Research papers

Tylosis formation and fungal interactions in an Early Jurassic conifer from northern Victoria Land, Antarctica

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ABSTRACT

Well-preserved fungi occur in permineralized conifer axes from the Lower Jurassic of northern Victoria Land, Antarctica. The fungus is characterized by septate hyphae extending through the vascular ray system via penetration of cross-field pits. Tyloses are present in large numbers and might have been effective as a physical restraint to the spread of the fungus. However, knotted fungal hyphae within and around the tyloses suggest that the fungus was able to surmount the barriers. Hyphae are also present in the secondary phloem. This plant–fungal interaction contributes to a better understanding of the antagonistic relationships that existed between pathogenic fungi and conifers in the Jurassic paleoecosystems of Antarctica, as well as providing evidence of interactions between fungi and tyloses in Mesozoic wood.

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1. Introduction

Fungi are an integral part of virtually all modern ecosystems. One of the most recognized and important ecological roles fungi perform includes decomposition and nutrient cycling. In extant forest ecosystems, fungi are the primary organisms responsible for the delignification and degradation of wood (Dighton et al., 2005). Some wood-decay fungi may also be effective as parasites and causal agents of mild to severe diseases. Tracheary elements in the heartwood of living plants (i.e., tracheids and/or vessels) are hollow and dead at maturity, and thus do not provide any physiological barrier against the spread of pathogenic fungi. The living outermost wood portion, i.e., sapwood, however, exhibits various types of defense strategies in order to deter or prevent the infestation of wood by pathogenic microorganisms. An initial process includes wood discoloration caused by the accumulation of a variety of extractives (e.g., tannins, dyestuffs, oils, gums, resins, salts of organic acids) that are deposited around an infected area (Pallardy, 2008). When these extractives are overcome by the pathogen, additional defense

measures include the production of tyloses (e.g., Barry et al., 2001). Tyloses are suberized structures that develop from ray parenchyma cells and project through pits to occlude the lumina of tracheids and vessels (Pearce, 1996). Tylosis formation is one of the main processes in the compartmentalization of decay in trees (CODIT model, e.g., Shigo, 1984) and serves to slow down or prevent the spread of pathogens. In addition, tyloses can form around wounds to prevent water loss, even in the absence of decay, in the nonfunctional xylem. Morphologically and functionally comparable structures in the sieve cells of phloem are termed tylosoids (Evert, 2006).

An extensive fossil record of tylosis formation demonstrates that the production of these protrusions has been a common process in woody plants since at least the late Paleozoic. The earliest reports of tyloses in fossil plants come from the Carboniferous, and include a progymnosperm (Scheckler and Galtier, 2003) and several ferns (Williamson, 1876; Weiss, 1906; Phillips and Galtier, 2005, 2011). Tyloses or tylosis-like structures have also been described in the Triassic gymnosperm wood, *Protocedroxylon mineense* (Ogura) Nishida et Oishi (Ogura, 1960; Nishida et al., 1977; Nishida and Oishi, 1982), as well as the Jurassic woods *Metacedroxylon scoticum* Holden (Holden, 1915) and *Xenoxylon morrisonense* Medlyn et Tidwell (Medlyn and Tidwell, 1975). Cretaceous and Cenozoic permineralized woods have yielded abundant reports on the presence of tyloses in fossil angiosperms (Jeffrey, 1904; Bancroft, 1935; Spackman, 1948; Brett, 1960; Manchester, 1983; Nishida et al., 1990; Privé-Gill et al., 1999; Castañeda-Posadas et al., 2009). However,

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information on whether tyloses in fossil plants formed specifically in response to infestation with fungi or other pathogens has so far been lacking and thus the evolutionary history of tylosis formation as a particular defense strategy against pathogens remains unresolved.

In this contribution, we present permineralized conifer axes from the Lower Jurassic of Antarctica that contain numerous tyloses in both the wood and bark in association with fungal remains. What is most significant about these fossils is that the tyloses co-occur with fungal hyphae in the tracheids in a pattern suggestive of tylosis formation as a direct response to fungal colonization.

2. Materials and methods

The three permineralized axes used in this study were collected during the Ninth German Antarctic North Victoria Land Expedition (GANOVEX IX 2005/2006) on Suture Bench, a small bench east of the Gair Mesa in northern Victoria Land, Transantarctic Mountains, East Antarctica. At this site, *in situ* tree trunks occur within the early Toarcian (late Early Jurassic) Kirkpatrick lavas of the Ferrar Group (Bomfleur et al., 2011). The specimens were collected from slope debris directly underneath the base of the lava flows. Acetate peels (Galtier and Phillips, 1999) and thin sections were prepared according to standard techniques (Hass and Rowe, 1999). Pieces of the specimens were mounted on microscope slides using a Hillquist epoxy compound and cut with a Buehler Petrothin® thin-sectioning machine to a thickness of ~250 μm. The wafer was subsequently ground down to a thickness of ~65 μm and analyzed using a Leica DM5000B transmitted-light compound microscope. Digital images were taken with a Leica DC500 digital camera attachment and minimally processed using Adobe Photoshop CS4 Version 11.0.2 (1990–2010, Adobe Systems). Multiple micrographs of the same specimen at different focal planes were compiled to produce composite images (e.g., Bercovici et al., 2009). The images were stacked in Adobe Photoshop CS4 and specific areas were erased to reveal the full three-dimensional view that can be seen through the thin sections. Measurements were taken using ImageJ 1.43u software (Abramoff et al., 2004). Specimens and slides are temporarily deposited in the Paleobotanical Collections, Natural History Museum and Biodiversity Institute, University of Kansas, under specimen accession numbers GIX-SB-007; GIX-SB-014; GIX-SB-036, acetate peel slide accession number AP-GIX-SB-007-CT2-01, and thin section slide accession numbers TS-GIX-SB-007-01; TS-GIX-SB-014-01; TS-GIX-SB-036-01; TS-GIX-SB-036-02.

3. Description

3.1. Wood and secondary phloem

Specimens represent segments of conifer axes with secondary xylem and phloem (Plate I, 1). The most complete and best-preserved specimen is a stem portion with an estimated original diameter of approximately 15 cm. Most of this axis consists of secondary xylem with numerous intercalated rays. Tracheids are polygonal in transverse section and about 20–30 μm in diameter (Plate I, 2). The wood has abundant, evenly distributed uniseriate rays that are 5–8 cells tall (Plate I, 3). Extraxylary tissue is preserved along the outer portion of the axis. Secondary phloem cells are of two principal types: a larger and more prevalent type with diameters up to 75 μm and a smaller, less common type with diameters between 18 and 35 μm (Plate I, 4). The larger cells show distinct concentric layers within the cell wall. The radial walls of the tracheids are further characterized by uniseriate circular-bordered pits with wide borders and narrow apertures (Plate I, 5).

Many of the conifer axes from the Suture Bench locality are *in situ* trunks with well-preserved secondary phloem layers; however, the preservation of the wood is overall very poor. In many sections of the specimen described here, the thick S_2 layer of the tracheid walls appears diffusely degraded and somewhat translucent. The cell walls may further show a separation and detachment of intact S_3 layers, which occur isolated and twisted within the cell lumens (Plate I, 6). In other cases, the boundaries of individual cells are represented by translucent outlines in which it is difficult to determine tracheid wall thickness. Discrete damage structures, such as erosion channels, lysis zones, bore holes, or cavities have not been observed. The ray parenchyma is decomposed to varying degrees; in some areas, the original distribution of rays is recognizable only by opposite pairs of tyloses.

3.2. Tyloses

Abundant tyloses are found along rays in the specimens and are not concentrated in any specific area, e.g., close to ring boundaries. They originate from ray parenchyma cells and each ray cell may produce more than one tylosis; most commonly, tyloses occur in the form of one or more opposite pairs per ray cell (Plate I, 7, 8). One ray parenchyma cell will balloon out through cross-field pits into the adjacent tracheids (Plate I, 9). Tyloses occur in different size ranges (8–25 μm in diameter), and have different morphologies that occlude the tracheid lumen entirely. During development, tyloses are initially small, bulbous protrusions with an undistinguishable base (Plate I, 10). Intermediate stages are

Plate I.
1. Overview of specimen with secondary xylem and phloem cells. Scale bar = 500 μm. AP-GIX-SB-007-CT2-01.
2. Transverse section of secondary xylem in thin section. Due to the relatively poor preservation of the wood, note the difficulty of distinguishing tracheids from rays. Scale bar = 100 μm. TS-GIX-SB-036-02.
3. Tangential section of secondary xylem; note narrow rays. Scale bar = 200 μm. TS-GIX-SB-036-01.
4. Transverse section of preserved phloem in thin section, showing large cells (#) and small cells (*). Note the hypha crossing one of the small cells and the thick, coiled contents of the larger cells. Scale bar = 25 μm. TS-GIX-SB-007-01.
5. Radial section of a tracheid with uniseriate circular-bordered pits. Scale bar = 25 μm. TS-GIX-SB-036-01.
6. Wood in transverse section showing degraded S_1–S_2 layers of the tracheid cell walls. Scale bar = 25 μm. TS-GIX-SB-036-02.
7. Transverse section of wood showing crushed vascular ray (dark line in center), with tyloses in adjacent tracheids. Scale bar = 25 μm. TS-GIX-SB-036-01.
8. Longitudinal section of wood with vascular ray (R) and tyloses in adjacent tracheids. Scale bar = 25 μm. TS-GIX-SB-036-01.
9. Tangential section of tracheids showing a large tylosis (center) ballooning through a cross-field pit into an adjacent tracheid. Scale bar = 25 μm. TS-GIX-SB-036-01.
10. Initial stage of tylosis development. Tyloses at this stage are small, bulbous protrusions with no discernable base. Scale bar = 10 μm. TS-GIX-SB-036-01.
11. Intermediate stage of tylosis development. Tyloses are morphologically similar to initial stage but are large and have a more distinguishable base. Scale bar = 10 μm. TS-GIX-SB-036-01.
12. Final stage of tylosis development. Fully developed tyloses are large bulbous structures that occlude the lumen of the tracheid and have a characteristic narrow base. Scale bar = 10 μm. TS-GIX-SB-036-01.
13. Tylosis with dark, filled lumen. Scale bar = 25 μm. TS-GIX-SB-036-01.
14. Fungal hypha with a right-angled septation. Scale bar = 25 μm. TS-GIX-SB-036-01.
15. Longitudinal section of a tracheid with a hypha extending through its lumen (arrows). Scale bar = 25 μm. TS-GIX-SB-036-01.
16. High degree of hyphal knotting inside a single tylosis. Wall of tylosis indicated by arrows. Scale bar = 10 μm. Note this is a composite image. TS-GIX-SB-036-01.
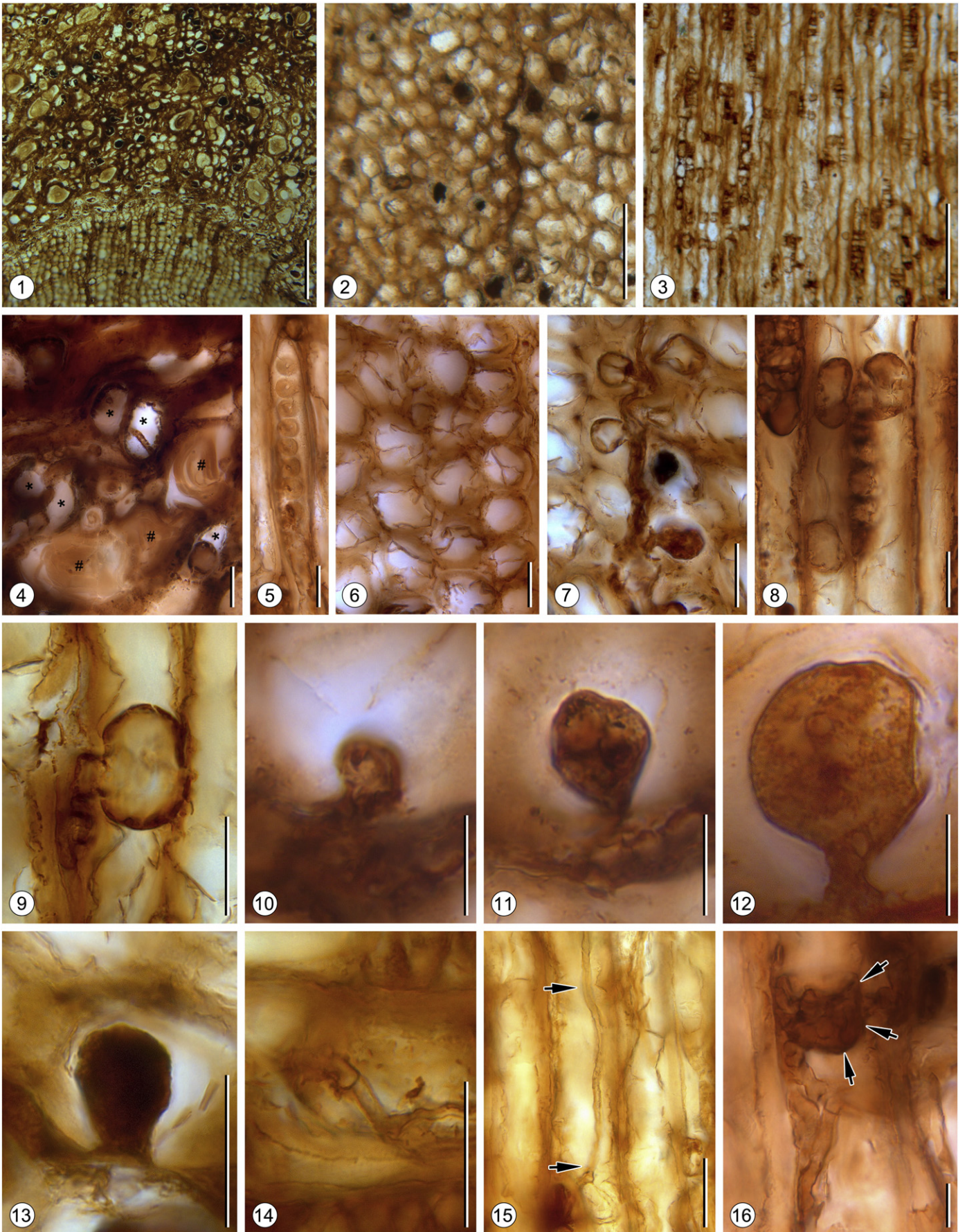
morphologically similar to these small protrusions but larger in size and with a more recognizable base (Plate I, 11). Fully developed and mature tyloses are large, globose structures characterized by a narrow base, which is often the same diameter as the cross-field pit (Plate I, 12). The main body of the tylosis may contain dark amorphous or granular material (Plate I, 13); they are occasionally empty and more or less translucent. Evidence for wood pathogenic response other than tylosis formation, such as the accumulation and deposition of secondary metabolites (i.e., extractives) in adjacent cells, were not observed. Such features, however, are overall not likely to become preserved in the fossil record.

3.3. Fungus

Fungal remains occur throughout the specimens. The hyphae are septate and relatively uniform in size, ranging from 1.5 to 3.0 μm in diameter (Plate I,14). Hyphal septations are irregularly spaced, at right angles to the hyphal wall, and commonly associated with a slight constriction of the hypha. Hyphae in tracheids may be irregularly swollen, with bare knob-like protuberances and short, irregularly forking branches. The mycelium extends horizontally in the wood via the rays and vertically via the tracheids. Hyphal propagation from cell to cell is essentially through pit apertures. In some sections, individual hyphae can be traced over a vertical distance of about 1 cm as they extend through the wood. Hyphae usually occur in a relatively straight or slightly curving course (Plate I, 15). Within the tyloses, hyphae may form dense loops, whereas knots or twisted configurations occur inside tracheid cells in close proximity to tyloses (Plate I, 16; Plate II, 1). In addition to being found within the tylosis, there is evidence that hyphae can penetrate the tylotic wall and either exit or enter the tylosis (Plate II, 2). In places where hyphae change direction, they may branch to form Y- or T-shaped dichotomies (Plate II, 3). In a ray cell, for instance, branching of a horizontal hypha commonly results in two hyphal branches that leave the ray in opposite directions through the cross-field pits. Similarly, a hypha within the main body of a tylosis may dichotomize and send off two hyphal branches that penetrate into the surrounding tracheid in opposite directions through the wall of the tylosis. Hyphae that depart a ray through a tylosis generally extend only a short vertical distance through the tracheid before re-entering into an adjacent ray parenchyma cell through the aperture of a cross-field pit. There is no evidence for penetration hyphae, boring, or any other form of hyphae penetrating the actual tracheid cell walls.

Fungal remains also occur in the secondary phloem cells, where they are particularly common in the small cell type. Hyphae are generally found along the surface of the cell wall in the lumen of the cells (Plate II, 4). Hyphae in the phloem are usually associated with the above-mentioned concentric layering. In contrast to those in the xylem, hyphae in the phloem are found penetrating the actual cell walls horizontally. Linearly aligned, spherical structures approximately 5 μm in diameter occur in close association with these hyphae. It remains unclear whether these structures are fungal in origin.

4. Discussion

Even though there has been increased scientific attention to the fossil record of plant–fungal interactions in recent years (Taylor and Krings, 2010), reports of Jurassic fungi are still sparse. This is likely the result of a major taphonomic bias, because most of our knowledge of Jurassic floras is based on impression/compression remains that usually yield very limited information on fungal and other microbial associations. Reports of Jurassic fungi include fungal trace fossils (Martill, 1989) and lichen-like organisms and lichen-forming fungi (Preat et al., 2000; Wang et al., 2010), as well as more readily identifiable fungal remains such as spores and hyphae (Stockey, 1980; Traverse and Ash, 1994; Ibáñez and Zamuner, 1996; García Massini et al., 2012). In addition, Jurassic fossil wood has been described with particular decay patterns that have been interpreted as the result of fungal activity (e.g., Müller-Stoll, 1936; Süss and Philippe, 1993; Falaschi et al., 2011). Few reports, however, provide a detailed description of the fungi. The new material described here therefore offers a rare opportunity to detail the wood infection and possible affinities of a Jurassic fungus from Gondwana. Moreover, our observations lead us to suggest that tylosis formation in the wood may have occurred as a non-specific host response to fungal infestation.

4.1. Tylosis formation as a host response to fungal attack

A conspicuous feature of the Antarctic conifer wood is the high number of tyloses. In contrast to the regular formation of tyloses in the (non-functioning) heartwood of angiosperms, tylosis formation in conifer tracheids generally occurs as a response to physical damage or pathogenic stimulants, i.e., traumatic tyloses. The apparent exception is the genus *Pinus* L., where they have been reported in unwounded tissue (Chrysler, 1908). They also form in resin canals in some conifers, although these are generally called tylosoids as they do not extend
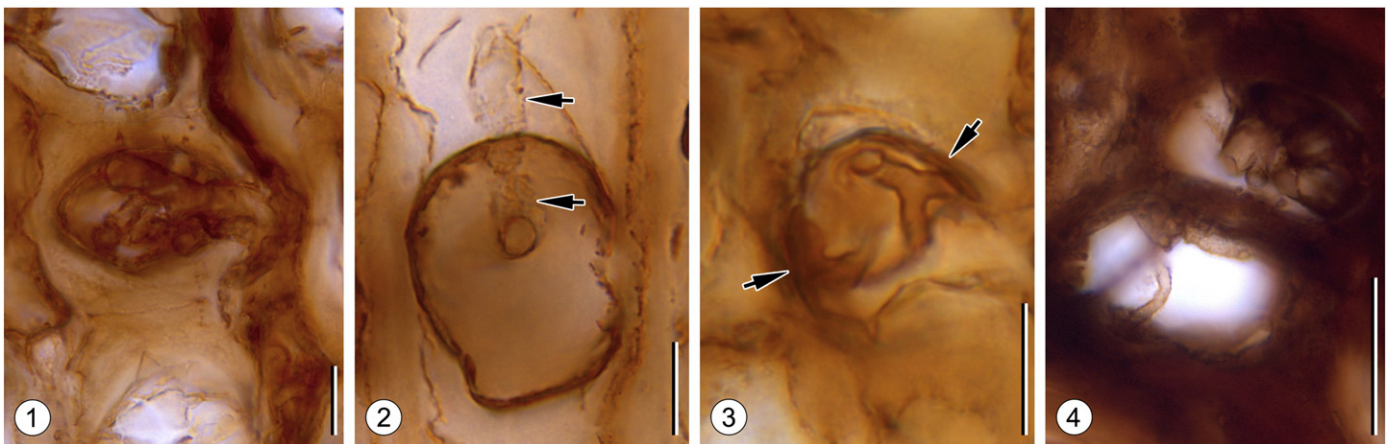
Plate II.
1.   Knotting hyphae inside of tylosis in transverse section. Scale bar = 10 μm. TS-GIX-SB-036-02.
2.   Hyphal (arrows) penetration of tylosis wall. Scale bar = 10 μm. TS-GIX-SB-036-01.
3.   Y-branching hypha inside of tylosis. Wall of tylosis indicated by arrows. Scale bar = 10 μm. TS-GIX-SB-036-02.
4.   Hypha inside lumen of smaller phloem cells. Scale bar = 25 μm. TS-GIX-SB-007-01.
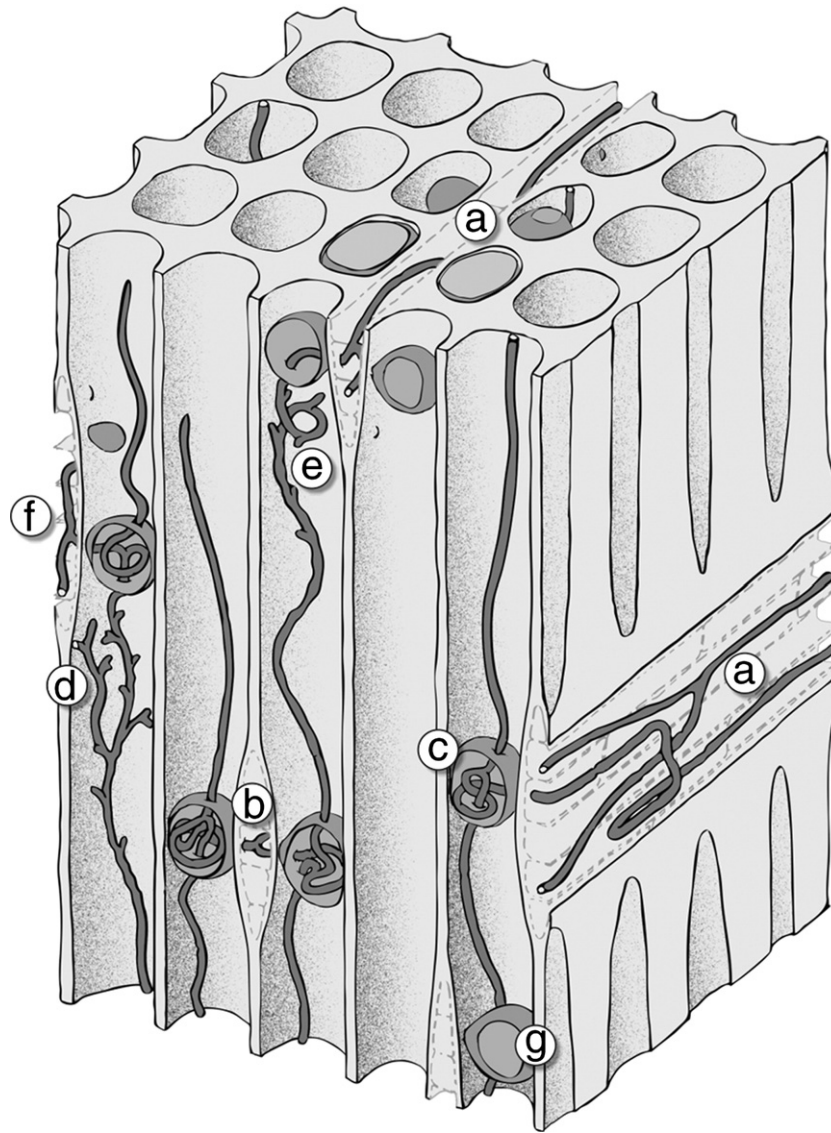
Fig. 1. Diagrammatic representation of the relationship between tylosis formation and fungal distribution in a three-dimensional block diagram of the wood presented in this study. (A): Hyphal distribution and pattern traversing the vascular ray system. Dashed lines represent the vascular ray. (B): Tyloses are often found in pairs on opposite sides of the vascular ray. (C): The lumen of the tyloses can contain highly coiled hyphae. The hyphae can exit and enter through the tylosis wall, including in opposite directions. (D): Hyphae that contain a high degree of dichotomies, which give the appearance of knotting structures. The knotting is often in close proximity to the tylosis, immediately outside of the tylosis wall. We hypothesize that this high degree of knotting increases the surface area of the fungus and the suberin-degrading enzymes can be concentrated and localized to the specific area. (E): Highly dichotomized or knotting hyphae can also form loops adjacent to tylosis; again, we hypothesize that this can also contribute to localization of degradational enzymes. (F): Hyphae travel through the ray system and enter tyloses through cross-field pits. (G): Many tyloses are filled with dark material. It has been suggested that fully developed, mature tyloses contain this amorphous, likely suberized material (Chrysler, 1908).

through pits (Chrysler, 1908; Evert, 2006). Tyloses serve to seal off damaged or infected wood areas, and to limit or retard further spreading of pathogenic agents, including wood-rotting fungi (Chrysler, 1908; Yamada, 2001). It has been shown that once a fungal pathogen has invaded the wood, tyloses can be produced in areas of wood not yet infected (Talboys, 1964). In *Lithocarpus densiflorus* (tanoak) wood, an increase in tylosis formation has been shown to correlate directly with an increase in fungi (Collins and Parke, 2008). It therefore appears possible that the prominent tylosis formation in this Antarctic fossil was a response to fungal infection of a wood-rot fungus and served to build up mechanical barriers against the advancing hyphae. The commonly occurring small, knob- to club-shaped tyloses may be interpreted as not fully developed. It has been shown in extant wood that fully developed tyloses are globose and contain dark lumina (Chrysler, 1908). Hence, there may be some evidence that tylosis formation and fungal infection occurred at least in parts synchronously in the fossil.

This is further supported by the common occurrence of fungal hyphae that appear to have grown around smaller tyloses.

At the same time, tylosis formation apparently occurred as a nonspecific host response, because its effectiveness against this particular fungus was only limited. Throughout the wood there is abundant evidence of fungal hyphae penetrating into the tyloses, where the hyphae usually coil and branch before extending into the adjacent tracheid or ray cell. Certain fungi are known to produce enzymes that break down plant suberin (Fernando et al., 1984; Ofong and Pearce, 1994). In this respect, the presence of knob-like swellings and short irregular branches on hyphae that occur inside or in close proximity to a tylosis is of particular importance; it may indicate that this fungus was capable of producing such degradational enzymes in order to break down the wall of the tyloses and thus surmount the defense mechanism of the plant. We hypothesize that hyphal swelling and branching would have facilitated the decay of suberic substances by

providing an increased surface area and thus increased enzyme concentrations at the contact site.

Overall, fungal hyphae are not extensive and the colonization of the host is limited. Therefore it is reasonable to suggest that the interaction between the tree and fungus is at the initial stage of fungal colonization. This relationship between tyloses and fungi are summarized and represented in Fig. 1.

4.2. Fungi and phloem relationships

In this report we provide evidence for fungi in the cells of the secondary phloem. Descriptions of fungal hyphae in fossil phloem are exceptionally rare (Stevens, 1912). The production of tylosoids in the phloem could also serve as a defense mechanism against external agents (Yamada, 2001). Tylosoids have been shown to develop in the roots of conifers (Wingfield and Marasas, 1980). In the phloem, tylosoids form similarly to tyloses in the xylem, i.e., parenchyma cells extend into the lumen of non-functioning sieve cells (e.g., Esau, 1977; Evert, 2006). The function of tylosoids is also hypothesized to be similar to that of tyloses in xylem, i.e., they serve to seal off non-functioning sieve elements (e.g., Ervin and Evert, 1967). They occur following a drop in pressure and cell death and are seasonal (Lawton and Lawton, 1971). Since tylosoids in the phloem can become lignified (e.g., Lawton and Lawton, 1971), the thicker, concentric structures present in the fossil phloem cell lumina may represent tylosoids formed in response to fungi. Whether these cell contents represent a preservational artifact or the actual deposition of some type of secondary metabolite in the phloem remains unknown.

4.3. Possible affinities of the fungus

Without additional evidence on reproductive and further anatomical features, the systematic affinities of the fungus cannot be determined with certainty at present. The morphology and colonization pattern of the fungus are, however, remarkably similar to those of some extant sap-stain fungi, including the dematiaceous hyphomycete *Verticicladiella wageneri* W.B. Kendrick (teleomorph: *Ceratocystis wageneri* Goheen et F. W. Cobb), the causative agent of black stain root disease in conifers (Hessburg and Hansen, 1987). Among the genus *Ceratocystis,* this fungus is unique because of the tracheid-limited pattern of colonization (Wagener and Mielke, 1961). Further key characters include longitudinal colonization of the host, serpentine and helical growth patterns without cell-wall penetration, traveling through the bordered pits, and branching near bordered pits. It has also been noted that in *Pseudotsuga menziesii* (Mirbel) Franco (Douglas-fir), tyloses frequently occluded cells adjacent to tracheids invaded *V. wageneri*, and that these structures seldom coalesced to block hyphal passage though lumina (Hessburg and Hansen, 1987). Additionally, the fungus in this study shares resemblance with blue-stain fungi (e.g., *Ceratocystis* sp., *Ophiostoma polonicum* Siemaszko) in colonization patterns that spread radially via the bordered pits of the xylem rays to enter the tracheid lumen (Ballard et al., 1982; Christiansen and Solhiem, 1990). The present fungus also resembles other sap-stain fungi, such as *Ophiostoma polonicum* and other *Ceratocystis* species that spread radially via the bordered pits of the xylem rays to enter the tracheid lumen (Ballard et al., 1982; Christiansen and Solhiem, 1990). Many sap-stain fungi, including *V. wageneri* and *Ceratocystis* spp., are spread via beetle vectors (Witcosky and Hansen, 1985; Goheen and Hansen, 1993; Solheim, 1994, 1995). In this context, it is interesting to note that Bomfleur et al. (2011) interpreted characteristic holes and tunnels in other wood specimens from the Suture Bench locality as possible arthropod borings, and that isolated beetle elytra have been described from two sites in the Lower Jurassic of Victoria Land (Tasch, 1973; Bomfleur et al., 2011). More direct evidence to link these occurrences, such as feeding galleries and coprolites in the wood, is still missing. We expect, however, that further studies may elucidate whether the complex biological interactions

between fungi, plants, and insects in modern forest ecosystems may already have existed in the Jurassic conifer forests of present-day Antarctica.

4.4. Antarctic Jurassic wood and tyloses

Although there is relatively little information available about continental Antarctic floras during the Jurassic, some areas were apparently dominated by conifers (Townrow, 1967; Jefferson et al., 1983; del Valle et al., 1997; Garland et al., 2007). The presence of fungi in these Jurassic conifers underscores the plasticity of these ancient organisms and their interactions. As in modern temperate forests, these trees must have encountered a diverse suite of microorganisms and developed several mechanisms for defense, including the production of tyloses to deter the spread of pathogenic fungi. Documentation of tylosis formation in fossil woods from Antarctica to date has been restricted to Cretaceous angiosperm wood (Poole and Francis, 1999; Poole and Cantrill, 2001). This report provides the first evidence of Jurassic conifer wood from Antarctica with well-preserved fungi and the formation of tyloses, as well as the first reports of fungi in fossil phloem from Antarctica and possible production of tylosoids in response to these fungi. Our results build upon our current understanding of the relationships in paleoecosystems and the coevolutionary processes that have developed between trees and external biotic agents through geologic time.

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