Original article

Evidence of fungal activity in silicified gymnosperm wood from the Eocene of southern Patagonia (Argentina)[☆]

Evidencia de actividad fúngica en madera silicificada gimnospérmica del Eoceno del sur de la Patagonia (Argentina)

Preuves d'une activité fongique dans des bois gymnospermiens de l'Éocène de la Patagonie méridionale (Argentine)

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Abstract

Evidence of fungal activity expressed as typical decay patterns is described from silicified podocarpaceous wood from the Eocene of Patagonia, Argentina. Decay features consist of tracheids of the secondary xylem that are degraded, resulting in thin-celled, lignin-free, translucent, circular to elliptical areas, some of which have cells devoid of all cell wall components including lignin, hemicellulose, and cellulose, and other areas that show only partial simultaneous decay of all cell wall layers. These patterns conform to the white rot and its variant white pocket rot decay patterns produced by basidiomycetes and ascomycetes in gymnosperm and angiosperm wood in modern terrestrial ecosystems. Coagulated opaque bodies in the lumen of some cells and enlarged secondary walls may represent host reactions to infection or remains of metabolic products of fungal enzymatic activity. Similar decay patterns and reaction features have been described from fossil woods ranging in age from the Devonian to the present. This record expands the fossil record of wood rot fungi and underscores their importance as drivers of biological cycles in ancient terrestrial ecosystems.

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Keywords: Fungal activity; Podocarpaceous wood; Eocene; Patagonia; Argentina

Resumen

Se describe evidencia de actividad fúngica expresada como patrones típicos de pudrición en una madera silicificada de Podocarpaceae del Eoceno de la Patagonia, Argentina. La pudrición consiste en traqueidas del xilema secundario con diferentes tipos de degradación observándose, áreas circulares a elípticas translúcidas con células de pared delgada, en algunas de estas áreas la pared celular, incluyendo la lignina, celulosa y hemicelulosa, fue degradada, mientras que en otras áreas solo se observa parcialmente degradación simultánea de las paredes celulares. Los patrones de descomposición observados son similares a la pudrición blanca y a la pudrición blanca alveolar producidas en ecosistemas terrestres actuales por basidiomicetes y ascomicetes en maderas de gimnospermas y angiospermas. Cuerpos opacos coagulados en el lumen celular y paredes engrosadas podrían representar una reacción del hospedador a la infección o remanentes del metabolismo de la actividad enzimática fúngica. Patrones de descomposición similares y patrones de reacción han sido descriptos en maderas fósiles desde el Devónico hasta la actualidad. Este

trabajo contribuye al registro fósil de pudrición de maderas por hongos y resalta el importante papel de este grupo en los ciclos biológicos de los ecosistemas del pasado.

Palabras clave : Actividad fúngica; Madera de Podocarpaceae; Eoceno; Patagonia; Argentina

Résumé

Des figures d'altération caractéristiques d'une activité fongique sont décrites dans du bois silicifié de l'Eocène de Patagonie proche des Podocarpacées. Ces figures consistent en des trachéides du xylème secondaire dégradées, avec des zones circulaires à elliptiques, translucides, à cellules à parois fines, dépourvues de lignine, certaines zones montrant des cellules dépourvues de tout composé pariétal y compris lignine, hémicellulose et cellulose, alors que d'autres ne montrent qu'une dégradation simultanée partielle des parois cellulaires. Ces figures sont conformes à celle d'une pourriture blanche et de sa variante alvéolaire produites par des Basidiomycètes et les Ascomycètes dans le bois d'Angiospermes ou de Gymnospermes des écosystèmes terrestres actuels. Des corps coagulés et opaques dans certaines cellules, ainsi que des parois secondaires élargies pourraient représenter des réactions de l'hôte à l'infection ou des restes de produits métaboliques de l'activité enzymatique fongique. Des figures de dégradation similaires ont été décrites pour des bois fossiles dont l'âge va du Dévonien à l'actuel. Notre observation étend l'enregistrement fossile des pourritures fongiques du bois et souligne leur importance dans les cycles biologiques des écosystèmes terrestres anciens.
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Mots clés : Activité fongique ; Bois ; Podocarpacées ; Éocène ; Patagonie ; Argentine

1. Introduction

Wood decay in modern terrestrial ecosystems is carried out by numerous organisms, of which fungi are the most important considering their relative abundance and enzymatic capacity (Schwarze et al., 2000; Carlile et al., 2001; Barron, 2003; Huhndorf et al., 2004; Martínez et al., 2005). In fact, cellulolytic and ligno-cellulolytic wood-inhabiting basidiomycetes and ascomycetes constitute a physiologically distinct group of saprotrophic, parasitic, and facultative parasitic fungi that are the main recyclers of carbon stored in wood and other organic debris produced in terrestrial ecosystems (Schwarze et al., 2000; Carlile et al., 2001; Barron, 2003; Martínez et al., 2005; Baldrian, 2008). Wood production dates back to the Devonian, but documentation of fungal decay has been sporadic and the record is incomplete for most periods and geographic regions (Taylor et al., 2009). This is evident in Patagonia, Argentina, where Phanerozoic deposits bearing wood and other fossil plants are abundant, but few fossil fungi have been documented and there is even less evidence of fungal mediated decay (Herbst and Lutz, 2001; García Massini et al., 2004). In this paper, we report variously degraded Podocarpaceae-like wood showing signs of fungal decay from the Eocene of Patagonia, Argentina. These fossils are compared to decay patterns of woods by fungi in modern terrestrial ecosystems and their paleoecological significance is discussed.
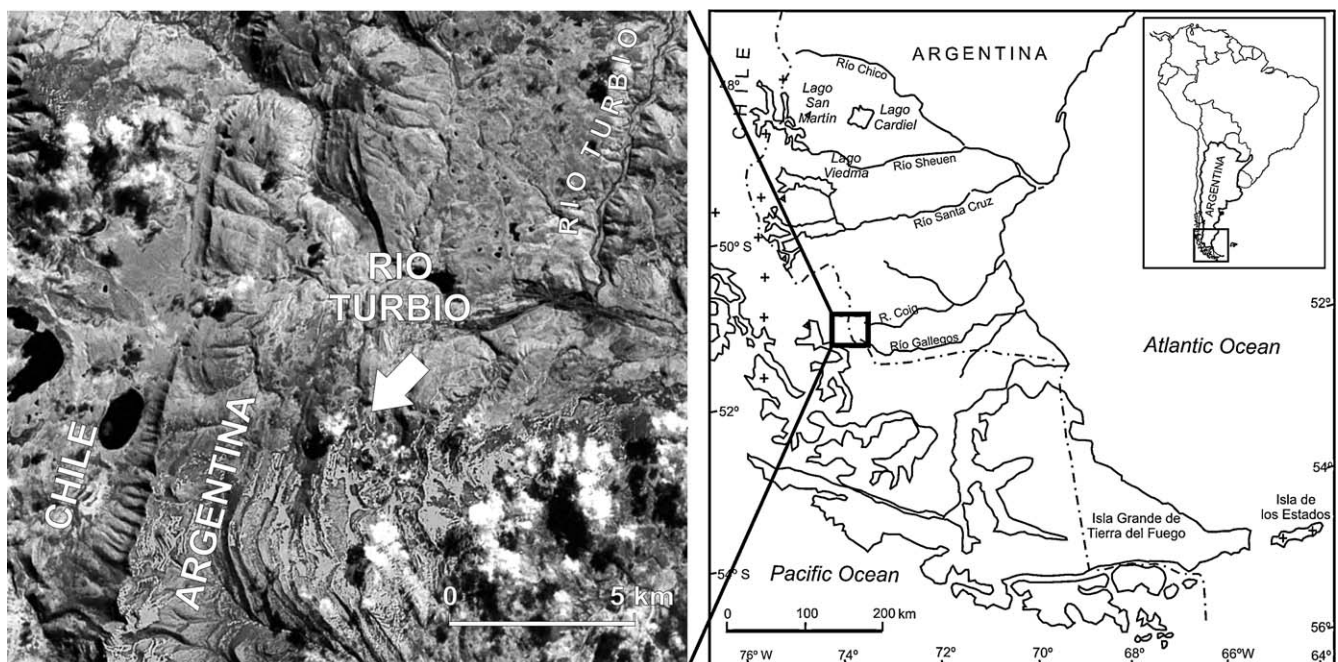

Fig. 1. Map showing the location of the fossiliferous locality. Enlarged area shows Middle to Upper Eocene Río Turbio Formation in southern Santa Cruz Province, Argentina.

2. Geological setting

The study area is part of the Austral (Magallanes) Basin, which includes marine and continental Jurassic to Miocene strata (Russo et al., 1980; Biddle et al., 1986). In particular, the fossils reported herein are from the Middle to Upper Eocene Río Turbio Formation in southern Santa Cruz Province, Argentina (Malumián, 2002). Strata of the Río Turbio Formation were deposited in wave- and tide-dominated shallow, coastal marine, temperate environments. They have a thickness of 598 m divided into a lower and an upper member, and are separated from the underlying Cerro Dorotea Formation and overlying Río Guillermo Formation by erosional contacts (Furque and Caballé, 1993; Azcuy and Amigo, 1991; Malumián, 2002). Palynology indicates that the deposits represent the oldest known forests in South America, which are dominated by *Nothofagus* (Nothofagaceae) along with conifers of the family Podocarpaceae, and they include fungal remains in the same strata bearing the wood described in this paper (Romero, 1977; Romero and Castro, 1986).

The fossil wood described herein was collected at a single locality (Fig. 1) along the slopes of the Santa Flavia Creek, near the city of Río Turbio, in southern Santa Cruz province, Argentina (51° 34' S, 72° 20' W). This new locality, which was exposed recently as a result of a landslide, contains a variety of petrified woods and compressed dicotyledonous leaves. A stratigraphic section of the locality is shown in Fig. 2. This consists of about 7 m of ripple-laminated limestones that alternate with sandstones displaying symmetric ripples. Overlying these is a 4 m section of cross-bedded sandstones with fossil woods. Sedimentological features in this section indicate progradation over a shallow tide-dominated mud flat. The fossil wood-bearing stratum is approximately 5 m above the *Complejo Carbonoso Inferior* stratigraphic unit described by Hünicken (1955).

3. Materials and methods

Thin-sections from the studied specimen were obtained following standard procedures (e.g., Hass and Rowe, 1999). The slides were examined using light microscopy and small fragments of wood were observed using SEM (Philips XL30) after being gold-coated. Terms for wood anatomy, when possible, are in accordance with the recommendations of the IAWA (Richter et al., 2004). The specimen, including four slides: a: transverse section; b: longitudinal radial section; c: longitudinal tangential section and d: acetate peel of transverse section, is permanently housed under accession number MPMPB 2249 at the Museo Regional Provincial Padre Manuel Jesús Molina, Santa Cruz province, Argentina.

4. Wood anatomy and affinity

4.1. Wood anatomy

The specimen consists of a 15 × 7 × 6 cm fragment of silicified pycnoxylic gymnosperm secondary xylem composed

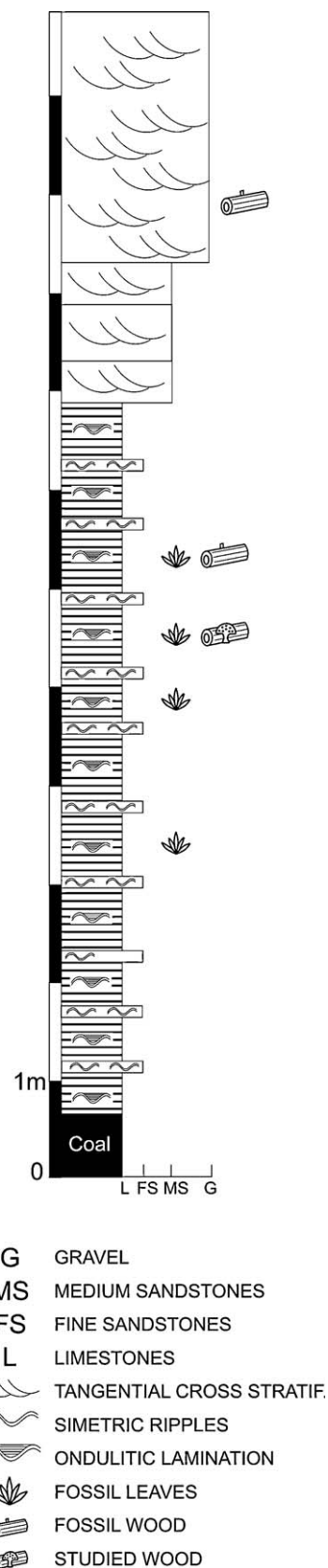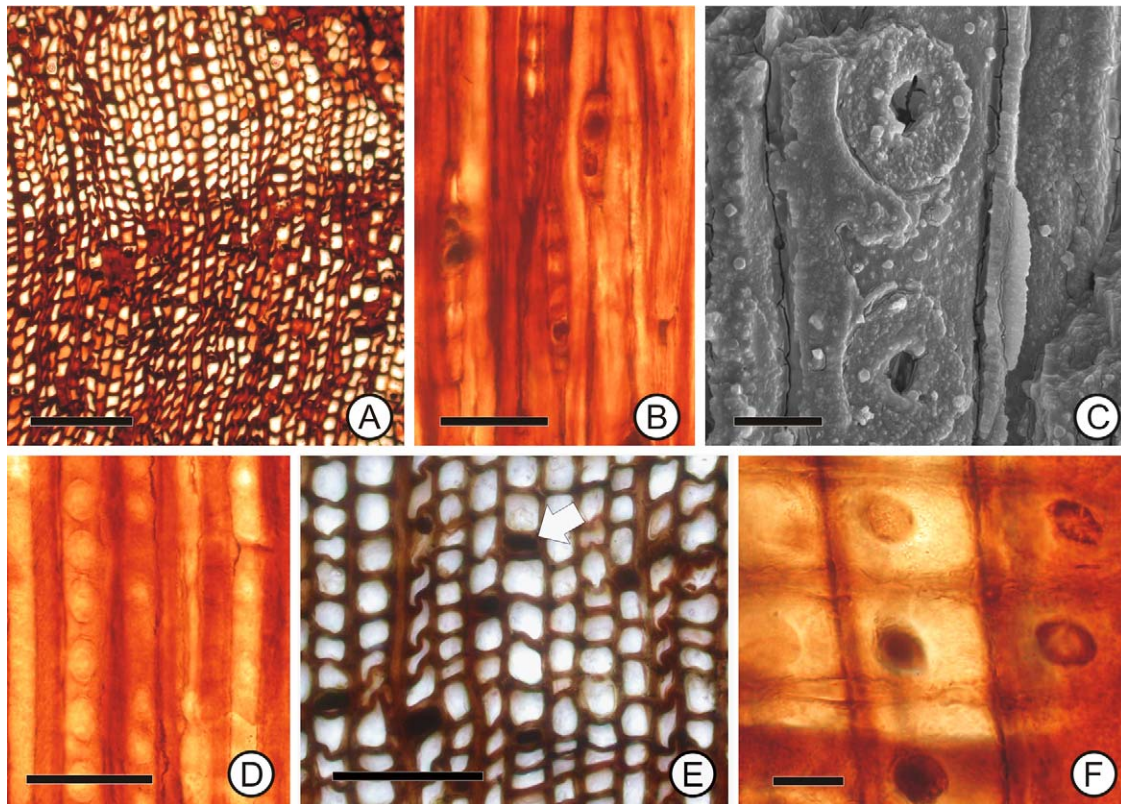|	
G	GRAVEL
MS	MEDIUM SANDSTONES
FS	FINE SANDSTONES
L	LIMESTONES
	TANGENTIAL CROSS STRATIF.
	SIMETRIC RIPPLES
	ONDULITIC LAMINATION
	FOSSIL LEAVES
	FOSSIL WOOD
	STUDIED WOOD

Fig. 2. Schematic log of the studied section.

Fig. 3. Sound wood anatomy. **A.** Growth ring boundaries in a transverse section (ts); scale bar: 200 µm. **B.** Tangential longitudinal section (tls) showing uniseriate rays; scale bar: 50 µm. **C.** Bordered pits at SEM; scale bar: 10 µm. **D.** Uniseriate pitting on radial wall in radial longitudinal section (rls); scale bar: 50 µm. **E.** Uniseriate rays and axial parenchyma (arrow) in ts; scale bar: 100 µm. **F.** Cross-field pits (rls); scale bar: 10 µm.

of rectangular to square tracheids in cross-section. Tracheids are 26 (13–35) µm in tangential diameter (Fig. 3[E]). The growth rings are indistinct, weakly marked by two to four rows of radially flattened latewood tracheids (Fig. 3[A]) and are approximately 2.4 mm in width. The tracheids have uniseriate pitting, exclusively on radial walls. Pits are bordered and ∼13 µm in diameter (Fig. 3[C, D]). Diffuse axial parenchyma is common (Fig. 3(E)). The rays are exclusively uniseriate and can reach 17 cells in height (Fig. 3[B]). There are 8 (6–10) rays per mm. Cross-fields usually have one, rarely two, oval bordered pits with oblique aperture (Fig. 3[F]) and ∼8 µm in diameter.

4.2. Affinity

Pitting on tracheids, bordered and spaced, of the fossil wood described here resemble those of Cupressaceae and Podocarpaceae. The axial parenchyma is also a feature shared with Cupressaceae and Podocarpaceae (Rancusi et al., 1987). Cross-field pits in Cupressaceae are bordered and have apertures narrower than the borders ("cupressoid"), while in this fossil the bordered pits have bigger apertures than the former, reminiscent of the "taxodiod" cross-field pits, present in some Podocarpaceae (Richter et al., 2004). In addition the growth rings in the fossil are much wider than those of extant Cupressaceae of Patagonia (Roig Juñent, 1992: Fig.

2[A]–4[A]). Therefore, the fossil wood anatomy resembles those of the extant Podocarpaceae from Patagonia.

5. Fungal evidence

The secondary xylem shows a mixture of degradation patterns that include numerous randomly distributed circular to irregular (in transverse section) to ellipsoid (in longitudinal section) areas ∼2 × 0.5 mm that are devoid of cells and other zones that, in transmitted light, show tracheid walls in various degrees of decay. Several of the circular to ellipsoidal areas are degraded to the point where there is no tissue left, while other areas show only partial removal of cell tissue resulting in the discoloring of the cells, leaving the wood with a "honeycomb" appearance (Figs. 4 and 5[A–C]). In some of the remaining cells in the circular to irregular areas, the middle lamella is selectively degraded, but the remaining wall layers are intact or only partially decayed and it appears as if individual cells were suspended in the matrix and separated from one another as seen in Blanchette (1984) (Fig. 5[D]). In addition, in some cells the secondary wall is partially or completely detached from the middle lamella and shifted toward the cell lumen (Fig. 5[E, H]). In the discolored areas some portions of the tangential and radial walls in individual cells are differentially degraded (Fig. 5[F, G]). In some cells, the lumen contains coagulated cell contents (Fig. 5[D, G]), and similar masses are present in some

Fig. 4. Macroscopic evidence of fungal decay. **A.** Longitudinal view showing pockets (arrow); scale bar: 10 mm. **B.** Transverse view (treated with HF); scale bar: 10 mm.

of the areas devoid of cells (Fig. 5[B]). Embedded within these mesh-like masses of degraded material, severely decayed cells are typical (Fig. 5[D]). The boundary between the degraded circular areas and surrounding tissue display cells whose wall layers are decreasingly degraded away from the center of the cavities (Fig. 5[B, D]).

6. Discussion

The occurrence of variously degraded podocarpaceous fossil wood from the Eocene of Patagonia raises questions about the affinity of the organism(s) responsible for the decay, the nature of the interaction between this and the vascular plant, and the paleoenvironmental characteristics of the depositional site. These kinds of interactions between the vascular plant and other organism(s) are difficult to discern when the organism(s) responsible for the decay of the wood is not preserved. However, the morphology of the decay pattern in the fossil wood allows comparison to those produced by modern taxa in woody plants.

Decay patterns exhibited by woods in modern terrestrial ecosystems are largely the result of fungal activity and include different kinds depending upon the type of fungus involved, its biochemical activity, the type of plant infected, and the microhabitat conditions (Carlile et al., 2001; Schwarze et al., 2000). Wood-inhabiting fungi are responsible for the degradation of cellulose and lignin, which results in characteristic decay patterns denominated soft rot, brown rot and white rot, respectively. A variation of the white rot decay pattern is represented by white pocket rot where only lignin is degraded (Otjen and Blanchette, 1986). Soft rots are typically caused by

soil-dwelling ascomycetes that decay the surface of woods in damp situations, creating a microscopic pattern characterized by conical cavities with pointed ends that are aligned with the cellulose microfibrils in the S_2 layer of the cell wall. Brown rots are most common in forests environments, where some basidiomycetes colonize recently felled woods as well as living trees and degrade lignin-associated cellulose in wood and non-woody pure cellulose. This results in a decay pattern characterized by generalized thinning of the secondary wall (mainly the cellulose-rich S_2 layer, while the S_3 layer remains intact to the latest stages of decay) and loss of cell shape. White rot and its variant white pocket rot are produced by basidiomycetes and ascomycetes. Fungi producing white pocket rot degrade and disassociate the tracheids in the secondary xylem, mainly affecting the middle lamella where lignin is abundant (selective lignin degradation), leaving fibrous, cellulose-rich areas that are spindle-shaped in longitudinal section (Otjen and Blanchette, 1982, 1984; Blanchette, 1991). White rot decay goes one step further since it degrades both lignin and cellulose (simultaneous degradation) in a process where, as it starts from the cell lumen (S_3 layer) outward, cells are first thinned to be later completely degraded, resulting in a rather fibrous residue with gradually coalescing microscopic erosion troughs in the decayed wood. Both of these two latter decay patterns can be produced by the same fungus, on the same tissue in the same plant, simultaneously or in sequence.

The morphological features of the decayed podocarpaceous wood from the Eocene of Patagonia differ from those of the soft-rot and brown-rot decay patterns in that there is no generalized decay of the secondary wall or a selective decay of
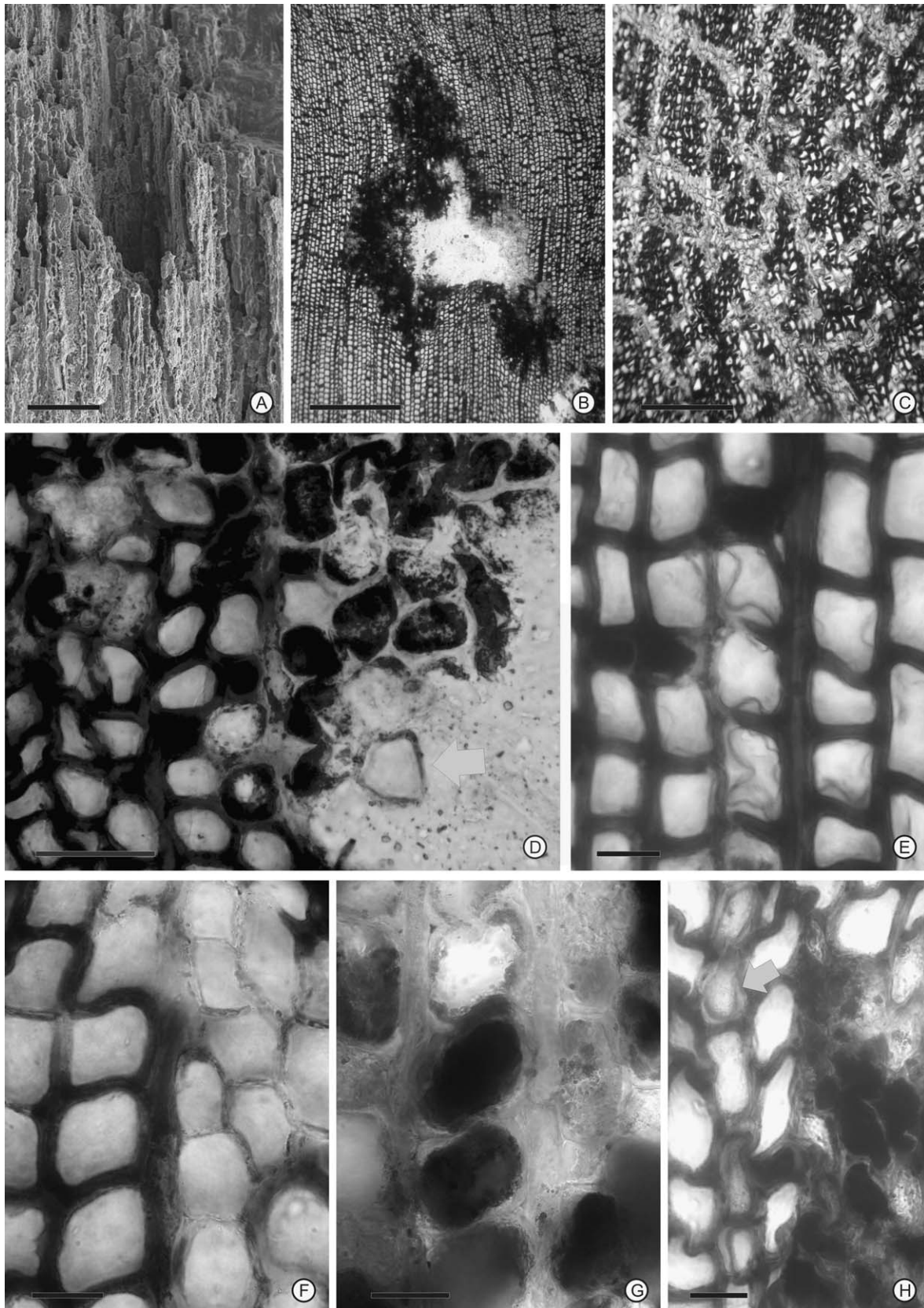
Fig. 5. Microscopic evidence of fungal decay. **A.** Longitudinal view of a pocket at SEM; scale bar: 100 μm. **B.** Ts showing a pocket. Note areas devoid of tracheids and areas with degraded tracheids; scale bar: 500 μm. **C.** Portions of wood (ts) showing only partial removal of cell tissue resulting in the discoloring of the cells, leaving the wood with a ''honeycomb'' appearance; scale bar: 200 μm. **D.** Transverse section of wood showing tracheids where the middle lamella has been degraded (selective delignification) (arrow); scale bar: 50 μm. **E.** Tracheids with their secondary wall partially or completely detached from the middle lamella (ts); scale bar:

any specific cell-wall component (e.g., the S_2 layer) except for the middle lamella, which is mainly of lignin and therefore not preferentially degraded by soft or brown rotters. Instead, silicified gymnosperm wood from Patagonia display variously degraded secondary xylem tracheids that are comparable to the white rot decay pattern (Carlile et al., 2001). In particular, the presence of areas devoid of cells (simultaneous degradation of cellulose and lignin) and areas where the cellular wall of the tracheids of the secondary xylem is distinctly discolored and degraded (selective delignification) conforms to the white rot and white pocket rot decay patterns, respectively (Figs. 4[A, B] and 5[A–C]) (Otjen and Blanchette, 1982, 1984; Blanchette et al., 1985; Blanchette, 1991). A white rot decay pattern is also suggested in other areas where the middle lamella and some of the inner secondary wall layers are variously thinned, although no wall layer is selectively decayed (Fig. 5(F)). The pocket areas where no cell structure is left (lignin and cellulose are removed) are elongated to semi-circular in longitudinal section, suggesting that a simultaneous rot decay pattern occurred (Figs. 4[A, B] and 5[A, B]). The presence of selectively delignified cells within the elongated to semi-circular empty areas, which in turn are bound by partially, but not selectively delignified, degraded cells supports the co-occurrence of these decay patterns (Fig. 5[B, D]). Similar cases, where complete degradation of cells from pockets of previously, selectively delignified cells are also known from hardwoods decayed by white rotters (Otjen and Blanchette, 1982, 1984). Moreover, the "honeycomb" morphological appearance of the fossil podocarpaceous wood resulting from the simultaneous decay of lignin and cellulose of some areas interspersed with areas characterized by selective delignification resembles what is referred to as mottle rot in extant hardwoods and softwoods (Otjen and Blanchette, 1986; Dill and Kraepelin, 1986; Blanchette, 1984, 1991).

White rot decay patterns are commonly observed in gymnosperms in moist temperate forests (e.g., Stokland and Kauserud, 2004; Asiegbu et al., 2005). In particular, the fossil decay patterns in the Eocene podocarpaceous wood are morphologically comparable to white rot and white pocket rot decay patterns produced by basidiomycetes (e.g., *Ganoderma*) in hardwoods from temperate rainforests in Chile (Zadrazil et al., 1982; Dill and Kraepelin, 1986; Agosin et al., 1990). Similarities include selective removal of lignin and the non-selective degradation of all cell wall components (Dill and Kraepelin, 1986: Figs. 1 and 2; Agosin et al., 1990: Figs. 1, 2, 4). However, while the fossils display discrete circular to ellipsoidal areas where cells appear to have been selectively delignified to completely degraded, selective delignification or simultaneous decay in modern hardwoods is not restricted to small pockets but extend into large areas inside the trunks (Zadrazil et al., 1982; Dill and Kraepelin, 1986; Agosin et al., 1990). Other variants in the modern hardwoods that were not

observed in the fossils include lignin removal from the secondary wall singly or along with that from the middle lamella (Agosin et al., 1990). This can be explained as the result of differences between hardwoods and softwoods in structural arrangement and accessibility of lignin relative to cellulose and other cell wall components (Adaskaveg and Gilbertson, 1986). Moreover, due to softwood/hardwood differences in lignin composition, selective delignification by white pocket rot fungi in softwoods might be more likely to affect the middle lamella individually (Blanchette, 1984), much like what we observed in the podocarp wood from Patagonia. The extensive delignification observed in extant hardwoods might be a result of low nitrogen content and the necessity of the fungus to access nitrogen stored in the middle lamella and other cell wall components (Dill and Kraepelin, 1986). Similarly, Dill and Kraepelin (1986) indicated that extensive delignification in the white pocket rot pattern interspersed with simultaneously decayed areas (mottled rot) may reflect uneven nitrogen distribution in some types of woods. Moreover, Agosin et al. (1990) indicated that rather discrete pockets of decay are more common in gymnosperm trees in temperate latitudes that include a dry season and that these might represent precursor areas for greater delignification, similar to what is observed in the Eocene fossil podocarp wood. Other factors, including microaerobic conditions, low average temperatures, high humidity, and the formation of pseudosclerotia plates around the decaying wood could be associated with extensive delignification by fungi (Zadrazil et al., 1982; Dill and Kraepelin, 1986; Agosin et al., 1990).

Bacteria are known to be part of the stages of wood decay in modern terrestrial ecosystems (Holt and Jones, 1983; Pointing, 2001). However, since no bacteria have been found in the fossil woods from Patagonia, their role in producing the decay pattern observed cannot be ruled out or even assessed (e.g., Zadrazil et al., 1982; Dill and Kraepelin, 1986). The role of wood-eating insects can be ruled out since excreted material (frass), which is the main subproduct of the processed wood, has not been found associated with the decay patterns. Moreover, the pockets are not connected and have gradually degraded borders, unlike wood bored by insects where galleries with well-defined borders are typical (Genise and Hazeldine, 1995). The possibility that the patterns in the fossil wood are the result of differential fossilization (i.e., pseudoborings, where calcite and silica replace different parts of the tissue) can also be excluded because the cellular structure of the fossil wood remains intact (Fisk and Fritz, 1984).

The morphological evidence from the decayed wood is consistent with white rot and white pocket rot decay patterns. However, those fungi are more common on hardwoods than on softwoods, and this, together with the absence of fungal hyphae in our fossils, could be used to argue for brown or soft rot fungi as the causative agent. A characteristic of wood invaded by

20 μm. **F.** Tracheid (ts) with all cell wall components differentially degraded (simultaneous decay) (ts); scale bar: 20 μm. **G.** Tracheids with simultaneously degraded walls and with opaque contents; scale bar: 20 μm. **H.** Tracheids with selectively delignified walls where the secondary wall (arrow) appears deformed and displaced toward the cell lumen (ts); scale bar: 20 μm. A: SEM micrograph; B–H: LM (light microscope) micrograph.

brown rot is a scarcity of hyphae, which are autolysed by the fungus as decay proceeds (Carlile et al., 2001). In contrast, hyphae are usually abundant in wood decayed by white rot fungi. However, selective lignin removal by such fungi (i.e., a white pocket rot decay pattern) can be a non-contact phenomenon such that the fungus degrades lignin without physical contact of hyphae with the degrading cell (e.g., Otjen and Blanchette, 1982, 1986; Blanchette et al., 1985). This, together with the overall morphology of the rot pattern and the possibility that the absence of hyphae in the fossil wood simply reflects preservation potential, leads us to conclude that the rot described herein is more likely a result of white rot fungi.

The presence of opaque and variously shaped bodies inside the lumen of some cells in the Eocene podocarps from Patagonia raises questions about whether these represent fungal activity. Similar ergastic material commonly occurs in the cell lumen of modern, healthy wood cells and cytoplasmic inclusions (e.g., phenolic) occur in parenchyma cells and resin ducts in the xylem of modern standing trees infected by wood decaying parasitic fungi (Otjen and Blanchette, 1982; Krekling et al., 2004). This has been referred to as "plugging" and is thought to represent a physical or chemical barrier developed by the infected plant to prevent the spread of the fungus (Otjen and Blanchette, 1982, 1984). In addition, what has been interpreted as a metabolic leftover from fungal lygnolitic activity in felled trees decayed by saprotrophic fungi consists of irregular masses of black manganese inside delignified wood cells (Agosin et al., 1990). The opaque bodies observed in the fossil from Patagonia are indistinguishable morphologically from similar inclusions in modern woods, and we cannot assess whether the decay described herein reflects the action of parasitic fungi on standing trees or saprotrophic fungi acting on dead material.

Saprotrophism is the most important activity carried out by fungi in terrestrial ecosystems since it recycles organic material transforming it into essential microelements, such as carbon available for other organisms. However, documentation of wood decaying fungi in the fossil record has been sporadic. Notwithstanding, direct and indirect evidence of their presence, via detection of a specific fungal morphology or a typical decay pattern, is known since the Upper Devonian (Stubblefield et al., 1985; Taylor and Osborn, 1992; Taylor et al., 2004, 2009). Wood decay fungi are known from all periods, except the Carboniferous where the relative absence of traces of this activity and their main producers (basiodiomycetes) has been attributed to the more efficient role of chytridiomycetes and zygomycetes as degraders of organic matter in the wetland habitats that were most characteristic of this period (Dennis, 1970; Smith et al., 2004; Taylor and Krings, 2005). Fossil fungi has received little attention in Argentina and as a result only a few references to wood decayed by fungi are known from the region (Herbst and Lutz, 2001 and references therein). The white pocket rot decay patterns in the Eocene podocarpaceous wood described herein are among the few that have recorded the activity of wood decaying fungi from Patagonia, Argentina, thereby expanding their geographic range during the Cenozoic.

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