THE BARK OF THE LATE TRIASSIC *ARAUCARIOXYLON ARIZONICUM* TREE FROM PETRIFIED FOREST NATIONAL PARK, ARIZONA

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SUMMARY

This paper contains a description of the only known non-banded bark in the geologic record. The bark is attached to a branch of the *Araucarioxylon arizonicum* tree that was found recently in the Late Triassic Chinle Formation (~220 Mya) in Arizona. In the fossil the vascular cylinder is almost totally enclosed in rough bark 2–11 mm in thickness. The inner bark is less than 1 mm thick and comprises a very narrow zone of presumed phloem containing infrequent fibers. The outer bark varies in thickness up to 10 mm, and consists of curving lenses of sequent periderm free of both dilation tissue and resin canals but is quite unlike the banded bark of *Araucaria heterophylla*. Wide zones of very thin-walled rectangular parenchyma cells arranged in radial files and groups of thin-walled spongy parenchyma, and small clusters as well as solitary sclerenchyma occur in the rhytidome. The vascular cambium contains 1–4 fusiform cells per radial file. Uniseriate rays are common in the secondary xylem and extend to the cambial zone. Small (1 mm in diameter), simple tunnels in the bark and wood indicate that the branch was attacked by phytophagous insects. A possible petrified beetle larva similar in form and size to *Anobium* is associated with these tunnels.

Key words: Late Triassic, *Araucarioxylon arizonicum*, bark, cambium, periderm, phloem, rhytidome, phytophagous insects.

INTRODUCTION

In contrast to petrified wood, fossilized bark, particularly the outer bark (rhytidome, periderm) of woody plants is comparatively rare in the geologic record. Furthermore, specimens of outer bark described in the past were relatively small and incomplete, and many came from roots (see Table 1). Recently, the senior author discovered a 0.7 m long bark-clad branch of the Late Triassic (.220 Mya) *Araucarioxylon arizonicum* Knowlton (1888) tree in Petrified Forest National Park, Arizona (Fig. 1A). This article contains the first detailed description of the bark on that branch which, coincidently, is the only known example of non-banded bark in the geologic record. There is an earlier unpublished report of *A. arizonicum* "cortex" on a small diameter twig (Turkel

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Table 1. Bark of selected woody plants in the geologic record. nr = not reported; est. = estimated from original illustrations; * a heterogeneous material existed where phloem was expected; phloem elements could not be unequivocally identified and may not have been present.

| Age	Location	Affinity	Species	Tissues recognised	Thickness	References
Early Paleogene	Western Greenland	Coniferophyta	*Cedroxylon saviarquatense*	inner bark	3–4 mm	Mathiesen 1961
Early Paleogene	Western Greenland	Magniolophyta	*Aphloioxylon groenlandicum*	sequent periderms and layers of phloem	5 mm	Mathiesen 1961
Late Cretaceous	Alberta, Canada	Coniferophyta	*Taxodioxylon gypsaceum*	sequent periderms and layers of phloem	62 mm	Ramanujam & Stewart 1969
Early Cretaceous	England	Coniferophyta	*Vectia luccombensis*	layers of phloem	26 mm	Stopes 1915
Cretaceous	Japan	Coniferophyta	*Paracupressinoxylon cryptomeriopsoides*	layers of phloem	nr	Shimakura 1937
?Late Jurassic	Franz Joseph Land	Coniferophyta	?*Pityoxylon* or *Cedroxylon*	sequent periderms	nr	Solms-Laubach 1904
Early Jurassic / Late Triassic	Wales	Coniferophyta	?*Cheirolepis*	outer bark	nr	Harris 1957
Late Triassic	Arizona	Coniferophyta	*Araucarioxylon arizonicum*	sequent periderms phloem*, and cambium	2–9 mm	Ash & Creber 2000; this paper
Late Triassic	Arizona	Coniferophyta	*Araucarioxylon arizonicum*	cortex	2 mm	Turkel 1968
Late Carboniferous	Kansas	Cordaitean	*Cordaixylon* sp.	sequent periderms and layers of phloem	5 mm	Taylor 1988
Late Carboniferous	Ohio	Cordaitean	*Mesoxylon priapi*	sequent periderms and layers of phloem	2 mm	Taylor 1988
Late Carboniferous	Kansas	Cordaitean	*Amyelon* type	layers of phloem	nr	Taylor 1988
Early Carboniferous	England	Cordaitean	*Mesoxylon sutcliffii*	sequent periderms and layers of phloem	3–5 mm (est.)	Maslen 1911
Later Devonian	New York	Progymnosperm	*Callixylon*	sequent periderms and layers of phloem	2–3 mm	Penhallow 1908; Arnold 1930; Scheckler et al. 2001
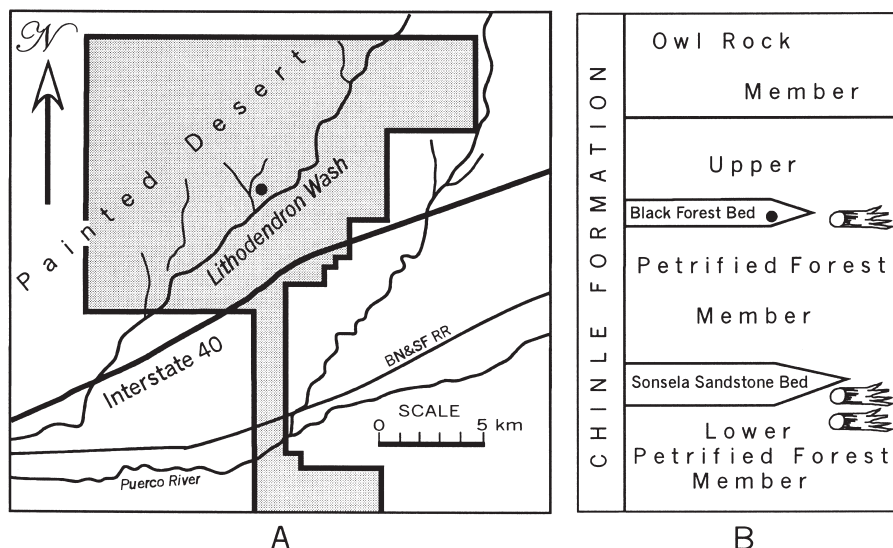
Fig. 1. – A: Sketch map showing some features of the Painted Desert Section of Petrified Forest National Park (shaded) and the location of the site (black dot) where the fossil described here was found. – B: Stratigraphic diagram showing the principal divisions of the Chinle Formation generally recognized in Petrified Forest National Park. The approximate stratigraphic position of the locality that contained the fossil described here is indicated by the black dot and the positions of the several "petrified forests" in the park are indicated by the "logs." Figures adapted from Ash (1987) and references cited therein.

1968), but otherwise there is only a cursory description of the periderm on the branch described here (Ash & Creber 2000). The fossil presents a rare opportunity to obtain information about several previously unknown anatomical and morphological aspects of the tree. In addition, tunnels in both bark and wood enable consideration of bark- and wood-boring insect activity of the time.

Background

When he described the wood of the *A. arizonicum* tree, Knowlton (1888) based his findings on two large decorticated logs collected a few years earlier from the Black Forest Bed in the Painted Desert Section of Petrified Forest National Park (Swaine & Hegewald 1882; Ash 1992) (Fig. 1A). Since 1888 such wood has been found at many localities and horizons in the Chinle Formation and is particularly common and generally very colorful in east-central Arizona. Logs attributed to *A. arizonicum* in Petrified Forest National Park are generally decorticated and range from 0.6 to 3 m in diameter near the base, and to 41 m in length (Ash & Creber 2000). In the park, which was established to protect some of the best of these deposits, the species is represented by literally hundreds of large prostrate logs that occur at high density in groups called "forests" (Ash 1987). Smaller fragments of the same species as well as a few stumps

that appear to be preserved in growth position also occur there. The trunk wood contains tracheids, axial parenchyma and uniseriate rays and lacks annual growth rings (Ash & Creber 1992). Abundant evidence indicates that many *A. arizonicum* trees were attacked by fungi (Daugherty 1941; Creber & Ash 1991) and a variety of phytophagous insects, probably beetles (Walker 1938; Ash 1997).

   The Chinle Formation of Arizona, which contained the bark-clad branch described here, was deposited during the Late Carnian and Early Norian Stages of the Late Triassic in a large continental basin by northward flowing streams and rivers and on adjacent flood plains and in lakes (Dubiel et al. 1999). At the time of deposition, the basin was situated about 18 degrees north of the equator near the west coast of the super-continent Pangea (Stewart et al. 1972; Blakey 1989). The formation is now exposed over broad parts of the southwestern United States, and as a result of its depositional environment, consists of several discontinuous units. In Petrified Forest National Park the formation is about 300 m thick and is conventionally divided into the Lower Petrified Forest Member, the Sonsela Sandstone Bed, the Upper Petrified Forest Member, and Owl Rock Member (see Fig. 1B and Dubiel et al. 1999).

MATERIALS AND METHODS

The remains of the branch described here were collected from the ground surface at the foot of a small, severely eroded, steep hill on the north side of Lithodendron Wash in the Painted Desert Section of Petrified Forest National Park (Fig. 1A). When found, they were lying loose, spread over an area of a few square meters together with many other fragments of black fossil wood, which may represent the same branch. However, this is uncertain because the fragments lack bark and do not fit any of the bark-clad fragments although they are similar in appearance to *A. arizonicum*.

   Since none of the bark-clad fragments were found *in situ*, their origin is somewhat debatable because the hill above the slope from which they were collected is underlain by red mudstones of the Petrified Forest Member of the Chinle Formation, a lithofacies that typically does not contain petrified wood. However, the Black Forest Bed, which occurs nearby and stratigraphically above the locality in the middle of the member, contains abundant, distinctive black petrified wood that is very similar. Furthermore, the holotype of *A. arizonicum* was collected from the Black Forest Bed at an adjacent locality in the Painted Desert (Ash 1992) and none of the petrified wood that occurs in the Chinle at other horizons and localities in the Petrified Forest National Park, such as Crystal Forest or elsewhere, is so darkly colored. Although the Black Forest Bed is no longer present above the collecting locality because it has been removed by erosion, it is still preserved on neighboring hill tops. Therefore, because petrified wood is not known to occur in the red mudstones of the Petrified Forest Member and identical fossilized wood occurs in large quantities in the Black Forest Bed, it appears most likely that the specimen described here was derived from the latter unit. It probably accumulated as a lag deposit at the base of the small hill where it was found while the Black Forest Bed on the top of the hill was being eroded. The presence and fresh appearance of the bark indicates that the branch was not transported any significant distance prior to burial in the Black Forest Bed or after being exposed sometime since the Triassic.

The fossil was studied using reflected light and with transmitted and differential interference contrast light using ground thin sections. All of the slides and uncut material are stored in the collections at Petrified Forest National Park, Arizona, under the number PEFO 3784. In describing this specimen, we have employed bark terminology as defined by Junikka (1994) and Trockenbrodt (1990).
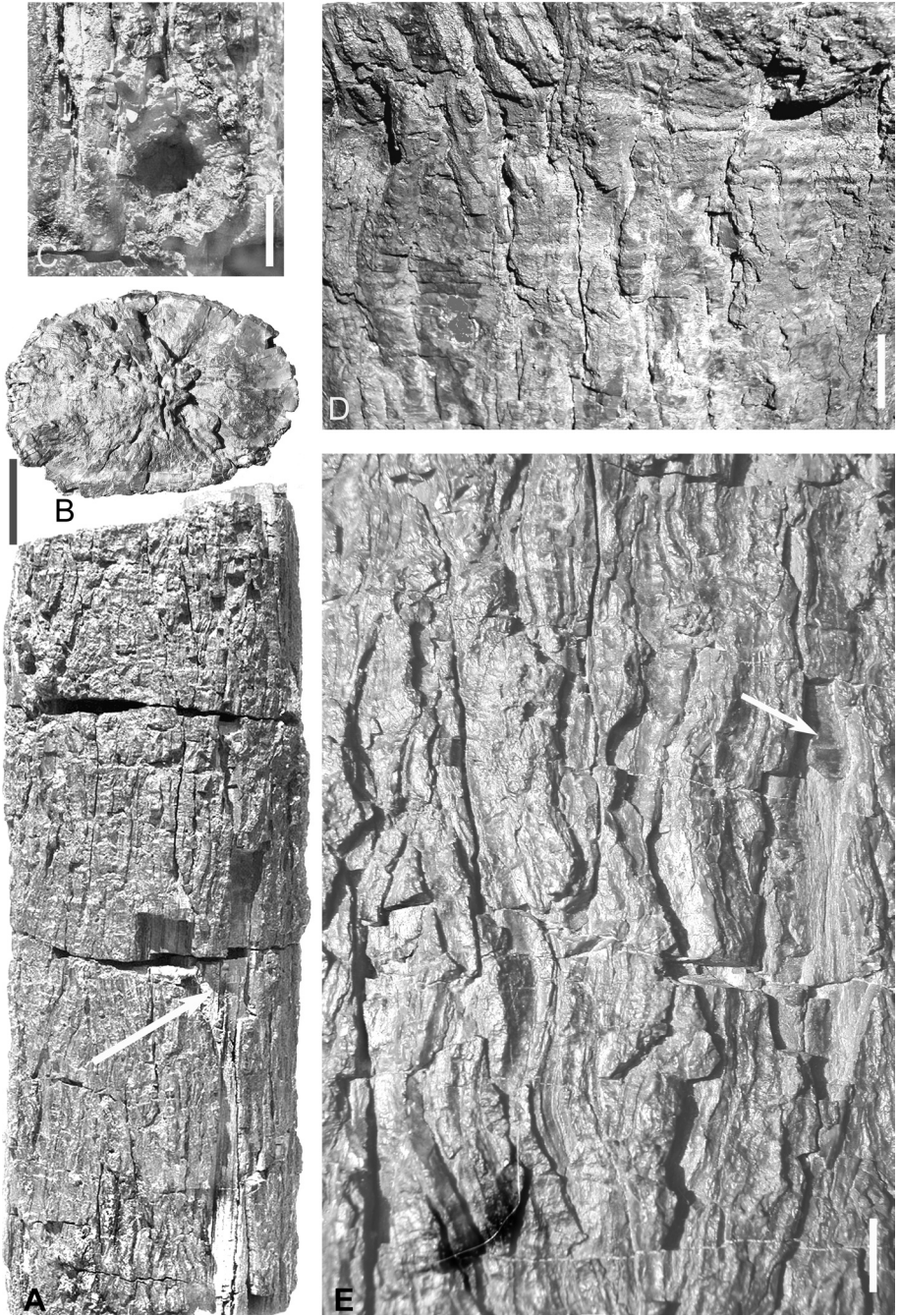
OBSERVATIONS

Macroscopic features

When discovered, the axis was in nine bark-clad fragments, five of which are more or less complete segments about 110 × 117 mm in diameter. Three of the longest fragments fit together forming a 470 mm long specimen (Fig. 2A). The other two segments and four of the fragments also fit together to form a second specimen about 230 mm long. Both reconstructed specimens are broadly oval in transverse section with one side slightly flattened in comparison to the opposite side (Fig. 2B). Although they do not fit together, the two reconstructed specimens probably came from closely adjacent parts of the same axis since they are about the same shape in cross section and diameter. If this is a valid conclusion, then they represent approximately 0.7 m of an axis which must have been much longer originally because neither of the reconstructed portions narrows significantly. The microscopy observations reported here are based on parts of the 230 mm long specimen.

The surface of the bark is very irregular and is broken into narrow (5–15 mm), axially oriented, short, usually undulating ridges and intervening shallow (1–3 mm) irregular fissures 1–8 mm wide (Fig. 2A, E). On the rounded side of the axis, the bark ranges from about 2 to 9 mm in thickness (averages about 3 to 5 mm), but it is generally somewhat thinner on the flattened side. It is possible that the bark could have been thicker before the axis was buried, but its general character seems to indicate otherwise.

The pith is present in each section, indicating that the axis is not a root. Several features of the fossil indicate that it is part of a branch and not a small diameter tree. For example, the diameter of the axis falls within the size range reported for branches of the *A. arizonicum* tree by Ash and Creber (2000) and in lateral view the reconstruction is slightly curved over its length. Near one end of the fossil the bark on the flattened side is transversely rippled. The ripples are formed of a series of low rounded ridges about 0.5 mm high and 2 mm wide, separated by flat valleys about 3 mm across (Fig. 2D). The rippled bark is similar to that often forming in bark on the undersides of branches (Esau 1960) and also to ridges observed beneath branch junctions of the *A. arizonicum* trees in the Petrified Forest (Ash & Creber 2000). Consequently, it appears likely that the flattened side of this branch is indeed its underside, and that the branch end having the compression ridges had been near its junction with the trunk.

Most of the fossil was permineralized by quartz, but some parts were completely replaced and therefore lack any cell structure. As is typical of petrified wood found in the Black Forest Bed, the fossil is black in color with grayish streaks. The original dark color of the exterior of the specimen has been heightened by the dark patina usually termed "desert varnish" which commonly develops on exposed rock surfaces in the southwestern United States and other arid regions of the world. The axis is longitudi-

nally cracked and, like so many logs in the Park, it is also transversely fractured. The pith region has been crushed and sheared but both the bark and secondary xylem near the surface of the specimen were little affected by the interior distortion. Evidently interior deformation occurred after the exterior layers had been sufficiently petrified to resist the force.

A few small, randomly distributed widely isolated lateral branches are present along the sides of the branch (Fig. 2A), a characteristic also displayed by *A. arizonicum* in the Petrified Forest (Ash & Creber 2000). The lateral branches are about 1.5 cm in diameter and are inclined upward at an angle of about 30°–40° to the surface of the branch. Some are represented by short (< 2 cm) lengths that protrude a short distance through the bark but others are partially overgrown by bark. Also, one is represented by a shallow depression in the surface of the bark (Fig. 2C).

Microscopic features

Pith – The pith in this specimen has been crushed slightly and fractured and is about 2–3 mm in diameter measured from the apices of inwardly protruding wedges of secondary wood. Quartz deposits in the fractures partially to completely obliterate anatomical detail in the pith (Fig. 2C, 4A, 5A) and elsewhere most of the cells have disintegrated to the point that they cannot be distinguished with certainty. Outlines of squarish isodiametric thin-walled parenchyma cells (about 30 μm in diameter) are faintly visible in places as the only discernible cell type in the pith. Some of these cells contain black material which may be resin. No evidence of a septate pith was found.

Primary xylem – The primary xylem is generally difficult to distinguish because of the compression fractures traversing the pith (Fig. 4A). It is most clearly demonstrated in longitudinal sections through the pith but it is also visible at places in cross sections. It appears to be represented by poles of small (~20 μm in diameter), round, compactly arranged cells at the apices of wedges of secondary xylem converging on the pith (Fig. 4A).

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Fig. 2. Surface features (A, C–E) and cross section of a branch (B) of the *Araucarioxylon arizonicum* tree. – A: Lateral view of the upper side of the longest length of the reconstructed bark-clad branch. The features on this surface are relatively sharp and fresh compared to those on the presumed under surface (see Fig. 2D). A few insect tunnels are present on the surface of the vascular cylinder just above the base of the specimen (arrow) and are shown at a higher magnification in Fig. 8C. PEFO 3784A, B, C. – B: Cross section of the base of the specimen shown in Fig. A. The rounded side of this figure is the upper surface of the branch shown in Fig. A. PEFO 3784A. – C: Scar of a lateral branch in the bark. Apical end of the branch is at the top of the figure. PEFO 3784C. – D: A series of compression ridges on the exterior of the bark on the underside of the branch. As is typical of the bark on the underside of the branch the strips and fissures are generally subdued in this view. The apical end of the branch is at the top of the figure. PEFO 3784A. – E: Surface of the bark on the upper side of the branch at natural size. Note the undulating strips and irregular fissures. The arrow points to a narrow strip of the vascular cylinder which was exposed when the bark fell away. The dark area at the top of the strip appears to be a bit of the inner bark that still adheres to the wood. PEFO 3784B. — Scale bars: A & B = 50 mm, C–E = 10 mm.
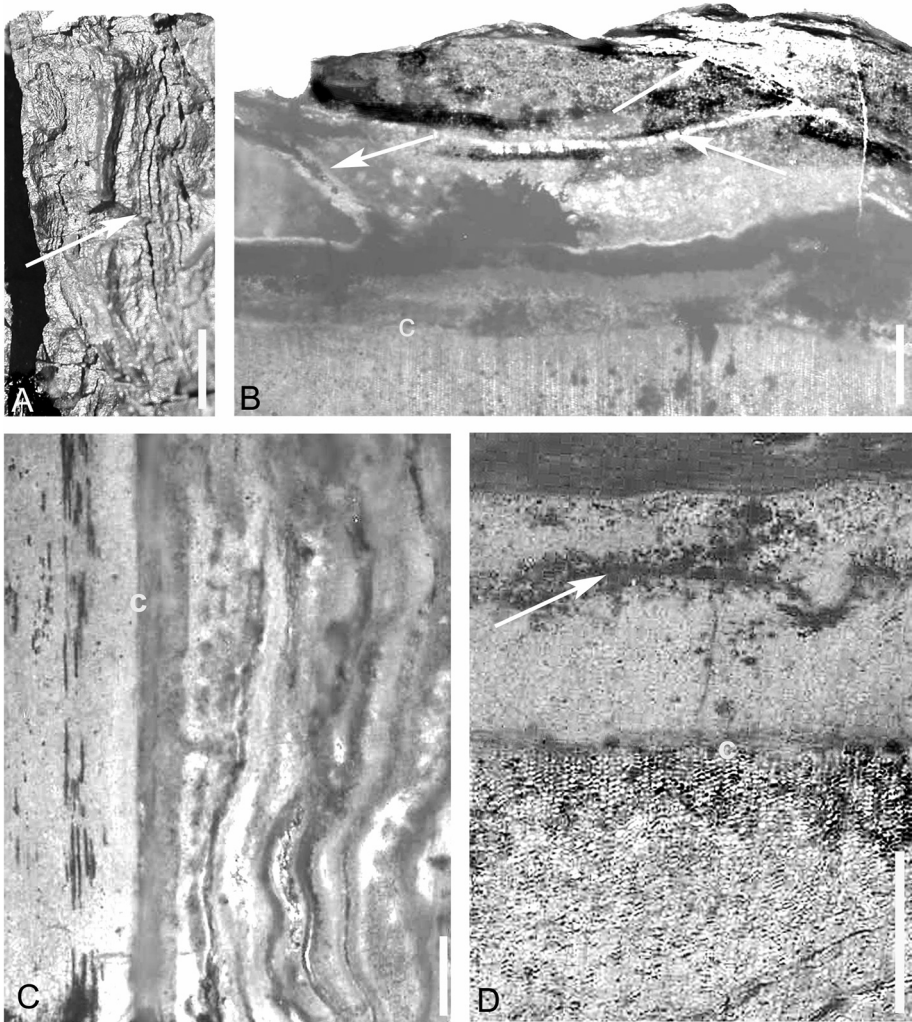
Fig. 3. Surface view and sections of the bark and wood of the *Araucarioxylon arizonicum* tree.
– A: Successive parallel layers of periderm (arrow) exposed on the upper side of the branch. PEFO
3784E. – B: Cross section of the outer part of the secondary xylem (at base of image) and the
bark The thick lens-shaped plates of periderm are demarcated by separation layers (arrows); c =
cambium. Slide PEFO 3784G2x. – C: Radial section of the outer part of the secondary xylem at
the left with the cambium (c), inner bark and periderm layers on the right. Note the dark streaks
of supposed resin in the tracheids a short distance below the cambium. The dark wavy bands in
the bark are sequent periderms separated by narrow zones of phellogen. Slide PEFO 3784G1p.
– D: Cross section of the secondary xylem (at the bottom) and the tissues external to it. Some of
the tracheids contain dark material which is probably resin. Note that external to the cambium
(c) the radial width of phloem is very narrow, with most of the bark consisting of inner and outer
peridermal layers. One of the separation zones between sequent periderms is indicated by an
arrow. Slide PEFO 3784D2m. — Scale bars: A–D = 10 mm.

Secondary xylem – The xylem cylinder is about 106 × 113 mm in diameter and the outside surface is completely covered by bark except in a few generally narrow longitudinal strips that range up to 20 mm in width (Fig. 2A, E). In these strips, the exposed surface of the xylem cylinder is smooth and somewhat wavy, suggesting the wood was dimpled (see Fig. 6G).

The secondary xylem (Fig. 3A, C, D) consists of radial files of axial tracheids and rays. In cross section, the tracheids are square, rectangular or hexagonal with ellipsoid lumens (Fig. 4B, E). Tracheid secondary walls are generally thick, 5 μm single wall thickness being common for radial walls, although tangential walls at their narrowest points are less than half that thickness. In places there appear to be intercellular spaces (Fig. 4B); however, the round to oval shape of the lumen is not necessarily linked to the presence of intercellular spaces and often is seen in tracheids that have tightly adjoined cell corners (Fig. 4F). Typically, the tracheids range from 12–54 μm in radial diameter, and tangential diameters from middle lamella to middle lamella as measured on cross sections across the largest diameter radial files varied from 40–56 μm. Narrower tangential dimensions were also seen and are evidence for tapering tracheid ends and the occurrence of anticlinal divisions in the cambium. Tracheid length could not be accurately determined but tracheids extend without interruption to > 5 mm (Fig. 4C, 5D). Resinous elements are scattered throughout the axial system of the secondary xylem (Fig. 3B, D).

Rays are numerous in the secondary xylem and, as viewed in cross section, are separated by 1–6 files of tracheids (Fig. 3B, D, 4B). The rays are uniseriate, 1–26 cells high (Fig. 4B). In tangential section the ray cells are round and about 9–22 μm in diameter and often contain dark material, possibly resin. The nature of cross-field pitting could not be determined due to poor preservation. Rays were not seen external to the cambium (Fig. 3A, B, 5B). Neither ray tracheids nor horizontal resin canals were seen in the wood.

Intertracheary bordered pits are in general poorly preserved, but are common on the radial walls (Fig. 4D). Pits are uniseriate, generally tightly packed with their margins contacting and not uncommonly appearing to have either a compressed or hexagonal outline (Fig. 4D). Bordered-pit diameter is fairly uniform at 16–20 μm with apertures about 5 μm in diameter. As shown in Figure 4D, there is the suggestion of a torus; however, this could not be determined conclusively because of poor preservation.

Growth rings that make a complete circuit of the branch are not present in the secondary xylem (Fig. 2B), although a few growth interruptions extend at least part way around the branch. As shown in Figures 4E and 5B, radial files of secondary xylem generally contain radially large diameter tracheids; however, just interior to the cambium the fully enlarged tracheids have radially small diameters with secondary walls up to 12 μm in single wall thickness, equal to their lumens. Thus, there is the impression of earlywood and latewood zones.

Vascular cambium – In most places cambial cells are not visible and have been replaced by mineral or disorganized organic matter (Fig. 5B), as occurs in other fossil woods, e.g., *Taxodioxylon gypsaceum* (Ramanujam & Stewart 1969) where the cambium is merely inferable by a contact line. However, in scattered locations evidence
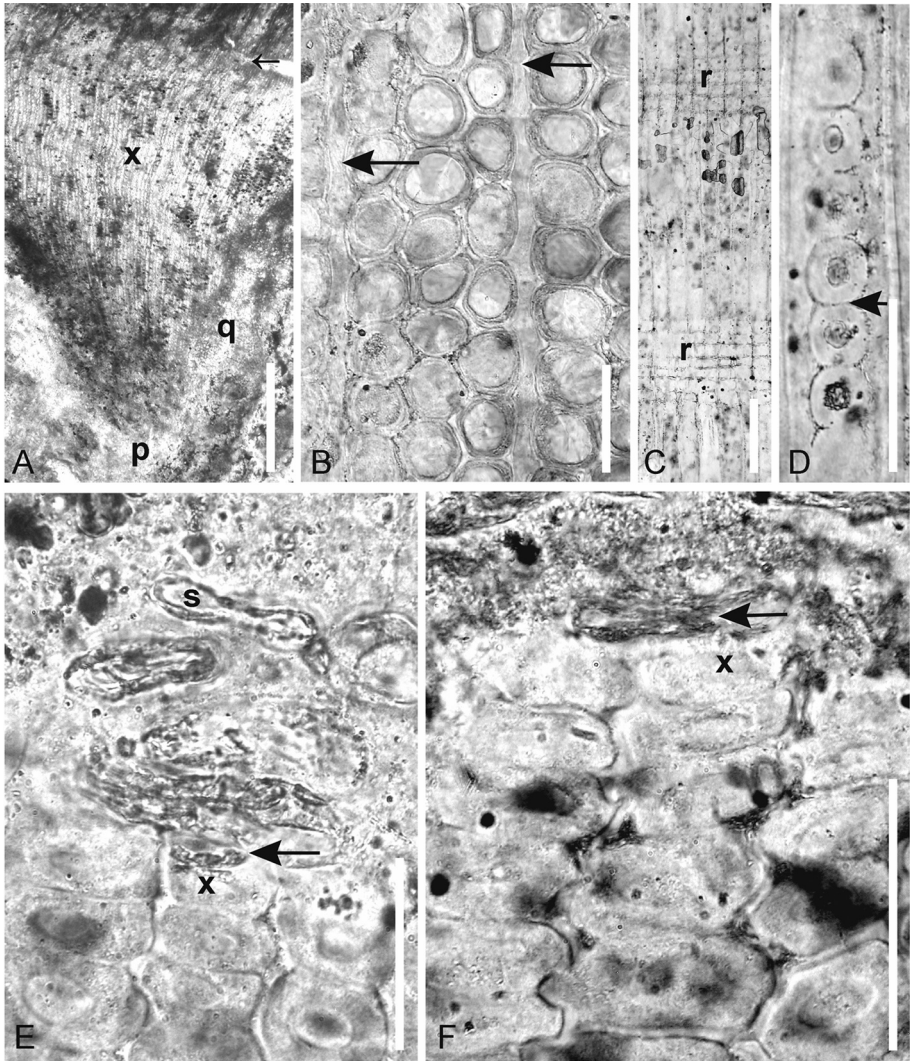
Fig. 4. Xylem in transverse section (A, B) and in radial section (C, D) and cambial region in transverse section (E, F). – A: A wedge of the first-produced secondary xylem (x) tapering to the pith (p), with quartz-infilled fracture zones on both sides (q). The separation of xylem shown in upper right (arrow) occurred at the boundary of a latewood-like zone (radially small diameter tracheids) with an earlywood-like zone. Slide PEFO 3784E2l. – B: Radial files of rounded compression-like tracheids. Two uniseriate rays are arrowed. Slide PEFO 3784G3a. – C: Secondary xylem axial tracheids with two rays (r) visible. Slide PEFO 3784G3b. – D: Uniseriate, rounded bordered pits somewhat flattened at their contacts (arrow). Slide PEFO 3784G3b. – E & F: Examples of the cambial region in transverse sections. The arrows point to what appear to be fusiform cambial cells, numbering 1–3 per radial file, in contact with the outermost tracheids (x). Thin-walled sieve cells (s) of similar appearance to fusiform cambial cells were rarely seen. Slide PEFO 3784G3a. — Scale bars: A = 500 μm; B, C = 100 μm; D–F = 50 μm.
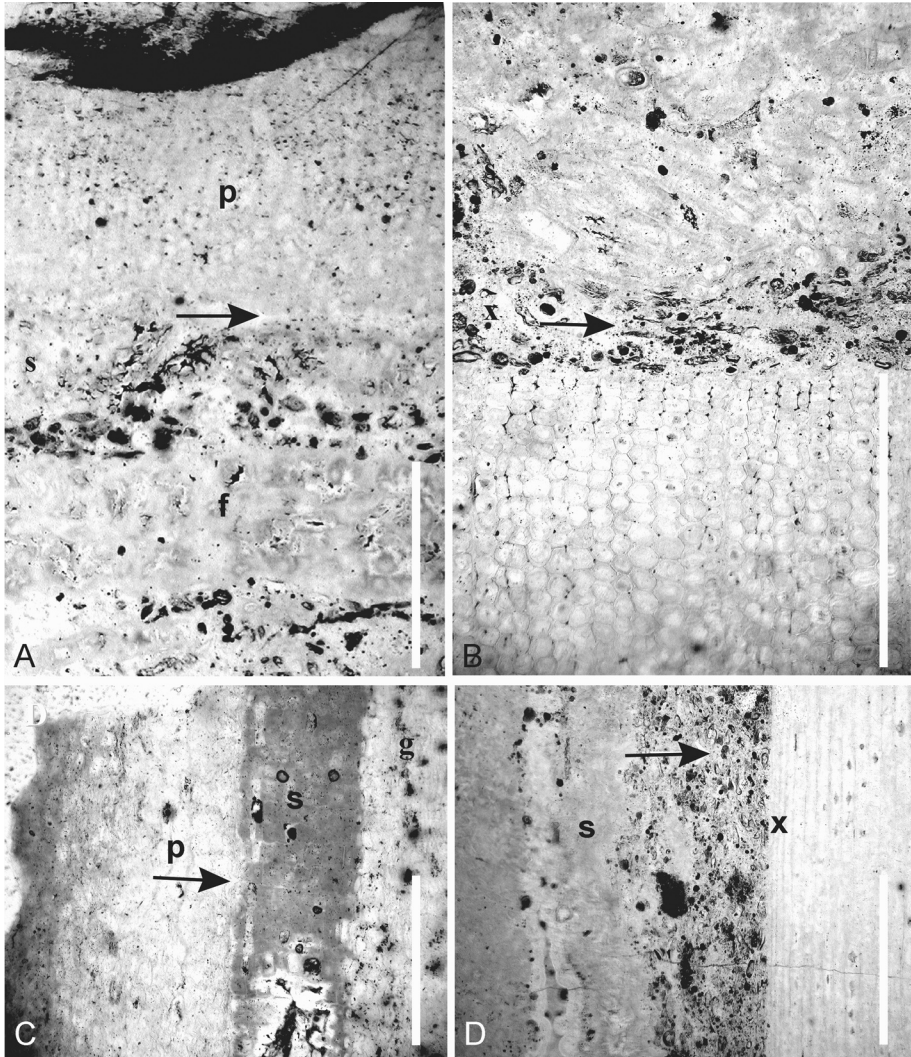
Fig. 5. Inner and outer barks in transverse (A, B) and radial sections (C, D). – A: Outer bark, the external boundary being the dark ragged layer at the top. A narrow detachment zone comprising light-coloured thin-walled cells (arrow) separates an outer periderm (p), consisting of files of radially expanded thin-walled parenchyma, from differentiating sclerenchyma (s) and a zone of mature fibers (f). Slide PEFO 3784G3a. – B: A zone of heterogeneous material (arrow) separates sclerenchyma (s) of the innermost periderm from phloem; x indicates a transitional point in the secondary xylem from radially wide to smaller diameter tracheids. Slide PEFO 3784G3a. – C: The outer periderm consisting of parenchyma (p) is separated from dark cork-like sclerenchyma (s) by a thin detachment zone (arrow). A zone of thin-walled cells appears to be phellogen (g). Darker cells also having thickened walls are at the external bark surface (left). Slide PEFO 3784G3b. – D: An inner periderm comprising mostly sclerenchyma (s) is separated from the phloem–cambial region by a zone of heterogeneous material (arrow), with xylem (x) on the right. Slide PEFO 3784G3b. — Scale bars: A–D = 500 μm.
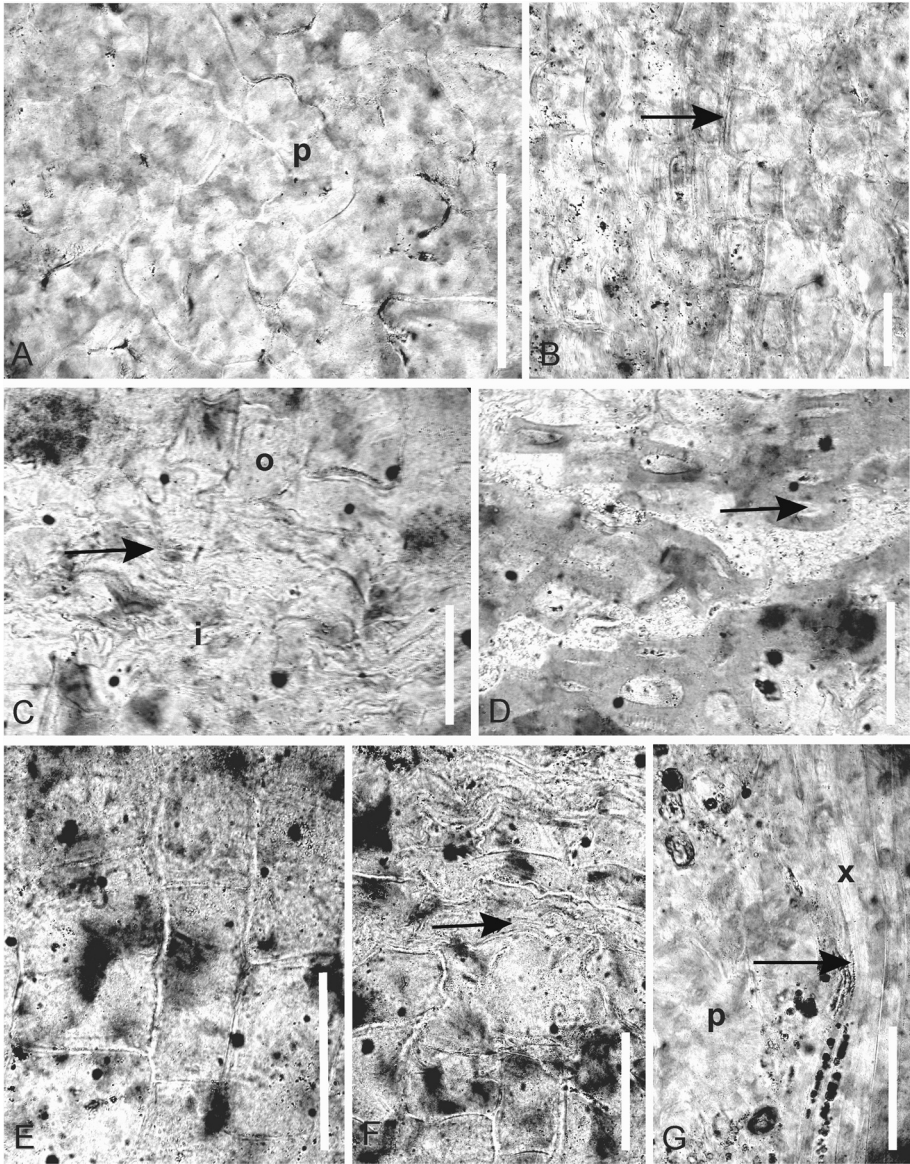
Fig. 6. Periderm in transverse section. – A: Elongated, curved and spongy parenchyma cells such as the one labeled (p) are common in the outer phelloderm; radial section. Slide PEFO 3784G3a. – B: Upright brick-like cells with thickened walls (arrow) occur within periderms in fairly discrete zones bordered on both sides by parenchyma; radial section. Slide PEFO 3784G3a. – C: A layer of phellogen (arrow) with phellem (i) and phelloderm (o); this narrow zone appears to serve as the detachment zone as well as the meristem for periderm generation; cross section. Slide PEFO 3784G3a. – D: Thick-walled fibers (one is arrowed) occur as groups in the phelloderm; cross section. Slide PEFO 3784G3a. – E: Thin-walled radially enlarged parenchyma predominate the phelloderm; cross section. Slide PEFO 3784G3a. – F: Thin-walled often misshapen and

was found for fusiform cambial cells in both cross and radial sections (Fig. 4E, F, 6G). The fusiform cells are thin-walled, and their radially compressed outlines in cross section appear dumbbell shaped, similar to those found in extant conifers, particularly during dormancy (Fig. 4E, F). Fusiform cell tangential width (up to 50 μm) is similar to that of the corresponding radial file of tracheids. No more than four fusiform cells per radial file were noted in the cambial zone. Thus, it is probable that the cambium was dormant, and this agrees with the above interpretation that latewood-like cells were in contact with the cambium. Evidence for rays in the cambium was not found.

Inner bark – Inner bark, or secondary phloem, is very limited in the specimen described here (Fig. 3D, 4E, F, 5B, D). In cross sections, thin-walled fusiform cells external to the cambium presumably are sieve cells (Fig. 4E); however, they appear to span only a very narrow radial width (Fig. 4E). Phloem appears to be entirely absent where the outer surface of the xylem is dimpled (Fig. 6G). Rays were not seen in the phloem. External to the narrow zone of sieve cells is a heterogeneous layer, less than 300 μm in radial width, consisting of dark and light colored objects (presumably a mixture of disorganized organic matter and cells) that separates the inner from the outer bark (Fig. 5B, D).

Outer bark – The outer bark appears to be a simple non-banded type because, other than the presence of sequential periderms containing cork-like cells (Fig. 3B, C, D), there is no evidence of alternating tangential bands of other cell types. The outer bark is 2–10 mm thick and averages 3–4 mm in thickness. It is composed of thin plates of sequent, tangentially overlapping periderms separated by thin detachment zones. The periderms are sharply curving, appearing as lenses in cross section, and as wavy layers in radial section (Fig. 3B, C, D). The individual peridermal lenses are up to 2 mm in thickness and as much as 9 mm in width.

Radial files of square to rectangular, thin-walled parenchyma, 15–30 μm in tangential width and 60–80 μm in radial length, are the prevalent cell type in the sequent periderms (Fig. 3C, D, 5A, C, 6E), although curved and spongy parenchyma reaching 100 μm in length and evidently having intercellular spaces are also common (Fig. 6A). Cork-like cells, 25–38 μm in diameter with conspicuous lumens and simple-pitted walls 6–8 μm in thickness, border the peridermal lens detachment zones (Fig. 6B, D). In cross section the cork cells may be mistaken as fibers (Fig. 6D); however, in radial section these 'fibers' are actually seen to be squat brick-shaped to cubical cells (Fig. 6B). These distinctive secondary-walled cells tend to occur in neatly arranged files; thus, it seems probable that they arose by continuing differentiation of the phelloderm's radial files of parenchyma (cf. Fig. 5A). Similar thick-walled cells were infrequently found to occur individually, or in small groups, at locations in the peridermal tissue

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probably physically collapsed parenchyma are common in phellem; cross section. Slide PEFO 3784G3a. – G: In association with dimpled regions (arrow) in the outermost secondary xylem (x), the phloem-cambial region is bordered by little if any heterogeneous material (some of which is present at upper and lower left) and instead appears to be in direct contact with nodules consisting of enlarged parenchyma (p) and occasional isodiametric sclereids; radial section. Slide PEFO 3784G3a. — Scale bars: A–G = 50 μm.

somewhat removed from the detachment layers. The sequent periderms are free of dilation tissue, and neither horizontal nor vertical resin canals were seen in any part of the bark.

The position of bark abscission evidently is that region comprising phellogen with associated immature phellem and phelloderm (Fig. 5A, C, 6C, E, F). This zone is about 0.3 mm in radial thickness. It generally consists of darker cells than the surrounding tissue, but in some locations the zone also appears lighter, the brightness evidently being associated with more severe petrifaction (cf. Fig. 3B, D). This detachment zone evidently arises within the outer bark following differentiation of phellem into the cork-like, presumably suberised, thick-walled, more or less isodiametric cells described above (Fig. 6B, D).

EVIDENCE FOR INSECT ACTIVITY

Small, simple tunnels occur at several places in the wood and bark on the rounded side of the branch described here (Fig. 2A, 7A–E, G, H). These tunnels are attributed to the boring activities of insects, based on their size and by the similarity of the tunnels to those of extant "powder post" beetles. Furthermore, the remains of a larva similar to those of the living powder-post beetle *Anobium* were observed in the wood of this branch (Fig. 7F). The fossil larva is about 0.5 mm in length and was found less than 1 mm beneath the cambium near one of these tunnels.

Typically, the tunnels are circular in cross section, but a few are somewhat angular (Fig. 7A, B, G). Most are slightly less than 1 mm in diameter and the longest are about 1.3 cm in length. All are straight to slightly curving and appear to be unbranched (Fig. 7G). No side chambers or "cradles" were observed and none of the tunnels contain frass or reaction tissue. Based on their position within the branch they can be subdivided into internal tunnels and surface tunnels. The internal tunnels occur sparsely in the xylem cylinder from 4–20 mm below the bark and are mostly visible in tangential and radial sections of the branch (Fig. 7B, E, H). Usually they are isolated some distance from each other and generally are perpendicular to the grain of the wood (Fig. 7B), although a few follow the grain (Fig. 7E) or are slightly inclined (Fig. 7B, H). No connections between the internal tunnels and the outer tunnels were observed.

The surface tunnels occur in the bark and the outermost part of the xylem cylinder, within 2 mm or less of the cambium. They are most abundant in the wood but a significant number occur also in the bark, particularly in the inner periderm (Fig. 7D, G).

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Fig. 7. Tunnels made by insects in the bark and wood of *Araucarioxylon arizonicum* (A–E, G, H) and what appears to be an insect larva embedded in the wood (F). – A: Isolated tunnels (arrow) on the outer surface of the vascular cylinder on the upper side of the axis that is shown in Fig. 2A. PEFO 3784A. – B: Polished tangential section about 1 cm below the xylem surface showing several isolated tunnels (arrow) that extend radially into the wood. Note that the wood is transversely fractured. PEFO 3784D1a. – C: A single upward inclined tunnel (arrow) on the outer surface of the bark. PEFO 3784G1. – D: Oblique view of part of the bark and xylem surface in Fig. G showing in the center of the field of view a broad cavity (arrow) created by insects under the bark (compare G). PEFO 3784D1a. – E: Tunnels (arrow) parallel to the wood grain in an
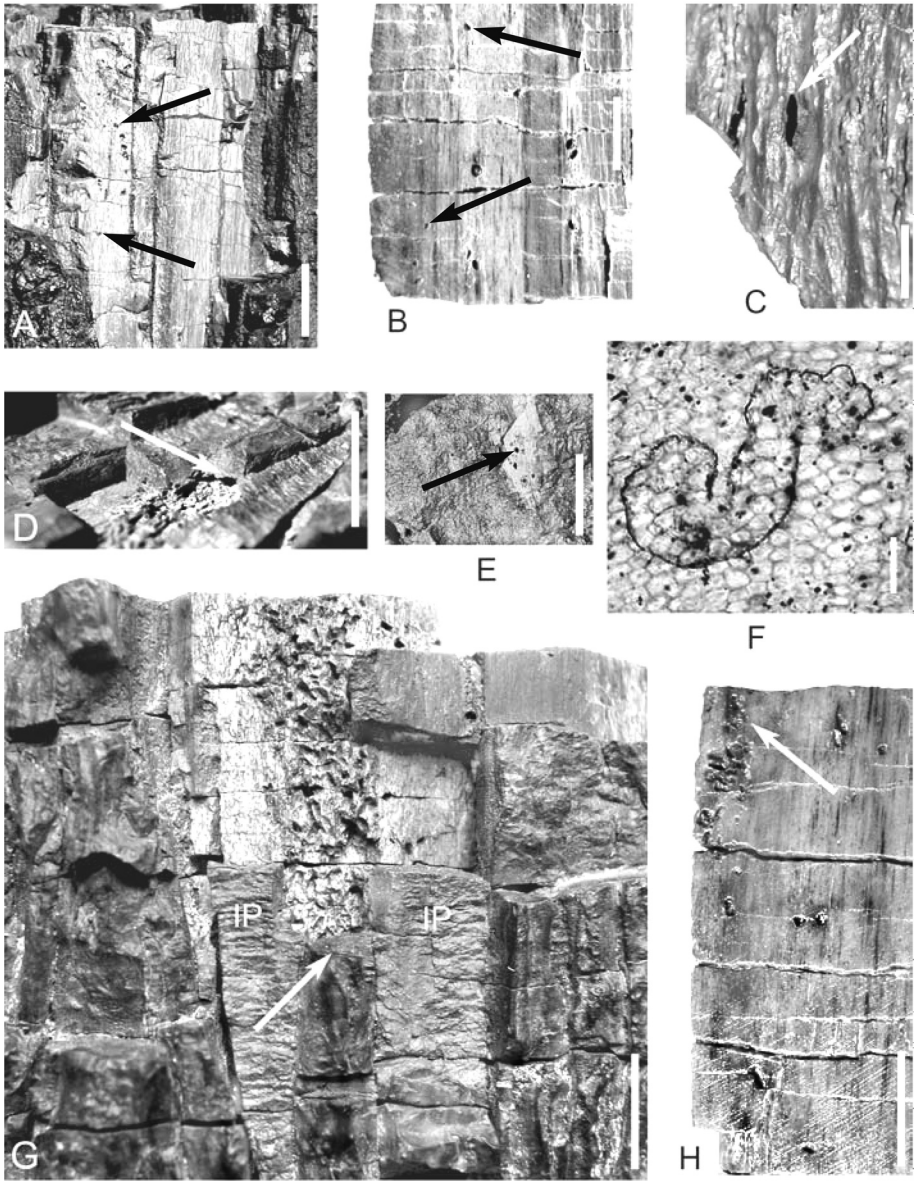
area about 2 cm beneath the xylem surface. PEFO 3784. – F: Cross section of a putative insect imbedded in the xylem about 1 mm in radial distance from the cambium. Slide PEFO 3784G3a. – G: A cluster of tunnels at the xylem surface. The wrinkled surface of inner periderm (IP) is visible where the outer scales of bark have disappeared. The arrow points to the roof of the cavity shown in Fig. D exposed at a different angle. PEFO 3784D1a. – H: Polished tangential section of xylem near its surface showing a cluster of tunnels (arrow) and several isolated tunnels. Note the dark streaks parallel to the grain which presumably are resinous zones in the tracheids comparable to those in Fig 4B. PEFO 3784D1. — Scale bars: A–E, G & H = 1 cm, F = 100 µm.

The tunnel entrances are scattered randomly on the surface of the bark (Fig. 7C) and xylem cylinder where it is exposed (Fig. 7A, G). Generally, the tunnels slope upward slightly in the bark (Fig. 7C) or are perpendicular to the grain and run through the wood more or less along radial lines (Fig. 7A, H). Most are separated, but in two places there are irregular clusters of short (< 10 mm) interconnected tunnels running in all directions along the surface of the vascular cylinder and in the lowest parts of the innermost outer bark (Fig. 7A, D, G). In surface view, the largest of these clusters is about 11 mm wide and more than 26 mm long (Fig. 7D, G). The total length of this cluster in surface view is unknown because one end extends for an unknown distance under the bark where it forms a cavity as much as 1 mm high and 6 mm wide in the cambial region (Fig. 7D). A somewhat similar cluster is present in the wood a few mm below the bark (Fig. 7H).

Two lines of evidence suggest that insects probably attacked the branch after it was dead and lying on the ground but before burial. First, the absence of reaction tissue in the tunnels indicates that the branch was not living when attacked. Second, the presence of tunnels on only the rounded side of the branch suggests that the opposite (flattened) side was inaccessible to the insects because the branch was lying on the ground surface and may have been partially buried in mud.

Although these tunnels are attributed to the boring activities of insects, they do not closely resemble any of the tunnels and other traces Walker (1938) described in fossil wood from the Chinle Formation in Petrified Forest National Park. However, slightly smaller, but otherwise comparable tunnels were described in Late Triassic wood from Germany by Linck (1949) as *Anobichnium simile* because they were similar to the tunnels produced by the living "powder-post" beetle *Anobium* (Anobiidae). Most of the Chinle tunnels reported here fall within the size range of the borings made by the living "powder-post" beetles that attack and breed in dry coniferous wood and bark (Wilson 1977). The resulting tunnels are unlike the traces produced by the bark beetles of the Scolytidae which principally bore galleries in regular patterns along the cambium, parallel to the surface of the xylem cylinder (Chamberlin 1958; Wood 1982). The clusters of short tunnels along the cambium of this branch (Fig. 7D, G) are comparable to the so-called gouges formed by the extant Southern Pine Sawyer (Cerambycidae) in dead and decaying pines (see Bennett et al. 1958). However, in spite of their similarity to those produced by the Cerambycidae and the Anobiidae, the tunnels described here and the fossil larva observed in the wood cannot be assigned unequivocally to either family at this time because the body fossil record of both only extends to the Early Paleogene (Carpenter 1992).

DISCUSSION

The fossil described here contributes to our limited knowledge of the geologic history of fossil bark of woody plants as summarized in Table 1. That history, which begins with the well known and modern appearing bark of the Devonian progymnosperm *Archaeopteris* (*Callixylon*) tree (Scheckler et al. 2001), consists mostly of reports of bark similar to that found in many extant woody plants. It also includes a few incompletely preserved examples of bark in which it is not possible to determine if there are sequent

periderms. In contrast, no fossil examples of the simple type of vertically oriented ridge-and-furrow sequent periderm bark structure described here seem to have been reported previously, although it occurs in a number of extant conifers (Smoot 1984). This pattern (= *Pseudotsuga taxifolia* type of Den Outer 1967) has been recognized in many members of the living Pinaceae (Chang 1954). Thus, this finding of non-banded vertical strip bark extends the history of this type of bark 220 million years into the Late Triassic.

Bark of extant *Araucaria heterophylla* (a 10-year-old stem) appears distinct from that of the *A. arizonicum* fossil branch. At the crushed phloem–outer bark interface of *A. heterophylla*, there is a zone of large diameter thin-walled parenchyma, variably sized and randomly oriented, and immediately external to that zone is a zone of poorly organized large diameter (many in excess of 200 μm) stone cells each exhibiting countless secondary wall lamellae with little or no lumen. It reasonably may be expected that the stone cell zone, had it been present in *A. arizonicum*, would have endured petrifaction with little or no alteration, particularly as more external radial files of thin-walled parenchyma did so (Fig. 5A). It is possible that the zone of sclerenchyma identified in Figures 5A and D is analogous to the stone cell zone in *A. heterophylla*, and that the heterogeneous zone interior to the sclerenchyma comprises crushed parenchyma and phloem. External to the stone cell zone, there are sequential periderms in *A. heterophylla* bark; however, those periderms are in the form of bands and are quite unlike the sequential periderm lenses found in *A. arizonicum*. In *A. heterophylla* the peridermal layers alternate between thin-walled parenchyma and thick-walled fibres, and both cell types have their long axes oriented circumferentially, perpendicular to the long axis of the stem. Consequently, the outer bark of *A. heterophylla* is strongly banded. As described and shown above (Fig. 3, 5), in *A. arizonicum* the peridermal strips and furrows comprise files of radially enlarged parenchyma and squat brick-shaped cork-like cells, and the bark is not banded, facilitating longitudinal splitting and creation of ridges and furrows. If bark features are definitive for the genus, as Chang (1954) concluded that they are for extant species, our observations raise doubt as to the existence of a close relationship between *Araucarioxylon* and extant *Araucaria*. However, the bark structure of more extant Araucariaceae need to be examined in order to confirm this conclusion.

Although resin canals, ducts and cysts are common in the bark of many conifers (Chang 1954), they do not occur in either the wood or the bark of the branch described here, nor were they reported in the *Araucarioxylon* wood described by Knowlton (1888). Turkel (1968) described irregularly arranged resiniferous parenchyma and fibers with "traumatic" resin canals in the outer cortex of the small branch that he investigated. Upon reexamination of Turkel's slides, however, we found no unequivocal evidence that canals or ducts are present. The absence of resin canals in the bark of the *A. arizonicum* tree compares with some living conifers in the Taxaceae and several members of the Pinaceae such as *Pinus*, *Larix*, and *Pseudotsuga* (Chang 1954). In contrast, resin canals were reported by Chang (1954) and De Magistris and Castro (2001) to be well developed in the bark of several members of the Cupressaceae including *Austrocedrus chilensis, Fitzroya cupressoides, Cupressus marocarpa,*and *Junipterus virginiana*.

We found only a very narrow zone of presumed sieve cells external to the cambium in the fossil branch bark of *A. arizonicum*. Otherwise we found no obvious phloem, nor evidence for phloem fibres or rays. However, in re-examining the inner bark of the small *A. arizonicum* branch investigated by Turkel (1968), phloem was found. In addition, rays clearly traverse the cambium into the phloem in that fossil but, on the other hand, fibres are not obvious.

The origin of bark presumably goes hand in hand with attainment of perennial survival. However, it remains to be deduced from the fossil record when plants first acquired fitness to tolerate severe seasonal changes, such as freezing and drought. A tree trunk of *Dadoxylon farleyense* (Permian, est. 260 Mya) from Beaver Lake, Antarctica, had growth ring-like layers, and there is evidence for cycles of primary growth in Permian lycopods (e.g., *Subsigillaria* sp.) (White 1990). Thus, cycles of growth and dormancy likely occurred in the Permian, if not earlier, at least in plants of the southern hemisphere. It remains unclear whether the latewood-like tracheids and dormant cambium found in the fossil branch of *A. arizonicum* were in response to annual or more or less frequent cycles, but our observations leave little doubt that cambial dormancy occurred near the equator in the late Triassic. One possible explanation for fossil logs in Petrified Forest National Park typically being devoid of bark is that the cambium was active when the trees fell, thus allowing the bark to become easily detached from the wood by weathering and erosional forces. Insect activity at the bark-wood interface, which is recorded in many specimens in the park (Ash 1997), is another probable explanation.

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