie basins, Western Australia. *Palaeontographica B* **118**, 113–52.
- ROYLE, J. F. 1833–1840. *Illustrations of the Botany and Other Branches of Natural History of the Himalayan Mountains and of the Flora of Cashmere*, 2 volumes. London: W.H. Allen & Company, 100 pp.
- RYBERG, P. E. 2010. *Lakkosia kerasata* gen. et sp. nov., a permineralized megasporangiate glossopterid structure from the central Transantarctic Mountains, Antarctica. *International Journal of Plant Sciences* **171**, 332–44.
- SCHIMPER, W. P. 1869. *Traité de Paléontologie Végétale ou la Flore du Monde Primitif*. Paris: J.B. Baillière et Fils, 740 pp.
- SCHOPF, J. M. 1982. Forms and facies of *Vertebraria* in relation to Gondwana coal. *Antarctic Research Series* **36**, 37–62.
- SINGH, A. S. 2009. Regional integration in South Asia and energy cooperation: opportunities and challenges. In *The Geopolitics of Energy in South Asia* (ed. M. Lall), pp. 51–82. Singapore: ISEAS Publications.
- SITHOLEY, R. V. 1944. Jurassic plants from the Tabbowa Series in Ceylon. *Spolia Zeylanica* **24**, 3–17.
- SLATER, B. J., MCLOUGHLIN, S. & HILTON, J. 2012. Animal-plant interactions in a Middle Permian permineralised peat of the Bainmedart Coal Measures, Prince Charles Mountains, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology* **363–4**, 109–26.
- SLATER, B. J., MCLOUGHLIN, S. & HILTON, J. 2015. A high-latitude Gondwanan lagerstätte: The Permian permineralised peat biota of the Prince Charles Mountains, Antarctica. *Gondwana Research* **27**, 1446–73.
- SMITH, R. M. H. 1990. A review of stratigraphy and sedimentary environments of the Karoo Basin of South Africa. *Journal of African Earth Sciences* **10**, 117–37.
- SRIVASTAVA, A. K. & AGNIHOTRI, D. 2011. Insect traces on Early Permian plants of India. *Paleontological Journal* **45**, 200–6.
- SRIVASTAVA, A. K. & RIGBY, J. F. 1983. *Sphenophyllum*, *Trizygia*, and *Gondwanophyton* from the Barakar Formation of Raniganj Coalfield, with a revision of Lower Gondwana Sphenophyllales. *Geophytology* **13**, 55–62.
- SRIVASTAVA, A. K. & TEWARI, R. 1996. Plant fossils from the Barakar Formation, Auranga Coalfield, Bihar. *Geophytology* **26**, 83–8.
- SRIVASTAVA, P. N. 1956. Studies in the *Glossopteris* flora of India – 4. *Glossopteris*, *Gangamopteris* and *Palaeovitaria* from the Raniganj Coalfield. *The Palaeobotanist* **5**, 1–45.
- VEEVERS, J. J. & TEWARI, R. C. 1995. Gondwana master basin of peninsular India between Tethys and the interior of the Gondwanaland province of Pangea. *Geological Society of America Memoirs* **187**, 1–73.
- WAYLAND, E. J. 1925. The Jurassic rocks of Tabbowa. *Ceylon Journal of Science* **13**, 195–208.

- WEBB, D. A. 1959. A physiognomic classification of Australian rain forests. *Journal of Ecology* **47**, 551–70.
- ZALESSKY, M. D. 1927. Permskaya flora ural'skikh predelov Angaridy. Atlas. Flore Permienne des limites ouraliennes de l'Angaride. *Mémoires du Comité Géologique, Nouvelle Série* **176**, 1–152.
- ZALESSKY, M. D. 1932. Observations sur les végétaux nouveaux paléozoïques de Sibérie. *Annales de la Société Géologique du Nord* **57**, 111–34.
- ZIMINA, V. G. 1967. On *Glossopteris* and *Gangamopteris* in Permian deposits of the Southern Maritime Territory. *Palaeontological Journal* **2**, 98–106.