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EPICORMIC SHOOTS IN A PERMIAN GYMNOSPERM FROM ANTARCTICA

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Two anatomically preserved gymnosperm trunks with clusters of epicormic shoots are described from the Late Permian of Antarctica. The best-preserved trunk is 14 cm long. It has a small circular parenchymatous pith and 9 cm of secondary xylem that contains at least 50 growth rings. The second specimen is slightly smaller (11 × 8 cm) and has 20 growth rings. Both specimens have pycnoxylic wood and produced more than 50 small shoots in a delimited zone on the surface of the trunk. Shoots have a wide parenchymatous pith that may be solid to septate with endarch primary xylem forming 8–10 sympodia and a small amount of secondary xylem similar to that of the parent trunk. The shoots branch and increase in number toward the outside of the trunk. Evidence based on anatomical comparisons and association at the site indicates that the specimens probably represent trunks of some glossopterid, the dominant group of seed ferns during the Permian in Gondwana. This is the first report of clusters of epicormic shoots in a Paleozoic gymnosperm. The ability to produce a large number of young shoots that were capable of developing into new branches indicates that these high-latitude trees possessed an architectural plasticity that allowed them to respond quickly to short- or long-term environmental stress.

Keywords: sprouting, gymnosperm, Late Permian, Antarctica, Gondwana.

Introduction

Sprouting, the production of new shoots from established stems or roots, is widespread among extant gymnosperms and angiosperms (Del Tredici 2001 and references therein; Bond and Midgley 2003). While this phenomenon does not automatically imply the potential for clonal growth, it does allow for the regeneration of the vegetative body of the plant, providing a replacement for damaged or aging organs (Del Tredici 2001). In extant plants, epicormic shoots are formed from the activation of dormant buds on a trunk or a branch (fig. 1A–1C; Kramer and Kozłowski 1979, p. 50). They can have either a preventitious or an adventitious origin (Büsgen et al. 1929). In the first case, the shoots arise from existing axillary buds and are connected to the pith of the parent stem; in the second, they arise outside the normal phyllotaxis and have a vascular connection only with the external tissues of the parent stem (Büsgen et al. 1929). Anatomical studies have shown that in some species, clusters of epicormic shoots apparently produced in an unorganized pattern actually have a strictly preventitious origin, the original axillary bud having formed several secondary latent buds (e.g., in *Quercus petraeae*; Fontaine et al. 1999).

Several causes have been linked to the release of apical dominance that induces the development of the dormant buds. Epicormic shoots are typically produced in trees undergoing significant short- or long-term environmental stress, and the presence of such shoots is used as a growth indicator in some species (Nicolini et al. 2003). They develop in trees

that suffer damage as a result of human activities, but they also develop as a result of pathogens, storm activity, or fire (Cooper-Ellis et al. 1999; Burrows 2002). They also have been reported on trees exposed to variations in light, either to a sudden increase in the amount of light received (“light suckers”) or, conversely, to an increase in shading by dominant trees (“agony branches”; Nicolini et al. 2001). Recent studies also show that in some cases, the production of epicormic shoots is part of the normal crown construction and maintenance in aging trees (Barthelemy and Caraglio 2007 and references therein).

While the mechanisms and causes of epicormic shoot production in extant gymnosperms and angiosperms have been the subject of numerous studies, in part because of their importance in forestry, there are only a few records of their occurrence in fossil plants. Within the lignophyte clade (progymnosperms and seed plants), the oldest evidence of epicormic branching is that found in Late Devonian trunks of *Archaeopteris* (Trivett 1993; Meyer-Berthaud et al. 2000), a progymnosperm genus that includes the first arborescent lignophytes and that has been suggested as the sister group of seed plants (Rothwell and Serbet 1994). Other reports of epicormic branching in Paleozoic lignophytes include the cones of the Pennsylvanian cordaite *Cordaixylon*, which can be borne as epicormic organs on proximal portions of stems (Rothwell 1993). Vascular traces to preventitious epicormic buds have also been documented in specimens of the conifer *Woodworthia arizonica* from the Late Permian of Brazil and the Triassic of the United States (Creber and Collinson 2006).

In this article, we report the presence of clusters of epicormic shoots in two small gymnosperm trunks from the Late Permian (260–251 Ma) of Antarctica. The anatomy of

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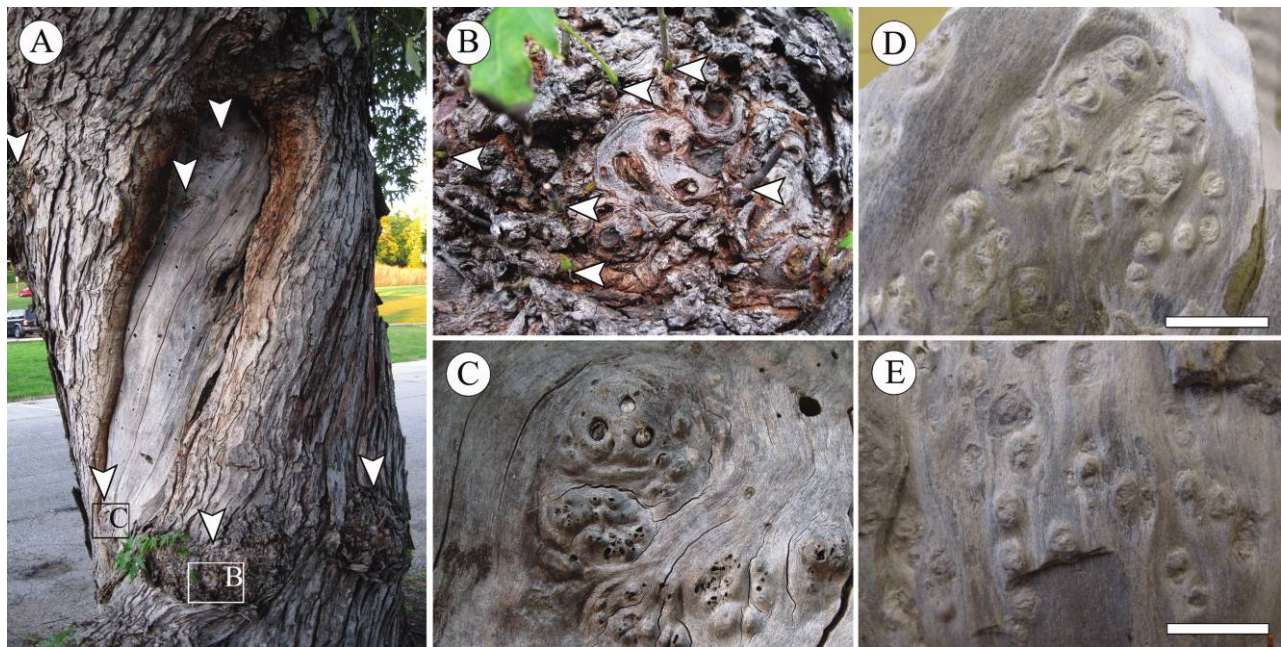


Fig. 1 General aspect of epicormic shoots in an extant maple tree (*Acer saccharinum*, Sapindaceae; A–C), and in fossil gymnosperm trunks from the Permian of Antarctica (D–E). A, General view of an *A. saccharinum* trunk with several clusters of epicormic shoots (arrows). B, Detail of A showing a cluster with the base of several living (arrows) and dead shoots. C, Detail of A showing a cluster of dead shoots in a decorticated zone of the trunk. D, General view of the cluster of shoots on the surface of one of the decorticated Permian trunks; scale bar = 1 cm; specimen 13691 A4. E, Detail of the shoots on one of the fossil trunks; scale bar = 1 cm; specimen 13691 C.

the trunks and shoots is compared to that of the Glossopteridales, the pteridosperm group that dominated the Permian floras of Gondwana, which are well represented at the locality (Taylor 1996). A comparison with previous evidence of epicormic branching in Paleozoic gymnosperms is provided. The possible causes leading to the development of these shoots are discussed in the context of the seasonal high-latitude environment that characterized Antarctica during the Permian (Taylor et al. 1992; Taylor and Ryberg 2007).

Material and Methods

The two anatomically preserved specimens were collected at the Skaar Ridge permineralized (silicified) peat locality in the Beardmore Glacier area, central Transantarctic Mountains, Antarctica (84°49'19.1"S, 163°20'28.0"E; elevation 2289 m). They were found isolated, not included in peat blocks. They occur within the Buckley Formation of the Beacon Supergroup, which is considered to be Late Permian based on palynological data (Farabee et al. 1991). The specimens were cut into slabs that were etched for 2–3 min in 49% hydrofluoric acid, and acetate peels were prepared of the etched surfaces (Galtier and Phillips 1999). Selected peels were mounted on standard microscope slides for study.

Digital images were taken using a Leica (Leica Microsystems, Wetzlar, Germany) DC500 digital camera attachment on a Leica MZ16 stereomicroscope (reflected light) and on a Leica DM5000 B compound microscope (transmitted light). Images were processed using Adobe Photoshop CS (Adobe Systems, San Jose, CA). Some images are composites

of several photos in different focal planes created with the Stack Focuser plug-in for ImageJ (Rasband 1997–2009); these are indicated in the figure legends. Drawings of the specimens were made from enlarged images of peels scanned at 1200 dpi using a flatbed Epson Perfection V750 Pro scanner. Cell and tissue measurements were made using ImageJ. Unless otherwise specified, averages correspond to a minimum of 50 measurements. Specimens, peels, and slides are deposited in the paleobotanical collections of the Natural History Museum and Biodiversity Institute, University of Kansas, under specimen accession numbers 13691 and 13692 and slide accession numbers 23967–23988, 26500, and 26501.

Results

General Aspect

The two specimens represent decorticated trunks, each showing a zone with small shoots forming cylindrical projections or depressions on the outermost tangential surface of the secondary xylem (figs. 1D, 1E, 2). Specimen 13691 (fig. 2A) is 14 cm long, has a maximum diameter of 10 cm, and represents about half of a small trunk. A circular area 2 mm in diameter is present in the basalmost sections, but the tissues in this area have been replaced by minerals, and the pith and primary xylem are not preserved. Secondary xylem is 8–9 cm thick and contains at least 45 growth rings (fig. 3). The second specimen (13692; fig. 2B) is 11 cm long, has a maximum diameter of 8 cm, and represents only the external portion of a trunk; that is, the central part is absent. The

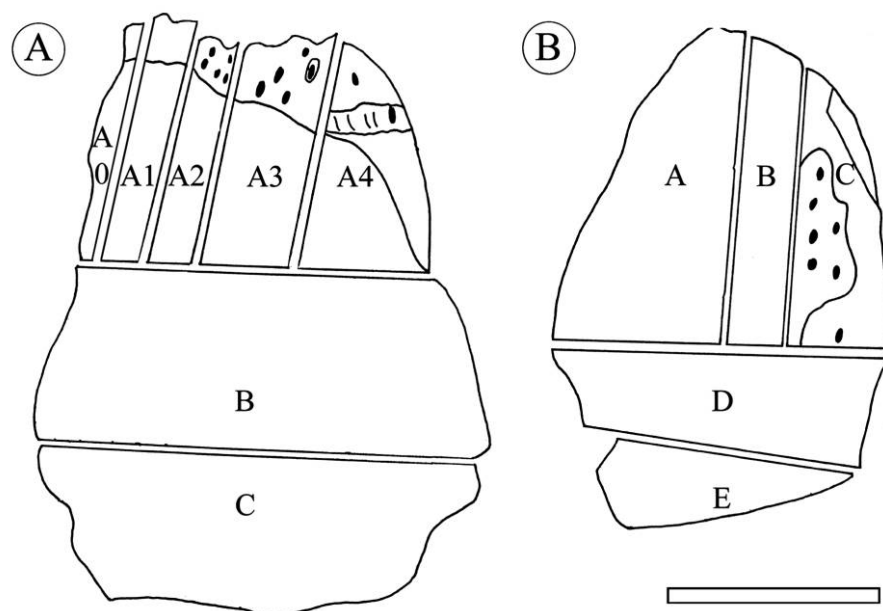


Fig. 2 Line drawings of the Antarctic specimens showing the position of the cluster of shoots and of the sections made. A, Specimen 13691; B, specimen 13692. Scale bar = 5 cm.

secondary xylem in this specimen is 4–5 cm thick and contains ~20 growth rings (fig. 3). Ring width ranges are 0.3–3.5 mm in specimen 13691 and 0.9–4.9 mm in specimen 13692. It is interesting to note that the pattern of ring width in the second specimen is relatively similar to that of rings 23–42 in the first one (fig. 3). As result of this, and because they were collected from the same site during the same field season and possess the same anatomy, we cannot exclude the possibility that they represent part of the same tree.

About 55 small shoots are visible on a zone ~8 × 5 cm on the surface of specimen 13692; more than 70 are present in an equivalent area in specimen 13692. There are no shoots on any other areas of the trunks. All of the shoots have approximately the same diameter (fig. 1D, 1E) and some are branching. They usually have no apparent arrangement but can locally be vertically aligned (fig. 1E).

Wood

The secondary xylem is exclusively composed of tracheids and parenchymatous rays. In transverse section, the tracheids are square to polygonal, and range from 20 to 40 μm in diameter. Growth rings are characterized by a small amount of latewood (fig. 4A) and are comparable to the rings in other trunks from the Permian of Antarctica (Taylor and Ryberg 2007). In tangential section, rays are uniseriate, rarely (~2%) partly biseriate (fig. 4B). They are 1–9 cells high, with an average of 2 cells ($n = 176$). Ray cells are oval and $24 \times 14 \mu\text{m}$ in tangential section. In radial section, they are 45–110 μm long, with vertical to slightly oblique walls and opaque contents. The radial walls of the tracheids display 1–4 but most commonly 2 rows of hexagonal to circular-bordered pits. Latewood tracheids typically have only 1 or 2 rows of pits (fig. 4C, left) with an opposite-to-alternate organization. In larger

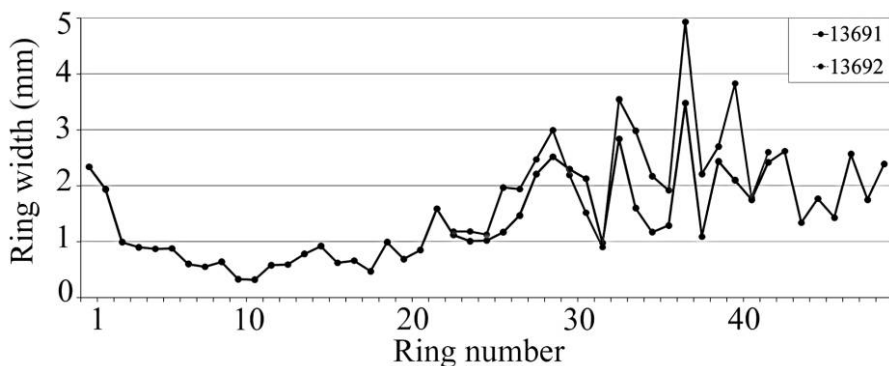


Fig. 3 Variation of growth ring width along the radius of the two trunks showing the similarity in ring width variation.

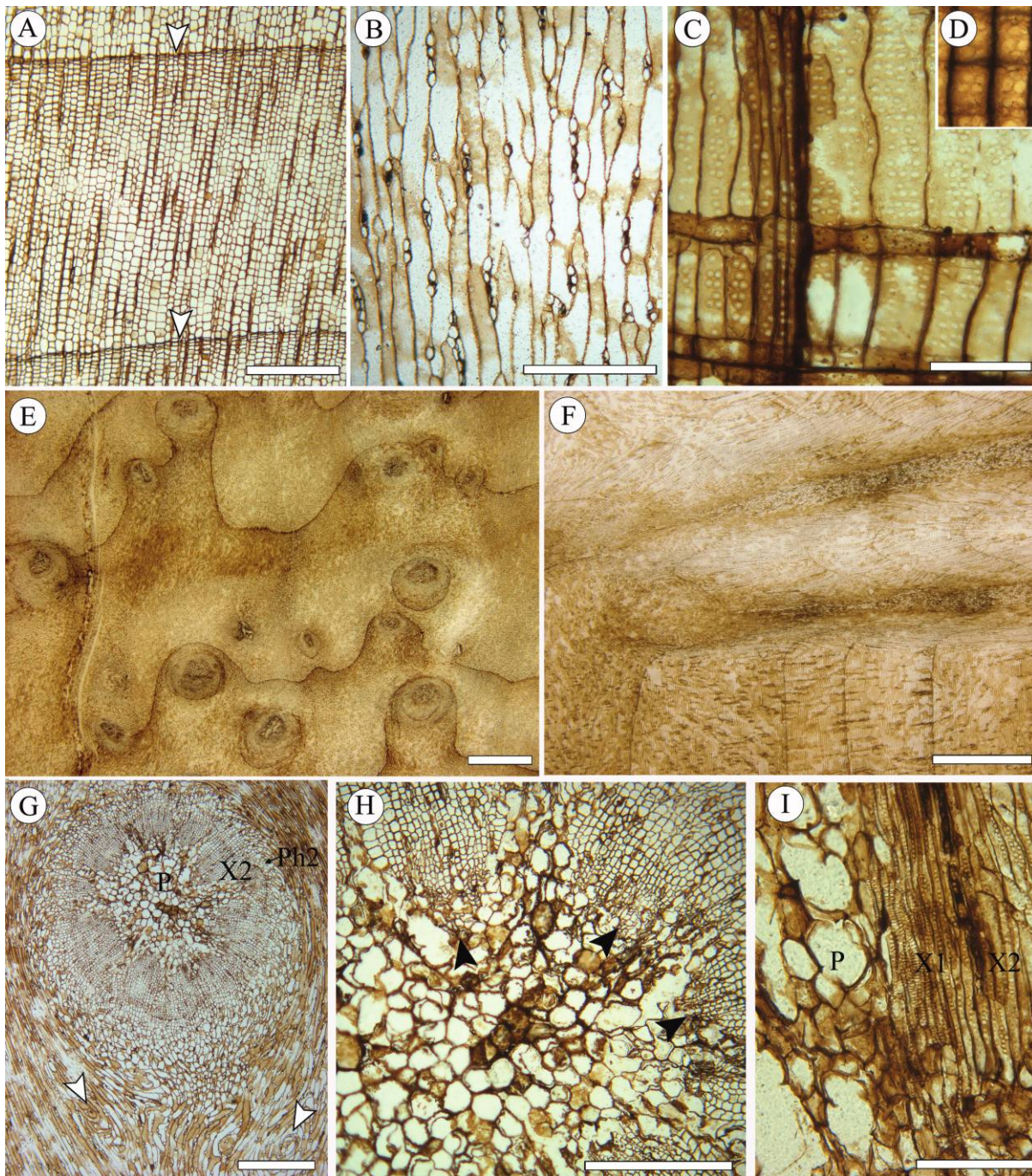


Fig. 4 Anatomy of the Permian trunks (A–E) and shoots (F–I). *P* = pith, *Ph2* = secondary phloem, *X1* = primary xylem, and *X2* = secondary xylem. *A*, Transverse section of the secondary xylem showing the limit of two growth rings with a small amount of latewood (arrows); scale bar = 500 μm ; slide 23967 (13691 A2-CT#2a). *B*, Tangential section of the secondary xylem showing uniseriate parenchymatous rays; scale bar = 250 μm ; slide 23971 (13691 A3-SR#2a). *C*, Radial section of the secondary xylem showing tracheids of the latewood (left) and earlywood (right) with 1–4 rows of circular bordered pits; scale bar = 100 μm ; slide 23983 (13692 B-SLR#2a); composite of four photos. *D*, Detail of the cross-field pitting; slide 23983 (13692 B-SLR#2a). *E*, Tangential section of the trunk in the zone of a cluster of shoots showing numerous small axes; scale bar = 2.5 mm; slide 26501 (13692 B-SR#2a). *F*, Radial section in the same zone showing the horizontal course of the shoots through several growth rings; scale bar = 2 mm; slide 23983 (13692 B2-SLR#2a). *G*, Tangential section of the trunk showing a shoot with a large parenchymatous pith and secondary vascular tissues in close association with the secondary xylem of the trunk; note the circular pattern of the secondary xylem on the side of the shoot (arrows); scale bar = 500 μm ; slide 26501 (13692 B-SR#2a); composite of three photos. *H*, Close-up of the pith and primary xylem of the shoot illustrated in *G*, showing several primary xylem strands (arrows); scale bar = 200 μm ; slide 26501 (13692 B-SR#2a). *I*, Radial section of the trunk with a shoot seen in radial section showing from left to right pith, primary xylem tracheids with helical pitting, and secondary xylem; scale bar = 200 μm ; slide 23983 (13692 B2-SLR#2a).

tracheids of the earlywood, the pits almost always appear in an opposite arrangement, forming horizontal rows of 3–4 pits (fig. 4C, right). These horizontal rows are not located at equal distances from each other on the wall and sometimes appear in groups of 1–5 rows. Pits are 7–10 μm wide, with an oblique oval aperture up to 4 μm wide ($n = 20$). Cross-field pitting consists of 3–6, rarely more, oval pits (fig. 4D).

Shoots

Longitudinal sections of the trunk in the zones where shoots are visible on the surface reveal the presence of numerous small eustelic axes (figs. 4E, 5), which decrease in number significantly toward the inner part of the trunk in both specimens (fig. 5). Most of these axes cross several growth rings and have an almost horizontal course through the wood (fig. 4F).

Anatomy. The shoots range from 0.7 to 3 mm in diameter and are composed of a parenchymatous pith, which may be solid or irregularly septate, and vascular tissues. They are closely associated with the secondary xylem of the trunk, which forms circular patterns on their side (fig. 4G). The pith is 0.2–1 mm wide, exclusively composed of parenchymatous cells, and represents up to 55% of the total shoot diameter. Along the margin, the pith appears stellate in transverse section due to the presence of conspicuous medullary rays (fig. 4G, 4H). Pith cells are rounded and some of them have opaque contents (fig. 4H). These cells range from 15 to 60 μm in transverse section and are as long as wide in longitudinal section (fig. 4I). Primary xylem strands are recognized by the smaller diameter of the tracheids; maturation appears to be endarch (fig. 4H). In longitudinal section, the walls of what are interpreted as protoxylem tracheids have helical secondary wall thickenings (fig. 4I). Observation of some of the best-preserved shoots suggests that the primary xylem is organized into 8–10 sympodia (fig. 6A, 6B). This organization is made clearer by the fact that in most cases the inner ring of secondary xylem, recognizable by its smaller and usually darker tracheids, is entirely dissected by the medullary rays (fig. 6A, 6B). At any given level in the axis, sympodia vary in size. Some have a single protoxylem pole (e.g., fig. 6A, sympodia 5 and 6) while others have two protoxylem poles (e.g., fig. 6A, sympodia 8 and 9), no doubt in relation with the tangential departure of traces to lateral appendages. Secondary xylem anatomy is similar to that of the trunks.

Branching. Almost all the shoots show branch departure (figs. 6, 7A, 7B). Branch traces appear to be produced in pairs from two adjacent sympodia (fig. 7A), but this is not evident for all the shoots. Each pair of traces then forms two circular zones with secondary xylem, located on both sides of a group of horizontal tracheids (figs. 6C, 7C). These subsequently fuse to form a branch that is tangentially elongated and usually assumes a more circular shape distally (figs. 6D, 7B). Most of the shoots show one to several lateral branches at the same level (fig. 7A, 7B), but no clear organotaxis could be determined. In addition to the branch traces, some small ephemeral traces that consist of a few tracheids and are produced in pairs might represent leaf traces (fig. 7D).

Decayed shoot. In the inner portion of specimen 13691, there are a few shoots located around another one that has a different aspect (fig. 7E). This shoot is preserved only in

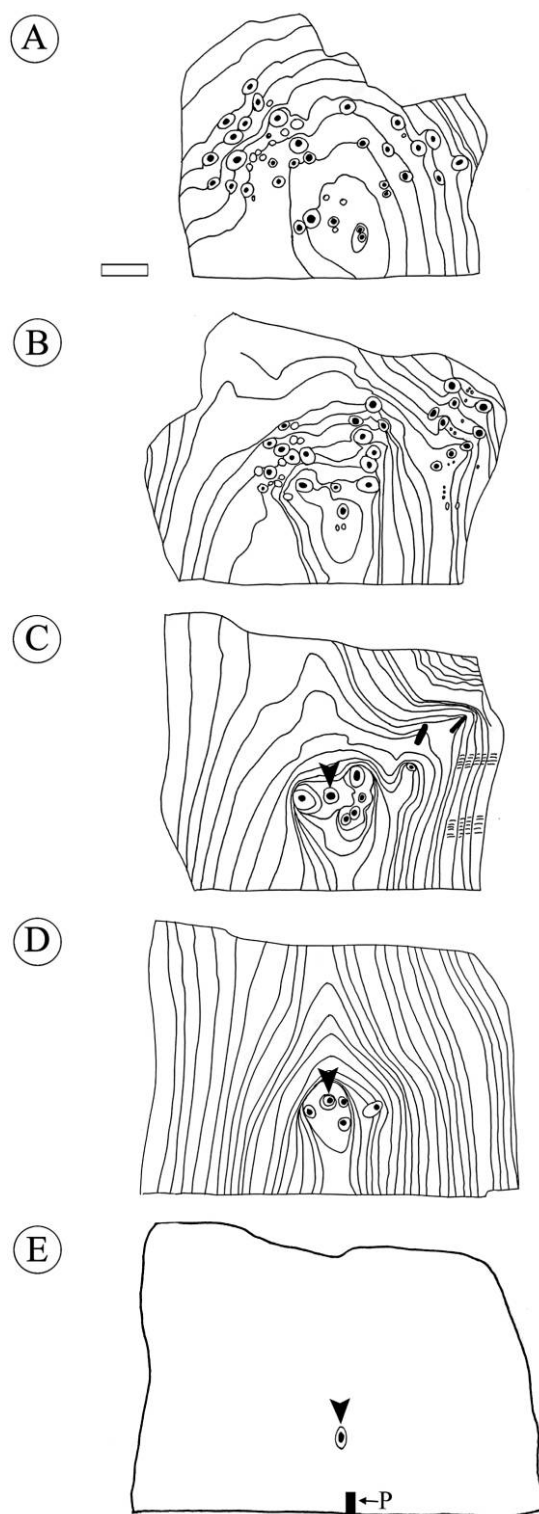


Fig. 5 Line drawing of the tangential sections in specimen 13691 showing the location of the largest shoots; black arrows indicate the position of the innermost, decayed axis (see text for explanation); scale bar = 1 cm. A, Peel 13691 A4-S#1; B, peel 13691 A3-S#1; C, peel 13691 A2-S#1; D, peel 13691 A1-S#1; E, outer surface of block A0 showing the remains of the pith (P) and the innermost axis.

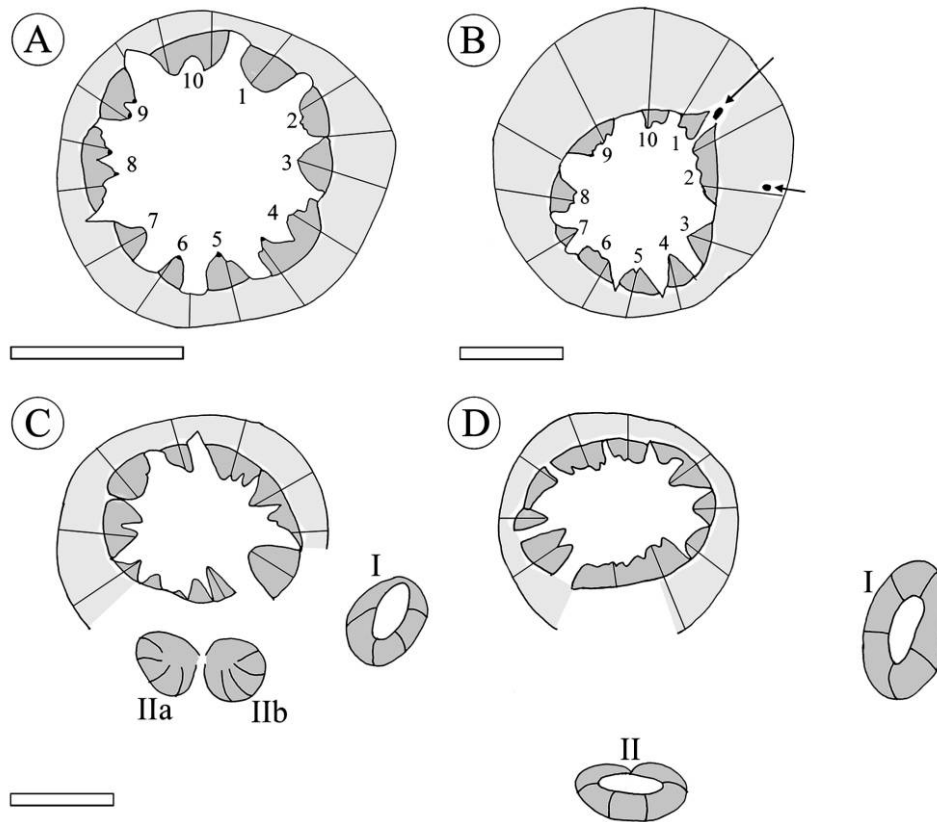


Fig. 6 Primary xylem organization and branching pattern of the shoots. *A*, Shoot with 10 sympodia: pith (white), conspicuous protoxylem poles (black), first (discontinuous) ring of secondary xylem (dark gray), and second ring of secondary xylem (light gray); scale = 500 μ m; redrawn from slide 26501 (13692 B-SR#2a). *B*, Shoot with 10 sympodia producing two small traces (arrows); scale = 500 μ m; redrawn from slide 26501 (13692 B-SR#2a). *C*, Shoot producing two branches, in the first one (*I*) the traces are already fused; the second branch is at an earlier stage, with a pair of traces with secondary xylem (*IIa* and *IIb*); scale = 500 μ m; redrawn from slide 23971 (13691 A3-SR#2a). *D*, Same shoot as in fig. 6C in a more distal section; traces *IIa* and *IIb* have fused to form branch *II*; scale = 500 μ m; redrawn from slide 23970 (13691 A4-S#2a).

the inner part of the trunk and is occluded ~ 2.5 cm into the wood (fig. 5C–5E). Its course in the wood is almost horizontal. Because the pith of the trunk is preserved only in a small portion of the block, it was not possible to determine whether this shoot is connected to the primary vascular system of the trunk or is adventitious in origin. However, it is present on the exterior of block A0 (fig. 5E) in a depression less than 2 mm from where the border of the pith of the trunk would be if it were preserved in this zone. At 1.5 cm from the center of the trunk, the shoot is ~ 3.2 mm in diameter. The pith is 1.2 mm wide and is almost completely degraded (fig. 7E, 7F). Primary xylem organization is difficult to distinguish, but there is evidence of paired traces to branches as in the other shoots (fig. 7F). In several places, cells of the secondary xylem appear decayed (fig. 7G). The shoot is separated from the wood of the trunk by several layers of a dark calluslike tissue up to 200 μ m in thickness (fig. 7H).

Discussion

Affinities of the Trunks

Anatomically preserved plants from Skaar Ridge and contemporaneous compression floras from the central Transant-

arctic Mountains document a vegetation dominated by the glossopteridalean seed ferns, with *Vertebraria* Royle roots (Schopf 1965), *Glossopteris* Brongniart leaves (Pigg 1990), several types of reproductive structures (Taylor and Taylor 1992; Ryberg 2009, 2010), and wood traditionally assigned to the *Dadoxylon* Endlicher or *Araucarioxylon* Kraus type (but see below). The presence of other gymnosperms in Late Permian localities of the central Transantarctic Mountains is evidenced by anatomically preserved wood and stems (Maheshwari 1972), several morphologically distinct seeds (Taylor and Taylor 1987, 1992; Klavins et al. 2001) and possibly by roots with a non-*Vertebraria* anatomy (Decombeix et al. 2009).

Young shoots of *Glossopteris skaarensis* with attached leaves (Pigg and Taylor 1993) are the only type of gymnosperm stems from Skaar Ridge for which the anatomy and affinities are well established. These axes range from 1 to 12 mm and display a broad (up to 1 mm wide) parenchymatous pith surrounded by pycnoxylic wood. The shoots reported here are similar to *G. skaarensis* axes with regards to the dimension and anatomy of the pith, which in both cases can be solidly parenchymatous, irregularly septate or more rarely hollow. The primary xylem of *G. skaarensis* stems was

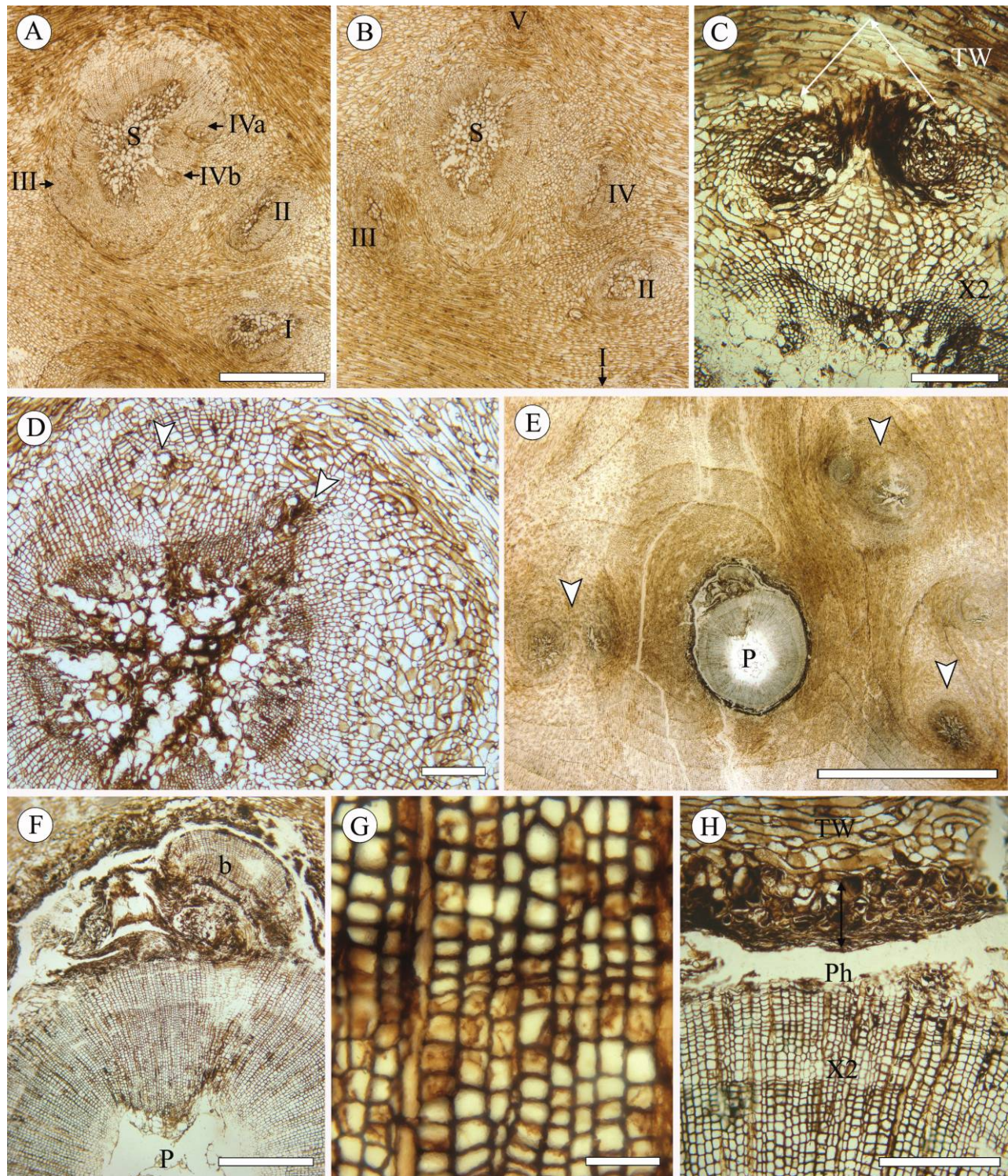


Fig. 7 Anatomy of the shoots; A–C, branching; D–H, decaying. *P* = pith, *Ph* = phloem, *S* = shoot, *TW* = secondary xylem of the trunk, *X2* = secondary xylem of the shoot. *A*, Branching of a shoot seen in transverse section; three branches are visible (*I–III*) and the double trace to a fourth one (*IVa* and *IVb*) is being produced from two sympodia; scale bar = 1 mm; slide 23988 (13692 A-SR#2a). *B*, Same shoot as in *A* on the following block (~1 mm apart); the branches visible in *A* are still present (*I–III*), the double trace has fused (*IV*), and a fifth trace has been produced (*V*); scale = 1 mm; slide 23989 (13692 B-S#2a). *C*, Detail of a pair of traces (arrows) to a branch about to fuse; scale bar = 200 μ m; slide 23970 (13691 A4-S#2a); composite of three photos. *D*, Shoot with two small traces in the inner part of the wood (arrows) that might correspond to leaf traces, the one on the left has almost disappeared while the second one is still visible; scale bar = 200 μ m; slide 23971 (13691 A3-SR#2a). *E*, Tangential section approximately 1.5 cm from the center of the trunk showing three groups of shoots (arrows) located around a shoot that has

described as indistinct, recognizable only by the presence of tracheids with a smaller diameter and helical or scalariform pitting in longitudinal section (Pigg and Taylor 1993). In the shoots borne on the specimens described here, the number of sympodia and endarch maturation of the primary xylem strands is relatively clear. The preservation of the shoots in these new specimens, however, is considerably better than that in most stems of *G. skaarensis*, so the difference may be due only to different preservation. For example, the primary xylem is difficult to distinguish in the decayed axis present in one of the new trunks. In *G. skaarensis*, the leaf traces are emitted in pairs, and the vascular trace to axillary branches is formed by the fusion of a pair of traces (Pigg and Taylor 1993). Although the relationship in position between the leaf and branch traces is not clear in the shoots of the new trunk, the mode of production of the branches is similar to that of *G. skaarensis*.

Secondary xylem anatomy of *G. skaarensis* and the new specimens is comparable in terms of ray anatomy and size. Cross-field pitting in *G. skaarensis* has been described as cupressoid to taxodioid (Pigg and Taylor 1993), while it seems to be only cupressoid in the new specimens. The radial pitting of the tracheids in *G. skaarensis* apparently compares to the wood morphogenus *Araucarioxylon*. However, the arrangement of the pits is often difficult to distinguish in these young stems that have narrow tracheids with only 1 or 2 rows of pits, and the arrangement of pits on larger tracheids remains unknown. The radial pitting in the two new trunks clearly differs from typical *Araucarioxylon* wood by the opposite arrangement of the pits observed on the largest tracheids and their tendency to occur in groups. It is considered significant that an identical type of radial pitting is present in the *Vertebraria* roots collected at the same locality (Decombeix et al. 2009; fig. 3D, 3E) and has been reported in several Permian Gondwanan axes attributed to or found in association with glossopterids (Marguerier 1973; Mussa 1978; Prasad and Chandra 1978; Weaver et al. 1997; Bamford 1999). These axes have generally been assigned to the morphogenus *Australoxylon* Marguerier 1973, characterized by a mixed araucarioid/abietoid radial pitting. While a discussion on the wood anatomy of glossopterids is beyond the scope of this article, the possibility that this distinctive radial pitting pattern might be a characteristic of the group, as suggested by Mussa (1978), is noteworthy.

In addition to the glossopterids, many Paleozoic gymnosperms have stems roughly comparable to the new shoots described in this article, that is, with a large pith, small endarch primary xylem strands and pycnoxylic wood. These include some putative arborescent seed ferns of Mississippian age (Galtier and Meyer-Berthaud 2006) as well as Pennsylvanian and Permian coniferophytes, including some cordaites (e.g., *Cordaixylon*; Rothwell and Warner 1984) and basal conifers (e.g., *Emporia*; Hernandez-Castillo et al. 2009 and

references therein). Stems with a similar anatomy are documented in Permian localities of Gondwana (Maheshwari 1972; Mussa 1986; Crisafulli and Herbst 2009); however, most are decorticated and their affinities remain equivocal. As a result of the overwhelming predominance of glossopterid remains in the permineralized peat from Skaar Ridge, together with the anatomical similarities of the new specimens with *Glossopteris skaarensis* and *Vertebraria*, we consider that the specimens described here most likely represent trunks of a glossopterid.

Interpretation and Comparison to Epicormic Shoots in Other Paleozoic Plants and in Extant Gymnosperms

The presence in the fossils described in this article of young shoots on trunks that are more than 20 years old indicates a delayed development, probably after some trauma. Evidence from the specimen with the central part preserved (13691) indicates that these shoots were borne on a trunk and not on roots or in the root-stem transition (collar) zone, and thus they are interpreted as similar to the epicormic shoots of extant trees. While the morphology of shoots produced from the roots, collar zone, or aerial axes is similar in extant trees, their function and fate are distinct since only root and collar sprouts have the potential to become independent from the parent tree under normal conditions (Del Tredici 2001). Epicormic shoots have a significant role in the regeneration of the plant vegetative body. The fact that all the shoots in the fossil trunks from Skaar Ridge are closely associated with the secondary xylem of the trunk is a possible indication of their adventitious nature. Because the information on the relationship between the primary vascular system of the trunks and the shoots is lacking, the adventitious or preventitious nature of the shoots is not entirely certain.

There is evidence, however, that the increase in the number of shoots toward the external part of the trunks is caused, at least in part, by the branching of the shoots. This pattern results in a cluster of more than 50 shoots in a relatively small zone on the surface of the trunk. In extant lignophytes, this pattern occurs in a number of angiosperms but is rare in gymnosperms (Bond and Midgley 2003). Among fossil lignophytes, Trivett (1993) reported the presence of groups of 1–10 small adventitious branches in an old trunk of the progymnosperm *Archaeopteris* from the Late Devonian of the United States. This report represents, to the extent of our knowledge, the only detailed study of epicormic shoots produced in clusters in a fossil tree before this report. Trivett interpreted the epicormic branches in her specimen of *Archaeopteris* as a method that might serve to repair the crown in aging trees. More recently, Meyer-Berthaud and her collaborators (2000) showed that latent meristematic zones were abundant in a young trunk of *Archaeopteris* from

a degraded pith and is partly surrounded by a dark tissue; scale = 500 μm ; slide 23969 (13691 A1-SR#2a). F, Detail of the central shoot in E showing a lateral branch (b); scale = 500 μm ; slide 23969 (13691 A1-SR#2a). G, Detail of the secondary xylem of the same shoot as in F showing signs of decay; scale = 100 μm ; slide 23969 (13691 A1-SR#2a). H, Outer part of the same shoot with secondary xylem, phloem, layer of dark tissue (double-headed arrow), and secondary xylem of the trunk; scale = 250 μm ; slide 23969 (13691 A1-SR#2a).

the Late Devonian of Morocco. They interpreted this as an indication that *Archaeopteris* had the ability to reproduce vegetatively through layered axes or cuttings. Since the ultimate fate of such meristems cannot be determined, it is also possible that they could have developed into epicormic shoots in response to some environmental factor.

In the Pennsylvanian cordaite *Cordaixylon dumusum*, cones are produced in an adventitious manner both in the distal portions of stems and in more proximal regions where leaves have been shed and a significant amount of wood has been produced (Rothwell 1993). This production of epicormic cones, compared by Rothwell (1993) to the cauliflory of some extant angiosperms, could have increased the reproductive output of the plant but does not have the regenerative implications of the epicormic shoots observed in the trunks from Skaar Ridge. The only other report of epicormic buds or shoots in a Permian gymnosperm is in Brazilian specimens of the conifer *Woodworthia arizonica*. In this species, Creber and Collinson (2006) report the presence of traces to preventitious epicormic buds or shoots. These traces are not branched, indicating that the epicormic buds/shoots were not produced in clusters like those in the specimens from Antarctica.

The production of clusters of epicormic shoots is documented in several extant gymnosperms, although the phenomenon is less frequent than in angiosperms (Del Tredici 2001; Bond and Midgley 2003). Redwoods (*Sequoia sempervirens*, Cupressaceae) produce structures commonly called “burls” on the lower portion of old or injured trunks and sometimes higher up in the tree. These burls form large outgrowths on the trunks that are several tens of centimeters in thickness. They correspond to masses of buds and cortical tissue and can produce numerous sprouts, as well as roots in the lower part of the trunks (Del Tredici 1999). Other extant conifers do not form specialized structures like the redwood burls but can produce clusters of epicormic shoots in response to environmental stresses. The bigcone Douglas-fir (*Pseudotsuga macrocarpa*, Pinaceae) of California for example is capable of producing numerous epicormic shoots following fire events or mechanical damage (Gause 1966). Burned bigcone Douglas-firs produce sprouts from dormant buds located on the upper surface of branches in the middle and upper third of the crown. In the case of mechanical damage to the trunk, buds proliferate around the wound and a cluster of shoots is developed, usually with one dominant stem (Gause 1966). Several species of *Pinus* (Pinaceae) possess dormant buds of preventitious origin that can branch, but they do not form large clusters (Stone and Stone 1943). Hoop pines (*Araucaria cunninghamii*, Araucariaceae) have latent axillary meristems that can develop into epicormic buds when apical dominance is released (Burrows 1990). The presence of buds that do not fit in the phylotaxis indicates that either the latent meristem of hoop pines can divide or that adventitious buds are also produced in addition to the preventitious ones.

Epicormic Shoots and Environment

All the epicormic shoots observed in the Permian specimens have a small diameter and only a small amount of secondary xylem. These shoots might have produced some

leaves, thus increasing photosynthetic capacity, but none of them actually developed into a large branch. Their presence indicates that these Permian trees were capable of producing epicormic branches. In extant trees, epicormic branching can be (1) part of the normal developmental pattern, (2) linked to long-term changes in light conditions, or (3) caused by a short-term environmental stress. What might have caused the development of epicormic shoots in the Permian trees from Antarctica?

In some cases, epicormic branching is part of the normal architectural development of a tree. This is the case in a number of extant species, including conifers such as *Larix occidentalis*, *Picea mariana*, *Pseudotsuga menziesii*, and *Thuja occidentalis* (Ishii et al. 2007 and references therein). Because the Skaar Ridge specimens represent the first evidence for the presence of these shoots in a gymnosperm from the Permian of Antarctica, it is unknown how frequently this phenomenon occurs in this taxon. The identification of all the developmental stages and reconstruction of the architecture are particularly difficult in fossil plants due to the rarity of complete young or mature trees with attached laterals.

Adaptive epicormic branches develop as a response to a change in the light regime in forest ecosystems. Such shoots tend to be formed continuously on trees growing in closed stands but have a very high mortality rates due to the small amount of light received (Yokoi and Yamaguchi 1996). In spite of this, they can develop into branches if thinning of the stand occurs. During the Permian, the South Pole was located either in Northern Victoria Land (Antarctica) or in southeastern Australia, which places the central Transantarctic Mountains above 75°S, and probably between 80° and 85°S (Grunow 1999; Scotese 2002). At these high latitudes, the light regime is quite different from that for temperate and tropical trees in which epicormic branching has been studied, with 24 h of daylight in summer and complete darkness during the winter. The study of 15 in situ stumps near Mount Acherar, in the central Transantarctic Mountains, provides some information about potential forest dynamics in Antarctica during the Late Permian (Taylor et al. 1992). The density extrapolated from the distance between the stumps is of 2000 trees/ha, and the tree ring structure indicates very rapid growth during the growing season. The interpretation of this stand is that it consisted of saplings. Colin and his collaborators (2008), however, showed that stand density had no significant effect on the production of epicormic shoots. Because the Permian Antarctic forest was a monospecific forest of Glossopteridales (Taylor et al. 1992), all trees are expected to have the same physiology (i.e., no species adapted to low vs. high light). Studies on tropical and temperate trees (Nicolini et al. 2003; Colin et al. 2008) showed that both the number of living epicormic branches already present on a tree and the number of new epicormic organs formed are inversely correlated with the vigor of the tree. The development of adaptive epicormic branches is thus often associated with a change in cambial activity (Nicolini et al. 2001 and references therein). Even in the high-latitude environment where the Permian specimens were growing, it is expected that such a change in growth or health of the tree would be reflected in its growth rings (Schweingruber 2007). The average ring width and range of variation in the two Permian specimens with epicormic

shoots does not significantly differ from other trunks from Skaar Ridge analyzed by Taylor and Ryberg (2007). Their sequence of ring widths shows important variations between successive rings, but there is no obvious trend indicating an increase or decrease in overall plant growth (fig. 3). This is consistent with the fact that the shoots present in the specimens did not develop into larger branches.

Traumatic epicormic branching may also be a response to a loss of part of the vegetative body of the tree and is common in some species growing in fire-prone environments (Burrows 2002). While charcoalified plant remains are found in younger (Middle Triassic) permineralized peat from the Beardmore Glacier area of Antarctica (Hermsen et al. 2009, p. 119), there is no evidence of fire events in the Late Permian peat from Skaar Ridge. Breakage of branches due to the fall of another tree, flooding events, snow, and strong winds represent other causes for the formation of epicormic branching (Cooper-Ellis et al. 1999). Wounds that might have been caused by these types of events are well documented in the Triassic of Antarctica (Putz and Taylor 1996), but again there is no conclusive evidence in any Permian specimens. Despite the fact that such short-term events would probably not be recognizable in the fossil record, such events could be the cause of this type of shoot development. Finally, traumatic epicormic branches can also develop in response to insect or pathogen interactions. To date, evidence of insect-plant interactions observed in specimens from Skaar Ridge occurs in the form of borings and coprolites (Kellog and Taylor 2004). These particular interactions are believed to have been caused by oribatid mites and probably took place after the death of the plants, but there is no a priori reason why other animal or fungal interactions could not involve living tissues and thus stimulate the production of epicormic branching. There is no indication of pathogenic infection in the trunks described here, such as the presence of the wood-decaying fungi that are known in other Permian woods from Antarctica (Stubblefield and Taylor 1986). It has been noted, however,

that the inner part of one of the specimens contains a partially decayed shoot that is isolated from the wood of the trunk by a dark calluslike tissue. Perhaps in this case the production of epicormic shoots was induced by the death of this axis.

Conclusion

The presence of epicormic shoots is documented for the first time in putative glossopterid trunks from the Permian of Antarctica. They represent the oldest evidence of epicormic shoots occurring in large clusters in a Paleozoic seed plant. The ability to produce a large number of epicormic shoots that could develop into new branches indicates that these trees had an architectural plasticity that allowed them to respond rapidly to short- or long-term environmental stresses. Data from multiple sources suggest that the Glossopteridales were probably good colonizers in these late Paleozoic ecosystems (Taylor 1996). The ability to produce opportunistic shoots would have been an important evolutionary adaptation that provided the opportunity for these plants to rapidly colonize new niches in the high-latitude environments of the Permian of Antarctica. Investigation of trunks from other localities in Gondwana could reveal whether the production of epicormic shoots in glossopterids followed a paleolatitudinal gradient.

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