

The Role of Wood in Understanding Saprophytism in the Fossil Record

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Columbus

With 1 Plate

Introduction

One of the most neglected areas in paleobiology is the study of fungi and the impact these organisms had on the developing ecosystem throughout geologic time. There are perhaps three reasons for this neglect. One concerns the long held belief that fungi were too fragile to be adequately preserved in the fossil record, and thus of little value in interpreting past ecosystems. Second, most paleobotanists are trained in vascular plant morphology and anatomy, and thus perhaps ill-equipped to deal with the complexities of fungal life histories, their organization and systematics. Third, there has been relatively little interaction between mycologists working with living fungi and paleobiologists studying fossil forms. All of the above have contributed to a general paucity of information about the diversity of fungi through geologic time, and especially the levels of interaction between fungi and other organisms.

In recent years, however, several reports of fossil fungi have demonstrated that preservation is not a major factor, and that several levels of interaction can be documented in the paleoecosystem. One of these involves the report by SHERWOOD PIKE & GRAY (1985) of branched hyphae with perforate septa and multiseptate and unicellular spores in sediments of Upper Silurian age. Included in some of their preparations were aggregations of frass containing hyphae, perhaps produced by fungivores. Another example of an interaction between fungi and animals involves the first fossil trichomycetous fungus (WHITE & TAYLOR 1989). Modern trichomycetes are obligate symbionts that live within the digestive tract of various arthropods. In the Triassic fossil, diagnostic features of the arthropod are lacking, nevertheless the presence of frass in the sediment and the morphology of the fungus provide documentation of the existence of this fungus/animal interaction. Examples of levels of interaction between fossil fungi and plants are widespread and variable, and include a variety of cases demonstrating parasitism (e.g. MILLAY & TAYLOR 1978, STIDD & COSENTINO 1975, ILLMAN 1984) and both direct and indirect occurrences of mutualism (e.g. STUBBLEFIELD et al. 1987a,b).

The most obvious, but least well documented example of fossil fungi interacting with plants, involves the decay of plant material through the generalized process of saprophytism. Although this level of interaction is one of the most common activities of fungi today, there are relatively few documented cases of saprophytism in the fossil record. The primary intent of this paper is to document the role of saprophytic fungi in the fossil record and to discuss this level of interaction as it relates to the anatomical features of fossil wood.

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Description

To date, the earliest known example of wood rotting fungi occurs in the Upper Devonian axis *Callixylon* (STUBBLEFIELD et al. 1985). Evidence for the existence of fungi in this example includes several forms. One is the direct presence of hyphae in both tracheids and ray cells (pl. 1 figs. 4, 8). Individual hyphae range up to 6 μm in diam. and are septate. In the *Callixylon* wood many of the hyphae branch; in others there are distinct terminal and intercalary swellings. The interaction of fungi and the *Callixylon* wood is even more apparent when one examines the surface of the tracheids. Many of the tracheid walls lacking hyphae show some evidence of fungal modification in the formation of decay features within the lignin. These may be in the form of narrow grooves (erosion troughs) (pl. 1 fig. 5) and/or oval cavities which extend into the lignin of the cell wall.

Other indirect evidence of fungal invasion in the *Callixylon* wood involves the presence of various structures within the ray cell lumens. These include spherical bodies that range from approximately 2.0 - nearly 50.0 μm in diam. (pl. 1 fig. 8). Many are solid and appear amber in color in transmitted light. Other inclusions are characterized by a hyaline zone that surrounds the dark body, or as collapsed spheres ranging up to 23 μm in diam. There can be little doubt that the fungal remains in the *Callixylon* wood represent several different types, as well as several levels of interaction. It is unclear even what major groups of fungi are present in the *Callixylon* wood, although at least some certainly have ascomycetous and basidiomycetous affinities. The distinct pattern of erosion troughs in the tracheid wall (pl. 1 fig. 5) is suggestive of wood rotting fungi, especially those of the white rot type.

In recent years there have been a number of reports of fungi preserved in silicified peats of both Triassic and Permian age from Antarctica (e.g. TAYLOR & WHITE 1989). Some are believed to be endogonaceous types, while at least one form constitutes the oldest evidence to date of an arbuscle from a vesicular arbuscular endomycorrhizal (VAM) type (STUBBLEFIELD et al. 1987a,b).

The fungi that are by far the most common at these sites include at least two types of wood rotting fungi that are believed to be of the white rot and white pocket rot types (STUBBLEFIELD & TAYLOR 1986). Characteristic perforate patterns in the wood, caused by these fungi, have been observed in several woody axes, including wood referred to as *Araucarioxylon* (pl. 1 fig. 1) and *Vertebraria* (pl. 1 fig. 2).

Although perforated wood may be produced by several causal agents (e.g. insects, differential mineralization), there is little doubt that the unique patterns present in *Vertebraria* and *Araucarioxylon* are the result of fungal activity. Both wood types are characterized by areas in the secondary xylem devoid of tracheids. The perforations range up to 3.5 mm in diam; in longitudinal section they may be spindle-shaped and 3.0 cm long. In both axes growth rings are conspicuous, with the pockets randomly scattered throughout the wood. Microscopically, the pockets may contain a few disorganized cells near the periphery, or may be completely devoid of tracheids (pl. 1 fig. 7).

In many of the pockets, septate, branched hyphae up to 6.5 μm in diam occur; a few have been identified with medallion clamp connections (pl. 1 fig. 9) suggesting basidiomycetous affinities. Hyphae extend through radial and tangential walls, or through pits. No well developed erosion troughs, like those reported in *Callixylon*, have been observed to date in either the Permian or Triassic woods.

Both woods demonstrate two patterns of decay. In one, the regions of wood closely associated with pockets show a reduction in the amount of organic material, with tracheid walls appearing light in color (pl. 1 fig. 11). A second pattern includes partially degraded cells near margins of the pockets, and in the modification of cells near the perforations. In many of these cells the middle lamella is not removed and the cells are held together at the corners (pl. 1 fig. 7). In this pattern the secondary cell wall also separates from the middle lamella and is generally lighter in color (pl. 1 fig. 12). At some levels the secondary wall of tracheids may be swollen (pl. 1 fig. 6). In this decay pattern it appears that the progression extends from the primary wall to the secondary wall, and finally to the middle lamella. The separation of adjacent tracheids has also been noted in the Gondwana wood type *Polysolenoxylon kraeuselii* (MAHESHWARI 1972). The thickened secondary cell wall is also similar to

the formation of appositions (pl. 1 fig. 13), a cell wall feature that functions to partition the fungus from uninfected tracheids of the wood.

In extant woody plants there are three principal types of decay (brown rot, soft rot and white rot). Dissociation of tracheids and formation of perforations in the Antarctic woods are identical to that type included in the white rot group of fungi, in particular white rot and white pocket rot. In extant plants, basidiomycetes are the principal cause of these two types of decay; the presence of clamp connections in the fossils suggests these fungi were operative in the Gondwana woods as well.

In white rot, enzymatic activities of the fungus begin in the S_3 layer (pl. 1 fig. 10) and continuously erode the cell wall to form erosion troughs. Studies of modern woods indicate that lignin and cellulose are degraded in a 1:1 ratio in this type of wood rot (COWLING 1961). Symptoms of white pocket rot are relatively easy to identify because fungal activities result in the formation of spindle-shaped pockets of decayed wood separated by regions of intact tracheids. This decay pattern, however, involves the removal of the middle lamella and ultimate separation of the cells (pl. 1 fig. 7). In this type of rot, tracheid surfaces lack erosion troughs and the fungus principally removes lignin from the wood leaving substantial amounts of cellulose. Thus, although these two types of fungal attack occur together in many woods, activities of the fungi result in quite different symptoms that are easily recognizable in fossil woods. It is interesting that although different fungi cause decay in softwoods as opposed to hardwoods, which obviously differ in a number of anatomical characters, the general decay pattern in both is quite similar.

In some extant woods, that have been studied to date, a substantial amount of lignin is degraded by bacteria and yeasts as well. In one study, tunnel-forming bacteria consisting of Gram-negative rods were demonstrated to remove total cell wall material (DANIEL & NILSSON 1987). Neither bacteria nor yeasts have been identified in any of the rotted fossil woods examined. This may simply reflect their small sizes, the inability to recognize them or simply the failure of bacteria and yeasts to be preserved. This level of interaction will need to be addressed in subsequent studies of fossil wood rot.

Discussion

It is surprising that there are not more accounts of wood rotting fungi in the fossil record, especially in light of the large number of studies dealing with Carboniferous coal ball plants. Although a variety of different types of fungi have been reported in association with coal ball plants (e.g. TAYLOR 1990) none of these involve documented examples of wood decaying forms. Even lacking well preserved mycelia in plant tissues, there are no examples demonstrating the symptoms of wood rotting fungi (e.g., spindle shaped pockets of white pocket rot, removal of lignin from cell walls). There may be several reasons for the absence of lignin and cellulose decaying fungi in Carboniferous sediments. One may simply be the inability to recognize the decaying activities of such fungi, especially if the decaying organisms produced more subtle effects such as erosion troughs on tracheids. Another plausible explanation for the absence of wood decaying fungi at this point in geologic time is belief that the higher fungi (basidiomycetes and ascomycetes), that today are responsible for cellulose and lignin decomposition, had not yet evolved the appropriate biochemical pathways. Both the ascomycetes and basidiomycetes were present by Pennsylvanian time, and at least one basidiomycete has been described in the xylem of a small fern (DENNIS 1970). Moreover, the report of erosion troughs in *Callixylon* tracheids indicates that lignin decaying organisms were active as early as the Upper Devonian. Nevertheless, we know of no examples of wood rotting fungi in any of the various wood types (e.g., lycopods, sphenophytes, seed ferns, cordaites) common in Carboniferous peat communities. Although the term peat swamp is widely used for heterogeneous assemblages of plant material throughout the geologic column, the conditions under which these deposits formed were highly variable (TAYLOR et al. 1989). For example, many of the mid-continent coal ball peats from North America generally formed in association with marine incursions into the peat swamps. In Europe and Britain, coal balls are generally more restricted stratigraphically while in North America they are found throughout the Pennsylvanian. This has caused SCOTT & REX (1985) to suggest that perhaps some tecto-

nic or climatic control influenced their formation. The apparent absence of wood decaying fungi in coal ball deposits perhaps encompasses a complex set of variables that range from pH of the swamp environment to climatic tolerances of the decaying organisms. Climatic variability alone does not appear to be a significant feature since there was a major shift in the climate from the Permian to the Triassic. In spite of these major changes, Antarctic woods from both geologic periods (Permian and Triassic) show evidence of exactly the same type of decay symptoms in the form of white pocket rot. Moreover, the fungi responsible for the fossil perforate wood have not only continued to the Recent, but also, as was the case in the Late Paleozoic and Early Mesozoic, continue to utilize a wide variety of hosts. As paleobiologists continue to gain greater resolution in understanding fossil plant communities, it will be necessary to better understand the role that fungi and other decaying organisms play in the development of the ecosystem. Interpreting fossil woods from all geologic periods provides an important source of information necessary in understanding the geologic history of saprophytism.

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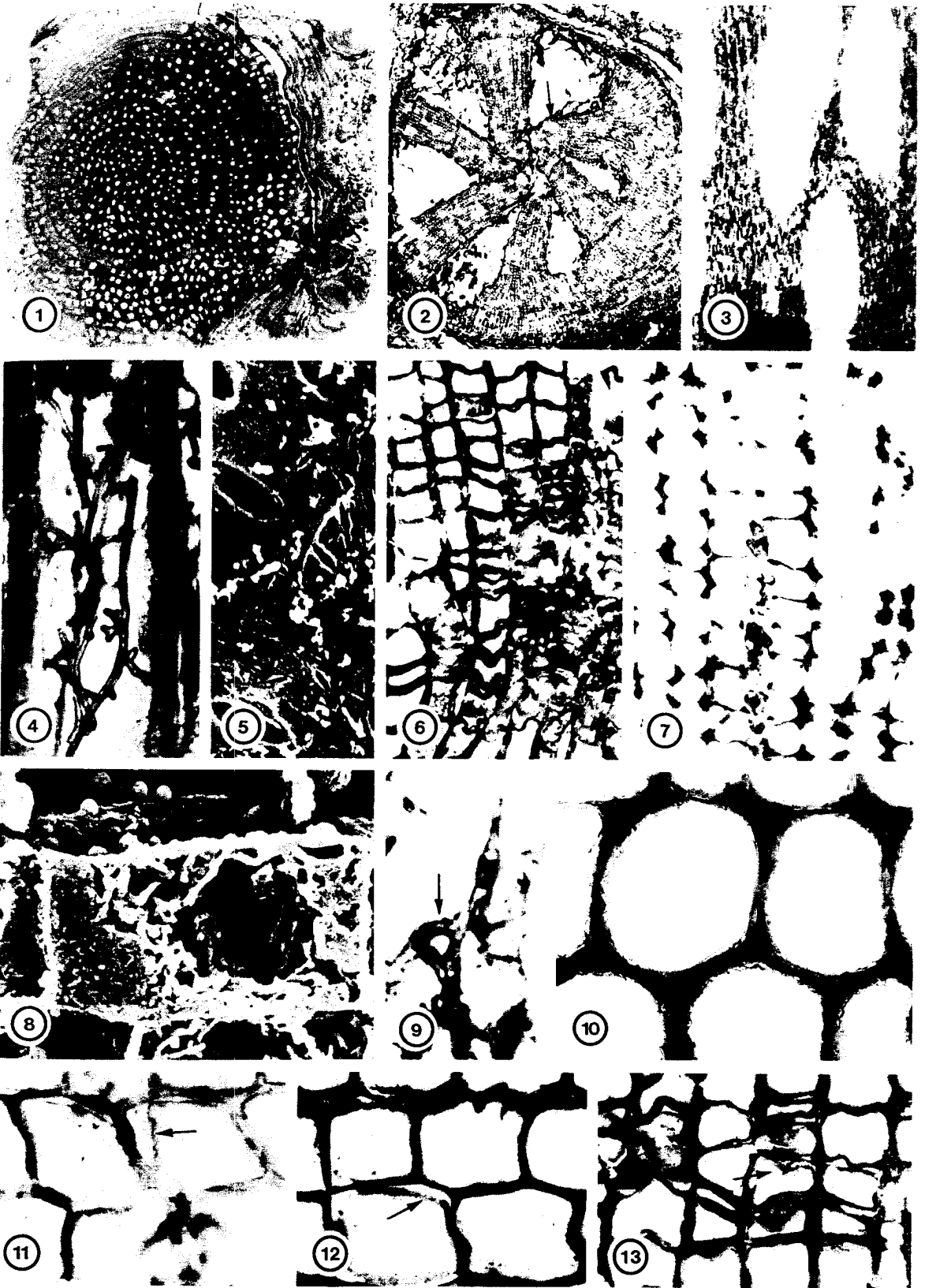
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Plate 1

- Fig. 1. Transverse section of *Araucarioxylon* axis showing numerous perforations of white pocket rot in the wood. -- x0.5.
- Fig. 2. Transverse section of small *Vertebraria* axis. Arrow indicates position of white pocket rot. -- x12.5.
- Fig. 3. Longitudinal section of white pocket rot in *Araucarioxylon* wood. -- x7.
- Fig. 4. Tracheid of *Callixylon* containing hyphae. -- x700.
- Fig. 5. Surface of *Callixylon* tracheid showing numerous ellipsoidal erosion troughs. -- x2000.
- Fig. 6. Early stage in the formation of a decay pocket in *Araucarioxylon* wood where wall layers become swollen and separated to fill cell lumen. -- x235.
- Fig. 7. Tracheids in vicinity of decay pocket showing persistent cell corners and middle lamellae. -- x400.
- Fig. 8. *Callixylon* ray parenchyma filled with hyphae. Note globular units in cell above. -- x750.
- Fig. 9. Medallion clamp connection (arrow) in *Araucarioxylon* wood. -- x1500.
- Fig. 10. *Callixylon* tracheids in transverse section showing irregular cell walls and lamellae. -- x400.
- Fig. 11. *Araucarioxylon* tracheids in various stages of degradation. Arrow indicates region of inner wall layer. -- x325.
- Fig. 12. Degraded tracheids of *Araucarioxylon* showing separation of secondary wall (arrow). -- x325.
- Fig. 13. Tracheids of *Araucarioxylon* containing wall appositions (arrow). -- x400.



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