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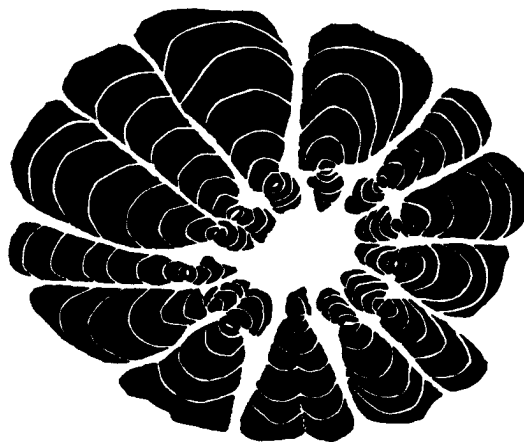
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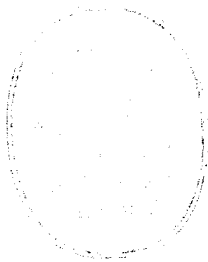
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**In memoriam Richard Kräusel**



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## Permineralized Conifer Axes from the Triassic of Antarctica

BRIGITTE MEYER-BERTHAUD & THOMAS N. TAYLOR\*

Columbus

With 1 Plate

### Introduction

Silicified wood occurs together with impression/compressions of leaves, stems and reproductive organs throughout the Permian and Mesozoic of Gondwana. Gymnospermous wood is abundant and has been studied during the late 1800's and in the beginning of the present century by prominent paleobotanists such as ZEILLER (1896), GOTHAN (1905), SEWARD (1914-19), KRÄUSEL (1919-49), WALTON (1925) and SAHNI (1933) (see references in MARGUERIER 1973). One of the principal xylotomists at this time was RICHARD KRÄUSEL who examined woods from South Africa, Brazil and Antarctica. His detailed studies provide an important starting point for subsequent investigations of permineralized stems. As early as 1928, KRÄUSEL recognized that these Late Paleozoic and Mesozoic woods represented a more diverse assemblage of plants than the genera *Dadoxylon* ENDLICHER and *Araucarioxylon* KRAUS suggested. Basing his hypothesis on the study of woods from the Karoo beds of South West Africa, he demonstrated that pith and primary xylem were crucial features as "...they exhibit far larger differences than the secondary wood..." (KRÄUSEL, MAITHY & MAHESHWARI 1961). In other words, one type of secondary xylem could correspond to different taxa based on the characters of the pith and the primary xylem. Another of KRÄUSEL's contributions was the recognition, in Mesozoic woods, of a type of pitting on the radial walls of the tracheids that he interpreted as mixed. In this type of pitting, the presence of both "araucarian" and "abietinean" features occur in the same wood. In modern representatives of the Araucariaceae, the pits are contiguous and flattened, polygonal when multiseriate. In all other living conifers, the pits are spaced and circular in outline; they are opposite when bi or tri-seriate. According to KRÄUSEL (1949), the Coniferales with a mixed type of radial pitting constituted a homogeneous group, which he termed the Protopinaceae. This group was characterized anatomically and stratigraphically, mostly from Jurassic and Cretaceous beds. This concept was challenged by GRAMBAST (1960) who demonstrated that such forms were not limited to the Mesozoic, but extended from the Late Paleozoic (in the southern hemisphere) to the present day (Podocarpaceae).

In this paper we will discuss KRÄUSEL's ideas using two types of gymnosperm axes found in a Triassic silicified peat in Antarctica. The flora at this site includes a variety of gymnosperm remains with woody axes representing a large percentage of the plant material (TAYLOR & TAYLOR 1989). The abundance and preservation of the fossil material at this locality provides an opportunity to characterize each taxon through a range of axes corresponding to roots, stems and different orders of branches.

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### Type A (Pl. 1 fig. 1-5)

Stems of this type range from 1 to 15 mm in diameter (fig. 1). Shoots bearing crowded small leaves are abundant in the peat (fig. 2). The pycnoxylic secondary xylem is well developed and contains uniseriate rays. The largest stems possess several growth rings with late wood made up of 1-2 cell layers (fig. 1). Ray cells are 20-25  $\mu\text{m}$  wide. Tracheids measure up to 50  $\mu\text{m}$  in diameter and possess a mixed type of pitting on the radial walls (figs. 3, 4). Pits, with a well developed torus, measure 7.5-10  $\mu\text{m}$  in diameter (fig. 4). In the cross field, the pits number from 1-4. They are large (9 to 7.5x17  $\mu\text{m}$ ) and simple, oval to rectangular and sometimes arranged alternately (fig. 4). In transverse section, the secondary phloem is composed of up to 15 rows of radially arranged cells. These elements are flattened and measure 20x35  $\mu\text{m}$  in average diameter. Fibers have not been observed.

The primary xylem appears endarch. Leaf traces are emitted as a single bundle and remain undivided through the secondary xylem. The pith is parenchymatous and contains cells that may have been secretory. It is characterized by the presence of large sclerotic nests dispersed throughout the tissue (fig. 5). Similar sclerotic nests are interspersed in the cortex. This tissue is limited, on the outside, by a periderm organized in a single superficial zone of variable thickness (fig. 5).

### Type B (Pl. 1 fig. 6-9)

Roots of type B range from 0.5 mm to more than 6 cm in diameter and aerial axes which comprise up to four orders of branching, from 5 mm to more than 20 cm in diameter. Leaves up to 10 mm long are awl-shaped and borne on the distal branches. They were apparently shed relatively early during development.

Secondary xylem in stems and roots is well developed and shows a variable number of narrow growth rings with little late wood (fig. 9). Rays are inconspicuous in transverse section due to the small size of the cells (20-25  $\mu\text{m}$  high, 10-14  $\mu\text{m}$  wide and up to 50  $\mu\text{m}$  long). Tracheids rarely exceed 50  $\mu\text{m}$  in diameter and show a mixed type of pitting on the radial walls (figs. 6, 8). Pits measure 8-14  $\mu\text{m}$  in diameter. Pits in the cross fields are large and few (1-2, up to 4), simple or slightly bordered, rectangular to oval, generally horizontal (fig. 7). Axial parenchyma occurs in some axes and is typically more abundant in roots and large stems. Secondary phloem is composed of alternating bands of sieve cells and parenchyma; fibers are present in stems with more than one ring of wood. The primary xylem in stems appears clearly endarch. Vertical strands of secretory cells are interspersed in the pith (fig. 9).

Cortical tissues are preserved in young stems and roots. In the roots, an endodermis with phi thickenings limits a two-zoned cortex with few intercellular spaces (MILLAY et al. 1987). The cortex in stems is parenchymatous, interspersed with secretory cells and canals. Periderm develops in stems with one or more growth rings, and involves a superficial first zone. Subsequent zones arise deeper in the cortex and the secondary phloem.

The primary vascular system of the stems consists of endarch sympodia, each primary strand giving rise to a single leaf trace which divides in the cortex. In a few specimens, leaf traces are arranged in a double helix (bijugate phyllotaxy). Leaves are short, with the distal part thin and flattened. Leaf bases are crescent-shaped and up to 2 mm wide. They possess canals interspersed in the parenchyma, and a vascular supply composed of at least 6 small bundles. Stomata are amphistomatic and sunken.

Branching is often profuse, along a helical pattern. Secondary branches arise from the primary axis at wide angles (close to 90°). Branches are widely separated in some areas of the plant and occur in pseudowhorls in other parts. Anatomically, branching may deeply affect the shape of the stele which, in some instances becomes temporarily triangular.

### Discussion

Axes of types A and B have a similar type of secondary xylem. In both, the wood is pycnoxylic with uniseriate rays; growth rings are characterized by little late wood; pitting on the radial walls of the tracheids is mixed and pits in the cross fields are few, large and simple. The secondary xylem in stems of the A type appear a little less compact as the ray

cells are larger; it is devoid of axial parenchyma and the climatic and/or systematic significance of the tori in the pits is presently unknown. The two types of axes, however, mostly differ in the anatomy of the pith and cortex (presence/absence of sclerotic nests), the structure of the secondary phloem (presence/absence of fibers), the anatomy of the periderm and its position (superficial/deep) in the bark. In addition, the abundance of leafy shoots of type A present in the peat may indicate that they were deciduous whereas axes of type B shed leaves.

Triassic woods from Gondwana localities are far less abundant than Permian ones. For this reason, we have found more similarities between some Permian genera and the axes of type A and B than with any of the Triassic taxa described to date. In a decorticated state, axes of type A could be assigned to *Kaokoxylo* KRAUSEL where scattered groups of sclerenchyma cells are present in the pith (KRAUSEL, MAITHY & MAHESHWARI 1961, PRASAD 1982). Like in type A stems, pits in cross field number from 1-4 in the species *K. sclerosum* from South Africa (MAHESHWARI 1972). Tori, however, are unknown in *Kaokoxylo*, as in any wood earlier than the Jurassic. Similarly, axes of type B might be most similar to *Megaporoxylo* KRAUSEL. This genus is characterized by a pith containing secretory cells and a secondary xylem with few (1-2), large, and simple pits in the cross fields (MAHESHWARI 1972, PRASAD 1982). Such comparisons provide little information about the affinities of the Triassic axes, however, they do suggest that, although both possess a similar type of secondary xylem, they probably belonged to different genera.

Both types clearly differ from the few silicified Gondwana stems of Triassic age included within the Cycadales. *Antarcticycas schopfii* from Antarctica (SMOOT et al. 1985) and *Michellioa waltonii* from Argentina (ARCHANGELSKY & BRETT 1963) are characterized by a small amount of manoxylic wood and a wide pith; pits on the radial walls of the tracheids are araucarian; leaf traces are girdling and their pattern of emission is complex. Finally, cycad leaves which are abundant as compressions are usually much larger than those observed on either types A or B.

Both of the Antarctic axes share features with the ginkgophytes which also have pycnoxylic wood and a mixed type of radial pitting; however, the Triassic stems possess leaves that are much smaller. In addition, some characters of the secondary xylem in *Ginkgo biloba* were already present in Mesozoic woods attributed to ginkgophytes (e.g. *Ginkgoxylon*; PRASAD & LEE 1984). These ginkgophyte woods possess very different characters than those of the Triassic Antarctic stems described in this paper. These include intermixed wide and narrow tracheids, inflated ray cells and the occurrence of small oculipores in the cross fields.

Based on the vegetative parts, neither of the Triassic axes resemble any of the few permineralized pteridosperm currently known from the Mesozoic of Gondwana (*Glossopteris/Vertebraria*, *Rhexoxylon*). PANT & SINGH (1974) described some small *Glossopteris* axes with pycnoxylic wood, mixed radial pitting and few large pits in the cross fields. However, the *Glossopteris* leaves associated with these axes are much larger than those borne on the Antarctic stems, and *Vertebraria* roots are unknown in Triassic peat. In *Rhexoxylon*, the vascular tissues are characteristically organized in separate bundles (ARCHANGELSKY & BRETT 1961). A similar dissected organisation of the xylem occurs in the stems of *Pentoxylon* (Pentoxylales) which, otherwise, possess a pycnoxylic wood with a mixed type of radial pitting and one large pit in the cross fields (BOSE, PAL & HARRIS 1985).

The characters shared by the Triassic stems and the cordaites and conifers are numerous and include the primary vascular organization, similar anatomy of the secondary xylem and leaves of small size. The natural affinities of the plants that produced these stems currently remain unknown since reproductive organs to date have not been observed. However, based solely on anatomy, it is our belief that both axes belonged to the Coniferales. This hypothesis indicates that the gymnosperms with dense wood, mixed type of radial pitting and large simple pits in the cross fields were widespread in the Mesozoic and belonged to different orders (e.g. Glossopteridales, Pentoxylales, Coniferales).

#### Acknowledgement

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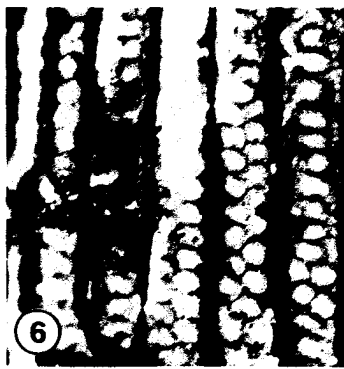
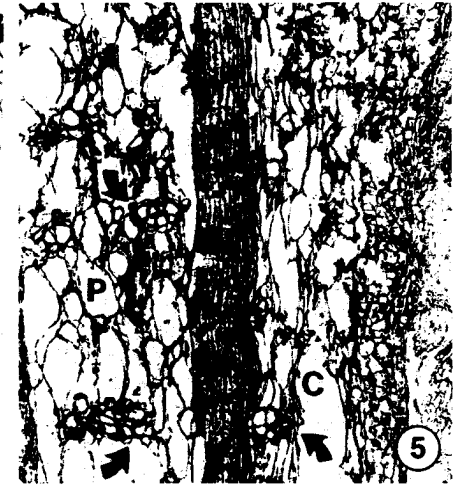
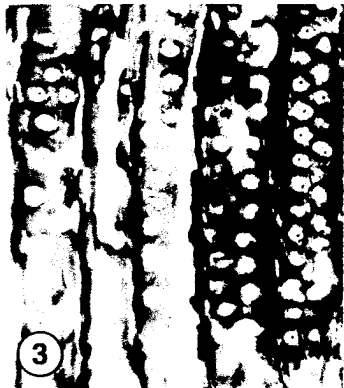
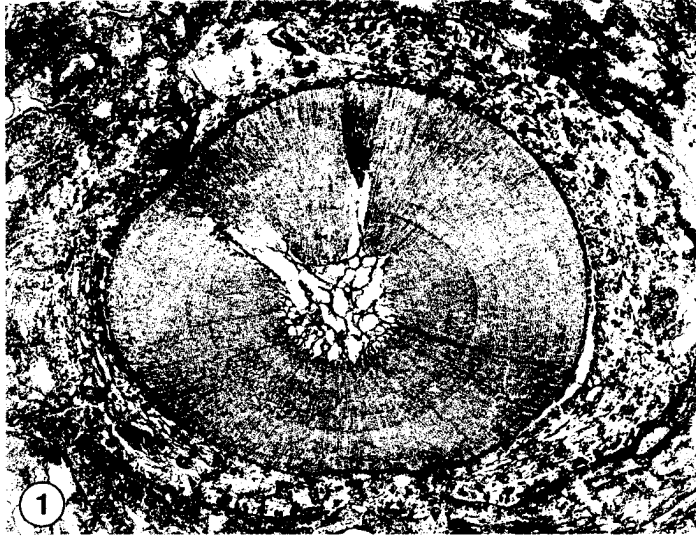
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**Plate 1****Fig. 1-5. Type A.**

1. Transverse section of a stem; 10,891 F2Top#5. -- x6.5.
2. Small leafy shoot in longitudinal section; CB 545 A(B2-a). -- x20.
3. Secondary xylem tracheids with a mixed type of pitting in radial section; 10,891 E5S#2. -- x350.
4. Radial section of secondary xylem tracheids. Cross field pits at arrows. Note the tori in the bordered pits; 10,891 E5S#2. -- x425.
5. Stem in radial section. Sclerotic nests at arrows, in the pith (P) and cortex (C). Note the compact periderm on the outer edge of the cortex; 10,891 E5S#2. -- x25.

**Fig. 6-9. Type B.**

6. Secondary xylem tracheids with "araucarian" pits on the radial walls; 10,145 GS#8. -- x256.
7. Radial section through secondary xylem showing cross field pitting; 10,246 CS#26. -- x200.
8. Spaced ordered pits on the radial walls of some secondary xylem tracheids.
9. Transverse section of a stem showing black secretory cells in the pith; 10,145 GS#2. -- x320.



section;  
s. Note  
tex (C).  
S#2. --

10,145

10,246

ds.  
10,145