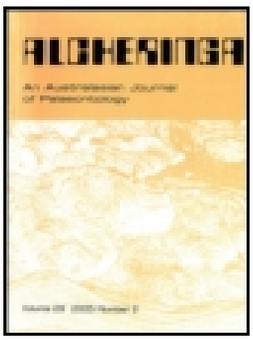

Alcheringa: An Australasian Journal of Palaeontology

ISSN: 0311-5518 (Print) 1752-0754 (Online) Journal homepage: http://www.tandfonline.com/loi/talc20

# Fungal wood-decay strategies in Nothofagaceae woods from Miocene deposits in southern Patagonia, Argentina

Carlos Daniel Greppi, Juan L. García Massini, Roberto R. Pujana & Sergio A. Marenssi

**To cite this article:** Carlos Daniel Greppi, Juan L. García Massini, Roberto R. Pujana & Sergio A. Marenssi (2018): Fungal wood-decay strategies in Nothofagaceae woods from Miocene deposits in southern Patagonia, Argentina, Alcheringa: An Australasian Journal of Palaeontology, DOI: 10.1080/03115518.2018.1471736

**To link to this article:** https://doi.org/10.1080/03115518.2018.1471736

# Fungal wood-decay strategies in Nothofagaceae woods from Miocene deposits in southern Patagonia, Argentina

CARLOS DANIEL GREPPI, JUAN L. GARCÍA MASSINI, ROBERTO R. PUJANA and SERGIO A. MARENSSI

Carlos Daniel Greppi, Juan L. García Massini, Roberto R. Pujana and Sergio A. Marenssi, May 2018. Fungal wood-decay strategies in Nothofagaceae woods from Miocene deposits in southern Patagonia, Argentina. Alcheringa xxx, xxx -xxx.

Decayed woods from the Miocene, Rio Leona Formation, Santa Cruz, Argentina having simultaneous decay patterns consistent with soft- and white rot characteristics are described. Samples were previously identified as *Nothofagoxylon scalariforme*. At low magnification, the permineralized woods appear mottled, with discoloured, degraded areas, scattered in apparently robust tissue, consistent with white-rot decay. At greater magnification, the woods reveal several micromorphological features, including differential decay of cellulose-rich cellular components that match soft-rot decay by extant ascomycetes and some basidiomycetes. In addition, decayed woods either appear differentially delignified or show simultaneous decay of all cellular components (lignin- and cellulose-rich), which are by-products of white-rot fungal decay. Additional anatomical characteristics of the decayed woods are consistent with a host response to the fungal attack. Co-occurrence of these two decay patterns suggests soft-rot decay and white-rot fungal decay. In addition, co-occurrence of all the decay features observed also suggests facultative soft rot by white-rot fungi, such as in some extant species that switch between these two types of decay strategies as a means to circumvent plant defences. These data indicate that fungi with soft-rot capacity for wood decay can be traced back to the early Miocene (*ca* 19 Ma). In addition, this report adds to the distribution and diversity of fungi in the geological record and underscores the ecological importance of wood as a preferred substrate for the association and interactions between fungi with different saprotrophic abilities, which have been fundamental for nutrient recycling in terrestrial ecosystems during the Cenozoic.

*Carlos Daniel Greppi [greppi.carlos.d@gmail.com] Museo Argentino de Ciencias Naturales-CONICET, Av. Ángel Gallardo 470, (1405) Ciudad Autónoma de Buenos Aires, Argentina; Juan L. García Massini [massini112@yahoo.com.ar] Centro de Investigaciones Científicas y Transferencia Tecnológica de La Rioja (CRILAR), Provincia de La Rioja, UNLaR, SEGEMAR, UNCa, CONICET, Entre Ríos y Mendoza s/n (5301) Anillaco, La Rioja, Argentina; Roberto R. Pujana [rpujana@gmail.com] Museo Argentino de Ciencias Naturales-CONICET, Av. Ángel Gallardo 470, (1405) Ciudad Autónoma de Buenos Aires, Argentina; Sergio A. Marenssi [smarenssi@hotmail.com] IGEBA-CONICET, Departamento de Geología, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Guiraldes 2620, (1428) Buenos Aires, Argentina.* *Received 7.9.2017; accepted 29.4.2018.*

Key words: white rot, soft rot, *Nothofagoxylon scalariforme*, secondary xylem, Río Leona Formation.

FUNGI comprise a very diverse group of heterotrophic eukaryotes (kingdom: Fungi) of cosmopolitan distribution that are fundamental to the functioning of terrestrial ecosystems as saprotrophs, mutualists and parasites (Carlile *et al*. 2001, Webster & Weber 2007, Dighton 2016). They are the primary decomposers and recyclers of organic remains in terrestrial ecosystems and, thus, play a key role in the continuity of life on Earth by maintaining the carbon cycle (Dighton 2016). Of particular significance is the role of fungi in the degradation of woody tissues, which has allowed fungi to monopolize the exploitation of a unique ecological niche, developing strategies specifically adapted to local conditions of each environment (Schmidt 2006).

The origin of fungi can be dated back to the Precambrian based on molecular data, but accepted fossils can be recognized in the Ordovician and younger sediments (Heckman *et al*. 2001, Taylor *et al*. 2009, Berbee & Taylor 2010, Taylor *et al*. 2015, Berbee *et al*. 2017). In comparison with other organisms, the fungal fossil record is less complete, which is partly a consequence of their low potential for fossilization owing to the fragility of their vegetative and reproductive structures and also owing to the difficult task of discerning and assigning simple vegetative fungal structures more commonly preserved in fossil contexts (e.g., wood) to extant groups (Taylor & Krings 2010). More easily identifiable fossil fungi come from a few deposits of restricted geographical and temporal distribution in the geological record (i.e., the Rhynie Chert, North American and Northern European coal balls, Deseado Massif, Princeton Chert, Apple Bay, Fremow Peak and Skaar Ridge, Transantarctic Mountain, Antactica, Bainmedart Coal Measures, Prince Charles Mountains, Antarctica), where typically fragile fungal structures along with their substrates are preserved (e.g., Stockey 2001, Taylor *et al*. 2004, Galtier 2008, Strullu-Derrien *et al*. 2011, Wacey *et al*. 2011, García Massini *et al*. 2012a, Schopf 2012, Slater *et al*. 2015, García Massini *et al*. 2016, Harper *et al*. 2016 2017). In addition, evidence of fungi and


https://doi.org/10.1080/03115518.2018.1471736

Published online 20 May 2018

their roles have also been documented based upon recognition of specific morphological and anatomical patterns resulting from consumption of their substrates. Thus, reports of fungal decayed secondary xylem and other woody debris are known in Paleozoic to Cenozoic deposits (e.g., Stubblefield *et al*. 1985, Stubblefield & Taylor 1986, Taylor & Osborn 1992, McLoughlin *et al*. 1995, Weaver *et al*. 1997, Pujana *et al.*, 2009, García Massini *et al*. 2012b, Gnaedinger *et al*. 2015). These reports provide information on the development of different metabolic strategies tailored to degradation of woody tissues and indirectly on the occurrence of different fungal groups in the geological record (Taylor *et al*. 2015).

A few reports of direct and indirect presence of fungi are known from Argentina, although, based on the abundance of wood-bearing sedimentary deposits, the potential of information they carry has been little investigated (Herbst & Lutz 2001, García Massini *et al*. 2004, 2012a, 2012b, 2016). The aim of this paper is to describe and illustrate the patterns of fungal degradation of woods of *Nothofagoxylon scalariforme* Gothan, 1908 in early Miocene deposits of Patagonia. These are compared with decay patterns in modern ecosystems and the various fungi that produce them. Their significance is analysed in the context of the evolution of different strategies known among fungi for wood degradation.

## Geological setting

Fossils described in this paper were collected from two outcrops, both exposing the upper part of the Río Leona Formation. The first, Arroyo de las Bandurrias, is within the Estancia 25 de Mayo and the second is a southern outcrop in Arroyo Oro (Fig. 1). Fossils from the Río Leona Formation include woods (Pujana 2007, 2009a, 2009b), pollen (Barreda *et al*. 2009) and leaves (César *et al*. 2015). These palaeobotanical remains indicate a temperate forest dominated by Nothofagaceae, together with accessory ferns, Typhaceaae, Myrtaceae, Rosaceae, Proteaceae, Lauraceae and Podocarpaceae, among others.

In the area of Estancia 25 de Mayo, the Río Leona Formation is up to 100 m thick and consists of an upward-fining succession of conglomerates to carbonaceous shales previously described by Marenssi *et al*. (2005). The succession is interpreted as being deposited in fluvial settings that range from high-energy braided systems at the base to low-energy meandering and anastomosing systems towards the top (Marenssi *et al*. 2005). The fossiliferous interval occurs in the upper 30 m of the unit, which is composed of mudstones (35%), sandstones (30%), carbonaceous shales (25%), tuffs (5%) and very scarce fine-grained conglomerates (5%). The distinctive character of this interval is the abundance of fine-grained rocks with greenish mudstones having a homogeneous and distinctive orange weathering colour, typical of Río Leona Formation outcrops. These fine-grained rocks form tabular beds of mainly massive or laminated sandy mudstones and include thin levels of very fine-grained massive or rippled laminated sandstones. Decimetre-thick, white tuff beds with normal grading are preserved within the mudstones. Some tree stumps are preserved in growth positions at the top of sandstone intercalations penetrated by roots. Carbonaceous shales forming black tabular beds, 10–100 cm thick, contain abundant though very poorly preserved plant remains. Coarser clastics form upward-

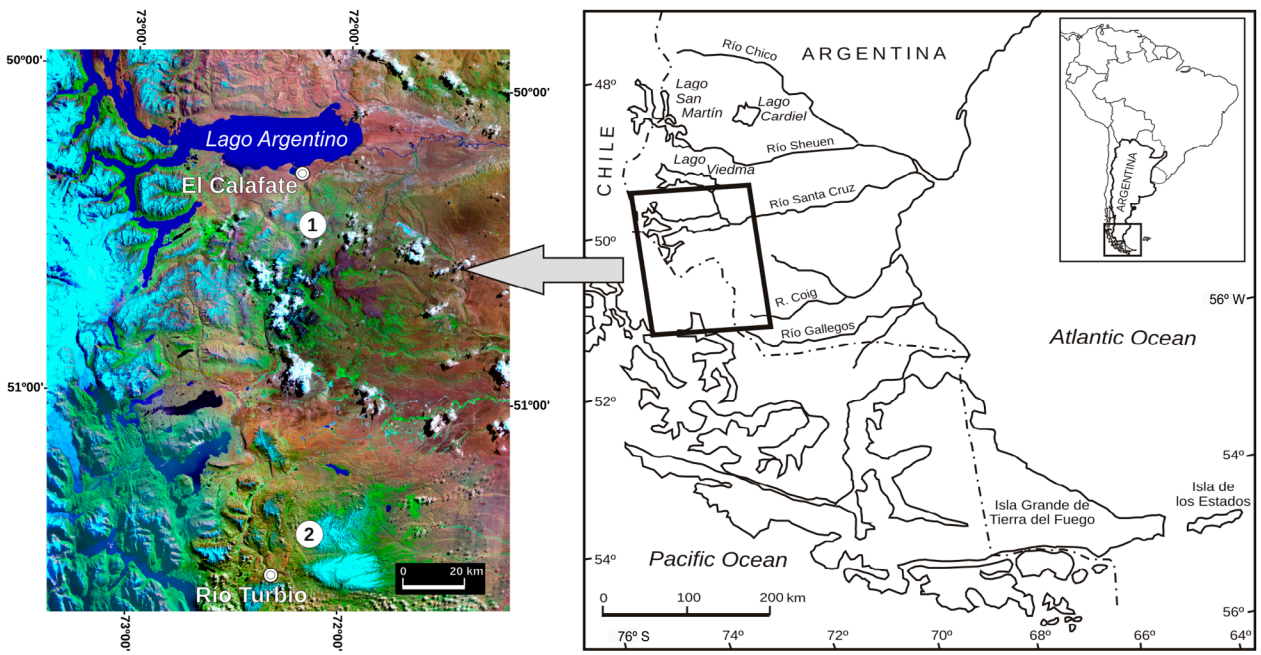


*Fig. 1.* Map of Argentina depicting the study localities in detail. **1**, Arroyo de las Bandurrias; **2**, Arroyo Oro.

fining cycles, 2–4 m thick, from very fine-grained, massive conglomerates to fine-grained, massive, tabular cross-bedded or ripple-laminated sandstones with some plant remains. Laterally continuous, low-angle internal surfaces are interpreted as lateral accretion surfaces. Channels are represented by low-relief erosional bases and coarse lag deposits, followed by upward-fining sandstone successions with low-angle lateral accretion surfaces that represent fine-grained point bar deposits. Floodplains are represented by fine-grained sediments formed by suspension settling, or more energetic, instantaneous floods, interpreted as crevasse splay deposits. The predominance of floodplain deposits with dark carbonaceous beds characterizes the two localities and indicates poorly drained interchannel areas. The crudely defined upward-fining cycles, high proportion of mudrocks and relatively low width-to-depth ratio of the channels suggest a fluvial system with small channels and oversized plains. A network of fluvial channels within a coastal plain environment is envisaged for this period (Marenssi *et al*. 2005).

An Oligocene age for the Río Leona Formation was assigned by Malumian & Panza (2000), Marenssi *et al*. (2003) and Barreda *et al*. (2009). However, more recent geochronological dating indicates an early Miocene age (Fosdick *et al*. 2011, 2015).

## Materials and methods

The studied specimens (four samples) were thin-sectioned in transverse, tangential longitudinal and radial longitudinal sections following standard techniques for petrified woods. Acetate peels were also made following the recommendations of Galtier & Phillips (1999). The slides were studied using light microscopy, photographed with a Leica 1295 DFC camera attached to a DM2500 light microscope and minimally edited with a Corel PhotoPaint X18. All the samples were assigned to *Nothofagoxylon scalariforme* Gothan, 1908 based on their anatomical characteristics (Pujana 2009b).

The specimens are housed in the palaeobotanical collection of the Museo Provincial Padre Molina, in Rio Gallegos, Argentina, under the numbers MPM PB 2149a, 2149b, 2149c, 2152a, 2152b, 2152c, 2152d, 2155a, 2155b, 2155c and 2218a, 2218b, 2218c, 2218d, 2218e, 2218f, 2218 g. Slides bear the specimen number followed by an arbitrary lower case letter for identification purposes.

## Results

### *Anatomical description of* Nothofagoxylon scalariforme

The specimens have a minimum estimated diameter of up to 25 cm. Growth ring boundaries are distinct. Porosity is diffuse to semi-ring porous, and the vessels are solitary or commonly in short radial multiples of up to four elements. Vessels have a tangential diameter of *ca* 50 µm and a density of *ca* 180 vessels per mm$^2$. Vessel elements are *ca* 140 µm long. Perforation plates are simple; scalariform perforation plates with few bars are rarely present in the latewood vessels. Intervessel pitting arrangement is scalariform to opposite. Vessel-ray pits are circular to scalariform. Diffuse axial chambered crystalliferous parenchyma, with one crystal per cell, is common. Axial parenchyma abundance varies among samples. Rays are uniseriate or partially biseriate and heterocellular (Pujana 2009b).

### *Wood decay pattern of* Nothofagoxylon scalariforme

This section describes the macro- and microscopic decay patterns of silicified secondary xylem and associated fungal vegetative and reproductive structures.

The macroscopic decay pattern of the secondary xylem is represented by discoloured, decayed areas, interspersed with darker areas of apparently undamaged tissue (Fig. 2A). At greater magnification, the discoloured areas contain deformed and degraded cells (Fig. 2B). In addition, extensive erosive channels of *ca* 150 µm in diameter are evident in those areas where individual cells appear most degraded (Fig. 2C). Within these two areas, decayed cells and fungal hyphae are preserved (Fig. 2D). Furthermore, the fibres are more frequently degraded than other cell types, such as vessels or parenchyma (Fig. 2E). The better-preserved vessels and rays are partially or completely filled by traces of ergastic substances and tyloses (Fig. 2E). In some cases, these sealed cells are grouped into certain areas of the secondary xylem (Fig. 2F).

At greater magnification, the $S_2$ layer of the cell wall of some fibres appears degraded following a diffuse pattern that is expressed as a lack of pigmentation of the wall (Fig. 3A). These same cells also express incipient deformation of their structure, consistent with the degradation of all lignified components of the wall (Fig. 3A). Some whitened but somewhat less deformed fibres display their middle lamella differentially degraded, except at the corners (Fig. 3B). In those fibres where the middle lamella is degraded, the primary wall appears disconnected from the secondary wall, and adjacent cells also appear incipiently separated from each other (Fig. 3B). In addition, some vessels appear variously deformed, individually detached from adjacent fibres, and have their lumens filled with fungal remains (Fig. 3B–C). In other regions of the decayed wood, however, the vessels, fibres and parenchymatous rays appear better preserved than other cell types and contain a high concentration of opaque substances that block their cell lumens (Fig. 3A, D).

Some degraded fibres have varied micromorphologies, which are discernible in cross-section as the partial degradation of the wall in a centrifugal pattern, from the lumen to the outer layers ($S_3$, $S_2$, $S_1$ wall layers and middle lamella), resulting in soft to sharp notches and

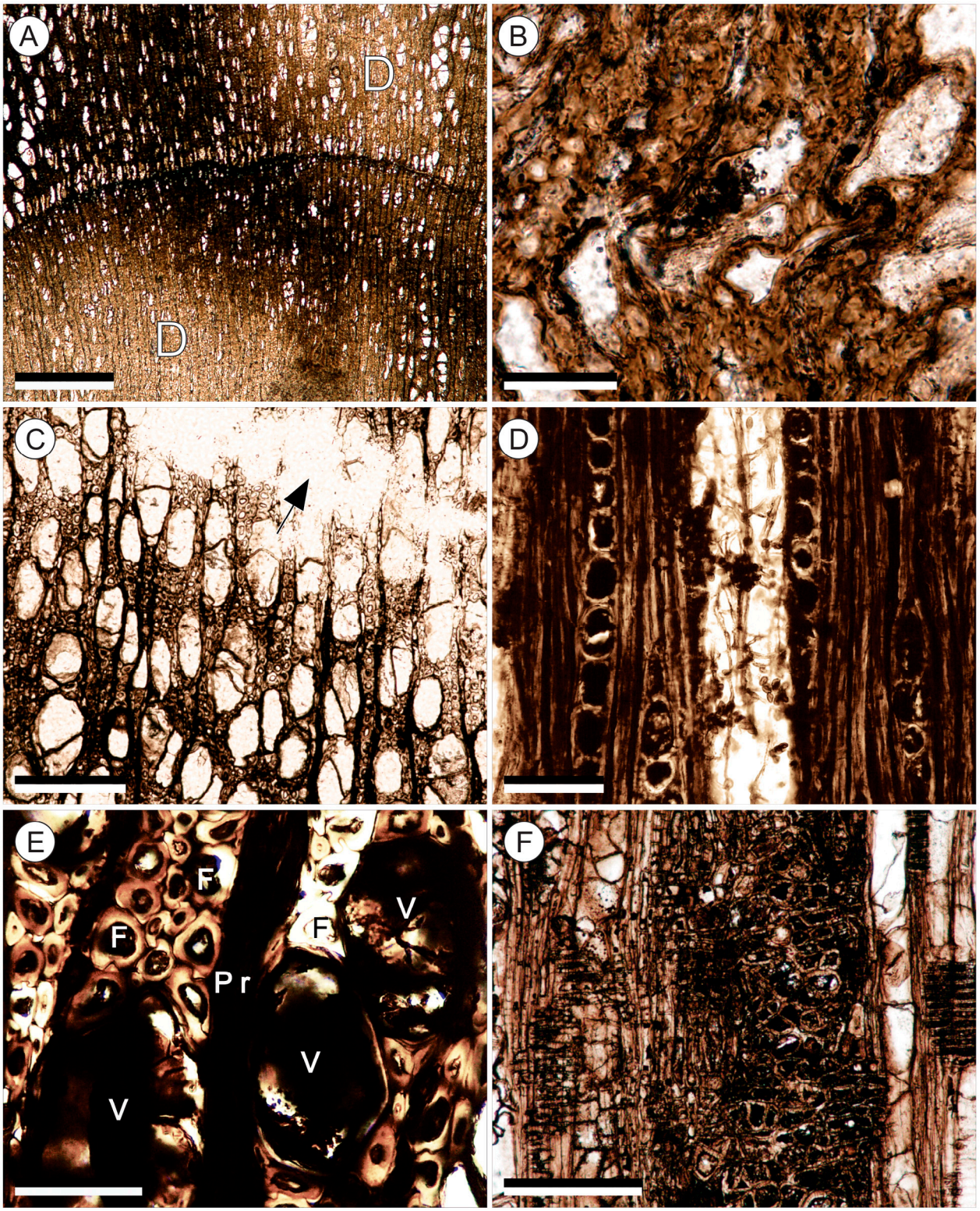


*Fig. 2.* General appearance of the various regions of the biodegradable wood of *Nothofagoxylon scalariforme*. **A**, Overview (cross-section) of secondary xylem with discoloured areas (D) interspersed in more pigmented tissue. MPM PB 2152a. Scale bar = 500 µm. **B**, Secondary xylem showing deformed and degraded cells in cross-section. MPM PB 2152a. Scale bar = 100 µm. **C**, Cross-section of secondary xylem showing extensive erosive channels (arrow). MPM PB 2218a. Scale bar = 200 µm. **D**, General view of secondary xylem in longitudinal section showing variously degraded cells colonized by fungi. MPM PB 2149c. Scale bar = 50 µm. **E**, Cross-section of secondary xylem showing vessels (V) and parenchymatous rays (P r) with opaque substances within their lumens. Note the degraded fibres (F). MPM PB 2218a. Scale bar = 50 µm. **F**, Radial longitudinal section showing cells with their lumens filled with opaque substances, grouped in discrete zones of the secondary xylem. MPM PB 2152b. Scale bar = 200 µm.

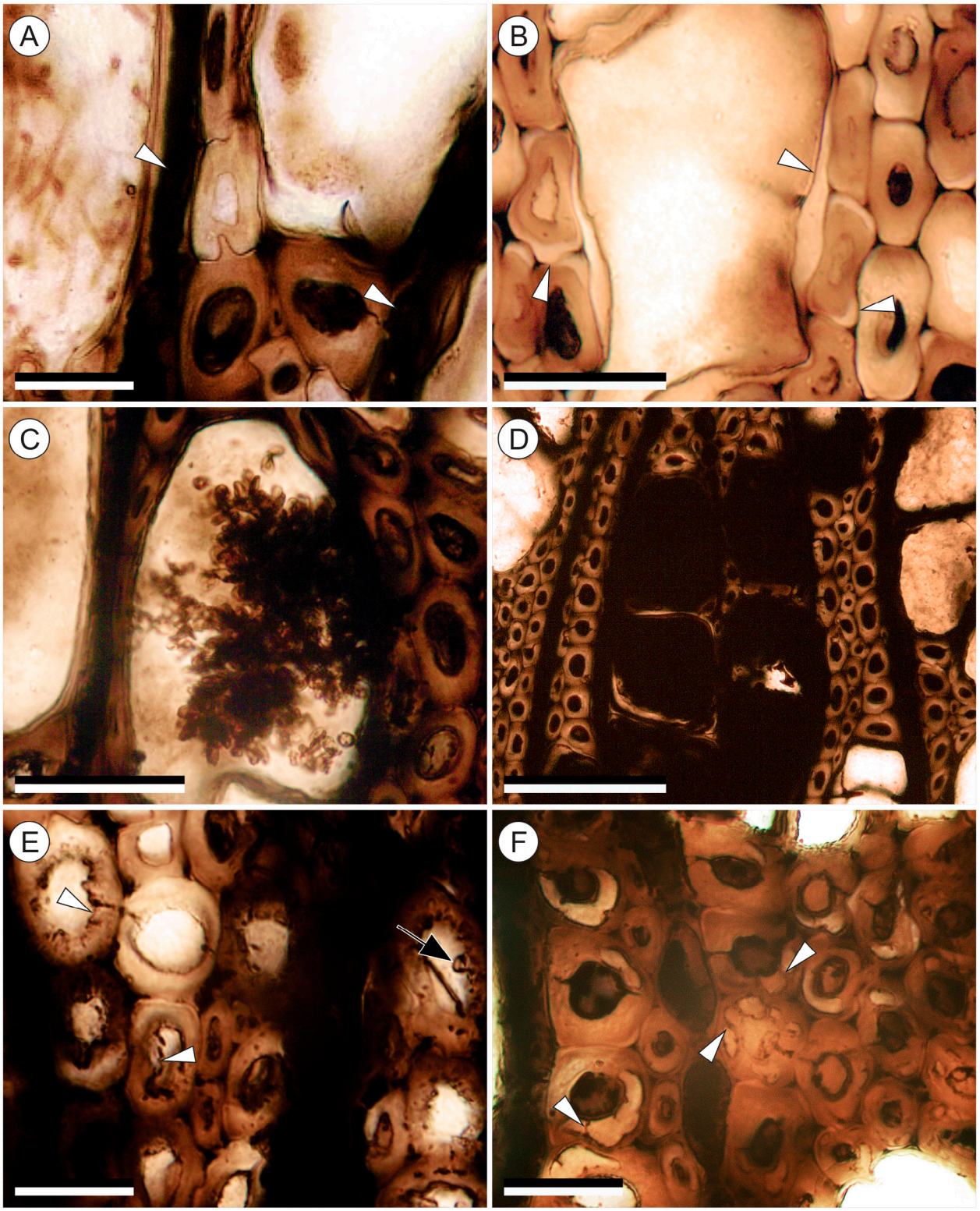


*Fig. 3.* Xylem anatomy preserved undergoing degradation. **A**, Cross-section showing deformed fibres, with the $S_2$ wall layer differentially discoloured and parenchymatous rays with their lumens filled with ergastic substances (arrowheads). MPM PB 2218a. Scale bar = 20 µm. **B**, Cross-section showing cells with their $S_1$ and $S_2$ wall layers detached from each other. Note the incipient detachement of some fibres with respect to neighbouring cells (arrowheads). MPM PB 2218a. Scale bar = 50 µm. **C**, Cross-section with vessel filled with fungal remains. MPM PB 2218a. Scale bar = 50 µm. **D**, Cross-section showing vessels, fibres and parenchymatous rays with their lumens filled with opaque substances. MPM PB 2218a. Scale bar = 100 µm. **E**, Cross-section showing decayed cells with wall layers degraded from the lumen outwards following centrifugal patterns. Note typical soft to sharp-edge notches on wall layers (arrowheads) and associated hyphae (arrow). MPM PB 2218a. Scale bar = 20 µm. **F**, Cross-section. Selective decay of the $S_2$ wall layer of fibres. Note approximately circular scars, which appear separated by septa-like wall remains or coalesced into voids in more intensely degraded cells (arrowheads). MPM PB 2218a. Scale bar = 20 µm.

irregularly corroded wall edges pointing in the same direction (Fig. 3E). In addition, the lumens of the decayed cells contain hyphal filaments observable at different planes, which are associated with further degradation of the wall layers (Fig. 3E). In other fibres, the $S_2$ layer appears selectively decayed, which results in a pattern characterized by circular to irregular cavities, 3– (4)–7 µm in diameter (Fig. 3F). In other fibres, circular cavities in the $S_2$ layer appear grouped and separated by radial septa-like wall residues (Fig. 3F). Where the wood appears highly degraded, cavities in the $S_2$ of fibres coalesce to form crescents or larger voids that ultimately result in the total degradation of this wall layer selectively (Fig. 3F, 4A–B). In addition, some cells show differential decay of $S_2$ layer, next to which are others that show synchronous decay of all cell wall components (Fig. 4A–B). Cells with differential decay of the $S_2$ layer host hyphae that can be traced as connecting cavities in individual cells to each other or through them in cells with lumens filled with opaque substances (Fig. 4C–D).

In addition, a series of longitudinally aligned, polygonal to circular perforations are evident in the $S_2$ layer in the tangential walls of the degraded fibres (Fig. 4E–F). Also, in the tangential plane, the wall appears interrupted by longitudinally aligned notches, which leave an approximately denticulate decay pattern denoting degradation in a centrifugal pattern from the lumen outwards (Fig. 4G). Only the middle lamella remains in those areas where the fibres appear most degraded (Fig. 4H). Another characteristic that can be observed in those fibres with $S_2$ layer more intensely degraded is the presence of variously oriented scars of different length and sharpness, which overall takes the appearance of perforated mesh (Fig. 5A).

In radial and tangential planes, some vessels contain abundant hyphae that ramify regularly in right to oblique angles and penetrate adjacent walls of neighbouring vessels, fibres and parenchymatous rays through wall pits and perforation plates (Fig. 5B). As a result, circular to irregular scars can be observed in the walls of the infected vessels (Fig. 5C). In cross-section, parenchymatous rays in the most degraded areas also have variably decayed walls following a circular to irregular centrifugal pattern (Fig. 5D). In addition, a variable number of incipient tyloses are evident in the parenchymatous rays (Fig. 5E).

Zones delimited by the sealed cells in the secondary xylem contrast markedly with the surrounding decay zones (Fig. 5F). At higher magnification, these obstructions are composed of opaque contents and tyloses that partly to completely fill the cell lumens (Fig. 5G–H).

### *Fungal remains in* Nothofagoxylon scalariforme

The decayed woods are also profusely invaded by hyaline and dark, septate hyphae 0.5–(2) to 3.5 µm long (Fig. 6A–B), which sporadically issue single or symmetrical branches at right to oblique angles, in an L and T fashion, respectively (Fig. 6A–B). Some hyphae have clamp connections (Fig. 6C). Hyphae occupy the cell lumens and in some cases they connect indivdual cells through lateral walls (Fig. 6D). In addition, some of the infected cells host dense clusters of small, elliptical, thick-walled spores (7 × 3 µm; Fig. 6E).

## Discussion

Fungi play a fundamental role as decomposers and recyclers of organic matter in terrestrial ecosystems, thereby maintaining the carbon cycle, essential to the continuation of life on Earth (Carlile *et al.* 2001, Dighton 2016). Lignicolous fungi are the main causes of wood decay within modern ecosystems because of their enzymatic ability to degrade lignin, hemicellulose and cellulose; the fossil record shows that this interaction is well represented deep into the geological past (Cridland 1962, Stubblefield *et al.* 1985, Stubblefield & Taylor 1986, Creber & Ash 1990, Taylor & Osborn 1992, Weaver *et al.* 1997, Cantrill & Poole 2005, Diéguez & López-Gómez 2005, Pujana *et al.*, 2009, García Massini *et al.* 2012b, Tanner & Lucas 2013, Gnaedinger *et al.* 2015, McLoughlin & Bomfleur 2016, Harper *et al.* 2017); however, the scarcity of direct fossil evidence of this kind of plant–fungi interactions, and the low representation of the current spectrum of known patterns of wood rot in the geological record, make the fossil woods from the Río Leona Formation especially important for better understanding the interaction between these organisms and the palaeoecological significance of the various strategies used by fungi as decomposers of wood in ancient ecosystems.

There are three basic types of fungal decay of wood that can be easily distinguished with transmitted light microscopy: brown, white and soft rot (Eriksson *et al.* 1990). Basidiomycetes and some ascomycetes are currently the main causes of white rot-producing similar macro- and microscopic decay patterns, consuming lignin before or synchronously with other components of the cell wall (Blanchette 1991, Schmidt 2006). Brown rot is the product of some specialized basidiomycetes, whereas mainly ascomycetes cause the soft-rot decay pattern, preferentially degrading the cellulose and hemicellulose, while lignin is consumed in a very limited manner (Nilsson *et al.* 1989, Worrall *et al.* 1997).

In our examples, the fibres are the elements of xylem that are relatively more structurally altered, followed by the parenchymatous rays and the vessels. In particular, in cross-section, the fibres of the degraded secondary xylem appear selectively delignified, with the $S_1$ layer and the middle lamella differentially decayed. This results in the deformation and disconnection of individual cells and the presence in others of highly degraded fibres joined just by their more intensely ligni-

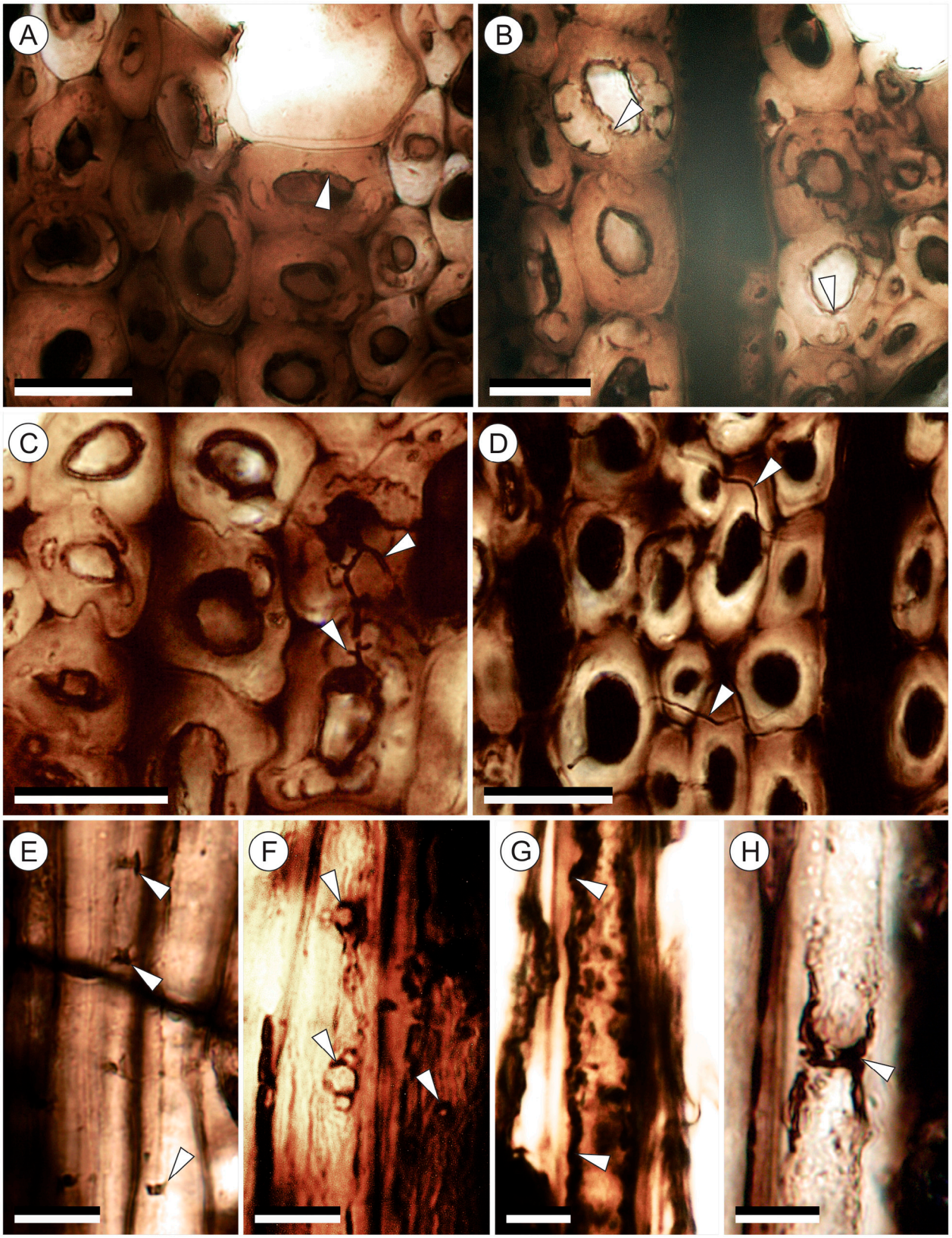


*Fig. 4.* Greater magnification of the vegetal anatomy involved in the decay wood. **A–B**, Cross-section showing fibres with the $S_2$ wall layer partial to completely degraded. Note the presence of two types of attack patterns on the same cells: centrifugal pattern in the lumens (arrowheads) and cavities in the $S_2$ layer. MPM PB 2218a. Scale bars = 20 µm. **C**, Cross-section showing branched hyphae (arrowheads) asociated with cavities in the $S_2$ layer in neighbouring cells. MPM PB 2218a. Scale bar = 20 µm. **D**, Cross-section showing hyphae (arrowheads) developing through the $S_2$ layer in cells with occluded lumens. MPM PB 2218a. Scale bar = 20 µm. **E–F**, Tangential longitudinal section showing aligned polygonal and circular perforations in the lateral walls of fibres (arrowheads). MPM PB 2155c and MPM PM 2218c. Scale bars = 20 µm. **G**, Tangential longitudinal section showing lateral walls of fibres with a denticulate pattern (arrowheads). MPM PB 2218c. Scale bar = 10 µm. **H**, Fibres almost completely degraded, only subtended by the middle lamella remaining in the corners of neighbouring cells (arrowheads) in tangential longitudinal section. MPM PB 2152c. Scale bar = 10 µm.

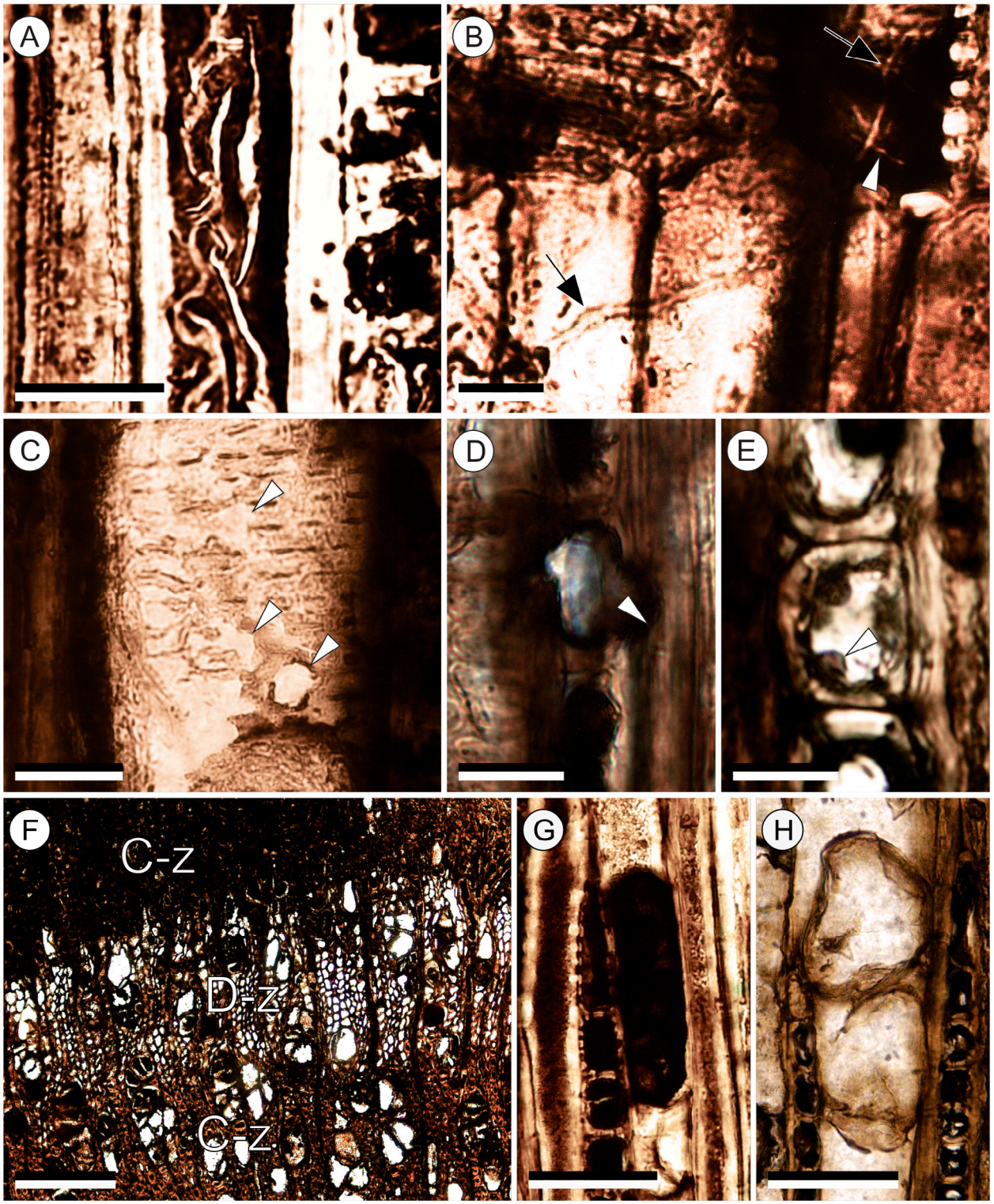


*Fig. 5.* Greater magnification of the vegetal anatomy involved in the decay wood. **A**, Tangential longitudinal section revealing a series of longitudinally to obliquely oriented scars in the $S_2$ wall layers of fibres, resulting in a mesh-like pattern. MPM PB 2155c. Scale bar = 20 µm. **B**, Vessel with hyphae ramifying at an oblique angle (arrows) and colonizing neighbouring cells and producing scars at right angles on the walls (arrowhead) (radial longitudinal section). MPM PB 2218b. Scale bars = 20 µm. **C**, Variably degraded vessel in tangential longitudinal section displaying circular and irregular scars (arrowheads). MPM PB 2155c. Scale bar = 25 µm. **D**, Degraded parenchymatous rays in a centrifugal pattern (arrowhead) in tangential longitudinal section. MPM PB 2218c. Scale bar = 50 µm. **E**, Parenchymatous rays with incipient tyloses (arrowhead) in their interior (tangential longitudinal section). MPM PB 2218c. Scale bar = 50 µm. **F**, General appearance of compact-zones (C-z) of blocked cells in cross-section. Contrast this with the adjacent tissue in which the cells are not clogged in degraded zones (D-z). MPM PB 2218a. Scale bar = 200 µm. **G–H**, Detail of opaque substances and tylosis by partially or completely filling the cell lumen (tangential longitudinal section). MPM PB 2218c. Scale bars = 50 µm.

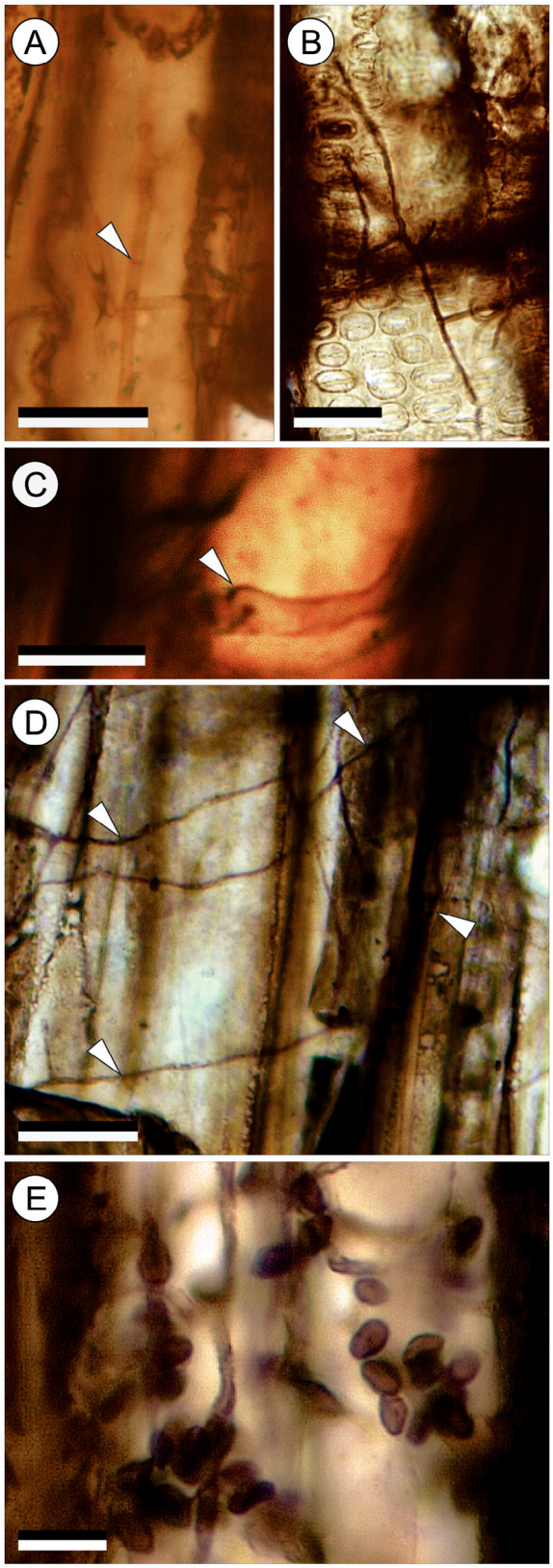


*Fig. 6.* Fungal remains. **A–B**, Tangential longitudinal section showing hyaline and dark hyphae branching at right angles and obliquely. Note the septum in the hyaline hypha (arrowhead). MPM PB 2218c. Scale bars = 20 µm. **C**, Hypha with clamp connections (arrowhead). MPM PB 2218c. Scale bars = 10 µm. **D**, Hyphae developing in cellular lumens and extending through adjacent cells (arrowheads). MPM PB 2218c. Scale bar = 50 µm. **E**, Detail of unicellular elliptical spores in clusters. MPM PB 2149d. Scale bar = 10 µm.

fied corners, which yields a decay pattern like that in modern white-rotted wood (Schwarze 2007). Other fibres, also in cross-section, show a centrifugal degradation pattern with numerous sharp to soft notches, denoting decay from the cell lumen to the outer layers of the cell wall, which look like the different by-products of the erosive mechanisms of soft- and white-rot fungi (Worrall *et al.* 1997, Anagnost 1998, Schwarze 2007). Although the tapered versus rounded shape of the edges of the scars has been used to differentiate the degradation by-products of soft rotters from white rotters, the form of erosion can be modified in advanced stages of decay as a result of the superposition of one type of decay on wood previously affected by the other (Worrall *et al.* 1997, Anagnost 1998). Given the advanced stage of alteration of the woods from Patagonia and the presence of both types of observable degradative notches in longitudinal and cross-section, the available evidence suggests that soft- and white-rot fungi caused the observed decay pattern. In more intensely degraded areas, larger erosive channels typical of simultaneous lignin and cellulose degradation are consistent with white-rot decay (Schwarze & Fink 1998).

The oldest example of white-rot decay occurs in progymnosperm woods (*Callixylon newberryi*) from the Upper Devonian of North America in which cells are invaded by septate hyphae comparable with basidiomycetes and ascomycetes producing extensive lyses of cell walls and characteristic erosion troughs. These plants include some cells with probable ergastic substances in their lumens that may represent a host response (Stubblefield *et al.* 1985). Other, younger examples from the Palaeozoic are also consistent with white-rot decay of Glossopteridales woods and in some cases also showing signs (e.g., secondary wall thickenings and cell lumen obstructed by ergastic substances) of reaction to fungal invasion (Stubblefield *et al.* 1985, Stubblefield & Taylor 1986; Weaver *et al.* 1997; Harper *et al.* 2017). These examples show that over the last 200 million years, fungi evolved the capacity to decay cellulose- and lignin-rich wall components of plants via multiple decay strategies (Harper *et al.* 2017).

The record of fungal decay of woods is also widespread in the Mesozoic and Cenozoic, with examples of white-rot decay and some of its variants produced by basidiomycetes in modern ecosystems, such as mottle rot from Triassic, Jurassic and Eocene deposits in Argentina, USA, China, Antarctica (Stubblefield & Taylor 1986, Pujana *et al.*, 2009, Tanner & Lucas 2013, Feng *et al.* 2015, Gnaedinger *et al.* 2015). A remarkable example from the Jurassic of Antarctica demonstrates white-rot decay resulting from invasion by a pathogenic fungus that triggered the development of tyloses in its plant host as a barrier against decay (Harper *et al.* 2012). Another interesting example is the massive fungal decay described in various tree trunks from the Late Triassic of North America, which was compared with similar widespread fungal attacks in

modern forests (Creber & Ash 1990). The current example from Patagonia supports the widespread presence in the geological record of white-rot fungi as carriers of wood decay either as saprotrophs or necrotrophs, which were critical for nutrient recycling through time.

An additional widespread feature of the degraded fibres observable in cross-section in the woods from Patagonia is the differential decay of the $S_2$ cell layer. Erosion of the $S_2$ layer is characterized by the presence of circular, irregular to crescentic cavities and by the complete absence in cells where the remaining wall components appear structurally sound. This is reminiscent of the selective degradation of the $S_2$ cell wall layer typical of soft-rot-causing ascomycetes (e.g., see Anagnost 1998). In more advanced stages of degradation, cavities appear separated by radial septa-like wall residues ($S_2$ layer), which subsequently can fuse to form larger cavities to finally end in the total consumption of the $S_2$ layer, also as in wood decayed by soft-rot ascomycetes (Schwarze *et al*. 1995). Additional features of the decay-wood consistent with soft-rot decay include aligned perforations in radial walls of fibres evident in longitudinal section. Directly associated with these decay zones are numerous septate hyphae that branch at right (L or T) to oblique angles. This is reminiscent of the erosive mechanism followed by soft-rot decay fungi, where thinner hyphae penetrate into the $S_2$ layer following the orientation of cellulose microfibrils (Savory 1954, Worrall *et al*. 1997, Schwarze 2007). There are other examples of woods in the fossil record with different soft-rot decay features as in the fossil from Rio Leona (Cantrill & Poole 2005, Harper *et al*. 2017). A few reports of apparently soft-rotted wood are also known from almost recent deposits, although decay features described correspond to highly degraded and deformed cells, where selective decay is difficult to discern, therefore, making those examples also comparable with white-rot decay (Blanchette *et al*. 1991, Filey *et al*. 2001). Cantrill & Poole (2005) have inferred soft-rot decay of Antarctic woods based on low structural alteration of plant cells, however, in comparison with the Rio Leona woods, we observed that those layers rich in cellulose show a preferential attack developing orifices of variable sizes, evidencing a more intense cellular decay during consumption of the substrate.

This decay pattern along with the white-rot features observable in the decayed woods also suggests facultative soft rot, which is caused by a few white-rot basidiomycetes that degrade lignin and cellulose via a strategy like that adopted by ascomycetes (e.g., Schwarze 2007). Facultative soft rot is a decay mechanism that allows some white-rot fungi to evade host-plant defence barriers, producing soft-rot-like traits in infected woods (e.g., Schwarze & Fink 1997). In particular, wood decayed by some pathogenic white-rot basidiomycetes (e.g., *Meripilus giganteus*) with the capacity to carry out soft-rot decay leave crescentic to circular or irregular cavities in the $S_2$ cell wall layer of the infected wood (Schwarze & Fink 1998). Such a strategy, followed by the advancing hyphae of some white-rot-causing fungi in the colonized tissue, is a response that avoids the presence of polyphenols and other toxic components present in the cell lumen released by the host to inhibit the spread of fungal pathogens (Schwarze *et al*. 1995, Schwarze & Fink 1997). The resulting branching pattern of the invading hyphae of these particular white-rot basidiomycetes (e.g., *Inonotus hispidus*), which branch at right angles after passing through the $S_3$ cell wall layer as they move within their host, is also like that of soft-rot ascomycetes (Daniel *et al*. 1992, Schwarze *et al*. 1995).

Additional features of the fibres, parenchymatous rays and vessels in the Patagonian woods are the presence of ergastic substances and tyloses in their lumens. In some cases, cells with these characteristics are clustered and represent compact or discrete regions defining cells without evident fungal decay. Tylosis production and secretion of ergastic substances, such as gums and phenolic compounds, represent common natural physicochemical barriers that prevent infection and development of pathogens, including fungi, in angiosperm trees (e.g., Blanchette *et al*. 1988, Christiansen *et al*. 1999, Krekkling *et al*. 2004). These deposits block the passage of hyphae of wood-degrading pathogens, inhibiting further propagation through the lumen and cell walls and, thus, cell degradation (Rioux *et al*. 1995, Pearce 1997, Yamada 2001). Thus, abundance and apparent grouping of cells with these features in the fossil woods from Patagonia suggests host tree response to fungal pathogen spread (Yamada 2001, Schwarze *et al*. 2004). Some examples of tylosis production as a defensive barrier against fungal attack in plants from the Permian of Antactica indicate that such a defence mechanism was used by plants as pathogen deterrents since at last the late Palaeozoic (e.g., Harper *et al*. 2012).

In addition, cells filled by ergastic substances and tyloses also appear invaded by hyphae that preferentially decay and spread from cell to cell via the $S_2$ layer, which is consistent with direct evasion of a structural barrier deployed by the host plants (Schwarze *et al*. 2004). This is also like the colonization mechanism of soft-rot-causing white-rot fungi (e.g., *Meripilus giganteus, Inonotus hispidus*, *Oudemansiella mucida*), which possess the ability to circumvent various plant defensive barriers, by switching from following a preferred invading path through the $S_3$ to the $S_2$ wall layer (Daniel *et al*. 1992, Schwarze & Fink 1997, 1998). In this syndrome, colonizing hyphae initially produce cavities with sharp edges that, as the $S_2$ becomes consumed, leave a series of scars that gradually coalesce giving to the decayed tissue the appearance of a perforated mesh of oblique to vertical orientation (in tangential section) in advanced decay stages (Schwarze *et al*. 1995, Schwarze & Fink 1998). Identical mesh-like degraded tangential walls are evident in the fossils from Patagonia. Facultative soft rot is how some white-rot fungi respond

to evade the so-called reaction zones that result from pathogenic fungus–tree interactions in modern ecosystems (Shain 1967, 1971, 1979). Although a reaction zone could not be detected in the Patagonian fossil, compact zones of comparatively better-preserved cells in otherwise decayed tissue might be the relicts of a more widespread defence deployed by the infected tree when it was alive, similar to relicts that remain in decayed woods in modern ecosystems (e.g., Pearce 1991, Schwarze & Fink 1997).

It is also possible that the observed colonization strategy indicates a means to colonize regions of the cell wall that are less lignified and, therefore, easier to degrade (Fengel & Wegener 1984, Schwarze 2007). With respect to this, other features of the host wood, including lignin to carbohydrate ratio, lignin monomer composition concentration, cell wall morphology and thickness, as well as environmental conditions (i.e., wet soils characterized by low oxygen concentration) could influence the degradational processes, e.g., by encouraging the descomposition of some cells over others, thus favouring one type of decay over the other, such as soft rot over white rot (e.g., Boddy & Rayner 1983, Blanchette *et al*. 1985, 1988, Schwarze *et al*. 1995, Pearce 1997).

Alternatively, it is also possible that these apparent defence symptoms in the Patagonian fossils could indicate an adaptive response to extreme environmental conditions, such as due to sudden flooding or hydric stress and resulting changes in soil physico-chemical characteristics; ageing of trees, such as during heartwood development, or, alternatively, mechanical injury, which can also trigger tylosis formation and deposition of ergastic substances (Chattaway 1949, Schweingruber 2007). Examples indicating tylosis development as a result of sudden environmental changes are known in the fossil record (e.g., Feng *et al*. 2013). Whatever the triggering mechanism for the presence of ergastic substances and tyloses in cell lumina might have been, these structures could have served as a barrier for fungal decay (Rayner 1993). Whether the apparent barrier formed by altered cells in the Patagonian woods indicates a defence mechanism triggered by an infecting fungal pathogen is difficult to determine without additional anatomical evidence (Rayner 1993). Nor is it possible to resolve whether the fungi only carried out decay as saprotrophs (Rayner 1993). Plant–fungi systems vary dynamically based on subtle changes in the decay strategies developed by fungi and responses to these by plants, such that shifts from different fungal nutrition modes (and consequently colonization and decay strategies) and plant perception of the invading agent vary frequently through the interaction processes (Rayner 1991, 1992, 1993).

The co-occurrence of the rich set of white- and soft-rot decay features evident in the same woods, is consistent with competition between fungi with complementary enzymatic capacities for substrate degradation (Boddy 2000, Schwarze *et al*. 2000a, 2000b). This is in fact what happens in most cases in modern ecosystems where living or dying stems become infected by several different fungi (and other organisms, such as bacteria) that compete for a common substrate (Rayner & Boddy 1988, Stokland *et al*. 2012). During the decay process, different species of wood-rotting fungi or hyphae from mycelia of the same species compete for space, nutrients, water and air (Rayner & Boddy 1988). These interactions gradually modify the nutrient quality of decaying woods, directly and indirectly influencing the ecological succession of species during the decay process (Schales 1992, Holmer *et al*. 1997). Strategies typical of competing fungi include rapid colonization of an unexploited and easily degradable substrate, defence of the occupied substrate or attack of competitor fungi occupying a preferred substrate, and adaptation to extreme environmental conditions, such as decay in very wet or low oxygen conditions typical of some soft-rot fungi (Schmidt 2006). Such adaptations in soft-rot fungi represent an efficient means of outcompeting white-rot basidiomycetes, which, become dominant in otherwise drier conditions (e.g., Levy 1987). Therefore, the decayed woods from the Miocene of Patagonia may be better envisioned as a microecosytem in which different fungi competed and interacted in multiple ways for adjacent resources. Under this regime, soft- and white-rot decay fungi left more easily detectable evidence of their activity.

Septate hyphae associated with the decayed woods indicate affinities to ascomycete and basidiomycete fungi (Watkinson *et al*. 2016). In addition, clamp connections are present, which are consistent with basidiomycetes and represent structures developed to maintain the dykarion status during sexual reproduction (Oberwinkler 1978), which have also been observed in various degraded fossil woods (e.g., Feng *et al*. 2015, Harper *et al*. 2017, Wan *et al*. 2017). Comparable thick-walled, septate, hyphae referred to as generative and skeletal hyphae are found in some extant genera of various basidiomycete families, including *Phellinus* (Hymenochaetaceae) and *Polyporus* (Polyporacea, Basidiomycota) (Rajchemberg 1996). These genera and other members of these families are common white-rot fungi present in modern Patagonian forests, where some are known to infect different *Nothofagus* species (Rajchenberg 1996). In addition, spores, especially inside decayed vessels, are elliptical and unicellular, and bear a characteristic longitudinal slit (germination opening), as in some ascomycetes in Xylariales (Ascomycota) (Watkinson *et al*. 2016). Similar dehisced conidia have been found extensively in the fossil record and grouped in the morphogenus *Hypoxylonites* based on its similarity to conidia of extant *Hypoxylon* in Xylariaceae (Kalgutkar & Jansonius 2000). This is interesting because soft-rot fungi are known to be present in extant Xylariaceae in the Andean forests of Patagonia (Wright & Deschamps 1972, Rajchenberg 1983, 1993,

Rajchenberg & Greslebin 1998, Deschamps & Wright 2001, Del Valle & Romero 2009). The preserved fungal structures conform to the features of white- and soft-rot fungi. Further refinement of the affinities of these fungi based on the structures preserved could be obtained if additional structures were found (e.g., fruiting bodies); however, it is likely that, as in modern ecosystems, several other wood rotters, including bacteria, and other fungi participated in the decay of the *Nothofagus* woods (Stokland *et al*. 2012), but these were not preserved; therefore, the full diversity of fungi involved in the decay process may never be known.

## Conclusions

We report the first fossil evidence of the decay of Nothofagaceae wood consistent with the co-occurrence of white- and soft-rot patterns. This evidence is reflected in the different decay strategies that the fungi followed at the time of colonization and decay of the host, which can be compared individually with those operating in modern ecosystems. This is consistent with decay carried out by at least two types of fungi. In addition, although less supported, it suggests facultative soft rot as in some extant white-rot fungi, which have the capacity to produce comparable patterns of wood decay. Pathogen–host interactions could also be argued to have occurred based on the widespread presence soft-rot features along with additional anatomical changes in infected tissue, including development of tyloses and deposition of ergastic substances, and the fungal hyphae colonization pattern of the infected woods. By analogy with extant examples, such a strategy could have been effective in avoiding physicochemical defensive responses induced by the host plant, thus, enabling continuity of the decay process. In addition, preserved fungal structures support the presence of typical ascomycete and basidiomycete families with extant taxa that cause soft- and white rot, respectively.

In summary, the Río Leona decayed woods indicate that at least by the Miocene some fungi had evolved an additional decay strategy involving multiple components of wood cells (i.e., soft-rot decay) that further enlarges the ecological capacity developed by wood-consuming fungi during their evolution. This provides a point of reference for the kinds of interactions between plants and fungi present in Cenozoic forest ecosystems. In particular, this record supports the key roles of fungi as recyclers of organic matter, essential for the completion of the carbon cycle in terrestrial ecosystems in Patagonia during the Miocene.

## Acknowledgements

We would like to thank the Cultural Bureau of Santa Cruz for granting us the permits to carry out this study.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by the ANPCyT and the CONICET through PICT 2012-0911, PIP 2014-0259 (to RRP) and PIP 2011–2013 and PICT-2014-3496 (to JGM).

## References

Anagnost, S.E., 1998. Light microscopic diagnosis of wood decay. *IAWA Journal 19*, 141–167.

Barreda, V.D., Palazzesi, L. & Marenssi, S.A., 2009. Palynological record of the Paleogene Río Leona Formation (southernmost South America): stratigraphical and paleoenvironmental implications. *Review of Palaeobotany and Palynology 154*, 22–33.

Berbee, M.L. & Taylor, J.W., 2010. Dating the molecular clock in fungi—how close are we? *Fungal Biology Reviews 24*, 1–16.

Berbee, M.L., James, T.Y. & Strullu-Derrien, C., 2017. Early diverging fungi: Diversity and impact at the dawn of terrestrial life. *Annual Review of Microbiology 71*, 41–70.

Blanchette, R.A., 1991. Delignification by wood-decay fungi. *Annual Review of Phytopathology 2*, 381–403.

Blanchette, R.A., Otjen, L., Efflan, M.J. & Eslyn, W.E., 1985. Changes in structural and chemical components of wood delignified by fungi. *Wood Science and Technology 19*, 35–46.

Blanchette, R.A., Obst, J.R., Hedges, J.I. & Weliky, K., 1988. Resistance of hardwood vessels to degradation by white rot Basidiomycetes. *Canadian Journal of Botany 66*, 1941–1947.

Blanchette, R.A., Cease, K.R., Abad, A.R., Koestler, R.J., Simpson, E. & Sams, G.K., 1991. An evaluation of different forms of deterioration found in a archaeological wood. *International Biodeterioration 28*, 3–22.

Boddy, L., 2000. Interspecific combative interactions between wood-decaying basidiomycetes. *FEMS Microbiology Ecology 31*, 185–194.

Boddy, L. & Rayner, A.D.M., 1983. Origins of decay in living deciduous trees: the role of moisture content and a re-appraisal of the expanded concept of tree decay. *New Phytologist 94*, 623–641.

Cantrill, D.J. & Poole, I., 2005. A new Eocene *Araucaria* from Seymour Island, Antarctica: evidence from growth form and bark morphology. *Alcheringa 29*, 341–350.

Carlile, M.J., Watkinson, S.C. & Gooday, G.W., 2001. *The Fungi*. Academic Press, London, 588 pp.

Césari, S.N., Panti, C., Pujana, R.R., Francis, J.E. & Marenssi, S.A., 2015. The late Oligocene flora from the Río Leona Formation, Argentinian Patagonia. *Review of Palaeobotany and Palynology 216*, 143–158.

Christiansen, E., Krokene, P., Berryman, A.A., Franceschi, V.R., Krekling, T., Lieutier, F., Lonneborgö, A. & Solheim, H., 1999. Mechanical injury and fungal infection induce acquired resistance in Norway spruce. *Tree Physiology 19*, 399–403.

Creber, G.T. & Ash, S.R., 1990. Evidence of widespread fungal attack on Upper Triassic trees in the southwestern U.S.A. *Review of Palaeobotany and Palynology 63*, 189–195.

Cridland, A.A., 1962. The fungi in cordaitean rootlets. *Mycologia 54*, 230–234.

Daniel, G., Volc, J. & Nilsson, T., 1992. Soft rot and multiple T-branching by the basidiomycete *Oudemansiella mucida*. *Mycological Research 96*, 49–54.

Del Valle, C.M. & Romero, A., 2009. Micromicetes asociados con corteza y/o madera de *Podocarpus parlatorei* Pilg. en la Argentina. V. Ascomycota anamórficos. *Lilloa 46*, 43–51.

Deschamps, J.R. & Wright, J.E., 2001. Micosis de importancia forestal en el Cono Sur de America. *Boletín de Sociedad Micologica 25*, 127–244.

Diéguez, C. & López-Gómez, J., 2005. Fungus-plant interaction in a Thuringian (Late Permian) *Dadoxylon* sp. in the SE Iberian

Ranges, eastern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology 229*, 69–82.

Dighton, J., 2016. *Fungi in Ecosystem Processes*. CRC Press, London, 408 pp.

Eriksson, K.E.L., Blanchette, R.A. & Ander, P., 1990. *Microbial and Enzymatic Degradation of Wood and Wood Components*. Springer, Berlin, 407 pp.

Feng, Z., Wan, J., Rößler, R., Kerp, H. & Wei, H.-B., 2013. Complete tylosis formation in a latest Permian conifer stem. *Annals of Botany 111*, 1075–1081.

Feng, Z., Wei, H.B., Wang, C.L., Chen, Y.X., Shen, J.J. & Yang, J.Y., 2015. Wood decay of *Xenoxylon yunnanensis* Feng sp. nov. from the Middle Jurassic of Yunnan Province, China. *Palaeogeography, Palaeoclimatology, Palaeoecology 433*, 60–70.

Fengel, D. & Weneger, G., 1984. *Wood: Chemistry, Ultrastructure, Reactions*. Walter de Gruyter, Berlin, 613 pp.

Filley, T.R., Blanchette, R.A., Simpson, E. & Fogel, M.L., 2001. Nitrogen cycling by wood decomposing soft-rot fungi in the 'King Midas tomb', Gordion, Turkey. *Proceedings of the National Academy of Science 98*, 13346–13350.

Fosdick, J.C., Romans, B.W., Fildani, A., Bernhardt, A., Calderon, M. & Graham, S.A., 2011. Kinematic evolution of the Patagonian retroarc fold-and-thrust belt and Magallanes foreland basin, Chile and Argentina, 51 30'S. *Geological Society of America Bulletin 123*, 1679–1698.

Fosdick, J.C., Bostelmann, J.E., Leonard, J., Ugalde, R., Oyarzun, J.L. & Griffin, M., 2015. Timing and rates of foreland sedimentation: New detrital zircon U/Pb geochronology of the Cerro Dorotea, Río Turbio, and Río Guillermo formations, Magallanes basin. *Actas XIV Congreso Geológico Chileno, Volumen 1*, 763–766.

Galtier, J., 2008. A new look at the permineralized flora of Grand-Croix (Late Pennsylvanian, Saint-Etienne basin, France). *Review of Palaebotany and Palynology 152*, 129–140.

Galtier, J. & Phillips, T.L., 1999. The acetate peel technique. In *Fossil Plants and Spores: Modern Techniques*. Jones, T.P. & Rowe, N.P., eds, Geological Society, London, 67–70.

García Massini, J.L., Channing, A., Guido, D.M. & Zamuner, A.B., 2012a. First report of fungi and fungus-like organisms from Mesozoic hot springs. *Palaios 27*, 55–62.

García Massini, J.L., Zamaloa, M.C. & Romero, E.J., 2004. Fungal fruiting bodies in the Cullen Formation (Miocene) in Tierra del Fuego, Argentina. *Ameghiniana 41*, 1–9.

García Massini, J.L., Falaschi, P. & Zamuner, A.B., 2012b. Fungal–arthropod–plant interactions from the Jurassic petrified forest Monumento Natural Bosques Petrificados, Patagonia, Argentina. *Palaeogeography, Palaeoclimatology, Palaeoecology 329*, 37–46.

Gnaedinger, S.C., García Massini, J.L., Bechis, F. & Zavattieri, A.M., 2015. Coniferous wood and wood decaying fungi from the El Freno Formation (Lower Jurassic), Neuquen Basin, Mendoza province, Argentina. *Ameghiniana 52*, 1–21.

Gothan, W., 1908. Die fossilen Hölzer von der Seymour und Snow Hill insel. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar Expedition 1901–1903*(3), 1–33.

Harper, C.J., Bomfleur, B., Decombeix, A.L., Taylor, E.L., Taylor, T.N. & Krings, M., 2012. Tylosis formation and fungal interactions in an Early Jurassic conifer from northern Victoria Land, Antarctica. *Review of Palaeobotany and Palynology 175*, 25–31.

Harper, C.J., Taylor, T.N., Krings, M. & Taylor, E.L., 2016. Structurally preserved fungi from Antarctica: Diversity and interactions in late Paleozoic and Mesozoic polar forest ecosystems. *Antarctic Science 28*, 153–173.

Harper, C.J., Decombeix, A.L., Taylor, E.L., Taylor, T.N. & Krings, M., 2017. Fungal decay in Permian glossopteridalean stem and root wood from Antactica. *IAWA Journal 38*, 29–48.

Heckman, D.S., Geiser, D.M., Eidell, B.R., Stauffer, R.L., Kardos, N.L. & Blair Hedges, S., 2001. Molecular evidence for the early colonization of land by fungi and plants. *Science 293*, 1129–1133.

Herbst, R. & Lutz, A., 2001. Catalogue of fossil fungi in Southern South America. *Acta Geológica Lilloana 18*, 241–248.

Holmer, L., Renvall, P. & Stenlid, J., 1997. Selective replacement between species of wood-rotting basidiomycetes: a laboratory study. *Mycological Research 101*, 714–720.

Kalgutkar, R.M. & Jansonius, J., 2000. Synopsis of fossil fungal spores, mycelia and fructifications. *AASP Contribution Series 39*, 1–428.

Krekling, T., Franceschi, P.K. & Solheim, H., 2004. Differential anatomical response of Norway spruce stem tissues to sterile and fungus infected inoculations. *Trees 18*, 1–9.

Levy, J.F., 1987. The natural history of degradation of wood. *Philosophical Transactions of the Royal Society of London A 321*, 423–433.

Malumian, N. & Panza, J., 2000. Hoja geológica 5172-III Yacimiento Río Turbio. *Boletín del Servicio Geológico Minero Argentino 247*, 1–108.

Marenssi, S.A., Casadío, S. & Santillana, S.N., 2003. Estratigrafía y sedimentología de las unidades del Cretácico superior-Paleógeno aflorantes en la margen sureste del lago Viedma, provincia de Santa Cruz, Argentina. *Revista de la Asociación Geológica Argentina 58*, 403–416.

Marenssi, S.A., Limarino, C.O., Tripaldi, A. & Net, L.I., 2005. Fluvial systems variations in the Río Leona Formation: Tectonic and eustatic controls on the Oligocene evolution of the Austral (Magallanes) Basin, southernmost Argentina. *Journal of South American Earth Sciences 19*, 359–372.

Chattaway, M.M., 1949. The development of tyloses and secretion of gum in heartwood formation. *Australian Journal of Biological Sciences 2*, 227–240.

García Massini, J.L., Escapa, I.H., Guido, D.M. & Channing, A., 2016. First glimpse of the silicified hot spring biota from a new Jurassic chert deposit in the Deseado Massif, Patagonia, Argentina. *Ameghiniana 53*, 205–230.

McLoughlin, S. & Bomfleur, B., 2016. Biotic interactions in a exceptionally well preserved osmundaceous fern rhizome from the Early Jurassic of Sweden. *Palaeogegraphy, Palaeoclimatology, Palaeoecology 464*, 86–96.

McLoughlin, S., Haig, D.W., Backhouse, J., Holmes, M.A. & Ellis, G., 1995. Oldest Cretaceous sequence, Giralia Anticline, Carnarvon Basin, Western Australia: late Hauterivian– Barremian. *AGSO Journal of Australian Geology and Geophysics 15*, 445–468.

Nisson, T., Daniel, G., Kirk, T.K. & Obst, J.R., 1989. Chemistry and microscopy of wood decay by some higher ascomycetes. *Holzforschung 43*, 11–18.

Oberwinkler, F., 1978. Was ist ein Basidiomycet? *Zeitschrift für Mykologie 44*, 13–29.

Pearce, R.B., 1991. Reaction zone relics and the dynamics of fungal spread in the xylem of woody angiosperms. *Physiological and Molecular Plant Pathology 39*, 41–55.

Pearce, R.B., 1997. Antimicrobial defences in the wood of living trees. *New Phytologist 132*, 203–233.

Pujana, R.R., 2007. New fossil woods of Proteaceae from the Oligocene of southern Patagonia. *Australian Systematic Botany 20*, 119–125.

Pujana, R.R., 2009a. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). Atherospermataceae, Myrtaceae. *Leguminosae and Anacardiaceae. Ameghiniana 46*, 523–535.

Pujana, R.R., 2009b. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). *Rosaceae and Nothofagaceae. Ameghiniana 46*, 621–636.

Pujana, R.R., García Massini, J.L., Rodríguez Brizuela, R. & Burrieza, H.P., 2009. Evidence of fungal activity in silicified gymnosperm wood from the Eocene of southern Patagonia (Argentina). *Geobios 42*, 639–647.

Rajchenberg, M., 1983. Basidiomicetos xilófilos de los Bosques Andinopatagónicos. Adiciones y correcciones. I. *Boletín de la Sociedad Argentina de Botánica 22*, 41–56.

Rajchenberg, M., 1993. Basidiomicetos xilófilos de los Bosques Andinopatagónicos. Adiciones y correcciones. III. *Boletín de la Sociedad Argentina de Botánica 29*, 115–121.

Rajchenberg, M., 1996. Los hongos pudridores de *Nothofagus pumilio* (Lenga): identificación de los cultivos puros. *Bosque 17*, 87–100.

Rajchenberg, M. & Gresbelin, A.G., 1998. Basidiomicetos xilófilos (Aphillophorales) de los Bosques Andinopatagónicos. Adiciones

y correcciones. V. *Boletín de la Sociedad Argentina de Botánica 33*, 191–194.

Rayner, A.D.M., 1991. The challenge of the individualistic mycelium. *Mycologia 83*, 48–71.

Rayner, A.D.M., 1992. Conflicting flows—the dynamics of mycelial territoriality. *McIlvainea 10*, 24–35.

Rayner, A.D.M., 1993. New avenues for understanding processes of tree decay. *Arboricultural Journal 17*, 171–189.

Rayner, A.D.M. & Boddy, L., 1988. *Fungal Decomposition of Wood: Its Biology and Ecology*. Wiley, Chichester, UK, 602 pp.

Rioux, D., Chamberland, H., Simard, M. & Ouellette, G.B., 1995. Suberized tyloses in tree: an ultrastructural and cytochemical study. *Planta 196*, 125–140.

Savory, J.G., 1954. Breakdown of timber by ascomycetes and fungi imperfecti. *The Annals of Applied Biology 41*, 336–347.

Schales, M., 1992. Totholz. Ein Refugium fur seltene Pilzarten. *Allg Forstz 47*, 1107–1108.

Schmidt, O., 2006. *Wood and Tree Fungi. Biology, damage, protection, and use*. Springer, Heilderberg, 334 pp.

Schopf, J.W., 2012. The fossil record of Cyanobacteria. In *The Ecology of Cyanobacteria*. Whitton, B.A., ed., Springer, Dordrecht, Netherlands, 15–36.

Schwarze, F.W.M.R., 2007. Wood decay under the microscope. *Fungal Biology Reviews 21*, 133–170.

Schwarze, F.W.M.R. & Fink, S., 1997. Reaction zone penetration and prolonged persistence of xylem rays in London plane wood degraded by the basidiomycete *Inonotus hispidus*. *Mycological Research 101*, 1207–1214.

Schwarze, F.W.M.R. & Fink, S., 1998. Host and cell type affect the mode of degradation by *Meripilus giganteus*. *New Phytologist 139*, 721–731.

Schwarze, F.W.M.R., Lonsdale, D. & Fink, S., 1995. Soft rot and multiple T-branching by the basiodiomycete *Inonotus hispidus* in ash and London plane. *Mycological Research 99*, 813–820.

Schwarze, F.W.M.R., Baum, S. & Fink, S., 2000a. Dual modes of degradation by *Fistulina hepatica* in xylem cell walls of *Quercus robur*. *Mycological Research 104*, 846–852.

Schwarze, F.W.M.R., Baum, S. & Fink, S., 2000b. Resistence of fibre regions in wood of *Acer pseudoplatanus* degraded by *Armillaria mellea*. *Mycological Research 104*, 1126–1132.

Schwarze, F.W.M.R., Engels, J. & Mattheck, C., 2004. *Fungal Strategies of Wood Decay in Trees*. Springer, Heidelberg, 185 pp.

Schwengruber, F.H., 2007. *Wood Structure and Environment*. Springer, Heidelberg, 279 pp.

Shain, L., 1967. Resistance of sapwood in stems of loblolly pine to infection by *Formes annosus*. *Phytopathology 57*, 1034–1045.

Shain, L., 1971. The response of sapwood of Norway spruce to infection by *Formes annosus*. *Phytopathology 61*, 301–307.

Shain, L., 1979. Dynamic responses of differentiated sapwood to injury and infection. *Phytopathology 69*, 1143–1147.

Slater, B.J., McLoughlin, S. & Hilton, J., 2015. A high-latitude Gondwanan lagerstätte: The Permian permineralized peat biota of the Prince Charles Mountains, Antarctica. *Gondwana Research 27*, 1446–1473.

Stockey, R.A., 2001. The Princeton Chert. In *Palaeobiology II*. Briggs, D.E.G. & Crowther, P.R., eds, Blackwell Science, Oxford, 359–362.

Stokland, J.N., Siitonen, J. & Jonsson, B.G., 2012. *Biodiversity in Dead Wood*. Cambridge University Press, New York, NY, 521 pp.

Strullu-Derrien, C., Kenrick, P., Rioult, J.P. & Strullu, D.G., 2011. Evidence of parasitic Oomycetes (Peronosporomycetes) infecting the stem cortex of the Carboniferous seed fern *Lyginopteris oldhamia*. *Proceedings of the Royal Society: Biological Science 278*, 675–680.

Stubblefield, S.P. & Taylor, T.N., 1986. Wood decay in silicified gymnosperms from Antarctica. *Botanical Gazette 147*, 116–125.

Stubblefield, S.P., Taylor, T.N. & Beck, C.B., 1985. Studies of paleozoic fungi. IV. Wood-decaying fungi in *Callixylon newberryi* from the Upper Devonian. *American Journal of Botany 72*, 1765–1774.

Tanner, L.H. & Lucas, S.G., 2013. Degraded wood in the Upper Triassic Petrified Forest Formation (Chinle Group), Northern Arizona: Differentiating fungal rot from arthropod boring. *New Mexico Museum of Natural History and Science Bulletin 61*, 582–588.

Taylor, T.N. & Krings, M., 2010. Paleomycology: the rediscovery of the obvious. *Palaios 25*, 283–286.

Taylor, T.N. & Osborn, J.M., 1992. The role of wood in understanding saprophytism in the fossil record. *Courier Forschungsintitut Senckenberg 147*, 147–153.

Taylor, T.N., Klavins, S.D., Krings, M., Taylor, E.L., Kerp, H. & Hass, H., 2004. Fungi from the Rhynie chert: a view from the dark side. *Transactions of the Royal Society of Edinburgh, Earth Science 94*, 457–473.

Taylor, T.N., Taylor, E.L. & Krings, M., 2009. *Paleobotany. The biology and evolution of fossil Plants*. Elsevier Academic Press, Burlingon, 1253 pp.

Taylor, T.N., Taylor, E.L. & Krings, M., 2015. *Fossil Fungi*. Elsevier Academic Press, Kidlington, 384 pp.

Wacey, D., Kilburn, M.R., Saunders, M. & Brasier, M.D., 2011. Microfossils of sulphur-metabolizing cells in 3.4-billion-year-old rocks of Western Australia. *Nature Geoscience 4*, 698–702.

Wan, M., Yang, W., He, X., Liu, L. & Wan, J., 2017. First record of fossil basidiomycete clamp connection in cordaitalean stem from the Asselian–Sakmarian (lower Permian) of Shanxi Province, North China. *Palaeogeography, Palaeoclimatology, Palaeoecology 466*, 353–360.

Watkinson, S., Boddy, L. & Money, N., 2016. *The Fungi*. Elsevier Academic Press, Oxford, 466 pp.

Weaver, L., McLoughlin, S. & Drinnan, A.N., 1997. Fossil woods from the Upper Permian Bainmedart Coal Measures, northern Prince Charles Mountians, East Antarctica. *Jounal of Australian Geology and Geophysics 16*, 655–676.

Webster, J. & Weber, R.W.S., 2007. *Introduction to Fungi*. Cambridge University Press, New York, NY, 841 pp.

Worrall, J.J., Anagnost, S.E. & Zabel, R.A., 1997. Comparison of wood decay among diverse lignicolous fungi. *Mycologia 89*, 199–219.

Wright, J.E. & Deschamps, J.R., 1972. Basiodiomicetos xilófagos de los Bosques Andinopatagónicos. *Revista de Investigaciones Agropecuarias, INTA, Serie 5. Patología Vegetal 7*, 111–204.

Yamada, T., 2001. Defense mechanisms in the sapwood of living trees against microbial infection. *Journal of Forest Research 6*, 127–137.