Glossopteris-like leaves from the Triassic of eastern Australia

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Holmes, W. B. K. 1992. *Glossopteris* - like leaves from the Triassic of eastern Australia. *In* : Venkatachala, B. S., Jain, K. P. & Awasthi, N. (eds) – *Proc. 'Birbal Sahni Birth Centenary Palaeobotanical Conference.' Geophytology* **22** : 119—125.

Glossopteris plants which dominated the vegetation in the late Permian coal measures in Australia, suffered a sudden and dramatic extinction close to the transition from the Permian to the Triassic periods. *Glossopteris*-like leaves which may represent surviving remnants from this catastrophic event are recorded from Triassic localities in the Sydney and Clarence-Moreton basins of eastern Australia. Leaves described and illustrated are *Glossopteris moribunda* Johnston, *G. grandis* (Walkom) comb. nov., *G. nymboidensis* sp. nov. and *G. lacerata* sp. nov.

Key-words - Plant megafossil, *Glossopteris*, Triassic, eastern Australia.

INTRODUCTION

THE origin of the *Glossopteris* Flora and the reason for its sudden demise before the close of the Permian Period are the great unsolved mysteries of Gondwana palaeobotany. This paper relates to the latter problem. Some leaves from the Triassic are described which may represent possible survivors of the catastrophic decline.

The Permian macrofloras in Gondwana countries, while generally lacking in diversity of species, were extremely rich in individuals. The prodigality of that vegetation resulted in the formation of some of the world's largest coal reserves within Gondwana basins. The bulk of the organic matter which produced the coals was from the stems and leaves of the *Glossopteris* plant.

The large, simple leaf of the glossopterids indicates an abundant availability of moisture (Kovaks-Endrody, 1979) and a temperate climate (Maheshwari *et al.*, 1991; Rigby & Shah, 1980). The distinct growth rings in the wood of petrified stems of glossopterid plants are evidence of marked seasonal temperature changes (Retallack, 1980). *Vertebraria*, the root of the later glossopterid plants (Gould, 1975b) exhibits a structure largely composed of aerenchyma cells. The presence of air spaces in plant internal architecture invariably is the result of adaptation to water-logged conditions (Williams & Barber, 1961). However, freezing is usually destructive to aerenchyma tissue. Therefore, it may be assumed that the environment that supported the *Glossopteris* vegetation was one with a high water-table and distinct seasonal changes in temperature, but in which the temperature did not drop low enough to cause freezing of the ground water. While some *Glossopteris* leaves possessed surface hairs and papillae (Pant, 1962) there is little evidence that they developed sufficient sclerophyllous characters that would allow them to diversify into drier or upland situations. For over 50 million years, the glossopterid vegetation flourished in the stable lowland habitat, and then suddenly it disappeared, to be replaced by the impoverished and short-lived "*Thinfeldia*" *callipteroides* Flora, which was possibly of Sub-Angara origin (Meyen, 1987). That flora in turn was replaced by the *Dicroidium* Flora which persisted through the Triassic Period in most Gondwana countries (Retallack, 1977).

In Australia, the sudden changes in vegetation are supported by palynological evidence. The widespread and diverse *Dulhuntyispora* Assemblage with its high content of disaccate pollen with striate proximal faces, persisted through the Middle and Upper Permian sediments (Balme, 1964). It was replaced by a new assemblage, Unit Tr 1a (Helby, 1973) in which *Quadrisporites horridus* is abundant-especially in the Sydney Basin- and new forms of striate saccate and monosaccate pollen made their first appearances (Hennelly, 1958). The succeeding Unit Tr 1b contains no vestiges of the older Permian microfloras (Evans, 1966). *Taeniosporites* made its first appearance and there was a fairly abundant content of *Alisporites* (*Pteruchus* types attributed to *Dicroidium*). A similar sequence of assemblages has been recorded from the Salt Range of Pakistan by Balme (1970).

In the past, the Permian-Triassic boundary was generally regarded as the time of the disappearance of *Glossopteris* and the introduction of the *Dicroidium* Flora (Walkom, 1936; David, 1950). By correlation with invertebrate faunas (Balme, 1970). Unit Tr 1a is latest Permian and the Triassic boundary is placed between Units Tr 1a and Tr 1b.

The abrupt change from the *Dulhuntyispora* Assemblage to Assemblage Tr 1a took place within the topmost Permian coal seam (de Jersey, 1979). Hennelly (1958) and Grebe (1970) who described the microfloral sequences across the Illawarra Coal Measures and Newcastle Coal Measures boundary with the overlying Narrabeen Group, found that there was little or no evidence of a sedimentary break at this horizon. This is strong evidence that, in this region at least, climatic rather than physical evironmental factors were responsible for the change. However, it must be noted that Helby (1973) suggested a possible hiatus between the respective palynological zones. A climatic factor, possibly an extreme heating event in association with tectonic upheaval may have been responsible for the great worldwide extinctions of invertebrates and other life that occurred near the Permian-Triassic boundary. However, the reasons for this event are not well understood and continue to be debated.

Were any of the glossopterids able to survive by adapting to the changing conditions or by migrating into suitable refugia?

Much speculation has taken place on the origin of the angiosperms. The glossopterids have been considered likely ancestors by Plumstead (1956), Melville (1983), and more convincingly by Krassilov (1971, through *Caytonia*) and Retallack & Dilcher (1981). For the glossopterids to be the ancestors of the angiosperms, it would be necessary for at least one glossopterid line to have survived the late Permian extinction.

In India, *Glossopteris* remains are recorded from the earliest Triassic in association with *Dicroidium*-like leaves (Pant & Pant, 1987). Du Toit (1927) and Thomas (1952, 1958) described a whorl of leaves as *G. verticillata* from the Triassic Molteno Formation of South Africa. From the evidence of not well preserved cuticle, Anderson and Anderson (1989) have transferred *G. verticillata* to a new genus *Gontriglossa* which also includes another two newly described species. There have been a number of records of *Glossopteris*-like leaves in Triassic floral asemblages from eastern Australia (Johnston, 1887, 1888; Walkom, 1928; Flint & Gould, 1975; Retallack, 1980). These leaves, plus some newly discovered material, are illustrated and described below. I have placed them in *Glossopteris* in the broad sense that it is a form genus for simple leaves having a midrib and reticulate venation.

Glossopteris moribunda Johnston 1887
Pl. 1, figs 1,2

1887 *Glossopteris* (?) *moribunda*, Johnston, p.169; pl. 1, figs 5, 5A.

1888 *Glossopteris moribunda*, Johnston, p1, 28, figs 5, 5A.

1980 *Glossopteris moribunda*, Johnston *in* Retallack, p.429; figs 21, 13C.

Material–Specimens of two almost complete leaves which are preserved as impressions are housed in the collections in the Australian Museum, Sydney; from Glenlee, SW of Sydney in the Bringelly Shale of the Wiannamatta Group of the Sydney Basin. Age - late Anisian to Ladinian (Retallack, 1980). Specimen AMF 26336 (Pl. 1, fig. 1) is a linear spatulate leaf, 7 cm in length and 1 cm in width; apex missing; tapering basally to an attenuated petiole 1 cm in length. The lateral veins leave the midrib at a very acute angle at a density of ca 7 per cm, then curve slightly outwards, forking and joining with adjacent veins to reach the margin at an angle of ca 45^0 and with a density of ca 16 veins per cm. Efforts to obtain a cuticle preparation from the carbonised surface of this leaf were unsuccessful. Specimen AMF26325 (Pl 1, fig. 2) is a narrow elliptic leaf 5 cm in length and 1.4 cm in width; apex obtuse, base missing. The venation pattern appears to be similar to the above leaf but is not clear.

Discussion—Johnston (1887) described and illustrated fragments of two linear-spatulate leaves from the Triassic shales of Lords Hill, in Hobart, Tasmania. Both leaves had the base missing. The larger fragment was 42 mm in length and 13 mm at the broadest part near the apex. The midrib was distinct; about 12 lateral veins in the length of the fragment branched off at an acute angle, curving outwards to the margin while forking and anastomosing to form 2 to 4 open meshes. Johnston surmised that the leaves "represented dwarfed or degraded descendants of *Glossopteris* which gave such a peculiar

Plate 1 →

1. *Glossopteris moribunda* Johnston. AMF 26336. To illustrate venation, x2.
2. *Glossopteris moribunda* Johnston. AMF 26325, x1.
3. *Glossopteris grandis* (Walkom) comb. nov. AMF 78254, x1.
4. *Glossopteris grandis* (Walkom) comb. nov. AMF 78254, x2.

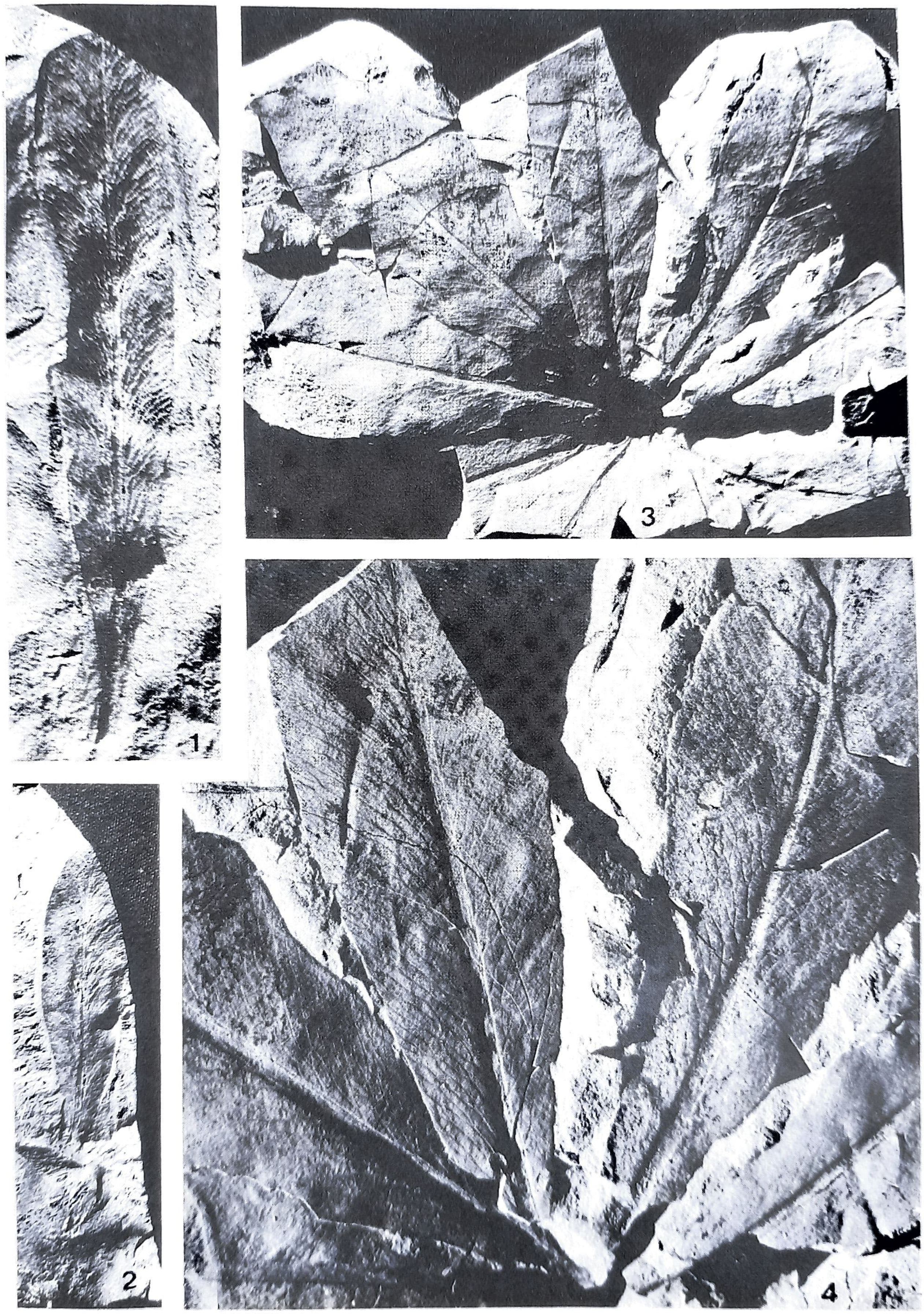

Plate 1

character to the Lower Coal Measures (Permian) by its wonderful profusion and were an indication of the fast approaching extinction of the genus".

The two specimens illustrated herein (Pl. 1. figs 1 & 2) closely resemble the description and illustrations of Johnston. Johnston's material cannot now be located (N. Kemp. pers. comm.). Retallack (1980) stated that he had seen Johnston's material. He considered that the specimens from Glenlee "were indistinguishable from the Type".

When compared with Permian material. *G. moribunda* shows a remarkable similarity to the Type of *G. angustifolia* described and illustrated by Brongniart (1828, p. 224, pl. 63, figs. 1, 1A).

Glossopteris grandis (Walkom) comb. nov.
Pl. 1, figs 3, 4; Pl.2, fig. 1

1928 *Anthrophyopsis grandis* Walkom, p. 464; text-fig. 2; pl. 26. fig. 5.

1965 *Anthrophyopsis grandis* Walkom in Hill *et al.*, pl. T7. fig. 3.

1975a *Anthrophyopsis grandis* Walkom in Gould, fig. 5C.

Material—The specimen re-illustrated here as Pl.2 fig. 1 to show the venation, is University of Queensland specimen UQF1725. This is counterpart of the type specimen. UQF1724 of Walkom (1928). The type locality is Sheep Station Creek, near Wivinhoe Crossing of the Brisbane River, Esk Trough. Age, Anisian-Ladinian. Walkom's type specimen was re-illustrated by Hill *et al.* (1965) and by Gould (1975a). The type specimen as preserved is incomplete at the basal end. It is 15 cm long and 9.5 cm wide; the apex is broadly obtuse. Secondary veins leave the midrib at an acute angle and for about one third of the width of the lamina. they form wide, elongate mesh with a general inclination of ca 45^0 to the midrib; for the remainder of the lamina they form a narrower elongate mesh inclined at ca 65^0 to 70^0 to the midrib; closer to the midrib the meshes are 1-2mm wide, wider in the proximal than the apical part, while towards the margin they approximate to 7 or 8 meshes in 5mm of width. A recently collected specimen of *G. grandis* (AMF 78254, figs 3, 4) from the Nymboida Coal Measures of the Southern Clarence-Moreton Basin shows about 10 leaves apparently attached in a whorl or a close spiral. Other specimens from Nymboida of detached leaves which are in the Australian Museum's Fossil Collection (AMF 78255-78258) show the range of variation which exists in the size of the leaves of this species. The age of the Nymboida Coal Measures is also Anisian-Ladinian (Retallack *et al.*,1977).

Discussion—The genus *Anthrophyopsis* Nathorst, which is restricted to the Northern Hemisphere, has a markedly different venation and is not considered appropriate for this material.

In gross morphology, the leaves of *G. grandis* are closely similar to and may be conspecific with *Gontriglossa verticillata* (Thomas) Anderson & Anderson (1989) from the Triassic Molteno Formation of South Africa. *G. verticillata* was first described as *Sagenopteris longicaulis* by Du Toit (1927), then transferred to *Glossopteris longicaulis* by Thomas (1952). As this name was preoccupied, the specific name was changed to *verticillata*. Anderson and Anderson (1989) have described a poorly preserved cuticle of this leaf and consider it to be significantly different from *Glossopteris*. They have therefore placed it in a new genus *Gontriglossa*. All known specimens of *Glossopteris grandis* are impressions without preserved cuticle. The leaf arrangement of *Gontriglossa verticillata* differs from *Glossopteris grandis* by having whorls comprised of opposite fascicles of three leaves, each attached at regularly spaced nodes.

Glossopteris nymboidensis sp.nov.
Pl.2, figs 2,3

1975 *Anthrophyopsis grandis* Flint & Gould; pl.1, fig.9.

Diagnosis—A leaf of unknown length, tapering distally to an acute (?) apex. Midrib distinct, striated. Lateral veins leaving midrib at an acute angle of ca 20^0-30^0 and intervals of ca 0.5mm quickly curve outwards over a distance of ca 5mm where they bifurcate and then run straight and parallel to margin at an angle of 70^0 to the midrib. After the initial bifurcation the veins fork again two or three times, joining with adjacent veins to form long, narrow meshes, each subsequent mesh being narrower than the preceding one. The density of veins halfway across the lamina, ca 12-14/cm and at the margin ca 18/cm.

Material—Holotype : University of New England UNEF 13528, and paratype UNEF 13639. The holotype is the distal portion of a leaf, the paratype is the midportion of a leaf. Each fragment is 8.5cm in length and the

Plate 2 →

1. *Glossopteris grandis* (Walkom) comb. nov. U.Q.F. 1725. Counterpart of Holotype, x1.
2. *Glossopteris nymboidensis* sp.nov. UNEF 13528. Holotype. x1.
3. *Glossopteris nymboidensis* sp.nov. UNEF 13639. Paratype. x1.
4. *Glossopteris lacerata* sp.nov. AMF 78261. Holotype, x1.

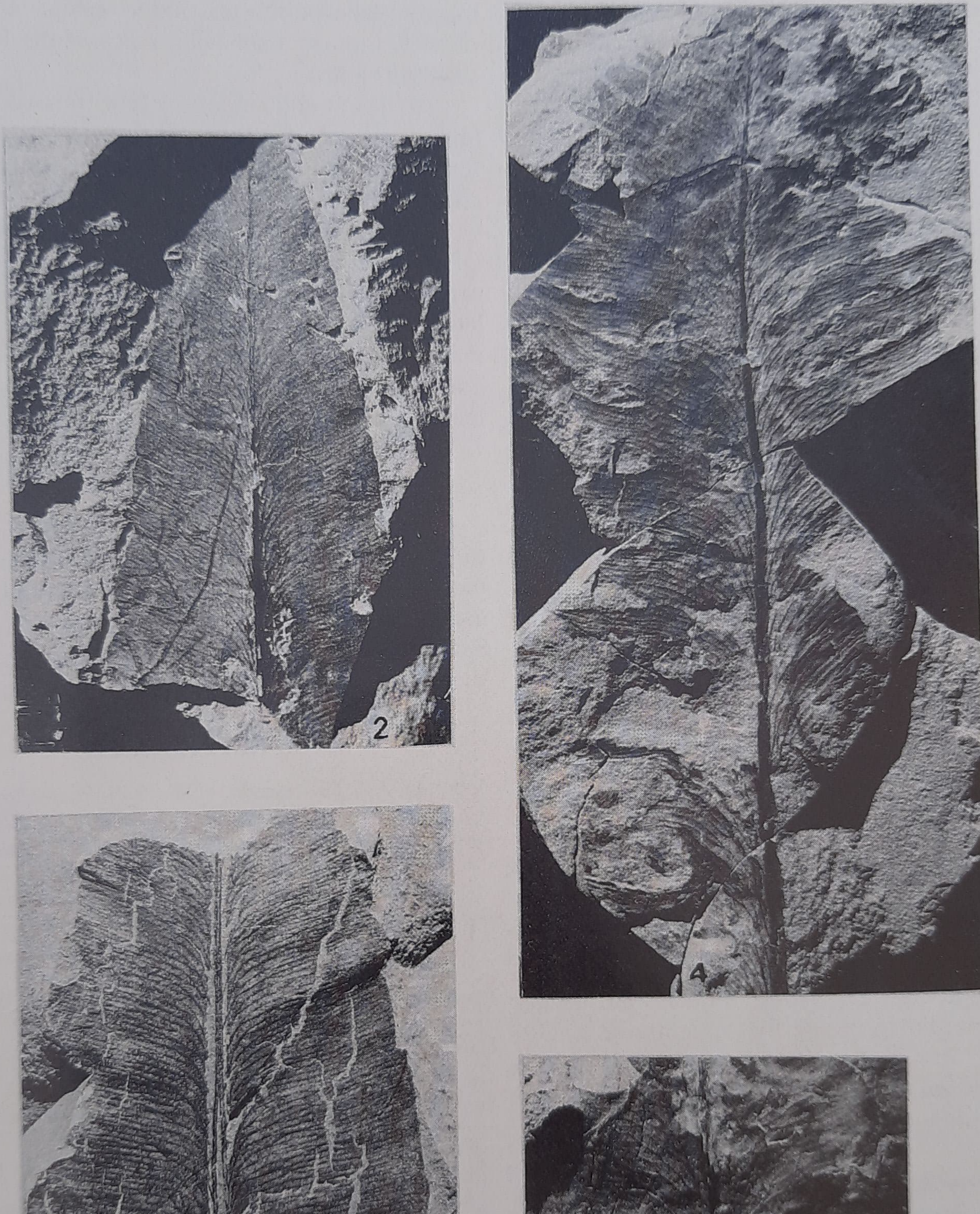

Plate 2

paratype is 5cm in width at its widest point. It is possible that both specimens are portions of the same leaf.

Type locality—Nymboida Quarry. University of New England Locality 1489. Nymboida Coal Measures. Clarence-Moreton Basin, Aniso-Landinian.

Discussion—*Glossopteris nymboidensis* differs from all other described Triassic *Glossopteris* and *Gontriglossa* species by the very fine narrow parallel meshes formed by the lateral veins. The venation pattern distinguishes it from *Anthrophyopsis* species.

Glossopteris lacerata sp. nov.
Pl.2, fig. 4

Diagnosis—A broad elliptic leaf with glossopterid venation, and with an irregularly lacerated margin. Base and apex missing. The leaf as preserved is 14cm in length and 6.5cm at its widest point, and appears to be broadly spatulate in outline. The lamina is deeply dissected into irregular widths and varying depths from the margin. The venation pattern is similar to that of *G. nymboidensis*.

Material—A single specimen, the holotype AMF 78259 Australian Museum, Sydney.

Type locality—Nymboida Quarry, University of New England Locality 1489, Nymboida Coal Measures. Clarence-Moreton Basin, Aniso-Ladinian.

Discussion—*Glossopteris lacerata* is a bizarre leaf with a most unnatural-looking appearance. *Glossopteris* leaves from Permian deposits sometimes show evidence of marginal damage from chewing by insects, however it would be a strange chewing pattern indeed that would damage a leaf margin to create the appearance of *G. lacerata*.

G. lacerata resembles *G. nymboidensis* in its venation pattern but differs from the latter by its dissected margin.

A *Glossopteris*-like leaf with a dissected margin from the late Permian Raniganj Coalfield of West Bengal was placed by Srivastava (1987) in a new genus *Gondwanophyllites* as *G. dissectus*. That leaf differs from *Glossopteris lacerata* by the venation pattern and by the deeper and more regular incisions of the lamina.

CONCLUDING NOTE

The leaves described above have been placed in the form genus *Glossopteris*. I stress, that on present evidence, there is no natural relationship between these leaves and the fructification- bearing *Glossopteris* leaves that have been placed variously in the Glossopteridales, Arberiales or the Ottokariales. The purpose of this paper is to draw attention to these leaves which occur in Triassic macrofossil assemblages, and to speculate that they may possibly represent surviving relics of the Permian *Glossopteris* Flora.

Anderson and Anderson (1989) have noted the difference between the cuticle of *Gontriglossa* and *Glossopteris*. Could this difference be the result of evolutionary change?

Leaves from the northern Permian floras such as *Glossopteridium* and *Glossophyllum* resemble *Glossopteris* in gross morphology but are obviously not related. If Meyen's suggestion that southern Triassic floras may have evolved from Permian Angaran ancestors is correct (Meyen, 1987), then the possibility arises that the leaves described herein may have had a northern origin.

ACKNOWLEDGEMENTS

I wish to thank Dr D.K. Chauhan for his endeavours to obtain a cuticle preparation from the Glenlee *G. moribunda* material, and Dr A.K. Srivastava for drawing my attention to *Gondwanophyllites*. The C.S.R.I.O. Science and Industry Endowment Fund and the Joyce Vickery Research Fund have provided valuable assistance.

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