THE PRESERVATION OF CONIFER WOOD: EXAMPLES FROM THE LOWER CRETACEOUS OF ANTARCTICA

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(deceased September 1983)

ABSTRACT. The non-marine, upper part of the Fossil Bluff Formation (Lower Cretaceous) in Alexander Island, Antarctica, contains abundant fossil wood. Fine details of cell wall structures (including those produced by fungal and bacterial delignification) and relatively coarse cell-fill mineral textures indicate that silicification took place in two main stages. A silica overgrowth on cellulose microfibrils suggests early cell wall impregnation involving the precipitation of a very thin (?monomolecular) silica film on these structures. A later and much slower lumen fill is indicated by centripetal, euhedral quartz crystals and by collophane and apatite within cells.

ABUNDANT silicified wood is found in the upper part of the Fossil Bluff Formation which is exposed on the south-east coast of Alexander Island, Antarctica, as a series of cliffs, ridges, and isolated nunataks (text-fig. 1). This part of the formation is thought to be of Barremian to Albian age (Taylor *et al.* 1979; Jefferson 1981). The exposures are separated by glaciers up to 10 km across and from the mainland Antarctic Peninsula by the ice-bound George VI Sound. The formation was deposited in a fore-arc basin to the west of a calc-alkaline volcanic arc (Taylor *et al.* 1979; Suarez 1976). During the late Early Cretaceous, delta-top fluvial and lacustrine processes dominated sedimentation in the south of this basin. Most of the sediment was deposited as channel sands, overbank-flood sands, and crevasse-splay sands and silts, but finely laminated silt and fine sand deposits were also important.

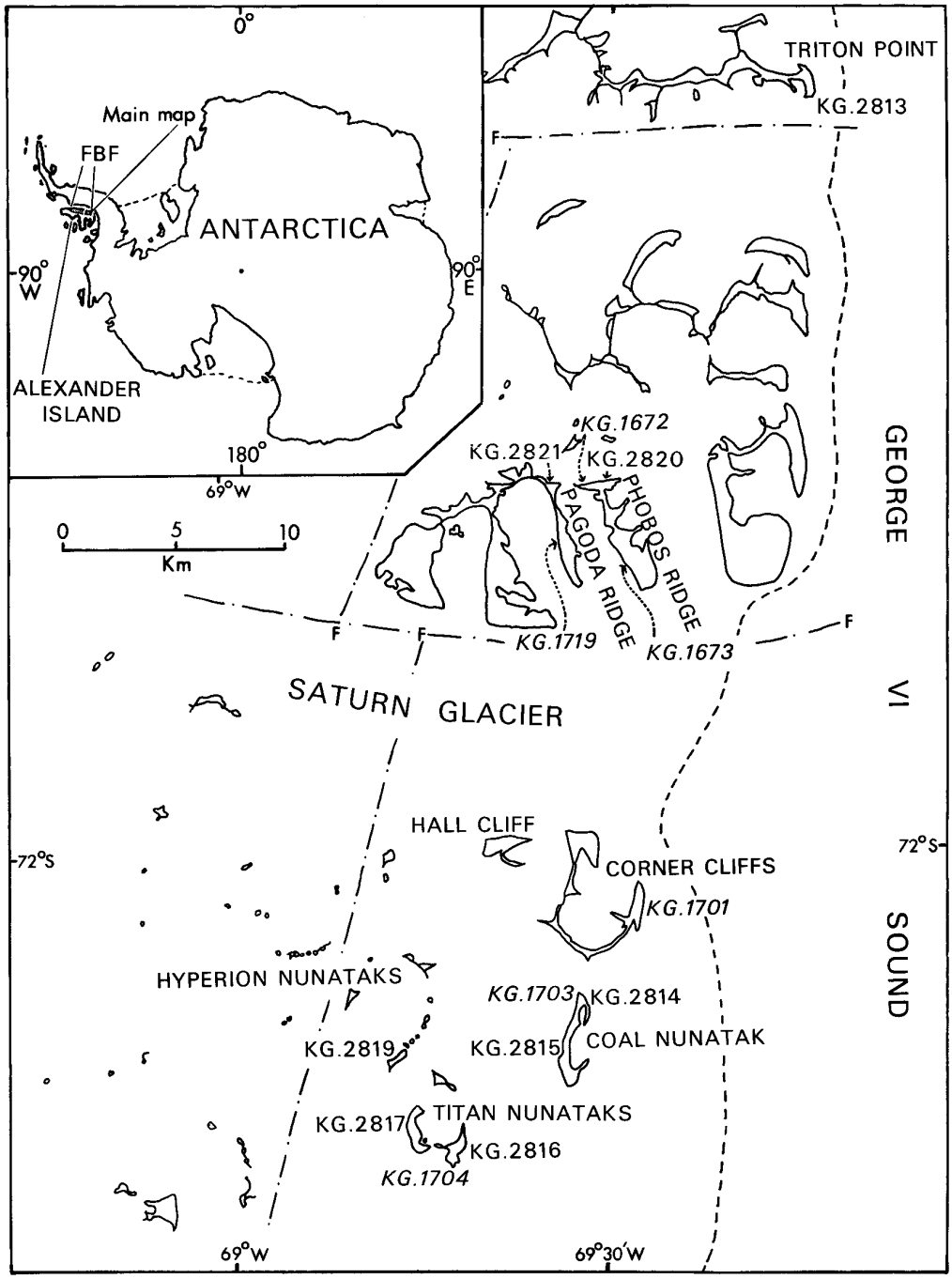
These sediments incorporated a large amount of plant material. Although diverse assemblages of leaves, stems, and seeds were preserved as compressions in mudstones, siltstones, and fine sandstones (Jefferson 1981, 1982*a*), the best preserved wood is found in coarse-grained porous volcaniclastic sandstones. Silicification depended on the early breakdown of volcanic components and the mobility of the resultant mineralizing fluids. Groups of trees were silicified in growth position as fossil forests. Growth rings within these trees are well preserved. The locations and stratigraphic positions of well preserved fossil wood were given, and the forests and their palaeoclimatic significance were discussed by Jefferson (1982*b*).

Although two types of wood mineralization (silicification and calcification) were found in fossil wood from the Fossil Bluff Formation, calcified wood fragments were found at only one locality in a marine sequence. This paper is concerned only with the silicified wood from the non-marine rocks in this formation.

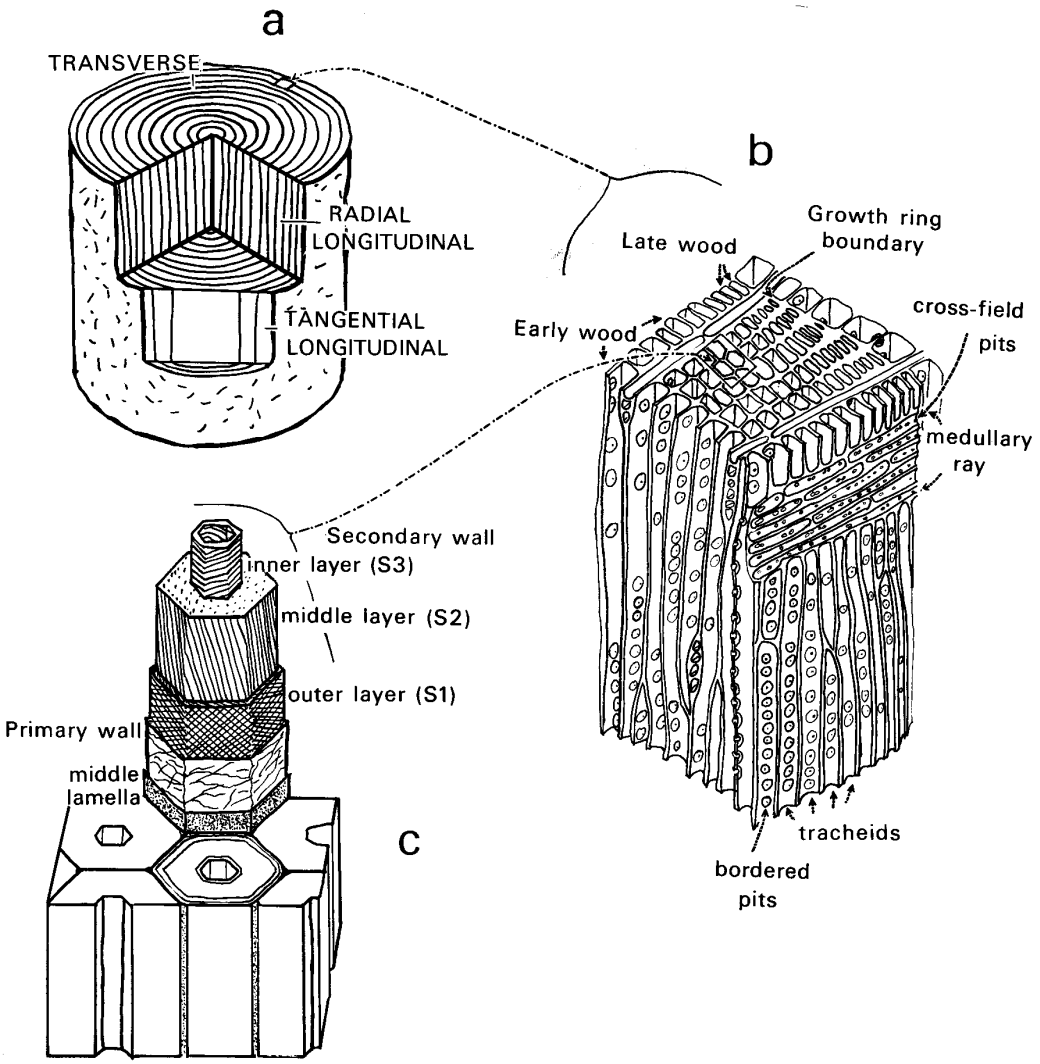
METHODS

Cell structures and preservational textures were studied both by microscopic examination of acetate peels and thin sections made in the radial longitudinal, tangential longitudinal, and transverse planes (text-fig. 2a), and by examination under the SEM. Acetate peels were prepared by etching material in 10 % hydrofluoric acid for 3 to 5·5 minutes and using the standard palaeobotanical peel techniques (Taylor 1981). Fractured surfaces were prepared for SEM work by cleaving blocks up to 1 cm^3 from specimens. Fragments were then glued to

[Palaeontology, Vol. 30, Part 2, 1987, pp. 233–249, pls. 28–30.]



TEXT-FIG. 1. Locality maps. a, Antarctica, showing the position of Alexander Island, the Fossil Bluff Formation (FBF), and the position of text-fig. 1b. b, Southeastern Alexander Island showing the localities mentioned in the text.



TEXT-FIG. 2. The structure of wood. a, The three planes in which fossil wood was sectioned or split in order to study its structure. b, Diagram of the structure of coniferous wood showing the anatomical features seen in the Alexander Island fossil woods. c, The constituent layers of the tracheid wall in extant conifers (after Wardrop and Bland 1959).

aluminium stubs and sputter coated with gold-palladium. Because files of medullary rays run out in a radial direction from the centre of woody stems (text-fig. 2b), the wood of extant conifers splits in a radial longitudinal plane. Similarly, the Alexander Island fossil wood cleaved naturally in this plane and produced some excellent radial surfaces. However, cleavage in transverse and tangential longitudinal planes is 'against the grain' of tracheids or rays, and resultant surfaces were irregular and rarely show clear anatomical details. Some specimens were polished, and other were polished and then etched in 10% hydrofluoric acid. Polishing and etching of specimen surfaces did not improve their quality, and destroyed many of the features seen on broken

radial surfaces. The etching of material not only removed silica from the cell lumen, but also caused collapse of the cell wall; this is thought to be a result of the intimate mineralization of the wall (see below). Although there is sufficient residual organic material in the cell wall to allow differential etching for peel preparation, there is not sufficient to prevent the wall from collapsing when deep etching occurs.

Qualitative energy dispersive analysis by X-ray (EDAX) was carried out on several SEM stubs to establish the relative quantities of silica and organic material in cell wall structures. This was substantiated with quantitative EDAX using an electron microprobe on polished and gold palladium-coated thin-sections; this method was also used to determine the distribution of other minerals filling cell lumina.

PRESERVATION OF THE CELL WALL

Arnold (1941) recognized that, because of the inert nature of cell materials and their very different reactions with possible solvents, molecular replacement of cells by silica would be extremely unlikely. He considered that silicification was by a process of infiltration, a view which has been supported by detailed study of fossil material (e.g. Buurman 1972; Leo and Barghoorn 1976). Experiments on silicification have resulted in the coating of the cell wall and in the filling of the cell lumen (Leo and Barghoorn 1976). The present study, however, strongly suggests that infiltration and impregnation of the cell wall was the first phase of silicification in all the well preserved Alexander Island fossil wood. In cases in which the cell walls were not impregnated by silica the walls have been reduced to lines of inclusions within quartz or chalcedony and the wood is poorly preserved. Although in thin-sections of well-preserved wood the cell wall appears to be continuous and up to 10 μm thick (Pl. 28, figs. 1 and 2), electron microprobe analysis using EDAX indicates that very little of the dark cell wall area is wholly occupied by carbon. Analyses in the centre of the cell wall show 82 % to 87 % silica (mean 85·35 %), and other low atomic weight elements (i.e. hydrogen and oxygen in hydrated silica) may make up part of the remaining 15 %. This clearly indicates that the various components of the cell wall have been silicified. The dark colouration in the wall is due to the even distribution of residual organic material throughout the cell wall area. It is thought that this organic material represents remnant microfibrillar 'threads' around which silica grew (see below).

When Alexander Island fossil wood is viewed under the SEM the cell walls can be seen to be composed of three layers, each with a silica overgrowth (Pl. 28, figs. 4–7). These can be compared with the constituent layers of the tracheid wall in modern gymnosperm wood (text-fig. 2c). Although the most common and steepest of the fossilized helical structures could have been a result of helical thickening, checking, or splitting, this is considered unlikely. Helical 'checks' follow the orientation of the S2 layer microfibrils in the reaction wood of living conifers (Côté and Day 1965; Meylan and Butterfield 1972), but checks do not overlap in the primary walls or S1 cell layers, and the S3 layer is absent. In the Alexander Island fossil woods the primary cell wall, the S1 layer, and probably the S3 layer, bear helical structures very similar to those interpreted as comprising the S2 layer.

EXPLANATION OF PLATE 28

Preservation of the cell wall in silicified conifer wood.

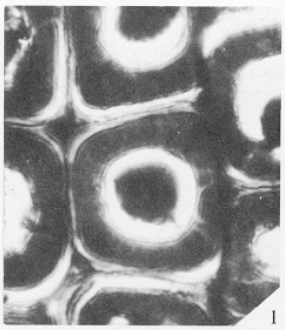
Figs. 1 and 2. Transverse thin sections. 1, KG.2815.71, late-wood tracheid with thick cell walls, × 1000. 2, KG.1702.2, early wood tracheids with thin cell walls, × 400.

Fig. 3. Tangential longitudinal acetate peel, KG.1719.3c, continuous middle lamelli within cell walls, × 250.

Figs. 4–7. Scanning electron micrographs of tangential fracture surfaces of tracheids, KG.2817.23. 4, the two outer layers of the cell wall, × 1000. 5 and 6, two cell wall layers, × 250, and detail, × 500. 7, the thickest layer (steep helix) underlying a thinner layer (flat helix), × 500.

Fig. 8. Scanning electron micrograph of radial fracture surface, KG.2817.5, helical thickenings in inner wall layer of tracheid, × 1000.

Figs. 9–13. Radial longitudinal thin sections. 9, KG.1704.10, showing steep helical structure, × 1000. 10, KG.1704.10, flat helical structures, × 400. 11, KG.1719.3c, fibrillar structures on bordered pits, × 800. 12, KG.2817.16, fungal hyphae, × 400. 13, KG.1704.10, ?fungal spores, × 400.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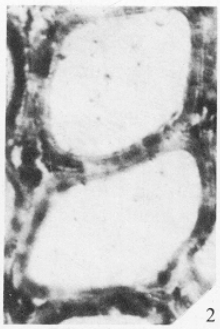
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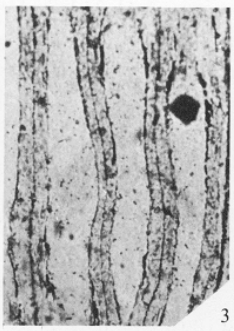
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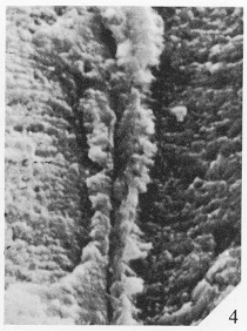
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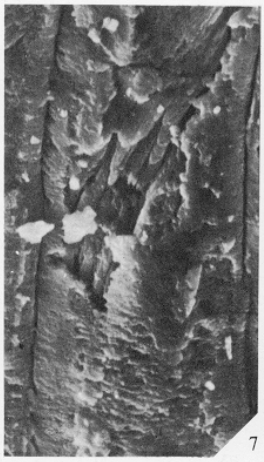
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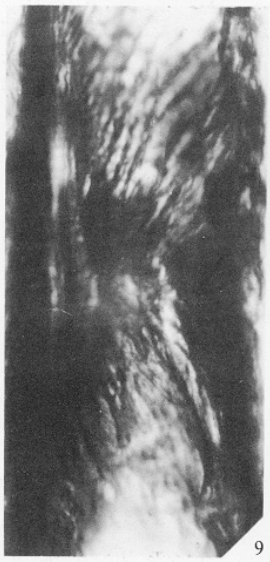
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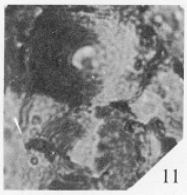
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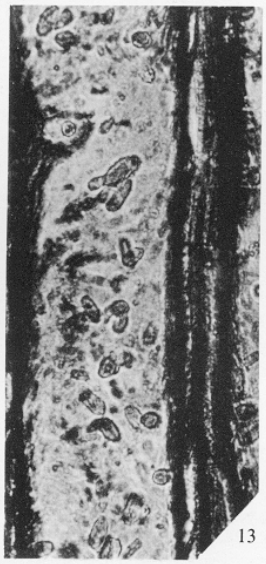
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JEFFERSON, silicified conifer wood

Furthermore, much of the fossil wood from Alexander Island comes from areas of trunks which show no sign of the development of reaction wood. Helical thickenings on tracheid walls in a few living conifers are on the same scale as the helical structures in the Alexander Island fossil woods, but they are considered to be extensions of the S3 layer and do not form the characteristic steep helices (Meylan and Butterfield 1972). Drying and splitting of cell wall layers parallel to microfibrils produce helical structures in modern woods which are more irregular and have angular terminations (Côté and Day 1965). The most likely origin for the fossilized structures is growth of silica on to the microfibrils and macrofibrils (microfibrillar bundles) within the individual layers of the cell wall. The difference in scale between the fossilized fibrillar structures and the microfibrils in extant woods is thought to be related to biogenic decay and is discussed below. Carbonized remnants of the original cell walls, including the walls around pits, can sometimes be seen in thin section (Pl. 28, figs. 9–11), providing further evidence that the process is one of growth of silica on to and within the cell wall layers rather than one of replacement.

Although all the silica seen in cell walls was in the form of chalcedony or cryptocrystalline quartz, silicic acid monomers probably formed the first phase of silica precipitation (Leo and Barghoorn 1976). Subsequent transformation and ordering of silica through Opal CT would be expected to take place within 10 my to 100 my (Stein 1982).

Morphology of cell wall layers

Although a complete section through all of the cell wall layers has not been seen, most of the layers can be recognized individually.

Middle lamella. This is generally poorly preserved. Silica has often grown between adjacent cells exerting little disruptive pressure and leaving the middle lamella intact (Pl. 28, fig. 3). Sometimes the middle lamella is present only as a line of carbon inclusions. This may be because of early fungal breakdown of the middle lamella as seen in modern woods (Kaarik 1974). In modern woods the thickness of the middle lamella varies considerably; at simple cell to cell boundaries it is often less than 0·2 μm thick and is often difficult to distinguish, whereas at triple point boundaries, or where cells taper, it may reach 2 μm across (Harada 1965). In the Alexander Island fossil woods the middle lamella cannot be positively identified under the SEM, although where the tracheids taper and the inter-cellular space is at a maximum a structureless layer can be seen (Pl. 28, fig. 4). This may represent the middle lamella or an 'intercellular substance' (Harada 1965) but is more likely to be an intercellular space created by post-mortem decay and shrinkage, and filled by silica.

Primary cell wall. Of the three wall layers recognized in Alexander Island fossil wood, the outer layer is discontinuous, very thin, and possesses an indistinct structure almost perpendicular to the tracheid axis (Pl. 28, fig. 7). This is similar to the regular transverse orientation of the microfibrils on the internal surface of the primary cell wall in extant gymnosperms (Wardrop and Bland 1959; Mark 1967). The more irregular arrangement of microfibrils on the internal surface of this wall in extant gymnosperms may explain the indistinct nature of the structures in the Alexander Island fossil wood.

Outer layer of the secondary cell wall (S1 layer). The second layer seen in Plate 28, figs. 4 and 7 is composed of distinct helical structures at an angle of 80–85° to the axis of tracheids. This layer is thought to represent the S1 layer and it is often so thin that the next layer is clearly visible underneath it when viewed with the SEM (Pl. 28, fig. 7). When seen in longitudinal thin-section the structures appear as dark, organic-rich strands spiralling in either direction (Pl. 28, fig. 10). Harada (1965) and Mark (1967) stated that the microfibrils of both the S1 layer and the S3 layer in extant gymnosperm woods form flat helical layers and spiral in alternate directions. Since it is not possible to determine whether the helical structures are internal or external to the S2 layer, it is not known whether they represent the S1 or the S3 layer. The structures are seen in only 15–20 % of cell walls in the Alexander Island fossil woods. This frequency in fossils is consistent with the relatively small thickness of both the S1 layer and the S3 layer in the tracheid walls of extant conifers; in *Pinus*

densiflora the S1 layer comprises only 12·5 %, and the S3 layer only 7 %, of the total wall thickness (S1 + S3 = 19·5 %) (Harada 1965).

Middle layer of the secondary cell wall (*S2 layer*). When broken surfaces are prepared for SEM study the outer layers of the cell wall often break off to expose the thickest of the cell wall layers (Pl. 28, fig. 7). This layer is composed of 'sublayers' comprising helical strands at 20–30° to the tracheid axis. Up to three 'sublayers' with strands 0·2–1·5 μm across, which spiral in alternate directions, can be recognized in thin-section (Pl. 28, fig. 9). The S2 layers of tracheids in extant conifer woods are by far the thickest of the cell wall layers; 1·93 μm across in *Pinus densiflora*, making up 78 % of the total cell wall thickness (Harada 1965). Such layers are made up of microfibrils with a steep helical arrangement which also spiral in alternate directions. It appears that the S2 layer in the Alexander Island fossil wood was similar in thickness and form to that of extant woods. Early decay and delignification are thought to have been important in opening up the cell wall, and promoting silica impregnation. Silica is thought to have grown on to microfibrils, and particularly on to groups of microfibrils, and to have filled interfibrillar porosity within the cell wall. The cryptocrystalline quartz seen on and within this wall probably resulted from the later ordering of the original silicic acid monomers likely to have been involved in this impregnation.

Inner secondary cell wall (*S3 layer*). In no case can any layer internal to the S2 layer be distinguished, using SEM techniques, from material filling the cell lumen. However, some of the flat helical fibrillar structures seen in thin section, and described above, probably represent the S3 layer.

Origin and silicification of fibrillar structures

Harada (1965) stated that the microfibrils making up the cell wall layers are from 0·01 to 0·03 μm (100–300 Å) across. The helical structures in all the cell wall layers of the Alexander Island fossil woods are far larger than this, ranging from 0·2–1·5 μm across. Although this may be due in part to the irregular growth of silica, the original microfibrils were probably only 10 % of the width of the fossilized structures. The relatively large size of the fibrils in the fossil wood is thought to relate to biogenic delignification of cell walls. Cowling (1965) and Kaarik (1974) showed that enzymatic activity of white rot fungi (which remove lignin) isolates and separates individual microfibrils and groups of microfibrils. The growth of silica on to fibrillar bundles produced by fungal delignification probably led to the preservation cell wall structures in the Alexander Island fossil woods. Fungal hyphae and lensoid-ovoid organic bodies 9–12 μm long (probably vegetative yeast cells since ascomycetes and basidiomycetes rarely produce spores within wood) are common within tracheids (Pl. 28, figs. 12 and 13).

Cowling (1965, p. 341) stated that 'the specificity of microbial organisms and the very mild conditions under which their reactions proceed, make them potentially ideal reagents for delicate study of structure'. Fine structures were probably preserved in some of the Alexander Island fossil woods because of these properties of microbial activity.

Some Tertiary permineralized woods bear fossilized fibrillar structures of the S2 layer on the same scale as those of extant gymnospermous woods (Buurman 1972, fig. 34). Buurman (1972) suggested that silicification was by impregnation *or* replacement of the cell wall layers. In the Alexander Island fossil woods silicification of the cell wall layers involved the growth of silica on to the component microfibrils and microfibrillar bundles of at least three, if not four, of the cell wall layers. The carbonized remnants of the original cell wall layers can be seen in thin section and have not been replaced. Buurman (1972) also stated that the preservation of fine details in silicified fossil wood was normally confined to opalized material and that details of those preserved in quartz or chalcedony were obscured or disrupted by crystal growth. X-ray diffraction (XRD) of bulk samples of fossil wood and electron microprobe analysis of thin sections indicate an absence of a hydrated silica phase in Alexander Island fossil woods; silica is in the form of low quartz or chalcedony. SEM studies show a cryptocrystalline structure to the silica which has impregnated the cell wall (Pl. 28, figs. 4–7). It is likely that all original opaline silica has transformed into chalcedony or quartz. An increase in the volume of silica, due to ordering and/or subsequent growth, may have

accompanied a reduction in the volume of organic material as oxygen and hydrogen were given off over time; silica may have filled this secondary porosity as it developed, or soon after. The cell wall structures seen in the Alexander Island fossil woods are much coarser than those seen in many opalized woods and are preserved because of the pre-mineralizational decay which opened up the cell wall and allowed silicification of delignified fibrillar bundles and interfibrillar space.

Helical thickenings

In addition to, and readily distinguishable from, the fine helical structures of the S2 layer, some tracheids bear regular helical bands 7·5 μm across and 5 μm apart, which have the same orientation (Pl. 28, fig. 8). They are clearly not caused by splitting of the cell wall; they are far too regular and many are rounded at each end. The distribution of these 'helically thickened' tracheids has no apparent pattern; they occur adjacent to non-thickened cells and often isolated from any other thickened tracheids. Although their relationship with areas of reaction wood cannot be demonstrated, they probably formed in cells which were growing under stress, in the same way as helical 'checking' forms in the tracheids of modern conifer reaction wood. Slit pits often separate these thickenings and follow their helical shape (Pl. 29, fig. 1). Despite the fact that they have no apparent border, the other side of the pit pair is often formed by a normal bordered pit.

Greguss (1967) figured 'spiral thickenings' in fossil gymnospermous wood from Hungary. He considered that these were characteristic of the genus *Platyspiroxylon*, although he recognized similar thickenings in members of the Ginkgoaceae and Araucariaceae and rarely in other genera of the Cupressaceae. These are usually regular, widely spaced (5–8 μm) and broad (2–5 μm), and bear a close resemblance to the structures in the Alexander Island fossil woods described above. However, some of the structures which Greguss (1967, plate XXXIV, 11) figured may well be artefacts of a decay process and not true anatomical characters. This highlights one of the major problems encountered in the taxonomy of fossil wood; a number of the structures which have been used as diagnostic properties may be artefacts of pre-mineralization decay.

Chemical hypothesis for silicification of the cell wall

The most likely silicifying agent involved in permineralization is molecular silicic acid (H_4SiO_4) which is the only common natural form of soluble silica, and the form released in the devitrification of volcanic glass and diagenesis of clay minerals (Murata 1940; Sigleo 1979). Leo and Barghoorn (1976) suggested that it was the potential for hydrogen bonding between silicic acid and holocellulosic complexes of the cell wall which led to exact replication of cell wall structures. The process

EXPLANATION OF PLATE 29

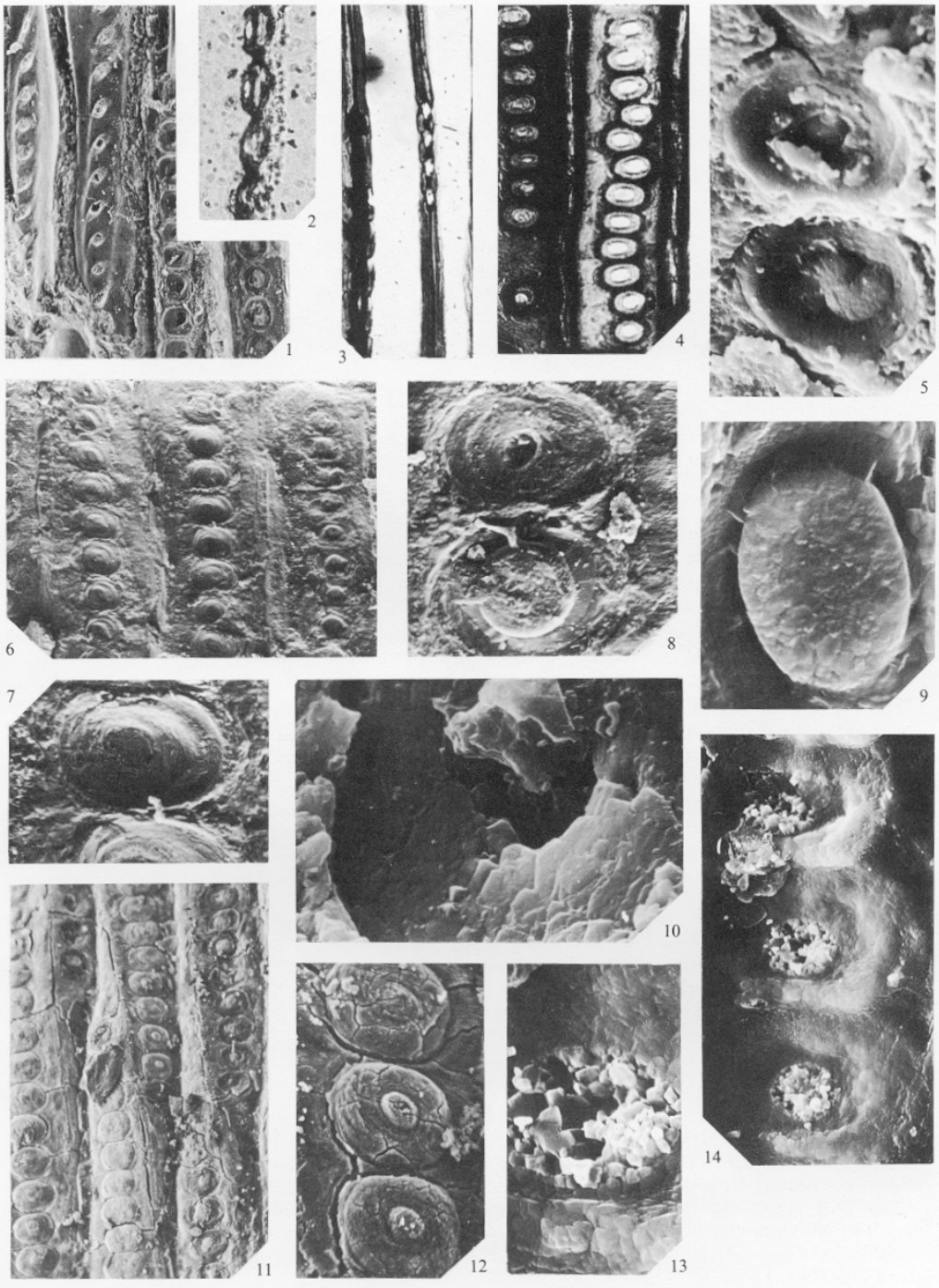
Bordered pits in silicified conifer wood.

Fig. 1. Scanning electron micrograph of radial longitudinal fracture surface, KG.2817.16, rare slit pits associated with helical thickenings ('normal' pits are seen on the right), × 250.

Figs. 2 and 3. Tangential longitudinal thin sections through bordered pits. 2, KG.1704.10, × 250. 3, KG.2817.16, × 150.

Fig. 4. Radial longitudinal thin section, KG.1702.6, × 250, showing contiguous bordered pits.

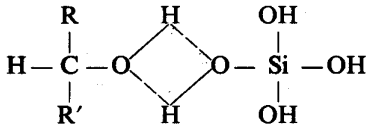
Figs. 5–14. Scanning electron micrograph radial longitudinal fracture surfaces. 5, KG.2817.23, view of internal surface of pit chamber, note 'S' and ring-shaped structures in the centres of the pits, possibly representing the collapsed tori, × 1000. 6–8, KG.2817.16, views of concave cast of pits in the silica filling a cell lumen. 7, detail, × 1000. 8, internal view of pits, in the lower pit fracture through the cell wall exposed the silica-fill of the pit chamber, in the upper pit fracture was external to the cell wall, × 1000. 9, KG.1702.3, internal view of pit, fracture through the silica-fill of the pit chamber, × 2500. 10, KG.2817.23, view of concave cast of pit in silica filling the cell lumen, × 2500. 11 and 12, KG.2817.23, external views of pits. 11, × 250. 12, × 1000. 13 and 14, KG.2817.16, external view of slightly collapsed pits, showing microcrystalline quartz in the pit aperture. 13, × 1000. 14, detail, × 2500.



JEFFERSON, bordered pits in silicified wood

proposed for the Alexander Island fossil woods involves permineralization of the cell wall structures, rather than replication, and is as follows:

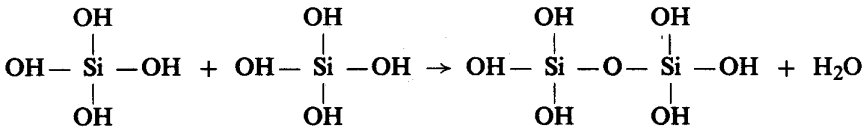
1. Dilute silicic acid infiltrates and permeates the cell wall and forms hydrogen bonds with hydroxy functional groups in the molecular constituents of the cell wall (Leo and Barghoorn 1976).



Ligno-holocellulosic complex — silicic acid

Because of the four active hydroxyl groups per molecule, silicic acid has a high potential for the formation of hydrogen bonds.

2. Silicic acid monomers build up on cell wall structures and begin to interact and polymerize, eliminating water in the formation of siloxane bonds.



3. A film of silica develops on microfibrils and fibrillar bundles, and along cell wall surfaces, and silica fills interfibrillar space.

4. The molecular film is converted over tens to hundreds of years into an opaline state ($SiO_2 \cdot nH_2O$), or disordered low-cristobalite (opal-CT) may be formed as an intermediate phase (Stein 1982).

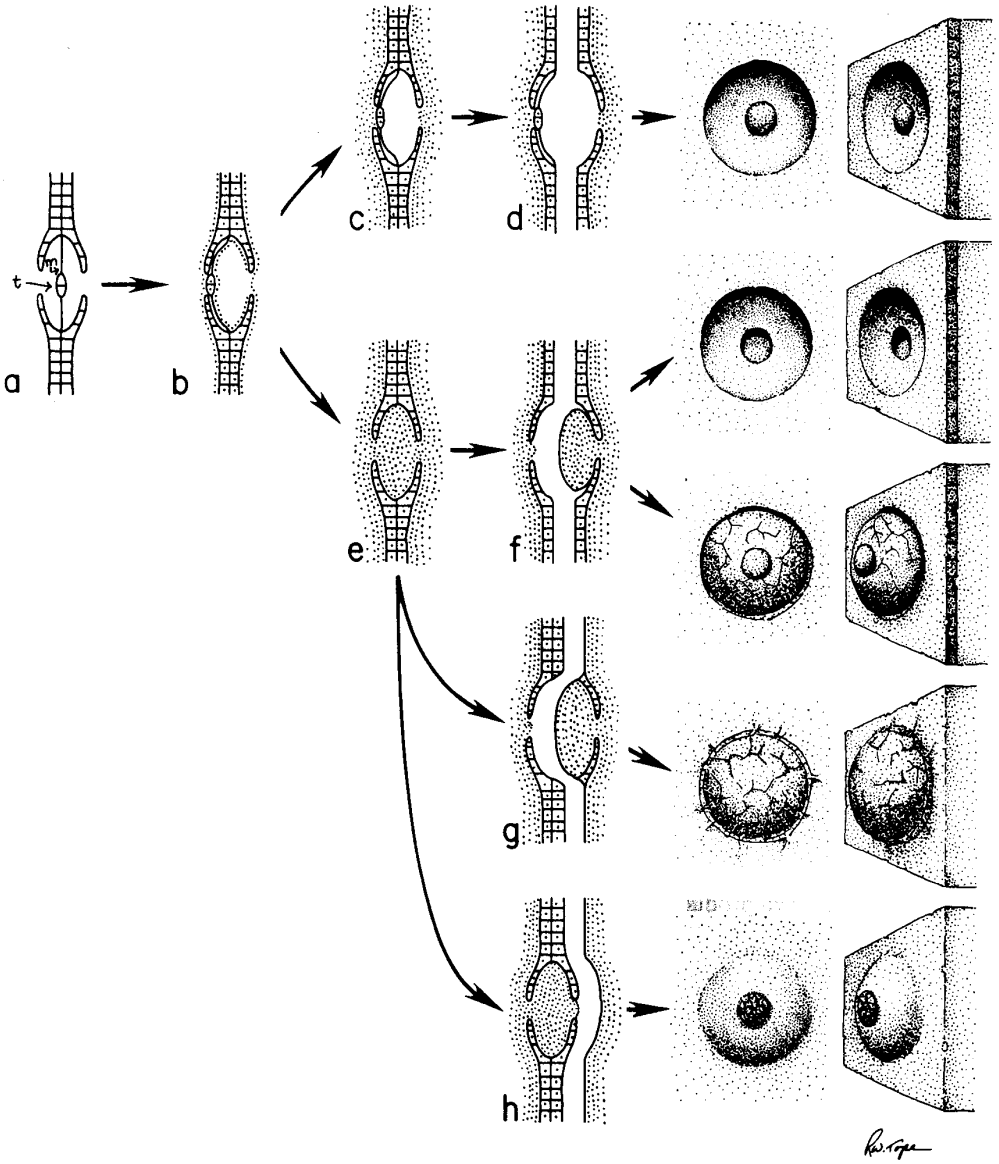
5. Opal is transformed to chalcedony and low quartz over 10^7 to 10^8 years.

The early decay demonstrated in the Alexander Island fossil wood is likely to promote the first part of this process by increasing cell permeability and surface area and producing chemical entities with more active sites for hydrogen bonding.

The final stage in the silicification of these woods was a cavity-fill process, in which silica filled the cell lumen (see below). In parts of some specimens this is the only form of mineralization and there has been no impregnation of the cell wall. Within such areas, cell structure is poorly preserved because of disruptive growth of chalcedony or quartz, and cell walls are marked only by inclusions of organic material.

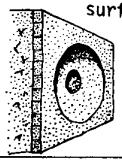
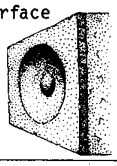
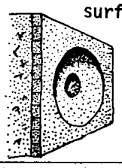
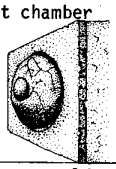
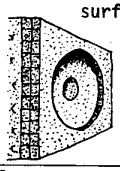
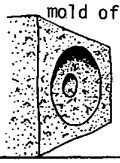
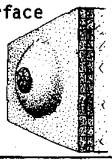
Preservation of bordered pits. The walls of bordered pits have been silicified by the same infiltration processes as is outlined above. Pits are seen in thin section as dark, organic-rich walls (the pit borders) enclosing a pit chamber and possessing a central aperture (Pl. 29, figs. 2–4). Using the SEM, however, the appearance of pits is highly variable and depends on the position of the fracture when specimens are prepared. Fractures are likely to pass along the cell walls, the planes of least resistance. The results of a range of fractures are shown in text-fig. 3. Although fractures are illustrated as passing along the line of the middle lamella between cell walls, there is likely to be some fracture through cell walls themselves. The process and results are shown in Table 1 (the numbers below (1a–4b) refer to the numbers on this table), and are summarized as follows:

1. When the pit aperture is blocked and the pit chamber is unfilled, fracture between cell walls will expose the internal surfaces of both halves of the pit pair (1a–b, text-fig. 3a–d). The circular to S-shaped body and the ring of irregularities over or around the pit aperture in Plate 29, fig. 5, probably represent the remains of the collapsed tori, indicating early silicification before the degradation of these structures, although there is no evidence of the margos, the delicate membranes which support the tori.



TEXT-FIG. 3. Preservation and form of bordered pits (see also Table 1). a, Wood prior to mineralization, showing two adjacent tracheid walls and their bordered pit pair interconnection. The torus (t) and margo (m) form the pit membrane. b, Cell wall permineralized and coated by silica (stipple). c-d, Cell lumina filled by silica; pit chamber unfilled; d, Fracture along cell wall through chamber. e-h, Cell lumina filled by silica; pit chamber filled; f, Fracture along cell wall, through pit chamber, around chamber-fill; g, Fracture between cell wall and lumen-fill, then through pit chamber; h, Fracture between cell wall and lumen-fill.

TABLE 1. Morphology of bordered pits. See text and text-fig. 2 for explanation.

	Text fig.1	Pit Chamber	Fracture	Pit 1 of pair	Features	Pit 2 of pair	Features	Plate 2 figs.
1	a-d	no fill	Between cell walls, through pit chamber	Concave internal surface 	Torus may be preserved; quartz crystals only in aperture	Concave internal surface 	Torus may be preserved, quartz crystals only in aperture	5
2	a-b e-f	filled	Between cell walls, around pit chamber	Concave internal surface 	Torus unlikely; quartz crystals only in aperture	Convex mold of pit chamber 	No torus; quartz crystals possible on surface	6-7
3	a-b e,g	filled	Between wall & lumen-fill as in 4 but around chamber as in 2	Concave internal surface 	Fractured cell wall visible outside & above pit	Convex mold of pit chamber 	Fractured cell wall visible outside & below pit; crystals possible on surface	8-9
4	a-b e,h	filled (may be no fill)	Between cell wall & silica lumen-fill	Concave external mold of pit 	Quartz crystals likely on surface; no torus	Convex external surface 	Quartz crystals unlikely except in aperture	10 11-14

2. When the pit chamber is filled, fracture between the cell walls will pass around the silica-filled chamber. This will produce an internal surface of one pit (2a) although the torus is less likely to have survived mineralization, and a concave surface of the internal silica mold of the pit chamber (2b). (This may be difficult to distinguish from an external view of the pit (Table 1, 4a; text-fig. 2h) unless a coarse crystalline structure is evident.)

3. When the pit chamber is filled, a fracture between a cell wall and the lumen fill may break through the cell wall in the area of this fill and pass around it producing an internal surface of one pit beneath the broken cell wall of the adjacent cell (3a), and a convex surface of the internal silica mold of the chamber, with the fractured cell wall around and beneath it (3b).

4. A fracture external to one of the cell walls (more common when the pit chamber is filled) will expose an external surface of one of the pits (4a), and a cast of this surface in the silica filling the lumen (4b). This will be similar to the internal surfaces of pits (1a-b) but may show a crystalline structure.

INFILL OF THE CELL LUMEN

The terminology applied by Storz (1933) and Buurman (1972) to cell-fill crystalline textures will be used here: (1) polyblastic—many crystals in the space of one cell, (2) oligoblastic—one crystal filling

each cell, (3) hyperblastic—single crystals filling a number of cells by growing through cell walls, (4) idioblastic—well shaped crystals in any part of the wood.

Although cell wall impregnation was probably in the form of silicic acid monomers which transformed via opal and disordered cristobalite to microcrystalline quartz, the variety of mineralization textures seen in the cell lumina suggests that the primary growth of silica was in several forms.

1. Cryptocrystalline chalcedony with a characteristic radial extinction in thin section (Pl. 30, figs. 1 and 5) and a granular appearance using the SEM at high magnification. It is usually polyblastic and post-dates cell wall silicification.

2. Microcrystalline quartz often found in association with chalcedony and consequently difficult to distinguish from it. It forms as individual crystals 0·5–2·0 μm across with poorly developed crystal faces and random orientation (Pl. 30, fig. 2).

3. Euhedral to subhedral polyblastic quartz crystals up to 30 μm long. These show characteristic cavity-fill textures; small anhedral crystals close to the cell wall and large euhedral crystals in the centre of the lumen (Pl. 30, figs. 3 and 4). The intercellular space may also be filled by polyblastic silica (Pl. 30, fig. 5).

4. Euhedral to subhedral hyperblastic quartz crystals which grew through cell walls and across several cells. Although preservation is inferior, the cell wall is usually preserved as a line of coaly inclusions and bordered pits are often seen (Pl. 30, fig. 6).

5. Single oligoblastic crystals of chalcedony filling whole cells in which the cell wall has been silicified. These crystals often contain spherical pores up to 10 μm across which do not represent the usual form of fluid inclusions (Pl. 30, fig. 7).

Although there are gradations between 1 and 2, and between 2 and 3, in terms of crystal size, there is no evidence for transformation of any of these forms to any other, or of pseudomorphed textures.

In the Alexander Island fossil woods the growth of chalcedony and microcrystalline quartz was usually polyblastic because silica filled cell lumina after the silicification of the cell wall and did not grow through them. Larger quartz crystals are often polyblastic; they grew away from previously silicified cell walls into cell lumina. In some specimens in which no cell wall mineralization took place (possibly those which had undergone extensive decomposition before mineralization), idioblastic silica grew in sub-spherical masses throughout the wood (Pl. 30, fig. 8). These masses range from 0·1–1·0 mm in diameter and also occur in small areas of many specimens which are otherwise well preserved. There is generally little evidence for the confinement of these silica masses to tracheid lumina.

In at least two specimens (KG.2815.252 and KG.2815.254) the first stage of lumen fill in approximately 1 % of tracheids involved the growth of isolated, euhedral, cubic iron sulphide crystals 20 μm across (Pl. 30, fig. 9). The crystals are completely enclosed in the silica which filled the cell lumen and are adjacent to, and sometimes penetrate, the cell wall. They represent a very early phase of crystallization under strongly reducing conditions promoted by the early decay of cells or their contents.

Partial fill of the cell lumen by apatite. When XRD analyses were carried out to determine the relative importance of the silica phases opal, disordered cristobalite and quartz/chalcedony, three specimens from the same unit (KG.2817.13, 16 and 17) were found to contain up to 70 % apatite and/or collophane (amorphous, hydrated apatite). This is difficult to distinguish from quartz by 'normal' petrographic techniques, particularly when the two minerals are in close association. Apatite and collophane formed as part of a two-stage lumen fill process in close association with chalcedony.

At the first stage, silica grew as spheroidal masses of chalcedony with radial extinction, occupying the full width of the cell, and sometimes coalescing to fill most of the tracheid (Pl. 30, fig. 10). Collophane then grew in the remaining cell lumen space as large masses composed of radiating needles, and apatite grew as fine crystals (polyblastic fill) (Pl. 30, figs. 11–13). In many cases tracheids

contain no silica but are completely filled by collophane. Series of microprobe analyses across the dark wall areas between adjacent apatite-filled and collophane-filled cells indicate that the first stage in mineralization, even in 'apatitized' wood, is the impregnation of the cell wall by silica. The cavity-fill growth of apatite and collophane is a late-stage alternative to the cavity-fill growth of quartz.

ORIGIN OF MINERALIZING FLUIDS

Silica. Murata (1940) considered that silicification of wood was due to the early decomposition of volcanic tuffs and ashes leading to the liberation of free silica and its deposition within tracheids. He demonstrated that permineralization in active volcanic areas in Yellowstone National Park, Wyoming, started within a few months of wood being surrounded by silica-rich fluids. Hunt (1972) supported this view and showed that silica in the form of silicic acid was released in the devitrification of volcanic material and the diagenesis of clay minerals. Sigleo (1979) conducted geochemical investigations on silicified wood and associated sediments in Petrified Forest National Park, Arizona, and showed that the silica precipitated within wood cells was derived from the breakdown of volcanic ash in the surrounding sediments. She found evidence in the external parts of the wood for co-precipitation of authigenic montmorillonite, a product of ash hydrolysis, and silica. Montmorillonite also constituted up to 15 % of the surrounding sediment. Trace and variable-valence element concentrations showed that silicification took place within the compositional ranges of modern stream and ground waters, SiO_2 concentrations less than 140 mg/l, and under anoxic, slightly acid conditions. Sigleo suggested that the most likely preservational environment was in stagnant pond water or in swamp bottom muds. Dorf (1964) regarded many of the forest beds in Yellowstone as volcanic debris flows but recent work by Fritz (1980) suggests that most of the trees were buried by alluvial sandstones and conglomerates (80–90 % water transported air fall ash, and 10–20 % reworked detrital volcaniclastic material).

Similar preservational and mineralizational settings are suggested by the composition of rocks associated with the Alexander Island fossil forests. The Fossil Bluff Formation sandstones in which fossil wood is found are coarse-grained, volcaniclastic sandstones with a high porosity. These are lithic arenites or greywackes when rock fragments are dominant, or arkosic arenites or greywackes when feldspar is dominant (Pettijohn 1975). The arkosic arenties may be composed of up to 50 % plagioclase feldspar, mostly andesine. Detrital plagioclase is common even in the lithic arenites. The prefix 'tuffaceous' should be used for most of these sandstones since fragments of volcanic glass, pumice, and chloritized volcanic material may constitute up to 60 % of the rock. The matrix is greatly altered by zeolite formation but is usually made up of chlorite, calcite and sericite.

EXPLANATION OF PLATE 30

Infill of the cell lumen in conifer wood.

Fig. 1. Transverse thin section, showing polyblastic fill, KG.1702.2a, × 250.

Figs. 2–4. Scanning electron micrographs of transverse fracture surfaces. 2, thick cell wall and microcrystalline fill, KG.1702.2a, × 1000. 3, euhedral polyblastic quartz, KG.2821.98, × 1000. 4, detail, × 2500.

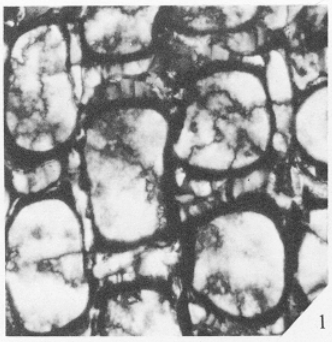
Figs. 5 and 6. Radial longitudinal thin sections. 5, polyblastic fill in tracheids and between cell walls, KG.1702.2a, × 250. 6, idioblastic fill in central area, KG.1704.10, × 100.

Fig. 7. Scanning electron micrograph of tangential fracture surface, showing oligoblastic chalcedony with ?fluid vesicles, KG.2814.252, × 500.

Fig. 8. Transverse thin section, showing hyperblastic masses of silica, KG.2817.257, × 100.

Fig. 9. Tangential thin section, showing pyrite crystal, KG.1704.10, × 250.

Figs. 10–13. Apatite filling the cell lumen, KG.2817.16. 10 and 11, tangential thin sections, × 250. 12 and 13, scanning electron micrograph of tangential fracture surface. 12, × 500. 13, × 1000.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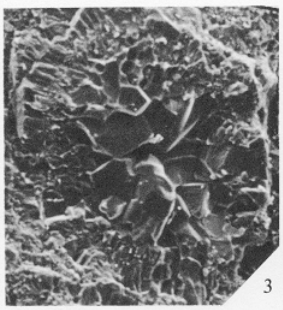
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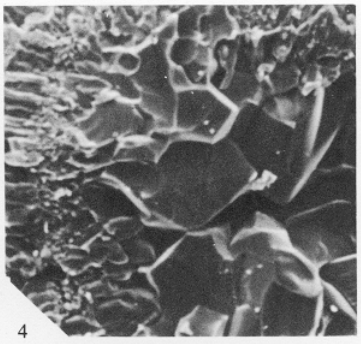
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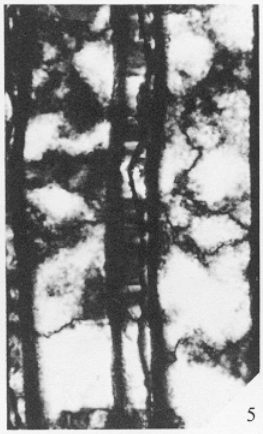
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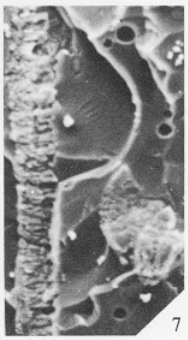
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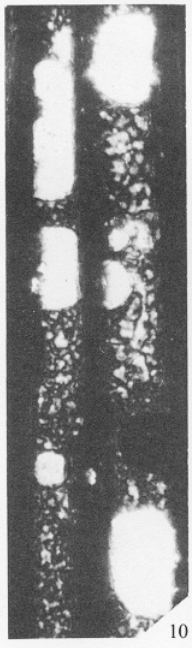
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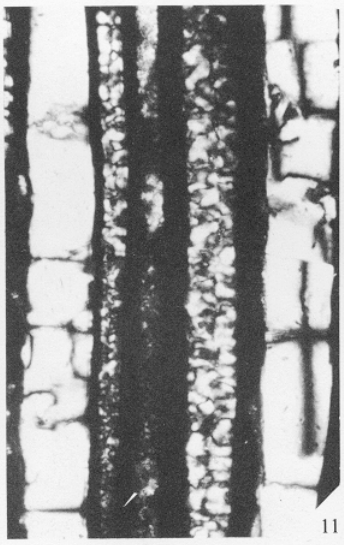
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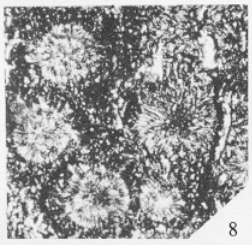
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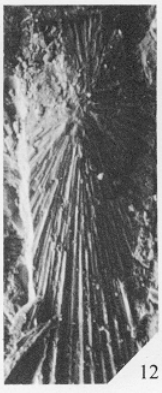
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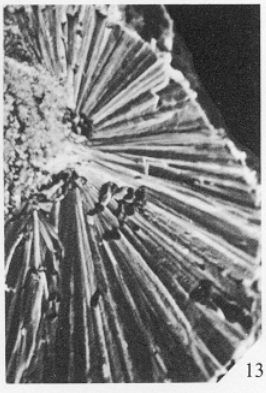
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JEFFERSON, silicified conifer wood

Mineralization of leaves by laumontite, chlorite, and calcite (Jefferson 1982*a*) suggests that the following diagenetic reactions took place under conditions of high PCO_2 and high PH_2O:

$$\text{clay minerals} \rightarrow \text{chlorite} + \text{silica} + H_2O$$
$$\text{glass} + H_2O + CO_2 \rightarrow \text{silica} + \text{chlorite} + \text{calcite}$$
$$\text{Ca-plagioclase} + H_2O + CO_2 \rightarrow \text{laumontite} + \text{calcite}$$

Some of the silica derived from these reactions was probably deposited in wood, early during diagenesis because of the hydrogen bonding outlined above, which makes the cell walls of wood optimum sites for the growth of silica. The anoxic conditions necessary for mineralization probably developed soon after the burial of trees by this fluvial volcaniclastic sediment.

Apatite. Apatite mineralization of fossil wood is little mentioned in the literature, but this may be because it is difficult to distinguish from silica without chemical analysis. The two phases of mineral growth within cells clearly indicate a change in pore water composition after the impregnation of the cell wall but before complete infill of the lumen. The high volcanic content of all the sediments in the non-marine part of the Fossil Bluff Formation indicates the close proximity of a volcanic area (Horne and Thomson 1972). Local influxes of ground water rich in phosphates, calcium, and other salts are common in present day volcanic environments like Yellowstone National Park, and similar ground waters might be expected to precipitate apatite into constrictions such as tracheid lumina.

CONCLUSIONS

Observations on Alexander Island fossil wood support the 'two stage' theory of wood silicification (Leo and Barghoorn 1976), but suggest that, in some fossil woods at least, impregnation of the cell wall, promoted by biogenic degradation, is more important than the subsequent coating or replication of the cell wall (Leo and Barghoorn 1976) or replacement of it (Buurman 1976).

The first stage in the mineralization of well-preserved wood from Alexander Island involved impregnation of the cell wall. Early biogenic delignification and decay opened up the cell wall, isolating bundles of microfibrils, and created interfibrillar porosity. Silica, in the form of a silicic acid monomer, grew on to these macrofibrils, and filled the inter-fibrillar porosity. The silica subsequently became ordered into chalcedony and microcrystalline quartz. Early silicification of the cell wall is thought to relate to the capacity for hydrogen bonding between silicic acid and cell wall components. Wood is therefore an optimum site for the early precipitation of silica. The second stage in mineralization involved the filling of the cell lumen by chalcedony, cryptocrystalline quartz, euhedral–subhedral quartz crystals, and/or apatite and collophane. The presence of apatite within the lumina of cells whose cell walls had already been silicified further supports the hypothesis that cell wall silicification occurred at an early stage and that lumen fill occurred later, in some cases after major changes in pore water composition.

Acknowledgements. The paper was written when the author was a visitor in 1981–1982 to the Department of Botany, and Institute of Polar Studies, Ohio State University, Columbus, Ohio 43210, USA. It was prepared for publication by Dr N. F. Hughes with the assistance of Dr J. Francis.

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Typescript received 16 October 1985
Typescript accepted 11 June 1986