

New records of Late Triassic wood from Argentina and their biostratigraphic, paleoclimatic, and paleoecological implications

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We report gymnospermous wood found in sandstone and siltstone beds of the Upper Triassic Hilario Formation, Sorocayense Group at Hilario Creek located in San Juan province, Argentina. The identified xylotaphoflora comprises *Baieroxylon cicatricum* (Ginkgoales) and a new species of *Protophyllocladoxylon* (Coniferales), it constitutes the first reports of these taxa from the Triassic in Argentina. *Protophyllocladoxylon hilarioense* sp. nov. differs from the other species by the following combination of anatomical characters: radial pits araucarian, mixed and some with abietinian tendency, uni-biseriate; contiguous, separated; tangential pits uni-biseriate; cross-field pits are simple elliptic, oblique, one to two in number and low uni-biseriate rays. The growth rings in the reported woods show a gradual transition from earlywood to latewood, suggesting little change in the climatic conditions experienced during their growth. The type of growth rings observed is consistent with a humid but seasonally dry subtropical climate. These woods are representatives of the arboreal stratum of a mesophytic association.

Key words: Ginkgoales, Coniferales, Pinales, *Baieroxylon*, *Protophyllocladoxylon*, Triassic, Hilario Formation, Argentina, San Juan.

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Introduction

The wood records from the Cuyana Basin of Argentina are scarce and poorly known. This basin is filled up with sediments of two groups: Sorocayense Group and Rincón Blanco Group, and it is located in the southwest of the San Juan province. These sedimentary units yielded rich taphofloras composed of Bryophyta, Lycophyta, Sphenophyta, Corystospermales, Peltaspermales, Cycadales, Coniferales, and Gnetales (Artabe et al. 2001, 2007a, b; Gnaedinger and Lutz 2008; Bodnar et al. 2018, 2019; Drovandi et al. 2020). The Upper Triassic Hilario Formation of the Sorocayense Group has yielded petrified wood that is an important addition to the Triassic lignoflora of Gondwana and the importance of this finding is discussed in this paper, both in systematic and palaeoenvironmental aspects.

Institutional abbreviations.—CTES-PB, Paleontological Collections of the National University of the Northeast Dr. Rafael Herbst at the CECOAL-CONICET-UNNE, Corrientes, Argentina.

Nomenclatural acts.—This published work and the nomenclatural acts it contains have been registered in Plant Fossil Names Registry (PFNR): urn:lsid:plantfossilnames.org:ref:967

Geological setting

The Cuyana, Ischigualasto-Villa Unión, and Marayes-El Carrizal basins are part of a series of basins that extended along the western margin of Gondwana in the early Mesozoic. They represent a continuous record of the Triassic in Argentina exhibiting several common paleofloristic elements (Drovandi et al. 2020). The Triassic sediments of the Cuyana Basin expose diverse taphofloras and are located from the southwest region of San Juan to the north of Mendoza. The taphofloras found in San Juan are located in two regions: Barreal-Calingasta, along the eastern flank of Los Patos river valley, and in Rincón Blanco in the Sierra del Tontal (Kokogian et al. 1999) (Fig. 1). The Barreal-Calingasta successions are assigned to the

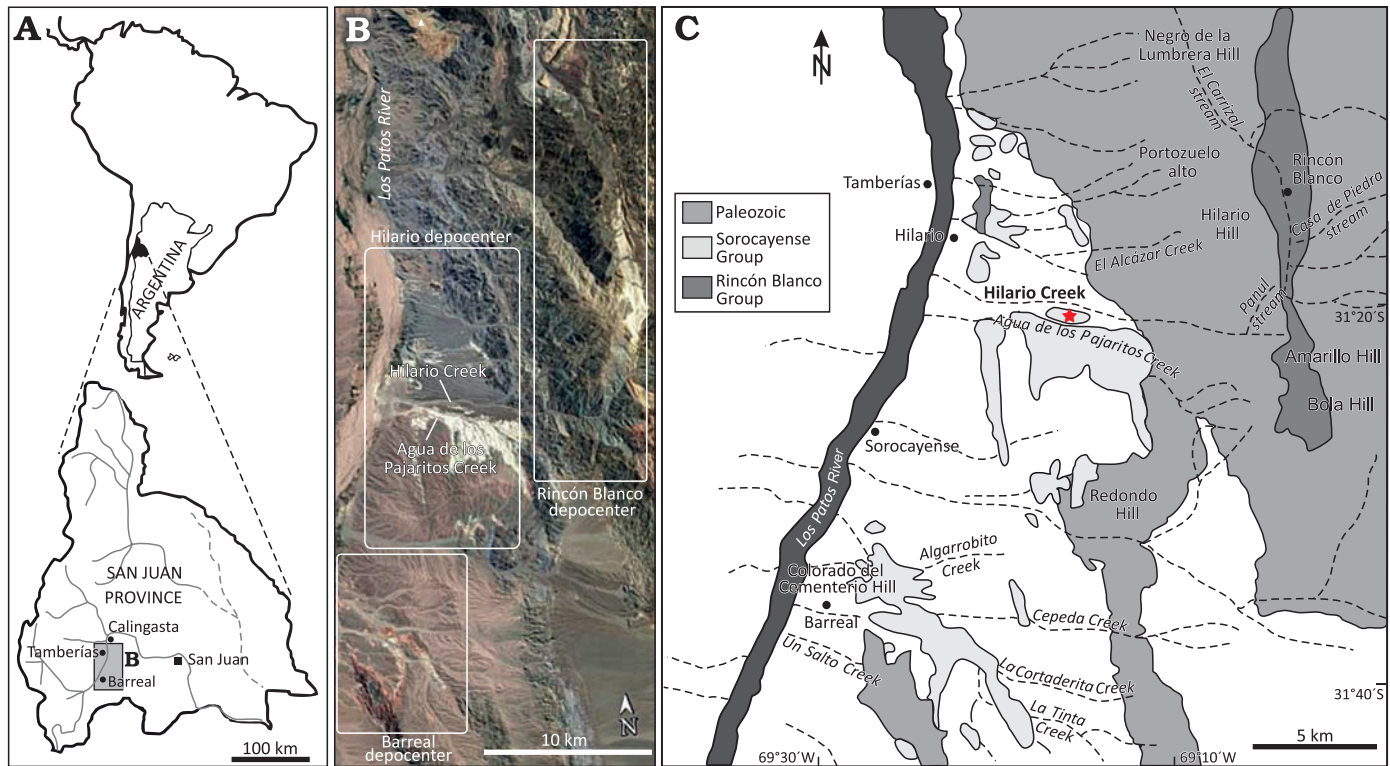


Fig. 1. Location of petrified woods. **A.** Location of the study area at San Juan province, Argentina. **B.** Hilario (northern), Barreal (southern) and Rincón Blanco depocenters of Cuyana Basin. The satellite image taken from Google Earth Pro. **C.** Location map of the Hilario Creek, in the Hilario (northern) depocenter. Modified from Ruiz and Bodnar (2019).

Sorocayense Group (Groeber and Stipanovic 1953; Baraldo and Guerstein 1984; Spalletti 1995; Barredo et al. 2016). This group is divided into the northern and the southern regions. Stratigraphically, the northern region is composed of the formations Agua de los Pajaritos, Monina, Hilario, and El Alcázar; in the Hilario area (Stipanovic 1979; Groeber and Stipanovic 1953; Baraldo and Guerstein 1984; Baraldo et al. 1990; Barredo 2012; Barredo et al. 2016; Table 1) while in the southern region of the Sorocayense Group, the Barreal, Cortaderita and Cepeda formations crop out in the Barreal area (Bodnar et al. 2019).

The stratigraphic framework of the Sorocayense Group in the Barreal (southern) area is overlapping on the discordance of Paleozoic sediments and Devonian diabases, and Hilario on “schists”, graywacke and diabases of the Lower Paleozoic (Stipanovic 1972; Barredo et al. 2016).

The Triassic sequence in the Hilario depocenter (northern) of the Sorocayense Group begins with the Agua de los

Pajaritos Formation, which represents the onset of the basin filling with fluvial-sandy elements and abundant pyroclastic input followed by levels of bituminous pellets from the Monina Formation (Baraldo and Guerstein 1984).

The filling is completed by the El Alcázar Formation characterized by clastic and pyroclastic sediments of fluvial and lacustrine environments alternating with tuff deposits (Baraldo and Guerstein 1984; Baraldo et al. 1990; Barredo et al. 2016; Table 1).

In the Barreal (southern) depocenter, the Hilario Formation correlates with the Don Raúl member of the Cortaderita Formation, which corresponds to an anastomosed fluvial system and flood plains where temporal ponds or lakes developed (Bodnar et al. 2019).

The Hilario Formation consists of sandstone-pelite deposits, and intercalations of tuffs, corresponding to a lacustrine environment that passes into a fluvial environment with flood plains and a palustrine environment.

Table 1. Table of historical comparison of the different stratigraphic nomenclatures of the Sorocayense Group (modified from Barredo et al. 2016).

Pozzo (1948)	Groeber and Stipanovic (1953)	Stipanovic (1972)	Baraldo and Guerstein (1984)	Barredo et al. (2016)
Hilario Triassic Series	Hilario Series	Sorocayense Group (North)	Sorocayense Group (North)	Sorocayense Group (North)
			El Alcázar Formation	El Alcázar Formation
Tobiferous-sandy Trias	Strata of Hilario	Hilario Formation	Hilario Formation	Hilario Formation
Clay Trias	Strata of El Alcázar	El Alcázar Formation	Monina Formation	Monina Formation
Basal or conglomerate Trias	Strata of Agua de los Pajaritos	Agua de los Pajaritos Formation	Agua de los Pajaritos Formation	Agua de los Pajaritos Formation

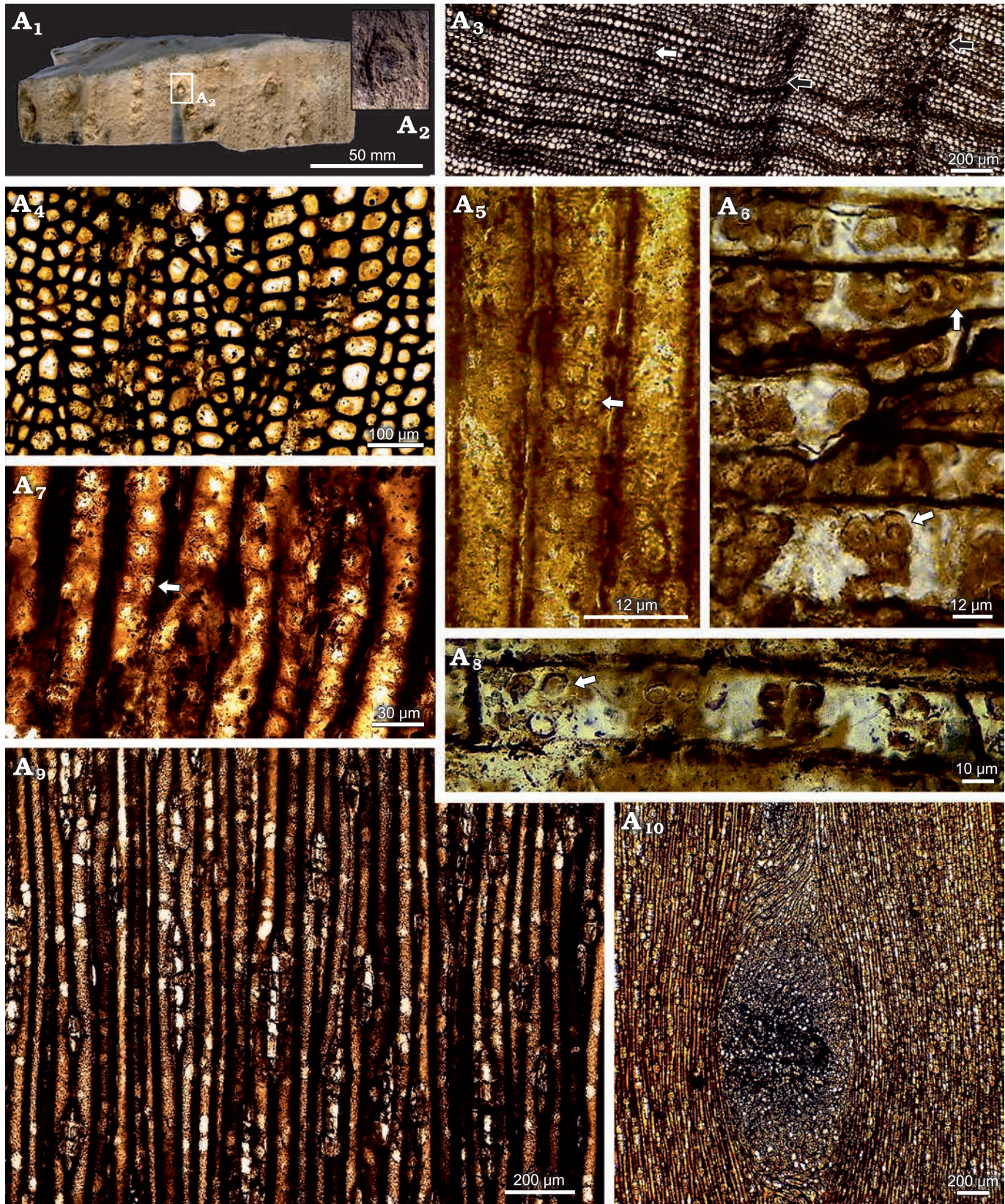


Fig. 2. Ginkgoalean wood *Baieroxylon cicatricum* Prasad and Lele, 1984 (CTES-PB 14411) from Hilario Creek, San Juan province, Argentina, Upper Triassic. General aspect of the wood showing the “eye-shaped” traces (A₁). Detail of the “eye-shaped” trace (A₂). Transverse sections of the secondary wood showing growth rings (white arrow) and “shearing zones” (black arrows) (A₃) and tracheids of unequal size (A₄). Radial longitudinal sections showing partially biseriate uniseriate pits, opposite biseriate pits (arrow) (A₅, A₇) and cupressoid cross-fields and others with the pits grouped in a cluster (A₆, A₈). Radial longitudinal sections showing rays (A₉) and trace detail (A₁₀).

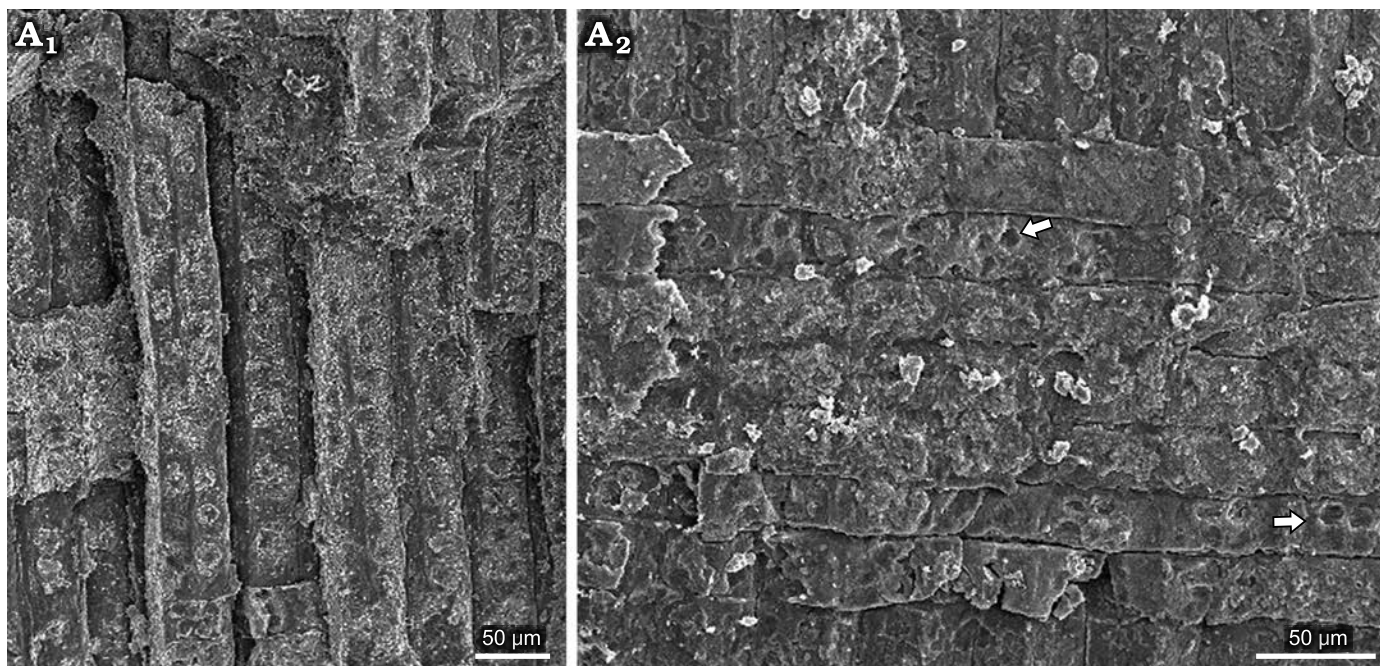


Fig. 3. Ginkgoalean wood. *Baieroxylon cicatricum* Prasad and Lele, 1984 (CTES-PB 14411) from Hilario Creek, San Juan province, Argentina, Upper Triassic. Longitudinal radial section of tracheids with biseriate pits (A_1), Pits in the cross-fields (A_2 , arrows).

(2–10) between adjacent rays. Latewood forms one or two rows of tracheids (Fig. 2A₃). The cell radial diameter is 16 µm (13–18 µm) and the tangential diameter is 23 µm (14–35 µm) (Fig. 2A₄). The mean sensitivity is 0.3 (Fritts 1976; Gou et al. 2021). In some sectors, false growth rings are observed.

In longitudinal radial section, the tracheids present uniseriate araucarian pitting (50%), biseriate (25%) and uniseriate partially biseriate (15%) and mixed (10%) pitting with fine spiral thickenings inclined at an angle of 52° in a clockwise direction. Uniseriate pits are circular, contiguous, or widely spaced. Their average measurements are 10 µm wide and 12 µm high, with a flattening coefficient of 0.83. Biseriate pits are circular, contiguous, alternate, opposite, and some of them are spaced. (Figs. 2A₅, A₇, 3A₁). They measure an average of 9 µm wide by 9 µm high. The opening of the areola measures 7 µm on average. Some cross-fields have up to 5 cupressoid pits, with an araucarioid arrangement, others with 3–4 pits grouped in a cluster measure 5 µm on average (Figs. 2A₆–A₈, 3A₂).

In longitudinal tangential section, the rays are homocellular and uniseriate. The height of the rays is 1–12 cells; the average height is medium (6 cells). The average diameter of the cells is 23 µm high by 22 µm wide (Fig. 2A₉). The density of rays is 23 per mm². In this section, it is possible to visualize a rameal trace that has preserved a homogeneous medulla composed of parenchymatic cells with an oval to circular contour surrounded by the rays. Their average diameter is 13 µm (7–23 µm) (Fig. 2A₁₀).

Remarks.—The anatomical characters of the wood branch under description allow to assign it to *Baieroxylon*, which is characterized by the presence on the radial walls of the tracheids of uni-biseriate pits, often araucarian, flattened, mixed

type pitting with helical thickenings; and rays 1–15 cells high, mostly uniseriate (Greguss 1961; Philippe and Bamford 2008). Based on the radial pitting, *Baieroxylon* unites a group of heterogeneous woods; some species show an araucarioid type and others a mixed type (Gnaedinger 2012).

Baieroxylon has a wide stratigraphic distribution. It is present in sediments from the Permian to the Cretaceous (Crisafulli 2001; Gnaedinger 2012), and includes seven species: *Baieroxylon multiseriale* Prasad, 1982, from Kamthi Formation from upper Permian of India; *Baieroxylon implexum* Greguss, 1961 from Permian of Hungary and Upper Triassic of Germany; *Baieroxylon graminovillae* Prasad and Lele, 1984, from Keuper (Upper Triassic of Germany);

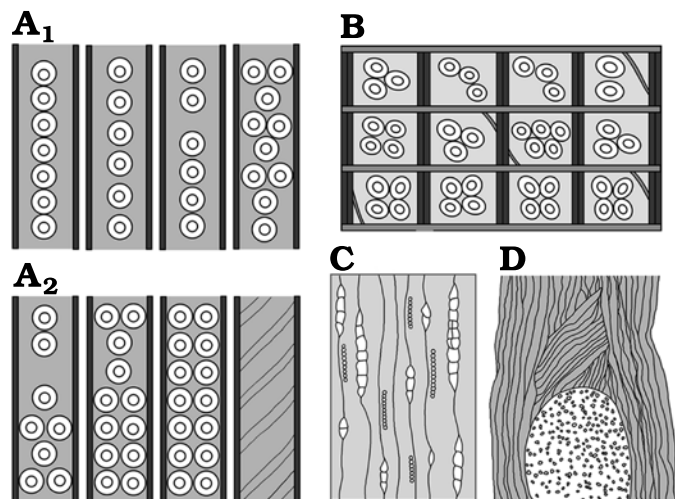


Fig. 4. Schemes showing anatomical characters of *Baieroxylon cicatricum*. A. Tracheid radial pitting patterns (A_1 , A_2). B. Cross field pitting. C. Radial system. D. Detail of scar.

Baieroxylon cambodiense Serra, 1966a, from Mesozoic of Cambodia; *Baieroxylon lindicianum* Philippe, 1995, from Liassic (Lower Jurassic) of France and Hungary; *Baieroxylon chilense* Torres and Philippe, 2002, from Upper Triassic of Chile and Argentina; *Baieroxylon rocablanquense* Gnaedinger, 2012, from Lower Jurassic of Argentina.

According to the comparison made between the species of *Baieroxylon* (SOM: table 1, Supplementary Online Material available at http://app.pan.pl/SOM/app67-Vallejos-Leiz_etal_SOM.pdf), the studied specimen of the Hilario Formation fits the diagnosis of *B. cicatricum* due to a similarity in types, size, shape, and seriation of radial pits, cross-fields, and uniseriate woody rays in the secondary wood and numerous “eye-shaped scars”.

The analyzed species is similar to *B. graminovillae* and *B. cambodiense*, due to similarities in radial pitting of tracheids and cross-fields (pits grouped in a cluster). However, *B. graminovillae* has tracheids with some triseriate pits and *B. cambodiense* has crassulae in the pits and a greater number of them in the cross-fields and also the presence of biseriate rays.

Our material supports the assignment of *Baieroxylon* to the woods of Ginkgoales due to the following anatomical characters: intercellular spaces between tracheids pointed ends in recurvate tracheids, simple or cupressoid pits in cross-fields, low rays and the variable size of the secondary wood tracheids (compare Greguss 1955; Prasad and Lele 1984; Crisafulli 2001; Leiva Verón et al. 2012; Gnaedinger 2012). It is also worth mentioning that Prasad and Lele (1984) found impressions of *Baiera digitata* (Brongniart 1828) Heer, 1876, from the Permian of Hungary, in the same outcrops as *Baieroxylon* sp.

Stratigraphic and geographic range.—Recognised from the Late Permian of Paraguay, Uruguay, and Africa, Upper Triassic of Argentina (this paper), Brazil and India, and Cretaceous of India.

Order Pinales Dumortier, 1829

(= Coniferales Gorozhankin, 1904)

Family Podocarpaceae Endlicher, 1847

Genus *Protophylocladoxylon* (Kräusel, 1939)

Mussa, 1958

Type species: *Protophylocladoxylon dolianitii* Mussa, 1958; Tubarão Series, Guatá Group, Rio Bonito Formation, Santa Catarina System of Santa Catarina, Brazil, lower Permian; see Zijlstra and Philippe (2020).

Protophylocladoxylon hilarioense sp. nov.

Figs. 5–7.

PFNR: PFN002690.

Etymology: In reference to the location where it was found.

Type material: Holotype CTES-PB 11409. Paratype CTES-PB 11406; both silicified wood fragments from the type locality and horizon.

Type locality: Hilario Creek, Cuyana Basin, San Juan province, Argentina.

Type horizon: Hilario Formation, Upper Triassic.

Diagnosis.—Secondary pycnoxylic wood with growth rings slightly marked. Radial tracheid pitting of the earlywood uni-biseriate. Radial tracheid pitting of the latewood uniseriate. Uniseriate pits are circular, contiguous, flattened, and spaced with a tendency to abietinoid type. Biseriate pits circular, opposite and alternate, contiguous, and flattened. Cross-fields with 1–2 simple oblique to horizontal phyllocladoid oopores. Very low-medium uniseriate rays and some uniseriate rays with a short biseriate portion, 1–8 cells high. Tangential walls of tracheids with contiguous, circular and uniseriate pits.

Description.—Decorticated, silicified, dark brown wood fragments. CTES-PB 11409 (Fig. 5A₁) has been selected as the holotype, and CTES-PB 11406, as the paratype. The holotype measures 3.5 cm in length, 5.5 cm in the largest diameter and 3.5 cm in the smallest diameter.

In transverse section, the growth rings are slightly marked (Fig. 5A₂, A₃). The tracheids are circular, oval to quadrangular, and with wide lumens. The average tangential is 33 µm, and the radial diameter is 34 µm. The thickness of the tracheal wall is 5 µm. It presents “shearing zones” sensu Erasmus (1976). It shows false growth rings.

In longitudinal radial section, the walls of the tracheids present uniseriate (70%) and biseriate (30%) araucarian pitting. When uniseriately arranged the pits are circular, contiguous (araucarioid type), and mixed, others are spaced (abietinoid type) and some are flattened (Fig. 5A₄, A₅, A₇, B). It measures an average of 18 µm wide × 16 µm long, with a flattening coefficient of 0.89. When biseriately arranged the pits are circular, sub-opposite, contiguous, and flattened, some are spaced. They have an average width of 14 µm × 16 µm long (Figs. 5A₆–A₈, 6A₁, A₂). The aperture of the areole measures 8 µm on average. The cross-fields present 1–2 simple oblique to horizontal elliptical phyllocladoid-type oopores, with an average aperture of 14 µm (Figs. 5A₉, A₁₀, 6A₃).

In longitudinal tangential section, the radial system is homogeneous. Some rays are uniseriate and some are uniseriate with a short biseriate portion. The rays are very low and medium; the average height is 4 (1–8) cells. Cells average is 26 µm high × 23 µm wide. The density of rays is 22 per mm². The cells of the rays are oval in the central portion and triangular to ellipsoidal at the ends. The tangential walls of the tracheids have contiguous, circular, uniseriate areolate pits (Fig. 5A₁₁, A₁₂).

Remarks.—The specimens present araucarioid, abietinoid and mixed pitting on the radial walls of the tracheids and simple phyllocladoid pits in the cross-fields, consistent with the diagnosis of the genus *Protophylocladoxylon* (Kräusel, 1939) Mussa, 1958. Vozenin-Serra (1970) classified *Protophylocladoxylon* species according to four characters: types of radial pitting, various aspects of pits in cross-fields, presence or absence of axial parenchyma and seriation of rays. Pant and Sing (1987) include it in the group of araucarioid woods for the Paleozoic and Bamford and Philippe

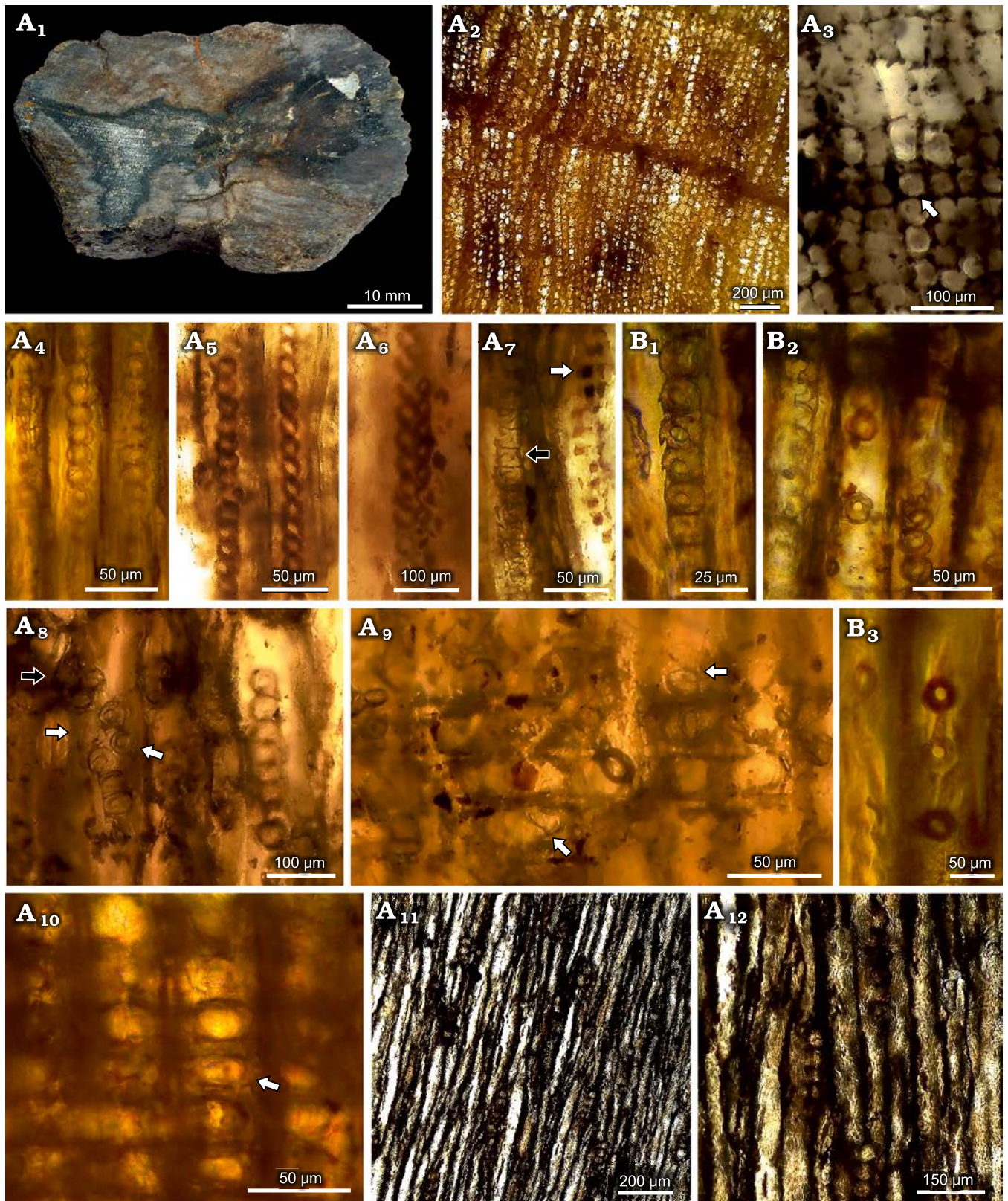


Fig. 5. Podocarpacean wood, *Protophyllocladoxylon hilarioense* sp. nov. from Upper Triassic, Hilario Creek, San Juan province, Argentina. Transverse sections (A₁–A₃); radial longitudinal sections of earlywood (A₄–A₁₀, B); tangential longitudinal sections (A₁₁, A₁₂). A. CTES-PB 14409, the general aspect of the wood (A₁), secondary xylem with growth rings (A₂), tracheids of late wood (arrow, A₃); uniseriate pits and flattened pits (A₄, A₅), biseriate and alternate pits (A₆), uniseriate flattened pits (black arrow) and biseriate opposite pits (white arrow) (A₇), opposite pits (black arrow) and subopposite pits (white arrows) (A₈), cross-fields with oblique to horizontal phyllocladoid oopores (A₉, A₁₀), uniseriate rays (A₁₁, A₁₂). B. CTES-PB 14406, uniseriate pits and flattened pits (B₁), mixed pits with a tendency to abietinoid (B₂), uniseriate separate pits (B₃).

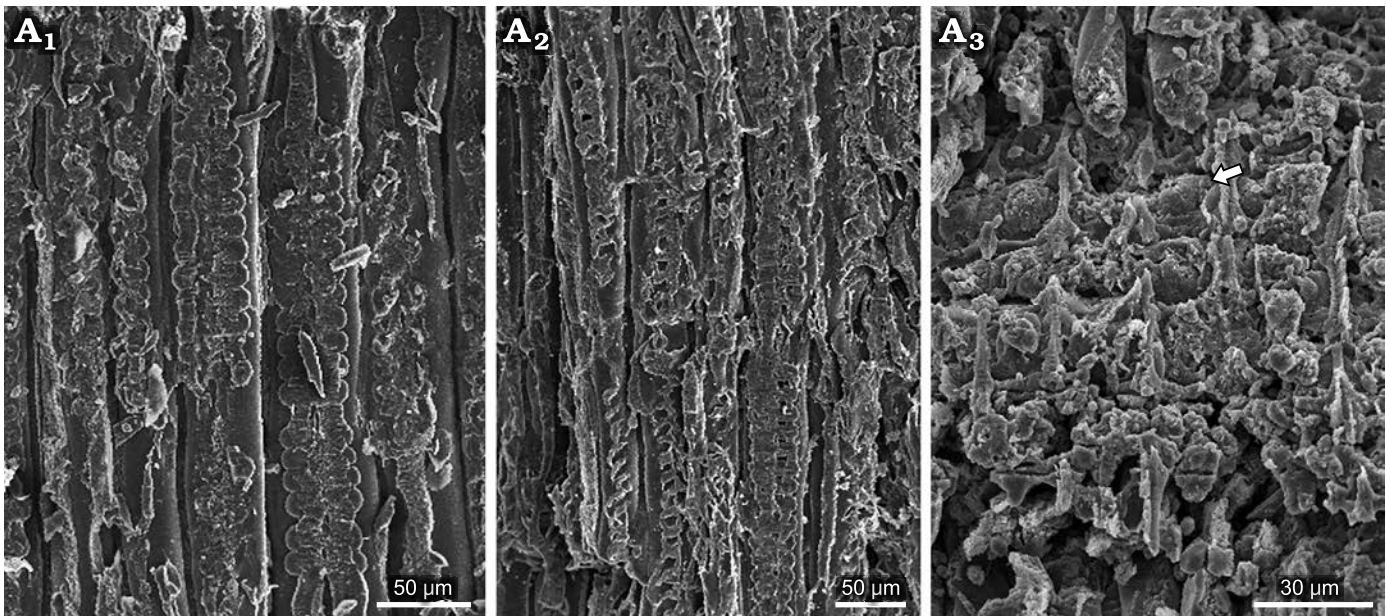


Fig. 6. Podocarpacean wood *Protophyllocladoxylon hilarioense* sp. nov. (CTES-PB 14409) from Upper Triassic, Hilario Creek, San Juan province, Argentina. Longitudinal radial section. Flattened biseriate and uniseriate pits (A_1); flattened uniseriate and biseriate pits (A_2); cross fields with phyllocladoid oopores (A_3 , arrow).

(2001) in the mixed type for Mesozoic woods. Gnaedinger (2007) and Philippe and Bamford (2008) according to the described species show that *Protophyllocladoxylon* is characterized by species with an araucarioid woody plan and others with a mixed woody plant. Therefore, the key of the latter authors includes *Protophyllocladoxylon* in Group B (araucarian or xenoxylean radial pitting) and in Group D (with mixed type radial pitting). The described specimens of the Hilario Formation correspond to the mixed type or group D.

Wan et al. (2019) point out that *Protophyllocladoxylon* species can have three types of pits in the cross-fields: phyllocladoid type (Philippe and Bamford 2008), window-type (Richter et al. 2004) and others with small to medium-sized oval/circular pits, being all simple without borders. Some species have two types such as *Protophyllocladoxylon owensii* Fletcher, Cantrill, Moss, and Salisbury, 2014, showing phyllocladoid oopores and less circular pits. In the Hilario Formation specimens, the cross fields have only the phyllocladoid type of pits.

For the specific determination of the wood, the comparisons were established with species from the Triassic (SOM: table 2). It is worth mentioning that this specimen has similarities with *P. korubaense* Serra, 1966b, and with *P. xenoxylodes* Serra, 1966b, both from Cambodia, regarding the pitting of the radial walls of the tracheids, and the cross-field pits. However, it differs from *P. korubaense* because the specimen from Argentina does not have axial parenchyma, nor tyloses, and presents flattened pits, a greater number of tangential pits and the pits of the cross-fields with elliptical oopores. Similarly, *P. xenoxylodes* is distinguished from the Hilario Formation specimen by presenting axial parenchyma, tyloses, spaced pits and the percentage of flattened

pits is different from the specimens analyzed here. However, Boura et al. (2013) synonymise the species *P. korubaense* and *P. thylloides* (from Upper Triassic of Vietnam) with *P. xenoxylodes* Serra, 1966a (Triassic–Jurassic) based on a reassessment of quantitative anatomical parameters and the presence of tyloses.

According to the indicated differences with the two closest species shown in SOM: table 2, it is proposed to assign the materials from the Hilario outcrop to a new species *Protophyllocladoxylon hilarioense* sp. nov.

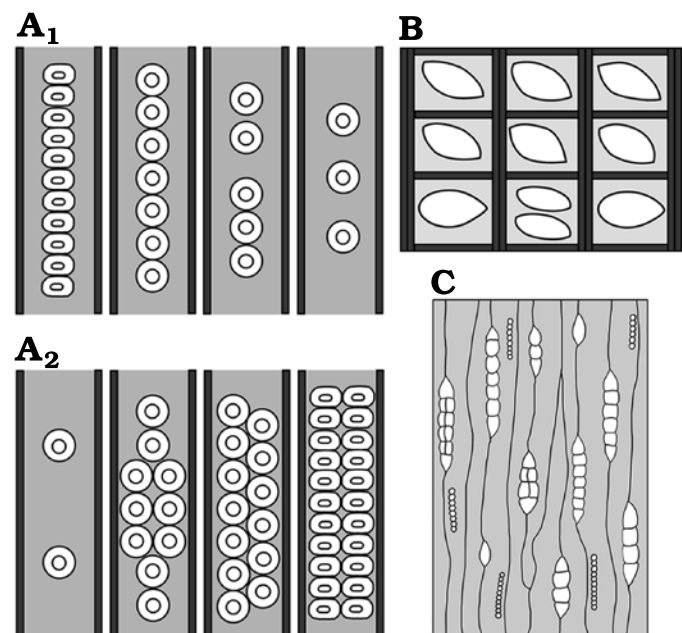


Fig. 7. Schemes showing anatomical characters of *Protophyllocladoxylon hilarioense*. A. Tracheid radial pitting patterns (A_1 , A_2). B. Cross field pitting. C. Radial system.

This new taxon is added to others from South America such as *Protophyllocladoxylon dolianitii* Mussa, 1958, *Protophyllocladoxylon derby* (Olivera, 1936) Maheshwari, 1972, and *Protophyllocladoxylon rosablancaense* Pons, 1971. *Protophyllocladoxylon derbyi* comes from the upper Carboniferous of Brazil. *Protophyllocladoxylon dolianitii* is recorded in the Permian formations of Brazil, Paraguay, Antarctica, and Australia (Mussa 1958; Crisafulli and Herbst 2009; Maheshwari 1972; Wan et al. 2020, respectively) and *P. rosablancaense* was found in Rosa Blanca Formation (Middle Valley of Rio Magdalena, Colombia) in Cretaceous sediments (Pons 1971). The SOM: table 3 compares the anatomical characters of these three taxa with the Hilario specimen. *Protophyllocladoxylon rosablancaense* is the one that shows the most similarity with the material studied herein; although *P. rosablancaense* does not show spaced radial pitting or tangential pitting and the height of the rays is high.

Following the criteria of Gnaedinger (2007), Zhang et al. (2010), and Pujana et al. (2014, 2015), *Protophyllocladoxylon* is most likely related to the basal forms of Podocarpaceae, due to the presence of cross-field pits of phyllocladoid-type, characteristic of some current members of Pinaceae and Podocarpaceae (Ritcher et al. 2004) and for presenting araucarian and mixed pitting on the radial walls of the tracheids. Likewise, in the Triassic, this type of woody axis was found close to *Rissikia* sp. (Podocarpaceae) leaves with female (*Rissikistrobis* sp.) and male (*Rissikianthus* sp.) cones (Townrow 1967; Anderson and Anderson 2003; Gnaedinger and Herbst 2008; Gnaedinger 2010; Holmes and Anderson 2013; Gnaedinger and Zavattieri 2017).

Stratigraphic and geographic range.—Upper Triassic, Hilario Formation, Hilario Creek, Cuyana Basin, San Juan province, southwest Argentina.

Discussion

Biostratigraphic implications.—*Baieroxylon cicatricum* is known from the upper Permian of the Tacuary Formation in the localities of Arroyo Vino (Crisafulli and Herbst 2009) and Guavirá in Paraguay (Leiva Verón et al. 2012), the Yaguari Formation in Uruguay (Crisafulli 2001), and the Ecca Group in Africa (Crisafulli and Herbst 2010). It has also been found in the Upper Triassic of the Tiki Formation (Prasad and Lele 1984) and in the Cretaceous of the Gangapur Formation (Muralidhar-Rao and Ramanujan 1986), both in India, and in Rio Grande do Sul, Brazil (Bardola et al. 2009). Here we present the first record from the Triassic of Argentina. The presence of Ginkgoales in the Sorocayense Group is further corroborated by the record of leaf impressions.

Ginkgophyta had its acme in the Mesozoic times. Then, the group declined during the Cenozoic, with only *Ginkgo biloba* persisting to the present times (Taylor et al. 2009). According to the considerations made by Gnaedinger (2012),

Ginkgoales fossils present secondary xylem of the araucarian or mixed type from the Permian to the Cretaceous and an abietinian type from the Late Cretaceous to the Tertiary (similar to the living species of *Ginkgo biloba*). Moreover, the stratigraphic and paleogeographic distributions of these woods in terms of anatomical changes (from mixed type to abietinian type) are concurrent with the morphological changes in leaves (lamina and petiole differentiation) and reproductive structures (reduction of numbers of seeds and increase in their size) reported in Zhou and Wu (2006) and Zhou (2009).

This group is recorded throughout Gondwana, presenting a large number of endemic forms in the southwest. Meanwhile, the greatest biodiversity is recorded in the high paleolatitudes (around 60° south paleolatitude), in the Karoo Basin (South Africa) and El Tranquilo Group (Patagonia, Argentina).

Protophyllocladoxylon is a cosmopolitan taxon. Its oldest record is from the Carboniferous. Zhang et al. (2010) presented a comparative table that includes most of the known Paleozoic and Mesozoic species. Then Boura et al. (2013), Fletcher et al. (2014), Pujana et al. (2014, 2015), Iamandei et al. (2018), Wan et al. (2019), and Gou et al. (2021) detailed other species of *Protophyllocladoxylon* and extended their range to the Eocene.

Protophyllocladoxylon hilarioense sp. nov. is the thirty-sixth species of the genus and its first record from the Triassic of Argentina.

Paleoclimatic and paleoecological implications.—*Baieroxylon* and *Protophyllocladoxylon* species occur in various paleoclimates, both in warm and humid and temperate to cold conditions (Crisafulli and Herbst 2009; Zhang et al. 2010; Gnaedinger 2012).

The presence of variations in the growth rings of the analyzed woods may indicate slight seasonal changes characterized by the alternation of dry and humid periods in response to variables such as rainfall, temperature and light availability (Creber and Chaloner 1984; Taylor and Ryberg 2007; Pires and Guerra Sommer 2011; Yang et al. 2013).

The rings analyzed correspond to type “E” of the classification proposed by Creber and Chaloner (seen in Brison et al. 2001). It means that these plants went through relatively uniform growing seasons but each one with a terminal event represents a cessation or delay of cambium activity.

The presence of narrow latewoods, such as in these specimens (composed of 2–5 radially compressed cells), probably reflects a rapid onset of unfavourable growth conditions and/or the result of a water deficit during the summer. However, it is not ruled out that it could be associated with the genetic makeup load of the species (Creber and Chaloner 1984; Brea et al. 2005).

A value of 0.3 of mean sensitivity (SM) was obtained for *Baieroxylon cicatricum*, which corresponds to a complacent wood, equivalent to little marked climatic changes (Brea et al. 2005; Pires and Guerra Sommer 2011).

The presence of false growth rings observed in these woods could be attributed to a cold season, or also by drought, or by defoliation caused by insects (Jefferson 1982; Zamuner 1986). Another anatomical feature with paleoenvironmental significance is the value of the flattening coefficients of the pits. The numbers obtained here indicate openings of considerable size and tracheids with a wide lumen, which denotes that they grew in subtropical conditions with little marked seasons (Creber 1977).

According to these data, it can be inferred that these trees grew in a humid but seasonally dry subtropical climate, in an environment that corresponds to a fluvial system with flood plains and paludal environments. This is suggested by the sandy-limolitic sediments of the Hilario Formation inferred by Baraldo and Guerstein (1984) and Barredo et al. (2016) that are the hosts of the woods of this xylotaphoflora.

Conclusions

The first wood species found in the Hilario Formation are described and assigned to *Baieroxylon cicatricum* (Ginkgoales) and *Protophylladoxylon hilarioense* sp. nov. (Coniferales: Podocarpaceae). The new specie contributes to the diversity and confirms the presence of the Podocarpaceae.

These taxa are added to the impressions of *Neocalamites carrerei* and *Neocalamites* sp. found in this Upper Triassic formation of San Juan province, described by Groeber and Stipanovic (1953). The wood of *Baieroxylon cicatricum* found in the Hilario Formation constitutes its first occurrence in the Triassic of Argentina, thus adding a new Gondwanan occurrence to those already known from Brazil and India. The species has wide both stratigraphic and geographic ranges occurring from the Permian in sediments of Paraguay, Uruguay, and Namibia to the Cretaceous of India.

From the paleoenvironmental point of view, the type of growth rings observed is consistent with a humid but seasonally dry subtropical climate. False growth rings were probably formed due to drought during the growing season, and/or arthropod damage during the life of these trees. These woods are probably representatives of the arboreal stratum of a mesophytic association where the Sphenophytes found would represent the understory. The described taxa extend the paleobotanical spectrum of the Sorocayense Group, composed of Corystospermales, Ginkgoales and Coniferales (Podocarpaceae, Cupressaceae).

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SUPPLEMENTARY ONLINE MATERIAL FOR

New records of Upper Triassic wood from Argentina and their biostratigraphic, paleoclimatic, and paleoecological implications

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Supplementary Online Material

SOM Table 1. Comparison of the anatomical characters of the secondary xylem of *Baieroxylon* species

SOM Table 2. Comparison of the anatomical characters of related Triassic species of *Protophyllocladoxylon hilarioense* sp. nov.

SOM Table 3. Comparison of the anatomical characters of South American species of *Protophyllocladoxylon*.

References

SOM Table 1. Comparison of the anatomical characters of the secondary xylem of *Baieroxylon* species.

AP= axial parenchyma, HT= helicoidal thickenings, A= absent, P= present, r= rare, d= diffuse. Modified from Gnaedinger (2012).

Taxon	Age and country	Pith	Secondary xylem					
			Tracheid radial pitting	AP	HT	Cross-field pits	Xylem rays	
							Seriation	Height
<i>Baieroxylon multiseriale</i> Prasad, 1982	late Permian India	A	1–4 seriate, circular and hexagonal, alternate, opposite, contiguous and separate	A	P	1–15 circular and oval to simple	1 seriate	1–15
<i>B. cicatricum</i> Prasad and Lele in Crisafulli, 2001	late Permian Uruguay	Scars, homogeneous parenchymatous pith	1–2 seriate, alternate, opposite, contiguous and separate	A	p	Mean 4	1 seriate	3–12
<i>B. cicatricum</i> Prasad and Lele in Crisafulli and Herbst, 2009	late Permian Paraguay	Scars, homogeneous parenchymatous pith	1–2 seriate, alternate, opposite, contiguous and separate	A	p	Mean 4	1 seriate	3–12
<i>B. implexum</i> Greguss, 1961	Late Triassic, Germany Permian, Hungary	A	1–3 seriate, contiguous	r	p	1–4 elliptical, simple	1 seriate	1–8
<i>B. chilensis</i> Torres and Philippe in Crisafulli and Herbst, 2010	Late Triassic, Argentina	A	1 seriate, contiguous, some separate, rarely biseriate alternate	P	P	Cupressoid, 1–4	1 seriate	1–13
<i>B. cicatricum</i> Prasad and Lele, 1984	Late Triassic, India	A	1–3 seriate alternate-opposite, contiguous and separate	A	P	Up to 9	1 seriate	1–10
<i>B. cicatricum</i> Prasad and Lele in Bardola et al., 2009	Late Triassic, Brazil	A	1–2 seriate, alternate, contiguous and separate, mixed type	A	P	1–4	1 seriate	1–14
<i>B. cicatricum</i> Prasad and Lele, 1984 (Vallejos Leiz et al. 2022)	Upper Triassic, Argentina	A	1–2 seriate, alternate, contiguous and separate, mixed type	A	P	Up to 5 arranged in crowns	1 seriate	2–12
<i>B. graminovillae</i> (Zimmermann, 1953) Prasad and Lele, 1984	Late Triassic, Germany	A	1–2 seriate, rarely 3 seriate, araucarioid type	A	P	1–4 oval, simple	1 seriate	1–15
<i>B. cambogdiense</i> Serra, 1966a	Mesozoic, Asia	A	1–2 seriate, opposite, alternate, with crassulae	A	A	4–19 arranged in crowns	1–2 seriate	4–19
<i>B. chilense</i> Torres and Philippe, 2002	Early Jurassic Chile	A	1–2 seriate, contiguous or separate, sometimes alternate	P	A	1–2	1 seriate, some locally 2 seriate	1–7(–15)

<i>B. sp. cf. B. chilense</i> Torres and Philippe in Gnaedinger and Herbst, 2009	Early Jurassic Argentina	A	1–2 seriate, contiguous or separate, alternate or opposite	A	A	1–2	1 seriate, some locally 2 seriate	2–6
<i>B. lindicianum</i> Philippe, 1995 (Philippe and Barbacka 1997)	Early Jurassic, France and Hungary	A	1–2 seriate, alternate- subopposite	A	A	4–7 oval	1–2 seriate	—
<i>B. rocablanquense</i> Gnaedinger, 2012	Early Jurassic Argentina	A	1 seriate, contiguous and separate	A	P	1–6 circular cupressoid pits, in horizontal rows, sometimes 8 arranged in groups or crowns.	1 seriate	2–8
<i>B. cicatricum</i> Prasad and Lele in Rao and Ramanujan, 1986	Cretaceous India	A	1–2 seriate, alternate, opposite, contiguous and separate, occasionally 3 seriate, alternate	d	A	1–8 simple pits, elliptic or oval and oblique	1 seriate	1–11

SOM Table 2. Comparison of the anatomical characters of related Triassic species of *Protophyllocladoxylon hilarioense* sp. nov. AP= axial parenchyma, GR= growth rings, T= tylosis, A= absent, P= present, ?= uncertain, n.o= not observed, ab= abundant, r= rare.

Taxon	Age and country	GR	AP	T	Radial pits	Tangential pits	Cross-field pits	Xylem rays	
								Seriation	Height
<i>Protophyllocladoxylon zhaobishanensis</i> Wan, Yang, and Wang, 2019	Zhaobishan, Shanshan, Turpan, Xinjiang, China.	P	A	P	1–2- seriate, rarely 3 seriate; rounded to polygonal rarely flattened in outline, with circular apertures, uniseriate contiguous rarely arranged in groups. Multiseriate pits contiguously and alternatively arranged.	1–2 seriate	1–2; window-like, sometimes circular, oval simple pits	1 seriate	1–28
<i>P. xenoxylodes</i> Serra, 1966a	Phnom-Ker, Cambodia	A	P	P	1–2 seriate; alternate, rarely opposite, flattened, elliptic or circular	n.o.	1 occasionally 2; oval to circular horizontal	1, rarely 2 seriate	1–12
<i>P. thylloides</i> Serra, 1966a	Ho-Hom, Quang-Nam, Vietnam	P	?	ab	1–2 seriate; uniseriate flattened; biseriate, alternate, rarely opposite, contiguous or separate, hexagonal	n.o.	1–2; elliptic, oblique to almost vertical, rarely horizontal	1 seriate, rarely 2 seriate	1–29
<i>P. lechangense</i> Wang, 1993	South China	A	A	A	1–3, rarely 4 seriate; 2–3 seriate in earlywood, alternate, hexagonal, uniseriate in latewood, contiguous, subcircular	r	1–2; rectangular with rounded angles or elliptic, horizontal	1 seriate	1–11
<i>P. korubaense</i> Serra, 1966b	Rovieng, Kompong Thom, Cambodia	A	P	P	1–2 seriate; uniseriate, contiguous or separate circular; biseriate, alternate, rarely opposite	r	1–2; oval to circular	1–2 seriate	1–28
<i>P. parathylloides</i> Vozenin-Serra, 1970	Quang-Nam, Vietnam	A	?	ab	1–2 seriate; araucarian, with a mixed tendency	n.o.	1–2; small more or less oval, obliquely disposed, sometimes with a vertical tendency	1-2 seriate	1–48
<i>P. szei</i> Wang, 1991	Guangdong, Mongolia	A	A	A	1 seriate; contiguous or sometime separate, circular or sometimes flattened	n.o.	1; large, circular, broadly oval or elliptic, vertical or oblique	1 seriate	1–10
<i>P. hilarioense</i> (Vallejos Leiz et al. 2022)	Hilario, San Juan, Argentina	P	A	A	1–2 seriate; uniseriate, contiguous to flattened, sometimes separate with abietinoid tendency circular; biseriate, subopposite, contiguous and flattened, rarely separate circular	1, rarely 2 seriate	1–2; elliptic, oblique, rarely horizontal	1 seriate; partly 2 seriate	1–10

SOM Table 3. Comparison of the anatomical characters of South American species of *Protophyllocladoxylon*.

AP= axial parenchyma, GR= growth rings, A= absent, P= present, n.o= not observed, r= rare.

Taxon	Locality and country	Age	Secondary xylem						
			GR	AP	Radial pits	Tangential pits	Cross-field pits	Xylem rays	
								Seriation	Height
<i>Protophyllocladoxylon dolianitii</i> Mussa, 1958	Brazil	late Carboniferous (Mississippian)	A	A	1–3 seriate; alternate and polygonal	n.o.	1–2, horizontal or oblique	1 seriate	1–30
<i>P. derby</i> (Oliveira, 1936) Maheshwari, 1972	Brazil	late Carboniferous (Pennsylvanian)	P	A	1 seriate; oblique and oval	r	1–2	1 seriate; partly 2 seriate	1–47
<i>P. rosablancaense</i> Pons, 1971	Colombia	Early Cretaceous	A	A	1–2 seriate; uniseriate, contiguous, flattened, rarely circular; biseriate, alternate, flattened	n.o.	1–2, elliptic, oblique, rarely horizontal	1-2 seriate	1–20
<i>P. hilarioense</i> (Vallejos Leiz et al. 2022)	Argentina	Upper Triassic	P	A	1–2 seriate; uniseriate, contiguous to flattened, sometimes separate with abietinoid tendency, circular; biseriate, subopposite, contiguous and flattened, rarely separate, circular	1, rarely 2 seriate	1–2; elliptic, oblique, rarely horizontal	1 seriate; partly 2 seriate	1–10

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