

DEGRADED WOOD IN THE UPPER TRIASSIC PETRIFIED FOREST FORMATION (CHINLE GROUP), NORTHERN ARIZONA: DIFFERENTIATING FUNGAL ROT FROM ARTHROPOD BORING

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Abstract—Permineralized wood from the middle of the Upper Triassic Petrified Forest Formation in Arizona, in strata correlative with the Sonsela Member, displays various forms of heartwood degradation. Pitting of the wood exhibits two primary morphologies. Elongated cavities are up to several mm long, parallel to the wood grain and may merge to form channels that extend longitudinally through the wood for lengths of several cm. Circular to elliptical cavities that cross-cut the wood grain are up to several mm wide. Both forms of degradation are interpreted as the result of pre-burial biotic activity. The pitting appears to be caused by pathogenic fungi (white rot and white pocket rot in particular) that degraded and removed tracheids in the secondary xylem. The size and shape of some of the features, such as the longitudinal channels, may be consistent with some forms of arthropod burrowing, but the weight of the evidence, in particular the lack of frass, suggests that these also resulted from fungal decay.

INTRODUCTION

Correct attribution of trace fossils is essential to the fullest understanding of paleoecological systems, and the misidentification of insect borings as wood rot, and vice versa, compromises the ability to attain this goal (cf. Genise et al., 2012). Furthermore, as arthropod trace fossils have been used to augment and extend the ranges of some orders, the correct identification of the trace maker is essential to avoid errors in extending the ranges of organisms for which the fossil record is limited. For example, Lucas et al. (2010) were able to demonstrate in convincing fashion that Upper Triassic traces previously attributed to nesting bees (Hasiotis and Dubiel, 1993; Hasiotis, 1997) represented instead borings by beetles (also see Tapanila and Roberts, 2012).

We report here several features of biotic degradation from Late Triassic wood that on superficial inspection invite multiple interpretations of origins, including both insect herbivory and fungal decay. Closer inspection allows the elimination of the former hypothesis. This recognition may pertain to the stratigraphic record of wood predation by various arthropod groups and aid in the future identification of fungal rot in fossilized wood.

MATERIAL AND METHODS

The samples we describe here were collected north of Cameron, Arizona, from sandstone beds below the base of redbeds correlated with the Painted Desert Member of the Petrified Forest Formation. Consequently, we correlate these sandstones as the uppermost strata of the Sonsela Member (Fig. 1; Lucas et al., 1997). Here we found numerous silicified logs up to 30 cm in diameter exposed at the surface of a badlands topography (Fig. 2A), as well as embedded in the hillsides, where poorly lithified sandstone beds have eroded. The logs exposed at the surface are fragmented and form roughly rectangular segments typically less than 20 cm long, elongated along the longitudinal axis (following the wood grain) of the trees (Fig. 2B). Fragments with the features described here were collected from the central part of the pattern of the tree fragments, and presumably represent mainly heartwood material. No rigorous attempt was made to identify the trees fossilized here, as taxonomic classification may require specific description of the tracheid structure, which is difficult in partially degraded wood. Nonetheless, the wood most likely can be attributed to *Araucarioxylon arizonicum* Knowlton, the most common woody taxon in Chinle strata, as other genera are known primarily

only from a single horizon in the Chinle, the Black Forest Bed in the Painted Desert Member (Creber and Ash, 1990), which occurs well above the Sonsela Member (Heckert and Lucas, 2002).

The dimensions of the longitudinal features of the wood degradation were examined by cutting specimens transverse to the grain. Fragments of wood displaying pitting were studied microscopically using a JEOL JSM6510-LV model scanning electron microscope. Samples were cleaned with acetone and alcohol before imaging. Images were obtained on uncoated samples in a partial vacuum (at 20–38 Pa) with an accelerating voltage of 20 kV using a backscattered electron detector.

Evidence of fungal activity in Chinle fossil wood was first described by Daugherty (1941), who described and interpreted structures formed by a pocket rot fungus. Creber and Ash (1990) presented more detailed evidence of widespread fungal decay in fossil wood from the Chinle at Petrified Forest National Park (PFNP), possibly reflecting rapid spread of a pathogenic fungus. They reported that this instance was confined to a single horizon occurring below the Sonsela Member, but using the stratigraphy of Heckert and Lucas (2002), this wood occurs within the Sonsela Member (above the Rainbow Forest Bed). Correlation of the beds within the Sonsela Member from PFNP to the study area, approximately 220 km to the northwest, is somewhat problematic. Nevertheless, we feel confident that the material we describe was collected within the uppermost strata of the Sonsela Member, and therefore occurs stratigraphically above the horizon containing the material described by Creber and Ash (1990).

OBSERVATIONS

Macromorphology

The collected samples mainly have a light tan to reddish brown color. Some fragments are dark gray-brown; typically, these are clustered in the centers of the tree remains. The grain of the wood is clearly visible on the surfaces of most specimens.

Several forms of degradation or pitting of the wood occur in the samples. Most common are small diameter pits, 0.2 to 0.4 mm wide, that range from nearly circular to ovoid (Fig. 3A); these pits are commonly elongated in the longitudinal dimension, i.e., parallel to the wood grain, and are up to 4 mm long. Locally, these elongated pits are heavily concentrated, creating a nearly alveolar texture in the permineralized wood (Fig. 3B). Within these zones, coalesced axially-oriented pits form axial chan-

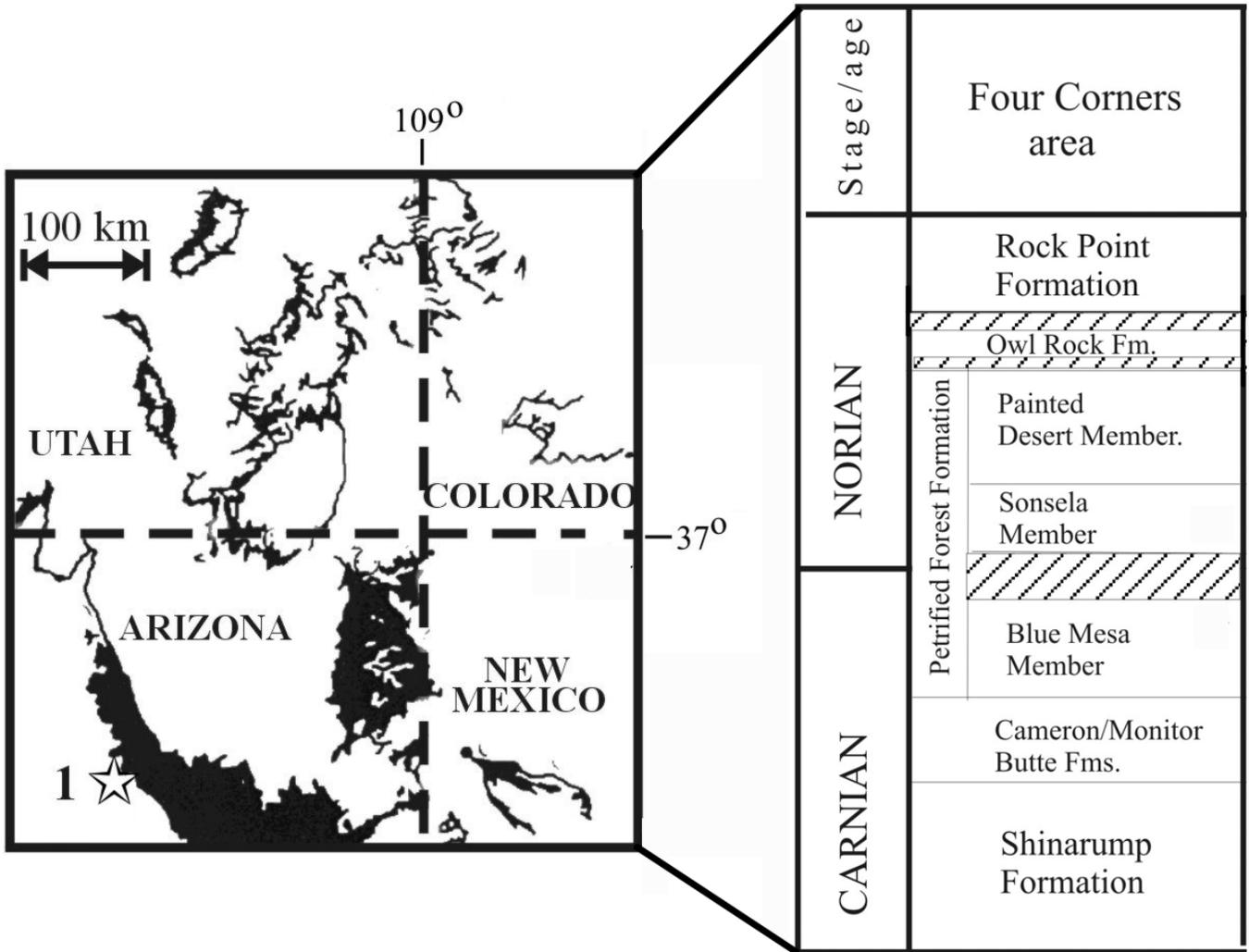


FIGURE 1. Location map of the sample site (star) with outcrops of Chinle Group strata shaded and stratigraphy of the Chinle Group in the study area (after Lucas et al., 1997).

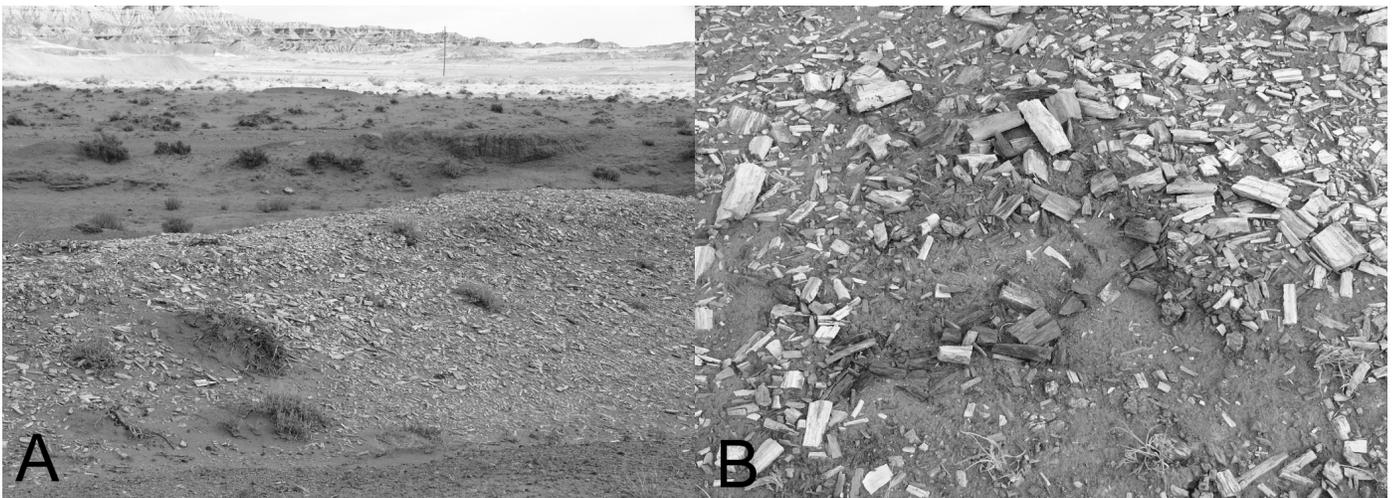


FIGURE 2. Sample site north of Cameron, Arizona. **A**, View of weathered sandstone hill covered by silicified wood fragments. **B**, Darkened fragments occur only in the center of the outline of the wood fragments and may represent heartwood.

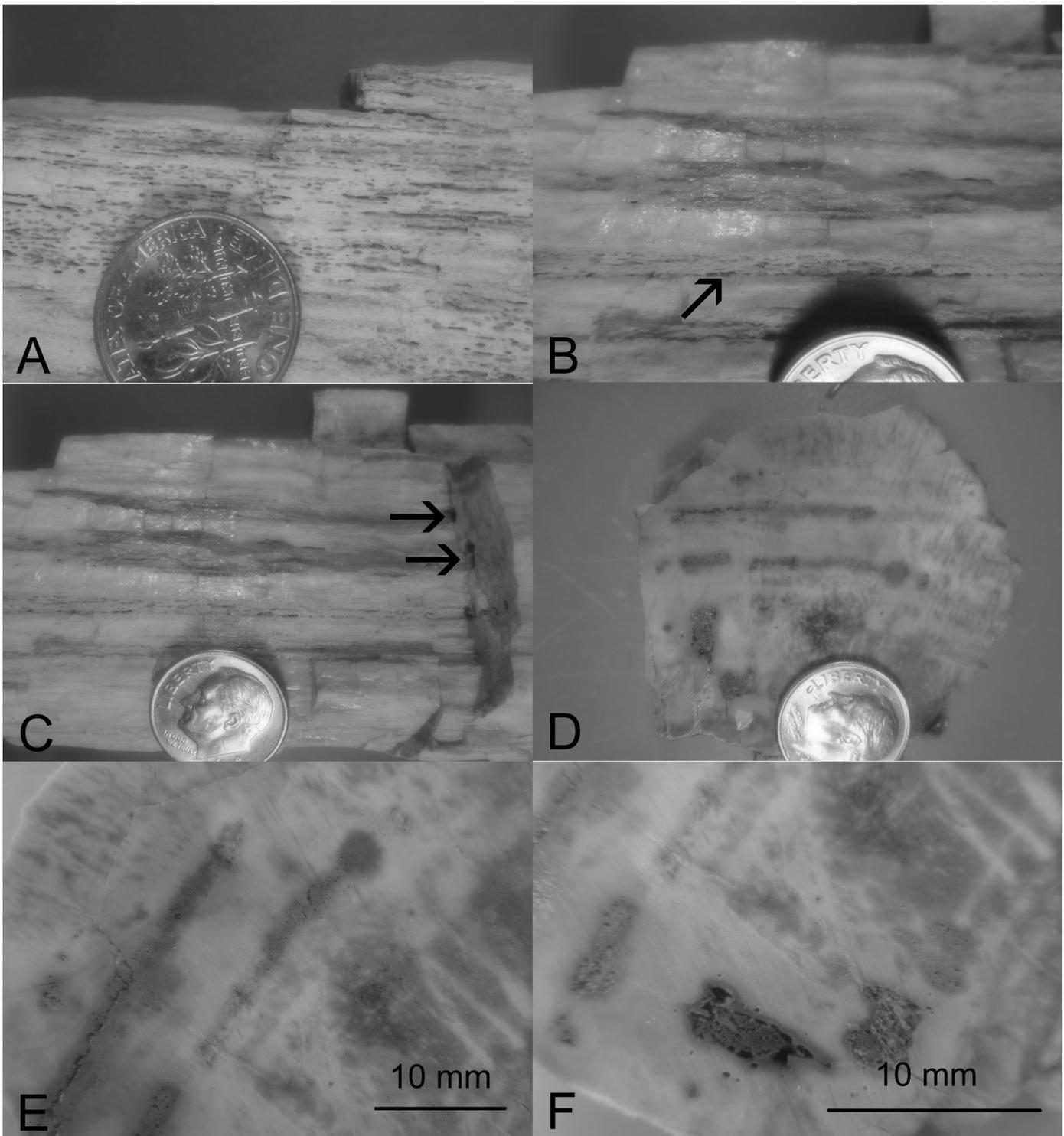


FIGURE 3. Features of wood pitting. **A**, Small pits elongated parallel to the wood grain are visible on the surface of this sample from the tree interior. Coin has a diameter of 18 mm. **B**, Zone with an alveolar texture (arrow) confined to a narrow zone. **C**, Alveolar zones, with staining, that are visible on the wood surface are continuous with channels that penetrate the wood interior (arrows). **D**, Transverse view of the wood illustrates the intersection of the alveolar zones (visible by their staining). **E**, Detail of view in 3D illustrates the fine scale of the longitudinal channels that penetrate the wood axis. **F**, Patches of the alveolar fabric are mainly confined to individual growth bands, as in 3E, but here can be seen also to cut across growth rings.

nels, or tunnels, with shapes that are circular to elliptical to very irregular in cross section, up to 3 mm in diameter (Fig. 3C). Transverse cuts demonstrate that the wood degradation characterized by the channels and alveolar texture is concentrated in localized axial zones in the softwood that are stained light orange-red and extend for 5 cm or more along the wood axis (Fig. 3D). In transverse view, the alveolar texture is produced by a nearly honeycomb-like porosity formed by numerous, small adjacent channels, some at the cellular scale (Fig. 3E). Commonly, these zones are confined (or nearly so) within individual growth bands, although they do also cross between growth bands (Fig. 3F).

Less common than the small, axial pits are larger pits with an ovoid to rectangular shape, up to 4 mm wide, that cut across the wood grain (Fig. 4A-B). These are closely spaced locally, with distances of several mm between pits. Notably, these pits co-occur with the smaller, longitudinally-oriented pits, and cross-cut them in some instances, although the relative order of their formation is not evident.

Micromorphology

Scanning electron microscopy reveals details of the wood degradation not readily apparent macroscopically. In particular, the pits can be seen as open cavities formed by the removal of the tracheid walls in the secondary xylem. This degradation is expressed by cell wall openings with a diverse range of sizes and shapes, from circular pits less than 100 μm , to ovoid to elongated, irregular depressions with lengths of 1 mm or more (Fig. 5A). Pits with the differing macromorphologies described above share the characteristic that the edges of the pits are smooth to moderately irregular; i.e., they lack distinctly angular edges (Fig. 5A). Planar to semi-circular elements on the margins of the cavities generally correspond to the boundaries of adjacent cells (Fig. 5B), but there is no sense of angular elements within a single cell wall bordering a cavity.

Microscopic examination of transverse sections of the specimens confirms the macromorphology described above in that the alveolar zones consist of longitudinal channels of various sizes, in which cells are completely missing, surrounded by or adjacent to patches of xylem in which the cells are thin-walled and completely open, rather than filled by silica, as in the wood adjacent to these patches (Fig. 5C-E). Commonly, however, the channels are surrounded by a dense network that appears to consist of collapsed tracheids (Fig. 5E).

Many of the cavities contain sedimentary grains that typically are silt-size (20 to 60 μm) grains, but in some instances are larger (i.e., >100 μm). These grains generally lack any discernible pattern of shape or size distribution (Fig. 5F). A few voids are occupied by clusters of grains with similar sizes, but even in these instances, the grains have diverse shapes.

INTERPRETATION

Fungal decay

The two distinctive morphologies of wood degradation described above invite attribution to separate origins. Fungi do produce borings in hard substrates such as bone and shell (e.g., Sarjeant, 1975). According to Sarjeant (1975), fungal borings in wood are very small (generally less than 25 μm in diameter) tunnels that may fork, but because they typically follow borings made by animals it is often difficult to identify them. Nevertheless, we interpret the features described above as resulting from a common cause, fungal rot, as described below.

Creber and Ash (1990) described features of degradation in *Araucarioxylon* in a laterally extensive zone of the Chinle that occurs within the Sonsela Member. They observed axially oriented cylindrical structures, that they termed "rods," with diameters of 1.2-2.5 cm. These appear to be zones of damaged, necrotic wood that have preferentially mineralized to form elongated resistant structures. These rods are significantly larger than any features we observed in our samples, none of which are associated with preferential silicification. However, they also described smaller, axial "tubes." These are longitudinal channels that are similar in size and morphology to the axial channels we find.

Creber and Ash (1990) attributed these features (of both scales) to the degrading actions of pathogenic fungi, a pocket rot fungus in particular, such as *Polyporus amarus*. They noted that fungus does not abrade the tracheids, as an invertebrate burrower might, and that it travels through the heartwood of the tree. As noted above, the edges of the pits in the samples we studied are indented where the edges intersect individual tracheid walls, but show no sign of the gnawing activity of arthropod mandibles. Moreover, the location of the samples we collected in relation to the overall pattern of distribution of the fossil wood fragments is consistent with an original position in the heartwood of the trees, suggesting that the decay occurred, or at least began, in still-living wood through the action of a pathogenic organism. Consequently, we interpret the perforation of wood we observe as the result of fungal decay, possibly similar to the heart-rot fungus interpreted by Creber and Ash (1990).

Stubblefield and Taylor (1986), in a pioneering paper on this topic, stated that arthropods, and beetles in particular, are one of the most common causes of pitting or perforation of woody tissues. However, their examination of features of Triassic wood from Antarctica (including *Araucarioxylon*) suggested instead an origin through fungal decay. They described spindle-shaped pockets, circular to irregular in cross-section and up to 3.5 mm wide, and up to 3 cm long. The pockets are voids within the wood that are free from cells. These pockets are

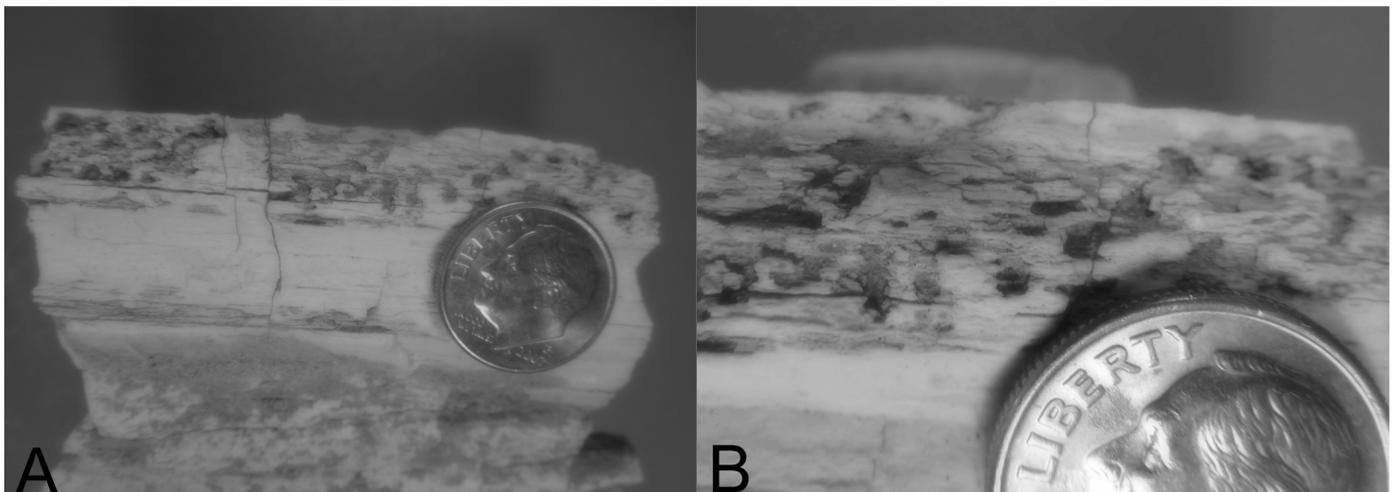


FIGURE 4. Views of cross-cutting pits. **A**, General view of circular to elliptical pits that have an orientation transverse to the wood grain. **B**, Detail of **A**.

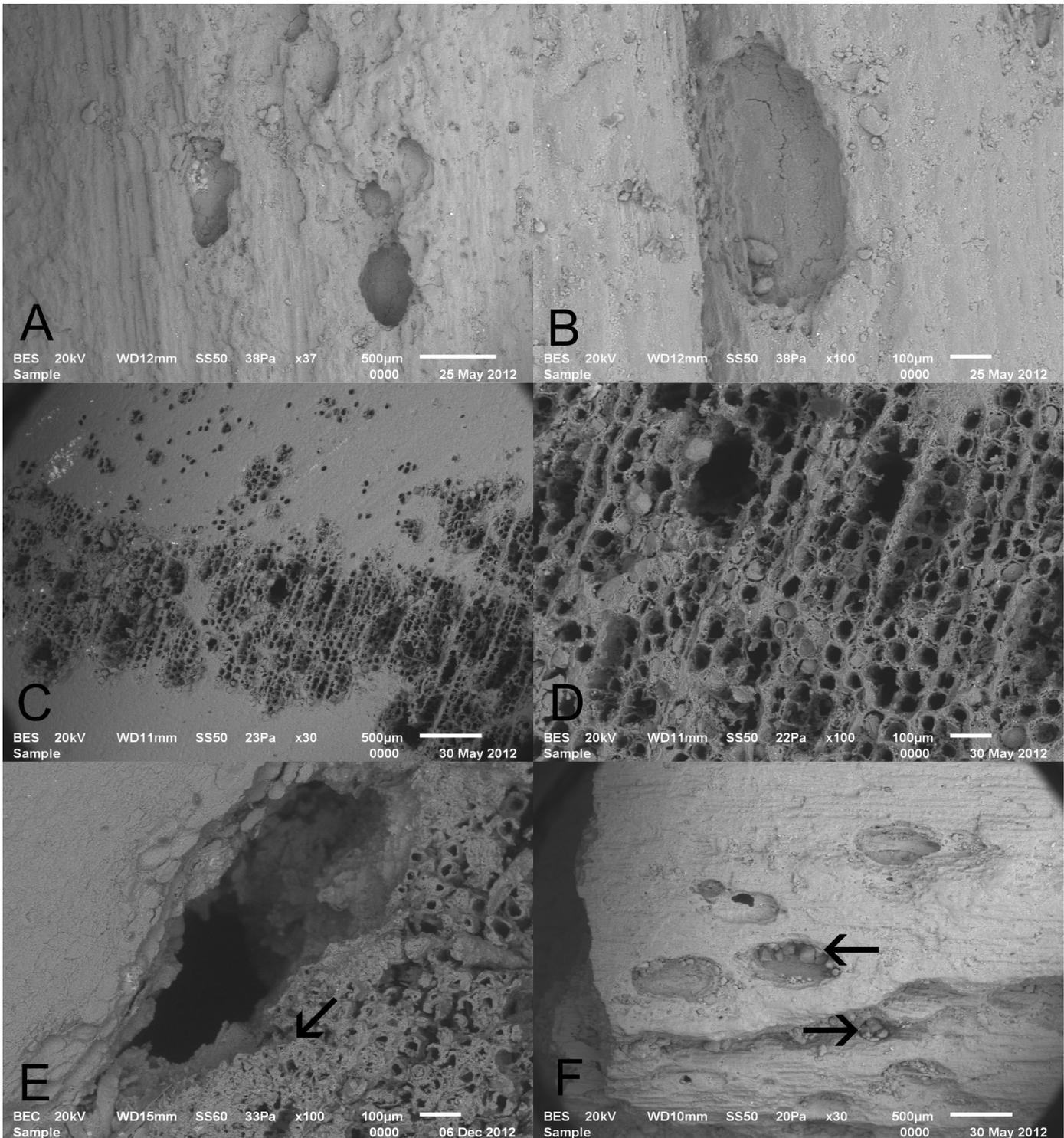


FIGURE 5. Micromorphology of the wood pitting as viewed by scanning electron microscopy. **A-B, F**, Images of surface of wood samples oriented longitudinally. **C-E**, Images of surfaces produced by cutting samples perpendicular to grain. **A**, Sizes and shapes of the pits vary greatly. Larger pits are oriented primarily parallel to the wood grain. **B**, The edges of the pits are mainly smooth where the sides are parallel to the wood grain, but show indentations, primarily at the bottom, where the edge intersects individual wood cells. **C**, Transverse view of an alveolar zone illustrating the distinctive texture formed by the combination of longitudinal channels and open wood cells. **D**, Higher magnification view of the field in 5C illustrating the thin-walled nature of many of the open cells adjacent to the channels. **E**, View of open channel in transverse section. Tracheids to the right of the channel are collapsed (arrow), while those to the left are whole and silica-filled. **F**, Wood pits contain particles that are varied in size and shape.

most often confined to a single growth ring, but may cut across adjacent growth rings. We see a similar distribution of voids with nearly identical sizes and shapes in our Chinle samples.

Additionally, Stubblefield and Taylor (1986) described regions of degraded and collapsed tracheids adjacent to the pockets, much as we observed. Further, they noted the presence of fungal hyphae, both within the tracheids and in the rays of the secondary xylem. These observations, combined with the lack of an anastomosing network of tunnels or frass (insect excrement), both of which are features characteristic of insect infestation, led them to conclude that the perforations they observed were caused by fungal activity. In particular, the degradation and removal of tracheids is consistent with the process of delignification of the wood cells by the enzymatic action of members of the fungal group Basidiomycotina, including both white rot and white pocket rot. White rot and white pocket rot differ in that the former removes both lignin and cellulose, and so will produce open cavities, while the latter selectively removes only the lignin, leaving weakened cell walls of cellulose. Based on the microscopic features they observed, Stubblefield and Taylor (1986) interpreted the simultaneous action of both fungal variants. The features we report compare well with those observed by Stubblefield and Taylor (1986), with the exception of the presence of fungal hyphae. No such features are confidently identified in our Chinle wood samples, although this may be a result of degradation during weathering.

The features we describe here also compare well with those described by Pujana et al. (2009, fig. 4A-B) in pycnoxylic Eocene gymnosperms, similar to the conifer *Araucarioxylon* that is the most common fossil wood found in the Chinle Group. They also described degraded tracheids in the secondary xylem, characterized by circular to ellipsoidal features formed by the partial to complete removal of cells, as seen in the Chinle samples. Most, but not all of the pits and channels described by Pujana et al. (2009, fig. 4A), are elongated parallel to the wood grain; some are circular pits that cut the grain of the wood transversely. These pits also match well the morphology we observe in the Chinle samples and match the example of white rot in modern wood presented by Genise et al. (2012, fig. 4G). Pujana et al. (2009) interpreted all features of wood degradation as due to the decay by white rot produced by basidiomycetes. We note again that basidiomycetes produce hyphae, which were not observed in the Chinle specimens, whereas ascomycetes do not. Nevertheless, the morphology of the features in our Chinle samples is consistent with an origin by the decaying action of white rot and/or white pocket rot fungi.

Other Potential Origins

Some of the features we describe in Chinle wood resemble also the termite borings in Early Cretaceous conifers described by Pires and Sommer (2009). Like *Araucarioxylon*, these conifers grew in a warm, equatorial setting with a strongly seasonal climate (in the Araripe basin, Brazil). Features described by Pires and Sommer (2009) include oval-shaped cavities 1-2 mm long near the exterior of the woody tissues; these are interpreted as the openings of tunnels to the exterior of the tree. The Chinle material, in contrast, exhibits no evidence of exterior openings, although the fragmentary preservation of the wood may hinder recognition.

Pires and Sommer (2009) described individual tunnels that are oriented axially to the grain of the wood, e.g., parallel to tracheid orientation, circular in radial view, and typically 1 mm in diameter. Although

generally straight and unbranching, adjacent tunnels coalesce laterally to form tunnels with widths of 2-5 mm. Hence, the morphology and scale of the tunnels in the Chinle wood is quite similar to the features described by Pires and Sommer (2009). But these authors note that an origin of wood degradation by arthropod herbivory is evidenced by the observation of visibly gnawed margins of the tracheids surrounding the borings. As noted above, this is a characteristic missing from the Chinle samples. Additionally, termites produce hexagonal coprolites that occur in some tunnels. Another potential wood-boring arthropod group, the oribatid mites, has a range extending as far back as the Devonian, but these also produce very characteristic coprolites (Labandeira et al., 1997). The Chinle wood pits contain grains, but they lack a consistent size or shape, and so appear more likely to be detrital siliciclastic sediments. Collectively, then, the key features to demonstrate an origin by burrowing behavior (gnawed tracheid margins and identifiable coprolites) are clearly missing from the Chinle wood. Therefore, an origin through arthropod herbivory is unlikely for the features we describe here. Furthermore, contra Hasiotis (2003), there is no evidence of termites before the Cretaceous (e.g., Grimaldi and Engel, 2005), which rules out termites as the specific tracemaker.

We note also that arthropod boring in Chinle Group (Upper Triassic) wood has been well-known and published on since the 1930s (e.g., Brues, 1936; Walker, 1938; Lucas et al., 2010; Tapinala and Roberts, 2012). These borings are characterized by their well demarcated tubular shapes and much larger size than the features we describe here. These published Chinle borings do not form complex galleries and closely resemble those of modern beetles such as anobiids (e.g., Haack and Slansky, 1987).

Finally, Fisk and Fritz (1984) examined fossils of silicified sequoia of Eocene age that displayed numerous small (0.5-1.5 mm) holes and channels that resemble the burrows of powder-post beetles. The lack of insect coprolites, or frass, which often fills insect burrows, led Fisk and Fritz (1984) to interpret these features as the result of differential weathering of calcite cement that had impregnated the wood prior to silicification. The features described in that study occurred only near the exterior surface of the wood, however, unlike the Chinle features, which are concentrated in the heartwood. Therefore, we discount this mode of origin in the formation of the Chinle wood features.

CONCLUSION

The Late Triassic wood samples collected from beds correlative with the upper Sonsela Member of the Petrified Forest Formation (Chinle Group) near Cameron, Arizona, present multiple morphologies of degradation, but all involve perforation of the original woody tissues in the heartwood. Macroscopic and microscopic examination demonstrates that the pits resulted from the complete removal of tracheids, and the degradation and collapse of tracheid walls adjacent to the voids. The lack of visible evidence for arthropod herbivory on the edges of the tracheids, and the absence of frass in the voids suggests that the pitting did not result from arthropod excavation, but instead from fungal decay. Enzymatic delignification of the wood cells by white pocket rot created zones of thin-walled tracheids, while simultaneous removal of both lignin and cellulose by white rot created the open cavities.

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REFERENCES

- Brues, C.T., 1936, Evidence for insect activity preserved in fossil wood: *Journal of Paleontology*, v. 10, p. 637-643.
- Creber, G.T. and Ash, S.R., 1990, Evidence of widespread fungal attack on Upper Triassic trees in the southwestern U.S.A.: Review of Palaeobotany and Palynology, v. 63, p. 189-195.
- Daugherty, L.H., 1941, The Upper Triassic flora of Arizona: Carnegie Institution of Washington Publication 526, 108 p., 40 pls.
- Fisk, L.H. and Fritz, W.M., 1984, Pseudoborings in petrified wood from the Yellowstone "fossil forests": *Journal of Paleontology*, v. 58, p. 58-62.
- Genise, J.F., Garroute, R., Nel, P., Grandcolas, P., Maurizot, P., Cluzel, D., Cornette, R., Fabre, A.-C. and Nel, A., 2012, Asthenopodichnium in fossil wood: Different trace makers as indicators of different terrestrial environments: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 365-366, p. 184-191.
- Grimaldi, D. and Engel, M., 2005, *Evolution of insects*: New York, Cambridge University Press.
- Haack, R. and Slansky, F., 1987, Nutritional ecology of wood-feeding Coleoptera and Hymenoptera; in Slansky, F., ed., *Nutritional ecology of insects, mites, spiders, and related invertebrates*: New York, Wiley and Sons, p. 449-486.
- Hasiotis, S.T., 1997, A buzz before flowers...: Plateau [Journal of the Museum of Northern Arizona], v. 1, p. 20-27.
- Hasiotis, S.T., 2003, Complex ichnofossils of solitary and social soil organisms: Understanding their evolution and roles in terrestrial ecosystems: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 192, p. 259-320.
- Hasiotis, S.T. and Dubiel, R.F., 1993, Continental trace fossils of the Upper Triassic Chinle Formation, Petrified Forest National Park, Arizona: *New Mexico Museum of Natural History and Science, Bulletin* 3, p. 175-178.
- Heckert, A.B. and Lucas, S.G., 2002, Revised Upper Triassic stratigraphy of the Petrified Forest National Park, Arizona, U. S. A.: *New Mexico Museum of Natural History and Science, Bulletin* 21, p. 1-42.
- Labandeira, C.C., Phillips, T.L. and Norton, R.A., 1997, Oribatid mites and the decomposition of plant tissues in Pennsylvanian coal-swamp forests: *Palaios*, v. 12, p. 319-353.
- Lucas, S.G., Heckert, A.B., Estep, J.W. and Anderson, O.J., 1997, Stratigraphy of the Upper Triassic Chinle Group, Four Corners Region: *New Mexico Geological Society, Guidebook* 48, p. 81-107.
- Lucas, S.G., Minter, N.J. and Hunt, A.P., 2010, Re-evaluation of alleged bees' nests from the Upper Triassic of Arizona: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 286, p. 194-201.
- Pires, E.F. and Sommer, M.G., 2009, Plant-arthropod interaction in the Early Cretaceous (Berriasian) of the Ararape Basin, Brazil: *Journal of South American Earth Sciences*, v. 27, p. 50-59.
- Pujana, R.R., Massini, J.L.G., Brizuela, R.R. and Burrieza, H.P., 2009, Evidence of fungal activity in silicified gymnosperm wood from the Eocene of southern Patagonia (Argentina): *Geobios*, v. 42, p. 639-647.
- Sarjeant, W.A.S., 1975, Plant trace fossils; in Frey, R.W., ed., *The study of trace fossils*: New York, Springer-Verlag, p. 163-179.
- Stubblefield, S.P. and Taylor, T.N., 1986, Wood decay in silicified gymnosperms from Antarctica: *Botanical Gazette*, v. 147, p. 116-125.
- Tapanila, L. and Roberts, E.N., 2012, The earliest evidence of holometabolous insect pupation in conifer wood: *Plos ONE*, v. 7, issue 2, p. 1-10.
- Walker, M.V., 1938, Evidence of Triassic insects in the Petrified Forest National Park, Arizona: *Proceedings of the U. S. National Museum*, v. 85, p. 137-141.