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

LAURA VALLEJOS LEIZ, ALEXANDRA CRISAFULLI, and SILVIA GNAEDINGER


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 Sorocayense Group (Groeber and Stipanicic 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 (Stipanicic 1979; Groeber and Stipanicic 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 (Stipanicic 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 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).

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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).

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

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<td>Hilario Triassic Series</td>
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<td>El Alcázar Formation</td>
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<td>Tuberous-sandy Trias</td>
<td>Strata of Hilaro</td>
<td>Hilaro Formation</td>
<td>Hilaro Formation</td>
<td>El Alcázar Formation</td>
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<tr>
<td>Clay Trias</td>
<td>Strata of El Alcázar</td>
<td>El Alcázar Formation</td>
<td>Monina Formation</td>
<td>Hilaro Formation</td>
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<td>Basal or conglomerate Trias</td>
<td>Strata of Agua de los Pajaritos</td>
<td>Agua de los Pajaritos Formation</td>
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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.

The Hilario Formation was first described as a part of the Hilario Triassic Series (Pozzo 1948; Groeber and Stipanicic 1953) and later, within the Hilario Group, as an informal denomination of Stipanicic (1969). According to the nomenclature of the “Comité Argentino de Estratigrafía (1992)” (Argentine Committee of Stratigraphy), the denomination of “Hilario Triassic Series” and “Hilario Series” were not valid due to the use of the same toponym for two entities of different hierarchies such as Formation and Group (Stipanicic 2002; Table 1).

The age of the Hilario Formation would correspond to the Norian–Rhaetian (Upper Triassic), based on the stratigraphic correlations elaborated by Spalletti et al. (1999) and Stipanicic (2002).

Historical background

Bodnar et al. (2019) suggested that the taphofloras of the Barreal (southern), Hilario (northern), and Rincón Blanco (eastern) depocentres display similarity in plant paleocommunities, in which the main components are Corystospermales: of arboREAL species of Zabaria and shrubs Dicroidium, Xylopteris, Peltaspermales (Lepidopteris, Pachydermophyllum), and Cycadales (Pterophyllum and Pseudocotinus). Wood taxa reported from the Sorocayense Group are as follows: Rhexoxylon sp. from the Barreal Formation (Lutz and Herbst 1992); Rhexoxylon sp., Tranquiloxylon sp., and Protocircoporoxylon sp. from the El Alcazar Formation (Ganuza et al. 1998; Drovandi et al. 2016). Rhexoxylon cortaderitaense, Juniperoxylon zamunerae from the Cortaderita Formation, and Protocircoporoxylon sp. from the Monina Formation (Drovandi et al. 2020).

However, the detailed descriptions of fossils from the Hilario Formation are only those of the sphenopsids NeoCalamites carrerei, NeoCalamites sp. and the conchostracans Estheria sp. (Groeber and Stipanicic 1953).

Material and methods

The studied material consists of silicified, decorticated specimens, with good preservation of cellular elements, which are deposited in the Colecciones Paleontológicas de la Universidad Nacional del Nordeste “Dr Rafael Herbst”, Sección Paleobotánica de Corrientes (CTES-PB). They were collected in various expeditions in the decades 1980–1990 by Rafael Herbst, Alicia Lutz, Susana Morton, Oscar Gallego and collaborators in Hilario Creek (Fig. 1). This site is located 122 m above sea level, and its coordinates are 31°20’S and 69°15’W.

The specimens were processed according to the standard methodology by making cuts in the transverse, radial longitudinal, and tangential longitudinal sections, and polishing with abrasives of different granulometry up to a thickness of 40 μm (Hass and Rowe 1999). The thin sections were studied in detail with a Leica microscope (DM500), the photomicrographs were taken with a digital camera (Leica ICC50). The scanning electron microscope (SEM JEOL 5800LV) from the Universidad Nacional del Nordeste, Corrientes, Argentina, has been used in pertinent cases.

The measurements of the different anatomic elements were obtained after with a minimum of 30 measurements. The mean and, between parent, the minimum and maximum values were recorded in the descriptions.

The terminology used corresponds to the list of microscopic characters for the wood identification of the International Association of Wood Anatomists (Richter et al. 2004) and Garcia Esteban et al. (2002, 2003). Systems of nomenclature and nomenclatural reviews are those of Philippe and Bamford (2008) and Zijlstra and Phillippe (2020).

Systematic palaeontology

Class Spermoptopsida Serbet and Rothwell, 1995
Order Ginkgoales Engler, 1897
Genus Baieroxylon Greguss, 1961
Type species: Baieroxylon implexum Greguss, 1961; Löwenstein Formation, Keuper, Upper Triassic of Germany.

Baieroxylon cicatricum Prasad and Lele, 1984
Figs. 2–4.
2009 Baieroxylon cicatricum Prasad and Lele, 1984; Crisafulli and Herbst 2009: 103–106, figs. 5H, 6A–E.

Material.—CTES-PB 11411, a piece of silicified wood branch from Hilario Creek, San Juan province, southwest Argentina, Upper Triassic.

Description.—Decorticated secondary wood fragment, silicified, dark grey, 10 cm in major diameter and 9 cm in minor diameter, and 3.5 cm in length. Externally, it presents a branch with numerous simple scars (from smaller branches or leaves) that follow a helical disposition (Fig. 2A). These are ovoid or eye-shaped (sensu Prasad and Lele 1984) in outline and range in diameter from 5 to 7 mm. In transverse section, the transition from earlywood to latewood is gradual. The tracheids of the earlywood are round to quadrangular in shape, with variable size and with intercellular spaces of varying
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 (*A*₁). Detail of the "eye-shaped" trace (*A*₂). Transverse sections of the secondary wood showing growth rings (white arrow) and "shearing zones" (black arrows) (*A*₃) and tracheids of unequal size (*A*₄). Radial longitudinal sections showing partially biseriate uniseriate pits, opposite biseriate pits (arrow) (*A*₅, *A*₇) and cupressoid cross-fields and others with the pits grouped in a cluster (*A*₆, *A*₈). Radial longitudinal sections showing rays (*A*₉) and trace detail (*A*₁₀).
shape and dimensions, which give the wood a disorganized appearance in some sectors. They have an average radial diameter of 48 μm (30–65 μm) and a tangential diameter of 46 μm (26–62 μm). These present an average of 6 tracheids (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, 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* Gressu, 1961 from Permian of Hungary and Upper Triassic of Germany; *Baieroxylon graminovillae* Prasad and Lele, 1984, from Keuper (Upper Triassic of Germany); *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 recablanquense* 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 Gressu 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 Protophyllocladoxylon** (Kräusel, 1939)

**Mussa, 1958**

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

*Protophyllocladoxylon hilarioense* sp. nov.

Figs. 5–7.

*PFN:* 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 rectangular, 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. 5A8, A9, A10, A11). 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. 5A12, A13, A14).

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 elliptoidal at the ends. The tangential walls of the tracheids have contiguous, circular, uniseriate areolate pits (Fig. 5A12, A13).

**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 *Protophyllocladoxylon* (Kräusel, 1939) Mussa, 1958. Vozenin-Serra (1970) classified *Protophyllocladoxylon* species according to four characters: types of radial pitting, various aspects of pits in cross-fields, pres-
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).
ence 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 (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. xenoxyloides* 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. xenoxyloides* 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. xenoxyloides* 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

![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).](image1)

![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.](image2)
the materials from the Hilario outcrop to a new species *Protophyllocladoxylon hilarioense* sp. nov.

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 derby* 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 (*Rissikistrobus* 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.—***Baieroxyylon cicatricum* is known from the upper Permian of the Taecuary 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 and Herbst 2001), and the Ecca Group in Africa (Crisafulli and Herbst 2009). 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 furthermore 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 *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.—** *Baieroxyylon* 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 *Baieroxyylon cicatricum*, which corresponds to a complacent wood, equivalent to little marked climatic changes (Brea et al. 2005; Pires and Guerra Sommer 2011).
Conclusions

The first wood species found in the Hilario Formation are described and assigned to *Baieroxylon cicatricum* (Ginkgoales) and *Protophyllocladoxylon hilarioense* sp. nov. (Coniferales: Podocarpaceae). The new species 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 Stipanicic (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 Sphenophyta found would represent the understory. The described taxa extend the paleobotanical spectrum of the Sorocayense Group, composed of Coryospermales, Ginkgoales and Coniferales (Podocarpaceae, Cupressaceae).

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References


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