# *OGURACAULIS BANKSII* GEN. ET SP. NOV., A MID-MESOZOIC TREE-FERN STEM FROM TASMANIA, AUSTRALIA

by William D. Tidwell, Harufumi Nishida and Neri Webster

(with one text-figure and five plates)

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*Oguracaulis banksii* gen. et sp. nov. is described from permineralised specimens from Upper Jurassic–Lower Cretaceous strata near Ida Bay, Tasmania. The specimens consist of large fern stems and adhering petiole bases covered with thick root mantle. Their stems are characterised by a dictyostele with a sclerenchymatous sheath, numerous medullary bundles, an undivided leaf and petiolar vascular trace and multicellular epidermal hairs. This fossil fern provides evidence for the common origin for many of the modern cyatheaceous tree ferns including the cibotioids. **Key Words: Mid-Mesozoic, Tasmania, Cyatheaceae, *Oguracaulis, Cibotium, Angiopteris.***

## INTRODUCTION

Permineralised specimens of the tree fern comprising this report, up to 80 mm across by 110 mm long with petiole bases on their surfaces, were collected from strata of either Late Jurassic or Early Cretaceous age at a locality south of Ida Bay in southern Tasmania. This locality lies a few metres to the east and west of South Cape road immediately north of its junction with the Leprena Track. Other plant remains at this locality include species of *Osmundacaulis* (*O. nerii*, Tidwell & Jones 1987, and *O. jonesii*, Tidwell 1987), a fossil tree fern (*Cibotium tasmanense* Gould 1972), fossilised leaf material (Tidwell *et al.* 1987), and as yet undescribed conifer remains.

## MATERIALS AND METHODS

The permineralised specimens are incomplete remains from various fern axes. These specimens were collected and donated by Ross Jones of Blackmans Bay, Tasmania, Neri Webster of Bicheno, Tasmania, and Dr M.R. Banks of the University of Tasmania. The specimens were photographed, thin-sectioned and studied. The fossils and their thin-sections provided the basis for morphological comparisons between these specimens and various cyatheaceous forms.

## SYSTEMATIC DESCRIPTION

### Filicales

**Cyatheaceae *sensu* Holttum (1963)**
*Oguracaulis banksii* gen. et sp. nov.
(pls 1–5, fig. 1)

**Diagnosis**
Fossil tree-fern stem with radial symmetry encircled by persistent petiole bases and adventitious roots; stem vasculature dictyostelic, containing numerous medullary bundles; meristeles surrounded by a sclerenchymatous sheath; tangential cells in phloem; leaf trace omega-shaped with incurved margins and lateral constrictions (omega open adaxially), fusion of medullary bundles forms adaxial arc of leaf trace, undivided throughout; stem surface with multicellular epidermal hairs; numerous adventitious roots arise from stele on each side of leaf trace; roots rarely inside stele.

**Generitype**
*Oguracaulis banksii.*

**Repository**
Tasmanian Museum and Art Gallery Z2286 (holotype), Z2287, Z2288, Z2289, Z2290 (paratypes); Hobart, Tasmania. Brigham Young University 3258 (paratype).

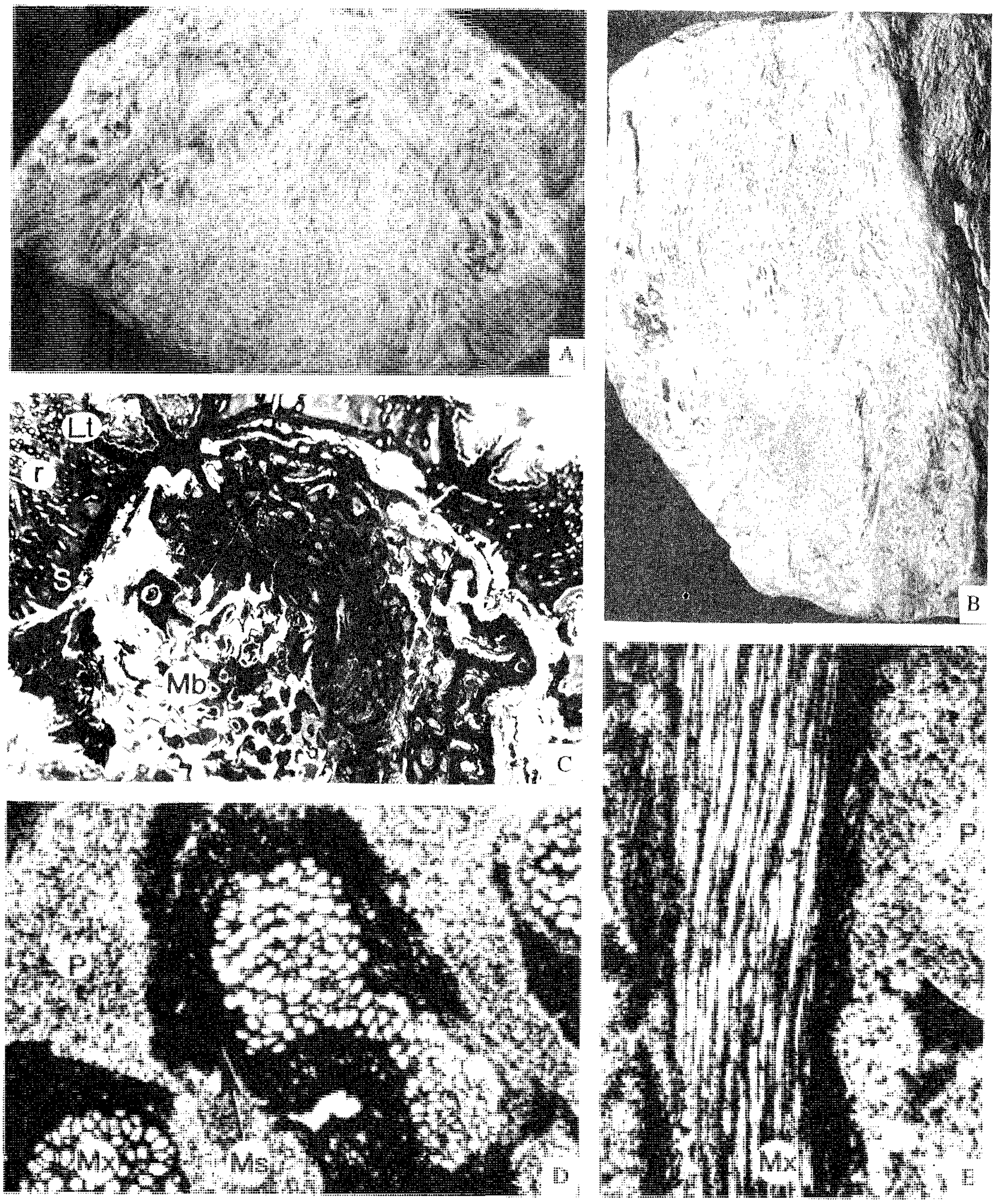

*PLATE 1*

Oguracaulis banksii *gen. et sp. nov. (A) Top view of holotype Z2286; × 1. (B) Side view of holotype Z2286, note leaf bases and roots on surface; × 1. (C) Cross sectional slide of holotype Z2286; × 1.6. (D) Cross section of medullary bundles, note fusion of bundles, Z2286; × 20. (E) Longitudinal section of a medullary bundle, Z2290; ×20. Stele (S), medullary bundles (Mb), medullary bundles xylem (Mx), roots (R), leaf traces (Lt), medullary bundle sheath (Ms) and pith of stem (P).*

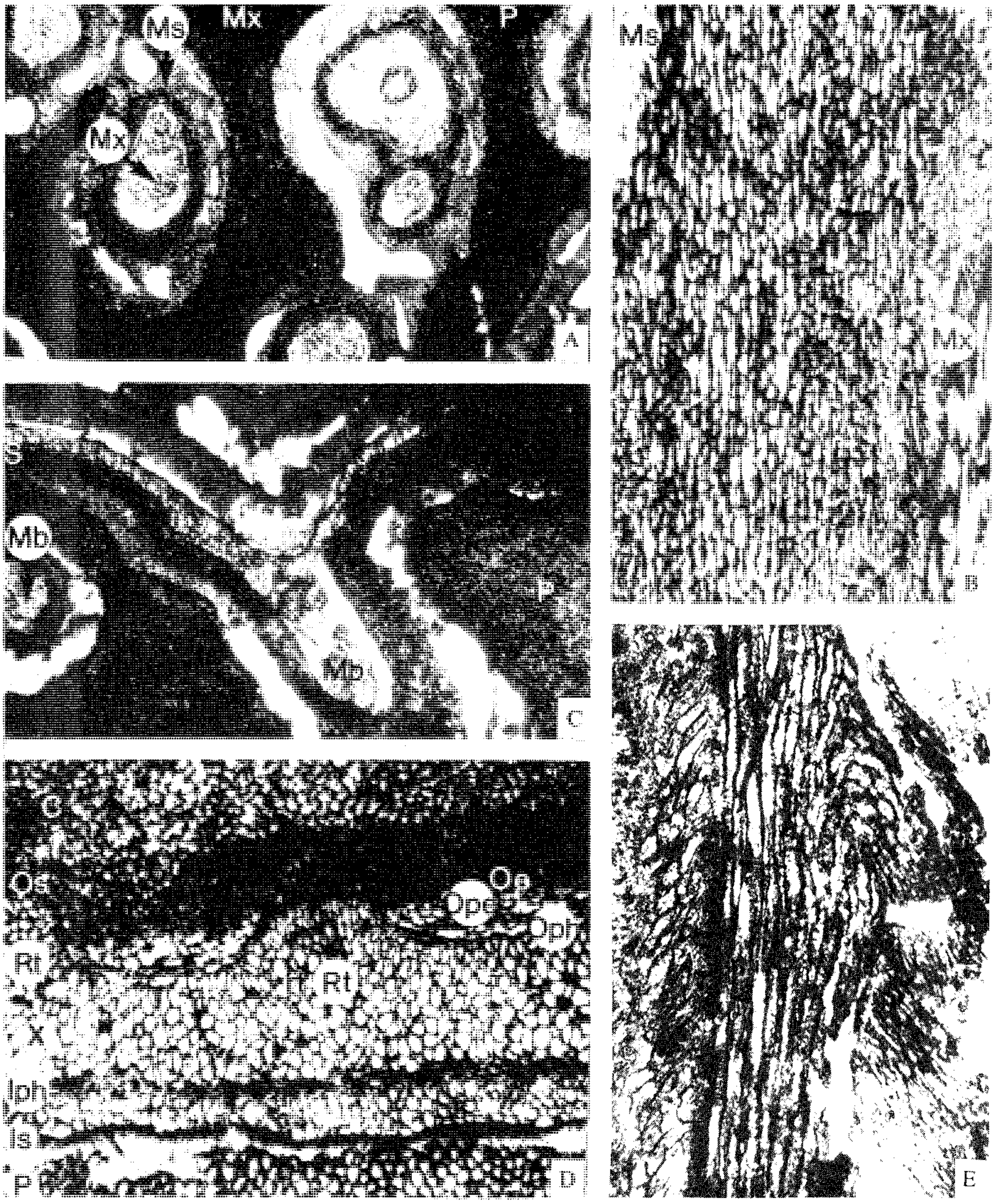

*PLATE 2*

Oguracaulis banksii *gen. et sp. nov. (A) Cross-sectional view of medullary bundles, Z2286; × 10. (B) Longitudinal section of a medullary bundle, Z2290; × 30. (C) Cross section of stelar strand with an occasional medullary bundle (Mb) connecting with vascular strand, thinner xylem strand to right is the beginning of a trace, Z2286; × 10. (D) Enlarged portion of the stele with two departing root traces, Z2286; × 20. (E) Longitudinal view of xylem strand of the stele with departing root trace, Z2290; × 30. Medullary bundle xylem (Mx), medullary bundle sheath (Ms), xylem (X), inner phloem (Iph), inner pericycle (Ipe), inner endodermis (Ie), inner sclerenchyma sheath (Is), pith (P), outer phloem (Oph), outer pericycle (Ope), outer endodermis (Oe), root trace (Rt), outer sclerenchyma sheath (Os), cortex (C).*

### Etymology

The generic name honours Professor Yadzuru Ogura for his many studies on extant and extinct tree ferns, and the specific epithet honours Dr M.R. Banks of the Department of Geology, University of Tasmania, for his assistance with this study and for his interest in the study of fossil plants of Tasmania.

### Locality

Near Ida Bay, Tasmania, Australia (Tidwell *et al.* 1987).

### Age

Late Jurassic–Early Cretaceous.

### Description

The stem of *Oguracaulis banksii* is radially symmetrical, 45–60 mm in diameter, and surrounded by petiole bases (pl. 1A,C). These petiole bases are elliptical in section, up to 30 mm in vertical dimension and 12 mm horizontally (pl. 1B), and are helically arranged in ten orthostichies with each base alternating with those of adjacent rows. Bases of these specimens being separated from each other, their stems having short leaf gaps, and their roots crowding the stems, invading and collapsing their leaf bases, suggest that these specimens are from near the lower portions of older tree ferns.

Leaf scars are visible on the surfaces of the specimens and show the characteristic arrangement of the petiolar vascular strands for this fern. These strands are an unbroken, fluted or corrugated, modified reverse omega (incurved horseshoe) configuration along the periphery of the elliptical petiole bases.

Numerous adventitious roots cover all sides of the specimens and occur between the petiole bases. Many run downward through the specimens. These roots have their origin from the external surface of the stele (pl. 3D,E) and separate from this tissue near the base of the developing leaf trace on each side of the future gap. After departing from the stele, they pass obliquely through the cortex, hypodermis and epidermis, eventually becoming free on the stem surface (pls 1B,4A,5B). They are almost equal in diameter (0.25–1.5 mm) and are diarch, with the xylem elements being surrounded by phloem, pericycle and endodermis (pl. 5D). The cortex of the roots consists of thick-walled fibres and prosenchyma enclosed by a single layered epidermis. Softer tissues are rarely preserved in these structures (pl. 4B) and root hairs were not observed.

Single, unbranched, filamentous hairs arising from the epidermis of the stem are straight and very long, reaching 20-50 mm in length and 1.4 µm in width (pls 4B,5A,B). The multicellular hairs are of the same diameter from their bases with their cells separated by straight septae. The walls of the single row of cells composing these trichomes are thin. The closely-packed hairs are persistent, densely covering the stem surface and extending outward surrounding the roots and petiole bases. Hairs derived from the epidermal cells of the petiole bases are the same as those from the stem.

Beneath the epidermal layer is the hypodermis which is 0.7–2.5 mm wide and sclerenchymatous. This sclerenchymatous layer consists of thick-walled fibrous elements that are 20–25 µm in diameter and 250 µm long.

The cortex is homogeneous and, where preserved, is composed of thick-walled parenchyma cells (30–40 µm in diam.) (pl. 2C,D,E).

The stele is 42–58 mm in diameter, dictyostelic, circular to square in transverse section (pl.1A,C) and appears lobed due to the bulging outward of the leaf traces. It is a hollow cylinder with wall perforated by a few leaf gaps. The stele is variable in thickness, generally 0.5-1.5 mm wide. The amphicribral bundles of the main dictyostele are composed predominantly of xylem with thin layers of phloem, pericycle and endodermis on each side (pl. 3D). The xylem consists of large, angular tracheids with interspersed, smaller, thin-walled xylem parenchyma (pl. 3A). The metaxylem tracheids are variable in size, varying from 40–60 µm in diameter by 1170 µm long. They are radially flattened and have scalariform pitting (pl. 2B). Some distinct protoxylem clusters of 4–6 cells (15–20 µm across) were noted and appear to be mesarch to subendarch.

Compared to the xylem, the phloem is thin (pl. 3A). It is 4–5 cells thick in the inner phloem and 3–4 cells wide in the outer. Sieve cells composing this tissue are 20–30 µm in diameter and tangential cells are present. A several-layered pericycle and a single-layered endodermis occur outside of the phloem. The outer endodermis is prominent, but the inner is obscure. The cells of the inner endodermis are also smaller, 20–30 µm versus 40–70 µm for the outer.

A discontinuous sclerenchymatous sheath occupies the area round the stele and the inner sheath is continuous with the sclerenchyma masses surrounding the adjacent medullary bundles. Therefore, the face of the sheath towards the pith is irregular in outline due to the numerous medullary bundles of the pith, whereas the stelar side of the sheath is regular.

In these fossil specimens, 300–350 medullary bundles are scattered throughout the pith (pls 1A,C–E,3A,C,4A,B,E). They vary in size (0.5–2.5 mm) and shape, and occur in clusters. The bundles are closely packed in the pith, which causes distortion in their shape. They are circular to elliptical in outline, often containing a flattened string of tracheids (pl. 1D). Sometimes bundles divide or fuse together to form a network, resulting in an elliptical shape or an elongated chain. These medullary bundles are usually protostelic, with an occasional bundle having parenchyma in the centre of the xylem. Softer tissues, which are often not well preserved, surround the xylem. In some specimens a black line (probably degraded protophloem), a pericycle 1–2 cells wide, and an endodermis with Casparian thickenings can be observed. A thin space between the black line and the xylem corresponds to the metaphloem. Outside of the endodermis is a ring of sclerenchymatous tissue of varying shape and thickness. The sclerenchymatous ring corresponds to the sclerenchymatous sheath of the stele and has the same general structure. Occasionally bundles fuse with the main stelar structure.

Although parenchymatous tissue may also be present in the pith, the major portion of the pith consists of a network of sclerenchyma (pl. 2A). Thus, the medullary bundles appear to be enclosed by double sheath-layers, of which the outer is parenchymatous and the inner sclerenchymatous. There are no mucilage cells in the fundamental tissues.

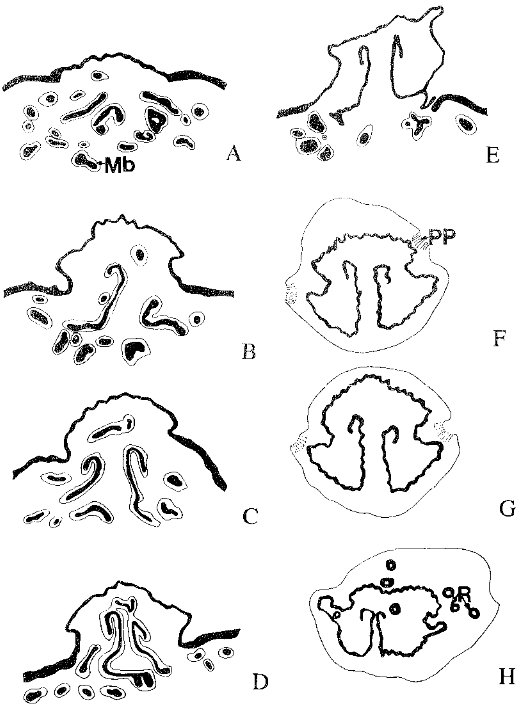

*FIG. 1A-H*— Oguracaulis banksii *gen. et sp. nov. Various stages in the development of a leaf trace, medullary bundles (Mb), roots (R), possible pneumathode (Pp); × 1.66.*

The boundary between the leaf gap, the stem vascular bundle and the leaf trace is indistinct. The position of the developing leaf trace can be noted where the xylem strand of the main stelar ring is only one to three tracheids thick (pl. 3C). Upward this section of the strand expands outward as a rounded protrusion to form the abaxial portion of the beginning leaf trace (fig. 1). The beginning trace gradually enlarges into the cortex, forming the abaxial arc of the typical cyatheaceous petiole vascular pattern (pl. 4A; Nishida 1984). Two circular medullary bundles that are side by side generally appear in the bulge (fig. 1A). Two more medullary bundles elongate into the forming gap and ultimately fuse with the previous two bundles. As they fuse, these bundles develop hooks at their tips (fig. 1B,C). Enlarging outward, the beginning trace remains as a semicircular, continuous band. This structure eventually becomes wavy, resulting in a fluted or corrugated structure. Protoxylem points occur at the outer projection of each bend of the fluted trace. The elongated medullary bundles fuse with the adaxial part of the trace to form a pair of adaxial arms of the petiole vascular bundle (fig. 1F). The trace then separates from the main stele of the stem, leaving a leaf gap (fig. 1F; pls 1C,4A,C). A pair of shallow lateral constrictions are developed in the leaf trace. In some petiole bases, a pair of medullary bundles remain in the pith, isolated from the continuous omega-shape of the standard leaf trace. These traces soon disappear distally in the petiole. Medullary bundles occasionally fuse with the gap end of the vascular strands of the stele immediately upon departure of the leaf trace (pl. 3C). This gives the impression that the vascular strands turn pithward on at least one, sometimes both, sides of the gap. The strands soon approach each other and finally the gap is closed. The trace becomes enclosed with part of the sclerenchymatous sheath of the xylem and the hypodermis as it progresses through these tissues of the stem. The sclerotic tissue of the petiole is

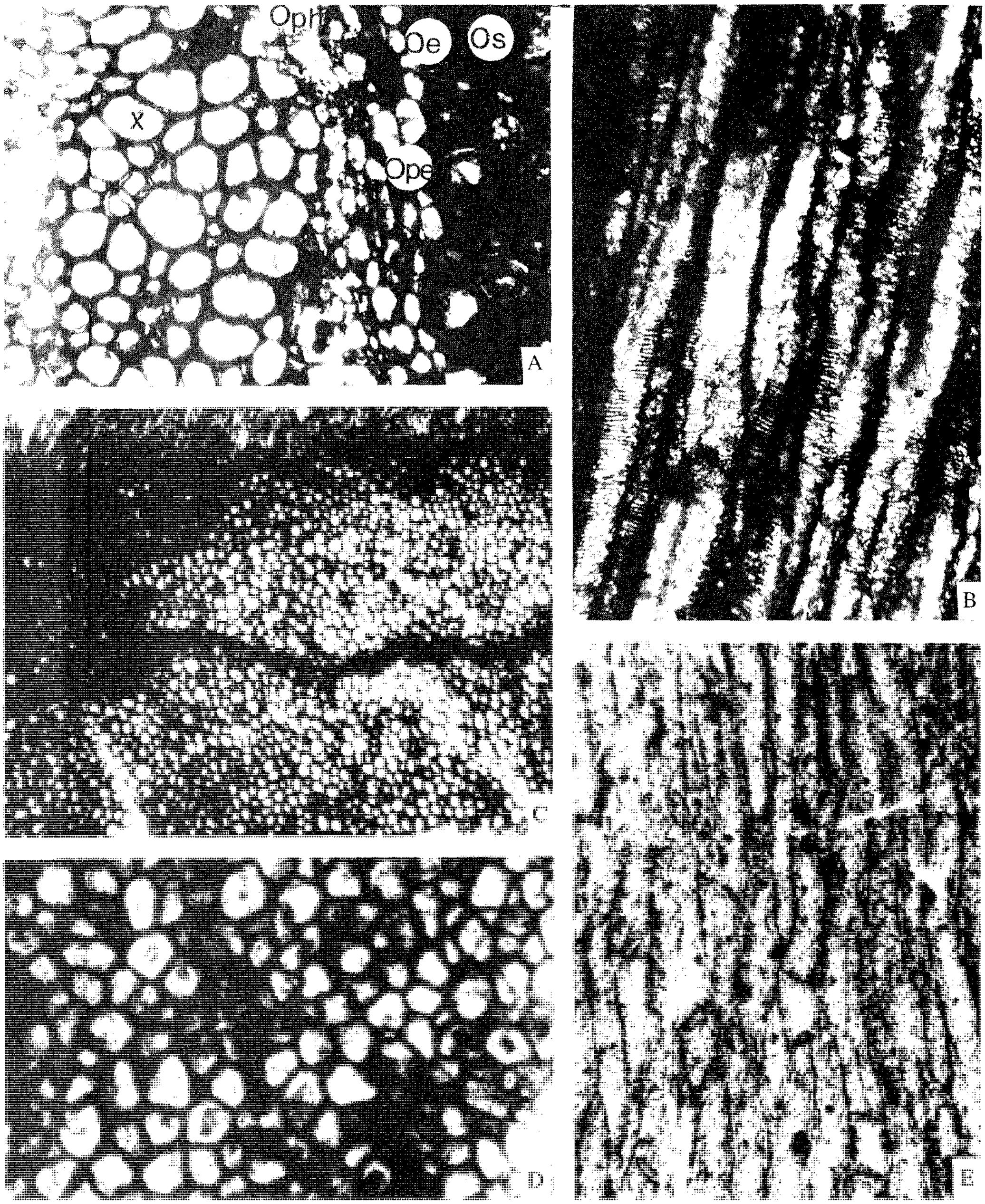

PLATE 3

Oguracaulis banksii *gen. et sp. nov. (A) Closeup of xylem (X), outer phloem (Oph), outer pericycle (Ope), outer endodermis (Oe) and outer (external) sclerenchyma sheath (Os); Z2286; ×60. (B) Longitudinal section of xylem strand, note scalariform thickenings on the tracheid walls, Z2240; ×60. (C) Cortex, Z2286; ×33. (D) Closeup of cells of the cortex, Z2286; ×90. (E) Longitudinal view of the cortex, Z2290; ×90.*

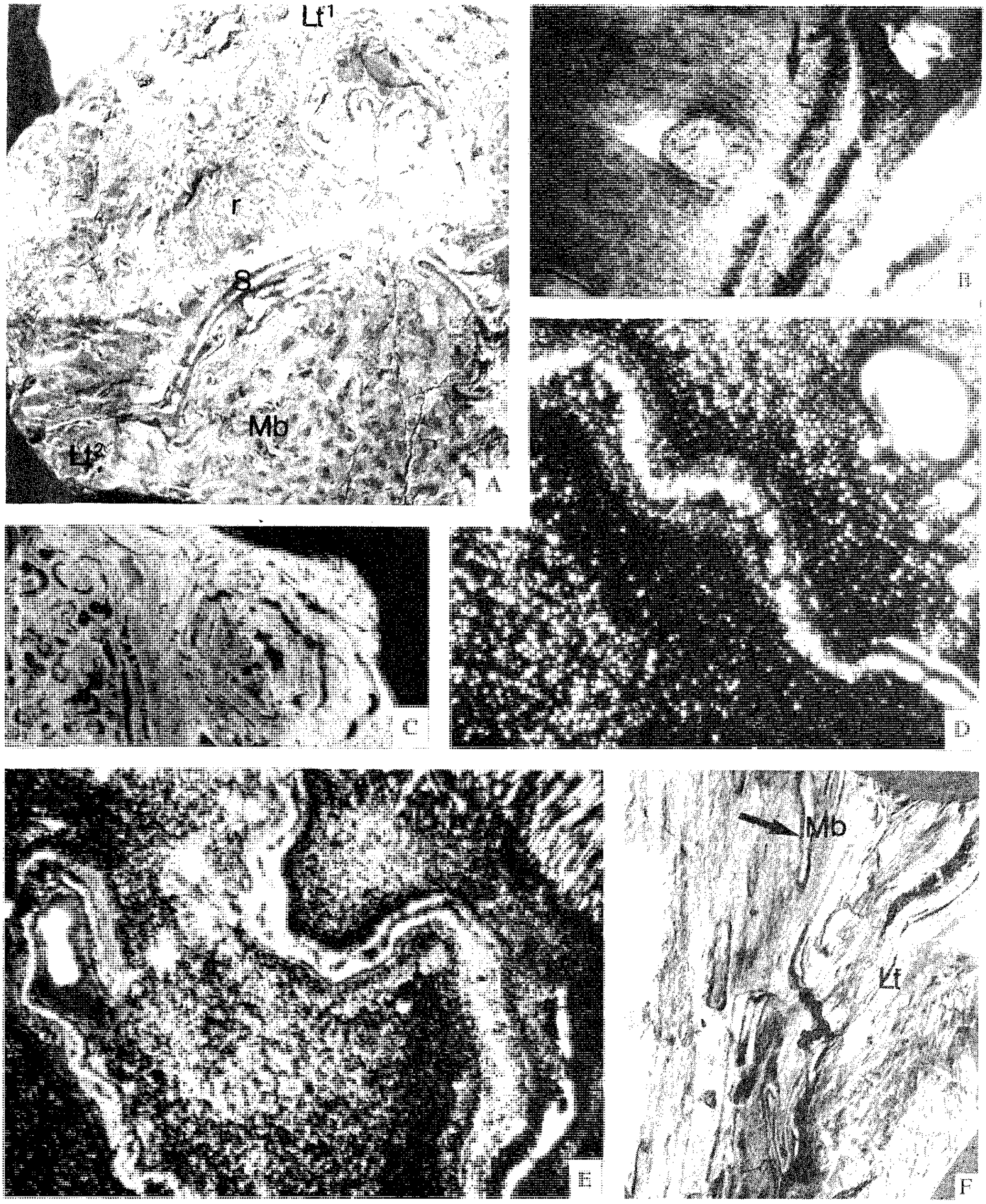

*PLATE 4*

Oguracaulis banksii *gen. et sp. nov. (A) Specimen showing a leaf trace ($Lt^1$), a forming leaf trace ($Lt^2$) and roots (R), note medullary bundles (Mb) inside the stele (S), Z2287; × 2. (B) Cross section of cortex with attached epidermal hair (arrow) surrounding roots, Z2286; × 10. (C) Cross section of specimen with leaf trace, note characteristic shape, Z2288; × 1. (D) Closeup of vascular strand of a leaf trace, Z2286; × 20. (E) Part of a leaf trace, note the possible pneumathode at upper right, Z2286; × 12. (F) Specimen showing leaf trace (Lt) departing the stele, medullary bundles (Mb), Z2289; × 1.4.*

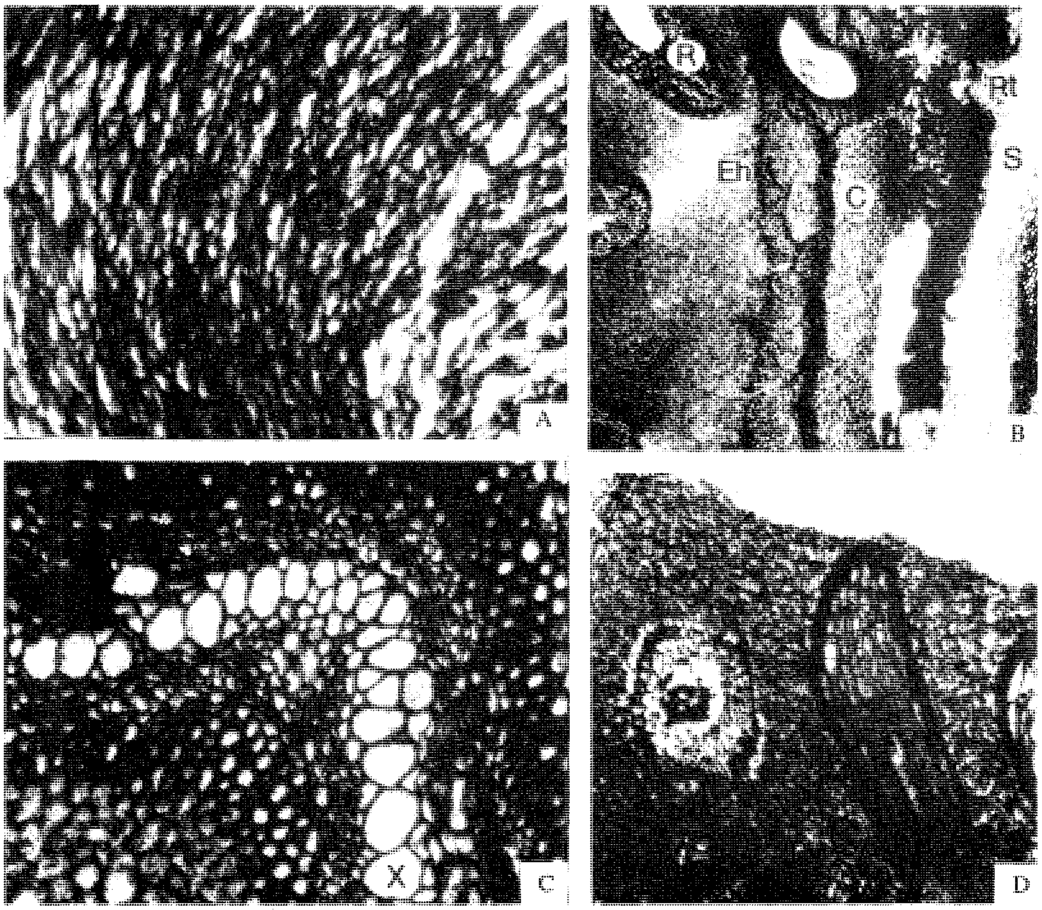

*PLATE 5*

Oguracaulis banksii *gen. et sp. nov. (A) Closeup of epidermal hair, Z2286; ×90. (B) Stelar strand (S), cortex (C) and epidermal hair (Eh), note departing root traces (Rt) and roots (R), Z2286; ×10. (C) Closeup of xylem of a leaf trace, Z2286; ×60. (D) Cross- and longitudinal sections of roots, Z2286; ×15.*

interrupted laterally by possible pneumathodes (pl. 4E; Williams 1925).

Petioles in transverse section vary in shape from circular to elliptical with lateral grooves (fig. 1F–H). They arise at a steep angle (10–20°) to the stem (pl. 4F) and vary in size from 10 mm in the cortex to 12 x 30 mm toward the outside of the specimen.

The vascular strand of the petiole is bisymmetrical, U-shaped with incurved ends. The U of the trace is adaxially open and has lateral constrictions on each side, resulting in a modified reverse omega-shape (pl. 4D,E).

A single layer of cells with attached uniseriate, multicellular hairs constitutes the petiolar epidermis. The hypodermis of this structure consists of a uniform layer of sclerenchyma. There is a gradual transition from hypodermis to the cortex. Cells of the latter tissue vary in size. The sheath surrounding the vascular strand appears to be two-layered with the outer layer composed of fibrous cells and the inner parenchymatous. An endodermis and a pericycle of several layers lie inside the sheath. The layer of protophloem is thin, discontinuous and not very distinctive. The outer metaphloem, composed of sieve cells and parenchyma, is one to several layers thick and has larger cells than the inner metaphloem which is generally difficult to distinguish. Large mucilage cells, 97–150 µm in diameter and containing dark brown substances, are present in the external phloem. Xylem strand is continuous and wavy with protoxylem occurring on the inner portion of the outer projection of the strand.

## COMPARISONS AND DISCUSSION

*Oguracaulis banksii* is characterised by having a radially symmetrical stem with dictyostelic main stelar ring, undivided leaf and petiolar vascular traces, an internal and external sclerenchymatous sheath, numerous irregular, anastomosing, medullary bundles, some of which form the adaxial arcs of the petiolar vascular strand, epidermal hairs and tangential cells in its phloem.

White (1986) preliminarily compared specimens of *O. banksii* with *Angiopteris*. *Oguracaulis*, however, differs from *Angiopteris* in having (1) a well-developed sclerenchyma sheath around the vascular bundles, (2) a less dissected dictyostele (Tansley 1907), (3) a continuous omega-shaped petiole trace composed of a wavy vascular bundle, and (4) V-shaped units of vascular bundles enclosed by a complete endodermis. These features are lacking in *Angiopteris*.

Cyatheaceae is the family with stems most similar in structure to this fossil tree fern. Generally, this family exhibits a typical arborescent habit. Its members are distributed in both the palaeo- and neotropics, particularly in moist, temperate mountain regions (Holttum 1963, Tyron 1970). The Cyatheaceae has been variously classified by different authors into one or two or more families (see discussion by Holttum 1963, Tyron 1970, Lucansky 1974a,b, Lucansky & White 1974, Nishida 1984). In the general classification of the Cyatheaceae as a single family and its subdivisions, we have followed Holttum (1963).

*Oguracaulis banksii* is most closely comparable to species of the Cibotioideae and Cyatheoideae of the Cyatheaceae. The cibotioids, including *C. tasmanense* Gould (1972) from this Tasmanian locality, differ from *O. banksii* in generally having a lateral discontinuity in their petiole vasculature and in lacking medullary bundles and stelar parenchyma (Williams 1925, Ogura 1930, Barrington 1983) that occur in the fossil form. Most living members of the squamate cyatheoids are anatomically similar to *O. banksii* but can be distinguished from it principally by their leaf traces being formed of a series of traces and their possessing dermal scales rather than hairs (Ogura 1927, 1938). *Metaxya* and *Lophosoria*, also of the Cyatheaceae (Lucansky 1974a, 1982), are similar to the fossil but differ from it mainly in their lack of medullary bundles.

The Thyrsopteridoideae, consisting of *Thyrsopteris* and *Culcita* (Holttum & Sen 1961) shares very few characters with *O. banksii*. They differ in the structure of their medullary bundles, the way these bundles contribute to petiole vascularisation (Bower 1913, Sen 1968) and the clear lateral discontinuity in their petiole vasculature. Both *Thyrsopteris* and *Culcita* lack the numerous medullary bundles that occur in *O. banksii*.

*Cyathocaulis* and *Cyathorachis*, from the Cretaceous of Japan, Korea and the Philippines, may be the only representatives of or, at least, closely related to the ancestors of the squamate cyatheoids (Ogura 1941, Nishida 1981, 1984, Nishida & Tanaka 1982). *Cyathocaulis* has hairs similar to *O. banksii*, but differs from the latter in having a number of medullary roots in its dictyostelic stem and leaf traces that consist of many individual traces.

*Dendropteridium cyatheoides* Bancroft (1932), *Alsophilocaulis calveloi* Menendez (1961) and *Cyathodendron texanum* Arnold (1945) of Tertiary age are similar to *Cyathea* and therefore unlike *O. banksii*.

*Lophosoriorhachis japonica* H. Nishida (1982) is a fossil rachis of uncertain affinity. Hair-like structures are present on the surface of *L. japonica* (Nishida 1984), and its vasculature is a continuous corrugated horseshoe-shaped structure with lateral folds and incurved margins similar to those in *O. banksii*. *Oguracaulis banksii* differs from *L. japonica* by having a much longer median pair in its petiolar vascular trace and in lacking large mucilage cells in its fundamental tissue.

Leaves and sori of *O. banksii* are unknown. Although dicksonioid in appearance, *Coniopteris websterii* Tidwell, Kim and Kimura from this locality cannot be assigned to any of the anatomically preserved taxa from this site.

*Oguracaulis* is important in considering the evolution of the scaly cyatheoids. *Oguracaulis*, the *Cyathocaulis* group of the Cretaceous and recent scaly cyatheoids appear to comprise a morphological sequence from primitive to advanced respectively. A Late Jurassic to Early Cretaceous age for *Oguracaulis* chronologically fits well into this sequence. The dermal hairs, stelar pattern and undivided leaf traces of *Oguracaulis*, however, are features similar to the primitive genera *Metaxya* and *Lophosoria* of the Cyatheoideae, as well as members of the Cibotioideae. Based upon this comparative anatomical data, *Oguracaulis banksii* appears to be a new, relatively primitive genus and species in the Cyatheaceae.

The presence of *Cibotium tasmanense* Gould in the same locality as *O. banksii* indicates cibotioid tree ferns also occurred at the same geologic time. *Oguracaulis banksii* lacks the long adaxial arcs of the leaf trace which are characteristic of *Cibotium*. Ferns with this characteristic are known as early as the Late Cretaceous (Nishida 1984). Since *C. tasmanense* was first described as Tertiary in age and having an internal structure too primitive to be assigned to *Cibotium*, Nishida (1984) doubted its affinity with *Cibotium*. The geologic age of this material has, nevertheless, been reconsidered and assigned to a Late Jurassic or Early Cretaceous age (White 1986, Tidwell *et al.* 1987), which is older than the oldest permineralised stem that definitely belongs to *Cibotium* (*Cibotium iwatense* Ogura, Coniacian-Santonian). *Cibotium tasmanense* is, therefore, a possible ancestral form of *Cibotium*. This, and the possible relationship of *Oguracaulis* with the squamate cyatheoids, suggest that the cyatheaceous tree ferns were diversified by the Late Jurassic or Early Cretaceous.

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