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General palaeontology, systematics and evolution (Palaeobotany)

# Gymnosperm trees from the Permian of Antarctica: An anatomically preserved trunk of *Kaokoxylon* sp.

## *Arbres gymnospermiens du Permien d'Antarctique : un tronc anatomiquement préservé de Kaokoxylon sp.*

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A B S T R A C T

Anatomically preserved gymnosperm axes are relatively abundant in Permian localities of Antarctica, but their anatomy has rarely been studied in detail, which limits comparison with other Gondwanan morphotaxa. Here we describe a silicified trunk collected from the Upper Permian Buckley Formation at Coalsack Bluff, in the central Transantarctic Mountains. The trunk has a small heterogeneous pith approximately 4 mm in diameter containing conspicuous sclerotic nests, endarch primary xylem maturation, paired leaf traces, and secondary xylem of the *Araucarioxylon* type. Comparison with contemporaneous gymnosperm axes from Antarctica indicates that the Coalsack Bluff trunk represents a new Permian morphotaxon for the region. The anatomical characters of the pith and secondary xylem suggest an affinity with the genus *Kaokoxylon* Kräusel, previously reported from Permian and Triassic localities of Southern Africa, South America, India, and Australia.



R É S U M É

Les axes de gymnospermes anatomiquement préservés sont relativement abondants dans les localités permiennes d'Antarctique, mais leur anatomie a rarement été étudiée en détail, ce qui limite la possibilité de les comparer avec d'autres morphotaxa du Gondwana. Nous décrivons ici un tronc silicifié collecté dans la Upper Buckley Formation à Coalsack Bluff, dans la région centrale des Monts transantarctiques. Ce tronc a une petite moelle hétérogène de 4 mm de diamètre qui contient des nids scléreux, une maturation endarche du xylème primaire, des traces foliaires doubles et un xylème secondaire de type *Araucarioxylon*. La comparaison avec les axes gymnospermiens contemporains d'Antarctique indique que le tronc de Coalsack Bluff représente un nouveau morphogenre Permien pour cette région. Les caractères anatomiques de la moelle et du xylème secondaire suggèrent des affinités avec le genre *Kaokoxylon* Kräusel, déjà documenté dans des localités permiennes et triasiques du Sud de l'Afrique, d'Amérique du Sud, d'Inde, et d'Australie.



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## 1. Introduction

The affinities of isolated fossil gymnosperm stems are usually hard to establish, especially in the case of decorticated specimens. However, anatomical characters of the primary and secondary vascular system (e.g., cross-field pitting, primary xylem maturation, mode of production of leaf traces) can have taxonomic value and are often included in cladistic analyses (e.g., Hilton and Bateman, 2006; Rothwell and Serbet, 1994). It is thus important to document the diversity of these stems in order to be able to circumscribe the anatomical variations occurring within a group of plants when more information becomes available.

Permineralised wood and isolated axes have been documented from numerous Permian localities of Antarctica. These axes, which range from small stems to large trunks, have provided valuable information on climate and forest growth at high latitude during the Permian (e.g., Taylor and Ryberg, 2007; Taylor et al., 1992). Axes with typical lacunae in the secondary xylem are assigned to *Vertebraria* Royle (Decombeix et al., 2009), the morphogenus representing the roots of the glossopterid seed ferns, which dominated the Antarctic vegetation during the Permian (e.g., Decombeix et al., 2009; Gould, 1975). The detailed anatomy of other axes, however, has been little studied. They are often assigned by default to the morphogenus *Araucarioxylon* Kräusel and considered to represent the stems and trunks of some glossopterid. There is evidence, however, that more than one type of gymnosperm axis was present in Antarctica in the Late Paleozoic. Maheshwari (1972) in particular described six distinct morphogenera of stems from Permian localities in Victoria Land, the Queen Maud Mountains, and the Horlick Mountains (*Araucarioxylon*, *Dadoxylon*, *Protophyllocladoxylon*, *Damudoxylon*, *Megaporoxylon*, and *Polysolenoxylon*). These morphogenera are distinguished not only based on their secondary xylem anatomy but also on their primary xylem maturation patterns and on characters of the pith such as the presence and arrangement of secretory canals. This diversity might represent variations of stem anatomy within the glossopterids, but probably also reflects the presence in Antarctica of other gymnosperms, as indicated for example by *Noeggerathiopsis/Cordaites, Gangamopteris*, and *Buriadia* leaves (e.g., Cúneo et al., 1993; McLoughlin and Drinnan, 1996; Serbet et al., 2010; Taylor et al., 1989).

To date, the only type of stem from the Permian of Antarctica whose affinities have been clearly established is *Glossopteris skaarensis* (Pigg and Taylor, 1993), based on young stems bearing *Glossopteris* foliage from permineralized peat of Skaar Ridge, in the central Transantarctic Mountains. The secondary xylem of *G. skaarensis* was compared to that of *Araucarioxylon*; however, the small amount of wood does not provide for a detailed observation of pitting variation, and ontogenetically young axes can have a wood anatomy different from that of mature axes (Falcon-Lang, 2005 and references therein). Our more recent studies of large *Vertebraria* roots (Decombeix et al., 2009) and of trunks producing branches comparable to *G. skaarensis* from Skaar Ridge (Decombeix et al., 2010a) showed that in these specimens, the radial pitting of the tracheids differed from that of typical *Araucarioxylon* and was more comparable to *Australoxylon* Marguerier, a wood morphogenus reported from throughout Gondwana (Marguerier, 1973). This wood type is also often associated with glossopterid remains.

In this contribution, we describe a Permian gymnosperm trunk from Coalsack Bluff in the central Transantarctic Mountains, which represents a new morphotaxon. The trunk is compared to Permian and Triassic gymnosperm axes from Antarctica and from other localities in Gondwana. It shows the most similarities with *Kaokoxylon* Kräusel, a stem morphogenus previously documented from Permian–Triassic localities of Africa, South America, India, and Australia.

## 2. Material and methods

The trunk was collected during the 1969–1970 expedition at Coalsack Bluff in the central Transantarctic Mountains, Antarctica (Fig. 1, 84° 14′ 00.0″ S, 162° 25′ 00.0″ E). This locality is famous as the first site on the continent where the Triassic therapsid *Lystrosaurus* was found, which provided support for the contiguity of Antarctica, Africa, and India at that time (Elliot et al., 1970). At Coalsack Bluff, the sandstones of the Triassic Fremouw Formation overlay gray shales and coals that correspond to the upper part of the Buckley Formation, which is Late Permian in age and was deposited within a foreland basin (Collinson and Elliot, 1984; Collinson et al., 1994; Farabee et al., 1991). The fossil trunk described in this paper was collected in the Permian part of the section, 15 m below a shaly coal, according to J.M. Schopf's notes about the specimen.

The trunk is silicified (permineralized) and was studied using the acetate peel technique (Galtier and Phillips, 1999) after etching transverse, tangential, and radial surfaces for about 2 min in 49% hydrofluoric acid. Eighteen representative portions of peels were mounted on slides for observation of anatomical details under the microscope. Images were taken using a Leica (Leica Microsystems, Wetzlar, Germany) DC500 digital camera attachment on a Leica MZ16 stereomicroscope and a Leica DC500 digital camera attachment on a Leica DM5000 B compound microscope. Images were processed using Adobe Photoshop (Adobe Systems). The trunk, peels, and slides are deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Institute, University of Kansas, under specimen number 13824 and slide numbers 24,150–24,168.

### 2.1. Remark

While we recognize that the taxonomy of Paleozoic woods and isolated stems is complex and that some morphotaxa are now considered to be invalid (such as *Araucarioxylon*, see Philippe, 1993, 2011), it is beyond the scope of this article to discuss the validity of previously described taxa. In the comparison section of the paper, we therefore use the generic and specific names as proposed by the original authors.

## 3. Systematic paleontology

**Class**: SPERMATOPSIDA Serbet and Rothwell 1995

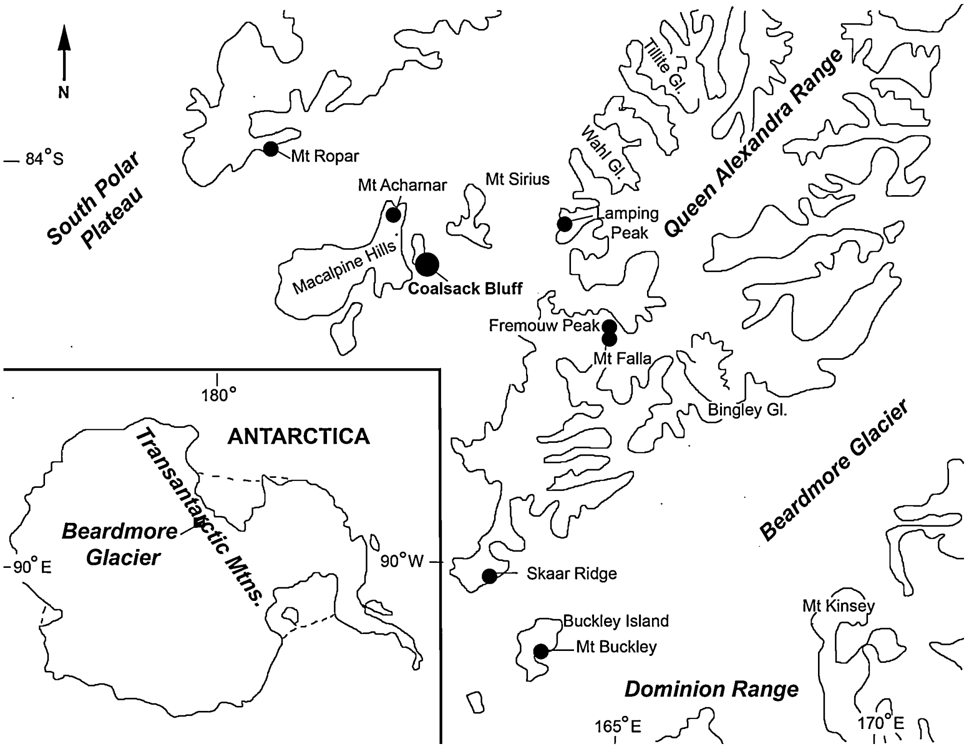


**Fig. 1.** Location of the Beardmore Glacier within the Transantarctic Mountains and detail of the region showing the location of Coalsack Bluff and other Permian and Triassic plant localities (modified from Collinson and Elliot, 1984).
**Fig. 1.** Position du Beardmore Glacier dans les Monts transantarctiques et détail de la région montrant la position de Coalsack Bluff et d'autres localités à plantes du Permien et Trias (modifié d'après Collinson et Elliot, 1984).

**Genus**: ***Kaokoxylon*** Kräusel, 1956
**Species**: *Kaokoxylon* sp.

### *3.1. Description*

The specimen is 4 cm in length and represents half of a decorticated trunk with about 8 cm of preserved radius (Fig. 2). The central part (i.e., pith and primary xylem) is present in the basal-most part of the specimen. A well-preserved branch about $13 \times 1$ mm in diameter is included in the outer part of the wood cylinder.

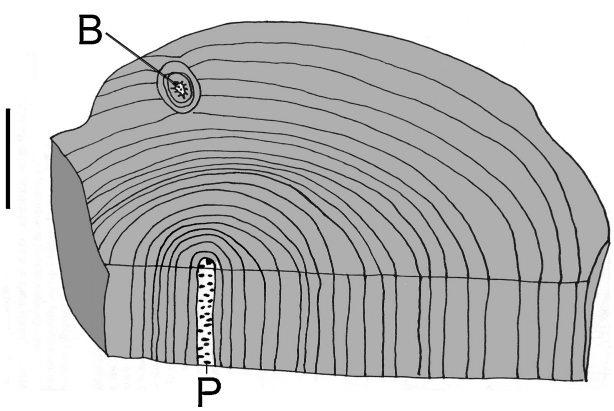


**Fig. 2.** General features of the silicified trunk. P: pith of the trunk; B: branch. Scale bar = 2 cm.
**Fig. 2.** Caractéristiques générales du tronc silicifié. P : moelle du tronc ; B : branche. Échelle = 2 cm.

*Pith*. The pith of the trunk is circular and 4 mm in diameter in the trunk (Fig. 2; Fig. 3

A, B), slightly oval and $3 \times 5$ mm in the branch. It is heterogeneous and contains parenchyma and clusters of sclereids forming sclerotic nests (Fig. 3A–C). Parenchyma cells are polygonal in shape both in transverse and longitudinal section, and have an average diameter of 53 μm. In the region of the clusters of sclerotic cells, parenchyma cells are often more rectangular in shape and sometimes elongated, up to 150 μm in diameter (Fig. 3C). Sclerotic nests are 90 to 400 μm in diameter in transverse section and up to 900 μm in height (Fig. 3 A, B). Individual sclereids are polygonal and generally similar in shape and size to the parenchyma cells, except for their thickened walls (Fig. 3C, D). There is evidence of a gradient in cell wall thickness among the pith cells, probably indicating the ongoing differentiation of sclereids from the parenchyma. The periphery of the pith also contains lacunae of various dimensions that seem to be associated with primary xylem strands and departing leaf traces (Fig. 3A–C, E). Some of the largest lacunae, however, contain coprolites (Fig. 3B, C, arrows) and the spaces may have been caused by arthropods.

*Primary xylem and traces to lateral organs*. The primary xylem is difficult to distinguish in cross section. Small groups of primary xylem tracheids are, however, visible at the pith-secondary xylem boundary (Fig. 3E). In longitudinal section, the anatomy of the strands appears more

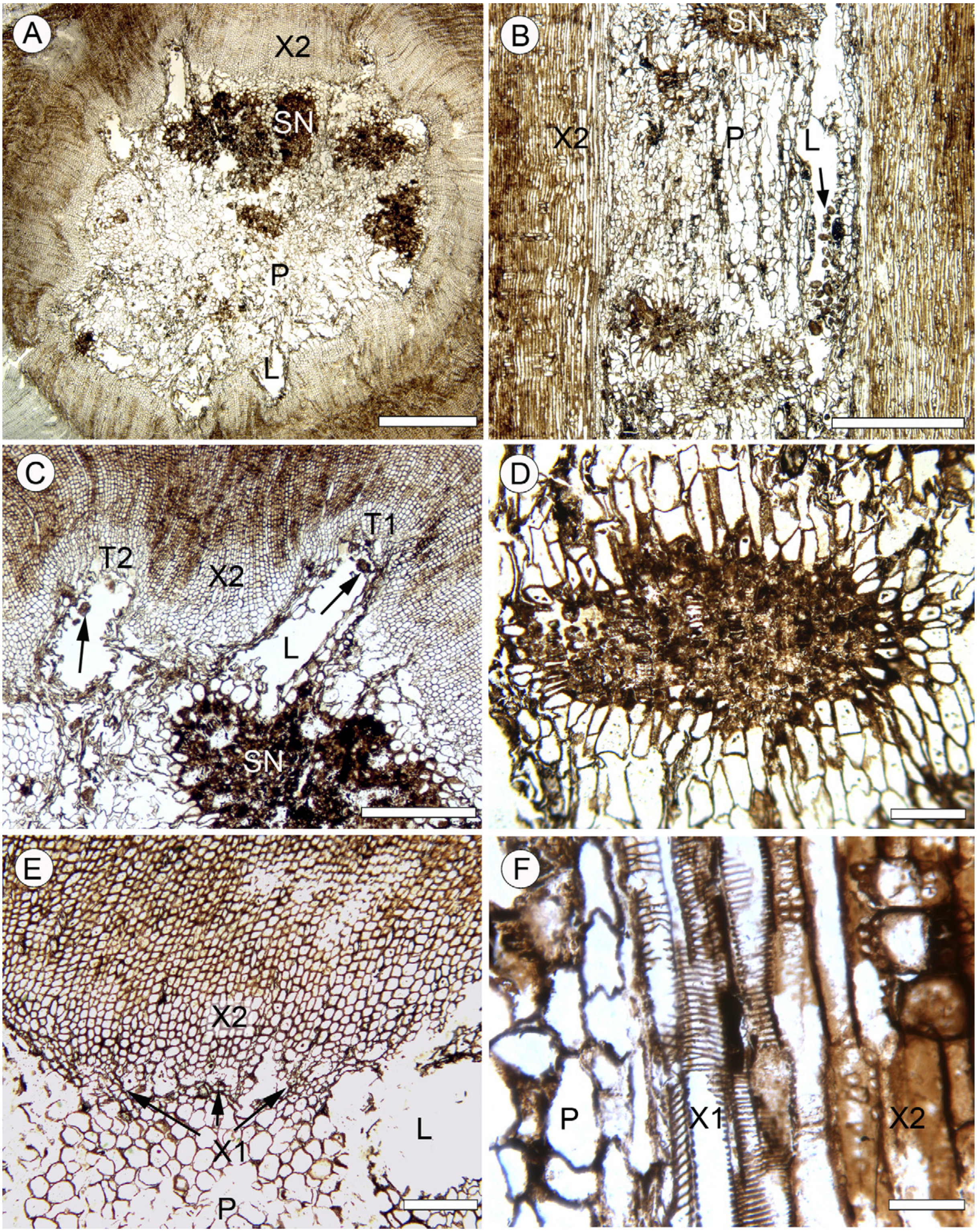


**Fig. 3.** *Kaokoxylon* sp. trunk from the Permian of Antarctica: general aspect and pith anatomy. P: parenchyma, SN: sclerotic nests, L: lacunae, X1: primary xylem, X2: secondary xylem. A. Central part of the trunk in transverse section showing the pith composed of parenchyma, conspicuous sclerotic nests and lacunae, as well as the inner part of the secondary xylem. Slide 24,150 (peel 13824 A B-2a). Scale bar = 1 mm. B. Central part of the trunk in longitudinal section showing the same elements as in A. Note coprolites in the lacuna on the right side of the pith (below L). Slide 24,159 (peel 13824 B S1-5a). Scale bar = 1 mm. C. Detail of the pith in transverse section showing a pair of departing leaf traces (T1 and T2) and a sclerotic nest. Slide 24,150 (peel 13824 A B-2a). Scale bar = 250 μm. D. Sclerotic nest in longitudinal section showing elongated, radiating parenchyma cells. Slide 24,159 (peel 13824 B S1-5a). Scale bar = 200 μm.

conspicuous and maturation is endarch (Fig. 3F); the walls of protoxylem and metaxylem tracheids contain helical to reticulate thickenings (Fig. 3F). Two different types of traces to lateral organs are present, leaf traces and a single branch trace. Leaf traces depart in pairs at the margin of the pith (Fig. 3C), with one trace slightly more advanced developmentally than the other (Fig. 3A, C). These vascular traces are truncated relatively close to the margin of the pith, indicating that the leaves were short lived. The branch exhibits anatomy comparable to that of the trunk (Fig. 4 A) although sclerotic nests in the pith are less prominent. The branch trace extends out from the sympodia at an angle of about 45°.

*Secondary xylem*. The secondary xylem of the trunk and branch is composed exclusively of tracheids and small parenchymatous rays. About 20 growth rings are preserved in the trunk (Fig. 4B). These are accompanied by a few false rings, each characterized by three to four rows of tracheids with reduced radial diameters. Although some parts of the secondary xylem have been distorted, it is possible to estimate that the width of the growth rings ranges from about 1 mm towards the center of the axis to about 5 mm in the outer part. This is comparable to other woods described from the Permian of Antarctica (e.g., Taylor and Ryberg, 2007 and references therein). Tracheids are rectangular to polygonal in cross section, and their radial diameter varies between 5 μm (in the latewood) and 55 μm (earlywood). Rays are uniseriate, rarely partly biseriate (Fig. 4C). They are one to ten cells high, occasionally up to 15 cells high. The radial walls of the tracheids contain one to three rows of bordered pits about 10 to 12 μm in diameter, each with a circular aperture (Fig. 4D–F). In tracheids with uniseriate pitting, the pits are circular in shape and do not occupy the whole width of the wall (Fig. 4D). Tracheids with bi- or triseriate pitting have the pits arranged alternately (Fig. 4D–F); pits are circular but can also appear hexagonal when crowded (Fig. 4E). Cross-field pitting consists of one to four oval, simple pits about $9 \times 6$ μm in diameter (Fig. 4G, H). The most common arrangement is four pits organized in two rows.

## 4. Affinities

### 4.1. Comparison with other Permian stems from Antarctica

A comparison with previously described Permian axes from Antarctica shows that the trunk from Coalsack Bluff probably represents a new morphotaxon for this region. A summary of the comparison for some anatomical characters of the primary and secondary vascular system is presented in Table 1. The new trunk differs from stems of *G. skaarensis* (Pigg and Taylor, 1993), which have a smaller pith (1 mm in diameter) composed entirely of parenchyma cells. Some of the stems from the Skaar Ridge permineralized peat observed by Pigg and Taylor have cells with opaque contents in their pith but none ($n > 150$) have sclereids, and this is also true for branches produced by two putative glossopterid trunks from the same locality (Decombeix et al., 2010a). *G. skaarensis* also has smaller rays than the new trunk (two cells high on average, $n = 176$), although this might be a developmental difference.

Two other genera reported from Antarctica by Maheshwari (1972), *Polysolenoxylon* and *Damudoxylon*, differ from the new trunk by their lack of sclereids in the pith. *Polysolenoxylon* has a pith with secretory cells and canals. *Damudoxylon* species have either a homogeneous parenchymatous pith or, as is the case in the Antarctic specimen *Damudoxylon* sp., a pith with interspersed secretory cells. The new trunk is also easily distinguished from other Antarctic taxa by anatomical characters of the secondary xylem. In a piece of wood assigned to *Dadoxylon weaverense* from Mt Weaver, up to 75% of the rays are biseriate (Maheshwari, 1972), a condition found in a small number of Permian gymnosperm axes and clearly different from the new trunk. In *Megaporoxylon* and *Protophyllocladoxylon*, cross-field pitting consists of a single, rarely two, large pits, versus several small pits in the Coalsack Bluff specimen. In addition, *Megaporoxylon* is characterized by a large pith up to 3 cm in diameter that can contain secretory cells but has no sclereids.

Maheshwari (1972) also described three species of *Araucarioxylon* based on wood fragments with no pith preserved. In one of them, *A. bengalense*, the radial pitting of the tracheids is opposite to subopposite with a tendency for the pits to form groups, as in the genus *Australoxylon* (Marguerier, 1973). This is different from the arrangement in the Coalsack trunk and more similar to what is observed in some *Vertebraria* roots and in two putative glossopterid trunks from Skaar Ridge (Decombeix et al., 2009, 2010a). Whether these specimens and *A. bengalense* represent the same taxon is, however, difficult to assess given the lack of information on primary structures in the *A. bengalense* specimen. The two other species of *Araucarioxylon* described by Maheshwari, *Araucarioxylon* sp. cf. *ningahense* and *A. allanii,* have secondary xylem anatomy

**Fig. 3.** E. Transverse section of the margin of the pith in the branch showing the primary xylem. Note the lacuna on the right. Slide 24,155 (peel 13824 C B-4a). Scale bar = 200 μm. F. Longitudinal section of the edge of the pith showing an endarch primary xylem strand with helical to reticulate secondary wall thickenings on the tracheids and the inner secondary xylem tracheids) with bordered pits. Slide 24,159 (peel 13824 B S1-5a). Scale bar = 50 μm.

**Fig. 3.** Tronc de *Kaokoxylon* sp. du Permien d'Antarctique : aspect général et anatomie de la moelle. P : parenchyme, SN : nids scléreux, L : lacunes, X1 : xylème primaire, X2 : xylème secondaire. A. Partie centrale du tronc en coupe transversale montrant la moelle composée de parenchyme, nids scléreux et lacunes, ainsi que la partie interne du xylème secondaire. Lame 24,150 (peel 13824 A B-2a). Échelle = 1 mm. B. Partie centrale du tronc en coupe longitudinale montrant les mêmes éléments qu'en A. Noter les coprolites dans la lacune du côté droit de la moelle (sous L). Lame 24,159 (peel 13824 B S1-5a). Échelle = 1 mm. C. Détail de la moelle en coupe transversale montrant le départ d'une paire de traces foliaires (T1 et T2) et un nid scléreux. Lame 24,150 (peel 13824 A B-2a). Échelle = 250 μm. D. Nid scléreux en coupe longitudinale montrant des cellules de parenchyme allongées et irradiant autour du nid. Lame 24,159 (peel 13824 B S1-5a). Échelle = 200 μm. E. Coupe transversale du bord de la moelle de la branche montrant le xylème primaire. Noter la lacune sur la droite. Lame 24,155 (peel 13824 C B-4a). Échelle = 200 μm. F. Coupe longitudinale du bord de la moelle montrant un faisceau de xylème primaire endarche avec des épaississements spiralés à réticulés de la paroi secondaire des trachéides et les trachéides les plus internes du xylème secondaire avec des ponctuations aréolées. Lame 24,159 (peel 13824 B S1-5a). Échelle = 50 μm.

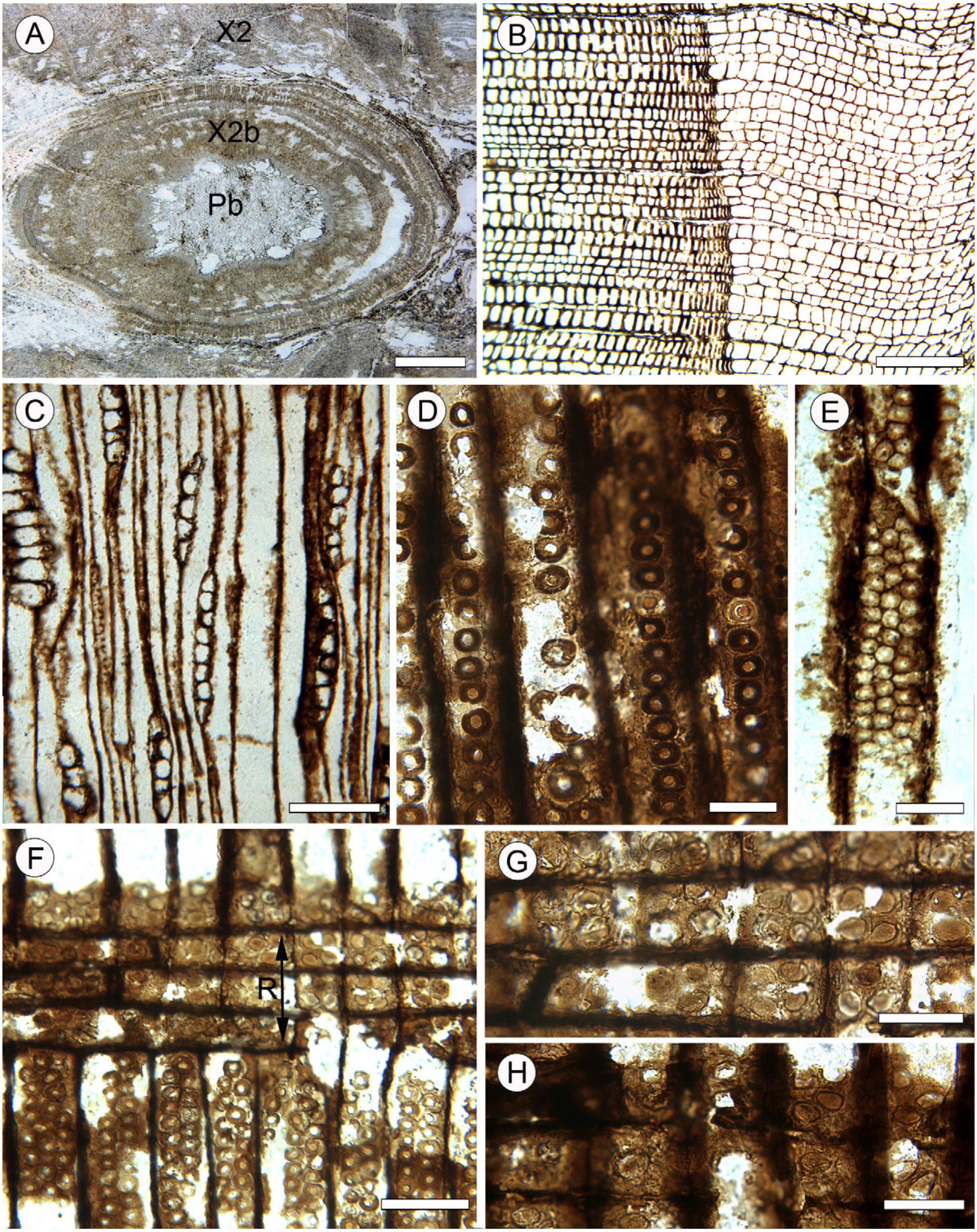


**Fig. 4.** *Kaokoxylon* sp. trunk from the Permian of Antarctica: branch and secondary xylem anatomy of the trunk. A. Slightly oblique transverse section of the branch as it departs the trunk. X2: secondary xylem of the trunk; X2b: secondary xylem of the branch; Pb: pith of the branch. Slide 24,155 (peel 13824 C B-4a). Scale bar = 2 mm. B. Growth ring boundary in the secondary xylem of the trunk. Slide 24,155 (peel 13824 C B-4a). Scale bar = 200 μm. C. Tangential section of the wood of the trunk with uniseriate to partly biseriate and low rays (usually less than ten cells high). Slide 24,157 (peel 13824 B S1-1). Scale bar = 100 μm. D. Radial section of secondary xylem tracheids in the trunk with uniseriate circular pits. Slide 24,159 (peel 13824 B S1-5b). Scale bar = 25 μm. E. Radial section of a large tracheid with three rows of crowded, hexagonal pits. Slide 24,159 (peel 13824 B S1-5b). Scale bar = 25 μm. F. Radial section of the

**Table 1**
Comparison of the new trunk and contemporaneous axes from Antarctica.
**Tableau 1**
Comparaison du nouveau tronc avec les axes contemporains d'Antarctique.

| | Pith size (cm) | Pith composition | X1 maturation | Ray width | Radial pitting | Cross-field pitting |
|---|---|---|---|---|---|---|
| New trunk | 0.4 | Sclerotic nests | Endarch | Mostly uniseriate | 1–3 alter | 1 to 4 |
| *Glossopteris skaarensis* | **0.1** | **Only parenchyma** | ? Endarch | Mostly uniseriate | 1–2 alter | ? 2 to 4 |
| *Polysolenoxylon lafoniense* | 0.4 | **Secretory canals** | Endarch | Mostly uniseriate | 1–2 alter | 2 to 4 |
| *Polysolenoxylon kraeuselii* | **1.5** | **Secretory canals** | Endarch | Mostly uniseriate | 1–5 alter | 1 to 8 |
| *Damudoxylon sp. cf. waltonii* | 0.5 | **Some dark cells** | Endarch | Mostly uniseriate | (1) to 3 alter | 2 to 11 |
| *Megaporoxylon antarcticum* | ? | ? Only parenchyma | Endarch | Mostly uniseriate | 1–3 alter | **1 large pit** |
| *Megaporoxylon canalosum* | **1.8** | **Elongated secretory cells** | Endarch | Mostly uniseriate | 1–3 alter | **1 large pit** |
| *Protophyllocladoxylon dolianitii* | – | – | – | Mostly uniseriate | 1–3 alter | **1 large pit** |
| *Dadoxylon weaverense* | **> 3?** | – | – | **Often biseriate** | 1–2 up 4 alternate | 1 to 7 |
| *Araucarioxylon bengalense* | – | – | – | Mostly uniseriate | 1–3 **opposite to subopposite, groups** | 1 to 5 |
| *Araucarioxylon sp. cf. ningahense* | – | – | – | Mostly uniseriate | 1–4 alternate | 2 to 6 (up to 10) |
| *Araucarioxylon allanii* | – | – | – | Mostly uniseriate | 1–3 altern to subop | 2 to 12 |

Anatomical differences are indicated in bold.

comparable to that of the new trunk but again it is difficult to assess their affinities with certainty in the absence of preserved primary tissues.

### *4.2. Comparison with Permian stems from other Gondwanan localities*

A significant number of Permian stem genera have been described from other regions of Gondwana, in particular India and South America. Among those that have secondary xylem anatomy generally comparable to that of the new trunk, several can be distinguished by a lack of sclereid clusters in the pith, including *Atlanticoxylon* (Mussa, 1986), *Barakaroxylon* (Surange and Maithy, 1961), *Brasilestiloxylon* (Mussa, 1978), *Paulistoxylon* (Mussa, 1986), *Petalopitys* (Mussa, 1986), *Solenobrasilioxylon* (Mussa, 1978), and *Solenoxylon* (Kräusel, 1956). *Piracicaboxylon* from the Permian of Uruguay (Mussa, 1986) has groups of sclerified cells in the pith but they are fibers and not isodiametric sclereids as in the Antarctic trunk.

Morphogenera that have both secondary xylem and pith anatomy most similar to the trunk from Coalsack Bluff are *Austroscleromedulloxylon* Mussa et al., 1980 and *Kaokoxylon* Kräusel (1956). These two taxa show a number of similarities and might represent the same morphogenus. The best-known species of *Austroscleromedulloxylon* is the type species, *A. geraldini*, from the Permian of Brazil (Mussa, 1986) and Uruguay (Crisafulli, 1998). The Brazilian specimen is characterized by a pith up to 4 mm in diameter, while in the Uruguayan specimen it is $1.5 \times 0.8$ cm. Both have lacunae on the periphery of the pith and sclerotic nests. The general wood anatomy of the Brazilian specimen also agrees with that of the Coalsack Bluff trunk, with tracheid pitting consisting of two to three rows of araucarioid pits, uniseriate rays usually one to five cells high, and several small pits in the cross field. A difference, however,

**Fig. 4.** wood of the trunk showing tracheids with biseriate circular pits and a ray (R) with cross-field pits. Slide 24,159(peel 13824 B S1-5b). Scale bar = 50 μm. G. Detail of a ray in radial section showing two to four simple, oval-to-circular pits. Slide 24,159 (peel 13824 B S1-5b). Scale bar = 25 μm. H. Detail of another ray in radial section showing two to four simple, oval-to-circular pits. Slide 24,159 (peel 13824 B S1-5b). Scale bar = 25 μm.

**Fig. 4.** Tronc de *Kaokoxylon* sp. du Permien d'Antarctique : branche et anatomie du xylème secondaire du tronc. A. Coupe transversale légèrement oblique de la branche quittant le tronc. X2 : xylème secondaire du tronc ; X2b : xylème secondaire de la branche ; Pb : moelle de la branche. Lame 24,155 (peel 13824 C B-4a). Échelle = 2 mm. B. Limite d'un cerne de croissance dans le xylème secondaire du tronc. Lame 24,155 (peel 13824 C B-4a). Échelle = 200 μm. C. Coupe tangentielle du bois du tronc avec des rayons unisériés à partiellement bisériés et bas (généralement moins de dix cellules de haut). Lame 24,157 (peel 13824 B S1-1). Échelle = 100 μm. D. Coupe radiale des trachéides de xylème secondaire du tronc, avec des ponctuations circulaires unisériées. Lame 24,159 (peel 13824 B S1-5b). Échelle = 25 μm. E. Coupe radiale d'une trachéide large, avec trois rangs de ponctuations hexagonales serrées. Lame 24,159 (peel 13824 B S1-5b). Échelle = 25 μm. F. Coupe radiale du bois du tronc montrant des trachéides, avec des ponctuations circulaires bisériées, et un rayon (R), avec des ponctuations de champ. Lame 24,159 (peel 13824 B S1-5b). Échelle = 50 μm. G. Détail d'un rayon en coupe radiale montrant 2-4 ponctuations simples ovales à circulaires. Lame 24,159 (peel 13824 B S1-5b). Échelle = 25 μm. H. Détail d'un autre rayon en coupe radiale montrant deux à quatre ponctuations simples ovales à circulaires. Lame 24,159 (peel 13824 B S1-5b). Échelle = 25 μm.

is that primary xylem maturation is mesarch in *A. geraldini* versus endarch in the Coalsack Bluff specimen. The Brazilian specimen assigned to *A. geraldini* differs from both the Uruguayan example of this species and the Coalsack Bluff trunk by having secondary xylem with rays that are often biseriate (Crisafulli, 1998).

*Kaokoxylon* Kräusel is a widespread taxon known from Permian and Triassic localities of South Africa, Australia, India, Brazil, and Argentina. The genus was established to include Gondwanan taxa with *Araucarioxylon*-type wood that have a heterogeneous pith with groups of sclerenchymatous cells. Seven species have been described and all of them have a small pith (< 1 cm in diameter, usually around 5 mm) and endarch primary xylem maturation. Two species, *K. reuningi* from the Permian of Namibia (Kräusel, 1956) and *K. rioclarense* from the Permian of Brazil (Mussa, 1982, as cited in Crisafulli and Dutra, 2009), differ from the Coalsack trunk in having secretory canals in the pith. In addition, the sclereids in *K. rioclarense* are located only at the periphery of the pith, usually in association with the secretory cells. *Kaokoxylon sclerosum,* the type species from the Triassic of Namibia (Kräusel, 1956), also differs from the Antarctic trunk by the arrangement of its medullar sclerenchyma cells, which form large columns in the pith. Based on pith anatomy, the Antarctic specimen is thus closer to the species that have spherical to lenticular sclerotic nests, i.e., *K. zalesskyi* from the Permian of India and Argentina (Herbst and Crisafulli, 1997; Maheshwari, 1967) and the Triassic of Brazil (Crisafulli and Dutra, 2009), *K. durum* from the Permian of Namibia (Kräusel, 1956), *K. farleyense* from the Permian of Australia (Maheshwari, 1972), and *K. pseudotrimedullaris* from the Permian of India (Prasad, 1982). All of these species also agree with the trunk from Coalsack Bluff in terms of secondary xylem anatomy, except for *K. durum*, which has numerous cross-field pits (Maheshwari, 1972). It is also interesting to note that Prasad (1982) reported the presence of double vascular traces to lateral organs in *K. pseudotrimedullaris,* although he described them as branch traces while we have interpreted them as leaf traces in the Coalsack Bluff specimen. The mode of emission of lateral organs in other species of *Kaokoxylon* remains unknown.

### *4.3. Comparison with Triassic stems from Antarctica*

Finally, it is necessary to provide a comparison of the Coalsack Bluff trunk with Antarctic gymnosperm axes described from the same area but occurring in Triassic deposits. Two genera with preserved primary vascular structures have been described from the Fremouw Formation of the central Transantarctic Mountains, *Kykloxylon* (corystosperm) and *Notophytum* (conifer). Both are found preserved in silicified peat from Fremouw Peak, about 30 km from Coalsack Bluff. They represent young stems with attached leaf bases, which make it possible to determine their affinities with much more accuracy than in the case of decorticated stems. *Notophytum* is easily distinguished from the Coalsack Bluff trunk by characters such as the lack of sclerotic nests in the pith, simple leaf traces, and podocarp type of pitting with one or rarely two large cross-field pits (Meyer-Berthaud and Taylor, 1991). *Kykloxylon*, on the other hand, shows some significant similarities with the new trunk, including the presence of sclerotic nests in the pith, endarch maturation of primary xylem, and double leaf traces. Interestingly, in a preliminary description of *Kykloxylon*, Meyer-Berthaud and Taylor (1992) noted that if found without the attached *Dicroidium* leaf bases, this type of stem would probably be assigned to *Kaokoxylon*; however, *Kykloxylon* has typical secretory structures in the pith that are not found in the Coalsack Bluff specimen. It is possible that these structures were only present in young axes (Decombeix et al., 2010b), but they are also missing in the branch of the new trunk. The pith of *Kykloxylon* is also smaller, only 0.05 to 0.26 cm in diameter, compared to 0.5 cm in the new trunk. Another difference is that cross-field pitting in *Kykloxylon* consists of oval-to-elongated pits that range from $7 \times 10$ μm to $10 \times 25$ μm (Meyer-Berthaud et al., 1993) while there is no evidence of such elongated cross-field pits in the new trunk. Thus, while both *Kykloxylon* and the Coalsack Bluff trunk would fit in the concept of *Kaokoxylon*, they apparently represent distinct stem morphotaxa.

## 5. Conclusions

The silicified trunk from Coalsack Bluff described here represents a new taxon for the Permian of Antarctica. Comparisons with other anatomically preserved axes from Gondwana show that it belongs to the morphogenus *Kaokoxylon*, which increases the geographic distribution of this type of stem during the Permian. The affinities of *Kaokoxylon* remain uncertain, due to the lack of knowledge of the type of leaves and reproductive structures that these trunks bore. Previous authors (e.g., Crisafulli and Dutra, 2009; Herbst and Crisafulli, 1997) have assigned *Kaokoxylon* to the Coniferales based on the wood anatomy. However, the fact that some non-conifer axes, such as the Triassic corystosperm *Kykloxylon* from Antarctica (Meyer-Berthaud et al., 1993) would fit into the general concept of *Kaokoxylon* underlines once more the need for caution in the taxonomic assignment of decorticated stems (Philippe, 1993, 2011).

Although the new trunk described here represents only a single specimen, it is critical that permineralized stem fragments and trunks be described from Permian and Triassic rocks of Antarctica for several reasons. One of these concerns the necessity of more accurately understanding what types of plants existed during these time periods based on reconstructing the entire organism and utilizing a variety of preservation modes. Details of the anatomy of fossil plants from polar latitudes is a major step forward, not only in understanding the diversity in these floras, but also in providing a base level of comparison on how plants adapted to changing climatic conditions from the Permian icehouse into a warmer Triassic world.

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