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Araucariaceous fossil woods from the Upper Triassic Ischigualasto Formation (San Juan Province, Argentina): paleofloristic and paleoclimatic implications

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Abstract.—In this contribution, fossil woods from the Valle de La Luna Member of the Upper Triassic Ischigualasto Formation at Ischigualasto Provincial Park, San Juan Province, Argentina, are described. The specimens are preserved as silica permineralization in tuffs intercalated with carbonaceous mudstone beds interpreted as distal floodplain facies. The fossil woods were assigned to the new species *Agathoxylon argentinum* since their anatomy differs from the known Mesozoic Gondwanan species of the genus *Agathoxylon*. The combination of characters present in the new taxon indicates an affiliation with the conifer family Araucariaceae. Signals of fungal-mediated wood decay were observed, comparable to the activity of basidiomycetes. Spherical structures attached to the walls of the tracheids were recognized and are interpreted as holocarpic chytrid fungi. The growth rings were quantitatively analyzed. Low values of percentage diminution, percentage latewood, and Ring Markedness Index, and a mean percentage skew of +11.5, were obtained, suggesting that the new species was an evergreen gymnosperm. The stratigraphic distribution and taxonomic composition of the Ischigualasto Formation fossil-plant-bearing levels were studied. A vegetation change is recorded in the fossil level bearing *Agathoxylon argentinum* n. sp., marked by the replacement of the corystosperm genera and a diminution of arboreal corystosperms. This floristic change, in addition to other evidence, indicates humid paleoclimatic conditions for the uppermost part of the Valle de La Luna Member of the Ischigualasto Formation.

Introduction

During the Mesozoic, the conifer family Araucariaceae was distributed throughout the Northern and Southern Hemispheres (Stockey, 1982, 1994; Stockey and Ko, 1986; Hill, 1995; Del Fueyo and Archangelsky, 2002; Axsmith et al., 2008). Its fossil record is remarkably rich from the Lower Jurassic to the Upper Cretaceous, although Triassic occurrences are less common and often have doubtful affinities with the family (Stockey, 1982; Dettmann et al., 2012; Rothwell et al., 2012). Fossil woods similar to Araucariaceae (i.e., isolated pieces of secondary xylem with araucarian tracheid radial pitting and araucarioid cross fields, together with mostly uniseriate rays) have been given mainly three generic names, *Araucarioxylon* Kraus, 1870, *Dadoxylon* Endlicher, 1847, and *Agathoxylon* Hartig, 1848 (Rößler et al., 2014). The generalized characters shared by these genera could correspond to other gymnosperm groups besides Araucariaceae. Although the Triassic fossil record of South America comprises several fossil woods similar to Araucariaceae, their affinities with the family have been questioned because of the absence of other araucariacean macrofossils (e.g., leafy twigs, cones) in the same strata (Panti et al., 2012).

Southern South American Triassic basins are narrow and elongated depressions oriented northwest–southeast and filled by continental sedimentation in Argentina and marine to transitional in Chile (e.g., Charrier, 1979; Spalletti et al., 2003). The Ischigualasto-Villa Unión Basin, located in west-central Argentina (Fig. 1), has one of the most extended and complete continental Triassic sections in the world (Colombi and Parrish, 2008). The Upper Triassic Ischigualasto Formation is one of the upper units of this basin and comprises fluvial sandstone, mudstone, and paleosols (Milana and Alcober, 1994). This formation is known worldwide for its diverse and exceptionally well-preserved vertebrate assemblage (e.g., Rogers et al., 1993; Martínez et al., 2011, 2013). However, the paleobotanical studies have not received the same attention, and during recent decades published contributions have been scarce.

In this work, we describe permineralized araucariaceous woods from the Ischigualasto Provincial Park (San Juan, Argentina), discuss their systematic position, and report the results of a

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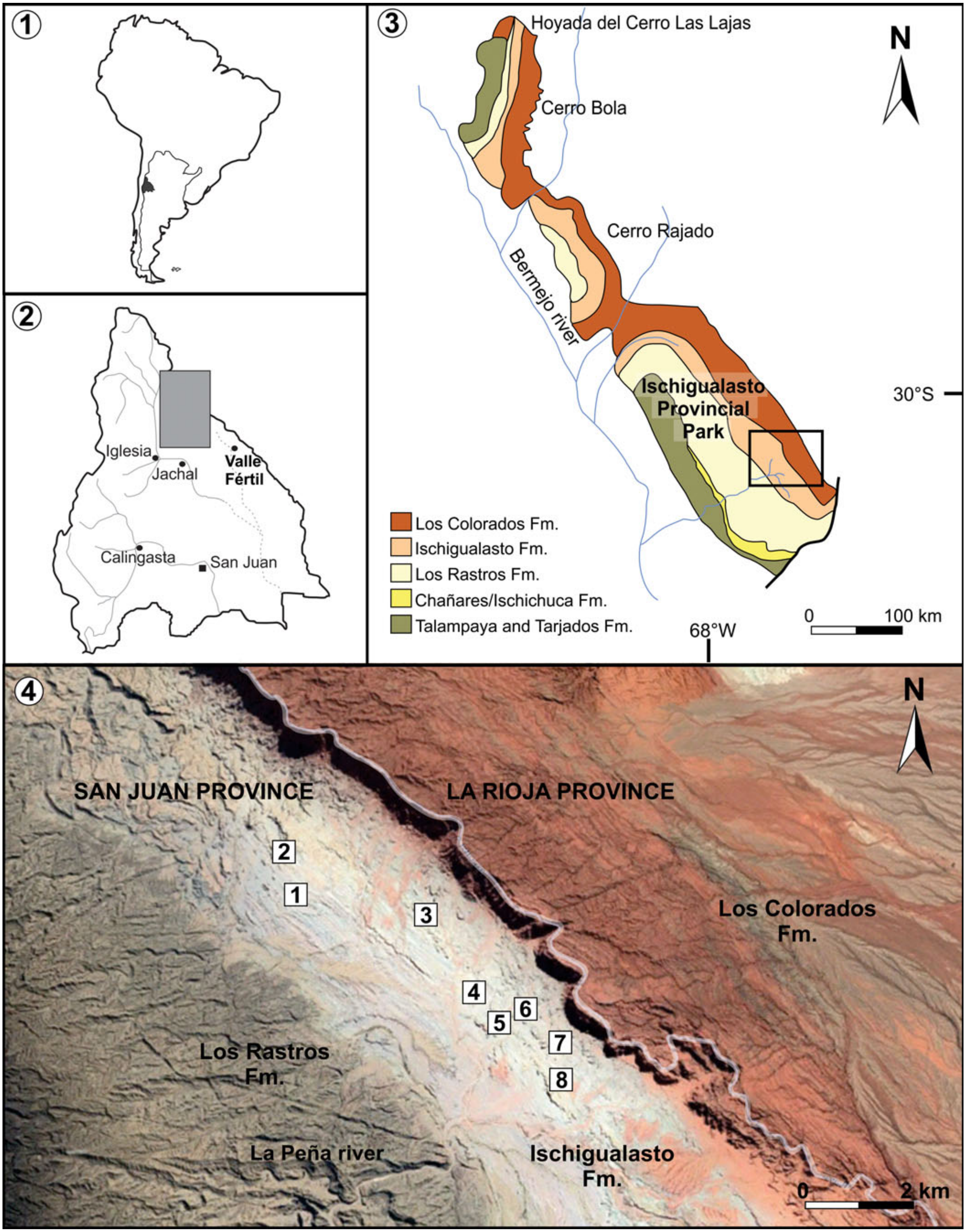

Figure 1. (**1**) Geographic location of the San Juan Province, at South America and Argentina. (**2**) Geographic location of the Ischigualasto-Villa Unión Basin at San Juan Province. (**3**) Geological map of the Ischigualasto-Villa Unión Basin, with the location of the studied area at the Ischigualasto Provincial Park. (**4**) Outcrops of the Ischigualasto Provincial Park showing the localities with PFLs (1–8). Modified from Colombi et al. (2021). Satellite image taken from Google Earth.

growth-ring analysis. The stratigraphic distribution and taxonomic composition of the plant-fossil-bearing levels (PFLs) were studied to analyze the paleofloristic changes along the Ischigualasto Formation. Furthermore, structures related to the degradation of wood are interpreted and characterized. Finally, the paleoclimatic implications of these findings are evaluated.

Geological setting

The Ischigualasto-Villa Unión Basin is located between ∼29°S and ∼31°S in northeastern San Juan and southwestern La Rioja provinces, Argentina (Golonka, 2007; Césari and Colombi, 2016; Fig. 1). This basin corresponds to an extensional half-graben, part of a series of Triassic basins that developed parallel to and cratonward of the proto-Andean arc (Uliana et al., 1988; Ramos and Kay, 1991; López-Gamundí et al., 1994). The filling of the Ischigualasto-Villa Unión Basin began during the late Permian and continued until the Late Triassic and is represented by a 2,500 to >4,000 m thick succession of continental deposits subdivided into a lower red alluvial package of the Talampaya and Tarjados formations and the overlying Agua de la Peña Group (Melchor, 2007; Gulbranson et al., 2015; Césari and Colombi, 2016). The Agua de la Peña Group comprises, from base to top, the Chañares, Ischichuca, Los Rastros, Ischigualasto, and Los Colorados formations.

The thickness of the Ischigualasto Formation varies between 300 m and 700 m (Currie et al., 2009); nevertheless, the lack of intraformational unconformities indicates that deposition was relatively continuous (Milana and Alcober, 1994). The formation includes deposits of fluvial channels characterized by massive and trough cross-stratified sandstones and conglomerates intercalated with finer-grained proximal and distal floodplain facies, mainly sandstones and mudstones (Colombi and Parrish, 2008; Currie et al., 2009; Césari and Colombi, 2016; Fig. 2.1). The proximal floodplain deposits are composed of fine-grained sandstones and mudstones with horizontal and ripple lamination and are frequently disturbed by paleosol development; the distal floodplain facies consist of massive or finely laminated siltstones and mudstones that are always overprinted by mature paleosol development (Césari and Colombi, 2016). At the base of the formation there are many ash layers and a basalt (Colombi and Parrish, 2008). The Ischigualasto Formation was subdivided into four members (Fig. 2.1), from base to top: La Peña, Cancha de Bochas, Valle de la Luna, and Quebrada de la Sal. These subdivisions are based on variations in the sedimentary architecture and paleosol development (Currie et al., 2009).

The Ischigualasto Formation is Carnian to Norian (231.4 to 225.9 Ma) according to radioisotopic information (Rogers et al., 1993; Martínez et al., 2011). The Carnian Pluvial Event, also known as Carnian Humid Episode (Ruffell et al., 2016), was recognized in the underlying Los Rastros Formation at 234.47 ± 0.44 Ma (Dal Corso et al., 2020; Mancuso et al., 2020). The Carnian Pluvial Event was linked to a major extinction event and might have been the trigger to major diversifications and originations of conifers, insects, dinosaurs, crocodiles, lizards, turtles, and mammals on land (Dal Corso et al., 2020). The appearance and rapid diversification of dinosaurs in the overlying Ischigualasto Formation represent a major biotic event recorded in the basin (Martínez et al., 2011, 2012), corresponding with the Dinosaur Diversification Event (Benton et al., 2018). Martínez et al. (2011, 2012) characterized vertebrate biozones and recognized a crucial turnover between the *Hyperodapedon–Exaeretodon–Herrerasaurus* (HEH) and the *Exaeretodon* (E) biozones after the Carnian Pluvial Event and before the End-Triassic Extinction. Concerning the Ischigualasto Formation plant assemblages, including impressions, cuticles, and permineralized trunks, they were referred to as the BNP Biozone (*Yabeiella brackebuschiana/Scytophyllum neuburgianum/Rhexoxylon piatnitzkyi*; Spalletti et al., 1999) assigned to the Carnian (Morel et al., 2003).

Paleobotanical background

The first paleobotanical contribution about Ischigualasto Formation was made by Bodenbender (1911), who indicated the presence of fossil leaves assigned to *Thinnfeldia*, *Cladophlebis mesozoica* (Kurtz) Frenguelli, 1947, and *Podozamites elongatus* (Morris) Feistmantel, 1889 and "*Araucarites*" fossil trunks. Afterward, Frenguelli (1948) published the first detailed study on the stratigraphy, paleontology, and correlation of the Triassic succession that crops out at Ischigualasto Provincial Park. This author presented a list of fossil plants, mentioning the following taxa for the Ischigualasto Formation: *Neocalamites carrerei* (Zeiller) Halle, 1908, *Dicroidium lancifolium* (Morris) Gothan, 1912, *D. odontopteroides* (Morris) Gothan, 1912, *Desmiophyllum* sp. (=*Heidiphyllum elongatum* (Morris) Retallack, 1981), and "*Araucarites*" fossil trunks.

In the 1960s, the paleobotanical studies were resumed by Archangelsky (1960, 1968), Archangelsky and Brett (1961, 1963), Bonetti (1966), and Brett (1968), focusing on permineralized trunks and leaf cuticles. Their investigations described new species of great systematic, paleophytogeographic, and biostratigraphic importance (i.e., *Rhexoxylon piatnitzkyi* Archangelsky and Brett, 1961 emend. Brett, 1968 [corystosperm], *Michelilloa waltonii* Archangelsky and Brett, 1963 [cycad], and *Protojuniperoxylon ischigualastense* Bonetti, 1966 emend. Bodnar and Artabe, 2007 [conifer]) and proposed for the first time that the *Dicroidium* leaves and *Rhexoxylon* stems corresponded to the same plant. Petriella (1978) followed this idea in his whole-plant reconstruction of the tree corystosperm dominant in the Ischigualasto Formation. Baldoni (1980) studied leaves with preserved cuticles from that unit and confirmed the occurrence of the corystosperm species *Xylopteris argentina* (Kurtz) Frenguelli, 1943 and *X. elongata* (Carruthers) Frenguelli, 1943.

In addition to the megafloras, the palynofloras of the Ischigualasto-Villa Unión Basin have been studied since the 1970s. Herbst (1970, 1971) stated that in the Ischigualasto Provincial Park area, well-preserved palynomorphs occur only in the Los Rastros Formation. However, in the Cerro Bola area at La Rioja Province, Yrigoyen and Stover (1970) recognized a palynological assemblage at the base of the Ischigualasto Formation composed of trilete spores and bisaccate, monosulcate pollen grains. In the same stratigraphic level, these authors identified poorly preserved impressions of *Podozamites*, *Yabeiella*, *Pterophyllum*, and *Phyllotheca*. From this information,

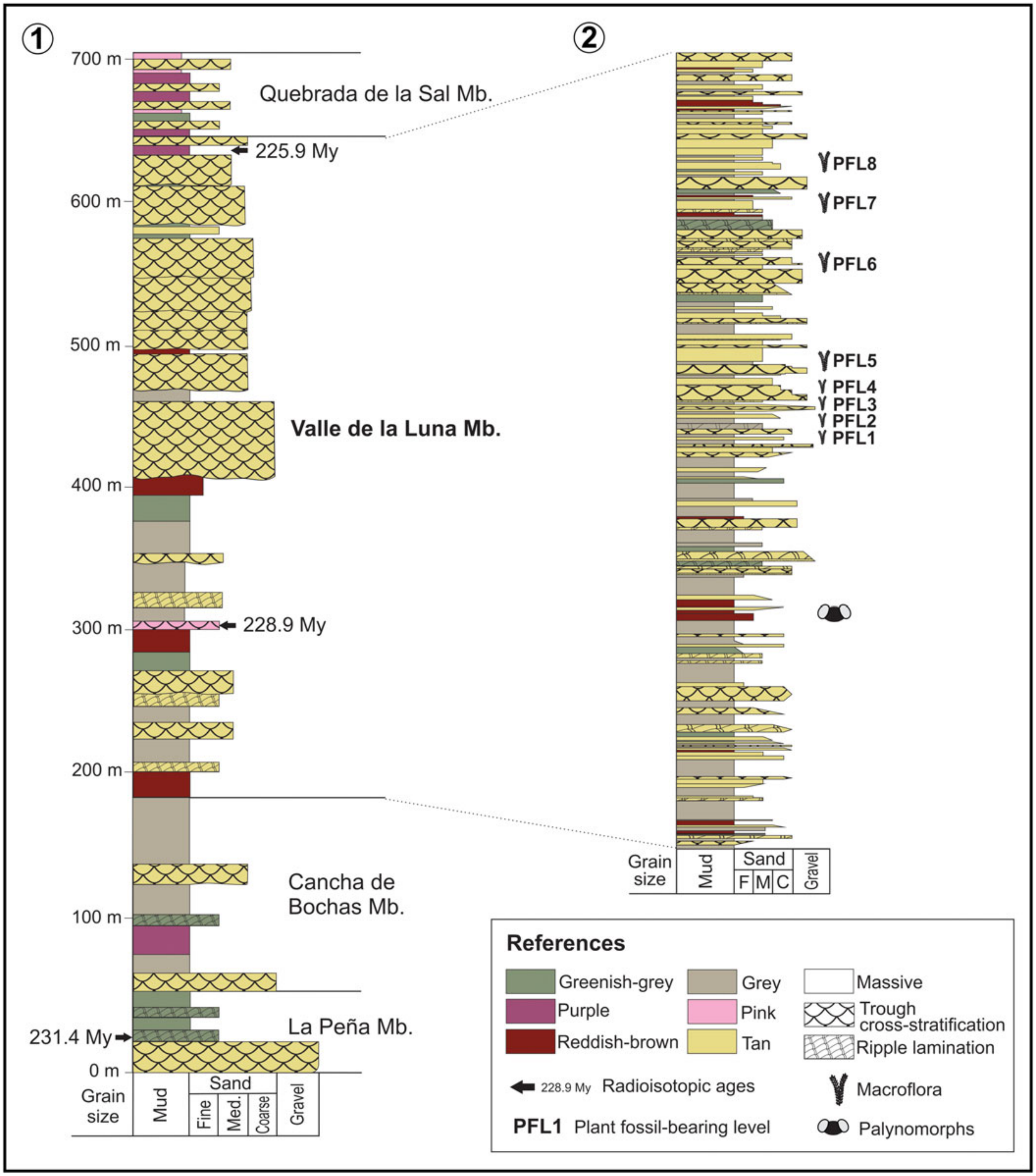

Figure 2. (**1**) General sedimentological section of the Ischigualasto Formation. (**2**) Detailed sedimentological section of the Valle de La Luna Member showing the stratigraphic position of the PFLs. Modified from Currie et al. (2009).

Yrigoyen and Stover (1970) correlated the lower section of the Ischigualasto Formation with the Quebrada de la Mina Formation and the upper section with the Carrizal Formation; both units crop out at the Marayes-El Carrizal Basin located at the southeast of Ischigualasto-Villa Unión Basin.

Zamuner (1992) completed a doctoral thesis on a paleofloristic assemblage from the Ischigualasto Formation at Ischigualasto Provincial Park, in which she analyzed in detail the anatomy and development of *Rhexoxylon piatnitzky* trunks and rhizomes, peltasperm leaves with preserved cuticles (*Lepidopteris*

Table 1. Megafossil plant content of the eight PFLs recognized in the Ischigualasto Formation at the Ischigualasto Provincial Park, San Juan Argentina. Information taken from Frenguelli (1948) Archangelsky (1968), Brett (1968), Zamuner (1992), and Zamuner et al. (2001). *The informal name of each plant group precedes the formal names of orders and families in brackets.

Taxon*	PFL1	PFL2	PFL3	PFL4	PFL5	PFL6	PFL7	PFL8
Sphenophytes (Equisetales, Neocalamitaceae)								
1. *Neocalamites carrerei* (stems)					x			x
Corystosperms (Umkomasiales, Umkomasiaceae)								
2. *Dicroidium lancifolium* (leaves)								x
3. *Dicroidium odontopteroides* (leaves)								x
4. *Johnstonia coriacea* (Johnston) Walkom, 1925 (leaves)		x		x				
5. *Xylopteris elongata* (leaves)		x		x			x	
6. *Zuberia papillata* (Townrow) Artabe, 1990 (leaves)				x				
7. *Zuberia zuberi* (Szajnocha) Frenguelli, 1943 (leaves)	x	x	x	x			x	
8. *Rhexoxylon piatnitzkyi* (stems)			x	x		x	x	
Peltasperms (Peltaspermales, Peltaspermaceae)								
9. *Scytophyllum neuburgianum* (leaves)		x						
10. *Lepidopteris stormbergensis* (leaves)			x	x				
Cycads (Cycadales)								
11. *Michelilloa waltonii* (stems)						x		
Conifers (Voltziales, Voltziaceae)								
12. *Heidiphyllum elongatum* (leaves)								x
Conifers (Pinales, Cupressaceae)								
13. *Protojuniperoxylon ischigualastense* (wood)				x		x	x	
Conifers (Pinales, Araucariaceae)								
14. *Agathoxylon argentinum* n. sp. (wood)								x

stormbergensis (Seward) Townrow, 1956 and *Scytophyllum neuburgianum* Dobruskina, 1969), and conifer wood assigned to a new species of *Araucarioxylon*. However, only the studies on *Scytophyllum neuburgianum* were published (Zamuner and Artabe, 1990), while the other results remain unpublished. Later, Zamuner et al. (2001) and Artabe et al. (2001) summarized the paleobotanical content and interpreted the preserved paleocommunities of the Ischigualasto Formation, respectively. Bodnar and Artabe (2007) revised the anatomy of the fossil wood *Protojuniperoxylon ischigualastense* and analyzed the growth rings, inferring that the species was an evergreen cupressaceous conifer.

Subsequent contributions included taphonomic, paleobiogeographic, and paleoclimatic analyses. The taphonomic characterization of the Ischigualasto Formation paleoflora was carried out by Colombi and Parrish (2008), who defined nine preservation styles (including root impressions, silicified trunks and stumps, cuticles, and palynomorphs) and seven taphofacies. Césari and Colombi (2013, 2016) reported the first Argentinian occurrence of a rich palynofloral assemblage with European Tethys and Northwestern Australia characteristic species (Onslow Microflora) and a dominance of species indicative of humid climatic conditions. Later, Pérez Loinaze et al. (2018) conducted a cluster analysis of palynological assemblages from Gondwana (including the Chañares, Ischigualasto, and Los Rastros formations), which recovered the Ischigualasto Formation palynoflora as transitional between Ipswich and Onslow subprovinces (Pérez Loinaze et al., 2018). The authors inferred a warm climatic belt that resulted in mixed Onslow–Ipswich microfloras for the Chañares and Ischigualasto formations, while the Los Rastros Formation would correspond to a pure Ipswich microflora of cooler and wetter conditions (Pérez Loinaze et al., 2018).

Materials and methods

Locality information.—The four fossil samples studied herein come from the Ischigualasto Provincial Park, San Juan Province, located between 29°56′6″S, 68°10′17″W and 30°12′34″S, 67°49′53″W (Fig. 1). The specimens come from the Valle de La Luna Member, which consists of 250–470 m of mudstone and sandstone. Distal floodplain facies including abandoned channel and swamp deposits are characterized by laminated mudstone deposits intercalated with abundant seams of compressed plant cuticles and abundant palynomorphs (Colombi and Parrish, 2008; Currie et al., 2009; Césari and Colombi, 2013). At Ischigualasto Provincial Park, Brett (1968) and Zamuner (1992) recognized eight localities where fossil plants are abundant. These correspond to different PFLs and were numbered from 1 to 8 according to their stratigraphic position (Fig. 1, Fig. 2.2, Table 1). Following the current stratigraphic scheme, all these levels are located in the top two-thirds of the Valle de La Luna Member of the Ischigualasto Formation. Both lower levels, PFL1 and PFL2, consist of compact layers of black plant compressions with preserved cuticles in a sandstone matrix. The PFLs 3 to 7 correspond to medium to coarse-grained sandstones and gray mudstones, where compressions with cuticles and permineralizations are preserved. The PFL 4 exhibits many large permineralized trunks, while in PFLs 3, 6, and 7, this type of fossil is less abundant. Most of the large permineralized trunks correspond to the corystosperm *Rhexoxylon piatnitzkyi* and usually consist of the basal part or stump. In PFLs 4, 6, and 7, conifer woods of the species *Protojuniperoxylon ischigualastense* were found. In PFL 6, together with the large *Rhexoxylon piatnitzkyi* specimens, a juvenile stem of the same species and fragments of cycad *Michelilloa waltonii* stems occur. At PFL 8, carbonaceous mudstones are intercalated with tuff beds in which silicified trunks, including those described here, occur in vertical position along with abundant compressions of *Neocalamites carrerei* and rare impressions of *Dicroidium odontopteroides*, *D. lancifolium*, and *Desmiophyllum* sp. (=*Heidiphyllum elongatum*) (Frenguelli, 1948).

Fossil study.—Four fragments of permineralized wood from trunks preserved in vertical position with respect to the strata

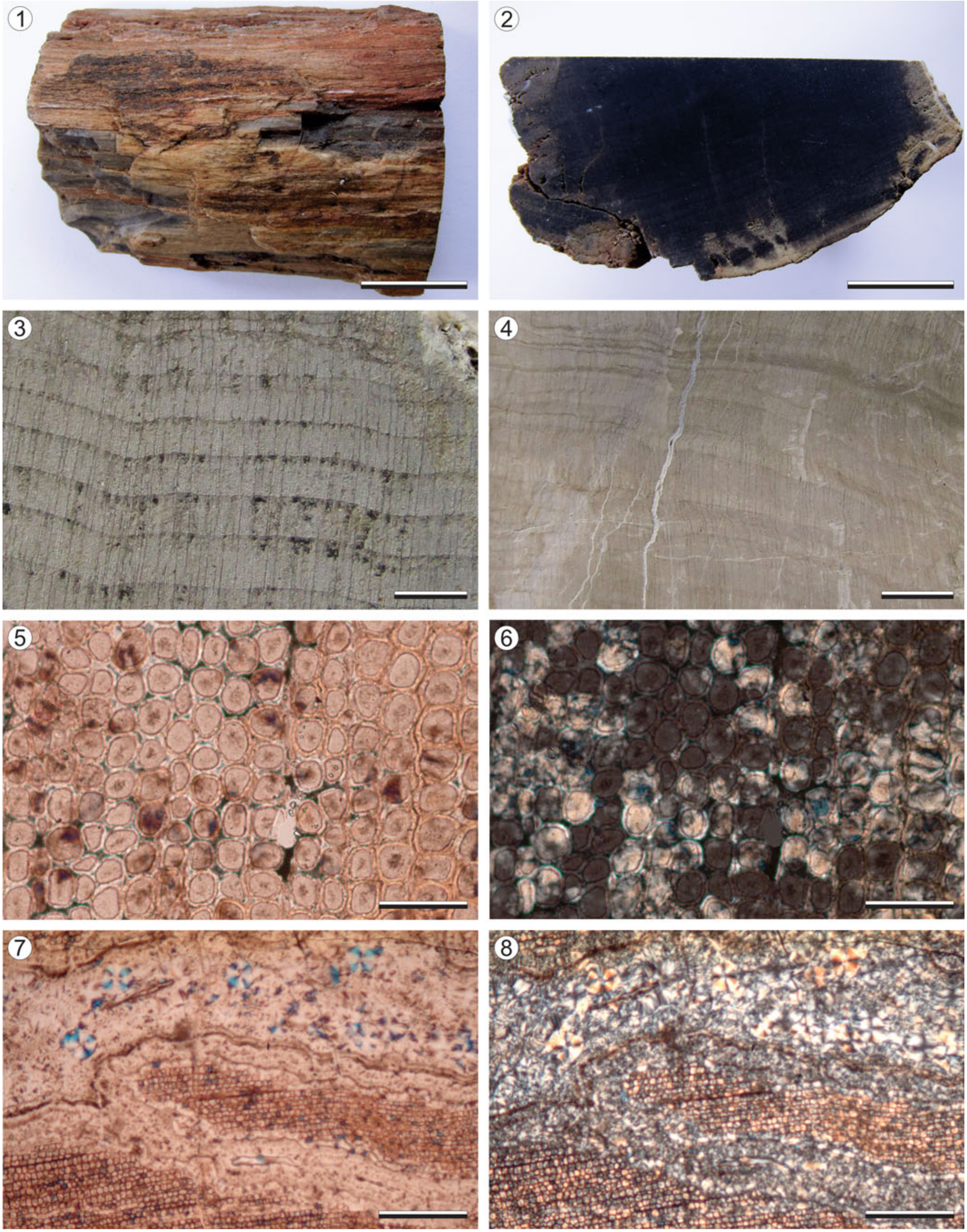
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Figure 3. *Agathoxylon argentinum* n. sp. (**1, 2**) General view of the silicified wood, paratype LPPB 495. (**3, 4**) Surface view of growth rings in transverse section; (**3**) paratype LPPB 495; (**4**) holotype LPPB 492. (**5, 6**) Tracheids in transverse section showing the form of silicification; (**5**) under plane polarized light; (**6**) under crossed nicol, paratype LPpm 1375. (**7, 8**) Transverse section of the secondary xylem showing a crack filled with amorphous silica and microcrystalline quartz; (**7**) under plane polarized light; (**8**) under crossed nicol, holotype LPpm 1367. (**1, 2**) Scale bars = 20 mm; (**3**) scale bar = 2 mm; (**4**) scale bar = 5 mm; (**5, 6**) scale bars = 100 µm; (**7, 8**) scale bars = 500 µm.

(probably in living position) were collected by Joaquín Frenguelli on field trips made during the 1940s. Zamuner (1992) studied one of the specimens. All samples are preserved by silica cellular permineralization, with excellent preservation (Fig. 3); only one shows evidence of diagenetic deformation. Although the amorphous form of silica is dominant (Fig. 3.5, 3.6), small quartz crystals occur inside fossil cracks (Fig. 3.7, 3.8).

Thin sections (transverse, longitudinal tangential, and longitudinal radial) obtained from the cellulose-acetate peel and polished surface techniques by Frenguelli (1948) and Zamuner (1992) were studied. Furthermore, new microscopic slides were prepared by polished surface technique. The thin sections were studied under a Leica DM2500 light microscope and photographed with a Leica DMC2900 camera mounted on the microscope. Furthermore, the minerals were observed and photographed under polarized light with the same microscope. Small fragments were observed, mostly in longitudinal radial view, under JEOL JSM6360 LV scanning electron microscope, with low vacuum, at the electronic microscopy service of the Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata. Wood anatomic sections of extant species *Araucaria araucana* (Molina) K. Koch, 1869, *A. angustifolia* (Bertoloni) Kuntze, 1898, and *A. cunninghamii* Aiton ex D. Don in Lambert, 1837 were also observed under transmitted light microscope for comparison.

A minimum of 30 measurements of each anatomical character were made using a ruler installed in the light microscope. The measurements are expressed as the mean followed by the range between parentheses and correspond to the type specimens (holotype and paratype). We calculated percentages of tracheid radial pitting types using the method of Philippe et al. (2014). The description followed the wood anatomy terminology of IAWA Committee (2004) and the template for the description of fossil tracheidoxyls (Boura et al., 2021). For the nomenclatural and systematic treatment, the International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code, Turland et al., 2018) was used, and the classification criterion of Philippe and Bamford (2008) was followed.

The growth rings of the fossil wood were quantitatively analyzed through the method of Falcon-Lang (2000a, b). This method uses the term "ring boundary" to describe the discontinuity between the latewood cells of one ring and the earlywood cells of the following ring, and the term "ring increment" to describe the region between two adjacent ring boundaries. The radial diameters of successive tracheid cells were measured across each ring increment; five adjacent rows of tracheids were measured for each ring increment, and their values were averaged to obtain the final estimate. Using these averages, the cumulative algebraic sum of each cell's deviation from the mean of the tracheid radial diameters was calculated and plotted as a zero-trending curve (CSDM curve; after Creber and Chaloner, 1984). For each ring increment, the percentage skew of the zenith of the CSDM curve with respect to the center of the graph was calculated (Falcon-Lang, 2000a, b). The percentage diminution (x) in a ring increment was obtained using the following formula: $x = (b/a) \times 100$, where a = maximum cell diameter, and b = maximum cell diameter minus minimum cell diameter. The percentage latewood (y) in each ring increment was calculated using the Creber and Chaloner (1984) method: $(y) = (d/c) \times 100$, where d = number of cells after the CSDM curve turns to zero for the last time, and c = number of cells in each ring increment. The product of these two parameters $(x \times y/100)$ provides the Ring Markedness Index (RMI) (Falcon-Lang, 2000a). Only ring increments derived from mature stems (as indicated by the fact that the growth ring boundaries were nearly straight in transverse section) and formed by continuous uniform growth were included in this study (Falcon-Lang, 2000a, b).

Repositories and institutional abbreviations.—The four fossil specimens examined in this study are deposited in the collection of the División Paleobotánica of the Museo de La Plata, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Buenos Aires Province, Argentina, under the acronyms LPPB and LPpm (microscopic slides). The wood sections of extant species analyzed are housed at the didactic xylotheque of the Cátedra de Xilología, also of the Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata.

Systematic paleontology

Order Pinales (=Coniferales) Gorozhankin, 1904
Family Araucariaceae Henkel and Hochstetter, 1865
Genus *Agathoxylon* Hartig, 1848 sensu Philippe, 1995

Type species.—*Agathoxylon cordaianum* Hartig, 1848, p. 188, by simultaneous publication of a single species name. Triassic, Coburg, Germany.

Agathoxylon argentinum new species
Figures 3–6

1992 *Araucarioxylon argentinum* Zamuner, p. 57, pl. 24, figs. 1–7.
1999 *Araucarioxylon argentinum*; Kokogian et al., p. 395.
1999 *Araucarioxylon argentinum*; Spalletti et al., p. 448.
2001 *Araucarioxylon* sp. A, Zamuner et al., p. 184.
2001 *Araucarioxylon* sp. A, Morel et al., p. 238.
2007 *Araucarioxylon* sp. A, Artabe et al., p. 82.
2016 *Araucarioxylon* sp., Césari and Colombi, p. 380.

Holotype.—LPPB 492 (microscopic slides LPpm 1178–1183, 1365–1373).

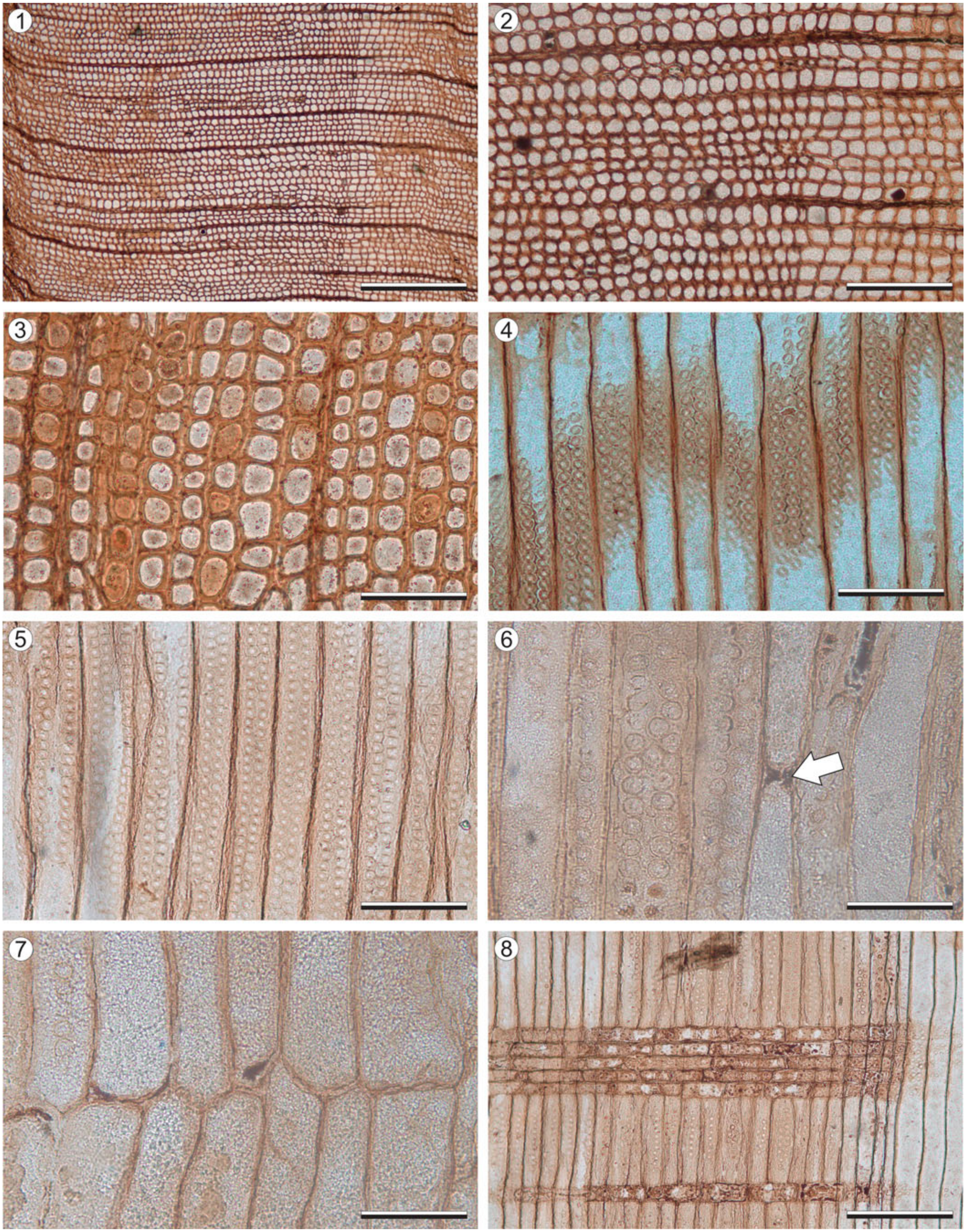
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Figure 4. *Agathoxylon argentinum* n. sp. (**1**) General view of the transverse section of the secondary xylem, holotype LPpm 1367. (**2**) Detail of the growth-ring boundary in transverse section, holotype LPpm 1367. (**3**) Detail of transverse section of tracheids, paratype LPpm 1375. (**4, 5**) Tracheid radial pitting, with uniseriate to triseriate, contiguous to compressed and alternating pattern; (**4**) holotype LPpm 1370; (**5**) paratype LPpm 1376. (**6**) Detail of the tracheid radial pitting and the resin plate in a tracheid (arrow), holotype LPpm 1180. (**7**) Detail of tracheids with truncate terminal walls, holotype LPpm 1181. (**8**) General view of radial section of the secondary xylem, paratype LPpm 1376. (**1**) Scale bar = 650 µm; (**2**) scale bar = 250 µm; (**3–5**) scale bars = 120 µm; (**6**) scale bar = 60 µm; (**7**) scale bar = 70 µm; (**8**) scale bar = 200 µm.

Paratype.—LPPB 495 (microscopic slides LPpm 1374–1377).

Diagnosis.—Tracheidoxyl with slightly distinct to distinct growth rings, with gradual transition from earlywood to latewood. Tracheid pitting in radial walls distinctly bordered, uniseriate to triseriate, with contiguous or compressed and alternating arrangement, very rarely with spaced and subopposite arrangement. Tracheid pitting in tangential walls absent. Frequent resin plates in tracheids. Axial parenchyma absent. Cross fields of araucarioid type, with 2–9 oculipores per field. Homocellular and homogeneous rays, mainly uniseriate, occasionally biseriate in part, medium to high.

Occurrence.—Ischigualasto Provincial Park, Ischigualasto-Villa Unión Basin, San Juan Province, Argentina; PFL 8, Valle de la Luna Member, Ischigualasto Formation, Agua de la Peña Group, Upper Triassic (Carnian-Norian)

Description.—The studied samples correspond to wood fragments 6–8 cm in diameter with only secondary xylem preserved (Fig. 3.1–3.4). The secondary xylem is homoxylic and pycnoxylic. Growth rings are slightly distinct to distinct, with a gradual reduction of the radial diameter of tracheids toward the ring's outer margin (Fig. 4.1, 4.2). Growth-ring thickness varies from 11 to 81 cells. Secondary xylem tracheids are circular or polygonal (quadrangular to rectangular) in transverse section (Figs. 3.5, 4.1–4.3). The radial diameter of earlywood tracheids is 41.30 (25.61–66.97) µm, and the tangential diameter is 44.30 (27.80–57.35) µm. The earlywood tracheids are thin walled, with a double-wall thickness of 7.25 (3.79–9.54) µm and a radial lumen diameter of 38.47 (21.51–59.17) µm. The radial diameter of latewood tracheids is 22.95 (14.70–29.09) µm, and the tangential diameter of tracheids is 37.97 (26.06–47.20) µm. The latewood tracheids are thin walled, with a double-wall thickness less than 7.37 (4.77–11.06) µm and a radial lumen diameter of 17.87 (9.01–27.83) µm. The number of rows of tracheids between rays is 7 (2–19) (Fig. 4.1–4.3).

Tracheids with bordered pits on radial walls. The pits are uniseriate (27.43%), biseriate (63.28%), and triseriate (9.29%) in the earlywood and exclusively uniseriate in the latewood (Figs. 4.4–4.6, 4.8, 6.1–6.3). Pits in the earlywood have a compressed or contiguous arrangement for the most part (98.23%) and, very rarely, a spaced arrangement (1.77%) (Figs. 4.4–4.6, 4.8, 6.1–6.3). In the latewood, tracheid pits have mainly a compressed or contiguous arrangement (79.17%) and, less frequently, a spaced arrangement (20.83%). Because of fossilization, some contiguous pits may appear spaced ("steinkern" preservation sensu Gothan, 1905). When biseriate or triseriate, pits are mainly alternating (92.07%), rarely subopposite (7.93%) (Figs. 4.4–4.6, 4.8, 6.1–6.3). This pattern belongs to the araucarian type of radial pitting sensu Philippe and Bamford (2008). Uniseriate pits are circular to flattened while biseriate and triseriate pits are circular to hexagonal; in all cases, they show circular apertures. Pits measure 12.98 (9.96–16.16) µm high and 16.26 (12.05–19.740) µm wide. Tracheids lack helical thickenings. Resin plates in tracheids are frequent (Figs. 4.6, 5.5, 5.6). Some tracheids have truncate terminal walls (Fig. 4.7). Spiral fissures, with a spiral angle of about 45° (Figs. 5.6, 6.6), were observed in some tracheids, which could be compression wood.

Cross fields have 2–9 oculipores with an oval outline, placed in one or two opposite to alternating vertical rows, contiguous (Figs. 4.8, 5.1, 5.2, 5.3, 6.4). They measure 6.60 (3.63–10.49) µm in minor diameter and 9.26 µm (5.81 µm–14.51 µm) in major diameter. Pit aperture is horizontal or oblique. Individual pits are of cupressoid type sensu Boura et al. (2021). Cross fields correspond to the araucarioid type sensu Boura et al. (2021). As in tracheid pits, some contiguous cross-field pits may appear spaced due to steinkern preservation.

Rays are homocellular and homogeneous with rectilinear trajectory in transverse section, mainly uniseriate (92.77%), occasionally biseriate in part (7.23%), and medium to high, 6 (1–27) cells high (Figs. 5.4–5.6, 6.5). They are composed of procumbent parenchyma cells, 29.68 (18.16 –42.03) µm high and 131.44 (54.25–193.95) µm long (Figs. 4.8, 5.1). Horizontal and end walls of the parenchyma cells are thin, smooth, and straight. The end walls are vertical or in a few cases oblique (Figs. 4.8, 5.1, 5.3). Resin contents are present in ray cells (Fig. 4.8). Axial parenchyma and ray tracheids are absent.

Leaf traces can be recognized. They have a rhomboid outline in tangential view (Fig. 5.7, 5.8). Around the trace, tracheids and xylem rays are curved (Fig. 5.7). The leaf trace consists of parenchyma cells, many of which have resin contents, and tracheids with reticulate thickenings (Fig. 5.9). In the center of the trace, several cells are completely degraded (Fig. 5.7–5.9).

Etymology.—The specific name refers to the country where the specimens were collected. This name was chosen by Zamuner (1992) when she preliminarily described this species.

Materials.—LPPB 499 (microscopic slides LPpm 1378–1380), LPPB 503 (LPpm 1381–1382).

Remarks.—Fossil woods with the characters observed in the studied specimens, known as "*Araucaria*-like anatomy" (i.e., pycnoxylic secondary xylem, araucarian tracheid radial pitting, and araucarioid cross fields), have been assigned to three commonly known genera, *Araucarioxylon* Kraus, 1870, *Dadoxylon* Endlicher, 1847, and *Agathoxylon* Hartig, 1848. Philippe (1993, 2011) and Bamford and Philippe (2001) pointed out that *Araucarioxylon* and *Dadoxylon* are both

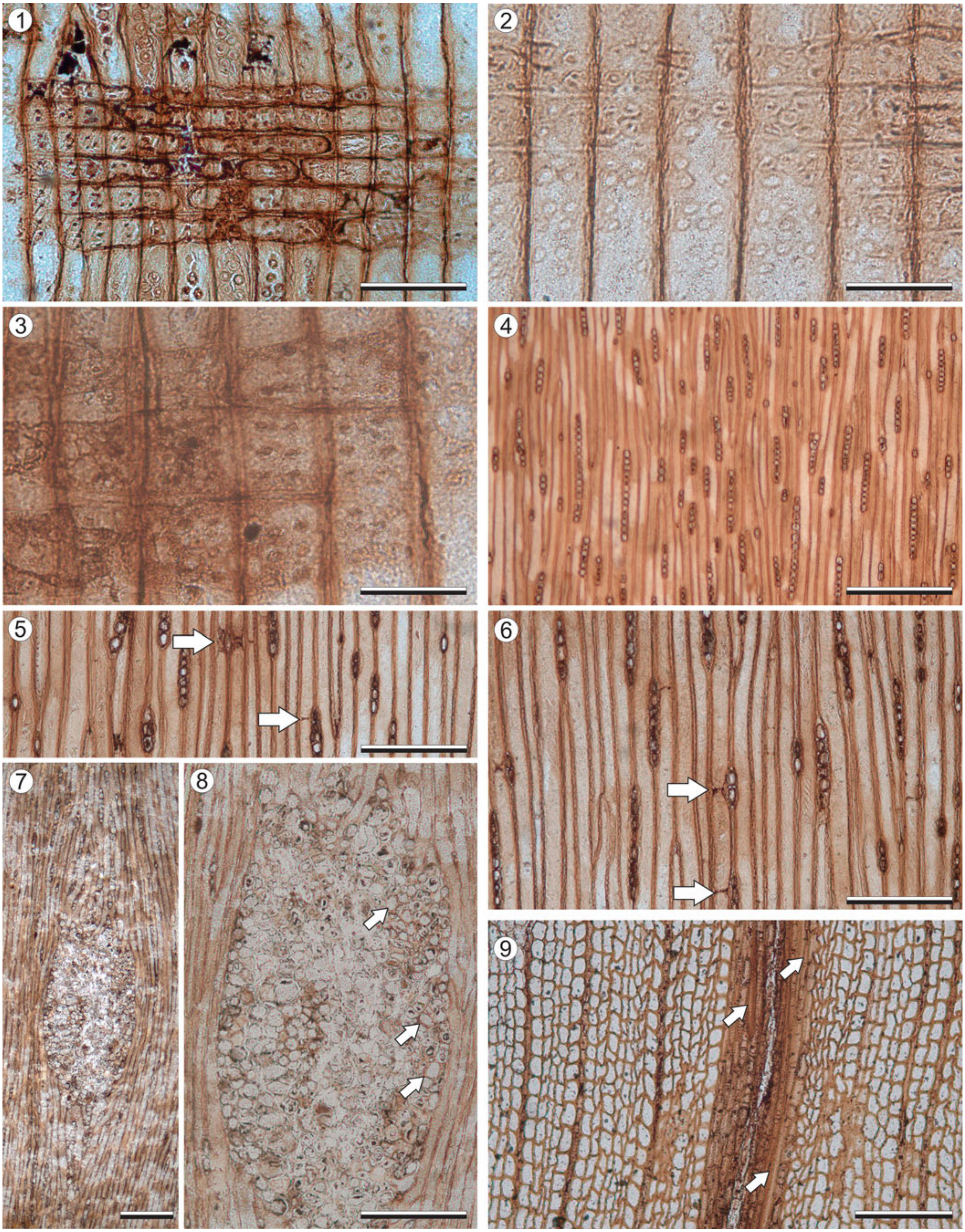
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Figure 5. *Agathoxylon argentinum* n. sp. (**1**) General view of the radial section of the secondary xylem showing the ray parenchyma cell types, the cross fields, and resin contents in ray cells, holotype LPpm 1370. (**2, 3**) Detail of araucarioid cross-field pitting; (**2**) paratype LPpm 1376; (**3**) holotype LPpm 1370. (**4**) General view of tangential section showing the mainly uniseriate rays and occasional biseriate in part rays, paratype LPpm 1377. (**5, 6**) Detail of rays and tracheid with spiral fissures and resin plates (arrows), holotype LPpm 1372. (**7**) Leaf trace in tangential section, holotype LPpm 1182. (**8**) Detail of leaf trace; arrows indicate tracheids. (**9**) Leaf trace in transverse section; arrows indicate tracheids, LPpm 1380. (**1**) Scale bar = 100 μm; (**2**) scale bar = 60 μm; (**3**) scale bar = 50 μm; (**4**) scale bar = 450 μm; (**5, 6, 8, 9**) scale bars = 250 μm; (**7**) scale bar = 350 μm.

illegitimate and superfluous synonyms of *Pinites* Lindley and Hutton, 1831, whereas *Agathoxylon* is a legitimate name having priority over the two other genera. Later, Rößler et al. (2014) argued for the use of *Agathoxylon* for fossil woods with *Araucaria*-like anatomy. Here we treat *Agathoxylon* as the appropriate genus for this type of fossil wood.

Agathoxylon is a widely distributed wood genus according to a brief list of characteristics that include araucarian tracheid pitting, araucarioid cross-field pits, axial parenchyma present or absent, and mainly uniseriate rays and smooth walls in the parenchyma cells (Hartig, 1848; Philippe, 1995). The studied fossil woods were compared with species of *Araucaria*-like tracheidoxyls of Mesozoic age from Gondwana to assess their identity (see Table 2). The wood anatomy of Ischigualasto specimens differs from the species of *Agathoxylon* previously recorded in the Argentinean Triassic—that is, *A. amraparense* (Sah and Jain, 1964) Crisafulli and Herbst, 2011, *A. cozzoi* Gnaedinger and Zavattieri, 2020, *A. dallonii* (Boureau, 1948) Crisafulli and Herbst, 2010, *A. lamaibandianus* Crisafulli and Herbst, 2011, and *A. protoaraucana* (Brea, 1997) Gnaedinger and Herbst, 2009—because of the presence of resin plates (see Table 2). Among other Mesozoic species, the here described tracheidoxyls show more similarities with *Agathoxylon pseudoparenchymatosum* (Gothan) Pujana et al., 2014, and *A. santalense* (Sah and Jain, 1964) because of the cupressoid type of individual cross-field pits; the absence of tangential tracheid pitting, septate tracheids, and axial parenchyma; and the presence of resin plates and occasional partially biseriate rays. However, the Ischigualasto fossil wood differs from these species due to the tracheid transverse section (both polygonal and circular in the studied specimens and exclusively polygonal in the other species), the presence of occasional subopposite and spaced tracheid radial pitting in the studied material, and the higher rays (up to 27 cells high in the studied material and up to 10 cells high in the other species), and the number of pits per cross field (up to nine in the Ischigualasto wood and up to six in *A. pseudoparenchymatosum* and *A. santalense*) (Table 2). Another difference with *A. pseudoparenchymatosum* is the presence of triseriate tracheid radial pitting in the studied material. *Agathoxylon santalense* also can be differentiated from the Ischigualasto wood by the indistinct growth rings in *Agathoxylon santalense* (Table 2). All these characteristics have taxonomic value in extant conifer woods (García Esteban et al., 2004) and are used to delimit *Agathoxylon* species (see Del Fueyo et al., 2021). Because of these differences, we proposed a new specific taxon for the Ischigualasto material.

Evidence of fungal activity

Structures related to the degradation of wood by fungi are preserved. It is common to observe resinous contents in the ray cells (Fig. 7.1, 7.2, 7.4). Two types of degradation patterns can be recognized: in some areas of the wood, differential degradation of cellulose and hemicellulose is observed, while lignin is at least partially preserved (Fig. 7.1, 7.2). This pattern is frequently associated with the boundary between earlywood and latewood (Fig. 7.1, 7.2) and is called brown rot (Schwarze et al., 2004; Schmidt, 2006; Schwarze, 2007). The differential degradation of the polysaccharide layers of the lignified ones can also be observed by the detachment of the S3 layer, which folds toward the lumen of the tracheids (Fig. 7.3). Alternatively, the S3 layer can appear strongly thickened.

In turn, areas with completely degraded secondary xylem cells were observed, which is evidenced as empty spaces, sometimes with associated resinous contents (Fig. 7.4). Complete degradation of the cell wall is called white pocket rot (Schwarze et al., 2004; Schmidt, 2006; Schwarze, 2007).

Although the presence of hyphae was not recognized, structures 3–6 μm in diameter that adhere to the cell wall can be observed in both areas affected by white rot and areas affected by brown rot (Fig. 7.4–7.6). These structures are approximately spherical and appear isolated (Fig. 7.5, 7.6) or in small groups (Fig. 7.4). The walls of these spheres are smooth, and they are surrounded by a thick translucent outer wall. The preservation of the samples did not allow us to observe the presence of openings or discharge papillae, although some of these spheres seem to present some type of process for anchoring (Fig. 7.6).

Growth-ring analysis

In total, 10 ring increments were included in this analysis. The results are summarized in Table 3 and Figure 8. Except for one curve, left-skewed CSDM curves correspond to ring increments smaller than 40 cells in width, while right-skewed curves belong to ring increments greater than 50 cells in width. The percentage skews of the CSDM curve are highly variable, from −27% to +75.6% (mean = +11.5). The percentage diminution ranges from 56.4% to 76.3% (mean = 62.9%). The percentage of latewood varies between 5.4% and 33.3% (mean = 22%). The RMI value varies from 3.2% to 25.4% (mean = 14.1%).

Composition of plant fossil assemblages

Fourteen species of plants are present in the Valle de la Luna Member of the Ischigualasto Formation as megafossils (Table 1). These include sphenophytes, corystosperms, and peltasperms and voltzialean, cupressaceous, and araucariaceous conifers. Other groups frequent in the Argentinean Triassic are not present, such as pleuromeialean lycophytes, ferns, petriellaleans,

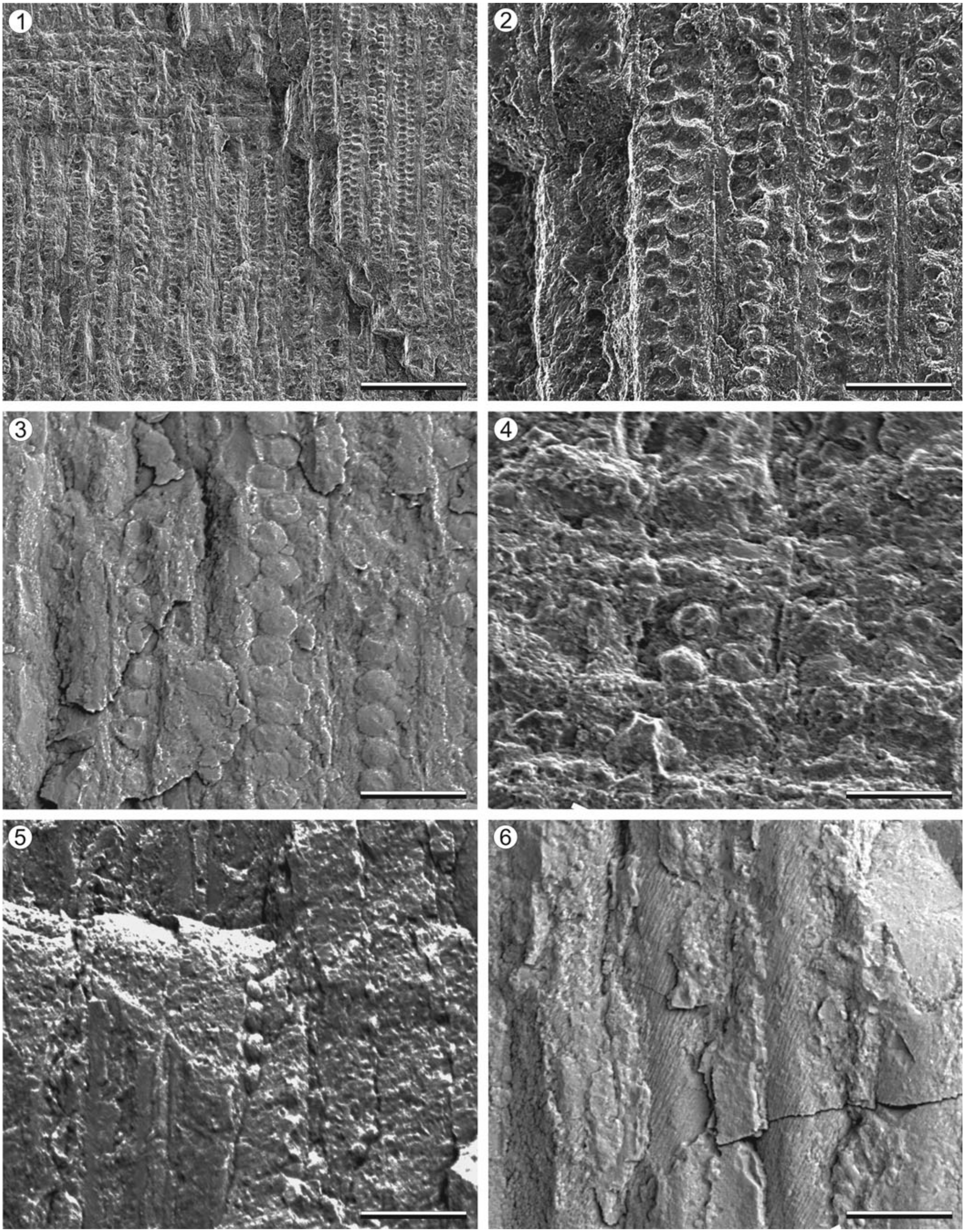

Figure 6. *Agathoxylon argentinum* n. sp., scanning electron microscope images LPPB 492. (**1**) General view of the tracheid radial pitting. (**2**) Detail of biseriate, compressed, and alternating tracheids pits. (**3**) Detail of uniseriate, compressed, and alternating tracheids pits. (**4**) Detail of a cross field. (**5**) Detail of a uniseriate ray in tangential section. (**6**) Spiral fissures in tracheid tangential walls. (**1, 5, 6**) Scale bars = 50 µm; (**2**) scale bar = 60 µm; (**3**) scale bar = 40 µm; (**4**) scale bar = 30 µm.

Table 2. Comparison among main Mesozoic *Agathoxylon* species recorded in Gondwana. SGD = stratigraphic and geographic distribution; GR = growth rings; TEL = transition from earlywood to latewood; TS = tracheid section; TTD = tangential diameter of earlywood tracheids (mean value or range when the mean value was not provided); TRPSE = seriation of tracheid radial pitting; TRPA = arrangement of (two or more seriate) tracheid pitting in radial walls; TRPSP = spacing of tracheid radial pitting; TRPD = diameter of tracheid radial pits (mean values or range when the mean value was not provided); TTP = tracheid tangential pitting; TRP = tracheids with resin plates or plugs; ST = septate tracheids; AP = axial parenchyma; RW = ray width; RH = ray height; CP = type of individual cross-field pits; CA = arrangement of cross-field pits; CPN = cross-field pit number; CPD = cross-field pit diameter (mean values or range when the mean value was not provided). Between () characters which appear less frequently. *Information not provided in the species protologue and taken from a subsequent contribution. [1]We used the combination *Agathoxylon antarticum* (Poole and Cantrill, 2001) Pujana et al., 2014, but we follow the original diagnosis of the basionym provided by Poole and Cantrill (2001). [2] The presence of resin plates is not mentioned in the diagnosis or in the description of Poole and Cantrill (2001), but some probable resin plates are observed in the photos (Poole and Cantrill, 2001, pl. 1, fig, 8). [3]*Agathoxylon dallonni* was previously cited in the Upper Triassic of Argentina by Crisafulli and Herbst (2010), but the specimens were reassigned to *Agathoxylon lamaibandianus* by Gnaedinger and Zavattieri (2020). [4]In the original diagnosis of Boureau (1948), the cross-field pits are described as simple and in the photos seems to be bordered (Boureau, 1948, pl. 1, fig. 5). [5]Although Pujana et al. (2014) proposed that *Agathoxylon matildense* is a junior synonym of *Agathoxylon antarticum*, we considered that the protologues of both species show enough differences to segregate them (i.e., tracheid section, the ray height, and the number of pits per cross field, see Poole and Cantrill, 2001, p. 1086, pl. 1, 2–10; Zamuner and Falaschi, 2005, p. 340, fig. 2).

Species	SGD	GR	TEL	TS	TTD	TRPSE	TRPA	TRPSP	TRPD	TTP
Agathoxylon africanum (Bamford, 1999) Kurzawe and Merlotti, 2010	Upper Permian–Upper Triassic, Botswana, Brazil, South Africa	distinct	gradual	polygonal	36 µm	uniseriate, biseriate	alternate	contiguous to slightly compressed	12–15 µm	absent
Agathoxylon agathioides (Kräusel and Jain, 1964) Kloster and Gnaedinger, 2018	Middle Jurassic, Argentina, India	indistinct	—	polygonal	33 µm*	uniseriate, biseriate (triseriate)	alternate	contiguous, compressed (in groups)	13–23 × 10–13 µm	present
Agathoxylon amraparense (Sah and Jain, 1964) Crisafulli and Herbst, 2011	Upper Triassic–Middle Jurassic, Argentina, India	distinct	gradual	polygonal	16–40 µm*	uniseriate to triseriate	alternate, opposite	contiguous or spaced	4 × 6 µm	absent
Agathoxylon antarcticum (Poole and Cantrill, 2001) Pujana et al., 2014[1]	Lower Cretaceous–Eocene, Argentina, Antarctica	distinct	gradual to abrupt	circular to polygonal	32.3 µm*	uniseriate (biseriate)	alternate	contiguous (confined to the ends of tracheids)	7–15 µm	absent
Agathoxylon cozzoi Gnaedinger and Zavattieri, 2020	Upper Triassic, Argentina	distinct	gradual	polygonal	31 µm	uniseriate to triseriate	alternate	contiguous, compressed	15–23 ×10–12 µm	absent
Agathoxylon dallonii (Boureau, 1948) Crisafulli and Herbst, 2010	Jurassic–Cretaceous, Egypt, Libya, Chad[3]	distinct	gradual?	polygonal	40–60 µm	uniseriate, biseriate	alternate	contiguous, compressed (spaced)	22 µm*	absent
Agathoxylon kellerense (Lucas and Lacey, 1981) Nishida et al., 1992	Early Cretaceous–Paleocene, Antarctica, Chile	distinct	gradual?	polygonal?	22–45 µm	biseriate, triseriate (uniseriate)	alternate	contiguous	9.5–12 ×11–14 µm	absent
Agathoxylon lamaibandianus Crisafulli and Herbst, 2011	Upper Triassic, Argentina	distinct	gradual	polygonal	38 µm	uniseriate, biseriate	alternate or opposite	contiguous, compressed	16–25 µm*	absent
Agathoxylon liguaensis Torres and Philippe, 2002	Lower Jurassic, Chile, Argentina	slightly distinct	gradual	polygonal	60 µm	uniseriate, biseriate	alternate (opposite)	contiguous, (compressed)	14–22 µm	present
Agathoxylon matildense Zamuner and Falaschi, 2005[5]	Middle Jurassic, Argentina	distinct	gradual	polygonal	24 µm	uniseriate (biseriate)	alternate	contiguous (compressed)	9.2 × 7.7 µm	absent
Agathoxylon mendezii Del Fueyo et al., 2021	Lower Cretaceous, Argentina	slightly distinct	gradual?	polygonal to circular	30.5 µm	uniseriate, biseriate	alternate, opposite	contiguous	13 µm	present
Agathoxylon protoaraucana (Brea, 1997) Gnaedinger and Herbst, 2009	Middle Triassic–Lower Jurassic, Argentina	distinct	gradual	polygonal	69.3 µm	uniseriate, biseriate	alternate (subopposite)	compressed or spaced	11.6–19.9 µm	present
Agathoxylon pseudoparenchymatosum (Gothan, 1908) Pujana et al., 2014	Early Cretaceous–Eocene, Antarctica, Argentina, Chile, New Zealand	distinct	abrupt	polygonal	35.8 µm*	uniseriate, biseriate	alternate	contiguous, compressed	10–12 µm	absent
Agathoxylon santacruzense Kloster and Gnaedinger, 2018	Middle Jurassic, Argentina	distinct	gradual?	Polygonal	37 µm	uniseriate, biseriate (triseriate)	alternate (opposite)	contiguous, compressed	10–20 µm	absent
Agathoxylon santalense (Sah and Jain, 1964) Kloster and Gnaedinger, 2018	Middle Jurassic–Lower Cretaceous, Argentina, India	indistinct	—	polygonal	50 µm	uniseriate, biseriate (triseriate)	alternate	contiguous, compressed	8 × 12–25 µm	absent
Agathoxylon termieri (Attims, 1965) Gnaedinger and Herbst, 2009	Lower–Middle Jurassic, Morocco, Tanzania, Argentina	distinct	gradual	polygonal	45 µm	uniseriate, biseriate (triseriate)	alternate (opposite)	contiguous, compressed	17–23 µm	present
Araucarioxylon arayaii Torres et al., 1982	Jurassic–Cretaceous, Antarctica	slightly distinct	gradual?	polygonal	45 µm	uniseriate, biseriate (triseriate)	alternate (opposite)	contiguous, compressed	16 µm	present[6]
Araucarioxylon floresii Torres and Lemoigne, 1989	Upper Cretaceous, Antarctica	slightly distinct or indistinct	—	polygonal	18–60 µm	uniseriate, biseriate	alternate	contiguous	12–21 µm	absent
Dadoxylon (=Araucarioxylon) jurassicum Bhardwaj, 1953	Jurassic–Lower Cretaceous, India	slightly distinct	gradual?	polygonal	30 µm	uniseriate, biseriate	alternate (opposite)	contiguous	5–7 µm	present
Agathoxylon argentinum n. sp.	Upper Triassic, Argentina	slightly distinct to distinct	gradual	polygonal or circular	44.3 µm	uniseriate to triseriate	alternate (sub-opposite)	contiguous, compressed (spaced)	13 × 16.3 µm	absent

Table 2. Continued.

Species	TRP	ST	AP	RW	RH	CP	CA	CPN	CPD	References
Agathoxylon africanum	present	absent	absent	uniseriate	2–18 cells	taxodioid	araucarioid	2–7	6–8 µm	Bamford (1999); Kurzawe and Merlotti (2010); Crisafulli et al. (2016); De Wit et al. (2018)
Agathoxylon agathioides	present	absent	absent	uniseriate (biseriate in part)	2–20 cells	cupressoid	araucarioid	2–8	10 µm	Kräusel and Jain (1964); Kloster and Gnaedinger (2018)
Agathoxylon amraparense	absent	absent	absent	uniseriate	1–15 cells	taxodioid?	araucarioid	2–4	8 µm	Sah and Jain (1964); Crisafulli and Herbst (2011)
Agathoxylon antarcticum	present?[2]	absent	absent	uniseriate (biseriate in part)	1–14 cells	cupressoid	araucarioid	2–9	6–12 µm	Poole and Cantrill (2001); Pujana et al. (2014); Vera et al. (2020)
Agathoxylon cozzoi	absent	absent	present	uniseriate (biseriate in part)	1–20 cells	cupressoid	araucarioid	2–8	10–12 µm	Gnaedinger and Zavattieri (2020)
Agathoxylon dallonii	absent	present	absent	uniseriate (biseriate in part)	2–20 cells	taxodioid?[4]	araucarioid?	1–4	9–10 µm*	Boureau (1948); Dupéron-Laudoueneix, (1976); Dupéron-Laudoueneix and Lejal-Nicol (1981)
Agathoxylon kellerense	absent	absent	absent	uniseriate	2–13 cells	cupressoid	araucarioid	2–5	6.6–7.5 ×6.6–10 µm	Lucas and Lacey (1981); Terada et al. (2006); Pujana et al. (2017); Mirabelli et al. (2018); Vera and Perez Loinaze (2022)
Agathoxylon lamaibandianus	absent	absent	absent	uniseriate	3–23 cells	cupressoid	araucarioid	1–4	18–20 µm*	Crisafulli and Herbst (2011)
Agathoxylon liguaensis	absent	absent	absent	uniseriate	1–56 cells	cupressoid	araucarioid	1–3	10 µm	Torres and Philippe (2002); Gnaedinger et al. (2015)
Agathoxylon matildense	absent	absent	absent	uniseriate	1–4 cells	cupressoid	araucarioid	4–5	6.7x 4.7 µm	Zamuner and Falaschi (2005)
Agathoxylon mendezii	present	absent	absent	uniseriate (biseriate)	3–20 cells	cupressoid	araucarioid	5–16	6 µm	Del Fueyo et al.. (2021)
Agathoxylon protoaraucana	absent	absent	scarce	uniseriate	2–9 cells	cupressoid, taxodioid?	araucarioid	3–9	6.6 µm	Brea (1997); Gnaedinger and Herbst (2009)
Agathoxylon pseudoparenchymatosum	present	absent	absent	uniseriate (biseriate in part)	2–10 cells	cupressoid	araucarioid	2–6	6.5 µm*	Gothan (1908); Stopes (1914); Torres et al. (2009); Pujana et al. (2014, 2017); Vera and Perez Loinaze (2022)
Agathoxylon santacruzense	absent	absent	absent	uniseriate (biseriate)	1–20 cells	cupressoid	araucarioid	2–20	8–10 µm	Kloster and Gnaedinger (2018)
Agathoxylon santalense	present	absent	absent	uniseriate (biseriate in part)	1–10 cells	cupressoid	araucarioid	2–6	6 µm	Sah and Jain (1964); Kloster and Gnaedinger (2018)
Agathoxylon termieri	absent	absent	absent	uniseriate	1–20 cells	cupressoid	araucarioid	2–10	5–6 µm	Attims (1965); Giraud and Hankel (1985); Giraud (1991); Gnaedinger (2006); Gnaedinger and Herbst (2009); Kloster and Gnaedinger (2018)
Araucarioxylon arayaii	present	absent	absent	uniseriate	2–20 cells	cupressoid	araucarioid	2–5	6–11 µm*	Torres et al. (1982, 2000)
Araucarioxylon floresii	present	present	present	uniseriate	2–12 cells	cupressoid	cupressoid?	1-4	10-15 µm	Torres and Lemoigne (1989)
Dadoxylon (=Araucarioxylon) jurassicum	present	absent	absent	uniseriate (biseriate in part)	1–11 cells	taxodioid	araucarioid	4-8	?	Bhardwaj (1953)
Agathoxylon argentinum n. sp.	present	absent	absent	uniseriate (biseriate in part)	1–27 cells	cupressoid	araucarioid	2-9	6.6 × 9.3 µm	This work

ginkgoaleans, and gnetaleans. The PFLs have low diversity, with one to six species in each one. The level PFL 1 is composed of only corystosperms, while levels PFL 2 and PFL 3 comprise both corystosperms and peltasperms. In PFL 4, cupressaceous conifers are recorded together with fossils of corystosperms and peltasperms. The level PFL 5 differs from the others since it bears exclusively sphenophyte remains. Corystosperms, cycads, and cupressaceous conifers occur in the level PFL 6, whereas only corystosperms and cupressaceous conifers continue at the level PFL 7. Finally, the PFL 8 consists of taxa that are not recorded in the previous levels (i.e., the corystosperm species *Dicroidium lancifolium* and *D. odontopteroides* and voltzialean, cupressaceous, and araucariaceous conifers) together with the sphenophyte *Neocalamites carrerei*, also present in PFL 5.

Discussion

Systematic affinities.—It has been suggested that several Paleozoic and Mesozoic plant groups may have an *Agathoxylon* type of wood: seed ferns, cordaitaleans, and araucarian and cheirolepid conifers (Philippe et al., 2004; Taylor et al., 2009; Degani-Schmidt and Guerra-Sommer, 2016). Besides the fact that Glossopteridales and Cordaitales became extinct at the Permian–Triassic boundary (see Bodnar et al., 2021), the new species show dissimilarities with the wood anatomy of these Paleozoic lineages. According to Noll et al. (2005), cordaitalean wood is characterized by predominant multiseriate tracheid radial pitting (with three to five pit series) and very subordinate uni- and biseriate pitting, in contrast to *Agathoxylon argentinum* n. sp., which shows a

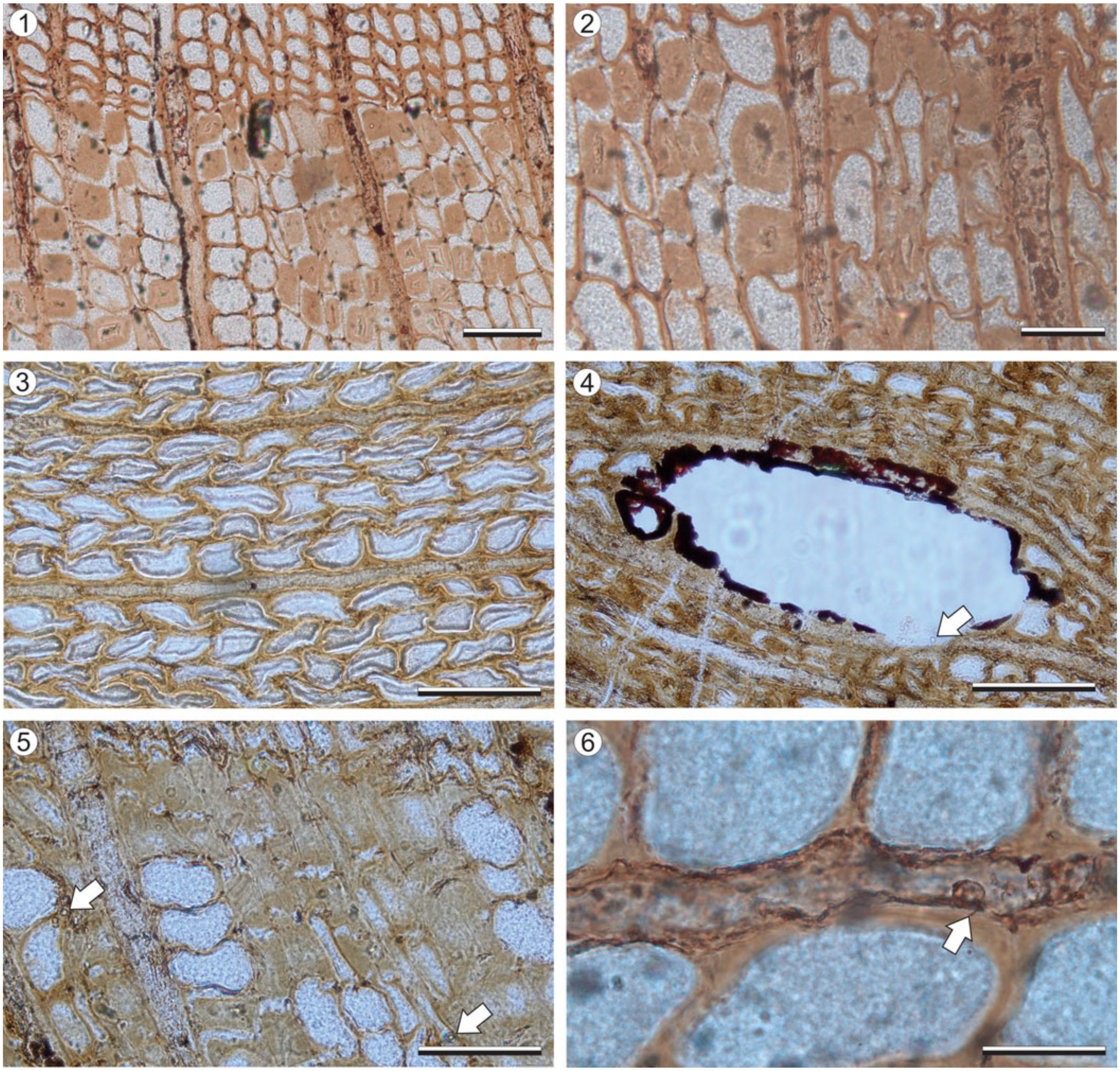

Figure 7. Structures related to the degradation of wood by fungi recognized in *Agathoxylon argentinum* n. sp. (**1, 2**) Transverse section showing resinous contents in the ray cells and tracheid walls with differential degradation of cellulose and hemicellulose and detached and strongly thickened S3 layer, LPpm 1380. (**3**) Collapsed tracheids in transverse section with detached S3 layer folded toward the lumen, LPpm 1380. (**4**) Complete degradation of the cell wall with small groups of spherical structures adhered to the cell wall (white arrow), LPpm 1380. (**5**) Tracheid walls with detached and strongly thickened S3 layer; white arrow indicates isolated spherical structures, LPpm 1379. (**6**) Isolated spherical structure adhered to a ray parenchyma cell; white arrow indicates a probable process for anchoring, LPpm 1379. (**1**) Scale bar = 70 μm; (**2**) scale bar = 50 μm; (**3, 4**) scale bars = 80 μm; (**5**) scale bar = 50 μm; (**6**) scale bar = 30 μm.

dominance of the uni- and biseriate tracheid pitting. Recently, most fossil woods of *Agathoxylon* type related to glossopterids were classified as or reassigned to the genus *Australoxylon* (see Gulbranson et al., 2014; Bamford, 2016; Decombeix et al., 2016; Bamford et al., 2020). The main character distinguishing *Australoxylon* from *Agathoxylon* is the presence of mixed-type pitting on the tracheid radial walls, whereas *Agathoxylon* has only araucarian radial pitting (Merlotti and Kurzawe, 2006; Gulbranson et al., 2014; Bamford et al., 2020). For its part, the secondary xylem of Mesozoic seed fern groups, such as Hermanophytales, Pentoxylales, and Umkomasiales (=Corystospermales), can be differentiated from *Agathoxylon* by mixed type of tracheid pitting in Hermanophytales and most Umkomasiales, and cross fields with oopores or oculipores of podocarpoid type in Pentoxylales and Umkomasiales (see Arnold, 1962; Sharma, 1969, 1972; Bose et al., 1985; Artabe and Brea, 2003; Artabe and Zamuner, 2007; Bodnar, 2008, 2012; Decombeix et al., 2014). In the case of Cheirolepidiaceae, three types of fossil woods have been related to the family—*Protocupressinoxylon*,

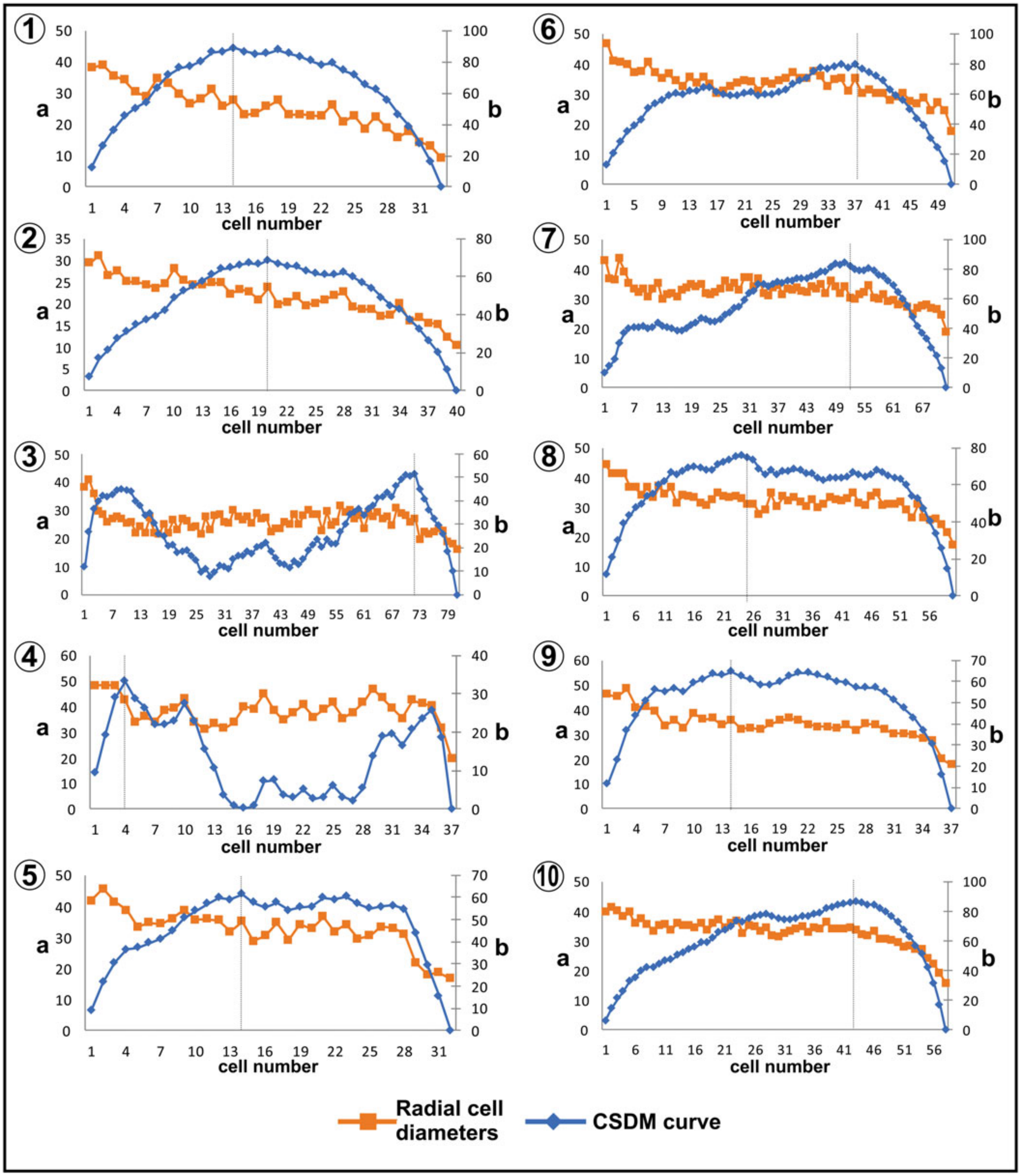

Figure 8. (**1–10**) Mean radial cell diameter (μm) curves (a and orange line) and CSDM curves (b and blue line) in *Agathoxylon argentinum* n. sp. from the measured ring increments 1 to 10. Vertical dotted gray line shows the zenith of each CSDM curve.

Protopodocarpoxylon, and *Brachyoxylon* (Harris, 1979; Alvin et al., 1981; Zhou, 1983), all of them characterized by mixed tracheid pitting (Axsmith, 2006; Bodnar et al., 2013) and not araucarian pitting as *Agathoxylon*.

Compared with extant conifer woods, the new species has a character combination present only in Araucariaceae, allowing us to assign it to this family, that is, presence of frequent resin plates in tracheids; compressed, polygonal, alternating, uniseriate to

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Table 3. Results of growth-ring analysis in *Agathoxylon argentinum* n. sp. using the Falcon-Lang (2000a, b) method.

	Number of cells	Mean cell radial diameter	Percentage skew	Percentage diminution	Percentage latewood	Ring markedness index
Ring 1	33	25.5	–12.5	76.3	33.3	25.4
Ring 2	40	21.8	0	66.2	32.5	21.5
Ring 3	81	26.3	+75.6	60.8	12.3	7.5
Ring 4	37	38.7	–27	59.2	5.4	3.2
Ring 5	32	32.8	–12.5	62.9	21.9	13.8
Ring 6	51	33.5	+34.6	62.4	29.4	18.3
Ring 7	72	32.5	+41.7	56.4	23.6	13.3
Ring 8	60	32.4	–20	60.7	15	9.1
Ring 9	37	34.5	–13.5	63.1	24.3	15.4
Ring 10	58	33.3	+48.3	61.5	22.4	13.8
Mean	50.1	31.1	+11.5	62.9	22	14.1

triseriate tracheid radial pits; absence of helical tertiary thickenings, Sanio's bars, and axial parenchyma (although this last character may be present in Araucariaceae, it is rare); and araucarioid cross fields with more than four pits (García Esteban et al., 2002, 2004; IAWA Committee, 2004; Table 4). In particular, the presence of resin plates or plugs in the tracheids is characteristic of the Araucariaceae (García Esteban et al., 2002, 2004; IAWA Committee, 2004). They are plate-like structures generally darker in color than the cell walls, which extend fully across the tracheid and are associated with adjacent rays (Heady et al., 2002). Resin deposits in tracheids were cited occasionally for a few species of Pinaceae (Penhallow, 1904; Record, 1918; Kukachka, 1960; García Esteban et al., 2007, 2021), but it is not considered as diagnostic for that family (García Esteban et al., 2021). However, resin plates or resinous tracheids were mentioned for some Paleozoic woods with Cordaitalean or uncertain affinities, but in most cases, they would not correspond to the same structures as those present in Araucariaceae woods. For example, the "meniscus-like" deposits in the tracheids described in *Dadoxylon brandlingii* (Lindley and Hutton) Frentzen, 1931 (Thomson, 1914, pl. 5, fig. 46) seem to be septa (i.e., transverse dividing walls inside the cells, Beck, 2010), while the resin plates cited for *Podocarpoxylon indicum* (Bhardwaj) Bose and Maheshwari, 1974 (Crisafulli and Herbst, 2008, fig. 10.2) and *Agathoxylon kurmarpurensis* (Bajpai and Singh) Crisafulli and Herbst, 2008 (Crisafulli et al., 2009, fig. 3.E) are not plate-like deposits since they filled whole tracheid cell lumen.

Although araucarian leaves and cones have not been found in the Ischigualasto Formation until today, fossil pollen grains often related to the Araucariaceae occur in the same strata (i.e., *Araucariacites australis* Cookson, 1947) (Césari and Colombi, 2016; Gnaedinger and Zavattieri, 2020), which supports the affinity of the studied fossil woods. When compared with the living species of Araucariaceae, the new species does not show a preferential affinity. *Agathoxylon argentinum* n. sp. shares the presence of resin plates in tracheids with *Agathis australis* (D. Don) Lindley in Loudon, 1829, *Agathis macrophylla* (Lindley) Masters, 1892, *Agathis ovata* (Vieillard) Warburg, 1900, *Agathis robusta* (C. Moore ex F. Mueller) Bailey, 1883, *Araucaria angustifolia, Araucaria montana* Brongniart and Gris, 1871, *Araucaria muelleri* (Carrière) Brongniart and Gris, 1871, *Araucaria rulei* Mueller, 1860, and *Wollemia nobilis* Jones et al., 1995 (Greguss, 1955; García Esteban et al., 2002, 2004; Heady et al., 2002; http://insidewood.lib.ncsu.edu/search [2004 onward]; Table 4). However, the average tangential diameter of earlywood tracheids of the new species is similar to that of *Agathis lanceolata* Warburg, 1900, *Agathis macrophylla*, *Araucaria columnaris* (G. Forster) Hooker, 1852, and *Araucaria montana* (Greguss, 1955; García Esteban et al., 2002, 2004; Table 4). The ray height of *Araucaria cunninghamii* and *Araucaria hunsteinii* Schumann in Schumann and Hollrung, 1889 wood is comparable to that of the new fossil taxon (Greguss, 1955; García Esteban et al., 2002, 2004; Table 4). Finally, the cross fields of *Agathoxylon argentinum* n. sp. resemble those of *Araucaria angustifolia*, *Araucaria araucana*, *Araucaria bidwillii* Hooker, 1843, and *Araucaria heterophylla* (Salisbury) Franco, 1952 because of the pit number per field (Greguss, 1955; García Esteban et al., 2002, 2004; Table 4).

Leaf phenology implication.—Quantitative analysis of growth rings, including CSDM curves and other parameters (percentage diminution, percentage latewood, and RMI), have proven to be powerful tools in understanding tree growth and leaf longevity as well as climate and environment (Falcon-Lang, 2000a, b). The CSDM method has been previously applied to three fossil wood species from the Triassic of Argentina: *Elchaxylon zavattierae* Artabe and Zamuner, 2007 (Upper Triassic Río Blanco Formation, Mendoza Province), *Protojuniperoxylon ischigualatense* (from same strata where the here studied species occurs, Upper Triassic Ischigualasto Formation, San Juan Province), and *Agathoxylon protoaraucana* (Middle Triassic, Paramillo Formation, Mendoza Province). All of them were interpreted as evergreen plants (Artabe et al., 2007; Bodnar and Artabe, 2007; Brea et al., 2008).

Unlike the other Argentinean Triassic species, *Agathoxylon argentinum* n. sp. shows both left-skewed and right-skewed CSDM curves (Fig. 8, Table 5); left-skewed curves correspond mostly to ring increments smaller than 40 cells. In narrow rings, values of percentage latewood are usually anomalously high compared with wide rings in the same tree (Creber and Chaloner, 1984), and this can explain our results. In general, the new species exhibits lower values of percentage diminution, percentage latewood, and RMI than the other Argentinean Triassic species (Table 5) because of the poorly defined growth rings observed in the studied specimens. The ring parameter values obtained in *Agathoxylon argentinum* n. sp. are comparable to those of extant evergreen conifers with leaf retention of one to two years (Table 5).

Table 4. Comparison among *Agathoxylon argentinum* n. sp. and the wood of extant Araucariaceae. GD = stratigraphic and geographic distribution; GR = growth rings; TEL = transition from earlywood to latewood; TS = tracheid section; TTD = tangential diameter of earlywood tracheids (mean values); TRPSE = seriation of tracheid radial pitting; TRPA = arrangement of (two or more seriate) tracheid pitting in radial walls; TRPSP = spacing of tracheid radial pitting; TRPD = diameter of tracheid radial pits (mean values); TTP = tracheid tangential pitting; TRP = tracheids with resin plates or plugs; ST = septate tracheids; AP = axial parenchyma; RW = ray width; RH = ray height; CP = type of individual cross–field pits; CA = arrangement of cross–field pits; CPN = cross–field pit number; CPD = cross–field pit diameter (mean values). *Measurements from the photo provided by Heady et al. (2002; fig. 13). Characters that appear occasionally are in parentheses. Information taken from Greguss (1955), García Esteban et al. (2002, 2004), Heady et al. (2002), IAWA Committee (2004), Farjon (2010), http://insidewood.lib.ncsu.edu/search (2004 onward), https://www.gbif.org, and this work.

Species	GD	GR	TEL	TS	TTD	TRPSE	TRPA	TRPSP	TRPD
Agathis australis	New Zealand	distinct or indistinct	gradual	polygonal	18–40 µm	uniseriate to triseriate	alternate	contiguous, compressed	4–7 µm
Agathis borneensis Warburg, 1900	Borneo, Malaysia, Sumatra	slightly distinct	gradual	polygonal	?	uniseriate to biseriate (triseriate)	alternate	contiguous, compressed	13–17 µm
Agathis dammara (Lambert) Richard, 1826	Borneo, Indonesia, Malaysia, Philippines, Sumatra	indistinct to distinct	gradual	rounded or polygonal	18–40 µm	uniseriate to triseriate	alternate	contiguous, compressed	6–16 µm
Agathis labillardieri Warburg, 1900	New Guinea	slightly distinct or indistinct	gradual	polygonal	35–37 µm	uniseriate to triseriate	alternate	contiguous, compressed	14–16 µm
Agathis lanceolata	New Caledonia	distinct	gradual	polygonal	45–50 µm	uniseriate to triseriate	alternate	contiguous, compressed	19–20 µm
Agathis macrophylla	Fiji, Solomon Islands, Vanuatu	slightly distinct or distinct	gradual	polygonal	45–50 µm	uniseriate to biseriate	alternate	contiguous, compressed	13–14 µm
Agathis microstachya Bailey and White, 1916	Australia	slightly distinct or indistinct	gradual	polygonal	70–80 µm	uniseriate to triseriate	alternate	contiguous, compressed	10–12 µm
Agathis moorei Masters, 1892	New Caledonia	slightly distinct or indistinct	gradual	polygonal	18–30 µm	uniseriate to biseriate	alternate	contiguous, compressed	12–18 µm
Agathis ovata	New Caledonia	distinct	gradual	rounded or polygonal	25–28 µm	uniseriate to biseriate	alternate	contiguous, compressed	10–12 µm
Agathis robusta	Australia, Papua New Guinea	slightly distinct or indistinct	gradual	rounded or polygonal	25–30 µm	uniseriate to triseriate	alternate	contiguous, compressed	8–10 µm
Araucaria angustifolia	Argentina, Brazil, Paraguay	slightly distinct or indistinct	gradual	polygonal	32 µm	uniseriate to biseriate (triseriate)	alternate	contiguous	10–11 µm
Araucaria araucana	Argentina, Chile	distinct	gradual	rounded or polygonal	22–24 µm	uniseriate to biseriate	alternate	contiguous	10–11 µm
Araucaria bidwillii	Australia	slightly distinct	gradual	polygonal	24–26 µm	uniseriate to biseriate	alternate	contiguous, compressed	14 µm
Araucaria columnaris	New Caledonia	slightly distinct to indistinct	gradual	polygonal	45–50 µm	uniseriate to biseriate	alternate	contiguous, compressed	10–13 µm
Araucaria cunninghamii	Australia, New Guinea	slightly distinct or distinct	gradual	rounded or polygonal	20–24 µm	uniseriate to triseriate	alternate	contiguous, compressed	13–14 µm
Araucaria heterophylla	Australia	distinct	gradual	polygonal	18–20 µm	uniseriate to biseriate	alternate	contiguous, compressed	11–12 µm
Araucaria humboldtensis Buchholz, 1949	New Caledonia	slightly distinct	gradual	rounded or polygonal	20–22 µm	uniseriate to biseriate	alternate	contiguous	11 µm
Araucaria hunsteinii	Papua New Guinea	distinct	gradual	rounded	50–60 µm	uniseriate to triseriate	alternate	contiguous, compressed	15–18 µm
Araucaria montana	New Caledonia	slightly distinct	gradual	rounded or polygonal	40 µm	uniseriate to triseriate	alternate	contiguous, compressed	11–12 µm
Araucaria muelleri	New Caledonia	slightly distinct	gradual	polygonal	28–30 µm	uniseriate to, biseriate	alternate	contiguous, compressed	10–12 µm
Araucaria rulei	New Caledonia	distinct	gradual	polygonal	30–40 µm	uniseriate, biseriate	alternate	contiguous, compressed	8–10 µm
Araucaria subulata Vieillard, 1862	New Caledonia	slightly distinct	gradual	polygonal	30 µm	uniseriate, biseriate	alternate	contiguous, compressed	9–11 µm
Wollemia nobilis	Australia, New Zealand	distinct	gradual	rounded or polygonal	31 µm	uniseriate to triseriate	alternate	contiguous, compressed	17.5 µm*
***Agathoxylon argentinum* n. sp.**	Argentina	slightly distinct to distinct	gradual	polygonal or rounded	44.3 µm	uniseriate, to triseriate	alternate (sub-opposite)	contiguous, compressed (spaced)	13 × 16.3 µm

Table 4. Continued.

Species	TTP	TRP	ST	AP	RW	RH	CP	CA	CPN	CPD
Agathis australis	present	present	absent	absent	uniseriate	8–10 cells	cupressoid	araucarioid	3–12	10–11 μm
Agathis borneensis	present	absent	absent	scarce	uniseriate	4–12 cells	cupressoid	araucarioid	2–5	8–10 μm
Agathis dammara	present	absent	absent	absent or present	uniseriate	1–15 cells	cupressoid	araucarioid	1–10	6–14 μm
Agathis labillardieri	absent	absent	absent	absent	uniseriate	1–10 cells	cupressoid	araucarioid	2–6	8–9 μm
Agathis lanceolata	present	absent	absent	absent or present	uniseriate or biseriate in part	1–40 cells	cupressoid	araucarioid	6–22	9–11 μm
Agathis macrophylla	present	present	absent	absent or present	uniseriate	1–18 cells	cupressoid	araucarioid	1–5	7–8 μm
Agathis microstachya	present	absent	absent	absent or present	uniseriate or biseriate in part	1–40 cells	cupressoid	araucarioid	2–12	7–9 μm
Agathis moorei	present	absent	absent	absent	uniseriate or biseriate in part	1–8 cells	cupressoid	araucarioid	3–6	10–12 μm
Agathis ovata	present	present	absent	absent	uniseriate	1–8 cells	cupressoid	araucarioid	1–16	6–7 μm
Agathis robusta	present	present	absent	absent or present	uniseriate	1–8 cells	cupressoid	araucarioid	1–18	7–9 μm
Araucaria angustifolia	present	present	absent	absent	uniseriate	1–15 cells	cupressoid	araucarioid	1–9	7–9μm
Araucaria araucana	present	present?	absent	absent	uniseriate	1–8 cells	cupressoid	araucarioid	1–8	4–5 μm
Araucaria bidwillii	absent	absent	absent	absent or present	uniseriate or biseriate in part	1–8 cells	cupressoid	araucarioid	1–8	4–11 μm
Araucaria columnaris	present	absent	absent	absent	uniseriate	1–16 cells	cupressoid	araucarioid	2–12	9–11 μm
Araucaria cunninghamii	present	absent	absent	absent	uniseriate	1–20 cells	cupressoid	araucarioid	1–12	7–8 μm
Araucaria heterophylla	absent	absent	absent	absent	uniseriate	1–12 cells	cupressoid	araucarioid	2–8	4–5 μm
Araucaria humboldtensis	present	absent	absent	absent	uniseriate	1–7 cells	cupressoid	araucarioid	2–6	6–7 μm
Araucaria hunsteinii	absent	absent	absent	present	uniseriate or biseriate in part	1–20 cells	cupressoid	araucarioid	2–6	10–12 μm
Araucaria montana	present	present	absent	absent	uniseriate	1–12 cells	cupressoid	araucarioid	8–14	10–11 μm
Araucaria muelleri	present	present	absent	absent	uniseriate	1–10 cells	cupressoid	araucarioid	4–8	6–7 μm
Araucaria rulei	present	present	absent	absent	uniseriate	1–6 cells	cupressoid	araucarioid	1–12	5–6 μm
Araucaria subulata	present	absent	absent	absent	uniseriate	1–6 cells	cupressoid	araucarioid	6–14	6–7 μm
Wollemia nobilis	present	present	absent	absent	uniseriate (biseriate in part)	1–11 cells	cupressoid	araucarioid	3–11	11 μm
Agathoxylon argentinum n. sp	absent	present	absent	absent	uniseriate (biseriate in part)	1–27 cells	cupressoid	araucarioid	2–9	6.6 × 9.3 μm

Paleofloristic changes.—Spalletti et al. (1999) recognized five assemblage biozones (*Dictyophyllum castellanosii/Johnstonia stelzneriana/Saportaea dichotoma* [CSD] Biozone, *Yabeiella mareyesiaca/Scytophyllum bonettiae, Rhexoxylon* (=*Protophyllocladoxylon*) *cortaderitaense* [MBC] Biozone, *Yabeiella brackebuschiana/Scytophyllum neuburgianum/Rhexoxylon piatnitzkyi* [BNP] *Biozone, Dicroidium odontopteroides/D. lancifolium* [OL] Biozone, and *Dictyophyllum tenuiserratum, Linguifolium arctum, Protocircoporoxylon marianaensis* [DLM] Biozone) in the Triassic System of Argentina based mainly on associations of characteristic plant taxa. In PFLs 1–7 of the Ischigualasto Formation, species diagnostics of the early Late Triassic (Carnian) Biozone *Yabeiella brackebuschiana/Scytophyllum neuburgianum/Rhexoxylon piatnitzkyi* (BNP) are recognized. However, the species present in the PFL 8 level are more related to the middle Late Triassic (Norian) Biozone *Dicroidium odontopteroides-D. lancifolium* (OL) (Spalletti et al., 1999; Morel et al., 2003). Among other floristic events, the OL Biozone is characterized by the dominance of shrubby corystosperms and a decline in diversity of tree corystosperms as the genus *Zuberia* (Spalletti et al., 1999).

Paleoenvironmental and paleoclimatic considerations.—The presence of compression wood in one of the studied samples (LPPB 492) suggests that it could be a stem growing on a hillside. As the growth ring boundaries are nearly straight in transverse section in the sample and it is a fragment of the main trunks preserved in vertical position, we infer that it was not a tree branch.

Both white and brown rot are the product of the activity of basidiomycetes fungi (Schwarze et al., 2004; Schmidt, 2006; Schwarze, 2007). Although no hyphal remains were observed in the studied materials, the degradation patterns are comparable to other examples of interactions between basidiomycetes fungi and Araucariaceae woods (e.g., Sagasti et al., 2018 and citations therein). The spherical structures attached to the walls of the tracheids are comparable to holocarpic chytrids (Taylor et al., 2015), whose parasitic activity has been suggested in vascular plants since the Devonian (e.g., Stubblefield et al., 1985; Taylor

Table 5. Comparison of growth-ring parameters of *Agathoxylon argentinum* n. sp. with other Triassic species from Argentina (*) and selected extant conifer species. Mean values in parentheses. Information taken from Falcon-Lang (2000a, 2000b), Artabe et al. (2007), Bodnar and Artabe (2007), and Brea et al. (2008).

Species	Leaf longevity	Number of cells	Percentage skew	Percentage diminution	Percentage latewood	Ring markedness index
Larix decidua Miller, 1768	deciduous	26–65 (46.3)	−40 to +7.7 (-6.8)	71.5–85.9	50–54.8	35.8–44.4
Taxodium distichum (Linnaeus) Richard, 1810	deciduous	14–41 (26.4)	−14.3 to +3.0 (-2.7)	—	—	—
Pinus sylvestris Linnaeus, 1753	evergreen, 1–3 years	28–49 (39.3)	−9.1 to +17.9 (+5.2)	70.5–77.3	41–50	31.6–35.3
Agathoxylon argentinum n. sp.*	unknown	32–81 (50.1)	−27 to +75.6 (+11.5)	56.4–76.3 (62.9)	5.4–33.3 (22)	3.2–25.4 (14.1)
Picea abies (Linnaeus) Karsten, 1881	evergreen, 3–5 years	19–65 (42.1)	0 to +38.2 (+12)	74–84	25.9–44.2	19.9–35.4
*Elchaxylon zavattierae**	unknown	64–69	+12.5 to + 24.6 (+ 17.9)	66.2–73.1 (69.9)	26.1–41.2 (32.6)	17.3–30.1
*Agathoxylon protoaraucana**	unknown	30–46	+13.3 to +26.3 (+21.3)	68.7–75.6 (72.1)	32.6–42.8 (35.4)	22.9–29.4 (25.5)
*Projuniperoxylon ischigualastense**	unknown	48–191	+8.3 to + 73.4 (38.1)	75.9–82.7 (79.3)	13.3–45.8 (31.9)	10.8–35 (25.2)
Araucaria araucana	evergreen, 3–15 years	40–192 (73.2)	+55.0 to +80.0 (+66.7)	28.7–51.8	10–22.5	3.2–10.3

et al., 1992; Hass et al., 1994; Krings et al., 2009; Sagasti et al., 2018). Members of Chytridiomycota are saprobes or parasites in or on organisms (Ogawa et al., 2001; Hurdeal et al., 2020). Chytrids are known to live on pollen grains, insect exoskeletons, protists, small invertebrates, amphibian skin, other fungi, pieces of plants, fruits, and water-logged twigs (Boyle et al., 2003). Fungal degradation of wood and the presence of probable chytrids would indicate at least locally humid conditions (Schmidt, 2006; Engelund et al., 2013; Thybring et al., 2018).

The palynoflora studied by Césari and Colombi (2016) from a level lower than the megaflora levels presents an association linked to humid conditions. PFLs 1–3 are composed exclusively of corystosperms and peltasperms, both considered xerophytic plants, which could show a change to drier conditions. At PFLs 4, 6, and 7, woods of Cupressaceae are recorded together with fossils of corystosperms and peltasperms. Cupressaceae grow in a wide variety of environments, but in general, they are xerophytic plants—with xeromorphic adaptations—that can live in arid or semi-arid environments or oligotrophic soils (Scagel, 1987). In PFL 8, Araucariaceae occurs, Cupressaceae and peltasperms are not recorded, and the large tree corystosperms are replaced by shrubby corystosperms. Members of the Araucariaceae family are currently restricted to the South American and Southwest Asia–Western Pacific region despite their extensive distribution in both hemispheres during the Mesozoic (Stockey, 1990; Kunzmann, 2007). They include three living genera, *Araucaria*, *Agathis*, and *Wollemia*, mostly distributed in tropical and subtropical humid regions (e.g., Kershaw and Wagstaff, 2001; Farjon, 2010). The history of the family indicates that araucarians prospered and became widespread forest dominants during periods of low fire frequency and generally wet climate (Kershaw and Wagstaff, 2001). Therefore, we infer a change to more humid climates for the PFL 8 level.

Conclusions

The studied fossil woods from the Triassic Ischigualasto Formation are assigned to a new species since they present anatomical differences of taxonomic importance from the other species of *Agathoxylon* recorded in Mesozoic strata from Gondwana. *Agathoxylon argentinum* n. sp. is characterized by uniseriate to triseriate radial tracheid pitting with mainly contiguous or compressed and alternating arrangement, frequent resin plates, cross fields of araucarioid type with 2–9 oculipores per field, uniseriate to occasional partially biseriate rays up to 27 cells high, and the absence of tangential tracheid pitting, septate tracheids, and axial parenchyma. This species is assigned to Araucariaceae because of the combination of uniseriate to triseriate alternating contiguous and compressed radial tracheid pitting, the presence of resin plates in tracheids, and araucarioid cross fields. These characters differentiate woods of Araucariaceae from those of other Mesozoic gymnosperms. Wood samples show evidence of moderate biodeterioration. Wood-decaying patterns comparable to the activity of basidiomycetes is recognized as white and brown rot. Moreover, spherical structures attached to the walls of the tracheids were recognized, which are interpreted as holocarpic Chytridiomycetes fungi that could have had parasitic or saprotrophic modes of life.

Quantitative growth-ring analysis results lead us to infer that *Agathoxylon argentinum* n. sp. was an evergreen gymnosperm with a low leaf-retention time. The fossil levels PFL 1–7 of the Ischigualasto Formation bear a floristic assemblage characteristic of the Carnian. *Agathoxylon argentinum* n. sp. occurs in the fossil level PFL 8, whose plant-fossil assemblage is typical of the Norian. The vegetation change recorded in the fossil level bearing the new species, in addition to evidence of fungal activity, indicates humid paleoclimatic conditions for the uppermost part of the Valle de La Luna Member of the Ischigualasto Formation.

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References

Alvin, K.L., Fraser, C.J., and Spicer, R.A., 1981, Anatomy and palaeoecology of *Pseudofrenelopsis* and associated conifers in the English Wealden: Palaeontology, v. 24, p. 759–778.

Archangelsky, S., 1960, Nota preliminar sobre el hallazgo de *Rhexoxylon* en la cuenca de Ischigualasto, límite de las provincias de San Juan y La Rioja: Acta Geológica Lilloana, v. 3, p. 187–190.

Archangelsky, S., 1968, Studies on Triassic fossil plants from Argentina. IV. The leaf genus *Dicroidium* and its possible relation to *Rhexoxylon* stems: Paleontology, v. 11, p. 500–512.

Archangelsky, S., and Brett, D.W., 1961, Studies on Triassic fossil plants from Argentina. I. *Rhexoxylon* from the Ischigualasto formation: Philosophical Transactions of the Royal Society of London B., v. 244, p. 1–9.

Archangelsky, S., and Brett., D.W., 1963, Studies on Triassic fossil plants from Argentina II: *Michelilloa waltoni* nov. gen. et. spec.: Annals of Botany N.S., v. 27, p. 147–154.

Arnold, C.A., 1962, A *Rhexoxylon*-like stem from the Morrison Formation of Utah: American Journal of Botany, v. 49, p. 883–886.

Artabe, A.E., 1990, Revalidación del género triásico *Zuberia* Frenguelli 1943, Familia Corystospermaceae: Revista del Museo de La Plata (n.s.) Paleontología, v. 9, p. 145–157.

Artabe, A.E., and Brea, M., 2003, A new approach to Corystospermales based on Triassic permineralized stems from Argentin: Alcheringa, v. 27, p. 209–229.

Artabe, A.E., and Zamuner, A.B., 2007, *Elchaxylon*, a new corystosperm based on permineralized stems from the Late Triassic of Argentina: Alcheringa, v. 31, p. 85–96.

Artabe, A.E., Morel, E.M., and Spalletti, L.A., 2001, Paleoecología de las floras triásicas argentinas, *in* Artabe, A.E., Morel, E.M., and Zamuner, A.B., eds., El Sistema Triásico en la Argentina: La Plata, Fundación Museo de La Plata ‘Francisco Pascasio Moreno’, p. 199–225.

Artabe, A.E., Morel, E.M., and Ganuza, D.G., 2007, Las floras triásicas de la Argentina: Asociación Paleontológica Argentina, Publicación Especial, v.11, p. 75–86.

Attims, Y., 1965, Etude anatomique et paléogéographique de quelques bois jurassiques du Maroc: Notes Du Service Geologique Du Maroc, v. 24, p. 33–52.

Axsmith, B., 2006, The vegetative structure of a Lower Cretaceous conifer from Arkansas: further implications for morphospecies concepts in the Cheirolepidiaceae: Cretaceous Research, v. 27, p. 309–317.

Axsmith, B.J., Escapa, I.H., and Huber, P., 2008, An Araucarian conifer bract-scale complex from the Lower Jurassic of Massachusetts: implications for estimating phylogenetic and stratigraphic congruence in the Araucariaceae: Palaeontologia Electronica 11.3.13A, 9 p., http://palaeo-electronica.org/2008_3/152/index.html

Bailey, F.M., 1883, Synopsis of the Queensland Flora: Brisbane, J.C. Beal, Government printer, 890 p.

Bailey, J.F., and White, C.T., 1916, Contributions to the Queensland flora: Botany Bulletin, Department of Agriculture, Queensland, v. 18, p. 1–16.

Baldoni, A.M., 1980, Revisión de las especies del género *Xylopteris* (Corystospermaceae) en el Triásico de Argentina, Australia y Sud África: Ameghiniana, v. 17, p. 135–155.

Bamford, M., 1999, Permo-Triassic fossil woods from the south African Karoo Basin: Paleontologia Africana, v. 35, p. 25–40.

Bamford, M.K., 2016, Fossil woods from the Upper Carboniferous to Lower Jurassic Karoo Basin and the environmental interpretation, *in* Linol, B., and de Wit, M., eds., Origin and Evolution of the Cape Mountains and Karoo Basin: Cham, Springer, p. 158–167.

Bamford, M.K., and Philippe, M., 2001, Gondwanan Jurassic–Early Cretaceous homoxylous woods: a nomenclatural revision of the genera with taxonomical notes: Review of Paleobotany and Palynology, v. 113, p. 287–297.

Bamford, M.K., Cairncross, B., and Lombard, H., 2020. Silicified fossil woods from the Late Permian Middleton Formation, Beaufort Group, Eastern Cape Province, South Africa and their palaeoenvironmental significance: South African Journal of Geology, v. 123, p. 465–478.

Beck, C.B., 2010, An Introduction to Plant Structure and Development: Plant Anatomy for the Twenty-First Century (second edition): Cambridge, Cambridge University Press, 459 p.

Benton, M.J., Bernardi, M., and Kinsella, C., 2018, The Carnian Pluvial Episode and the origin of dinosaurs: Journal of the Geological Society, v. 175, p. 1019–1026.

Bhardwaj, D.C., 1953, Jurassic woods from the Rajmahal Hills Bihar: The Palaeobotanist, v. 2, p. 59–70.

Bodenbender, G., 1911, Constitución geológica de la parte meridional de la Provincia de La Rioja y regiones limítrofes: Boletín de la Academia Nacional de Ciencias, v. 19, p. 5–221.

Bodnar, J., 2008, *Rhexoxylon cortaderitaense* (Menéndez) comb. nov., a species of permineralized stems newly assigned to the Corystospermaceae, from the Triassic of Argentina: Alcheringa, v. 32, p. 171–190.

Bodnar, J., 2012, Estudios evolutivos del desarrollo en tallos fósiles de Corystospermaceae (Corystospermales, Spermatopsida): Revista del Museo Argentina de Ciencias Naturales n.s., v. 14, p. 143–166.

Bodnar, J., and Artabe, A.E., 2007, Estudio sistemático y paleodendrológico del leño de una Cupressaceae triásica de la Formación Ischigualasto, provincia de San Juan, Argentina: Ameghiniana, v. 44, p. 303–319.

Bodnar, J., Escapa, I.H., Cúneo, R., and Gnaedinger, S., 2013, First record of conifer wood from the Cañadón Asfalto Formation (Early–Middle Jurassic), Chubut province, Argentina: Ameghiniana, v. 50, p. 227–239.

Bodnar, J., Coturel, E.P., Falco, J.I., and Beltrán, M., 2021, An updated scenario for the End-Permian Crisis and the recovery of Triassic land flora in Argentina: Historical Biology, v. 33, p. 3654–3672.

Bonetti, M.I.R., 1966, *Protojuniperoxylon ischigualastensis* sp. nov. del Triásico de Ischigualasto (San Juan): Ameghiniana, v. 4, p. 211–216.

Bose, M., and Maheshwari, H., 1974, Mesozoic conifers, *in* Surange, K., Lakhanpal R., and Bhardwaj, D., eds., Aspects and Appraisal of Indian Palaeobotany: Lucknow, Birbal Sahni Institute of Palaeobotany, p. 212–223.

Bose, M.N., Pal, P.K., and Harris, T.M., 1985, The *Pentoxylon* plant: Philosophical Transactions of the Royal Society, v. 310, p. 77–108.

Boura, A., Bamford, M., and Philippe, M., 2021, Promoting a standardized description of fossil tracheidoxyls: Review of Palaeobotany and Palynology, v. 295, 104525.

Boureau, E., 1948, Etude paléoxylologique du Sahara. I. Presence du *Dadoxylon* (*Araucarioxylon*) *dallonii* n. sp.: Bulletin du Muséum d’Histoire Naturelle, v. 20, p. 420–426.

Boyle, D.G., Hyatt, A.D., Daszak, P., Berger, L., Longcore, J.E., Porter, D., Hengstberger, S.G., and Olsen, V., 2003, Cryo-archiving of *Batrachochytrium dendrobatidis* and other chytridiomycetes: Diseases of Aquatic Organisms, v. 56, p. 59–64.

Brea, M., 1997, Una nueva especie fósil del género *Araucarioxylon* Kraus 1870, emend. Maheshwari 1972 del Triásico de Agua de la Zorra, Uspallata, Mendoza, Argentina: Ameghiniana, v. 34, p. 485–496.

Brea, M., Artabe, A.E., and Spalletti, L.A., 2008, Ecological reconstruction of a mixed Middle Triassic forest from Argentina: Alcheringa, v. 32, p. 365–393.

Brett, D., 1968, Studies on Triassic fossil plants from Argentina III. The trunk of *Rhexoxylon:* Palaeontology, v. 11, p. 236–245.

Brongniart, A., and Gris, A., 1871, Observations sur diverses plantes nouvelles ou peu connues de la Nouvelle-Calédonie: Annales des Sciences Naturelles; Botanique, v. 5, p. 340–404.

Buchholz, J., 1949, Addition to the Coniferous Flora of New Caledonia: Bulletin du Muséum National d'Histoire Naturelle, sér. 2, v. 21, p. 279–286.

Césari, S.N., and Colombi, C.E., 2013, A new Late Triassic phytogeographical scenario in westernmost Gondwana: Nature Communications, v. 4, n. 1889, https://doi.org/10.1038/ncomms2917

Césari, S.N., and Colombi, C.E., 2016, Palynology of the Late Triassic Ischigualasto Formation, Argentina: paleoecological and paleogeographic implications: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 449, p. 365–384.

Charrier, R., 1979, El Triásico de Chile y regiones adyacentes de Argentina: una reconstrucción paleogeográfica y paleoclimática: Comunicaciones, Departamento Geología, Facultad de Ciencias Físicas y Matemáticas, Universidad de Chile, v. 26, p. 1–37.

Colombi, C.E., and Parrish, J.T., 2008, Late Triassic environmental evolution in southwestern Pangea: plant taphonomy of the Ischigualasto Formation: Palaios, v. 23, p. 778–795.

Cookson, I.C., 1947, Plant microfossils from the lignites of Kerguelen Archipelago: Antarctic Research Expedition 1929–1931, Reports Series A, v. 2, p. 127–142.

Creber, G.T., and Chaloner, W.G., 1984, Influence of environmental factors on the wood structure of living and fossil trees: The Botanical Review, v. 50, p. 357–448.

Crisafulli, A., and Herbst, R., 2008, Maderas gimnospérmicas de la Formación Solca (Pérmico Inferior), provincia de La Rioja, Argentina: Ameghiniana, v. 45, p. 737–751.

Crisafulli, A., and Herbst, R., 2010, Leños gimnospérmicos de la Formación Llantenes (Triásico Superior), Provincia de Mendoza, Argentina: GAEA Journal of Geoscience, v. 6, p. 14–20.

Crisafulli, A., and Herbst, R., 2011, La Flora Triásica del Grupo El Tranquilo, provincia de Santa Cruz (Patagonia): Leños Fósiles: Ameghiniana, v. 4, p. 275–288.

Crisafulli, A., Herbst, R., and Storti, L.M., 2009, Maderas gimnospérmicas de la Formación Tres Islas (Pérmico Inferior) de Uruguay: GAEA Journal of Geoscience, v. 5, p. 1–14.

Crisafulli, A., Dutra, T.L., and Herbst, R., 2016, In-situ Late Triassic fossil woods from the fluvial channel deposits of the Caturrita Formation, Faxinal do Soturno, Rio Grande do Sul, Brazil: GAEA - Journal of Science, v. 9, p. 37–46.

Currie, B.S., Colombi, C.E., Tabor, N.J., Shipman, T.C., and Montañez, I.P., 2009, Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina: Journal of South American Earth Sciences, v. 27, p. 74–87.

Dal Corso, J. et al. 2020, Extinction and dawn of the modern world in the Carnian (Late Triassic): Science Advances, v. 6, n. 38, https://doi.org/10.1126/sciadv.aba0099

Decombeix, A.L., Bomfleur, B., Taylor, E.L., and Taylor, T.N., 2014, New insights into the anatomy, development, and affinities of corystosperm trees from the Triassic of Antarctica: Review of Paleobotany and Palynology, v. 203, p. 22–34.

Decombeix, A.L., Taylor, E.L., and Taylor, T.N., 2016, Bark anatomy of late Permian Glossopterid trees from Antarctica: IAWA Journal, v. 37, p. 444–458.

Degani-Schmidt, I., and Guerra-Sommer, M., 2016, Charcoalified *Agathoxylon*-type wood with preserved secondary phloem from the lower Permian of the Brazilian Parana basin: Review of Paleobotany and Palynology, v. 226, p. 20–29.

Del Fueyo, G.M., and Archangelsky, A., 2002, *Araucaria grandifolia* Feruglio from the Lower Cretaceous of Patagonia, Argentina: Cretaceous Research, v. 23, p. 265–277.

Del Fueyo, G.M., Carrizo, M.A., Poiré, D.G., and Lafuente Díaz, M.A., 2021, Recurrent volcanic activity recorded in araucarian wood from the Lower Cretaceous Springhill Formation, Patagonia, Argentina: palaeoenvironmental interpretations: Acta Palaeontologica Polonica, v. 66, p. 231–253.

Dettmann, M.E., Clifford, H.T., and Peters, M., 2012, *Emwadea microcarpa* gen. et sp. nov.: anatomically preserved araucarian seed cones from the Winton Formation (late Albian), western Queensland, Australia: Alcheringa, v. 36, p. 217–237.

De Wit, M., Bamford, M., and Van Waarden, C., 2018, Fossil trees from the basal Triassic Lebung Group at the Makgaba site, west of Mokubilo, Botswana: Palaeontologia Africana, v. 52, p. 194–200.

Dobruskina, I.A., 1969, Genus *Scytophyllum* (the morphology, epidermic texture and systematic position): Trudy GIN AN SSSR, v. 190, p. 35–58. [in Russian]

Dupéron-Laudoueneix, M., 1976., Sur la présence de *Dadoxylon* (*Araucarioxylon*) *dallonii* Boureau dans la région de Fardiallah (Tchad): Congrés nacional des Sociétés savantes, 97, Sect. Sciences, v. 4, p. 67–78.

Dupéron-Laudoueneix, M., and Lejal-Nicol, A., 1981, Sur deux bois homoxylés du Sud-Ouest de'l Égypte: Congrés nacional des Sociétés savantes, 106, Sect. Sciences, v. 1, p. 9–40.

Endlicher, S.L., 1847, Synopsis Coniferarum: St. Gallen, Scheitlin & Zollikofer, Sangalli, 368 p.

Engelund, E.T., Thygesen, L.G., Svensson, S., and Hill, C.A.S., 2013, A critical discussion of the physics of wood–water interactions: Wood Science and Technology, v. 47, p. 141–161.

Falcon-Lang, H.J., 2000a, A method to distinguish between woods produced by evergreen and deciduous coniferopsids on the basis of growth ring anatomy: a new palaeoecological tool: Palaeontology, v. 43, p. 775–783.

Falcon-Lang, H.J., 2000b, The relationship between leaf longevity and growth ring markedness in modern conifer woods and its implications for palaeoclimatic studies: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 160, p. 317–328.

Farjon, A., 2010, A Handbook of the World's Conifers, Volume 1: Leiden, Brill, 526 p.

Feistmantel, L., 1889, Obersichtliche Darstellung der Geologisch-Palaeontologischen Verhalmisse Sud-Afrikas. Th.1 Die Karroo-Formation und die dieselbe unterlagernden Schichten: Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften, v. 7, p. 1–89.

Franco, J. do A., 1952, Nomenclatura de algumas Coníferas: Anais do Instituto Superior de Agronomia (Lisboa), v. 19, p. 5–23.

Frenguelli, J., 1943, Reseña crítica de los géneros atribuídos a la "Serie de *Thinnfeldia*": Revista del Museo de La Plata (n.s.), Paleontología, v. 2, p. 225–342.

Frenguelli, J., 1948, Estratigrafía y edad del llamado "Rético" en la Argentina: Sociedad Argentina de Estudios Geográficos GAEA, v. 8, p. 159–309.

Frentzen, K., 1931, Studien uber die fossilen Hölzer der Sammelgattung *Dadoxylon* Endlicher: Abhandlungen der Heidelberger Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse, v. 16, p. 1–93 and v. 19, p. 1–51.

García Esteban, L., de Palacios, P., Guindeo, A., García-Esteban, Ly., Lázaro, I., González, L., Rodriguez, Y., García, F., Bobadilla, I., and Camacho, A. (eds.), 2002, Anatomía e identificación de maderas de coníferas a nivel de especie: Madrid, Ediciones Mundi-Prensa, 421 p.

García Esteban, L., de Palacios, P., Guindeo Casasús, A., and García Fernández, F., 2004, Characterisation of the xylem of 352 conifers: Investigación agraria, Sistemas y recursos forestales-INIA (España), v. 13, p. 452–478.

García Esteban, L., de Palacios, P., Guindeo, A., and Fernández, F.G., 2007, Comparative anatomy of the wood of *Abies pinsapo* and its two Moroccan varieties: IAWA Journal, v. 28, p. 285–300.

García Esteban, L., de Palacios, P., García-Iruela, A., García-Fernández, F., García-Esteban, L., and González de Vega, D., 2021, Comparative wood anatomy in Pinaceae with reference to its systematic position: Forests, v. 12, 1706.

Giraud, B., 1991, Les espèces du genre *Dadoxylon* depuis 1962: leur répartition et leur évolution du Permien à la fin du Mésozoïque: Review of Palaeobotany and Palynology, v. 67, p. 13–39.

Giraud, B., and Hankel, O., 1985, Bois fossiles des dépôts du Karoo du Bassin du Luwegu (Tanzanie méridionale): Annales de Paléontologie, v. 71, p. 159–185.

Gnaedinger, S., 2006, Maderas de la Formación Piedra Pintada (Jurásico Temprano), provincia de Neuquén, Argentina: Revista del Museo Argentino de Ciencias Naturales nueva serie, v. 8, p. 171–177.

Gnaedinger, S., and Herbst, R., 2009, Primer registro de maderas gimnospérmicas de la Formación Roca Blanca (Jurásico Inferior), provincia de Santa Cruz, Argentina: Ameghiniana, v. 46, p. 59–71.

Gnaedinger, S., and Zavattieri, A., 2020, Coniferous woods from the Upper Triassic of southwestern Gondwana, Tronquimalal Group, Neuquén Basin, Mendoza Province, Argentina: Journal of Paleontology, v. 94, p. 387–416.

Gnaedinger, S., García Massini, J.L., Bechis, F., and Zavattieri A.M., 2015, Coniferous woods and wood decaying fungi from the El Freno Formation (Lower Jurassic), Neuquén Basin, Mendoza province, Argentina: Ameghiniana, v. 52, p. 447–467.

Golonka, J., 2007, Late Triassic and Early Jurassic palaeogeography of the world: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 244, p. 297–307.

Gorozhankin, I.N., 1904, Lektsii po morfologii i sistematike archegonialnyh rastenij. II, Pteridophyta, I, Archispermae: Moskva, A.I. Mamontov, 104 p. [in Russian]

Gothan, W., 1905, Zur Anatomie lebender und fossiler Gymnospermen-Hölzer: Abhandlungen zur preuβischen geologische Landesanstalt, v. 44, p. 1–108.

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

Gothan, W., 1912, Über die Gattung Thinnfeldia Ettingshausen: Abhandlung der Naturhistorische Gesellschaft zu Nümberg, v. 19, p. 67–80.

Greguss, P., 1955, Identification of Living Gymnosperms on the Basis of Xylotomy: Budapest, Akadémiai Kiado, 508 p.

Gulbranson, E.L., Ryberg, P.E., Decombeix, A.L., Taylor, E.L., Taylor, T.N., and Isbell, J.L., 2014, Leaf habit of Late Permian *Glossopteris* trees from high-palaeolatitude forests: Journal of the Geological Society, v. 171, p. 493–507.

Gulbranson, E.L., Ciccioli, P.L., Montañez, I.P., Marenssi, S.A., Limarino, C.O., Schmitz, M.D., and Davydov, V., 2015, Paleoenvironments and age of the Talampaya Formation: The Permo-Triassic boundary in northwestern Argentina: Journal of South American Earth Sciences, v. 63, p. 310–322.

Halle, T.G., 1908, Zur Kenntnis der mesozoischen Equisetales Schwedens: Kungliga Svenska Vetenskapsakademiens Handlingar, v. 43, p. 1–56.

Harris, T.M., 1979, The Yorkshire Jurassic Flora. V. Coniferales: London, Trustees of the British Museum (Natural History), 196 p.

Hartig, T., 1848, Beiträge zur Geschichte der Pflanzen und zur Kenntnis der nordeutschen Braunkholen-Flora: Berlin, Bot. Zeitung, v. 6, p. 185–190.

Hass, H., Taylor, T.N., and Remy, W., 1994, Fungi from the Lower Devonian Rhynie chert: mycoparasitism: American Journal of Botany, v. 81, p. 29–37.

Heady, R.D., Banks, J.G., and Evans, P.D., 2002, Wood anatomy of Wollemi Pine (*Wollemia nobilis*, Araucariaceae): IAWA Journal, v. 23, p. 339–357.

Henkel, J.B., and Hochstetter, W., 1865, Synopsis der Nadelhölzer, deren charakteristischen Merkmale nebst Andeutungen über ihre Cultur und Ausdauer in Deutschlands Klima: Stuttgart, Verlag der J.G. Cottaschen Buchhandlung, 446 p.

Herbst, R., 1970, Estudio palinológico de la Cuenca Ischigualasto-Villa Unión, (Triásico), provincias de San Juan- La Rioja. I. Introducción. II. Monoaperturados: Ameghiniana, v. 7, p. 83–97.

Herbst, R., 1971, Estudio palinológico de la Cuenca Ischigualasto-Villa Unión (Triásico), provs. San Juan-La Rioja. III. Esporas triletes: Ameghiniana, v. 9, p. 280–288.

Hill, R.S., 1995, Conifer origin, evolution and diversification in the Southern Hemisphere, *in* Enright, N.J., and Hill, R.S, eds., Ecology of Southern Conifers: Melbourne, Melbourne University Press, 342 p.

Hooker, W.J., 1843, Figure and description of a new species of *Araucaria*, from Moreton Bay, New Holland, detected by J.T. Bidwill, Esq.: The London Journal of Botany, v. 2, p. 498–506.

Hooker, W.J., 1852, *Araucaria columnaris:* Botanical Magazine, v. 78, t. 4635.

Hurdeal, V.G., Gentekaki, E., Hyde, K.D., and Jeewon, R., 2020, Where are the basal fungi? Current status on diversity, ecology, evolution, and taxonomy: Biologia, v. 76, p. 421–440.

IAWA Committee, 2004, International Association of Wood Anatomists list of microscopic features for softwood identification: IAWA Journal, v. 25, p. 1–70.

Jones, W.G., Hill, K.D., and Allen, J.M., 1995, *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae: Telopea, v. 6, p. 173–176.

Karsten, H., 1881, Deutsche Flora. Pharmaceutisch-medicinische Botanik. Ein Grundriss der systematischen Botanik zum Selbststudium für Aerzte, Apotheker und Botaniker: Berlin, J.M. Spaeth, 1284 p.

Kershaw, P., and Wagstaff, B., 2001, The southern conifer family Araucariaceae: history, status, and value for paleoenvironmental reconstruction: Annual Review of Ecology and Systematics, v. 32, p. 397–414.

Kloster, A.C., and Gnaedinger, S.C., 2018, Coniferous wood of *Agathoxylon* from the La Matilde Formation, (Middle Jurassic), Santa Cruz, Argentina: Journal of Paleontology, v. 92, p. 546–567.

Koch, K.H.E., 1869, Dendrologie. Bäume, Sträucher und Halbsträucher, welche in Mittel- und Nord-Europa im Freien kultivirt warden 2.2: Erlangen, F. Enke, 424 p.

Kokogián, D.A., Spalletti, L.A., Morel, E., Artabe, A.E., Martínez, R.N., Alcober, O.A., Milana, J.P., Zavattieri, A.M., and Papú, O.H., 1999, *Los depósitos continentales triásicos,* in *Caminos, R., ed., Geología Regional Argentina*: Buenos Aires, Secretaría de Estado de Minería de la Nación, p. 377–398.

Kraus, G., 1870, Bois fossiles de coniferes, *in* Schimper, W.P., ed., Traite de Paleontologie vegetale, tome 2: Strasbourg, Baillere, p. 363–385.

Kräusel, R., and Jain, K., 1964, New coniferous wood from the Rajmahal Hills, Bihar, India: The Palaeobotanist, v. 12, p. 59–67.

Krings, M., Dotzler, N., Galtier, J., and Taylor, T.N., 2009, Microfungi from the upper Visean (Mississippian) of central France: Chytridiomycota and chytrid-like remains of uncertain affinity: Review of Palaeobotany and Palynology, v. 156, p. 319–328.

Kukachka, B.F., 1960, Identification of coniferous woods: Tappi Journal, v. 43, p. 887–896.

Kuntze, C.E.O., 1898, Revisio generum plantarum vascularium omnium atque cellularium multarum secundum leges nomenclaturae internationales cum enumeratione plantarum exoticarum in itinere mundi collectarum, 3.3: Leipzig, A. Felix, 576 p.

Kunzmann, L., 2007, Neue Untersuchungen zu *Araucaria* Jussieu aus der europäischen Kreide: Palaeontographica B, v. 276, p. 97–131.

Kurzawe, F., and Merlotti, S., 2010, O complexo *Dadoxylon-Araucarioxylon*, Carbonífero e Permiano do Gondwana: estudo taxonômico do gênero *Araucarioxylon*: Pesquisas em Geociências, v. 37, p. 41–50.

Lambert, A.B., 1837, A description of the genus *Pinus*, illustrated with figures; directions relative to the cultivation, and remarks on the uses of the several species: also descriptions of many other new species of the family of Coniferae (edition 2.3): London, Messrs, unnumbered.

Lindley, J., and Hutton, W., 1831, The Fossil Flora of Great Britain: or Figures and Descriptions of the Vegetable Remains Found in a Fossil State in this Country, Volume 1, Part 1 (first edition): London, James Ridgway and Sons, 370 p.

Linnaeus, C., 1753, Species Plantarum, Volume 2: Holmiae, Impensis Laurentii Salvii, p. 561–1200.

López-Gamundi, O.R., Espejo, I.S., Conaghan, P.J., and Powell, C.McA., 1994, Southern South America, *in* Veervers, J.J., and Powell, C.McA., eds., Permian–Triassic Pangean basins and foldbelts along the Panthalassan margin of Gondwanaland: Geological Society of America Memoir, v. 184, p. 281–329.

Loudon, J.C., 1829, An Encyclopædia of Plants (first edition): London, Longman, Rees, Orme, Brown and Green, 1159 p.

Lucas, R.C., and Lacey, W.S., 1981, A permineralized wood flora of probable Cenozoic age from King George Island, South Shetland Island: British Antarctic Survey Bulletin, v. 53, p. 147–151.

Mancuso, A.C., Benavente, C.A., Irmis, R.B., and Mundil, R., 2020, Evidence for the Carnian Pluvial Episode in Gondwana: new multiproxy climate records and their bearing on early dinosaur diversification: Gondwana Research, v. 86, p. 104–125.

Martínez, R.N., Fernandez, E., and Alcober, O.A., 2011, A new advanced eucynodont (Synapsida, Cynodontia) from the Carnian–Norian Ischigualasto Formation, northwestern Argentina: Ameghiniana v. 48, p. R109.

Martínez, R.N., Apaldetti, C., Alcober, O.C., Colombi, C.E., Sereno, P.C., Fernandez, E., Santi Malnis, P., Correa G.A., and Abelin, D., 2012, Vertebrate succession in the Ischigualasto Formation: Journal of Vertebrate Paleontology, v. 32, p. 10–30.

Martínez, R.N., Fernandez, E., and Alcober, O.A., 2013, A new non-mammaliaform eucynodont from the Carnian-Norian Ischigualasto Formation, northwestern Argentina: Revista Brasilera de Paleontología, v. 16, p. 61–76.

Masters, M.T., 1892, List of conifers and taxads in cultivation in the open air in Great Britain and Ireland: Journal of the Royal Horticultural Society of London, v. 14, p. 179–256.

Melchor, R.N., 2007, Changing lake dynamics and sequence stratigraphy of synrift lacustrine strata in a half-graben: an example from the Triassic Ischigualasto–Villa Unión Basin, Argentina: Sedimentology, v. 54, p. 1417–1446.

Merlotti, S., and Kurzawe, F., 2006, Estudo taxonômico do gênero *Australoxylon* Marguerier 1973 com a descrição de *A. catarinensis* sp. nov. para o Permiano Inferior, Bacia do Paraná, Brasil: Revista Brasileira de Paleontologia, v. 9, p. 73–81.

Milana, J.P., and Alcober, O., 1994, Modelo tectonosedimentario de la cuenca triásica de Ischigualasto (San Juan, Argentina): Revista de la Asociación Argentina, v. 49, p. 217–235.

Miller, P., 1768, The Gardeners Dictionary (eighth edition): London, John & Francis Rivington, 1344 p.

Mirabelli, S.L., Pujana, R.R., Marenssi, S.A., and Santillana, S.N., 2018, Conifer fossil woods from the Sobral Formation (lower Paleocene, Western Antarctica): Ameghiniana, v. 55, p. 91–108.

Morel, E.M., Artabe, A.E., Zavattieri, A.M., and Bonaparte, J.F., 2001, Cronología del Sistema Triásico, *in* Artabe, A.E., Morel, E.M., and Zamuner, A.B., eds., El Sistema Triásico en la Argentina: La Plata, Fundación Museo de La Plata "Francisco Pascasio Moreno," p. 227–253.

Morel, E., Artabe, A., and Spalletti, L., 2003, Triassic floras of Argentina: biostratigraphy, floristic events and comparison with other areas of Gondwana and Laurasia: Alcheringa, v. 27, p. 231–243.

Mueller, F., 1860, Essay on the plants collected by Mr. Eugene Fitzalan, during Lieut. Smith's expedition to the estuary of the Burdekin: Melbourne, Government Printer, 19 p.

Nishida, M., Ohsawa, T., Nishida, H., and Rancusi, M.H., 1992, Permineralized coniferous woods from the XI Region of Chile, Central Patagonia: Research Institute of Evolutionary Biology, Scientifical Report, v. 7, p. 47–59.

Noll, R., Rößler, R., and Wilde, V., 2005, 150 Jahre *Dadoxylon*. Zur Anatomie fossiler Koniferen- und Cordaitenhölzer aus dem Rotliegend des euramerischen Florengebietes; Veröffentlichungen des Museums für Naturkunde Chemnitz, v. 28, p. 29–48.

Ogawa, Y., Hayashi, S., Degawa, Y., and Yaguchi, Y., 2001, *Ramicandelaber*, a new genus of the Kickxellales, Zygomycetes: Mycoscience, v. 42, p. 193–199.

Panti C., Pujana, R.R., Zamaloa, M.C., and Romero, E.J., 2012, Araucariaceae macrofossil record from South America and Antarctica: Alcheringa, v. 36, p. 1–22.

Penhallow, D.P., 1904, The anatomy of the Coniferales (continued): The American Naturalist, v. 38, p. 523–554.

Pérez Loinaze, V.S., Vera, E.I., Fiorelli, L., and Desojo, J.B., 2018, Palaeobotany and palynology of coprolites from the Late Triassic Chañares Formation of Argentina: implications for vegetation provinces and the diet of dicynodonts: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 502, p. 31–51.

Petriella, B., 1978, La reconstrucción de *Dicroidium* (Pteridospermopsida, Corystospermaceae): Obra Centenario Museo de La Plata, v. 5, p. 107–110.

Philippe, M., 1993, Nomenclature générique des trachéidoxyles fossiles mésozoïques à champs araucarioïdes: Taxon, v. 42, p. 74–80.

Philippe, M., 1995, Bois fossiles du Jurassique de Franche-Comté (nordest de la France): systématique et biogéographie: Palaeontographica, Abteilung B, v. 236, p. 45–103.

Philippe, M., 2011, How many species of *Araucarioxylon*?: Comptes Rendus Palevol, v. 10, p. 201–208.

Philippe, M., and Bamford, M.K., 2008, A key to morphogenera used for Mesozoic conifer-like woods: Review of Palaeobotany and Palynology, v. 148, p. 184–207.

Philippe, M. et al., 2004, Biogeography of Gondwanan terrestrial biota during the Jurassic–Early Cretaceous as seen from fossil wood evidence: Review of Palaeobotany and Palynology, v. 129, p. 141–173.

Philippe, M., Boura, A., Oh, C., and Pons, D., 2014, *Shimakuroxylon* a new homoxylous Mesozoic wood genus from Asia, with palaeogeographical and palaeoecological implications: Review of Palaeobotany and Palynology, v. 204, p. 18–26.

Poole, I., and Cantrill, D., 2001, Fossil woods from Williams Point Beds, Livingston Island, Antarctica: a Late Cretaceous southern high latitude flora: Palaeontology, v. 44, p. 1081–1112.

Pujana, R.R., Santillana, S., and Marenssi, S., 2014, Conifer fossil woods from the La Meseta Formation (Eocene of Western Antarctica): evidence of Podocarpaceae dominated forests: Review of Palaeobotany and Palynology, v. 200, p. 122–137.

Pujana, R.R., Raffi, M.E, and Olivero, E.B., 2017, Conifer fossil woods from the Santa Marta Formation (Upper Cretaceous), Brandy Bay, James Ross Island, Antarctica: Cretaceous Research, v. 77, p. 28–38.

Ramos, V.A., and Kay, S.M., 1991, Triassic rifting and associated basalts in the Cuyo Basin, central Argentina, *in* Harmon, R.S., and Rapela, C.W., eds., Andean Magmatism and Its Tectonic Setting: Geological Society of America Special Paper 265, p. 79–91.

Record, S.J., 1918, Significance of resinous tracheids: Botanical Gazette, v. 66, p. 61–67.

Retallack, G.J., 1981, Middle Triassic megafossil plants from Long Gully, near Otematata, north Otago, New Zealand: Journal of the Royal Society of New Zealand, v. 1, p. 167–200.

Richard, L.C.M., 1810, Note Sur les Plantes dites Conifères: Annales du Museum National d'Histoire Naturelle, v.16, p. 196–299.

Richard, L.C.M., 1826, Commentatio Botanica de Conifereis et Cycadeis: Stutgardiae, Sumptibus J. G. Cottae, 212 p.

Rogers, R.R., Swisher C.C. III, Sereno, P.C., Monetta, A.M., Forster, C.A., and Martínez, R.N., 1993, The Ischigualasto tetrapod assemblage, Late Triassic, Argentina, and ^{40}Ar/^{39}Ar dating of dinosaur origins: Science, v. 260, p. 794–797.

Rößler, R., Philippe, M., van Konijnenburg-van Cittert, J.H.A., McLoughlin, S., Sakala, J., and Zijlstra, G, 2014, Which name(s) should be used for Araucaria-like fossil wood? Results of a poll: Taxon, v. 63, p. 177–184.

Rothwell, G.W., Mapes, G., Stockey, R.A., and Hilton, J., 2012, The seed cone *Eathiestrobus* gen. nov.: fossil evidence for a Jurassic origin of Pinaceae: American Journal of Botany, v. 99, p. 708–720.

Ruffell, A., Simms, M.J., and Wignall, P.B., 2016, The Carnian Humid Episode of the Late Triassic: a review: Geological Magazine, v. 153, p. 271–284.

Sagasti, A.J., García Massini, J.L., Escapa, I.H., and Guido, D.M., 2018, Multitrophic interactions in a geothermal setting: arthropod borings, actinomycetes, fungi and fungal-like microorganisms in a decomposing conifer wood from the Jurassic of Patagonia: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 514, p. 31–44.

Sah, S.C.D., and Jain, K.P., 1964, Some fossil woods from the Jurassic of Rajmahal Hills, Bihar, India: The Palaeobotanist, v. 12, p. 169–180.

Scagel, R.E., 1987, El reino vegetal: Barcelona, Ediciones Omega, 778 p.

Schmidt, O., 2006, Wood and Tree Fungi. Biology, Damage, Protection, and Use: Berlin, Springer, XII + 336 p.

Schumann, K.M., and Hollrung, M.U., 1889, Flora von Kaiser Wilhelms Land 11: Berlin, Asher und Co., 144 p.

Schwarze, F.W.M.R., 2007, Wood decay under the microscope: Fungal Biology Review, v. 21, p. 133–170.

Schwarze, F.W.M.R., Mattheck, C., and Engels, J., 2004, Fungal Strategies of Wood Decay in Trees (second edition): Heidelberg, Springer, 185 p.

Sharma, B.D., 1969, On Pentoxyleae remains from Amarjola in the Rajmahal Hills, India: Ameghiniana, v. 6, 50–56.

Sharma, B.D., 1972, *Guptoxylon endocentrica* sp. nov. du Jurassique D'Amarjola daus les Rajmahal Hills (Inde): Extrait, du Bulletin Mensuel de La Société Linnéenne de Lyon, v. 21, p. 114–120.

Spalletti, L.A., Artabe, A.E., Morel, E.M., and Brea, M., 1999, Biozonación paleoflorística y cronoestratigráfica del Triásico argentino: Ameghiniana, v. 36, p. 419–451.

Spalletti, L.A., Artabe, A.E., and Morel, E.M., 2003, Geological factors and evolution of southwestern Gondwana Triassic plants: Gondwana Research, v. 6, p. 119–134.

Stockey, R.A., 1982, The Araucariaceae: an evolutionary perspective: Review of Palaeobotany and Palynology, v. 37, p. 133–154.

Stockey, R.A., 1990, Antarctic and Gondwana conifers, *in* Taylor, T.N., and Taylor, E.L., eds., Antarctic Paleobiology: New York, Springer, 261 p.

Stockey, R.A., 1994, Mesozoic Araucariaceae: morphology and systematic relationship: Journal of Plant Research, v. 107, p. 493–502.

Stockey, R.A., and Ko, H., 1986, Cuticle micromorphology of *Araucaria* de Jussieu: Botanical Gazette, v. 147, p. 508–548.

Stopes, M.C., 1914, A New *Araucarioxylon* from New Zealand: Annals of Botany, v. 28, p. 341–350.

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

Taylor, T.N., Remy, W., and Hass, H., 1992, Fungi from the Lower Devonian Rhynie chert: Chytridiomycetes: American Journal of Botany, v. 76, p. 389–396.

Taylor, T.N., Taylor, E.L., and Krings, M., 2009, Paleobotany, the Biology and Evolution of Fossil Plants: London, Academic Press, 1253 p.

Taylor, T.N., Krings, M., and Taylor, E.L., 2015, Fossil Fungi: London, Academic Press, 384 p.

Terada, K., Asakawa, T.O., and Nishida, H., 2006, Fossil wood assemblage from Cerro Dorotea, Última Esperanza, Magallanes (XII) region, Chile, *in* Nishida, H., ed., Post-Cretaceous Floristic Changes in Southern Patagonia, Chile: Tokyo, Faculty of Science and Engineering, Chuo University, p. 67–90.

Thomson, R.B., 1914, On the comparative anatomy and affinities of the Araucarineœ: Philosophical Transactions of the Royal Society of London, Series B, Containing Papers of a Biological Character, v. 204, p. 1–50.

Thybring, E.E., Kymäläinen, M., and Rautkari, L., 2018, Moisture in modified wood and its relevance for fungal decay: iForest, v. 11, p. 418–422.

Torres, T.G., and Lemoigne, Y., 1989, Hallazgos de maderas fósiles de Angiospermas y Gimnospermas del Cretácico Superior en punta Williams, isla Livingston, islas Shetland del Sur, Antártida: Serie Científica Instituto Antártico Chileno, v. 39, p. 9–29.

Torres, T.G., and Philippe, M., 2002, Dos nuevas especies de *Agathoxylon* y *Baieroxylon* del Jurásico Inferior de La Ligua, Chile: datos paleoxilológicos en América del Sur: Revista Geológica de Chile, v. 29, p. 151–165.

Torres, T.G., Valenzuela, E., and González, I., 1982, Paleoxilología de Península Byers, Isla Livington, Antártida, Islas Sheetland del Sur. Antártica: Actas 3° Congreso Geológico Chileno (Concepción, 1982), v. 1, p. 321–341.

Torres, T.G., Galleguillos, H., and Philippe, M., 2000, Maderas fósiles en el Monte Flora, Bahía Esperanza, Península Antártica: Actas 9° Congreso Geológico Chileno, v. 2, p. 386–390.

Torres, T., Calderón, M., and Fadel Cury, L., 2009, Maderas fósiles de Gimnospermas en la Formación Yahgan, estratos de Tekenika, Isla Hoste, Chile: XII Congreso Geológico, abstract S12_020, p. 291.

Townrow, J.A., 1956, The genus *Lepidopteris* and its Southern Hemisphere species: Abhandlungen ut. Arbok d. Norske Videnskaps-Akademi, Oslo, I. Matematisk-Naturvitenskapelig Klasse, v. 2, p. 3–28.

Turland, N.J. et al., eds., 2018, International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code) Adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017: Regnum Vegetable, Volume 159: Glashütten, Koeltz Botanical Books.

Uliana, M.A., Biddle, K.T., and Cerdan, J., 1988, Mesozoic extension and the formation of Argentine sedimentary basins, *in* Tankard, A.J., and Balkwill, H.R., eds., Extensional tectonics and stratigraphy of the North Atlantic margins: American Association of Petroleum Geologists Memoir, v. 46, p. 599–614.

Vera, E.I., and Perez Loinaze, V.S., 2022, Ecological interactions in conifers (*Agathoxylon* and *Protocupressinoxylon*) from the Punta del Barco Formation (Baqueró Group, upper Aptian), Patagonia, Argentina: Cretaceous Research, v. 129, 105035.

Vera, E.I., Perez Loinaze, V.S., Llorens, M., and Passalia, M.G., 2020, *Agathoxylon* Hartig in the Lower Cretaceous Arroyo del Pajarito Member (Los Adobes Formation), Chubut Province, Argentina: Journal of South American Earth Sciences, v. 100, 102562.

Vieillard, E., 1862, Plantes utiles de la Nouvelle-Callédonie: Annales des Sciences Naturelles; Botanique, sér. 4, v. 16, p. 28–76.

Walkom, A.B., 1925. Notes on some Tasmanian Mesozoic plants: Papers and Proceedings of the Royal Society of Tasmania, v. 1, p. 73–89.

Warburg, O., 1900, Monsunia, Beiträge zur Kenntniss der Vegetation des Süd- und Ostasiatischen Monsungebietes: Leipzig, Verlag von Wilhelm Engelmann, 207 p.

Yrigoyen, M.R., and Stover, L.E., 1970, La palinología como elemento de correlación del Triásico en la Cuenca Cuyana: Actas IV Jornadas Geológicas Argentinas, v. 3, p. 427–447.

Zamuner, A.B., 1992, Estudio de una tafoflora de la localidad tipo de la Formación Ischigualasto (Neotrías), Provincia de San Juan [Ph.D. thesis]: La Plata, Universidad Nacional de La Plata, 97 p.

Zamuner, A.B., and Artabe, A.E., 1990, El género *Scytophyllum* Bornemann 1856 (Familia Peltaspermaceae Thomas), un nuevo representante de la Flora Triásica de Argentina: Revista del Museo de La Plata, n.s. paleontología, v. 54, p. 131–144.

Zamuner, A.B., and Falaschi, P., 2005, *Agathoxylon matildense* n. sp., leño araucariáceo del Bosque Petrificado del Cerro Madre e Hija, Formación La Matilde (Jurásico medio), Provincia de Santa Cruz, Argentina: Ameghiniana, v. 42, p. 339–346.

Zamuner, A.B., Zavattieri, A.M., Artabe, A.E., and Morel, E.M., 2001, Paleobotánica, *in* Artabe, A.E., Morel, E.M., and Zamuner, A.B., eds., El Sistema Triásico en la Argentina:La Plata, Fundación Museo de La Plata “Francisco Pascasio Moreno,” p. 143–184.

Zhou, Z., 1983, A heterophyllous conifer from the Cretaceous of east China: Palaeontology, v. 26, p. 789–811.

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