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WOUND RESPONSE IN FOSSIL TREES FROM ANTARCTICA AND ITS POTENTIAL AS A PALEOENVIRONMENTAL INDICATOR

by

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SUMMARY

Numerous permineralized axes of Middle Triassic age from Fremouw Peak, Antarctica show evidence of mechanical wounding and wound responses. These consist of both elongate and triangular-shaped scars. Some scars can be detected beneath subsequent secondary xylem, indicating that wounding occurred early in stem development. In other stems, scars remained open suggesting late wounding and the permanent disruption of the cambium. In cross section most stems display little callus tissue, but wound periderm can be seen along the margin of the scar. In some stems the wound phellogen has formed phellem and phelloderm within the wounded area oriented perpendicular to the growth rings. Although some scars resemble those produced by fires, we were unable to document the presence of charcoal around scars. In modern ecosystems wounds may be caused by other agents, including debris drifting in floods, flowing ice, avalanches, and animals. Each of these potential sources is reviewed in relationship to the paleoclimate in the region during the Triassic.

Key words: Antarctica, wound, fire, flood, fossil wood.

INTRODUCTION

Modern forest ecosystems are subject to natural disturbance of all types from fire and flood to insect and disease outbreaks (White 1979; Agee 1990). Fires, floods, animals, and other agents can also damage individual trees, causing their bark to be broken. Once the bark barrier is breached some type of wound response usually results. If damage is extensive, the wounded tree may die. But trees may also respond to mechanical wounding by callus formation and wound closure after being wounded (e.g., Shigo 1984). Examination of some types of tree scars can provide information not only about the environment, but also about plant/animal interactions. If we assume that many of the same mechanisms that affect modern forests were affecting forests in the past, we can infer disturbance events from the wounds found in fossil trees.

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Several silicified axes show a response to some form of mechanical wounding. Distinguishing between the various types of scars would allow us to reconstruct past disturbances and environments. Forest fires cause many of the scars seen in modern forests (Agee 1990), and fires could be the cause of scarring in fossil trees. Sedimentological evidence of fires in the Mesozoic and other time periods is extensive (Harris 1958; Komarek 1972; Cope & Chaloner 1985). However previous fusain/charcoal studies have only used isolated pieces of charcoal from sedimentary deposits and have not examined intact, scarred fossilized trunks (Herendeen 1991; Jones et al. 1993; Scott & Jones 1994). Insects and animals, floods and other agents can cause similar damage and resultant scars (Molnar & McMinn 1960; Sigafoos 1964; Mitchell et al. 1983). Wilkinson (1929–1930) examined and reviewed fossilized wounds and responses in some seed ferns and vascular cryptogams. However, no studies have looked at fossil scars in gymnosperm wood and few have attempted to identify the cause of scarring. While damage is obvious in fossil materials, its cause is more obscure. In this paper scars in Triassic wood from Antarctica will be described and likely wound sources for these scars will be discussed.

MATERIALS AND METHODS

All specimens represent fossilized pycnoxylic, gymnospermous wood and are preserved as silica permineralizations (i.e., the intercellular spaces and cell lumens have been infilled with silica; the cell walls remain organic). Based on other fossil plants previously described from this locality, the affinities of the wood may be with the Podocarpaceae (Meyer-Berthaud & Taylor 1991), or with the extinct Mesozoic seed ferns, the Corystospermales (Meyer-Berthaud et al. 1993).

The wood was collected from Fremouw Peak, in the Beardmore Glacier area, central Transantarctic Mountains, Antarctica (84° 18' S, 164° 20' E) (Jefferson & Taylor 1983; Smoot et al. 1985). Stems are preserved in silicified peat of the Fremouw Formation and are regarded as early Middle Triassic in age (approximately 240 m.y.) (Farabee et al. 1990). The peat was deposited in a paleostream channel, along with several silicified logs (Taylor et al. 1989).

The materials were studied both by light microscopy and by scanning electron microscopy (SEM). Cellulose acetate peels were made of each specimen by etching in 49% hydrofluoric acid for several minutes and neutralizing with a solution of sodium bicarbonate. Specimens for light microscopy were cut from peels and mounted on slides with Coverbond mounting medium. Several SEM preparation methods were used in attempts to view cell wall layers. Peels were mounted (rock side up) on SEM stubs with tape. Daghlian and Taylor's (1979) method for isolating pollen for SEM was modified for use on wood cell walls by using peels of stems rather than sporangia. Also several blocks (1 cm^3) were cut and fractured from specimens. Some of these blocks were etched in 49% hydrofluoric acid for about 15 minutes and neutralized in several dilutions of water. Cut, fractured, and etched blocks were glued to aluminum SEM stubs. All specimens were sputter coated with gold-palladium and viewed under SEM.

All materials are deposited in the Paleobotanical Collections of the University of Kansas Natural History Museum. Slide acquisition numbers are 15,243–15,254 and 19,704–19,736.

DESCRIPTION

When the transverse surface of an unscarred area of secondary xylem is viewed under SEM, the cell walls appear unlayered and homogeneous (Fig. 1). The middle lamella could not be positively identified under SEM using any method of preparation. Therefore, fusain (fossil charcoal) could not be identified using SEM due to the lack of recognizable features of the wood cell walls in any specimens.

Four types of scars were found in the Antarctic wood. Two axes were examined that contained triangular-shaped scars in transverse section (Fig. 2, 3), which is the most common scar morphology seen in modern woods. As the tree recovers from wounding, the surviving cambium spreads laterally to produce new bark and annual rings. The triangular shape is formed by the subsequent annual rings growing over the edges of the scarred tissue. If the scar is of moderate size and the tree lives long enough after wounding, surviving cambium eventually meets and covers the scarred area. In both specimens a small amount of bark has been included within the scar. Wood tissue is partially destroyed along the scarred area. Neither scar showed a black crust along the scarred area or within the scar. Scar width (parallel to growth rings) is 17–25 mm and scar length (perpendicular to growth rings) is 8–10 mm. Both trees were 29–30 yr old when the damage occurred and both trees lived for at least 13 yr after being wounded.

In addition to the above features, one of these specimens has a break in secondary xylem (Fig. 3) running parallel to the growth rings along the scar's boundary and 40 mm further (along the ring). Although there is a small amount of debris in this space, it does not resemble frass pellets or coprolites that have been described previously in fossil specimens (Scott & Taylor 1983).

A second type of scar, showing clear wound response, but no wound closure, was found in two other axes. These scars are elongate and remained open at the time of death of the tree; the surrounding woody tissue (annual rings) has a curved pattern but does not completely enclose the scar (Fig. 4, 5). Annual rings were partially destroyed along the scarred area. Callus tissue may be present but is hard to distinguish. These scars are 18–28 mm wide and 49–72 mm long. Both fossil specimens were large but broken. Therefore an age prior to wounding could not be determined. However, specimens did continue to grow for at least 23 and 40 yr after wounding. A third specimen with a similar scar 4 mm wide and 12 mm long was found to exhibit a comparable response (Fig. 6). It was younger than the others (13 yr old when damaged, approximately 31 yr old when fossilized), and in an early stage of wound response.

These scars were sealed with periderm, but the cambium had not yet grown over the scar and covered the scar with new secondary xylem. There was a band of regenerated tissue (wound periderm) growing perpendicular to the scar and to the growth rings, as well as along the scar's margin (Fig. 7, 8). The cellular constituents of the center of this band are hard to determine due to the fact that the tissue in this area is extensively

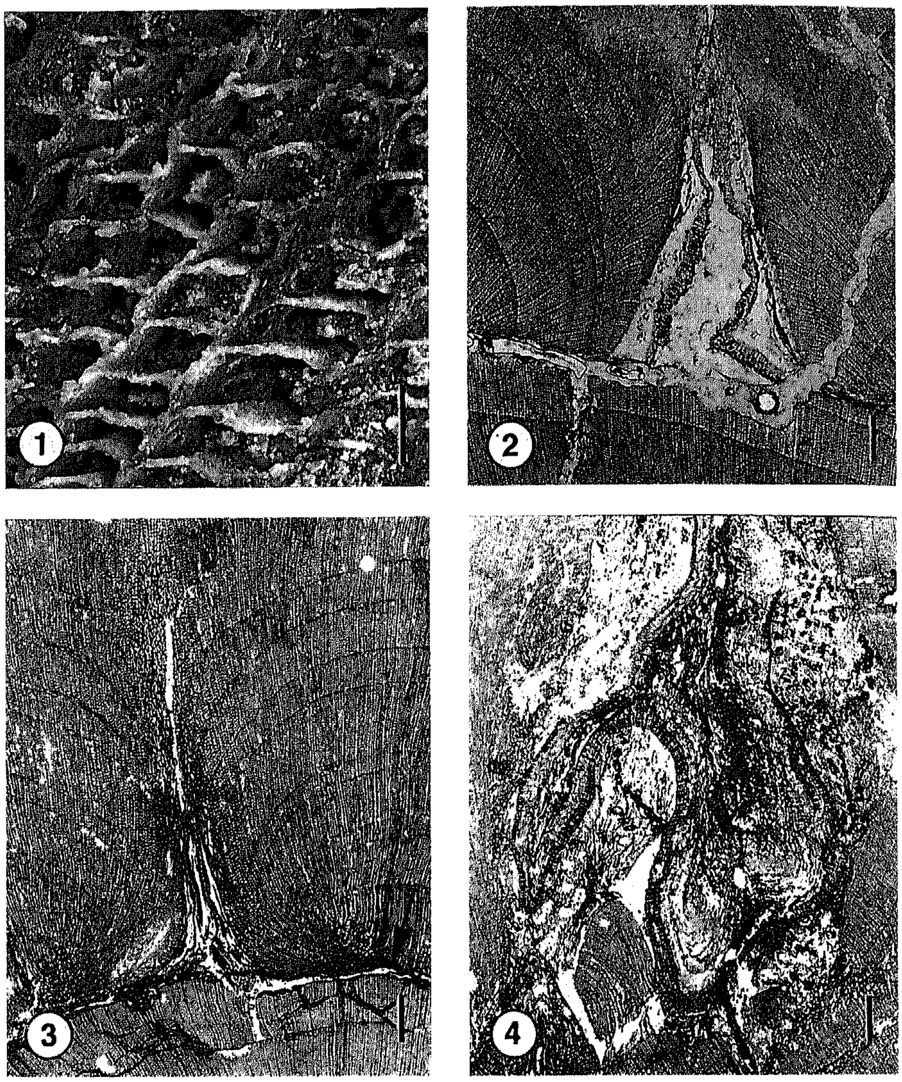

Fig. 1–4. Transverse sections of Triassic wood. In Fig. 2–7, the outside of the trunk is above and the cambium below. – 1: SEM of wood showing poorly preserved cell walls in non-scarred tissue; scale bar = 50 µm. – 2: Triangular-shaped scar (center) and curved rings of new wood growth (above); #70-9-129 Atop α. – 3: Triangular-shaped scar with tunnel that occurs parallel to growth rings (arrow); #10,822 Abot #1. – 4: Scarred area with wound response tissue inside of scar. Regenerated tissue runs perpendicular to the growth rings and extends from the scarred area to the outside of the tree; #11,500B top #2. – Scale bars of Fig. 2–4 = 1.0 mm.

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Fig. 5–7. Transverse sections of Triassic wood. The outside of the trunk is above and the cambium below. – 5: Scarred area with regenerated tissue inside of scar. Regenerated tissue continues from scar to the outside of the tree. Note growth of secondary xylem inside of wound periderm (arrow); #11,817B; scale bar = 1.0 mm. – 6: Young scar showing similar wound response tissue

inside of scar. Small circular objects are roots that penetrated the trunk after deposition; #11,763B top #1; scale bar = 500 μm. – 7: Wound response tissue showing bands of secondary cells; #11,500B top #1; scale bar = 200 μm.

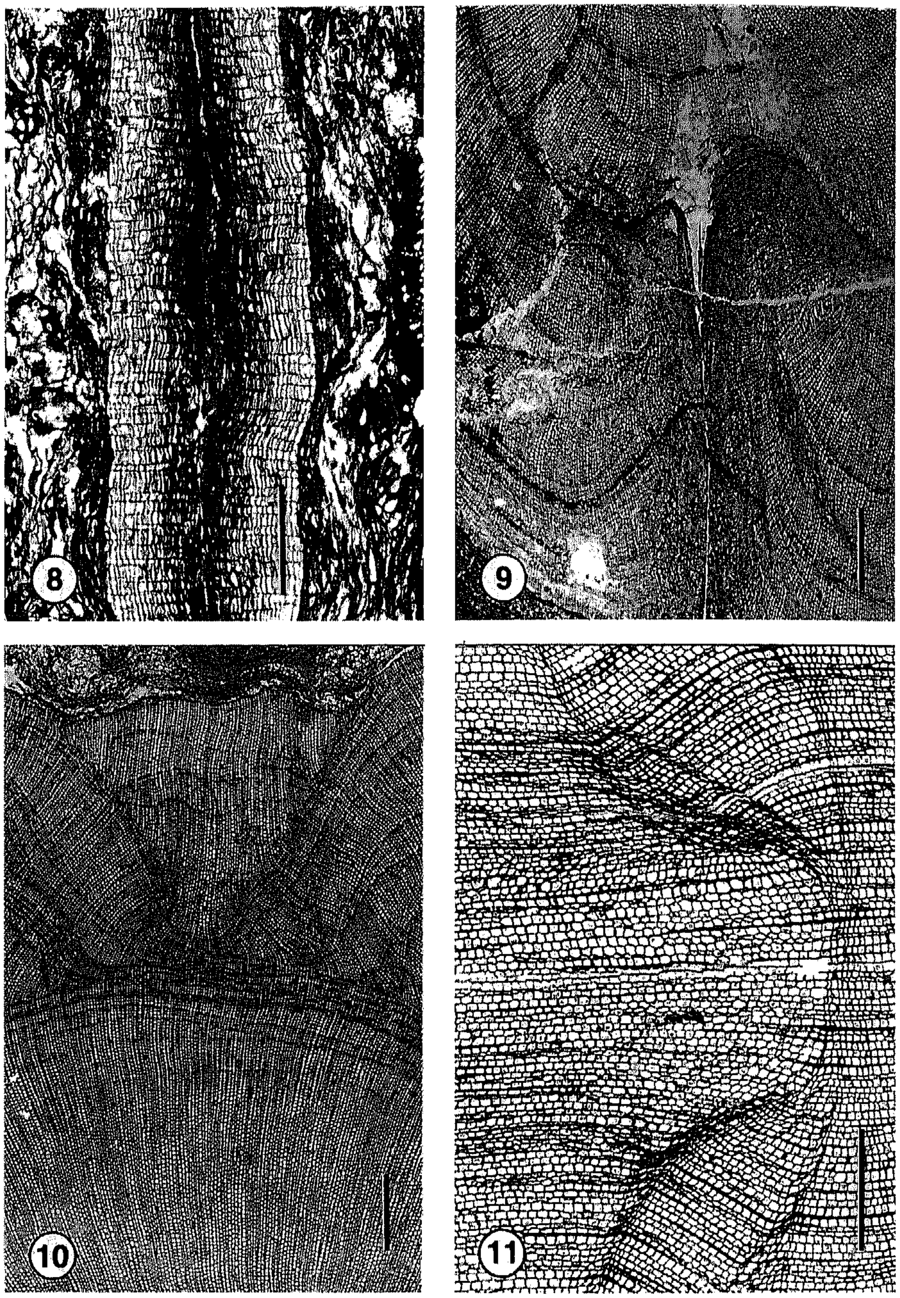

Fig. 8–11. Transverse sections of scarred Triassic wood. In 8 & 10 outside of trunk is above and cambium below. – 8: Wound response tissue showing bands of secondary cells; #11,817B; scale bar = 500 µm. – 9: Small, open scar exhibiting wound response; #10,345B_2 top; scale bar = 1.0 mm. – 10: Scar showing zone of crushed or missing earlywood (center); #10,033D_2; scale bar = 1.0 mm. – 11: Small scar showing area with no earlywood; #11,767Btop; scale bar = 500 µm.

crushed. However, this central dark band probably represents crushed phellem, since cork (phellem) in the form of stacked rectangular cells lines this dark band on both sides. These cork cells average 59 × 25 μm, and there are 10–20 layers of cork cells. Adjacent to the cork is a thin layer of rectangular, slightly thicker-walled cells which measure 48 × 25 μm; these may represent phelloderm.

One of the specimens that displays this wound response has an unusual growth of secondary xylem along the scarred area (Fig. 5). The cells in this secondary xylem resemble normal wood cells, but the xylem is surrounded on all sides by wound periderm.

A third type of scar resembles the previous two types in that the scar remains open, but the cambium appears to be in the process of closing over the wound (Fig. 9). This type of scar is elongate with curved annual rings. Damage can be seen along the annual ring at the level of the scar. No callus tissue could be distinguished. Some phellem (cork) can be seen in the scarred area, but it is difficult to distinguish different types of cells. The scar is 3 mm wide and 12 mm long and the axis was 8 yr old when scarred and approximately 21 when it died.

The fourth type of 'scar' may be due to wounding or it may be an unusual morphological feature. In cross section, the latewood of two or more annual rings converge in one area and no earlywood is present (Fig. 10, 11). Whether earlywood was crushed or never existed could not be determined, but these areas are unusual in that there is no obvious wound that resulted in the anomalous growth. Callus tissue and wound periderm are not evident. Scars are 1–2 mm wide and approximately 2 mm long. Axes were 3–4 yr old prior to scarring and trees lived at least 6–19 yr after scarring.

Other scars occurred in the fossil material. However, due to poor preservation, identifying the type of scar and the source of scarring was difficult. For this reason only well preserved axes with recognizable tissue and cellular preservation were used for this study.

DISCUSSION

Identifying the cause of injury, whether in modern or fossil trees, is difficult due to the wide variety of scar initiators. Fire is a major cause of modern tree scars in almost every habitat, including swamps, rain forests, and temperate forests (White 1979; Agee 1990; Scott & Jones 1994). Modern fire scars are characterized by an overall triangular shape (as viewed from the surface of the stem and in cross section), by the presence of black pieces of charcoalized wood, and by a black crust along the scar's margin (Molnar & McMinn 1960; Zackrisson 1977). One or more fire scars may be present on a single tree and these scars are generally on the same side of the tree (Agee 1990). In fact, this pattern of repeated scarring on one side of the tree can be used to date fires and to establish a tree's fire history. Often the ground litter will be charred and trees will show increased growth after the fire. Several trees in a large area may be burned and these scars originate in the same year.

Evidence for fossil forest fires has been based mostly on the presence of fusain in sediments (Harris 1958; Komarek 1972; Cope & Chaloner 1985). The presence or absence of fusain in sedimentary deposits has also been used to indicate atmospheric oxygen levels (Cope & Chaloner 1980; Robinson 1989; Jones & Chaloner 1991). Abundant fusain suggests abundant fires, and thus plenty of oxygen to sustain fires. Harris (1958) and Herendeen (1991) found abundant fusain in the Jurassic and Cretaceous, respectively, but little fusain has been found in Triassic deposits. Due to this, authors suggest that the Triassic had very low levels of atmospheric oxygen (Robinson 1989). But in her paper, Robinson (1989) goes on to say that abundant charcoal can be produced at very low oxygen levels. While high fusain levels may suggest high atmospheric oxygen, it is difficult to ascertain whether low fusain levels suggest low atmospheric oxygen content. Despite this debate, it is fairly certain that fusain does indicate the presence of fires in paleoecosystems (Harris 1958; Jones & Chaloner 1991; Scott & Jones 1994).

Most researchers use macroscopic and microscopic characteristics to identify fusain (Sander & Gee 1990; Jones & Chaloner 1991; Scott & Jones 1991; Jones et al. 1993; Jones 1994). Fossil and modern charcoal look much the same. Fusain is generally black, brittle, and fractures into blocks (Jones & Chaloner 1991). The most frequently suggested microscopic feature used to identify fossil charcoal is the presence of homogenized cell walls (Sander & Gee 1990; Jones et al. 1993). Under SEM, different layers of the cell walls of fusain cannot be identified. Middle lamellae may be fused or there may be cracks along the lamellae (Scott & Jones 1991). This lack of cell wall ultrastructure is one structural way of identifying fusain. Both Jones (1994) and Herendeen (1991) reiterate the necessity to use macroscopic as well as microscopic methods of fusain identification since cell wall fusion may or may not occur and it can be caused by mechanisms other than fire. Other methods for identifying fusain are available, including reflectance microscopy and nuclear magnetic resonance (Scott & Jones 1991; Jones 1994). However, due to the difficulties inherent in working with large pieces of silicified material, some of these other methods could not be used.

While some of the fossil wood from Antarctica exhibited triangular-shaped scars characteristic of the morphology of modern fire scars, no blackened surfaces resembling charcoal were present. Middle lamellae were not distinguishable on either scarred or unscarred specimens under SEM. Thus, a positive identification of fusain could not be obtained using this method. Sedimentologic data from the Fremouw site show no signs of fusain in similar age sediments of that area (Barrett et al. 1986). This evidence currently suggests that forest fires were not common in the Fremouw paleoenvironment and therefore perhaps were not the cause of these scars.

Avalanches and slope movements, such as landslides and mudslides, can cause distinctive scarring followed by unusual growth of tree rings. Snow, soil, and debris can create 'impact scars' on the uphill side of the tree. Scars are usually small, triangular shaped, abraded along the ring boundary, and sometimes sealed over by subsequent cambial growth. In addition, avalanches and landslides often tilt the tree resulting in eccentric growth. Compression wood (in conifers) grows on the lower (i.e., downslope) side of the tree (the side opposite the impact scar). Changes in the width of growth rings, either an increase or a decrease, can also indicate the presence of avalanches or landslides. Finally, large stems are more likely to break in avalanches than small stems. Thus, trees are not likely to show evidence of avalanche damage in their later years (Carrara 1979; Johnson 1987). Because these specimens were found in peat deposits, it is unlikely that the trees were growing on a slope steep enough to cause avalanches or landslides. Although many stems were not complete enough to detect reaction wood opposite the scar, the scars that are complete do not show signs of reaction wood growth. Frost rings (damage by frost during the growing season) are not evident in these specimens and appear to be rare in this time period (Taylor & Taylor 1993). Due to the lack of evidence for steep slopes, cold temperatures, and obvious signs of avalanche damage, it is likely that trees were not subject to damage by landslides or avalanches.

Many modern tree scars have biotic origins. Several species of mammals utilize the phloem layer of trees as a food source while other animals scratch trees with antlers or with claws. Scars of this type are usually triangular or irregularly shaped with tooth or claw marks along the scar margin. Trees may have several scars originating on different sides of the tree (Molnar & McMinn 1960; Spencer 1964). There is no evidence of tooth marks in any of our fossil specimens. The most common reptile of the Lower Fremouw Formation, *Lystrosaurus*, had beak-like jaws similar to modern turtles (Colbert 1982). This form of dentition is not well adapted to breaking the surface of bark. *Cynognathus*, reptiles, and capitosaurs, aquatic amphibians, were present in the upper Fremouw Formation. Their dentition suggests that they were carnivores (Hammer et al. 1990). It is not likely that any of these animals were utilizing fossil tree trunks as food (Tiffney 1992). The habits of these and other animals of the Fremouw area suggest that trees were probably not being scarred by large animals (Colbert 1982; Hammer et al. 1990).

Insects and other arthropods can also damage trees, with the resulting scar sometimes resembling a fire scar. Mitchell et al. (1983) describe 'catfaces' on lodgepole pine, *Pinus contorta*, caused by the mountain pine beetle, *Dendroctonus ponderosae*, as 1–3 m tall with fluted/triangular scars. Beetle exit holes, vertical galleries (tunnels), and blue (fungal) stain behind the scar are also common in scars caused by beetles. Insects could be the cause of some of the scars found in Triassic wood. Insects of the order Coleoptera, which includes the mountain pine beetle, were present in the Triassic period (Carpenter & Burnham 1985). Other wood-borers are known from as early as the Carboniferous (Scott & Taylor 1983). Also, one specimen which we examined did have a tunnel-like gallery running parallel to the growth rings (Fig. 3). However, no other positive evidence of insect damage, such as frass pellets or additional galleries, was found in the Antarctic specimens. Other biotic factors, such as damage to trees by fungi or other agents of disease, have been suggested as modern causes of basal scars (Molnar & McMinn 1960). While fungi and diseases may widen existing scars, some other outside factor is usually necessary to initiate the wound (Shigo 1984).

Flooding and the debris carried in floods, consisting of logs, branches and other vegetation, and/or ice, can also scar trees. Ice and other debris abrade the bark and sometimes break and uproot trees along the shore. Scars from flooding are often triangular shaped, may be large or small (a few mm to several cm), and may have damaged annual rings along the scar's margin. If flooding is common, several open or closed scars may be found on the upstream side of the stem (Sigafoos 1964). Some of the Triassic scars are triangular with abraded tree rings at the scar's surface. Perhaps the two scars which were closed by sealing the scar with cork used this method as an adaptation to high water. Phi thickenings have been found in the roots of several types of plants from the Fremouw Formation (Millay et al. 1987). These thickenings are believed to restrict water flow in the apoplast and they occur in modern plants that grow in environments with fluctuating water levels. This suggests that the fossil plants from Fremouw were dealing with water stress in their environment.

In addition to scarring, false rings may be formed when flooding occurs during the growing season (Yanosky 1983; Young et al. 1993). Since some tree ring boundaries in our specimens are not very distinct, some of these rings may be the result of flooding. The specimens themselves were probably deposited in a braided streambed during a flood. Peat was rafted into the area and left there as flood waters receded. Tree-covered islands may have been destroyed by heavy flooding allowing logs to be deposited with the peat (Taylor et al. 1989). Since floods occur in nearly all modern rivers (Sigafoos 1964), flooding in a Triassic stream is likely.

The importance of fossilized tree scars is not simply the scars themselves, but their potential as paleoenvironmental indicators. What caused the trees to be scarred in the first place? Clearly something damaged the trees while they were still living. The presence of distinct growth rings in our study specimens points to a seasonal climate. Jefferson and Taylor (1983) suggested that the Fremouw site was a coastal plain that remained ice-free during the summer. Taylor et al. (1989) described the Fremouw site as including trees living on forested islands within a braided stream. Based on the diverse flora and fauna, moisture was probably abundant and temperatures were warm with no significant snow or ice cover (Hammer et al. 1990).

Tree scars are not common in Triassic fossil wood from Antarctica, but they are present. Their potential causes vary from biotic to abiotic. Identification of wound source is difficult. However, given the various indicators within the scars and the paleoenvironmental data for a wet climate where flooding was likely, we believe the scars were probably caused by debris hitting trees during flood events. While working with scarred fossil trees has its difficulties, other investigators should be aware of and looking for scars, and be aware of their potential as paleoenvironmental indicators. As more scarred fossil material is found and studied, a better understanding of scarring mechanisms may be identified.

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