Anatomically preserved Glossopteris leaves from the Bowen and Sydney basins, Australia

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Abstract

Anatomically preserved vegetative Glossopteris leaves in silicified peat deposits of Late Permian age are described from the Bowen Basin of Queensland and the Sydney Basin of New South Wales, Australia. Glossopteris homevalensis Pigg et McLoughlin, sp. nov., a distinctive new species from the Fort Cooper Coal Measures, Bowen Basin, is characterized by mesarch vascular bundles with parenchymatous bundle sheaths, a prominent midrib, the occasional presence of secondary vascular tissues, a differentiated mesophyll, an ad- and abaxial hypodermis of isodiametric-cuboidal cells with abundant fibers, epidermal cells with sinuous anticlinal margins and simple, slightly sunken stomata. Anatomically preserved leaves similar to G. schopfii Pigg, originally described from the central Transantarctic Mountains of Antarctica are also documented from the Bowen and Sydney basins. Those from the Burngrove Formation (Bowen Basin) differ slightly from Antarctic G. schopfii in size, and possess more numerous bundle sheath fibers and sometimes a more pronounced palisade mesophyll. Those from Katoomba (Sydney Basin) are also similar but may differ in some cuticular details. Also occurring in the Katoomba and Burngrove floras are leaves resembling G. skaarensis Pigg, a second species originally described from Antarctica. The presence of G. schopfii and cf. G. skaarensis in Australia as well as in the Transantarctic Mountains demonstrates their widespread distribution in eastern Gondwana. In contrast, the apparent restriction of G. homevalensis to a single locality in the Bowen Basin may reflect a distinct, more local distribution of a floristic assemblage unlike those typical of other Australian and Antarctic floras. © 1997 Elsevier Science B.V.

Keywords: Glossopteris; leaves; anatomy; Australia; Antarctica; silicification

1. Introduction

Although Glossopteris leaves have been known from numerous Southern Hemisphere compression/impression floras for over a century, information concerning their internal anatomical structure has only been available recently. To date, two species of Glossopteris, G. schopfii Pigg and G. skaarensis Pigg have been named on the basis of anatomically preserved specimens from Skaar Ridge, in the central Transantarctic Mountains (Pigg, 1990; Pigg and Trivett, 1994). Other petrified glossopterid leaves have been figured from the Bowen Basin (Gould and Delevoryas, 1977; McLoughlin, 1990; Pigg and Trivett, 1994) and

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Fig. 1. Relationships of eastern Gondwanan landmasses during the Late Permian showing the distribution of sedimentary basins (stippled) and studied permineralized leaf localities (●). Map modified after Anderson (1973), Lawver and Scotese (1987) and Scotese and Langford (1995).
the Prince Charles Mountains of East Antarctica (Neish et al., 1993) but are not yet known in detail. Initial comparisons of these floras have suggested that they differ from one another, and particularly that anatomical details of glossopterid leaves in these different localities may be distinct (Pigg, 1990; Pigg and McLoughlin, 1992; Pigg and Trivett, 1994).

In the present paper, we describe *Glossopteris homevalensis* Pigg et McLoughlin, *sp. nov.* from Homevale Station, in the Bowen Basin, Queensland, based on a suite of distinctive anatomical features. *Glossopteris homevalensis* is the third species of *Glossopteris* leaves based on anatomically preserved remains and demonstrates further diversity within the taxon. We also document the presence of *G. schopfii* and cf. *G. skaarensis*, leaves known previously from the central Transantarctic Mountains of Antarctica, at localities in the Bowen and Sydney basins of Australia, demonstrating that they were widespread in eastern Gondwana.

Apart from *Glossopteris* leaves, peats from each locality contain a range of other anatomically preserved plant remains including: glossopterid ovulate and pollinate fructifications, wood referable to *Araucarioxylon* Kraus or *Australoxylon* Marguerier, roots (*Vertebraria* Royle), seeds, and pollen; fern axes, foliage, sporangia and spores; mosses; and fungal hyphae (Gould, 1970, 1975; Schopf, 1970; Gould and Delevoryas, 1977; Taylor and Taylor, 1990; McLoughlin, 1990, 1992; Pigg and Trivett, 1994). *Noeggerathiopsis* Feistmantel leaves and sphenophyte remains are also well represented in impression floras from the studied formations (Rigby, 1969; McLoughlin, 1992; Cüneo et al., 1993).

Within these eastern Gondwanan foreland basins, permineralized peats and woods are essentially restricted to Upper Permian strata and typically occur within volcanogenic sedimentary rocks whose sediments were sourced from orogenic terranes to the east. The siliceous permineralization of the plant remains was probably related to the liberation of copious amounts of silica from the
breakdown of unstable volcanic glass, plagioclase, ferromagnesian silicates, and clays in these sediments (Taylor et al., 1989; McLoughlin, 1990).

2. Materials and methods

Anatomically preserved leaves are described from two localities in the Bowen Basin, Queensland, at Homevale Station (Gould, 1970, 1975; Gould and Delevoryas, 1977; Pigg and McLoughlin, 1992; Pigg and Trivett, 1994), and Blackwater (McLoughlin, 1990), and at a single locality in the Sydney Basin near Katoomba, New South Wales (Pigg and McLoughlin, 1992): see Figs. 1 and 2.

Material from the Homevale locality originates from within the Fort Cooper Coal Measures exposed in the southwest corner of Homevale Station near the Homevale–Elphinstone Road [21°16'27"S, 148°16'28"E on maps 1:250,000 (Mt. Coolon) and 1:100,000 (Hillalong)]. Material studied includes the figured slides of Gould and Delevoryas (1977), housed at The Australian Museum (AM) and additional specimens from the collections of J. Beeston, Queensland Department of Mines and Energy (housed at Arizona State University (ASU). This material was cited as 'New type, Homevale Station' in Pigg and Trivett (1994, table 2).

Material from the Blackwater Mine was collected by Andrew Scott during a visit to central Queensland in 1984, and was studied by S. McLoughlin as part of his doctoral dissertation (McLoughlin, 1990, 1992; cited as 'McLoughlin locality #1' in Pigg and Trivett, 1994, table 1). This material is housed in The University of Queensland's Department of Earth Sciences (UQ) bearing the acquisition numbers UQ F79332 a–k. This material is strongly siliceous and grey to white in color. A second slab collected from the same area (UQ L4863) differs markedly in being slightly calcareous and red-brown in color (cited as 'McLoughlin locality #2' in Pigg and Trivett, 1994, table 1). The two slabs also appear to differ in their floristic composition.

The provenance of the Blackwater slabs remains uncertain. Four geological units containing permineralized plant remains crop out in the Blackwater area (viz., the MacMillan, Fair Hill and Burngrove formations and the Rangal Coal Measures). Most previous collections of permineralized plants from this area have been from the Burngrove Formation cropping out immediately

PLATE I
Glossopteris homevalensis Pigg et McLoughlin, sp. nov. Leaves in transverse section to show variation in anatomy.
1. Midrib of leaf with primary tissues. Note palisade mesophyll; F 758896-13502 (5 O Side3 #5). × 87.
2. Leaf with primary tissues. Specimen was originally figured by Gould and Delevoryas (1977, fig. 2A). Abaxial surface of leaf is distorted by poor preservation; AM UNEF 15276. × 100.
3. Midrib of leaf with primary tissues. Note epidermis (e) and palisade mesophyll (p); F 758896-13502 (5 O Side #18A). × 140.
4. Leaf with secondary tissues. Specimen was originally figured by Gould and Delevoryas (1977, fig. 2B). Note secondary xylem (sx) and secondary phloem (sp); AM UNEF 15277. × 125.
5. Lateral area of leaf showing thinner lamina and poorly preserved mesophyll. Note vascular bundle (v8); F 758896-13502 (5 O Side #15A). × 95.
6. Midrib of leaf in 1 at another level. Note fibers (f) in both ad- and abaxial hypodermis and palisade mesophyll (p); F 758896-13502 (5 O Side3 #18). × 100.

PLATE II (see p. 344)
Glossopteris homevalensis Pigg et McLoughlin, sp. nov.
1. Oblique/longitudinal section through leaf. Note epidermis (e) and vein (v) in oblique/longitudinal section; AM UNEF 15276. × 100.
2. Tracheids in vein showing helical-reticulate wall thickenings; AM F 758896-13502 (5 O Side #0). × 350.
3. Longitudinal section of leaf. Note tabular appearance of upper epidermis; AM UNEF 15280. × 150.
4. Longitudinal section of leaf originally figured by Gould and Delevoryas (1977, fig. 2E). Note palisade/spongy differentiation in mesophyll and position of stoma (arrow); AM UNEF 15280. × 88.
5. Longitudinal section through leaf showing appearance of palisade/spongy differentiation in mesophyll; AM UNEF 15280. × 150.
PLATE II

(for explanation see p. 343)
to the west of the Blackwater mine site (Gould, 1970; McLoughlin, 1992). This formation is considered to be the most likely source of the slabs (especially the strongly siliceous UQ F79332) although derivation from one of the other aforementioned units cannot be discounted. All of these formations are of Late Permian age. For the sake of distinction in this study, the strongly siliceous grey-white block (UQ F79332) is described under 'Burngrove Formation' whereas the slightly calcareous red-brown block (UQ L4863) is designated as 'undifferentiated Blackwater Group'. Plants from the latter block were not studied in detail.

In the Sydney Basin, material designated in this paper as being from the Katoomba locality was collected by John Davis and other members of the Blue Mountains Lapidary Club from the north bank of Katoomba Creek (Jamieson’s Valley) roughly 2.4 km south of the Three Sisters, Katoomba, N.S.W., where it was associated with a bed of fine-grained banded chert thought to be silicified volcanic ash. This material derives from the Upper Permian Illawarra Coal Measures and is housed at The Australian Museum where it bears the registration number AM 60885. Sections cut from this material prior to this study bear numbers AM 6962-4.

Material was prepared by a modification of the cellulose acetate peel technique adapted for use with hydrofluoric acid (Joy et al., 1956; Basinger and Rothwell, 1977). Specimens lacking enough organic material for obtaining peels were thin-sectioned by standard techniques. Specimens are housed at The Australian Museum, Sydney, N.S.W., Australia (AM), The University of Queensland, St. Lucia, Queensland, Australia (UQ) and Arizona State University, Tempe, Arizona, USA (ASU). The Gould and Delevoryas (1977) figured slides and accompanying collection are housed at the Australian Museum and bear the prefix UNEF.

3. **Systematic paleobotany**

3.1. **Leaves from the northern Bowen Basin**

**Genus Glossopteris** Brongniart

**Glossopteris homevalensis** Pigg et McLoughlin, sp. nov. (Plates I–III; Plate IV, 1–3)

**Holotype:** Specimen in AM F 75896-13502 (5 O Side, #5, 18) (Plate I, 1, 6).

**Paratypes:** Specimen in AM UNEF 15277 (Plate I, 4); specimen in AM F 75896-13502 (5 O Side # 19a) (Plate III, 1, 2); specimen in AM F 75896-13502 (5 Q-O Side #0, 2a) (Plate III, 3, 4, 6; Plate IV, 2, 3).

**Repository:** Housed at The Australian Museum, Sydney, N.S.W., Australia.

**Type Locality:** Homevale Station near the Homevale–Elphinstone Road [21°16′27″S, 148°16′28″E on maps: 1:250,000 (Mt. Coolon) and 1:100,000 (Hillalong)].

**Stratigraphic horizon:** Fort Cooper Coal Measures (Blackwater Group). Upper Permian.

**Etymology:** The species is named for its locality at Homevale Station, Queensland, in the Bowen Basin.

**Diagnosis:** Leaves with reticulate venation, midrib lamina 0.18–0.36 mm thick, lateral lamina 0.08–0.15 mm thick; midrib containing 6 vascular bundles, each up to 180 μm, round, mesarch, 4–6 protoxylem strands interspersed with parenchyma and ca. a dozen metaxylem elements; vascular bundles of lateral lamina 60–80 μm; primary tracheary elements with helical wall thickenings; secondary xylem up to 5 cells thick when present; secondary phloem 500 μm thick when present; vascular bundle sheath 1–2 cells thick, parenchymatous; mesophyll with palisade and spongy layers; ad- and abaxial hypodermis up to 3 cells thick in midrib, of isodiametric-cuboidal cells 10–18 μm, fibers abundant; epidermal cells 53 × 25 μm, intercostal cells with sinusoid anticlinal walls, cells over veins with straight-margined walls; stomata randomly arranged on abaxial surface, not in rows, slightly sunken, surrounded by unspecialized epidermal cells, guard cells 35 × 10 μm with radially striate thickening, stoma elongate, 30 × 10 μm.

3.2. **Description**

3.2.1. **Leaves from the Homevale locality**

**Glossopteris homevalensis** leaves have a distinctive anatomical structure unlike that of either of
the two currently known anatomically preserved species from Antarctica, G. schopfii and G. skaarensis. They have a prominent midrib 0.18–0.36 mm thick that contains 6 large vascular bundles (Plate I, 1, 2, 4, 6). The lamina is considerably thinner, 0.08–0.15 mm, in the lateral regions of the leaf (Plate I, 5). Vascular bundles in the midrib are up to 180 μm in diameter, round and mesarch with 4–6 small protoxylem tracheids interspersed with parenchyma and surrounded by about a dozen metaxylem elements (Plate I, 1–3, 6). Those of the lateral region of the leaf are 60–80 μm in diameter, and have a similar organization (Plate I, 5). Primary tracheary elements typically have helical wall thickenings (Plate II, 2, 6). Within the veins tracheids are typically elongate, but short, barrel-shaped tracheids may also be present, particularly within vein dichotomies (Plate II, 2, 6). The vascular bundle sheath is composed of parenchymatous cells and is 1–2 cells thick (Plate I, 5). Secondary vascular tissues are sometimes found in the midrib area of leaves (Plate I, 4). When present, secondary xylem is up to 5 cells thick. A narrow band of secondary phloem 500 μm thick may also occur, and typically appears amorphous because of poor preservation (Plate I, 4).

Leaves have both an ad- and abaxial hypodermis up to 3 cells thick that is particularly evident in the midrib (Plate I, 1, 4, 6; Plate III, 5). The hypodermis is composed of isodiametric-cuboidal cells, 10–18 μm in diameter, many of which are fibers. The mesophyll of G. homevalensis leaves is differentiated into palisade and spongy layers (Plate I, 1, 6). In leaves cut in oblique or longitudinal section the palisade and spongy mesophyll layers appear even more pronounced (Plate II, 1, 4, 5). Spongy-type mesophyll is also observed in paradermal section beneath the lower epidermis and/or the abaxial layer of hypodermis (Plate III, 1, 4).

The uniseriate epidermis is composed of cells up to 53 × 25 μm (Plate I, 1, 3, 5; Plate II, 1, 3–4). While intercostal cells have sinuous anticlinal walls (Plate III, 3, 4, 6), those covering the veins have straight-margined anticlinal walls (Plate III, 1, 2, 4). Stomata are randomly arranged on the abaxial leaf surface, not in rows, are slightly sunken, and are surrounded by unspecialized epidermal cells (Plate II, 4, at arrow; Plate IV, 1–3). Guard cells are 35 × 10 μm, have radially striate thickenings and surround elongate stomatal openings 30 × 10 μm (Plate IV, 2, 3). Cuticle is sometimes well preserved and appears fairly thick (Plate I, 3; Plate II, 1, 3, 4; Plate III, 4, 6; Plate IV, 2, 3).

Only small fragments of glossopterid leaves with G. homevalensis anatomy that show external morphology were recovered. They provide little infor-
(for explanation see p. 347)
Fig. 3. Line drawing of leaf type 1 with relatively broad meshes preserved on the surface of a peat block from the Homevale locality. Illustrated in Plate IV, 4. ASU GL 12 no. 1. Scale bar = 1 cm.

Fig. 4. Line drawing of leaf type 2 with narrow, elongate meshes preserved on the surface of a peat block from the Homevale locality. Illustrated in Plate IV, 5. ASU GL 10 leaf 3. Scale bar = 1 cm.

Fig. 5. Line drawing of leaf attributed to *G. schopfii*. Illustrated in Plate V, 5. UQ F79332 (specimen since sectioned for anatomical studies); Burngrove Formation, Blackwater Mine. Scale bar = 1 cm.

Information as to total leaf size and shape or details of the base or apex. Larger leaf fragments recovered from the same locality are either too highly weathered or poorly preserved to confirm their anatomy (Plate IV, 4, 5), although leaves with *G. homevalensis* anatomy appear to dominate the flora. All fragments so far recognized have narrow elongate meshes, although there is variation in mesh shape and midrib width (Figs. 3 and 4; Plate IV, 4, 5). Two representative leaf fragments are illustrated to demonstrate the characteristic features and their range of variation (Figs. 3 and 4; Plate IV, 4, 5).

The first fragment (Fig. 3; Plate IV, 4) is 5.3 cm long and up to 2.8 cm wide and lacks both base and apex. The midrib is up to 1.8 mm wide in the basal part of the leaf and composed of up to 5 veins. Meshes are elongate, 10.6 mm long × 1.1 mm wide. They diverge from the midrib at angles of 10–22° and meet the margin at an angle of 30° (venation degree of arching around 12° sensu McLoughlin, 1994a). In contrast, the second fragment (Fig. 4; Plate IV, 5) is 5 cm long and 2 cm wide with a half-width of the leaf from midrib to intact margin of 1.8 cm, suggesting leaves may...
Fig. 6. Line drawing of leaf comparable to \textit{G. schopfii} preserved on the surface of a peat block from the Katoomba locality. Illustrated in Plate VI, 5. AM 60885. Scale bar = 1 cm.

have been up to around 2.6 cm wide. Leaves of this type have a narrow midrib up to 1 mm wide composed of 1–2 veins that persists to near the apex. Meshes are long and narrow, 6 mm long × 0.4 mm wide and diverge from the midrib at an angle of 10–25° and meet the margin at an angle of 40–50° (degree of arching ca. 12°).

3.2.2. \textit{Leaves from the Burngrove Formation (Blackwater area)}

A single leaf fragment was obtained from a weathered surface of a block presumably derived from the Burngrove Formation at Blackwater Mine (Fig. 5; Plate V, 5). It is 1.7 cm long × 0.5 cm wide basally and up to 0.7 cm wide more apically, suggesting that the leaves may have been somewhat oblanceolate. Details of the leaf base and apex are lacking. This specimen has the narrow-meshed venation pattern characteristic of \textit{G. schopfii} (Fig. 5; Plate V, 5). The midrib is about 0.6 mm wide and composed of 4–5 parallel vascular strands. Meshes are around 1.3–1.6 mm long × 0.2 mm wide. Veins diverge from the midrib at an angle of 10° and meet the leaf margin at an angle of 55–75° (degree of arching ca. 25°).

In transverse section, the most common type of leaf in the Burngrove Formation sample (UQ F79332) has anatomical features that are strikingly similar to \textit{G. schopfii} (Plate V, 1–3). The only differences are that these leaves are slightly thicker than the Antarctic forms, may have a better developed palisade mesophyll (Plate V, 3), and generally show more bundle sheath fibers (Plate V, 2).

In addition to \textit{G. schopfii}-type leaves, a few leaf specimens have been observed from the Burngrove Formation that resemble \textit{G. skaarensis} (Plate V, 4). Only transverse sections are available of these leaves but they show the characteristic fibrous hypodermis, prominent midrib and parenchymatous vascular bundle sheaths of \textit{G. skaarensis}. Leaves of this type are 0.4 mm thick in the midrib and 0.24 mm thick laterally and have 3–4 rows of secondary xylem elements in the vascular bundles. Because of the limited information available for these leaves they are referred to \textit{G. cf. skaarensis}. McLoughlin (1990) noted the presence of epidermal cells with sinuous margins in this matrix, but their connection to either leaf type remains unknown.

3.2.3. \textit{Leaves from the Sydney Basin}

Two types of leaves have also been found in material from the Illawarra Coal Measures near

\begin{table}
\centering
\begin{tabular}{l}
\textbf{PLATE V} \\
Permineralized glossopterid leaves from the Burngrove Formation, Bowen Basin. \\
1. Transverse section of \textit{G. schopfii} leaf showing rounded, fibrous vascular bundle sheath (vb) and prominent phloem lacuna, UQ F79332 F. × 95. \\
2. Transverse section of \textit{G. schopfii} leaf showing prominent fibers (f) in vascular bundles, UQ F79332 J2. × 95. \\
3. Transverse section of lateral area of \textit{G. schopfii} leaf showing smaller fibrous vascular bundles and somewhat differentiated mesophyll, UQ F79332 J2. × 95. \\
4. Transverse section of \textit{cf. G. skaarensis} leaf showing characteristic vascular bundles (vb) and poorly preserved mesophyll, UQ F79332 E. × 95. \\
5. Weathered surface showing external morphology of \textit{G. schopfii} leaf. Note midrib (mr), UQ F79332. × 8.
\end{tabular}
\end{table}
Table 1
Directory of specimens studied

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Formation</th>
<th>Preservation</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>G. schopfii</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Skaar Ridge, Transantarctic Mountains</td>
<td>Buckley Formation</td>
<td>petrifaction</td>
</tr>
<tr>
<td>2. <em>G. schopfii</em>&lt;sup&gt;b,c&lt;/sup&gt;</td>
<td>Blackwater, Bowen Basin</td>
<td>Burngrove Formation</td>
<td>petrifaction</td>
</tr>
<tr>
<td>3. <em>G. sp. cf. G. schopfii</em>&lt;sup&gt;d&lt;/sup&gt;</td>
<td>Bowen Basin</td>
<td>Upper Permian units</td>
<td>petrifaction</td>
</tr>
<tr>
<td>4. <em>G. homevalensis</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Katoomba, Sydney Basin</td>
<td>Illawarra Coal Measures</td>
<td>petrifaction</td>
</tr>
<tr>
<td>5. Leaf #1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Homevale, Bowen Basin</td>
<td>Fort Cooper Coal Measures</td>
<td>petrifaction</td>
</tr>
<tr>
<td>6. Leaf #2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Homevale, Bowen Basin</td>
<td>Fort Cooper Coal Measures</td>
<td>weathered chert surface</td>
</tr>
<tr>
<td>7. <em>G. skaarensis</em>&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Skaar Ridge, Transantarctic Mountains</td>
<td>Buckley Formation</td>
<td>petrifaction</td>
</tr>
<tr>
<td>8. <em>G. skaarensis</em>&lt;sup&gt;e&lt;/sup&gt;</td>
<td>Blackwater, Bowen Basin</td>
<td>Burngrove Formation</td>
<td>petrifaction</td>
</tr>
<tr>
<td>9. cf. <em>G. skaarensis</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Katoomba, Sydney Basin</td>
<td>Illawarra Coal Measures</td>
<td>petrifaction</td>
</tr>
<tr>
<td>10. cf. <em>G. skaarensis</em>&lt;sup&gt;c&lt;/sup&gt;</td>
<td>Katoomba, Sydney Basin</td>
<td>Illawarra Coal Measures</td>
<td>petrifaction</td>
</tr>
</tbody>
</table>

<sup>a</sup>Pigg, 1990.
<sup>b</sup>McLoughlin, 1990.
<sup>c</sup>This paper.
<sup>d</sup>McLoughlin, 1994b.

Katoomba, N.S.W. The most common of these types is represented by five fragments showing external morphology and numerous leaves in transverse section (Fig. 6; Plate VI, 1, 3–6). The most extensive leaf fragment is 9.5 cm long and up to 2.4 cm wide and somewhat oblanceolate (Fig. 6; Plate VI, 5). The midrib is 3 mm wide at the base and tapers to 1.5 mm in the central region of the leaf where it is composed of 5–8 vascular strands. Meshes are long and narrow, up to 7 mm long × 0.5 mm wide. They diverge from the midrib at an angle of < 10° and meet the leaf margin at an angle of 45°–60°. Another similar specimen shows an obtuse leaf apex (Plate VI, 4).

In transverse section, leaves of this type have the characteristic anatomy of *G. schopfii* (Plate VI, 1, 3). Although the quality of preservation is limited by the large amount of iron oxide in the matrix and the high degree of weathering, the round vascular bundle sheaths with prominent fibers characteristic of *G. schopfii* are present. Leaves of this type are 0.28 mm thick in the midrib and 0.18 mm thick laterally. Vascular bundles fall within the same size range as *G. schopfii* leaves from Skaar Ridge. Details of the mesophyll are poorly preserved. Fragmentary cuticular remains of these leaves demonstrate that epidermal cells have straight anticlinal margins. Stomata are simple, with guard cells 45 × 13 μm and a stomatal opening around 16 × 8 μm. They appear to be surrounded by a ring of 4–5 subsidiary cells 63 × 29 μm (Plate VI, 6).

The second leaf type, known from only two specimens cut in transverse section, shows the characteristic anatomy of *G. skaarensis* (Plate VI, 2), but the lack of cuticle or venation patterns limits its characterization further. Leaves of this type are 0.22 mm thick in the midrib area and 0.17 mm laterally and have vascular bundles with 5–8 rows of secondary xylem cells. Although the mesophyll is poorly preserved, the hypodermis is prominent and composed of tabular cells 11.7 × 6.6 μm one cell thick (Plate VI, 2).

4. Discussion

4.1. Comparison of *G. homevalensis* to previously described species of Glossopteris

A detailed comparison of *G. homevalensis* with previously known compression–impression forms is limited by the small amount of *G. homevalensis* material showing both anatomy and morphology. For this reason the taxon is compared primarily with the two species for which anatomy is currently known: *G. schopfii* and *G. skaarensis* (Tables 1–4).

To date, the three species of *Glossopteris* known in anatomical detail can all be characterized by a reticulate glossopterid venation pattern, the fre-
quent presence of secondary xylem and a hypodermis, rounded to oval vascular bundles, and probably a hypostomatic condition (Tables 2-4). The relatively small sample of paradermal sections of epidermis and cuticle available for study limits the opportunity to verify this last feature. *Glossopteris homevalensis* shows a mosaic of anatomical characters that combine features seen in both previously described species with some features unique to this taxon. *Glossopteris homevalensis* is similar to *G. schopfii* in having narrow elongate meshes, relatively simple stomata that are only slightly sunken, and simple unspecialized epidermal cells surrounding the stoma (Tables 2 and 4). Similarities to *G. skaarensis* include a distinct midrib, parenchymatous bundle sheaths, abundant fibers in the hypodermis, sinuous margins on intercostal epidermal cells and straight-margined epidermal cells over veins (Tables 3 and 4). *Glossopteris homevalensis* is distinct from both previously described species in having a highly differentiated palisade and spongy mesophyll, although this feature appears intergradational and is sometimes difficult to interpret because of poor preservation in some leaves, and in some stomatal features (Tables 3 and 4).

Among the anatomically preserved forms, *G. schopfii* is unique in having prominent fibers in its vascular bundle sheath, a large phloem lacuna, stomata in rows, and epidermal cells with one central papilla per cell (Tables 3 and 4). Features unique to *G. skaarensis* among anatomically preserved forms are broad polygonal meshes, radially organized vascular bundles, highly sunken stomata with a ring of subsidiary cells with beak-like extensions, and epidermal cells with 2–3 small papillae per cell.

### 4.2. Comparison to other genera of permineralized leaves

Anatomically preserved Permian *Noeggerathiopsis* leaves from the Prince Charles Mountains, Antarctica, are distinguished from *Glossopteris* leaves by their prominent abaxial grooves and trichomes, and lack of vein anastomoses (McLoughlin and Drinnan, 1996). However, they are similar to *G. homevalensis* and *G. schopfii*, respectively, in having a moderately differentiated mesophyll and vascular bundle sheaths. Secondary xylem is sometimes present in the median veins of *Noeggerathiopsis* (McLoughlin and Drinnan, 1996), as in *Glossopteris*. In contrast, Euramerican, Paleozoic *Cordaites* leaves have anatomical features distinct from both *Glossopteris* and *Noeggerathiopsis*. Cordaita leaves are characterized by prominent longitudinal plates of sclerotic cells that occur between most veins or pairs of veins. Such plates typically are continuous from the ad- to abaxial surfaces of the leaf (Harms and Leisman, 1961; M.L. Trivett, pers. commun., 1996). In addition, there are other regularly occurring intercostal, longitudinal files of sclerotic cells that, in cross section appear as ad- and abaxial pads of cells.

To date, a very large number of *Glossopteris* species have been described from Gondwana based on gross morphological and/or cuticular features with any one fossil assemblage typically yielding up to 10 species (see, for example, Chandra and Surange, 1979; Anderson and Anderson, 1985; McLoughlin, 1994a,b). Studies of permineralized *Glossopteris*-bearing assemblages, although in their infancy, have not yet indicated an equivalent range of anatomically based species diversity. One of several factors may account for this:

1. The small number of anatomically preserved leaf assemblages, all of which derive from coeval units in eastern Gondwana, may, as yet, represent an insufficient sample to assess true glossopterid diversity based on leaf anatomy.

2. *Glossopteris* species may have undergone excessive taxonomic splitting by the use of subtle and gradational characters when defined on morphological or cuticular features (i.e., true diversity of glossopterids may have been substantially less than that indicated by leaf variation in impression floras).

3. *Glossopteris* leaves may have had a relatively conservative anatomy, particularly in terms of their vascular bundle and mesophyll structure, resulting in leaves with markedly different morphologies, and belonging to many natural species, having the same basic anatomy (i.e., the relatively slight anatomical variation amongst *Glossopteris*...
Table 2
Morphological characteristics of Australian and Antarctic permineralized Glossopteris leaves or leaves preserved as impressions but associated with permineralized peats (leaves 5, 9 and 10 omitted from chart)

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Locality</td>
<td>Skaar Ridge</td>
<td>Blackwater</td>
<td>Bowen Basin</td>
<td>Katoomba</td>
<td>Homevale</td>
<td>Homevale</td>
<td>Homevale</td>
<td>Skaar Ridge</td>
</tr>
<tr>
<td>Leaf area (cm²)</td>
<td>ca. 20</td>
<td>1.7</td>
<td>6 (18) 60</td>
<td>9.5</td>
<td>5.3</td>
<td>5</td>
<td>3.5 (10</td>
<td>ca. 25</td>
</tr>
<tr>
<td>Maximum length (cm)</td>
<td>6–8 (10–12 estimated)</td>
<td>1.3–1.8 (3.1 estimated)</td>
<td>1.3–5.6 (incomplete)</td>
<td>2.4</td>
<td>2.8</td>
<td>2 (6 estimated)</td>
<td>2.2 (2.7 estimated)</td>
<td></td>
</tr>
<tr>
<td>Width (cm)</td>
<td>0.5–0.7</td>
<td>1.3–5.6</td>
<td>oblongolate, narrowly oblongolate,</td>
<td>somewhat oblongolate</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>probably oblongolate</td>
</tr>
<tr>
<td>Leaf shape</td>
<td>slightly oblongolate</td>
<td>oblongolate, narrowly oblongolate, narrowly elliptical</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>L:W ratio</td>
<td>ca. 4:1–3:1</td>
<td>4:1</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>ca. 4:1 retuse, asymmetric</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Leaf apex</td>
<td>obtuse-retuse</td>
<td>–</td>
<td>–</td>
<td>obtuse</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Midrib width (mm)</td>
<td>1.6</td>
<td>0.6</td>
<td>4 at base, 0.4 near apex</td>
<td>3 at base, 1.5 centrally</td>
<td>1.8</td>
<td>1–2</td>
<td>1.1</td>
<td>–</td>
</tr>
<tr>
<td>Midrib veins</td>
<td>4–5</td>
<td>4–5</td>
<td>–</td>
<td>5–8</td>
<td>5</td>
<td>–</td>
<td>1</td>
<td>to apex broad, polygonal</td>
</tr>
<tr>
<td>Vein persistence</td>
<td>to apex narrow elongate</td>
<td>to apex narrow elongate</td>
<td>relatively broad, elongate</td>
<td>–</td>
<td>–</td>
<td>very narrow linear</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Vein angle with midrib</td>
<td>53°</td>
<td>–</td>
<td>1.2 × 0.8 center: 4; margin: 14–25</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Marginal vein angle</td>
<td>22°</td>
<td>55–75°</td>
<td>50–70°</td>
<td>45°</td>
<td>30°</td>
<td>40–50°</td>
<td>90°</td>
<td>–</td>
</tr>
</tbody>
</table>

PLATE VI
Permineralized glossopterid leaves from the Illawarra Coal Measures, Sydney Basin.
1. Transverse section of G. schopfii leaf showing prominent vascular bundles and characteristic phloem lacunae; AM 60885 (24 A botc #9). × 95.
2. Transverse section of cf. G. skaarensis leaf showing characteristic vascular bundles, prominent hypodermis, and poorly preserved mesophyll; AM 60885 (24 B botc #8). × 95.
3. Oblique/longitudinal section through G. schopfii leaf to show characteristic mesophyll; AM 60885 (24 C2 Top #2a). × 95.
4. Weathered surface showing leaf apex of G. schopfii leaf. AM 60885. × 2.3.
5. Weathered surface showing external morphology of most complete G. schopfii leaf. Illustrated in Fig. 6. AM 60885. × 2.5.
6. Transverse section of G. schopfii leaf showing cuticle with smooth epidermal cell margins and stoma surrounded by 3–4 subsidiary cells, AM 60885 (24 C2 Top 4b). × 200.
Table 3
Anatomical characteristics of Australian and Antarctic permineralized *Glossopteris* leaves (leaves 3, 6 and 7 omitted from chart)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Locality</th>
<th>Thickness of midrib (mm)</th>
<th>Thickness of lamina (mm)</th>
<th>Vascular bundle diameter (μm)</th>
<th>Vascular bundle anatomy</th>
<th>Wall thickenings: protoxylem</th>
<th>Wall thickenings: metaxylem</th>
<th>Secondary xylem: number of rows</th>
<th>Phloem lacuna (μm)</th>
<th>Mesophyll differentiation</th>
<th>Hypodermis thickness, surfaces present</th>
<th>Hypodermis cell type</th>
<th>Epidermal cell size (μm)</th>
<th>Epidermal cell size (μm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. <em>G. schopfii</em></td>
<td>Skaar Ridge</td>
<td>0.3 - 0.7</td>
<td>0.2 - 0.3</td>
<td>128</td>
<td>2-3 layers elongate parenchyma and fibers</td>
<td>annular and helical</td>
<td>scalariform, reticulate, annular and helical</td>
<td>3-8</td>
<td>200 × 80</td>
<td>poor but poorly preserved</td>
<td>1-3 cells, ad- and abaxial</td>
<td>parenchyma, cuboidal, dark contents</td>
<td>25-30</td>
<td>53 × 35</td>
</tr>
<tr>
<td>2. <em>G. schopfii</em></td>
<td>Blackwater</td>
<td>0.4</td>
<td>0.3</td>
<td>186</td>
<td>1-3 layers elongate parenchyma and numerous fibers</td>
<td>-</td>
<td>-</td>
<td>3-4</td>
<td>180 × 10</td>
<td>moderate</td>
<td>cr. 1-3 cells abaxial (at least)</td>
<td>parenchyma</td>
<td>-</td>
<td>ca. 20 × 30</td>
</tr>
<tr>
<td>4. <em>G. schopfii</em></td>
<td>Katoomba</td>
<td>0.28</td>
<td>0.18</td>
<td>158</td>
<td>1-3 layers elongate parenchyma and fibers</td>
<td>-</td>
<td>-</td>
<td>4</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>isodiametric, cuboidal, abundant fibers</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>5. <em>G. homevalensis</em></td>
<td>Homevale</td>
<td>0.18-0.36</td>
<td>0.08-0.15</td>
<td>up to 300</td>
<td>1-2 layers parenchymatous</td>
<td>helical</td>
<td>helical</td>
<td>5</td>
<td>500 μm²</td>
<td>poor but poorly preserved</td>
<td>up to 3 cells ad- and abaxial</td>
<td>cuboidal, dark contents</td>
<td>-</td>
<td>45 × 23</td>
</tr>
<tr>
<td>8. <em>G. skaarensis</em></td>
<td>Skaar Ridge</td>
<td>0.5</td>
<td>0.13-0.14</td>
<td>137</td>
<td>1-2 layers elongate parenchyma</td>
<td>helical</td>
<td>helical</td>
<td>3-4</td>
<td>180 × 10</td>
<td>moderate</td>
<td>prominent ad- and abaxial</td>
<td>-</td>
<td>-</td>
<td>36 (48)</td>
</tr>
<tr>
<td>9. cf. <em>G. skaarensis</em></td>
<td>Blackwater</td>
<td>0.4</td>
<td>0.17</td>
<td>140 × 260</td>
<td>not well preserved</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>(24-37) × (16-18) (av. 11.7 × 6.6)</td>
</tr>
<tr>
<td>10. cf. <em>G. skaarensis</em></td>
<td>Katoomba</td>
<td>0.22</td>
<td>0.17</td>
<td>not preserved</td>
<td>not well preserved</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>
Table 4
Epidermal characteristics of Australian and Antarctic permineralized Glossopteris leaves (leaves 2, 3, 6, 7, 9 and 10 omitted from chart)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>G. schopfii</th>
<th>G. schopfii</th>
<th>G. homevalensis</th>
<th>G. skaarensis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Locality</td>
<td>Skaar Ridge</td>
<td>Katoomba</td>
<td>Homevale</td>
<td>Skaar Ridge</td>
</tr>
<tr>
<td>Epidermal cell walls</td>
<td>straight</td>
<td>straight</td>
<td>sinuous in intercostal areas, straight over veins</td>
<td>sinuous</td>
</tr>
<tr>
<td>Papillae</td>
<td>1 central/cell</td>
<td>–</td>
<td>–</td>
<td>2–3 per cell</td>
</tr>
<tr>
<td>Papillae size (μm)</td>
<td>7.5</td>
<td>–</td>
<td>–</td>
<td>12.5</td>
</tr>
<tr>
<td>Stomatal occurrence</td>
<td>hypostomatic</td>
<td>hypostomatic</td>
<td>hypostomatic?</td>
<td>hypostomatic</td>
</tr>
<tr>
<td>Stomatal distribution</td>
<td>random</td>
<td>–</td>
<td>random</td>
<td>random</td>
</tr>
<tr>
<td>Stomatal alignment</td>
<td>parallel with long axis of leaf</td>
<td>–</td>
<td>–</td>
<td>irregularly oriented</td>
</tr>
<tr>
<td>Stomatal density (mm²)</td>
<td>39.2</td>
<td>–</td>
<td>–</td>
<td>90.6</td>
</tr>
<tr>
<td>Stomatal organization</td>
<td>loosely organized in a ring</td>
<td>–</td>
<td>–</td>
<td>ring of subsidiary cells, may be contiguous</td>
</tr>
<tr>
<td>Subsidiary cells</td>
<td>unspecialized</td>
<td>unspecialized</td>
<td>unspecialized</td>
<td>blunt and elongate with beak-like papillae</td>
</tr>
<tr>
<td>Number of subsidiary cells per stoma</td>
<td>4–5</td>
<td>4–5</td>
<td>–</td>
<td>5–6</td>
</tr>
<tr>
<td>Subsidiary cell size (μm)</td>
<td>65 × 35</td>
<td>63 × 29</td>
<td>not obvious</td>
<td>(40 × 28)–(59 × 30); beak-like papillae 12 × 7</td>
</tr>
<tr>
<td>Guard cell size (μm)</td>
<td>43 × 10</td>
<td>45 × 13</td>
<td>35 × 10</td>
<td>34 × 9</td>
</tr>
<tr>
<td>Guard cell specializations</td>
<td>thickened around opening</td>
<td>some thickenings</td>
<td>radially straite thickenings</td>
<td>thickened margins</td>
</tr>
<tr>
<td>Stoma size (μm)</td>
<td>25 × 2.5</td>
<td>16 × 8</td>
<td>30 × 10</td>
<td>9</td>
</tr>
<tr>
<td>Is stoma sunken?</td>
<td>slightly</td>
<td>–</td>
<td>slightly</td>
<td>yes</td>
</tr>
</tbody>
</table>

leaves enabling differentiation of only a few taxa may underestimate the true diversity of glossopterids).

The initial description of anatomically preserved G. schopfii and G. skaarensis demonstrated what appeared to be highly distinctive, mostly non-overlapping suites of characters between leaves whose anatomical diversity 'could not be predicted based on external morphology alone' (Pigg, 1990). With the present description of G. homevalensis, a third species, we recognize glossopterid leaf anatomy as a mosaic of variations of a basically similar theme. Glossopteris schopfii and G. skaarensis remain markedly distinct from one another both anatomically and morphologically, showing narrow-meshed and broad-meshed venation patterns, respectively, as well as distinctive epidermal features. Interestingly, these two species coexist in chert floras of at least three East Gondwanan basins, with G. schopfii being more frequently encountered in all cases. Whether this distribution represents true differences in occurrence, differential preservation or a combination of factors is not clear. Perhaps these two leaf types represent plants that successfully divided niche space between themselves over a wide area. The newly recognized G. homevalensis appears to be more limited in its distribution, but this impression may reflect sampling more than distribution. As more chert floras are investigated our understanding of the diversity and its distribution will continue to change.

Interestingly, Euramerican Cordaites leaves show a comparable disparity in diversity to glossopterids in that more species have been established on subtle morphological differences than on anatomical grounds (Harms and Leisman, 1961). Harms and Leisman (1961) attributed much of the apparent, morphology-based, Cordaites diversity to the establishment of many taxa based on inadequately or incompletely preserved impression/compression fossils. In the cases of both Cordaites and Glossopteris more extensive anatomical studies and the discovery of additional attached vegetative and fertile organs (e.g. Trivett and Rothwell, 1991; Pigg and Taylor, 1993) is
required to provide a realistic assessment of whole-plant diversity.

4.3. Distribution of permineralized Glossopteris leaves

Glossopteris species defined on anatomical characters are confined to Upper Permian strata of the central Transantarctic Mountains, and the Sydney and Bowen basins of Australia (Figs. 1 and 2) although undescribed material is also now known from equivalent strata in the Prince Charles Mountains, East Antarctica (Neish et al., 1993). McLoughlin (1994b) identified anatomically preserved specimens from the Burngrove Formation of the central Bowen Basin (leaves preserved in block UQ F79332) as Glossopteris sp. cf. G. schopfii that are here regarded as G. schopfii. He further considered that the surface morphological features of these leaves were indistinguishable, apart from their appreciably smaller size, from a large number of leaves (>500) preserved as impressions and distributed widely in the upper Back Creek Group and Blackwater Group of the central and southern Bowen Basin. The notably smaller dimensions of the few permineralized G. schopfii leaves with surface detail compared to those in the impression floras of the Burngrove Formation may reflect preservation at a different stage of leaf expansion. The broad distribution of leaves with either G. schopfii and G. skaarensis anatomy or surface morphology within eastern Australia and the central Transantarctic Mountains and their apparent absence from other Gondwanan basins favors interpretation of the continuity of the Bowen–Sydney–Transantarctic regions as a single phytogeographic province. The apparent floristic similarities between these basins is also highlighted by the shared occurrence of the same or similar species of Righya, Plumsteadia and some sphenophyte species (Rigby, 1963, 1977; Rigby and Schopf, 1969; Kyle, 1974; McLoughlin, 1995).

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