PETRIFIED STEMS BEARING *DICROIDIUM* LEAVES FROM THE TRIASSIC OF ANTARCTICA

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ABSTRACT. Anatomically preserved one to five year-old stems are described from a Triassic site in the central Transantarctic Mountains. They are assigned to *Kykloxylon fremouwensis* gen. et sp. nov. and are regarded as related to the corystosperm stem *Rhexoxylon* on the basis of wood and pith anatomy and leaf trace organization. *Kykloxylon* axes possess a solid vascular cylinder of secondary xylem of the *Dadoxylon* type, but lack centripetal wood and a narrow pith. The bases of leaves attached to one-year-old stems of *K. fremouwensis* are similar to the leaves of *Dicroidium fremouwensis* described from the same locality in Antarctica. The '*Dicroidium*/*Kykloxylon* plant' from Antarctica is branched and more complex than the hypothetical '*Dicroidium*/*Rhexoxylon* plant' reconstructed from disarticulated remains from the Ischigualasto Formation of Argentina. It is suggested that the '*Dicroidium*/*Rhexoxylon* plant' may have been dominant in western Gondwana, whereas the *Dicroidium* plants with *Kykloxylon* stems might have had a wider geographical distribution in Gondwana.

PETRIFIED plant stems from the late Palaeozoic and Mesozoic are common throughout Gondwana (Kräusel *et al.* 1962; Maheshwari 1972; Prasad 1982; Smoot *et al.* 1985; Bose *et al.* 1989; Taylor and Taylor 1990). They are represented typically by isolated trunks and branches that have been transported to the site of deposition. These fossils are generally decorticated axes and have resulted in a profusion of form genera based almost exclusively on features of the secondary xylem. One of the most interesting aspects of these stems is the potential information that is available on past climates based on growth ring analysis (Jefferson 1982; Jefferson and Taylor 1983; Francis 1986; Taylor 1989). Of biological interest are the *in situ* stumps from the Cretaceous of Alexander Island (Antarctica) described by Jefferson (1982). An analysis of the size and distribution of these stumps has provided the opportunity to reconstruct a Cretaceous forest. The species composition of such forests continues to remain problematic since the systematic affinities of the trees are still uncertain.

The excellent preservation of the plant assemblages occurring in the silicified peat at Fremouw Peak is significant in that it provides, for the first time, an accurate image of the vegetation that inhabited this Triassic site in Antarctica. Small herbaceous plants such as sphenophytes (Osborn and Taylor 1989) and a variety of ferns (Schopf 1978; Millay and Taylor 1990) have already been described as well as a cycad with a slender growth habit (Smoot *et al.* 1985) and a conifer with podocarpaceous affinities (Meyer-Berthaud and Taylor 1991). In addition, a *Pteruchus*-like pollen organ (DeVore and Taylor 1988), multiovulate cupules (Taylor and Taylor 1987) and leaves of *Dicroidium fremouwensis* (Pigg 1990) have also been reported from this locality. The present study is based on the distal parts of a plant that bore leaf bases of the *D. fremouwensis* type. This is the first report of stems and leaf bases with similar anatomy that differ significantly from the stems of *Rhexoxylon*, the Triassic genus generally believed to have borne *Dicroidium* foliage at some localities.

MATERIAL AND METHODS

Numerous twigs and stems were collected from a silicified peat in the Transantarctic Mountains during the 1985–1986 field season (Taylor *et al.* 1986). The collecting locality is a col at an elevation of 2408 m just north of Fremouw Peak in the Queen Alexandra Range (84° 17′ 409″ S, 164° 21′ 483″ E (Global Positioning System),

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Buckley Island Quadrangle; Barrett and Elliott 1973) (Text-fig. 1A). The locality occurs in the upper part of the Fremouw Formation and is considered to be early mid-Triassic in age based on palynostratigraphy (Farabee *et al.* 1990) and the occurrence of the vertebrate *Cynognathus* (Taylor and Taylor 1990) (Text-fig. 1B).

Cellulose acetate peels of the specimens were prepared for light microscopy by etching the rock surfaces with 48 per cent hydrofluoric acid for 1–5 minutes. The largest specimen was cut into two slabs and eighty serial transverse-oblique peel sections were prepared. This stem was less than 1 cm long and it was not possible to correct the original plane of section in order to obtain information about the phyllotaxy. One of the remaining slabs was re-cut longitudinally to provide anatomical details of the secondary xylem in both radial and tangential planes. Information on the pattern of leaf trace emission and vascularization of the leaf bases was obtained by a series of peel sections made from three leafy twigs (10,415 A; 10,525 A; 10,628 E1B).

Slides and peels are deposited in the Palaeobotanical Collections, Department of Plant Biology, The Ohio State University under the acquisition numbers 14,768–14,862

SYSTEMATIC PALAEONTOLOGY

Class GYMNOSPERMOPSIDA
Order CORYSTOSPERMALES
Family CORYSTOSPERMACEAE Thomas, 1933

KYKLOXYLON gen. nov.

Type species. Kykloxylon fremouwensis sp. nov.

Diagnosis. Gymnospermous plant with undivided cylinder of secondary xylem in 1–5 year-old stems. Stems with non-septate pith containing lacunae, sclerotic nests and occasional bands of periderm-like tissue. Primary xylem endarch, with small tracheids in radial files; secondary xylem pycnoxylic with growth rings, rays uniseriate and short with smooth cell walls. Tracheids with 1–3 rows of bordered pits with circular pores on the radial walls; pits sometimes spaced when uniseriate, either opposite or alternate when multiseriate. Pits in cross fields simple, oval-horizontal and variable in number. Cortex parenchymatous with lacunae and sclerotic nests as in pith; cortical periderm homogeneous and composed of several rows of cuboidal cells, often with dark contents. Vascular system to the leaf originating from four axial bundles and consisting of several endarch strands, dividing near periphery of cortex in a three-dimensional pattern; vascular supply in leaf base consisting of adaxial row of endarch bundles and two incomplete rings of abaxial vascular strands.

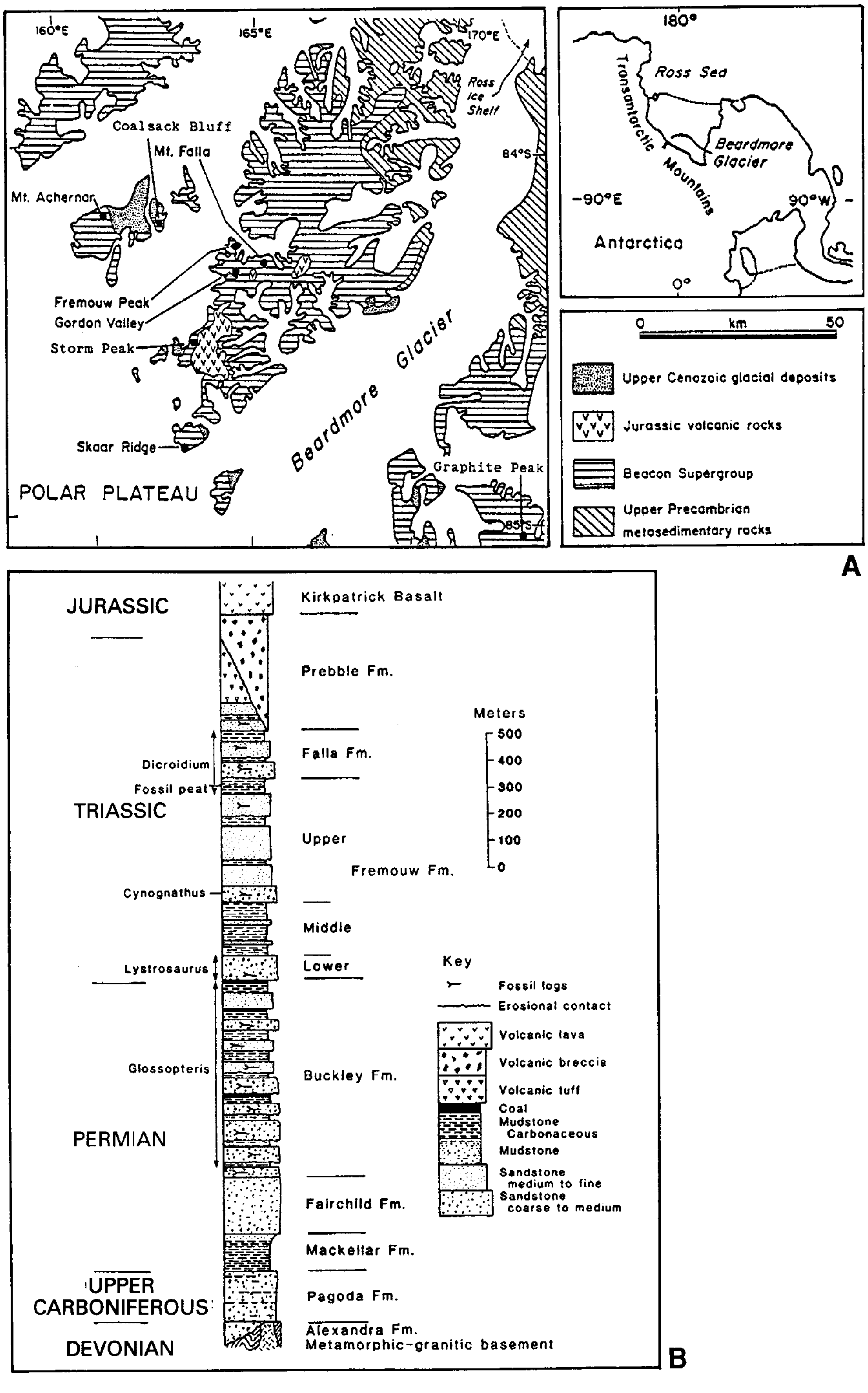
Kykloxylon fremouwensis sp. nov.

Plate 1, figs 1–5; Plate 2, figs 1–6; Plate 3, figs 1–6; Plate 4, figs 1–7; Text-figs 2–5

Derivation of name. The generic name *Kykloxylon* refers to the continuous cylinder of secondary xylem (Gr. '*kyklos*', ring; '*xylon*', wood) and the specific epithet *fremouwensis*, to the Fremouw Peak collecting locality.

Diagnosis. Gymnospermous axes up to 15 mm in diameter; pith composed of parenchyma, sclerotic nests up to 300 × 650 μm wide and 400 μm high and lacunae up to 250 μm in diameter; and occasional periderm-like tissue. Primary xylem of radially aligned tracheids 5–17 μm in diameter. Secondary xylem with growth rings of variable thickness; late wood of 1–3 cell rows; tracheids polygonal to square in transverse section, up to 55 μm both in radial and tangential dimensions, pits on radial walls bordered, 8 × 10 μm to 10 × 14 μm in diameter; 3–9 simple pits in cross fields arranged in vertical tiers; cross field pits oval–circular, horizontally elongate and 7 × 10 μm to 10 × 25 μm; rays uniseriate, 1–10 cells high, ray cells 15–20 μm wide and 35–65 μm high. Cells of cortical periderm up to 35 × 50 μm wide, frequently with dark contents. Leaf venation originating

TEXT-FIG. 1. A, Map of the Beardmore Glacier area, Transantarctic Mountains. B, Stratigraphical column of the Beacon Supergroup; Central Transantarctic Mountains.


160°E
165°E
170°E
Ross Ice Shelf
84°S
Coalsack Bluff
Mt. Falla
Mt. Achernar
Fremouw Peak
Gordon Valley
Storm Peak
Skaar Ridge
POLAR PLATEAU
Beardmore Glacier
Graphite Peak
85°S
180°
Ross Sea
Transantarctic Mountains
Beardmore Glacier
-90°E
90°W
Antarctica
0°
0 km 50
Upper Cenozoic glacial deposits
Jurassic volcanic rocks
Beacon Supergroup
Upper Precambrian metasedimentary rocks
A
JURASSIC
TRIASSIC
PERMIAN
UPPER CARBONIFEROUS
DEVONIAN
Dicroidium
Fossil peat
Cynognathus
Lystrosaurus
Glossopteris
Kirkpatrick Basalt
Prebble Fm.
Falla Fm.
Upper
Fremouw Fm.
Middle
Lower
Buckley Fm.
Fairchild Fm.
Mackellar Fm.
Pagoda Fm.
Alexandra Fm.
Metamorphic-granitic basement
Meters
500
400
300
200
100
0
Key
Fossil logs
Erosional contact
Volcanic lava
Volcanic breccia
Volcanic tuff
Coal
Mudstone Carbonaceous
Mudstone
Sandstone medium to fine
Sandstone coarse to medium
B

as two pairs of traces from four axial bundles; subsequent divisions in cortex and leaf base leading to a row of adaxial bundles and two incomplete rings of bundles toward the abaxial surface.

Holotype. Specimen 10,628 E.

Paratypes. Specimens 10,397 D(1); 10,415 A–B; 10,440 C(3); 10,525 A(6); 10,891 D(7)–E; 10,891 F(2).

Locality. Col just north of Fremouw Peak, GPS 84° 17′ 409″ S, 164° 21′ 483″ E (Buckley Island Quadrangle).

Stratigraphical level. Top of the upper portion of the Fremouw formation, Beacon Supergroup, early Middle Triassic.

Description

This paper is based on the description of twelve stem specimens that occur in the same peat blocks as *Antarcticycas schopfii* (Smoot *et al*. 1985), *Dicroidium* foliage (Pigg 1990) and filicalean fern stems and petioles (Millay and Taylor 1990). No specimens of *Kykloxylon* have been found associated with the conifer *Notophytum krauselii* (Meyer-Berthaud and Taylor 1991) or with sphenophyte twigs known from this locality which may be part of a different plant community (Taylor and Taylor 1990).

The smallest axis, which represents the apical portion of a leafy shoot, is 3·2 × 4·3 mm wide, and includes leaf bases (Text-fig. 2G). The six other leafy shoots range from 5 to nearly 10 mm in diameter. They show a single ring of xylem in transverse section and have a single year's growth (Pl. 1, figs 1–2; Text-fig. 2C–F). Leaves are densely arranged on the shoots. The occurrence of several bands of periderm just beneath the leaf bases suggests that the leaves were probably shed early, perhaps during the first year of growth.

Four stems have a vascular cylinder with more than one growth ring and contain no leaves (Pl. 1, figs 3–4; Text-fig. 2A–B). The largest stem has five rings of secondary xylem and measures 10 × 15 mm in diameter (Pl. 1, fig. 3; Text-fig. 2A). All of the axes that are approximately one year old possess axillary buds; a larger axis approximately five years old has what appears to be an axillary bud, but this may also represent an adventitious bud (Text-fig. 2A, C–D, F–G).

Pith. The diameter of the pith varies from 0·5 mm in the apical portion of the shoot to 1·8 × 2·6 mm in the largest stem (Pl. 1, figs 1, 3–5). This represents 16–40 per cent of the total diameter of the axes without leaf bases and 22–75 per cent of the diameter of the vascular cylinder. The pith parenchyma is rarely preserved except in the vicinity of what we interpret as sclerotic nests, which are present in all specimens including the apical portion of a shoot (Pl. 1, figs 2, 5; Pl. 2, fig. 1). These nests are up to 650 μm wide (transverse section) and 100–400 μm high (longitudinal section) in the largest stems; 110–150 μm in width (TS) and up to 150 μm high (LS) in the apical stem sections. Nests are composed of polyhedric cells, 30–80 μm wide, that sometimes possess reticulate or pitted thickenings on their walls. The parenchyma cells preserved in the vicinity of these nests measure up to 90 μm in diameter. Another conspicuous feature of the pith is the presence of ovoid-spherical cavities that do not exceed 250 μm in diameter (Pl. 1, figs 1–2, 5; Pl. 4, fig. 7). Some of these spheres superficially resemble chlamydospores of fungi, but it is our belief that most represent pith lacunae that are an anatomical feature of this taxon. Lacunae of this type have not been recorded in any other plant material from the Fremouw peak locality but they resemble the 'resinous cells' described in the cortex of *Dicroidium* leaves (Pigg 1990) and *Pteruchus*-like pollen organs (DeVore and Taylor 1988). One additional potentially important anatomical feature in *Kykloxylon* is a band of small rectangular cells arranged in files that occasionally traverse

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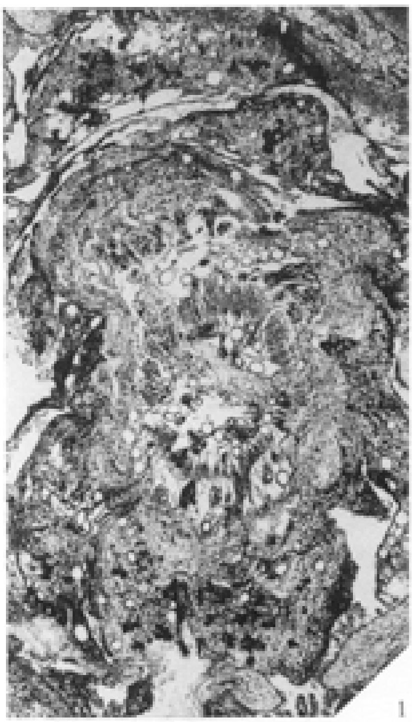
EXPLANATION OF PLATE 1

Figs 1–5. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,628 E(1)BT. 17; transverse section (TS) of a leafy shoot; holotype specimen, × 10. 2, 10,397 D(1)T. 5; longitudinal section (LS) of a leafy shoot with a bud at arrow, × 10. 3, 10,891 F(2)T. 5; TS 5 year-old stem with two leaf traces at arrows, × 6·5. 4, 10,891 D(3)T. 2; TS 3 year-old stem, × 20, 5, 10,440 C(3). 3; TS central pith region of the apical portion of a shoot; note sclerotic nests (N) and lacunae (L), × 25.

PLATE 1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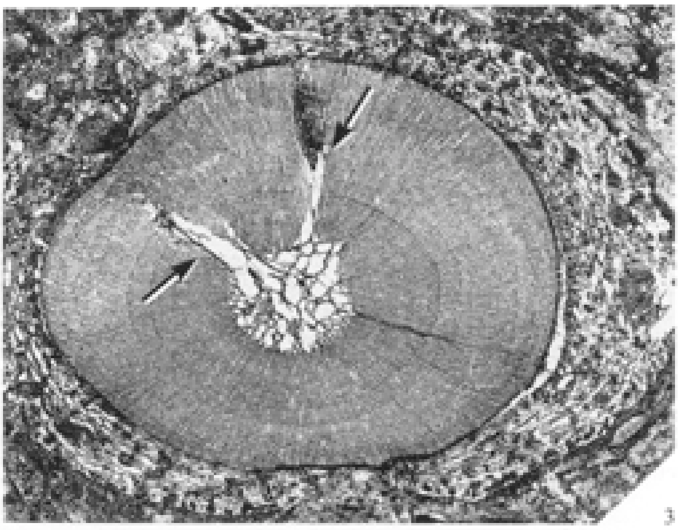
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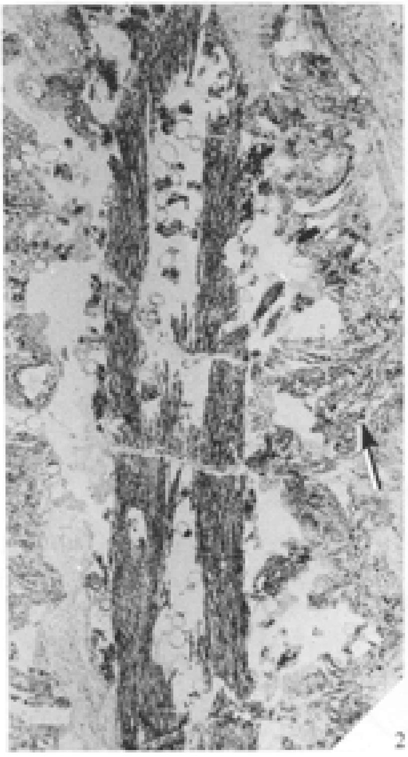
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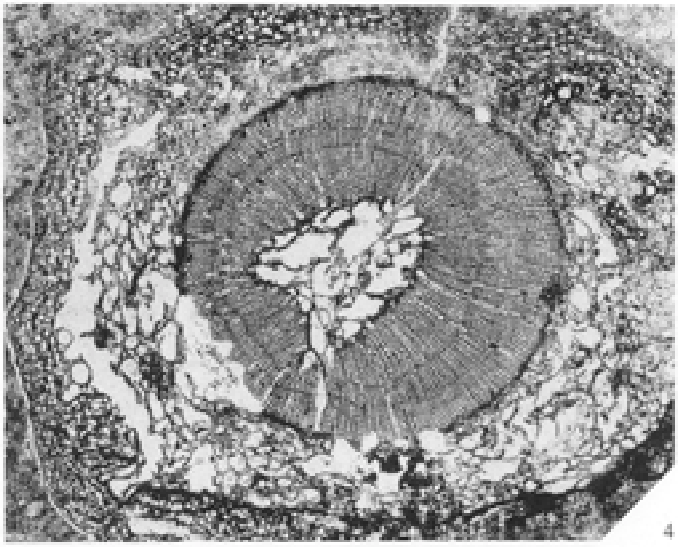
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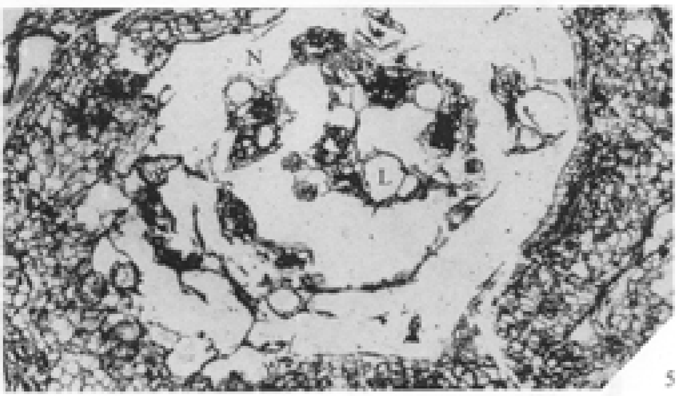

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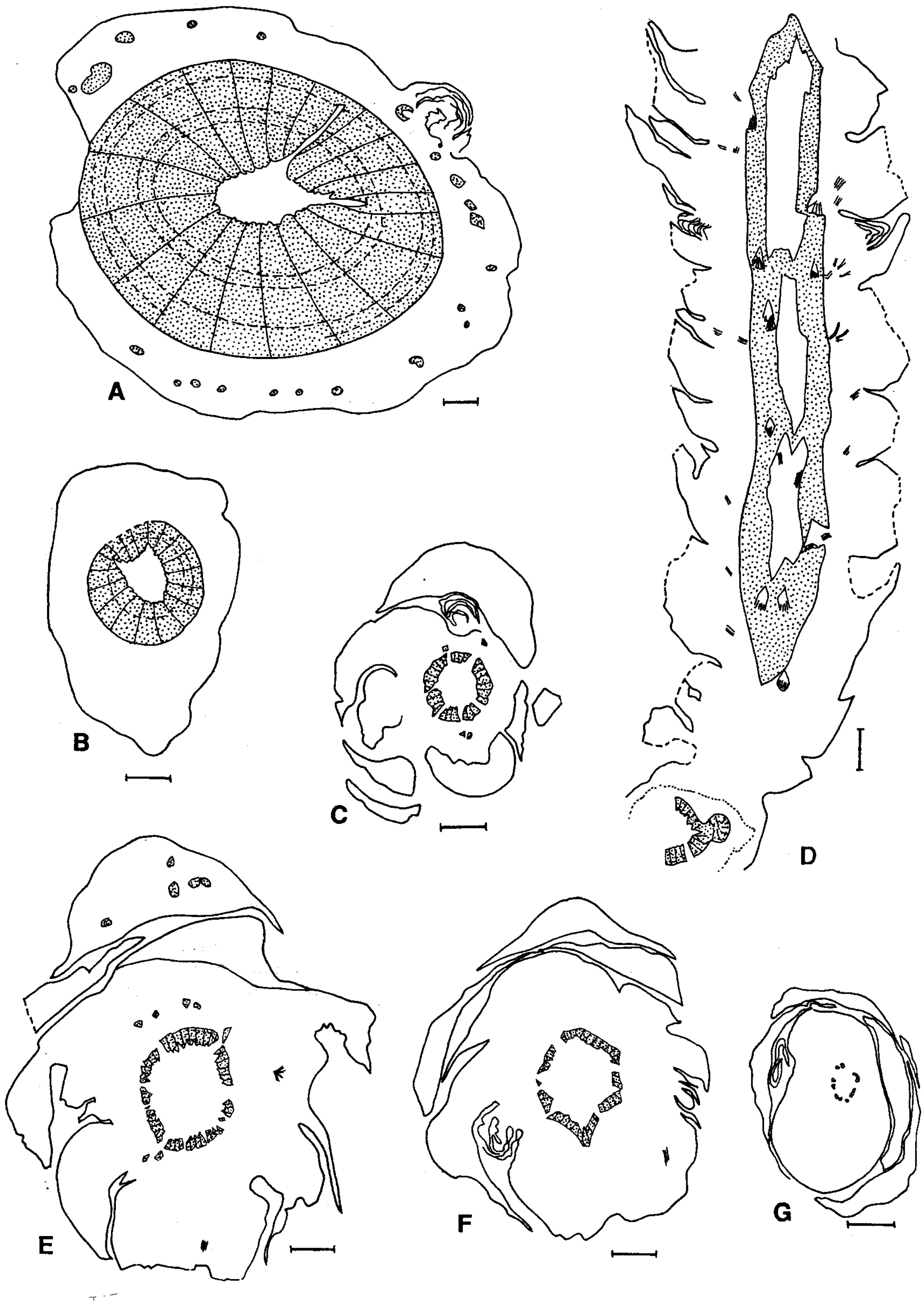
A
B
C
D
E
F
G

the pith. While this zone of cells superficially resembles a periderm-like tissue, the origin and subsequent fate of these cells is not known.

Primary xylem. The primary xylem in *Kykloxylon* is composed of a few rows of radially aligned tracheids that differ from those of the secondary xylem by their smaller diameters (5–17 μm wide) (Pl. 2, figs 1–2). A transverse section in the apical portion of a shoot clearly shows that the primary xylem is arranged in paired clusters of tracheids suggesting that the axial bundles also occur in pairs (Pl. 1, fig. 5; Pl. 2, fig. 1). Order of primary xylem maturation is endarch. Tracheids with scalariform to reticulate secondary thickenings compose the major portion of this tissue.

Secondary xylem. In transverse section, the secondary xylem ranges from 200 μm wide in the leafy twigs to 3·5 mm in the largest stem. Tracheids are polygonal in the region of the pith and square to rectangular in the outermost rings of the five year-old stem. In the early-wood, tracheids range from 25 to 70 μm in tangential dimension and from 25 to 55 μm radially. The radial dimension of the tracheids in stems with growth rings is reduced in the latewood which is composed of 1–3 rows of cells (Pl. 1, figs 3–4). Rays are 1–10 cells high and uniseriate (Pl. 2, fig. 5). Ray cells range from 15 to 20 μm wide and 35 to 65 μm high. Axial parenchyma is absent.

Pitting on the radial walls of the tracheids is variable. In the oldest specimen, most of the tracheids, including those close to the primary xylem, show contiguous biseriate pits that are arranged either in an alternate or opposite pattern; otherwise the radial pitting is uniseriate and either spaced or contiguous (Pl. 2, fig. 3). A few large tracheids possess triseriate radial pitting (Pl. 2, fig. 6). Pits are bordered and range from 8 × 10 μm to 10 × 14 μm wide. Apertures are circular to oval and average 6 μm in diameter. In most of the pits, the centre is occupied by a circular black dot up to 3 μm in diameter (Pl. 2, figs 3–4; Text-fig. 3). If this dot represents a torus, its small diameter compared with the size of the pith aperture makes its function questionable. An alternative hypothesis is that the pit aperture is conical rather than cylindrical (Text-fig. 3). The dot, then, would be the black image of the outer aperture (facing the pit chamber).

Pits in the cross fields are simple and range from 3 to 9 (Pl. 2, fig. 3). The shape of these pits is oval; in some, it is horizontally elongate. Pit size ranges from 7 × 10 μm to 10 × 25 μm. Oval pits are numerous and arranged more or less in an alternate pattern. Horizontally elongate pits occur in vertical tiers and give the cross field a scalariform appearance (Pl. 2, figs 3, 6). The dimensions and arrangement of the pits suggest that the large horizontally elongated ones may result from the fusion of two contiguous oval pits. The horizontal walls of the ray cells are smooth and approximately 4 μm thick. Periclinal walls are rarely observed.

Phloem. Some secondary phloem is preserved in the largest stem where it is sectioned obliquely (Pl. 3, fig. 5). This phloem zone is about 300 μm thick and composed of small sieve cells up to 30 μm in radial dimension. Uniseriate rays are also visible. Due to the relatively poor preservation of extraxylary tissues the exact organization of the phloem is uncertain, and thus it is not known whether fibres are present. Nothing is known about the primary phloem of *Kykloxylon.*

Cortex and periderm. Cortical tissues are similar to those of the pith and include numerous spherical cavities (Pl. 3, fig. 4; Pl. 4, figs 5–6). Some parenchyma cells may be present surrounding the sclerotic nests. These cells measure 20 × 50 μm to 55 × 65 μm in the largest stem. Almost all of the axes possess one to several bands of periderm just beneath the leaf bases (Pl. 3, fig. 4). The development of this tissue occurs early in the ontogeny of the stem since cortical cells of the apical fragment of a shoot show some evidence of periclinal divisions. The periderm is composed of cells that are square-rectangular in both transverse and longitudinal sections. These elements measure up to 35 × 50 μm wide and frequently possess dark contents.

Leaf trace emission and phyllotaxy. The vascularization of a leaf originates as four traces (Ia, Ib, IIa, IIb) arranged in two pairs (I, II) that are variously separated (650–800 μm) depending on the diameter of the stele

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TEXT-FIG. 2. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains; general views of a selection of representative axes; all specimens except D in transverse section. A, 10,891 F(2)aT. 41. B, 10,891 D(3)T. 2. C, 10,525 A. 6. D, 10,397 DT. 2. E, 10,628 E(1)BT. 28; holotype specimen. F, 10,743 DT. 3. G, 10,440 C(3). 3. Scale bars = 1 mm.

(Pl. 4, figs 1–4; Text-fig. 4A). The two traces of a pair (Ia, Ib) are emitted with a slight delay from two different bundles separated by a narrow parenchymatous zone (Pl. 4, figs 2–4, 7). Traces follow a slightly ascending course through the cortex (Pl. 4, figs 1–4, 6; Text-fig. 4B–C) until the two inner bundles (Ib, IIb) become reorientated at 90° (Pl. 4, fig. 5; Text-fig. 4D, F). As a result of this change in orientation the protoxylem of these bundles shifts from an adaxial to a lateral position. The inner and outer traces of each pair subsequently divide in different planes that are approximately perpendicular (Text-fig. 4F). In each pair of traces, the bundles arising from the division of the outer trace (either Ia or IIa) are arranged in a horizontal row; those arising from the division of the inner trace (either Ib or IIb) tend to be arranged in a ring rather than remaining vertically aligned (Pl. 3, figs 1–3, 6; Text-fig. 4E–F).

In leafy twigs, the leaves are crowded and the phyllotaxy difficult to interpret. A series of transverse sections has been prepared through a complete internode of a five-year-old stem and a selection of the most representative ones is illustrated in Text-figure 5A–C. In Text-figure 5D, which shows these sections superimposed, leaf vascular supplies I + II (including Ia, Ib, IIa, IIb) and I′ + II′ (including I′a, I′b, II′a, II′b) are separated by an angle approaching 130°. This suggests that the leaves were arranged in a single sinistrorse helix according to the Fibonacci series. On the basis of this specimen it would appear that the buds are axillary (Text-fig. 5A, C). However, additional specimens will have to be critically examined to confirm this hypothesis.

Leaf bases. Leaf bases are widely inserted on the twigs (Pl. 1, figs 1–2) and all are broken at a distance of 1–2 mm from the stem surface. The bases are flat or slightly concave on the adaxial surface, and hemispherical on the abaxial side (Pl. 3, figs 1–2; Text-fig. 4E); none of the leaf bases observed showed evidence of tapering. Bases measure up to 2 mm high and 5 mm wide. The ground tissue is composed of an outer part that consists of several rows of cuboidal cells with dark contents and an inner zone of parenchymatous cells that often appear disorganized. The inner zone also contains numerous sclerotic nests and lacunae (Pl. 3, fig. 1; Text-fig. 4E). The vascular system in the leaf bases is bilateral and complex. Each half of the leaf vascular supply consists of an adaxial series of bundles and, near the middle of the leaf base, an incomplete ring of traces that are close to the abaxial surface (Pl. 3, fig. 1; Text-fig. 4E). Bundles range from 150 to 350–550 μm wide and often occur in a lacuna. In the best preserved portions of the leaf bases, they are ensheathed by 2–3 rows of elongate cells that are slightly flattened in transverse section (Pl. 3, fig. 6). Each bundle consists of up to 10 rows of radially aligned tracheids that are 5 × 10 μm to 15 × 20 μm wide. Primary xylem maturation is endarch in the bundles of the adaxial series. Protoxylem has an inner lateral position in the traces of the ring (Pl. 3, figs 3, 6). External to the tracheids is a zone of phloem that consists of radially aligned thin-walled cells which are up to 45 μm wide. No further information is available of the leaf base or leaf distally.

DISCUSSION

Comparison with form genera based on petrified wood from Gondwana

There have been numerous reports of silicified wood fragments from the late Palaeozoic and Mesozoic of Antarctica since the initial description of *Antarcticoxylon* by Seward (1914). However, in most instances these reports lack information about anatomical features. To date, the best-known fossil woods from the Antarctic regions are those described by Maheshwari (1972) from different Permian localities of Antarctica, two specimens referred to as *Taeniopitys scotti* and *Dadoxylon allani* by Kraüsel (1962) from the Permian of the Allan Hills (South Victoria Land), and specimens of *Australoxylon* (*Dadoxylon*) *bakeri*, *D. lafoniense* and *Dadoxylon* cf. *D. angustum* from the Permian of the Falkland Islands (Halle 1911; Seward and Walton 1923; Marguerier 1973). In

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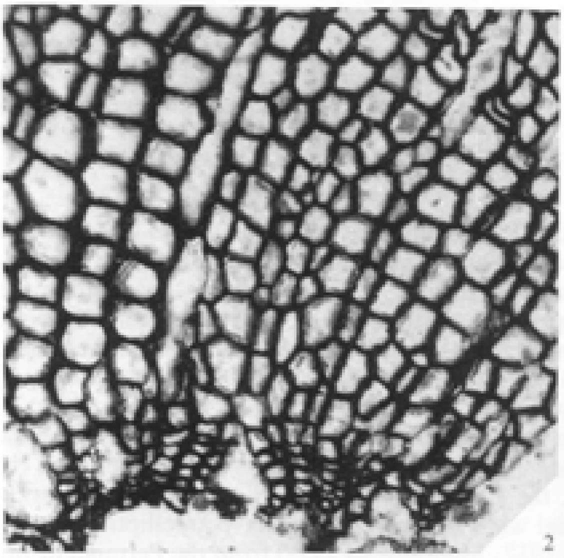
EXPLANATION OF PLATE 2

Figs 1–6. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,440 C(3). 3; detail of TS stele showing 2 pairs of bundles (arrows) in the apical portion of a shoot, × 100. 2, 10,891 D(3)T. 2; radially aligned tracheids of primary bundles seen in figure 1 and larger tracheids of the secondary xylem, × 170. 3, 10,891 F(2)IIS. 1; secondary xylem in radial section; cross fields at top, × 335. 4, 10,891 F(2)IIS. 1; bordered pits with a central black dot on the radial wall of a tracheid, × 800. 5, 10,891 F(2)IS. 1; secondary xylem with short uniseriate rays in tangential section, × 150. 6, 10,891 F(2)IIS. 1; triseriate pitting on the radial wall of a tracheid, × 200.

PLATE 2


1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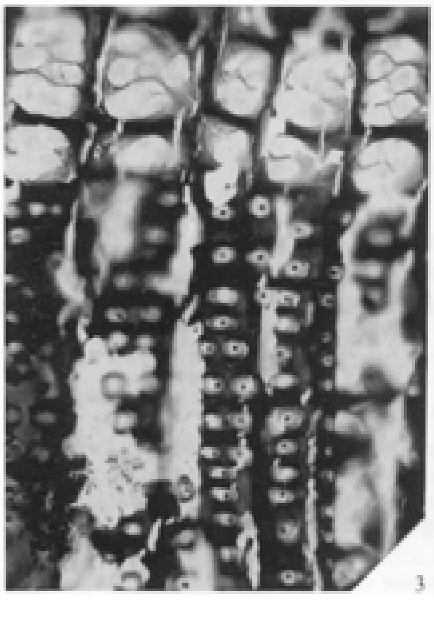
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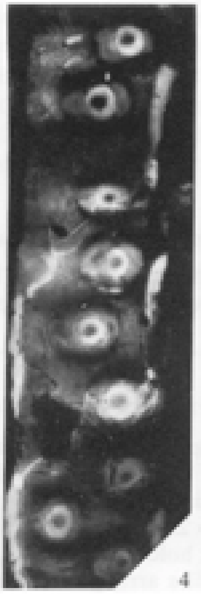
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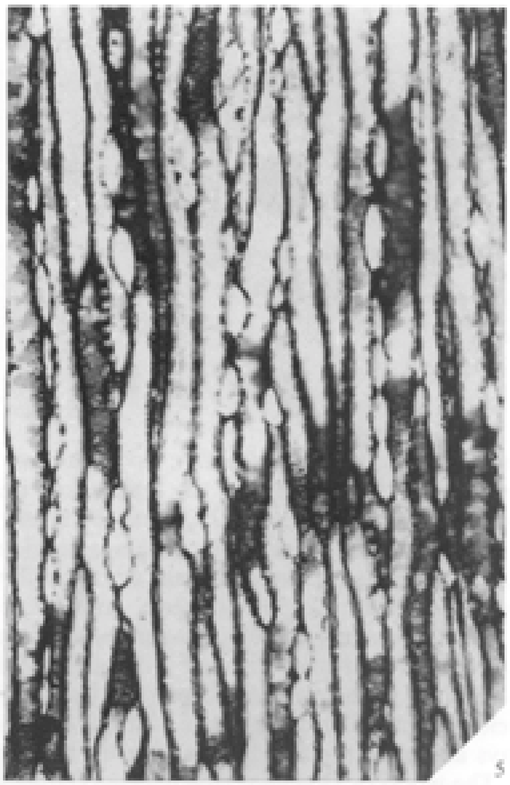
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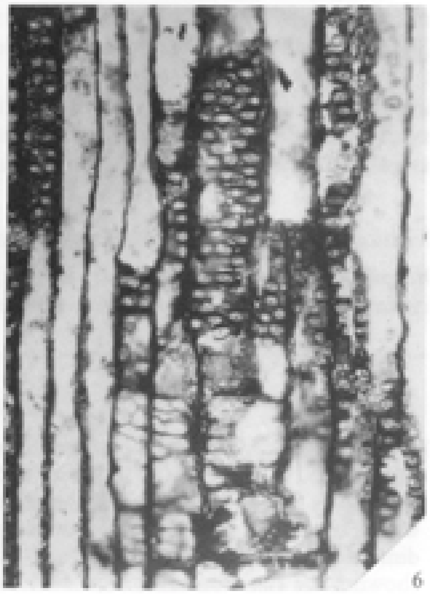
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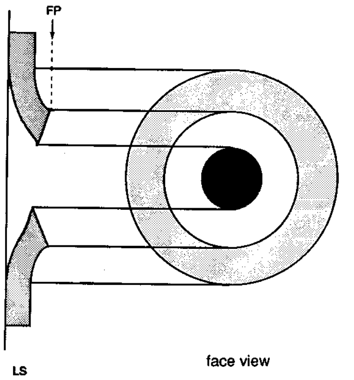

TEXT-FIG. 3. Interpretation of the features of a bordered pit on the radial wall of a secondary xylem tracheid. FP, focusing plane; LS, longitudinal section.

most species, as in *Kykloxylon*, ray cells have thin, unornamented walls and pits in the cross fields are simple. Depending on the taxa, cross field pits are either small and numerous or large and unique. In three species, *T. scotti*, *D. allani* and *A. bakeri*, variations in pit organization from one type to the other occur within a single specimen. Despite these variations, none shows the large, horizontally elongated pits arranged in vertical tiers that characterize some cross fields in the wood of *Kykloxylon*. In addition, unlike *Kykloxylon*, *T. scotti* and *A. bakeri* are characterized by a special outer parenchymatous 'sheet' that surrounds the pith (Kraüsel *et al.* 1962). The description by Halle (1911) of 2–5 small simple pits that are rounded or elliptical, and then almost horizontal in the cross fields of the wood of *Dadoxylon* cf. *D. angustum* is reminiscent of the cross field pits in *Kykloxylon*. In the former species, the ray cells are especially narrow (10–15 μm), the rays are taller (1–25 cells) and pits on the radial walls of the tracheids have an elliptical pore.

The wood of *Damudoxylon indicum* (Holden 1917; Maheshwari 1972) from the Permian of India has short rays (2–7 cells) and 1–4 simple pits that tend to fuse in the cross fields. But unlike *Kykloxylon*, the pith of *D. indicum*, which is devoid of sclerotic cells and lacunae, is lined by a sheath of small reticulate cells. In addition, the primary xylem is associated with a large amount of parenchyma at the nodes, a feature that has not been observed in the Antarctic specimens. One feature that deserves mention in a comparison with *Kykloxylon* is the report of paired leaf traces extending almost horizontally through the wood of *D. indicum* (Holden 1917).

Relationships of Kykloxylon fremouwensis *and* Dicroidium fremouwensis

Dicroidium fremouwensis occurs in the peat of Fremouw Peak and is the first species of *Dicroidium* known with anatomically preserved specimens. It includes bifurcating fronds that might have been

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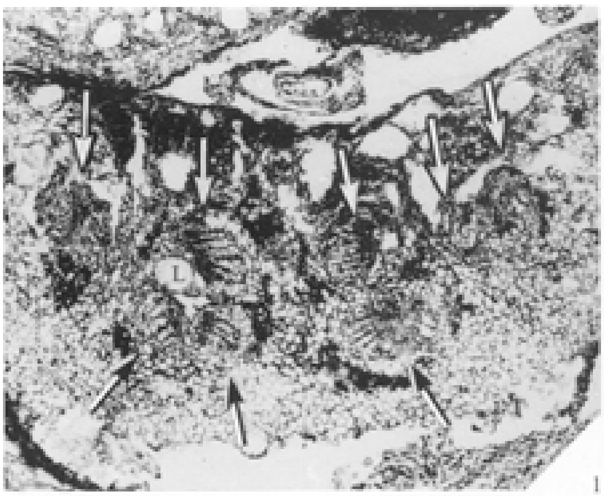
EXPLANATION OF PLATE 3

Figs 1–6. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1, 10,628 E(1)BT. 82; TS leaf base showing an adaxial line of bundles and two incomplete rings of bundles placed oppositely on the abaxial side (arrows); note sclerotic nest (N) and lacuna (L); compare with Text-fig. 4E; holotype specimen, ×22. 2, 10,628 E(1)BT. 22; oblique TS leaf base showing a 3-dimensional arrangement of the bundles; holotype specimen, ×22. 3, 10,628 E(1)BT. 82; detail of figure 1 showing the two abaxial groups of bundles arranged in opposite rings and two adaxial bundles at right (arrows), ×45. 4, 10,397 DT. 5; LS wood, cortex and periderm from right to left; note a leaf trace running through the cortex, ×40. 5, 10,891 F(2)B. 12; secondary phloem in oblique TS showing two rays with enlarged cells, ×80. 6, 10,415 A. 55; detail of a pair of perpendicularly arranged leaf traces within cortex of a leafy shoot; at left, outer trace with protoxylem pointing upwards and at right, inner leaf trace shifted; adaxial side at top, ×45.

PLATE 3



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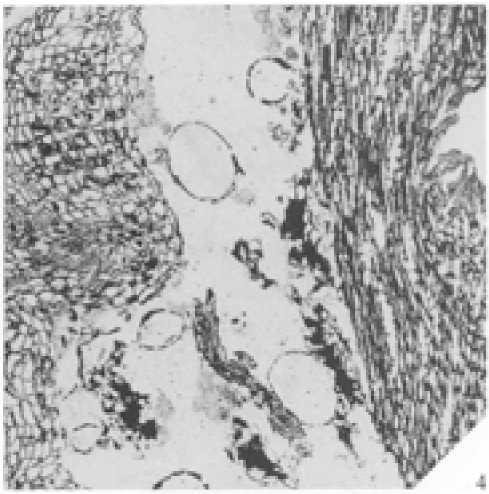
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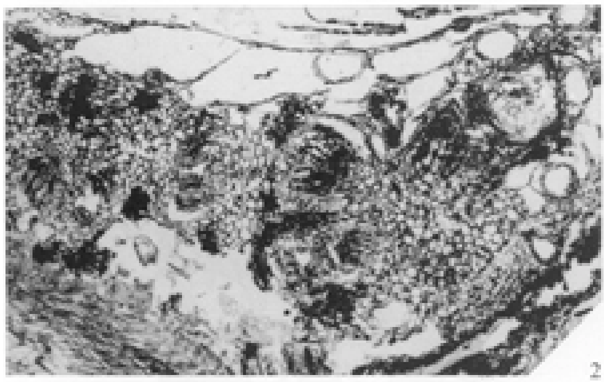
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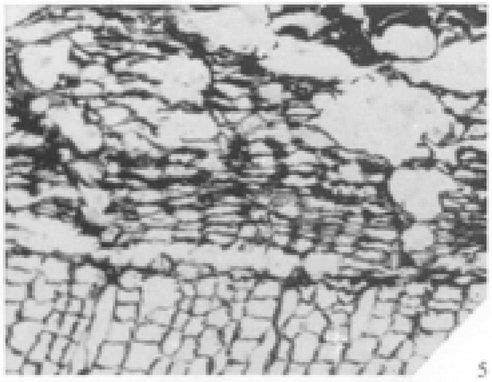
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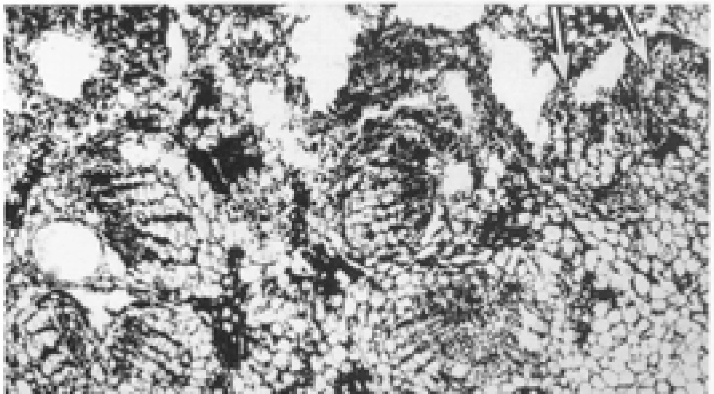
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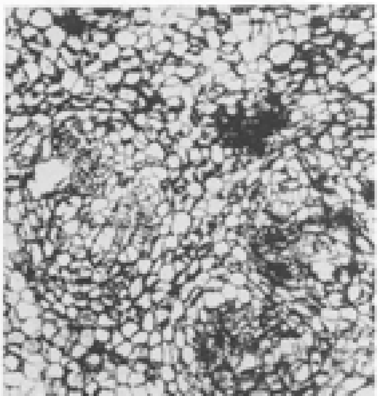
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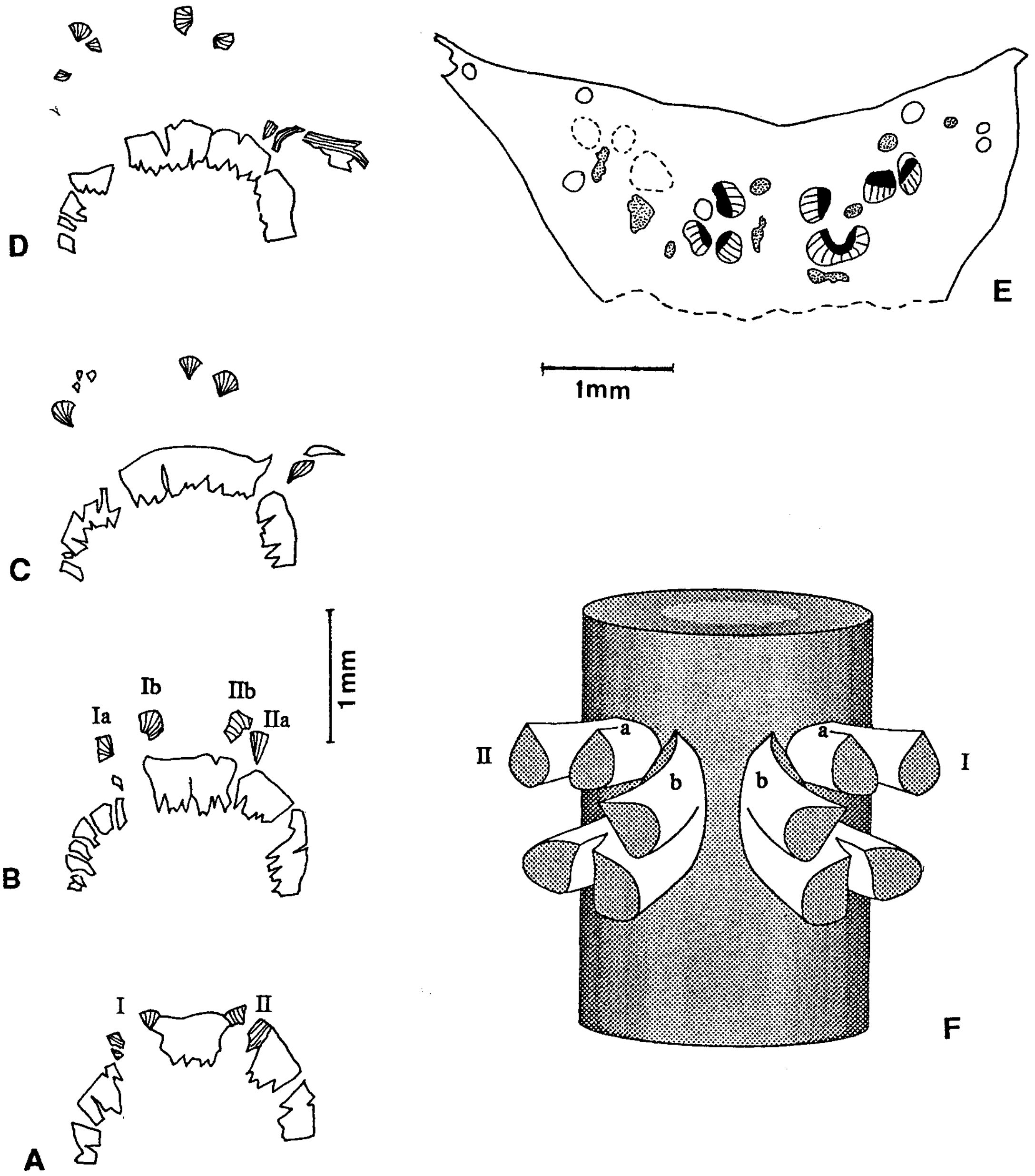

TEXT-FIG. 4. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. A–D. Series of sections from proximal (A) to distal levels (D) showing the emission of two pairs of leaf traces (Ia, Ib and IIa, IIb) that compose the vascularization of a leaf; compare with Plate 4, figs 5–7; holotype specimen; A, 10,628 E(1)BT. 41; B, 10,628 E(1)BT. 34; C, 10,628 E(1)BT. 26; D, 10,628 E(1)BT. 21; E, 10,628 E(I)BT. 82; oblique transverse section of a leaf base showing the three-dimensional arrangement of the leaf traces. Stippled areas = sclerotic nests; solid white circles = secretory cavities; areas encircled by a dotted line = putative position of unpreserved bundles; blackened areas in bundles = xylem; stripped areas in bundles = phloem. F, three-dimensional reconstruction showing the division of the leaf traces that form the vascularization of a single leaf.

up to 150 mm long with petioles measuring 5 mm proximally (Pigg 1990). Although remains of *D. fremouwensis* are abundant at Fremouw Peak, nothing is known of proximal petiole anatomy because specimens discussed in Pigg (1990) are known only at and distal to the frond bifurcation into pinna rachides. On the contrary, a wealth of information is known on the anatomy of the rachides and pinnae. Rachides are unique in possessing a three-dimensional vascular system with an adaxial row of bundles and one abaxial ring of strands. The strands are ensheathed by 1–3 layers of elongated cells. They consist of several rows of radially aligned tracheids limited abaxially by a zone of secondary phloem. Adaxial bundles are endarch (Pigg 1990, pl. 3, figs 2–5). Two zones are recognized in the ground tissue of the rachides: an outer zone of cuboidal cells with dark contents and an inner zone of loose parenchyma elements in which large 'resinous cells' are scattered.

Kykloxylon fremouwensis and *Dicroidium fremouwensis* are associated in the same plant assemblage within the Fremouw Peak peat and share a striking number of similar anatomical features. The dimensions of the petioles of *D. fremouwensis* are comparable to those of the leaf bases attached to *Kykloxylon*. The two-part organization of the ground tissue is similar in both species. The lacunae described in pith, cortex and leaf bases of *Kykloxylon* resemble the 'resinous cells' (Pigg 1990) of *Dicroidium*. The absence of sclerotic nests in *Dicroidium* rachides and pinnae may be related to the distal position of these parts in the frond architecture. The arrangement of leaf traces is dorsiventral both in *D. fremouwensis* rachides and *K. fremouwensis* leaf bases and differs only in the number of abaxial rings. The composition of the strands is similar in both species. Based on these anatomical features and the occurrence of both taxa within the same peat, we believe that *Kykloxylon fremouwensis* and *Dicroidium fremouwensis* represent parts of the same biological species. We interpret the reduction from two abaxial rings of strands in *Kykloxylon* leaf bases to one ring only in *Dicroidium* rachides as the result of the dichotomy that is known to occur in the distal part of *Dicroidium* petioles.

This is a different interpretation for the biological affinities of *Dicroidium* from that seen at Triassic localities in Argentina and elsewhere in South America, where *Dicroidium* is consistently associated with *Rhexoxylon* stems (Archangelsky 1968). This latter reconstruction was subsequently supported by Petriella (1981) and by Retallack and Dilcher (1988), who reconstructed the '*Dicroidium*/*Rhexoxylon* plant'. These two viewpoints as to the biological affinities of *Dicroidium* are not contradictory. Rather, they underscore a common situation in palaeobotany in which one type of leaf is ultimately demonstrated to have been produced by a variety of stem-genera. This is certainly the possibility with *Dicroidium*, a leaf morphotype which is highly variable throughout the Triassic of Gondwana.

The relationship between Rhexoxylon *and* Antarcticoxylon

Rhexoxylon has been described from various Triassic localities of South Africa and South America, and four species are currently recognized: *R. africanum* (Bancroft 1913), *R. tetrapteridoides* (Walton 1923), *R. piatnitzkyi* (Archangelsky and Brett 1961; Brett 1968) and *R. brasiliensis* (Herbst and Lutz 1988). *Rhexoxylon waltoni*, which was described by Kraüsel (1956) on the basis of a special tissue ('Fransenxylem') lining the secondary xylem, was synonymized with *R. africanum* by Archangelsky and Brett (1961), a decision that has been supported by the work of Herbst and Lutz (1988). In addition, a specimen with *Rhexoxylon*-like secondary anatomy was recently reported from the Triassic of Antarctica (Taylor 1992). All specimens assigned to these species are characterized by a cylinder of secondary xylem that is divided into sectors by large wedges of parenchyma and the development, within the pith, of strands of secondary xylem that are either centripetal or both centripetal and centrifugal. This vascular organization superficially resembles that of modern lianas (Walton 1923). In addition, the stems assigned to these species are characterized by a large pith, a pycnoxylic type of wood and tracheids of secondary xylem that show alternate and contiguous ('araucarian') bordered pits on the radial walls. Anomalous xylem development in tangential cracks of the wood is also a common feature of these taxa.

The problem of associating *Antarcticoxylon priestleyi* with *Rhexoxylon* is a complex one. Two decorticated specimens have been assigned to *Rhexoxylon* (*Antarcticoxylon*) *priestleyi* by Walton (1925); the original stem described by Seward (1914) from an erratic boulder on the Priestley Glacier (Antarctica) and a second, better-preserved specimen from the Triassic of South Africa (Walton 1925, 1956). The association of the Antarctic specimen with a two-winged pollen grain that resembles those produced by *Pteruchus* suggests a Triassic age for this specimen. Like the four species of *Rhexoxylon* mentioned above, both specimens have a pycnoxylic type of wood, tracheids of secondary xylem of the 'araucarian' type and anomalous xylem development in the wood. However, they also possess a massive undivided cylinder of secondary xylem and, in this respect, differ from these taxa. Because of the bad state of preservation of the Antarctic specimen, the presence of centripetal xylem at the periphery of the pith has never been established and many other critical characters of the primary and secondary xylem have not been observed in this stem. For these reasons, we propose to maintain *Antarcticoxylon* as a form genus including a single valid representative, the specimen from Antarctica (Meyer-Berthaud and Taylor 1991). The specimen from South Africa has a well-preserved ring of centripetal secondary xylem at the periphery of the pith and in this respect resembles *Rhexoxylon*. However, it is not clear whether stems with an undivided cylinder of secondary xylem should be included within *Rhexoxylon*. According to Walton (1923, 1925, 1956), the *Rhexoxylon* stems probably possess a continuous cylinder of secondary xylem at an early stage of development that becomes segmented radially by the secondary tissue development. During this phase of growth, vascular strands with both centripetal and centrifugal secondary xylem are formed at the periphery of the pith. However, after the discovery of a young stem of *R. piatnitzkyi*, Archangelsky and Brett (1961) suggested a different pattern of growth. They interpret the vascular tissues of *Rhexoxylon* as discrete vascular segments with both centripetal and centrifugal xylem from the earliest stages of development. According to this idea, the increase in diameter of the stems results from a tangential splitting of the original strands and the formation of secondary xylem along the margins of the wedges of wood that have become separated. In the present paper, the specimen from South Africa is referred to as '*Rhexoxylon priestleyi*'.

Comparison between Kykloxylon, Antarcticoxylon *and* Rhexoxylon

A comparison of the available anatomical features of *Kykloxylon*, *Antarcticoxylon* and *Rhexoxylon* indicates that these taxa have numerous characters in common (Table 1). The secondary xylem in all three is pycnoxylic with uniseriate rays. Pitting on the radial walls of the tracheids is uni- or biseriate, rarely triseriate. Pits are bordered with a circular, sometimes slightly elliptical, aperture. They are generally polygonal and contiguous (of 'araucarian' type) when multiseriate. Pits in the cross field are simple. Those in *Rhexoxylon* are few and wide. We mentioned a tendency for a reduction in the number of cross field pits, possibly by fusion, in the wood of *Kykloxylon*.

A consistent character of most *Rhexoxylon* and possibly *Antarcticoxylon* stems is the presence of sclerotic nests and lacunae (also called 'reservoirs' or 'cysts'; Table 1) that might have been secretory in the pith. These characters have been mentioned by some authors (Walton 1923; Archangelsky and Brett 1961) as indicators of the potential affinities with the medullosan

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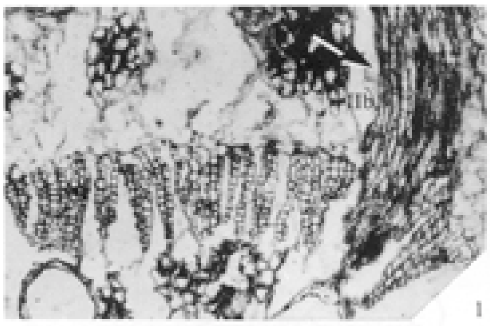
EXPLANATION OF PLATE 4

Figs 1–7. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. 1–4, series of oblique sections showing the pattern of emission in three traces (Ia, Ib, IIb at arrows) that are part of a single leaf vascular supply, from distal (1) to proximal levels (4); holotype specimen; all × 70. 1, 10,628 E(I)BT. 8. 2, 10,628 E(I)BT. 13. 3, 10,628 E(I)BT. 17. 4, 10,628 E(I)BT. 20. 5–7, series of transverse sections showing the pattern of emission of four traces (Ia, Ib, IIb, IIa) that are part of a single leaf vascular supply, from distal (5) to proximal levels (7); note the shift of the inner bundles (Ib, IIb) in fig. 5 (arrows); compare with Text-fig. 4A–D; holotype specimen; all × 45. 5, 10,628 E(1)BT. 21. 6, 10,628 E(1)BT. 28. 7, 10,628 E(1)BT. 41.

PLATE 4



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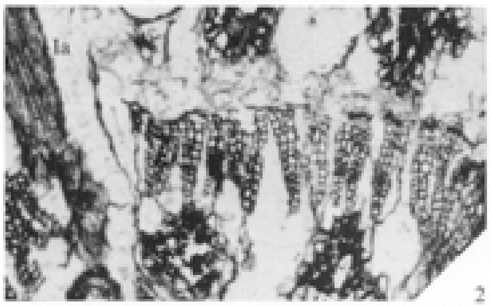

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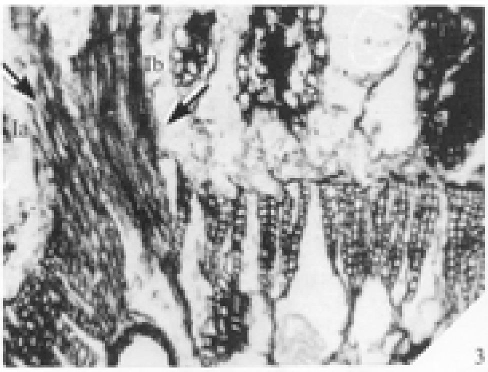

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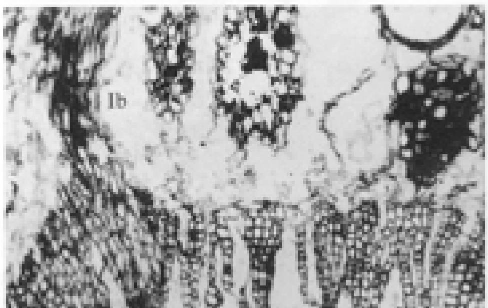

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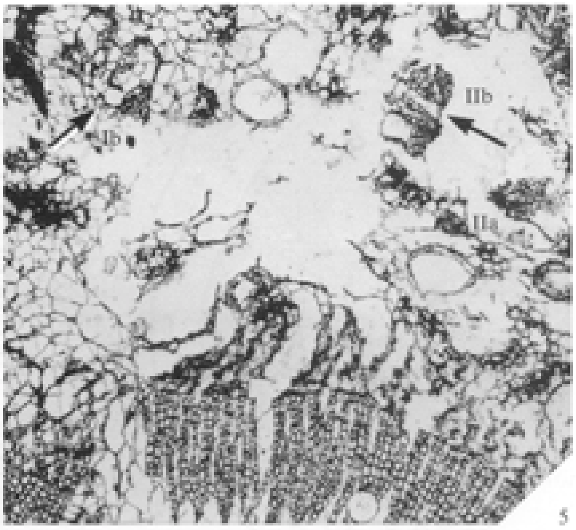

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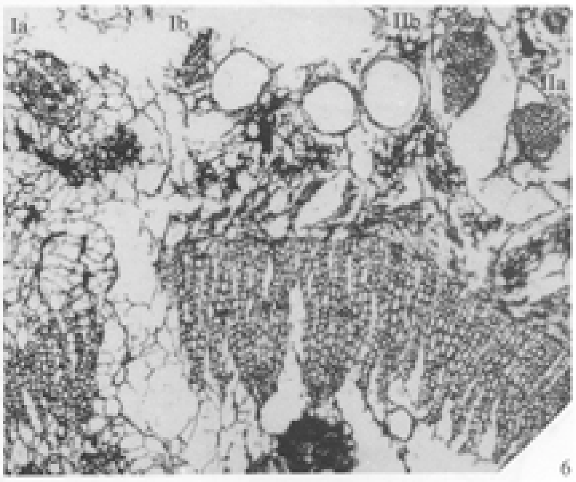

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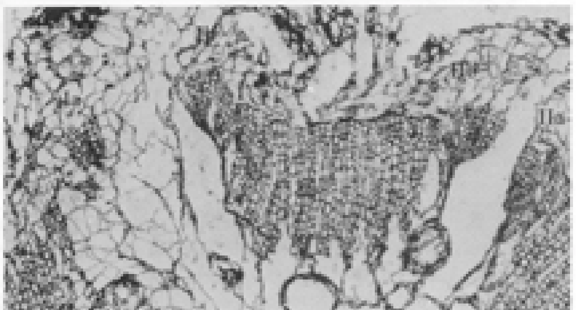

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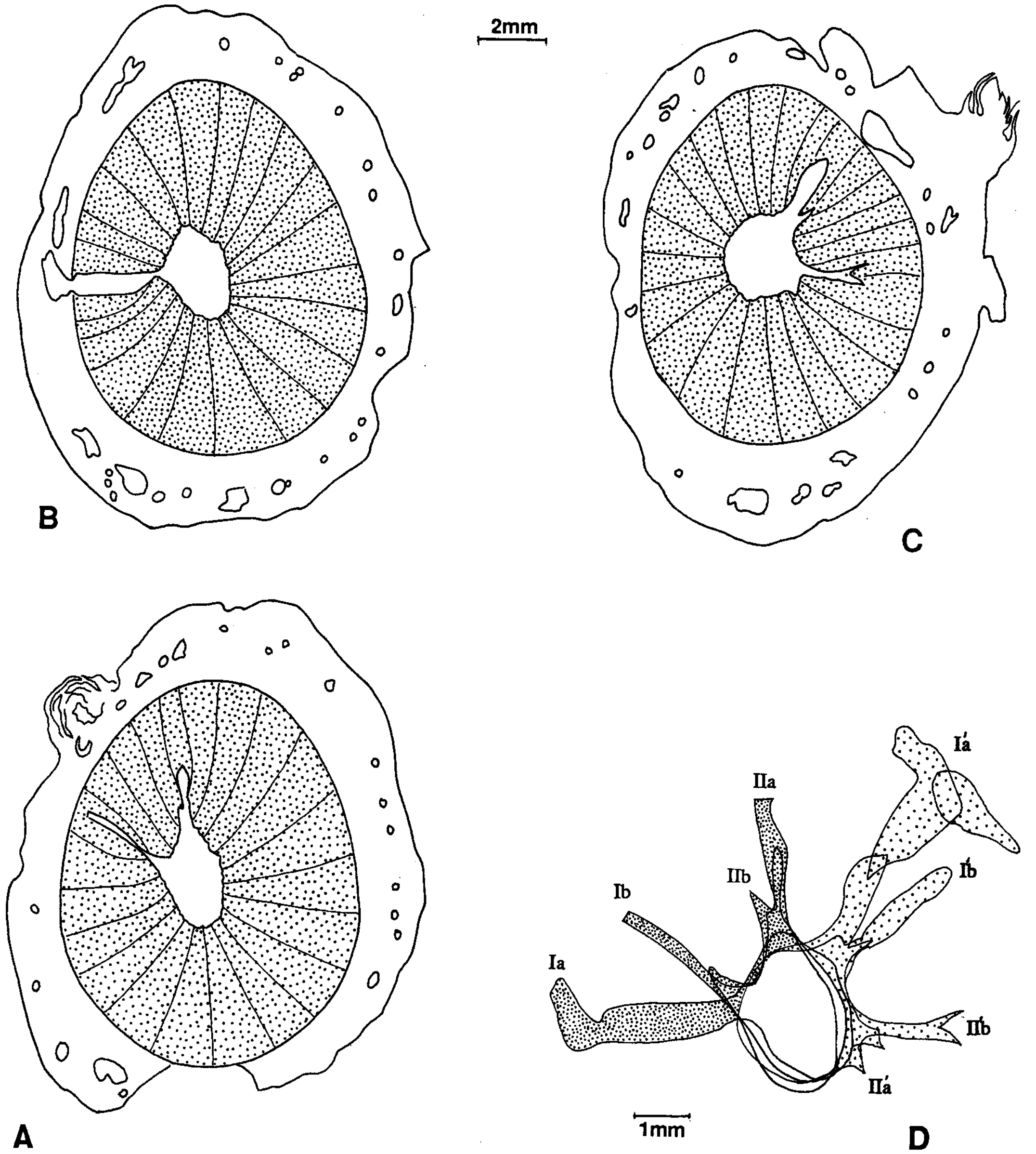

TEXT-FIG. 5. *Kykloxylon fremouwensis* gen. et sp. nov. Middle Triassic; Queen Alexandra Range, Transantarctic Mountains. A–C, emission of two successive leaf vascular supplies from proximal (A) to distal levels (C), × 3. A, 10,891 F(2)aT. 41; B, 10,891 F(2)aT. 4; C, 10,891 F(2)aT. 5. D, superimposed transverse sections showing the emission of two successive leaf vascular supplies (I+II and I'+II') separated by an approximate angle of 130°.

pteridosperms. We emphasized similar features in *Kykloxylon* with a special mention to the lacunae since within the Fremouw Peak flora the latter are known from these stems, the leaves and petioles of *Dicroidium* and certain reproductive structures. The bands of periderm-like tissue extending

TABLE 1. Comparison of anatomical characters of *Kykloxylon* gen. nov., *Antarcticoxylon* Seward and *Rhexoxylon* Bancroft.

	Kykloxylon fremouwensis	*Antarcticoxylon priestleyi*	*"Rhexoxylon priestleyi"*	*Rhexoxylon tetrapteridoides*	*Rhexoxylon africanum*	*Rhexoxylon brasiliensis*	*Rhexoxylon piatnitzkyi (small)*	*Rhexoxylon piatnitzkyi (trunks)*
AUTHOR(S)		Seward 1914 Walton 1923, 25	Walton 1925, 56	Walton 1923	Bancroft 1913 Walton 1923	Herbst & Lutz 1988	Archangelsky & Brett 1961	Brett 1968
LOCALITY	Antarctica	Antarctica	South Africa	South Africa	South Africa Rhodesia	Brasil	Argentina	Argentina
DIAMETER (cm)	up to 1 x 1.5	> 2 x 9	6	up to 17	> 25	up to 37 x 43	8	up to 100
SECONDARY XYLEM								
Divided in sectors	No	No	No	Yes	Yes	Yes	Yes	Yes
Centripetal wood	No	?	Yes	Yes	Yes	Yes	Yes	Yes
Type	Pycnoxylic	Pycnoxylic	Pycnoxylic	Pycnoxylic	Pycnoxylic	Pycnoxylic	Pycnoxylic	Pycnoxylic
Ray width	Uniseriate	Uni(bi)seriate	Uniseriate	Uniseriate	Uniseriate	?	Uniseriate	Uniseriate
Ray height	1 to 10	1 to 24 cells	1 to 8 cells	5 to 7 cells	1 to 17 cells	?	1 to 22 cells	1 to 22 cells
Radial pitting	Uni-triseriate	Uni-biseriate	Uni-biseriate	Uni-biseriate	Uni-triseriate	?	Uni-biseriate	Uni-biseriate
Cross field pits	3 to 9	Not preserved	4 to 7	1	1 to 3	"in 2 rows"	1 to 3	1 to 3
PROTOXYLEM	Endarch	Endarch ?	Endarch	Endarch	Endarch	Endarch	Mesarch	?
PITH								
Sclerotic nests	Yes	?	Yes	Yes	Yes	Yes	No	Yes
Lacunae	Cavities	?	"Reservoirs"	"Reservoirs"	?	"Cysts"	"Cysts"	"Cysts"
Periderm-like zone	Yes	No	No	Yes	Yes	No	No	Yes
CORTEX		Not preserved	Not preserved		Not preserved			Not preserved
Sclerotic nests	Yes			Yes		No	No	
Lacunae	Cavities			Secretory cells		No	"Cysts"	

through the pith in *Kykloxylon* have also been reported in *R. africanum* (Bancroft 1913), *R. tetrapteridoides* (Walton 1923) and *R. piatnitzkyi* (Archangelsky and Brett 1961). It is not known whether this tissue is the result of some wound or represents some form of growth that is a feature of these plants.

The pattern of leaf trace emission in *Kykloxylon* is complex and initially involves four bundles. As a result of repeated divisions the two pairs of traces that originate from the axial strands eventually give rise to an adaxial row of vascular bundles and two abaxial rings of strands in the leaf base. A comparable pattern has been reported in a young axis of *Rhexoxylon piatnitzkyi* (Archangelsky and Brett 1961). Here also the vascularization of the leaf is supplied by traces originating from several axial bundles that occur in pairs, the bundles of each pair being separated by a small amount of parenchyma. Within the cortex the traces divide to form a three-dimensional pattern. In *R. piatnitzkyi* this pattern results in the formation of seven to eight groups of bundles arranged in a semi-circle. It should be pointed out that the two leaf bases illustrated in Archangelsky and Brett's Figure 5 (1961) are incomplete and thus the possibility cannot be ruled out that the bases also contained bundles near the adaxial leaf base surface. The pattern of leaf base vascularization has not been studied in any other specimens of *Rhexoxylon* and *Antarcticoxylon*. But a horizontal or low-angled course of the leaf traces has been reported in *R. tetrapteridoides* (Walton 1923) and *R. piatnitzkyi* (Archangelsky and Brett 1961). This feature which has been observed in *Kykloxylon* may characterize the whole group of plants presently discussed. Finally, the presence of buds on small axes of *R. piatnitzkyi* (Archangelsky and Brett 1961) and *Kykloxylon* is noteworthy.

One of the primary difficulties in discussing the affinities of *Kykloxylon* with *Rhexoxylon* is brought about by the fact that the former are known only from young axes (with up to five years' growth) while most species of the latter are known only from fragments of trunks or older branches. According to Walton, the arrangement of the secondary xylem has no systematic value since young *Rhexoxylon* axes might have had an undivided cylinder of xylem. However, the single five year-old stem (based on ring count from Archangelsky and Brett 1961, fig. 2; pl. 1, fig. 21) of *R. piatnitzkyi* has the vascular tissue divided into sixteen vascular segments with both centripetal and centrifugal wood. The oldest specimen from Fremouw Peak, which is also approximately five years old, shows an undivided ring of wood and no centripetal development of the secondary xylem. In addition, the pith of *Kykloxylon* is much smaller and the vascularization of the leaf bases is quite different from that of *R. piatnitzkyi*. It is currently impossible to state with certainty that all of the young axes of *Rhexoxylon* species are anatomically similar to *R. piatnitzkyi*; however, at our current level of knowledge this feature is sufficient to distinguish those specimens from *Kykloxylon*.

The axis from South Africa referred to herein as '*Rhexoxylon priestleyi*' resembles *Kykloxylon* in having a continuous cylinder of pycnoxylic wood. However, the lack of information concerning the pattern of leaf trace emission and leaf base venation in this axis prevents any close comparison with the specimens from Fremouw Peak.

Finally, the differences between *Kykloxylon*, *Antarcticoxylon* and *Rhexoxylon* must not understate the unique set of characters shared by these taxa. It is our belief that they form a natural group, the Corystospermaceae, characterized by the following vegetative characters: pycnoxylic wood with uniseriate rays, possibly related to the tree habit of these plants; 'araucarian' type of pitting on the radial walls of the tracheids of secondary xylem; cross-field pits simple that tend to be few and wide; pith with sclerotic nests and lacunae or secretory structures; leaf vascular system complex, originating from several axial bundles, three-dimensional and dorsiventral in leaf bases.

CONCLUSION

This study represents the first step in the reconstruction of a '*Dicroidium* plant' from Antarctica. The distal parts of the plant are constructed of axes with a solid cylinder of pycnoxylic wood of the *Dadoxylon*-type, a form-genus that is widespread in the Mesozoic of Gondwana (Giraud 1991). Distal-most twigs bear helically arranged leaves of the *Dicroidium fremouwensis*-type. Because of the consistent occurrence of buds on stems, it is assumed that this plant possessed a more complex branching pattern than the tree fern-like habit of the '*Dicroidium*/*Rhexoxylon* plant' suggested by Petriella (1981) on the basis of specimens from the Triassic of Argentina. The presence of *Pteruchus* pollen organs at the same locality (DeVore and Taylor 1988), also with characteristic cortical lacunae, strongly suggests that this was the microsporangiate organ of the Antarctic *Dicroidium* plant.

Stems are assigned to a new genus, *Kykloxylon*, which differs from *Rhexoxylon* axes of comparable ontogenetic age by a different arrangement of the vascular cylinder and features associated with the leaf bases and their vascular pattern. The liana-like anatomy of *Rhexoxylon* can no longer be used to characterize all plants that produced *Dicroidium* foliage. Perhaps the '*Dicroidium*/*Rhexoxylon* plants' inhabited the western regions of Gondwana (South Africa, South America and rarely Antarctica) whereas the '*Dicroidium*/*Kykloxylon* plants' might have had a wider geographical distribution in Gondwana.

To date our knowledge of Triassic plants has been fragmentary, owing to the relatively few taxa described and especially to the few known permineralized specimens that provide a suite of anatomical features useful in whole plant reconstruction. The relationships between *Dicroidium* foliage and *Kykloxylon* axes illustrated here represent the first attempt to document the biological relationships of two Triassic taxa based on such a suite. It is important to underscore our belief that the plants that bore *Dicroidium* foliage may have been of several types and that the Antarctic *Dicroidium*/*Kykloxylon* plant was just one of many forms that inhabited the Triassic of Gondwana. Although the reproductive organs are still poorly known, the vegetative parts based on anatomical evidence suggest that at least two of the taxa (*Rhexoxylon* and *Kykloxylon*) shared a number of features, especially those relating to leaf trace emission. As subsequent studies of permineralized Triassic plants continue it may be possible to resolve more accurately the relationships between these Mesozoic seed ferns and their putative Palaeozoic ancestors based on both vegetative and reproductive organs.

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