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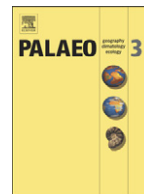
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Fungal–arthropod–plant interactions from the Jurassic petrified forest Monumento Natural Bosques Petrificados, Patagonia, Argentina

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ABSTRACT

Fungal–arthropod–plant interactions are described from the Middle Jurassic Monumento Natural Bosques Petrificados, Santa Cruz, Patagonia, Argentina. Fossils consist of a silicified araucarian log that appears differentially decayed and displays galleries bored in patterns resembling those produced by extant wood-boring beetles. Galleries are filled completely with frass that is reworked into smaller galleries containing spherical to ellipsoidal coprolites. The coprolites are of possible mite origin and contain fungal and plant remains. Fungi are also found growing from the walls of the smaller galleries and from the coprolites. Identifiable fungal propagules include asexual structures typical of extant imperfect fungi. Comparison with modern wood with similar patterns suggests a xilophagous role for the wood borer, whereas the smaller galleries and coprolites likely are products of a smaller xylophagous/fungivorous woodborer. Decay patterns in the silicified woods are like those produced by extant saprotrophic and pathogenic wood-rotting fungi in modern ecosystems. The fungus on the walls of the galleries and on the coprolites most likely was saprotrophic. However, additional indirect and direct interactions (i.e., phorisms) similar to those between conifers, mites, beetles, and fungi in modern ecosystems could be hypothesized. This report provides unique direct fossil evidence of multitrophic fungal–arthropod–plant interactions and suggests the possibility that complex interactions like those in modern conifers might have been in place by at least the Jurassic. These results underscore the importance of fungi as key elements of past ecosystems, acting as drivers of biological cycles and symbionts with a variety of organisms.

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1. Introduction

Interactions between plants, fungi, and arthropods have been pivotal in the evolution of terrestrial ecosystems (Labandeira, 2006). However, the scarcity of fossil records indicating such interrelationships precludes a thorough assessment of the origin and development of trophic relationships and symbiotic associations among taxa in modern ecosystems (Taylor et al., 2009). In part, this difficulty reflects inherent problems associated with the preservation of fossils, where documentation of interactions is dependent upon the fossilization potential of the organism(s) involved.

Fossil evidence of species interactions are only available when particular preservation conditions, such as the embedding of fossils in a mineral-charged solution or in plant resin matrix, capture the

interacting organisms as intimately associated as they were when they were alive (e.g., García Massini, 2007; Schmidt et al., 2008). Examples are rare, but the Devonian cherts of the Rhynie deposits of Scotland are a notable exception (Taylor et al., 2009). The Rhynie cherts have provided a rich record of interspecies associations and symbiotic interactions. These include fungi known to have direct and indirect interactions with other organisms, particularly with plants (Remy et al., 1994). The record of fungal associations and/or interactions with organisms other than plants is less well known and represented by relatively few examples (Hagwood et al., 2004). Despite the many examples of extant multi-species interactions involving fungal interactions with plants and other organisms, no definite examples of such interactions are known from the fossil record (Taylor et al., 2009). Here, we describe and discuss an example from the Jurassic of Argentina. In this system, a fungally decayed, petrified araucarian (Pinophyta: Araucariaceae) log displays beetle-bored galleries that are in turn hollowed into smaller galleries containing fungal propagules and coprolites of possible mite origin. In addition, the coprolites include plant and fungal remains.

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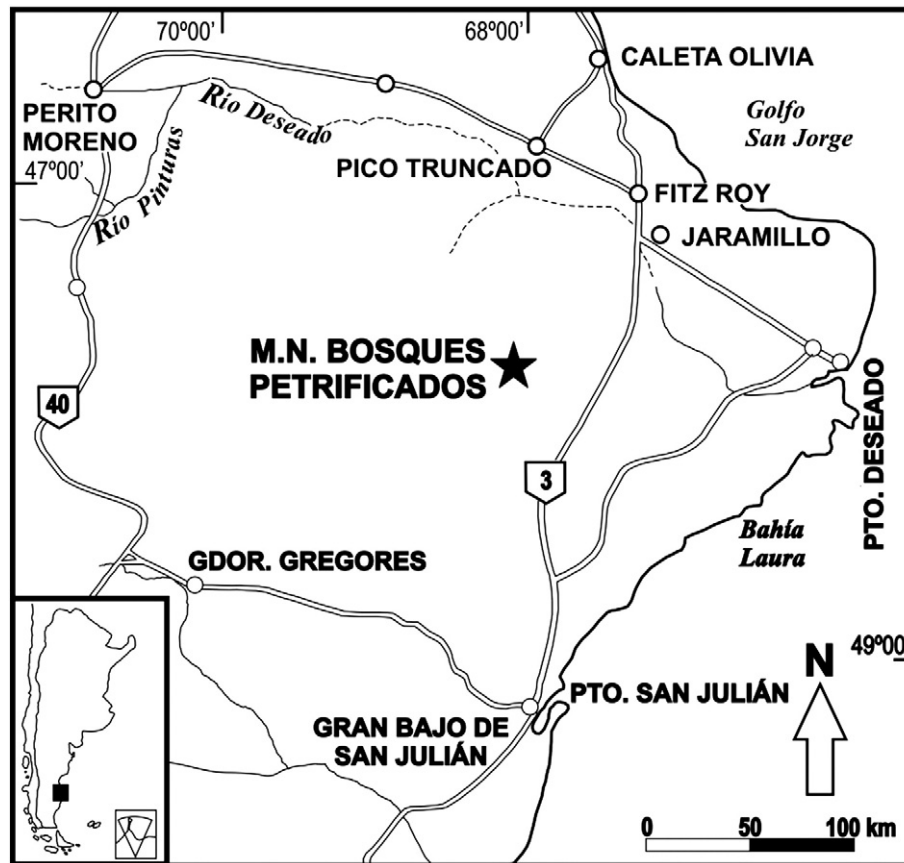


Fig. 1. Map of Argentina depicting in detail the study locality within the Monumento Natural Bosques Petrificados (Santa Cruz Province, Patagonia).

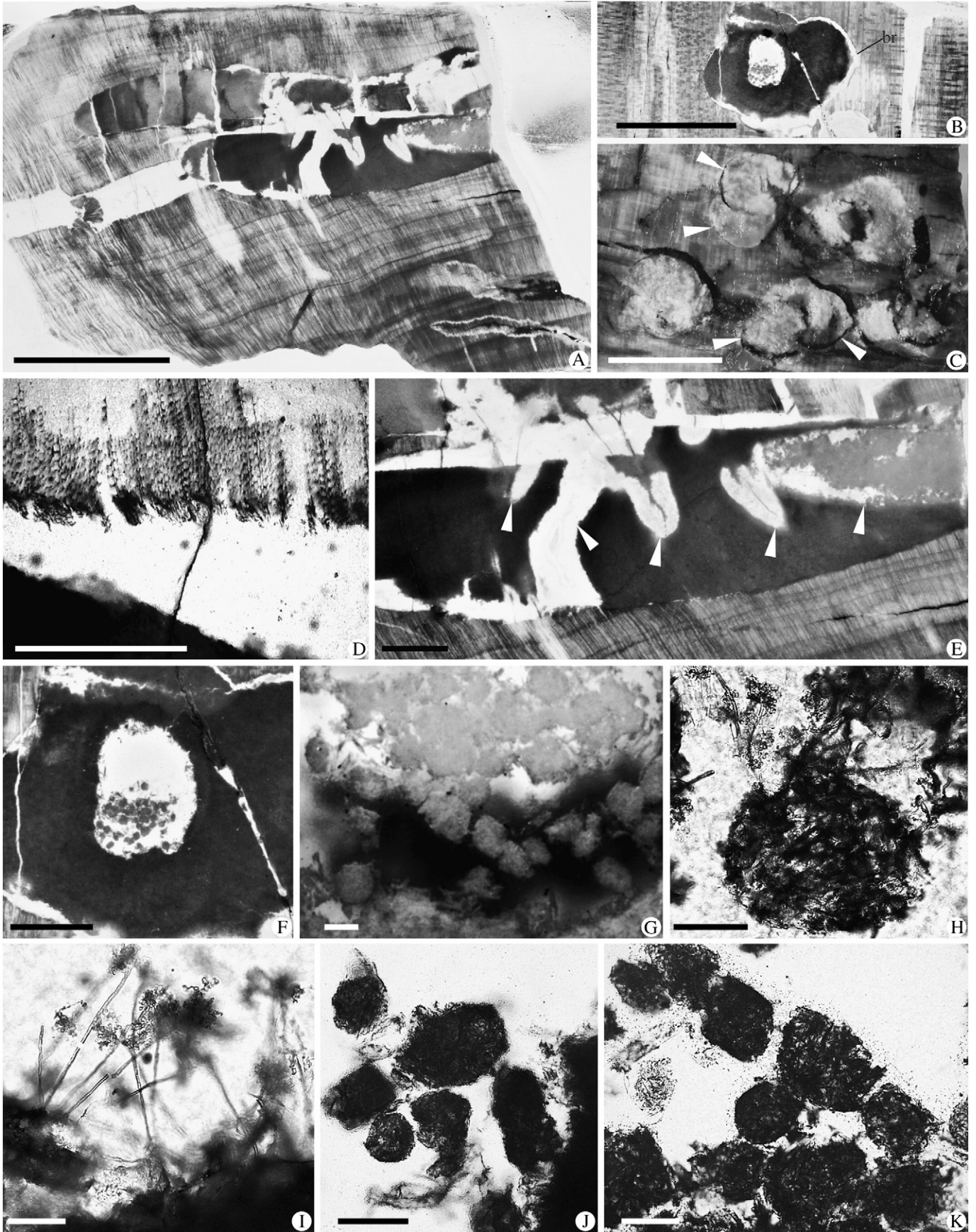
2. Geologic setting

The study area is set within the Monumento Natural Bosques Petrificados, northeastern Santa Cruz Province, Patagonia, Argentina (Falaschi et al., 2011). The fossil log described is from a single locality (47° 52'S 68° 00'O) that is part of the basal strata of the Jurassic La Matilde Fm, which is stratigraphically sandwiched between the Lower Jurassic Bajo Pobre Fm and the Lower Cretaceous Anfiteatro de Ticó Fm (Fig. 1) (De Barrio et al., 1999; Panza and Genini, 2001; Falaschi, 2009; Falaschi et al., 2011). La Matilde Formation is included in the Central Deseado Massif, whose origin is related to the development of the Patagonian cordillera Orogen during the Paleozoic and the opening of the proto-Atlantic Ocean in the Mesozoic (De Barrio et al., 1999; Ramos, 2002). In the studied section, it consists of a succession (~125 m thick) of volcanic strata intercalated with volcanoclastic sediments (Falaschi et al., 2011). The sedimentary succession and paleontological content indicate a terrestrial paleoenvironment characterized by subaerial deposition of volcanically originated sediments with occasional subaqueous reworking, periodically alternating with sedimentation in lacustrine settings

and with the formation of paleosols (Falaschi, 2009; Falaschi et al., 2011).

The fossil log studied in this paper is from an *in situ* fossil forest that is part of the sedimentary succession (Falaschi, 2009; Falaschi et al., 2011). Conifers, represented by permineralized woods, external molds of leafy branches, female cones and seedlings are the only plant group present in the petrified forest, which, at the study site, consists of a dominant araucarian species, *Agathoxylon matildense*, and another conifer possibly belonging to the Pararaucariaceae (Zamuner and Falaschi, 2005; Falaschi, 2009; Falaschi and Zamuner, 2010; Falaschi et al., 2011). Other fossils described from the La Matilde Formation include vertebrates, mollusks, arthropods, dinosaur and arthropod traces, fungi and a diversity of plant remains including ferns, Bennettitales, pteridosperms, Sphenophytes and conifers (Falaschi, 2009 and references therein). The age of the La Matilde Formation is constrained on the basis of its fossil content to the Middle Jurassic, while based on stratigraphic correlations of the fossil-bearing strata, a Middle-Upper Jurassic age was inferred (Stipanovic and Reig, 1955, 1956; Stipanovic and Bonetti, 1970). More recently, radiometric data have provided ages between 157

Fig. 2. Degraded *Agathoxylon matildense* log from the Jurassic Monumento Natural Bosques Petrificados in Patagonia (Santa Cruz Province), Argentina. A. Longitudinal section of beetle (cerambycid) galleries bored in the secondary xylem of *Agathoxylon matildense* (transverse section). Scale = 1.5 cm. B. Cross section of beetle (cerambycid) galleries bored in the secondary xylem of *Agathoxylon matildense* (radial section). Note circular to elliptical outline and lobed/notched borders (br). Scale = 1 cm. C. Un-cut external surface of *Agathoxylon matildense* showing several partly superposed galleries (arrowheads) bored in the secondary xylem. Scale = 1 cm. D. Close up of gallery borders showing harshly cut tracheids. Note the advanced state of decay of the bored plant tissue. Scale = 1 cm. E. Close up of frass-filled, beetle gallery with its frass reworked into smaller borings (arrowheads) of variable orientation, length and outline. Scale = 2.5 mm. F. Cross section of a smaller, mite, boring into a larger, beetle, gallery. Note the ovate to semi-circular outline, the irregular borders and the clustering of the coprolites on a single side of the boring. Scale = 2.5 mm. G. Close up of a smaller gallery showing coprolites and other reworked organic debris and fungi. Note the homogeneous distribution of the coprolites. Scale = 250 μ m. H. Close up on a coprolite showing fungi growing from it. Scale = 100 μ m. I. Close up on the borders of a smaller gallery and other reworked organic debris showing fungi growing from them. Scale = 25 μ m. J. Close up on a group of coprolites showing their different relative dimensions, rough texture, clear outline and spherical to ellipsoidal shape. Scale = 200 μ m. K. Group of coprolites partly aligned in a row. Scale = 200 μ m.



and 162 ± 5 – 10 Ma (Spalletti et al., 1982; De Barrio, 1993; Echeveste et al., 2001).

3. Materials and methods

Thin sections of a single silicified wood specimen were obtained following standard procedures (Hass and Rowe, 1999) and were analyzed using light microscopy. Description and classification of arthropod feces, fungal decay patterns and fungal remains were carried out by comparisons with modern and fossil examples (e.g., Labandeira et al., 1997; Grimaldi and Engel, 2005; Schmidt, 2006; Domsch et al., 2007; Krantz and Walter, 2009; Taylor et al., 2009). Slides representing transverse, longitudinal radial and longitudinal tangential sections of the specimens studied are deposited under accession numbers LPPB-13724 (megascopic sample), LPPm-1855, 1856, 1857, 1901, 1902 and 1903 (microscopic slides) in the Paleobotanical Division of the Natural Sciences Museum of La Plata, Argentina.

4. Results

This section describes a set of galleries bored in an araucarian log fragment (including only the external part of the secondary xylem; preserved width ~ 5 cm), decayed according to patterns of extant wood-decaying fungi, and coprolites and fungal remains present inside and on the walls of the galleries.

The fossil log was assigned to *Agathoxylon matildense* Zamuner and Falaschi (Araucariaceae; Zamuner and Falaschi, 2005) based on the identity of diagnostic characters in radial section including uni-biseriate bordered pits, which are contiguous, circular or oval. Biseriate bordered pits display an alternate pattern and are semi-circular or hexagonal. Cross-field pits (4–6) are cupressoid or taxodioid, rarely araucarioid, and they are arranged in two horizontal tiers or irregularly. Medullary rays are homocellular and moderately high.

4.1. Galleries

These consist of irregularly elongate to funnel-shaped cavities up to 4 cm long in the secondary xylem (sapwood) that are set transversal to the main axis of the affected log (Fig. 2A). Most galleries are homogeneously filled towards both ends with tightly packed frass made up of finely masticated plant remains (Fig. 2A). In cross section, the cavities are 1.5 to 13.0 mm in diameter, the overall shape is circular to nearly elliptical, and the edge is irregularly lobed/notched (Fig. 2B). The un-cut external surface of the bored log shows the exposed ends of several roughly linearly aligned, superposed galleries, producing larger and more irregular holes than individual cavities (Fig. 2C). Galleries are constructed in differentially decayed tissue and their walls are commonly composed of cut, tightly packed tracheids that give the wall a jagged appearance (Fig. 2D).

Some galleries are filled with frass that has been reworked into smaller, elongate to sinuous, sometimes ramified, borings of variable length (up to ~ 7 mm) (Fig. 2E). The smaller borings are oriented longitudinally to transversely relative to the main axis of the larger galleries (Fig. 2E). In cross section, the smaller borings are ovate to semi-circular with irregular borders and with dimensions of 2–4 \times 2.5–7 mm (Fig. 2F). They are usually associated with differentially degraded zones in the adjacent plant tissue and contain coprolites and fungi that grow from the latter and from the walls and fragments of frass reworked from the larger galleries (Figs. 2G–I).

4.2. Coprolites

These are ellipsoidal to cylindrical or hemispherical, rather compact bodies, of rugose texture, but generally with well delineated borders (Fig. 2J). They range in size (length \times diameter) between 170 \times

160 to 330 \times 250 μm . Coprolites are either grouped on one side of the galleries or homogeneously distributed inside the reworked galleries, and they are commonly aligned in rows (Fig. 2F, G, and K). They comprise plant material and fungal remains that vary from being disaggregated and finely comminuted to preserved to a degree where they can be identified (Fig. 3A and B). A number of coprolites appear covered to a large extent by fungi (Fig. 3C).

4.3. Fungal remains

Fungi grow from the walls of the smaller galleries and from the coprolites and make up part of the latter (Figs. 2H and I and 3A–C). Propagules present include regularly septate hyphae (2–3 μm wide) that are at times ramified and differentiated into intermittently apically branched, erect reproductive structures (conidiophores) of variable length (Fig. 3D and E). Conidiophores are mononematous and bear diffuse clusters or chains of unicellular, psilate, ovoid to cylindrical, hyaline conidia (spores) that are up to 4.5 μm wide (Fig. 3E). In addition, conidiophores have a basal swelling (\sim appresoria) by which they are attached to the substrate (Fig. 3F). Conidia are acropoleurogenous (formed at the end and on the sides) and originate polyblastically (from more than one point in a single cell) either from swollen terminal pyriform conidiogenous cells or from apparently undifferentiated terminal or intercalary conidiophore cells (cf. ampullae) (Fig. 3G and H). A single hilum (pore) is present in conidia and a rather inconspicuous denticle mark or a depression can be observed on both conidiogenous cells and undifferentiated conidiophore cells from where conidia dehisced (Fig. 3G and H).

4.4. Wood decay patterns

The decayed araucarian log displays elongate to diffuse areas in transverse section that appear translucent in transmitted light (Fig. 4A). In addition, some of these translucent areas are associated with darker areas that give them a mottled appearance (Fig. 4B). At a greater magnification translucent areas appear completely devoid of cells or have a fibrous and whitish appearance and consist of tracheids with differentially decayed cell wall components (Fig. 4C and D). Included are cells with differentially degraded middle lamella that sometimes appear still attached by their corners (Fig. 4E). Other regions of the decayed areas have cells ranging from nearly intact to almost completely degraded (sometimes filled with opaque irregular contents), but with no particular cell component differentially decayed (Fig. 4F and G). Decayed cells show a variety of textures, where their surface ranges from roughened with troughed, elongated, to irregular areas, to sometimes skeletonized, to mostly smooth and better preserved (Fig. 4H and I). Also present inside the lumen of some cells are psilate, septate, unbranched hyphal strands that are associated with differentially decayed cells and that sometimes connect several cells to each other (Fig. 4J and K).

5. Discussion

Plant–fungal interactions are better known than animal–fungal interactions in the fossil record (Taylor et al., 2009). Interactions inferred between fossil plants and fungi span the range of possibilities known from modern ecosystems, from mutualism to parasitism, and saprotrophism (Remy et al., 1994; Taylor et al., 2005; García Massini, 2007). A similarly diverse range of associations between animals and fungi is known from the fossil record, ranging from predation to fungivory to possible obligate and opportunistic symbioses (White and Taylor, 1989; Habgood et al., 2004; Schmidt et al., 2008; Jackson et al., 2009). However, this information is based on a limited number of records from scattered localities and geologic ages (Taylor et al., 2009).



Fig. 3. Contents of degraded *Agathoxylon matildense* log from the Jurassic Monumento Natural Bosques Petrificados in Patagonia (Santa Cruz Province), Argentina. A. Close up on the contents of a coprolite showing a variety of organic debris including partly broken tracheids (arrowhead). Scale = 50 μm . B. Close up on the contents of a coprolite showing fungal remains including masses of conidia (arrowhead). Scale = 50 μm . C. General view of a coprolite densely colonized by fungi. Scale = 100 μm . D. Apically branched conidiophores built on septate hyphae. Scale = 25 μm . E. Branched septate conidiophore bearing masses (lower arrowhead) and chains (upper arrowhead) of unicellular conidia. Scale = 15 μm . F. Close up on basal swelling present in conidiophores. Scale = 10 μm . G. Conidia arising terminally or from the side (acropleurogenous) of a conidiophore. Note lateral conidia arising from an undifferentiated conidiophore cell (cf. ampullae) and terminal conidia produced on inflated conidiogenous cells. Arrowhead points to a denticle mark left on places from where conidia dehiscid. Scale = 10 μm . H. Conidiophores showing conidiogenous cells bearing conidia from more than one point on its surface (polyblastic origin). Right arrowhead points to hilum present in dehiscid conidia and lower arrowhead points to depression left on places from where conidia dehiscid. Scale = 10 μm .

Fossils representing multitrophic interactions, such as those described herein for plants, fungi, and arthropods, are especially uncommon. Examples of possible direct tripartite interactions including plants, fungi and animals are those inferred from the presence of epiphyllous fungi and, independently, of fungally decayed wood inside dinosaurian coprolites from the Cretaceous of India and North America, respectively (Sharma et al., 2005; Chin, 2007). In another record, from the Jurassic of North America, transported pieces of wood bored according to patterns attributed to insects, that in turn displayed longitudinal cavities interpreted as fungal decay, were described as possibly reflecting tri-trophic interactions (Hasiotis, 2004). Co-occurrence of injured plant parts, coprolites and apparent fungal spores was also indicated as evidence of multiple biotic interactions from the Devonian of Canada (Banks and Colthart, 1993). Another possible example of multitrophic interactions is a Jurassic record from Germany of wood borings with signs of fungal decay and hyphae on the walls of the galleries (Müller-Stoll, 1936). Complex plant–fungal–arthropod interactions including epiphytes, endophytes, mites and other vascular plants have been described from the Permian of Germany (Barthel et al., 2010). A more recent example of the association between plants, arthropods and fungi consists of an insect/myriapod-bored fern stem with coprolites that are secondary colonized by fungi (D'Rozario et al., 2011). However, these records are almost anecdotal considering the scarcity of fossil evidence of possible biological interactions connecting more than two organisms (Taylor et al., 2009). In contrast, the fossils described here, from the Jurassic of Patagonia, consist of plant, fungal, and arthropod fossils physically associated with each other in a discrete microhabitat. This suggests that these organisms closely influenced each other during their life cycles. In addition, the fossil log containing the galleries and fungi-bearing coprolites appears degraded in patterns produced by extant wood-rotting fungi (Schmidt, 2006). This is interesting because anamorphic fungi associated with extant xylophagous insects include among their sexual counterparts wood-rotting fungi (Harrington, 2005; Schmidt, 2006), adding complexity similar to that observed in modern ecosystems to this Jurassic association.

Various characteristics of the larger galleries in the Jurassic wood from Patagonia are shared with galleries produced by extant beetles of the families Cerambycidae and Buprestidae (Solomon, 1995; Fierke et al., 2005). These traits include their transverse arrangement, location in the secondary xylem, variable to elongate outline, filling with frass, large dimensions, and notched borders in cross section. The nearly circular cross section of the fossil galleries is most similar to cerambycid borings (Solomon, 1995; Fierke et al., 2005). Furthermore, the high density and the resulting superposition of the bored tunnels resemble cerambycid entrance/exit holes in extant araucarian trees in Patagonia (Turienzo, 2006). The high density of frass inside the galleries is more characteristic of buprestid galleries, but it is possible that this reflects the effects of taphonomy and diagenesis. Moreover, high compaction of the frass inside the galleries is a feature previously attributed to cerambycids in Jurassic araucarian logs from Patagonia (Genise and Hazeldine, 1995).

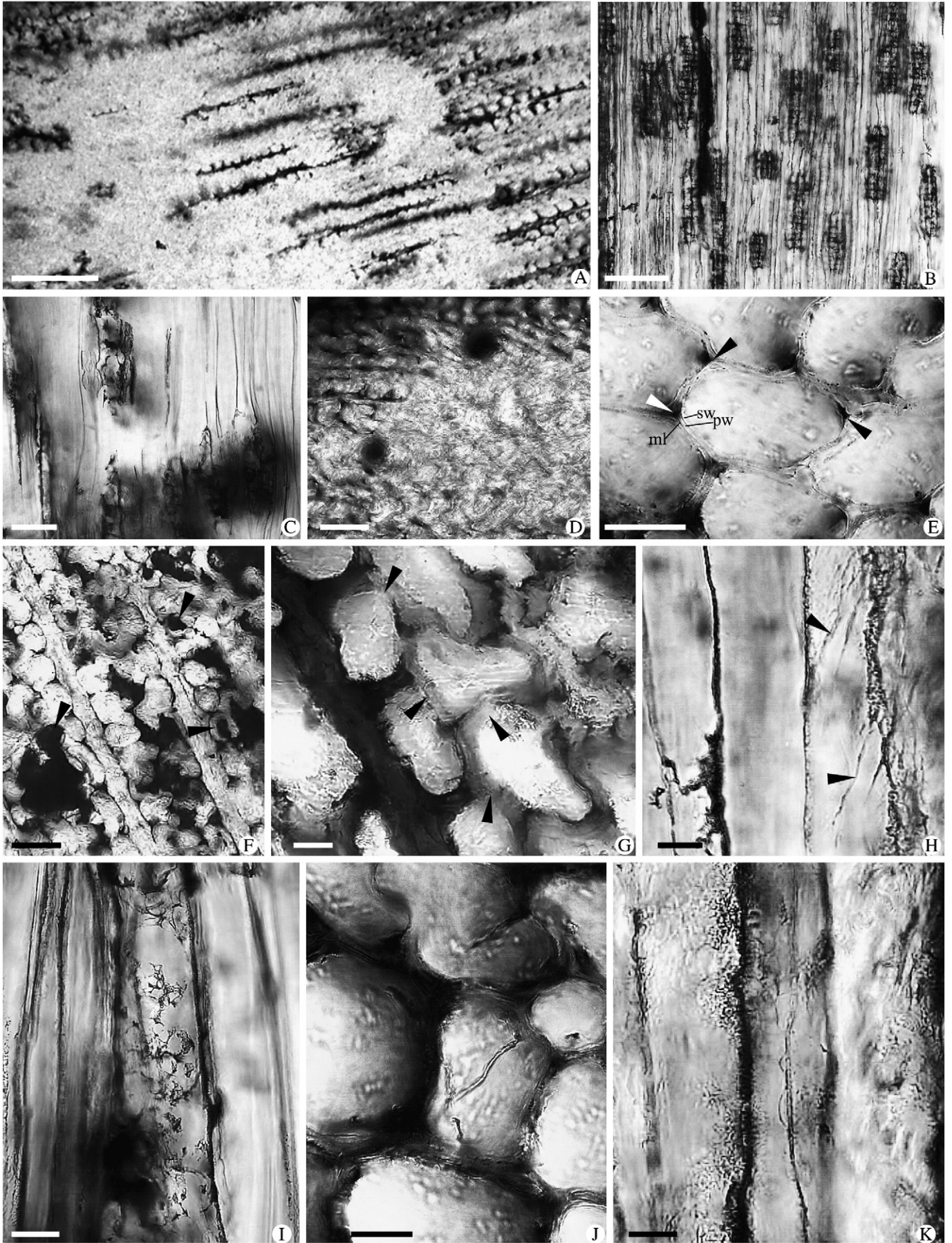
Additional features shared with the tunnels described by Genise and Hazeldine (1995) are the harshly cut borders of the galleries and the evidence of reworking of these into smaller components.

Those authors considered the reworking of the galleries into smaller components to be the result of cerambycid larvae boring through older galleries or the activity of parasites or inquilines. If the large and small galleries described here represent borings by different instars of the same organism, then the presence of frass and coprolites would indicate both foraging and nesting activities, as in extant cerambycids (Turienzo, 2006). However, the morphologically irregular secondary galleries containing coprolites are also similar to those produced by detritivorous microarthropods (Labandeira et al., 1997). Moreover, the variable orientation and dimensions of the smaller galleries do not indicate a determined path towards the exterior of the tree, as expected for beetle larvae emerging from previously bored entrance holes (Solomon, 1995; Fierke et al., 2005; Turienzo, 2006). We suggest that the secondary galleries were created by a detritivorous, microarthropod inquiline feeding on the fungus and the predigested plant material (frass) inside the galleries.

Various aspects of the coprolites inside the smaller galleries support the inference that these galleries are products of a collembolan or, more likely, a mite. About half of the coprolites fall within the upper range expected for mites and collembolans, whereas the others are larger and closer to the lower range for millipedes (Bal, 1970; Labandeira et al., 1997; Kellogg and Taylor, 2004). However, the commonly aligned arrangement of differently sized coprolites in continuous rows along the sides of the smaller galleries most likely reflects deposition by different instars of a single taxon (Bal, 1970; Feng et al., 2010). The commonly rough surface of the coprolites is seen in collembolan feces; however, as previously inferred for Mesozoic coprolites attributed to mites (Kellogg and Taylor, 2004), this pattern probably reflects decay by microorganisms, rather than the original texture of the coprolites. The presence of fungi on several of the coprolites, and the increasing degradation observed in the more densely colonized individuals, supports this assumption. Moreover, Kubienski (1955) and Sharma and Harsh (1989) reported extant and apparent fossil mite fecal pellets composed of identifiable plant remains and having a rough outer texture. The shape of the coprolites (spherical to ellipsoidal to cylindrical) coincides with that expected for both mites and collembolans with the variation attributable to diagenesis. Contents of the coprolites indicate a plant- and fungal-based diet consistent with either a mite or a collembolan origin (Grimaldi and Engel, 2005; Krantz and Walter, 2009). However, the apparent greater abundance of finely comminuted to less-chewed plant detritus over fungal remains might reflect a preference for cellulose- and lignin-rich vegetal tissues, as in most extant, detritivorous oribatid mites living in insect galleries in decomposing woods (Krantz and Walter, 2009).

The association of microfungi with collembolans and mites, in cavities in rotting wood, or as inclusions in their feces, is common in modern ecosystems (Visser et al., 1987; Abdel-Sater and Eraky, 2001; Ebermann and Hall, 2003; Renker et al., 2005). The fungi in these habitats represent opportunists or specialized symbionts (Kleipzig et al., 2001; Ebermann and Hall, 2003; Renker et al., 2005; Roets et al., 2007). A common outcome is predation of fungal propagules by fungi-eating arthropods (fungivory) and phoretic dispersal of fungal propagules (Afifi et al., 1989; Abdel-Sater and Eraky, 2001; Dromph, 2001; Ebermann and Hall, 2003; Renker et al., 2005).

Fig. 4. Degraded *Agathoxylon matildense* log from the Jurassic Monumento Natural Bosques Petrificados in Patagonia (Santa Cruz Province), Argentina. A. Transverse section of the bored *Agathoxylon matildense* log showing elongate to diffuse translucent degraded areas (transmitted light). Scale = 250 μ m. B. Tangential section of the bored *Agathoxylon matildense* log showing mottled pattern resulting from differentially degraded tissue. Scale = 250 μ m. C. Close up (tangential section) on translucent areas showing fibrous appearance and variously degraded tissue. Scale = 100 μ m. D. Close up (transverse section) of *Agathoxylon matildense* showing whitened and deformed differentially degraded cells. Scale = 100 μ m. E. Detail (transverse section) of *Agathoxylon matildense* showing cells with differentially decayed, lignin-rich, middle lamella (ml). Some cells shows partial decay of their middle lamellas (darker cell wall layer) and remain attached by their corners (arrowheads). Note preserved cell wall components arrangement towards the cell lumen: primary wall layer (pw) and secondary wall layers (sw). Scale = 25 μ m. F. Close up (transverse section) of *Agathoxylon matildense* showing variously decayed cells where no cell wall component has been differentially degraded. Note cells with their lumina filled with opaque contents (arrowhead). Scale = 100 μ m. G. Detail (transverse section) of undifferentially decayed cells. Arrowheads point to regions of the cell wall where all components have been synchronically degraded. Scale = 25 μ m. H. Close up (tangential section) on tracheids showing longitudinal erosion troughs (arrowheads). Scale = 25 μ m. I. Close up (tangential section) of *Agathoxylon matildense* showing variously decayed tracheids including skeletonized cells. Scale = 25 μ m. J. Close up (transverse section) of *Agathoxylon matildense* showing septate hyphae inside the lumen of a cell. Scale = 25 μ m. K. Close up (tangential section) of *Agathoxylon matildense* showing tracheids with septate hyphae connecting several cells with each other. Scale = 25 μ m.



It is difficult to evaluate how closely associated the fungus and the producer of the coprolites were in the araucarian wood from Patagonia. Predation on fungi can be inferred from the inclusion of hyphae and conidia in the coprolites and it is possible that the predator facilitated dispersal of the fungus. The clusters of unicellular conidia produced by the fossil fungus support the possibility that the coprolite producer played a role in dispersal of the fungus. A dispersal strategy of modern fungi is to produce clusters of sticky conidia which adhere to the body of their phoretic host (Harrington, 2005). Mites often play a role in the dispersal of the fungi preyed on, supporting this group as the producer of the coprolites (Hubert et al., 2003; Renker et al., 2005; Roets et al., 2007). However, fungivorous collembolans are commonly found with mites in the same microniches (Pherson and Beattie, 1979) and they cannot be disregarded as the producers of the coprolites.

Based on its morphology, the fossil fungus associated with the coprolites and smaller galleries can be classified within the Deuteromycota (Domsch et al., 2007). Deuteromycota groups extant fungi characterized by the exclusive formation of asexual reproductive structures (Kirk et al., 2008). In particular, based on the production of loose clusters of well-differentiated, hilate, polyblastic, 1-celled, spherical to ovoid, conidia from swollen conidiogenous cells in distinct, apically and irregularly branched, mononematous, conidiophores, the fossil fungus appears most similar morphologically to the genus *Botrytis* (Ellis, 1971, 1976; Barnett and Hunter, 1998; Domsch et al., 2007). Some differences, however, exist with *Botrytis*, including origin of conidia laterally from undifferentiated conidiophore cells and apparent clustered to catenulate arrangement of conidia (which may be the result of them being sticky). This latter feature, which results in the common agglomeration of conidia, suggests the presence of a sticky substance, making the patagonian fungus comparable to *Trichoderma*, although conidia arise from phyalidic cells in this latter genus and not from inflated-globose or undifferentiated cells as in the fossil (Ellis, 1971, 1976; Barnett and Hunter, 1998; Domsch et al., 2007). In addition, conidiophore branching is variable in the fossil, sometimes showing similarities also with other extant deuteromycetes (e.g., *Chrysosporium*) (Barnett and Hunter, 1998; Domsch et al., 2007). Other features of the fossil conidia (hyaline, psilate) and conidiophores (scabrate wall, basal swellings, denticle mark or a depression on conidiogenous and ampullae from where conidia dehisced) are also seen in a number of extant deuteromycetes (e.g., *Gonatobotrys/Gonatorhodiella*), but overall the combination of morphological features present makes the Jurassic fungus morphologically most similar to *Botrytis* (Barnett and Hunter, 1998; Kirk et al., 2008).

Occurrence of fossil *Botrytis* from Patagonia on degraded microarthropod coprolites and on walls of galleries reworked from larger, frass-filled borings is consistent with a saprotrophic habit. The fossil displays conidiophores with basal swellings that resemble appressoria or modified hyphal tips for infection of host tissue. Such features are seen in extant *Botrytis* and are common in both pathogens and mutualists (Ellis, 1971; Brundrett, 2002; Money, 2004; Domsch et al., 2007). This suggests the possibility of a facultative parasitic habit for the fossil fungus, much like *Botrytis* infections of *Araucaria* and other trees in modern forest ecosystems (Dingley, 1969; Butin and Peredo, 1986). Regardless, the direct association of the fungus with the mite-like coprolites and galleries is reminiscent of similar associations involving interactions between pathogenic *Botrytis* and mites in modern ecosystems (Hubert et al., 2003; Muñoz and Lucero, 2007).

The pattern of decay in the fossil araucarian log examined in this study suggests wood-rotting activity by ascomycetes and basidiomycetes as in modern ecosystems (Schmidt, 2006). The araucarian log from the Jurassic of Patagonia shows zones with indiscriminate decay of cellulose and lignin and others where only the latter is selectively degraded, which is consistent with white rot (Blanchette, 1984). The resulting spotty pattern of rot is seen in the fossil

araucarian log from Patagonia, indicating a mottle-rot decay, much like one of the products of white rotters on extant woody plants (Otjen and Blanchette, 1984; Blanchette, 1991). Differential and simultaneous decay, represented by tracheids still attached by their lignin-rich corners or completely lacking the middle lamella and zones devoid of cells, respectively, as well as intact areas, characterize the fossil log from Patagonia, supporting a white-rot fungus responsible for the patterns observed (Blanchette, 1991; Carlile et al., 2001; Schmidt, 2006). In addition, roughened tracheid walls of the fossil displaying variously broken walls and hyphal strands associated with longitudinal erosion troughs are like those made by white-rot fungi in woods in modern ecosystems (Blanchette, 1991; Carlile et al., 2001; Schmidt, 2006).

The presence of opaque substances inside the lumen of a number of cells within decayed zones of the fossil log suggests a host reaction possibly related to fungal activity on a living plant, such as happens between some white-rot fungi and conifers in modern ecosystems (Schmidt, 2006). In those instances, either phenolic substances and manganese oxides or ergastic material and resins accumulate inside cell lumina as a result of a parasitic interaction (Otjen and Blanchette, 1982, 1984; Agosin et al., 1990). However, a large surface area of the fossil log appears variously decayed (selectively and simultaneous decay, with galleries and fungi), which, together with the absence of other signs of host reaction suggests an advanced stage of decay of a fallen piece of wood rather than a branch of a living tree.

In modern ecosystems, fungally decayed wood appears to provide an ecological niche for xylophagous beetles, including cerambycids (Yee et al., 2006). In many instances these beetle–fungal associations result in positive interactions exemplified by exosymbiotic relationships, where the consumption of otherwise indigestible wood, pre-degraded fungally (lignin-free), by the beetle provides a means of dispersal among potential hosts for the fungus (Kukor and Martin, 1986; Kukor et al., 1988). Moreover, a number of the fungi-eating cerambycids have been indicated to be obligately dependent upon consumption of fungally degraded wood, through which they might acquire the enzymatic capability to degrade all cell wall components (including lignin) by themselves (Kukor and Martin, 1986; Kukor et al., 1988). In addition, larvae of cerambycids in fungally decayed wood have a faster growth rate than in sound wood (Martin, 1979). It is not known when such associations evolved, but it has been previously indicated that these were probably significant for the growth and development of cerambycids that feed on nutrient-limited sources (e.g., wood) (Yee et al., 2006; Geib et al., 2009). Through such associations beetles would have been able to gain access to essential nutrients in their hosts, bound by otherwise unsolvable structural and chemical barriers (Yee et al., 2006; Geib et al., 2009). The association of white-rot fungi and cerambycids has not been previously documented in the fossil record. However, based on the present evidence from the Jurassic of Patagonia showing galleries adjacent to and also probably bored into fungally decayed tissue, it seems reasonable to argue that such a kind of association, whether incidental or more specialized, was more common than yet recognized in ancient terrestrial ecosystems.

It is assumed that arthropod–fungi–plant interactions have been important since the early Mesozoic, when it is possible that fungi, conifers, mites and beetles coexisted on land (Grimaldi and Engel, 2005; Krantz and Walter, 2009; Taylor et al., 2009). The fossils from Patagonia described here represent the first direct evidence of close interaction among these groups in the fossil record. Xylophagy, fungivory, saprotrophism, possible parasitism and other more incidental interactions including phorism and inquilinism are apparent from the variety of fossils associated within the araucarian log we examined. These fossils provide evidence that, as in modern systems, mites relied on a fungal/plant diet and that they probably lived in association with borings made by wood-boring beetles, which may have

preferred fungally decayed wood. The fossil fungi present probably were opportunistic saprotrophs and possibly parasites that were transported among hosts by the arthropods associated with their microhabitat. In summary, the fungal–plant–arthropod interactions documented in this report provide a rare and unique glimpse on the ecological relationships and possible consequences between micro- and macro-components in forest stands during the Jurassic and a point of reference for modern studies on the food web structure and functional diversity in ancient terrestrial ecosystems.

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