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Podocarpaceae woods (Coniferales) from middle Jurassic La Matilde formation, Santa Cruz province, Argentina

Silvia Gnaedinger *

Centro de Ecología Aplicada del Litoral (CECOAL)-Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste (UNNE), Casilla de Correo 128, 3400 Corrientes, Argentina

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Abstract

The anatomy of Podocarpaceae petrified woods (Coniferales) from La Matilde Formation (Middle Jurassic), that crop out in the Gran Bajo de San Julián area, of Santa Cruz province, Argentina are studied. The following species are described: *Podocarpoxylon feruglioi* nov. sp., *Podocarpoxylon austroamericanum* nov. sp.; *Circoporoxylon sanjuliense* nov. sp. and *Circoporopitys argentinum* nov. gen. et. sp.. The first two morphogenera correspond to specimens based on their secondary xylem (tracheid pitting, cross-fields and ray characters), while *Circoporopitys* is defined considering features of the pith, primary and secondary xylem. Also, a new combination, *Circoporopitys shanense* (Sahni) is proposed. Comparisons are made with other Podocarpaceae species from Gondwana. *Podocarpoxylon* Gothan and *Circoporoxylon* Kräusel are recorded for the first time for the Argentine Jurassic. The growth ring information of the woods suggest that they developed under very favorable environmental conditions, with a warm and humid paleoclimate.

Keywords: Podocarpaceae; fossil wood; Middle Jurassic; Santa Cruz province; Argentina

1. Introduction

La Matilde Formation is a volcaniclastic or pyroclastic sequence, with chonites, tuffs and tufolites, carrying *in situ* silicified trees, many fallen ones and fragments and logs of wood. Geological and paleontological characteristics of this Formation have already been described by several authors, for example, Delhaes (1913), Frenguelli (1933), Feruglio (1949), Stipanicic and Reig (1957), Spalletti et al. (1982), Panza and Irigoyen (1995) and Panza (1998). Sediments of this formation crop out in several areas in Santa Cruz province (Argentina). Studies of petrified cones (Spegazzini, 1924; Calder, 1953; Menéndez, 1960; Stockey, 1977, 1978; Stockey and Taylor, 1978), as well as leaf impressions (Baldoni, 1981, 1990) silicified fungi (Singer and Archangelsky, 1957), and a wood, *Agathoxylon matildense* (Zamuner and Falaschi, 2005) have been described from the well known "Jaramillo Petrified Forests", including areas such as Cerro Madre e Hija and Cerro Cuadrado, among others. Herbst et al. (1995) found new outcrops with many petrified logs in the south of the province, in the Gran Bajo de San Julián area, in addition to other previously described known localities such Laguna del Carbón, Mina de Pareja and Puesto Raspuzzi, which show the same characteristics as those from the North of the province, *i.e.*, forests with *in*

* Fax: +54 3783 454421.
E-mail address: scgnaed@hotmail.com.

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situ petrified logs and rolled trees, that reach diameters of up to 2.4 m. Anatomical descriptions of Osmundales and leaf impressions of the orders Equisetales, Osmundales, Bennettitales and Coniferales were made from these outcrops (Feruglio, 1951; Archangelsky and De la Sota, 1962; Herbst, 1977; Herbst and Salazar, 1999; Herbst, 2003).

This study is part of a series of contributions with the objective of examining the xylotaphoflora of the La Matilde Formation that crops out in the Gran Bajo de San Julián area. In previous studies, species of the following genera were described: *Prototaxoxylon* Kräusel y Dolianiti of the Taxales; *Agathoxylon* Hartig (= *Araucarioxylon* Kraus), of the Araucariaceae, *Protelicoxylon* Philippe and *Herbstiloxylon* Gnaedinger, related to members of the Cupressaceae, and *Planoxylon* Stopes, of the group Protopinaceae, order Coniferales (Gnaedinger, 2001; Gnaedinger and Herbst, 2006; Gnaedinger, 2007). In this study, a new genus: *Circoporopitys* and new species of *Podocarpoxylon* Gothan and *Circoporoxylon* Kräusel (Podocarpaceae; order Coniferales) are created and also recorded for the first time for the Jurassic La Matilde Formation in Argentina.

2. Materials and methods

The specimens described in this paper have been collected from the following localities: Cerro Conito, Bardas Blancas (Estancia Meseta Chica), Mina de Pareja and Laguna del Carbón (Estancia La Silvita) (Gnaedinger and Herbst, 2006; Gnaedinger, 2007: fig. 1). Thirteen fragments from silicified logs with very good cellular preservation of the secondary xylem have been analyzed. Petrographic sections: transversal (TS), radial longitudinal (RLS) and tangential longitudinal (TLS) were made from these fragments. Also, cellulose acetate peels of the three sections were prepared with good results in most of the cases. Observations were carried out with a Leitz microscope (Ortholux–Orthomax), a Leitz stereoscope (LM) and a scanning electron microscope (SEM).

A minimum of 20 measurements of the different anatomical elements were carried out, and in the case of the woody ray heights, the mean, minimum–maximum and occasional maximum are indicated. The Glossary of Terms of the International Association of Wood Anatomists (I.A.W.A., 2004) and the standard measures established by Chattaway (1932) are followed.

Specimens are deposited in the paleobotanical collection of the Faculty of Exact and Natural Sciences of the National University of the Northeast (Corrientes, Argentina) under CTES-PB for specimens and CTES-PMP for the microscope slides.

3. Systematic paleobotany

Order CONIFERALES
Family PODOCARPACEAE Endlicher 1847

There are several form genera of fossil Podocarpaceae woods recorded from the Carboniferous to the Tertiary. These genera are the following:

A) Genera diagnosed on the basis of the secondary xylem:

1—Araucarioid-mixed woody plan: *Protophyllocladoxylon* Kräusel: with cross-fields of the "phyllocladoid type"; *Protocircoporoxylon* Vogellehner: characterized by cross-fields of the "circopores type". The wood anatomy of both genera characterizes a heterogeneous wood group; according to the tracheid pitting in radial walls some species show an araucarioid type, while others a mixed type (Pons, 1969). Therefore, there are authors, such as Pant and Sing (1987) who include these genera within the araucarioid group, for Paleozoic woods, while Bamford and Philippe (2001) include them within the mixed group, for Mesozoic woods.

2—Mixed woody plan: *Protopodocarpoxylon* Eckhold: with cross-fields of the "podocarpoid type".

3—Abietinoid woody plan: Gothan, in 1905 established *Podocarpoxylon* for cross-fields with areolate pits and large and elliptical aperture (podocarpoid type) and *Phyllocladoxylon* for cross-field with a single pit (phyllocladoid type). Later, Stopes (1915) considered that the difference between these two genera based on the cross-field pits was not clear enough, since both types of pits appear in several species of *Podocarpus* L'Hér. ex Pers. and *Phyllocladus* Rich. ex Mirb, and therefore she included both genera in *Podocarpoxylon*. Seward (1919) agreed with Stopes' criterium but established the genus *Mesembrioxylon* because this name does not imply a direct relationship with actual plants. This last genus is characterized by abietinoid type pits and cross-fields with 1 or 2 simple large pits or with a reduced areole.

Finally, Kräusel (1949) formally rehabilitated Gothan's genera (*Podocarpoxylon* and *Phyllocladoxylon*) and created a new one for Podocarpaceae: *Circoporoxylon*. There is a current tendency among the authors to use *Podocarpoxylon*, *Phyllocladoxylon* and *Circoporoxylon*. The main difference among these three genera is given by the type of pits in the cross-fields:
Podocarpoxylon Gothan: "podocarpoid type" cross-fields
Phyllocladoxylon Gothan: "phyllocladoid type" cross-fields
Circoporoxylon Kräusel: "circopore type" cross-fields

B) Genera created on the basis of the pith and primary and secondary xylem:

1—“Protophyllocladoxylon type” secondary xylem:

- *Phyllocladopitys* Kräusel: homo-heterocellular non-septate pith. Mesarch–exarch primary xylem.
- *Medullopitys* Kräusel: heterocellular non-septate pith. Endarch primary xylem.
- *Septomedullopitys* Guerra–Sommer: septate pith with ramified secretory canals. Endarch primary xylem.

These last three genera are constituted by an araucarioid type secondary xylem (Lepekhina and Yatsenko Khmelevsky, 1966; Lepekhina, 1972; Pant and Sing, 1987).

2—“Protopodocarpoxylon type” secondary xylem: *Protopodocarpitys* Mussa: heterogeneous pith (parenchymatic cells and secretory bands); endarch, tending to mesarch, primary xylem.

According to this classification, two species of *Podocarpoxylon* Gothan, one species of *Circoporoxylon* Kräusel and a new genus of *Circoporopitys* have been identified in the La Matilde Formation from the Gran Bajo de San Julián area.

Genus *Podocarpoxylon* Gothan, 1905

Type species: *Podocarpoxylon juniperoides* Gothan, 1905

Podocarpoxylon feruglioi Gnaedinger nov. sp.

Diagnosis: Growth rings distinct. Tracheid pitting of the abietinoid type. Pits are areolate, circular, uniseriate, spaced or contiguous in groups of two or three, or uniseriate with opposite–subopposite biseriate portions and rarely alternate. Cross-field pitting of the podocarpoid type with 1–2 oval, some circular pits. Radial system homogeneous, rays homocellular, uniseriate and low of 1–10 cells height. Tracheids show resins arrayed as biconcave plates (“resin plates”).
Holotype: CTES-PB 10694 (CTES-PMP 2384–2385)
Paratype: CTES-PB 10695 (CTES-PMP 2387–2388)
Locality: Cerro Conito, Gran Bajo de San Julián area, Santa Cruz province, Argentina.
Additional material. Locality: **Bardas Blancas:** CTES-PB 10661 (CTES-PMP 2341), CTES-PB 10662 (CTES-PMP 2357), CTES-PB 10663 (CTES-PMP 2359).
Stratigraphic position: La Matilde Formation, Middle Jurassic.
Derivatio nominis: Dedicated to Dr. E. Feruglio, for his contributions on geological and paleontological studies of the La Matilde Formation.

Description: Several fragments from trunks up to 30 cm in diameter, were analyzed.

The transversal section, show distinct growth rings and elements arranged in “S-shaped linear rows” (*sensu* Maheshwari, 1972) (Plate I.A). Tracheids are polygonal in shape. The early wood is constituted by 26 to 88 rows of tracheids, with a mean radial diameter of 22 μm (18–37 μm) and a tangential diameter of 26 μm (15–37 μm). The late wood is constituted by 3–5 rows of tracheids; it shows a mean radial diameter of 17 μm (11–22 μm) and a tangential diameter of 12 μm (7.5–18 μm). The mean number of tracheids that separate the rays is 5, with a range of 3–9 rows of tracheids.

In radial longitudinal section, tracheid pitting is of the abietinoid type. Pits are areolate, circular, uniseriate, spaced or contiguous in groups of two or three, or uniseriate with opposite–subopposite biseriate portions and rarely alternate (Fig. 1A; Plate I, B–D). The size of pits is 11–15 μm. Pits show a circular or oval aperture; they measure 4–7 μm, and their flattening coefficient is 0.5. Cross-fields show 1–2 oval, some circular podocarpoid pits of 7.5–12 μm size (Fig. 1B; Plate I, E–F).

In tangential longitudinal section, the radial system is homogeneous with homocellular, uniseriate and low rays of 1–10 cells height. Tracheids show resins arrayed as biconcave plates (“resin plates”) (Fig. 1C; Plate I, G).

In some specimens, there is a “callose tissue”, *i.e.*, parenchymatous structures originated as responses for a wound or lesion in the cambium of the living tree (Kuroda and Shimaji, 1984; Schweingruber et al., 1990) (Plate I.H).
Comparison: The structure of this wood allows one to assign it to *Podocarpoxylon* Gothan which is characterized by the tracheid pitting of the abietinoid type and a few small cross-field pits. According to the comparison made among the almost 24 described species of *Podocarpoxylon*, the specimens studied from the Gran Bajo de San Julián area, differs in diverse characters, therefore it is assigned to a new species, *P. feruglioi* Gnaedinger nov. sp. (Table 1).

This new species is more closely comparable to *P. tirumangalense* (Suryanarayana) Bose and Maheshwari from the Jurassic of India, but the latter species differs in the number of pits (1–4) in the cross-fields, ray height and absence resin plates. Also, it is comparable with two species of the Cretaceous from India. *P. trichinopoliense* Varma, presents axial parenchyma and lacks biseriate pits in the tracheid radial walls and resin plates. *P. sarmai* Varma lacks the resin plates and differs in the number of pits (1–4) in the cross-fields and ray height (Table 1).

Podocarpoxylon feruglioi Gnaedinger nov. sp. is distinguished from *P. austroamericanum* Gnaedinger nov. sp. because the second species has axial parenchyma, a higher frequency of biseriate pits in the tracheid

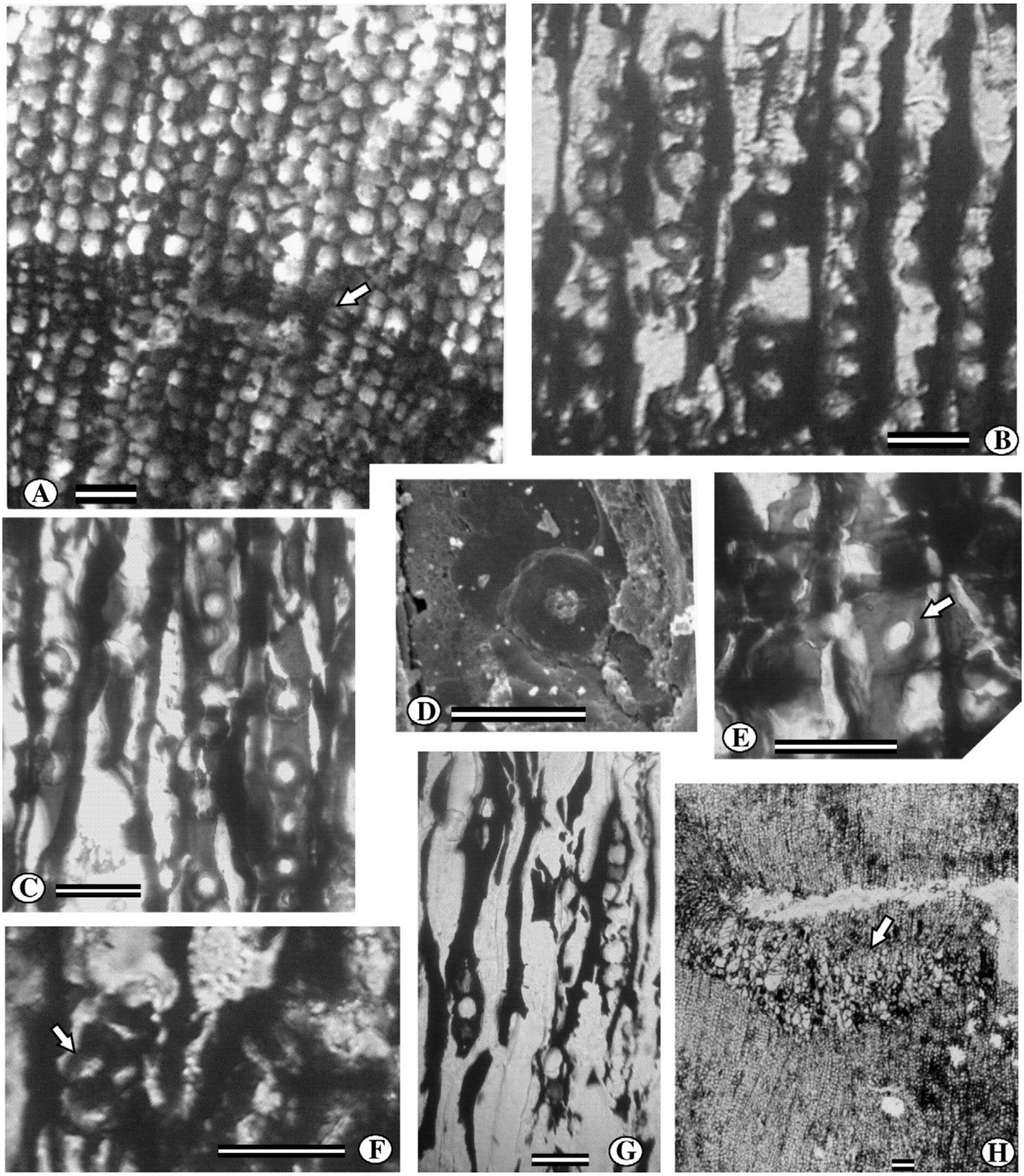


Plate I. A, H. *Podocarpoxylon feruglioi* Gnaedinger nov. sp. All LM, except D = SEM. Scale bar. A = 48 μm, B–C,E–G = 22 μm, D = 12 μm, H = 120 μm.

A. TS, detail of the tracheids and growth ring (arrow);

B–D. RLS, pits on tracheid radial walls;

E–F. RLS, cross fields pits (arrow);

G. TLS, rays;

H. TS, callous tissue (arrow). (CTES-PB 10694; A–G: CTES-PMP 2385, H: CTES-PMP 2384).

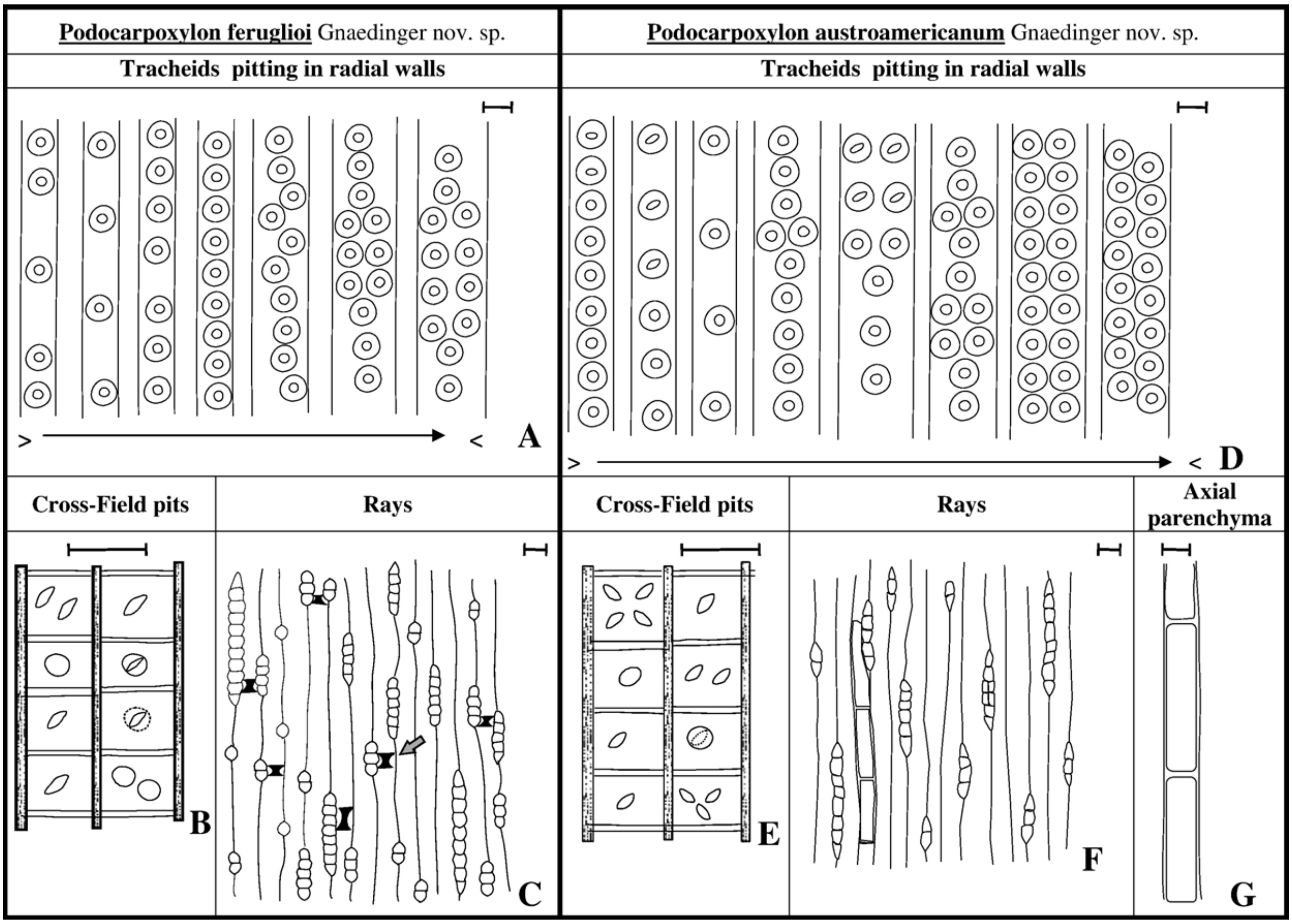


Fig. 1. Schematic diagram of the anatomical features. A–C. *Podocarpoxylon feruglioi* Gnaedinger nov. sp.; D–G. *Podocarpoxylon austroamericanum* Gnaedinger nov. sp.; A, D. RLS, pits on the radial tracheid walls (the arrow indicates a gradient percentage of the uniseriate–biseriate pits types presence); B, E. RLS, detail of cross fields; C, F. TLS, rays; G. TLS, axial parenchyma. Scale bar, A, D = 15 μm, B, E–C, F = 24 μm, G = 30 μm.

radial walls and greater number of pits in the cross-fields (Fig. 1).

Podocarpoxylon austroamericanum Gnaedinger nov. sp.

Diagnosis: Growth rings distinct. Tracheid pitting of the abietinoid type. Pits are circular areolate, spaced or contiguous, uniseriate or occasionally biseriate, where uniseriate they may have short opposite–subopposite biseriate portions and where biseriate the pits are opposite or rarely alternate. Cross-field pitting of the podocarpoid type with 1–4 oval, some circular pits. Radial system homogeneous, rays homocellular, uniseriate and low of 1–14 cells height, with a mean of 3–4 cells. Uniseriate rays with biseriate portions are rarely observed. Axial parenchyma present.
Holotype: CTES-PB 12016 (CTES-PMP 2437)
Paratype: CTES-PB 12015 (CTES-PMP 2436)
Locality: Laguna del Carbón, Gran Bajo de San Julián area, Santa Cruz province, Argentina.
Stratigraphic position: La Matilde Formation, Middle Jurassic.
Derivatio nominis: The name of the species refers to the region where the material comes from.
Description: Two log fragments collected from the Laguna del Carbón locality, with a good preservation of xylem elements, were analyzed. They measure 15–30 cm long and 8–18 cm wide .

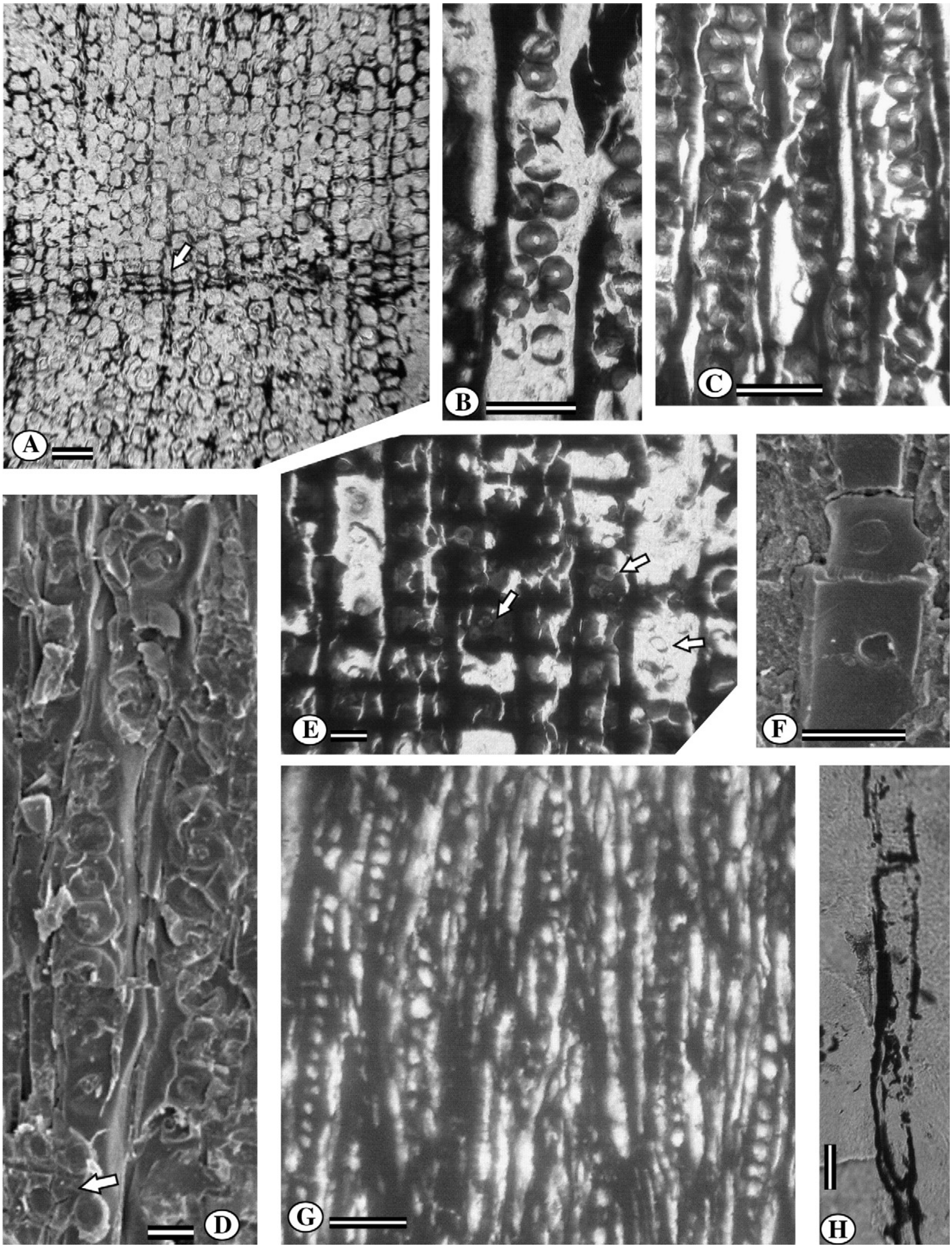
The transversal section, shows distinct growth rings; in some areas, elements are arranged in "S-shaped linear rows" (*sensu* Maheshwari, 1972) (Plate II, A). Tracheids are quadrangular–rectangular in shape. The early wood is constituted by tracheids with a mean radial diameter of 31 μm (22–41 μm) and a tangential diameter of 27 μm (15–37 μm). The late wood of 3–5 rows of tracheids shows a mean radial diameter of 18 μm (15–22 μm) and a tangential diameter of 36 μm (30–45 μm). The mean number of tracheids that separate the rays is 5, with a range of 2–8 rows of tracheids.

Table 1
Comparison among *Podocarpoxylon* Gothan species described from Gondwana (partially adapted from Bhardwaj, 1953; Ramanujan, 1953; Petriella, 1972; Agarwal and Rajanikanth, 2004)

Species	Age	Locality/ country	Characters					
			Radial walls pits	Axial parenchyma	Resin plates	Cross-Fields	Rays	
			Arrangement				Width	Height in cells
Podocarpoxylon indicum (Bhardwaj) Bose and Maheshwar (in Roberts et al., 1997)	Permo-Triassic	East London/ South Africa	Uniseriate Separate	Absent	Present	1–2	Uniseriate	1–6, 11
P. paralatifolium Vozenin-Serra and Grant-Mackie, 1996	Early Triassic	Murihiku Terrane/ New Zealand	Uniseriate Contiguous	Present	Absent	1–2	Uniseriate	1–12
P. tirumangalense (Suryanarayana) Bose and Maheshwari, 1974	Jurassic	Sripermatur/ Southern India	Uniseriate, rarely biseriate Contiguous or separate Subopposite to alternate	Absent	Absent	1–3, 4	Uniseriate (biseriate)	1–15, 23
P. feruglioi Gnaedinger nov. sp. [a]	Middle Jurassic	Santa Cruz Province/ Argentina	Uniseriate (biseriate portions) Separate or contiguous. Opposite, subopposite or rarely alternate	Absent	Present	1–2	Uniseriate	1–10
P. austroamericanu m Gnaedinger nov. sp. [a]	Middle Jurassic	Santa Cruz Province/ Argentina	Uniseriate–(biseriate) Separate or contiguous. Opposite or rarely alternate	Present	Absent	1–4	Uniseriate (biseriate portions)	1–14
P. trichinopoliense (Varma) Bose and Maheshwari, 1974	Cretaceous	Cauvery Basin, Tamil Nadu/India	Uniseriate Separate, rarely contiguous	Sparsely present	Absent	1–2	Uniseriate	2–6, 10
P. sarmai (Varma) Bose and Maheshwari, 1974	Cretaceous	Cauvery Basin, Tamil Nadu/India	Uniseriate Separate, rarely contiguous	Absent	Absent	2–4	Uniseriate	1–18
P. cf. sahnii Ramanujam (in Bamford andCorbett, 1994) [b]	Cretaceous	Namaqualand/ South Africa	Uniseriate (rarely biseriate) Separate or contiguous, opposite. Bars of Sanio.	Present	Absent	1 (2)	Uni–biseriate	3–30
P. umzambense Schultze-Motel, 1966	Early Cretaceous	Umzamba beds, South east coast/South Africa	Uniseriate (biseriate) Separate, opposite. Bars of Sanio.	Sparsely present	Present	1–2	Uniseriate	1–25
P. cf. umzambense Schultze-Motel (In Bamford and Corbett, 1994)	Early Cretaceous	Namaqualand/ South Africa	Uniseriate Separate, rarely contiguous	Not seen	Present	1	Uniseriate (biseriate)	3–20
P. indicum (Bhardwaj) Bose and Maheshwari, 1974	Early Cretaceous	Rajmahal Hills, Jharkhand/India	Uniseriate Separate	Absent	Present	1–2	Uniseriate	1–6
P. cf. umzambense Schultze-Motel (in Bamford and Corbett, 1994)	Early Cretaceous	Namaqualand/ South Africa	Uniseriate Separate	Sparsely present	Present	1	Uniseriate	3–18
P. garcie Del Fueyo 1998	Early Cretaceous	Río Negro Province/ Argentina	Uniseriate Separate	Present	Absent	1–2	Uniseriate	1–15

P. bansaense Prakash and Rajanikanth, 2004	Early Cretaceous	Marwar Ghat, Umaria District, Madhya Pradesh/India	Uniseriate (biseriate)	Absent	Present	2–3	Uniseriate (rarely biseriate)	2–14
P. kulakkalnattamensis Agarwal and Rajanikanth, 2004	Early Cretaceous	Cauvery Basin, Tamil Nadu India	Uni–biseriate Contiguous. Opposite	Absent	Present	1–2	Uniseriate (rarely biseriate)	2–16
P. woburnense (Stopes) Seward, 1919 (in Bamford and Corbett, 1995)[b]	Early Cretaceous	Namaqualand/South Africa	Uniseriate Separate–contiguous	Present and rare	Present	1	Uniseriate (rarely biseriate portions)	2–15, 25
P. cf. woburnense (Stopes) Seward, 1919 (in Bamford and Corbett, 1994)[b]	Early Cretaceous	Namaqualand/South Africa	Uniseriate (occasionally biseriate) Contiguous, opposite	Present	Present	1–2	Uniseriate (rarely biseriate portions)	1–15, 35
P. stokesii Thayn and Tidwell (in Bamford and Corbett, 1995)[b]	Early Cretaceous	Namaqualand/South Africa	Uniseriate Separate, rarely contiguous	Present and abundant	Absent	1	Uniseriate (partially biseriate)	1–28, 48
P. cf. stokesii Thayn and Tidwell (in Bamford and Corbett, 1994)[b]	Early Cretaceous	Namaqualand/South Africa	Uniseriate (rarely biseriate) Separate, rarely contiguous, opposite	Present	Present	1–3	Uniseriate (partially biseriate)	1–47
P. chapmanae Poole and Cantrill, 2001	Late Cretaceous	Williams Point Beds, Livingston Island/Antarctica	Uni–biseriate (rarely triseriate) Contiguous. Opposite or rarely alternate	Rare to absent	Absent	1–4	Uniseriate	1–42
P. comunis Poole and Cantrill, 2001	Late Cretaceous	Williams Point Beds, Livingston Island/Antarctica	Uniseriate (biseriate) Contiguous. Opposite or rarely alternate	Absent	Absent	1–3,4	Uniseriate	1–32
P. verticalis Poole and Cantrill, 2001	Late Cretaceous	Williams Point Beds, Livingston Island/Antarctica	Uniseriate or rarely biseriate Contiguous. Opposite or rarely alternate.	Absent	Absent	1–5	Uniseriate	1–36
Podocarpoxylon sp. 1 Falcon Lang and Cantrill, 2001	Cretaceous	Byers; Livingston Island, South Australia	Uniseriate Separate (contiguous)	Absent	…	1 – 2 , 3–4	Uniseriate	1–14, 21
Podocarpoxylon sp. 2 Falcon Lang and Cantrill, 2001 (= *P. comunis* Poole and Cantrill)	Cretaceous	Byers; Livingston Island, South Australia	Uniseriate (biseriate) Contiguous. Opposite or rarely alternate. Bars of Sanio.	Abundant	Absent	1–3, 4	Uniseriate	1–26
P. speciosum Ramanujan, 1955	Miocene–Pliocene	Cauvery Basin, Tamil Nadu/India	Uni–biseriate Opposite–subopposite	Abundant	Present	2–4	Uni–biseriate	1–18
P. mahabalei Agashe, 1969	Miocene–Pliocene	Cauvery Basin, Tamil Nadu/India	Uniseriate Separate, contiguous	Present	Present	1	Uniseriate	1–30
P. schmidianum Sahni, 1931	Miocene–Pliocene	Cauvery Basin, Tamil Nadu/India	Uni–biseriate Opposite	Absent	Present	1–2	Uni–biseriate	2–100
P. sahnii Ramanujam 1953[b]	Miocene–Pliocene	Cauvery Basin, Tamil Nadu/India	Uniseriate (rarely biseriate) Separate or contiguous, opposite	Absent	Absent	1 (2)	Uni–biseriate (triseriate)	1–20
P. tiruvakkaraianum Ramanujan, 1953	Miocene–Pliocene	Cauvery Basin, Tamil Nadu/India	Uni–biseriate Opposite	Absent	Present	1	Uniseriate	3–50

[a] This paper.
[b] Generic attribution to *Podocarpoxylon* realized by Philippe et al. (2004).


A
B
C
D
E
F
G
H

In radial longitudinal section, tracheids pitting is of the abietinoid type. Pits are circular areolate, spaced or contiguous, uniseriate or occasionally biseriate, where uniseriate they may have short opposite–subopposite biseriate portions and where biseriate the pits are opposite or rarely alternate (Fig. 1D; Plate II, B–D). The size of pits is 11–19 μm. Pits show a circular or oval aperture; they measure 2–4 μm, and their flattening coefficient is 0.5. Cross-field pitting is of the podocarpoid type with 1–4 oval, some circular pits of 6–7.5 μm size (Fig. 1E; Plate II, E–F).

In longitudinal tangential section, the radial system is homogeneous with homocellular, uniseriate and low rays of 1–14 cells height, showing a mean of 3–4 cells (Fig. 1F; Plate II, G). Uniseriate rays with biseriate portions are rarely observed. Marginal ray cells have a triangular shape while the rest are rectangular; their diameter is 15–22 μm. Axial parenchyma is present with cells of 90–227 μm height and 30 μm wide (Fig. 1G, Plate II, H).

Comparison: The studied specimens are included in *Podocarpoxylon* because of the tracheid pitting of the abietinoid type and cross-field pitting of the podocarpoid type. The comparison among the species described for Gondwana, justify the assignment of the patagonian specimens to a new species (Table 1).

Podocarpoxylon austroamericanum nov. sp. is more closely comparable to *P. tirumangalense* (Suryanarayana) Bose and Maheshwari described from the Jurassic of India but differs in that the latter species lacks axial parenchyma. *P. sarmai* (Shani) Bose and Maheshwari, described from the Cretaceous of India, is also similar but it differs in that the latter species lacks axial parenquima and biseriate pits in the tracheid radial walls. Also, it could be related to *P. speciosum* Ramanujan from India (Mio–Pliocene), but differs because of the higher frequency of biseriate pits in the tracheid radial walls and in the presence of resin plates.

Circoporoxylon Kräusel, 1949

Type species: Circoporoxylon goeppertii (Conwentz) Kräusel, 1949

When Kräusel (1949) described *Circoporoxylon*, he did not name a type species. Later, Andrews (1955) established *C. goeppertti* (Conwentz) as the type. However, Kräusel and Jain (1964) designated *C. priscum* Prill as type. Since this genus was created most of the authors design as type species *C. priscum* Prill. But, Bamford and Philippe (2001) while making a nomenclatural Jurassic–Early Cretaceous revision established that the lectotypification by Kräusel and Jain (1964) was irrelevant.

Circoporoxylon sanjuliense Gnaedinger nov. sp.

Diagnosis: Growth rings distinct. Tracheids pitting of the abietinoid type. Pits are circular, spaced or rarely contiguous; mostly uniseriate, some uniseriate with portions opposite–subopposite biseriate. Cross-fields with 1–2 (3) pits of the circopore type (circular), rarely oval. Radial system homogeneous. Rays homocellular, uniseriate, some partially biseriate in portions of 1–4 cells, with a mean height of 6 cells, varying between 1–15 cells (minimum–maximum). Axial parenchyma present and abundant.
Holotype: CTES-PB 12017 (CTES-PMP 2438)
Paratype: CTES-PB 12014 (CTES-PMP 2435)
Locality: Laguna del Carbón, Gran Bajo de San Julián area, Santa Cruz province, Argentina.
Stratigraphic position: La Matilde Formation, Middle Jurassic.
Derivatio nominis: The name of the species refers to the region where the material comes from.
Description: Wood fragments of 12–18 cm long and 14–23 cm wide.

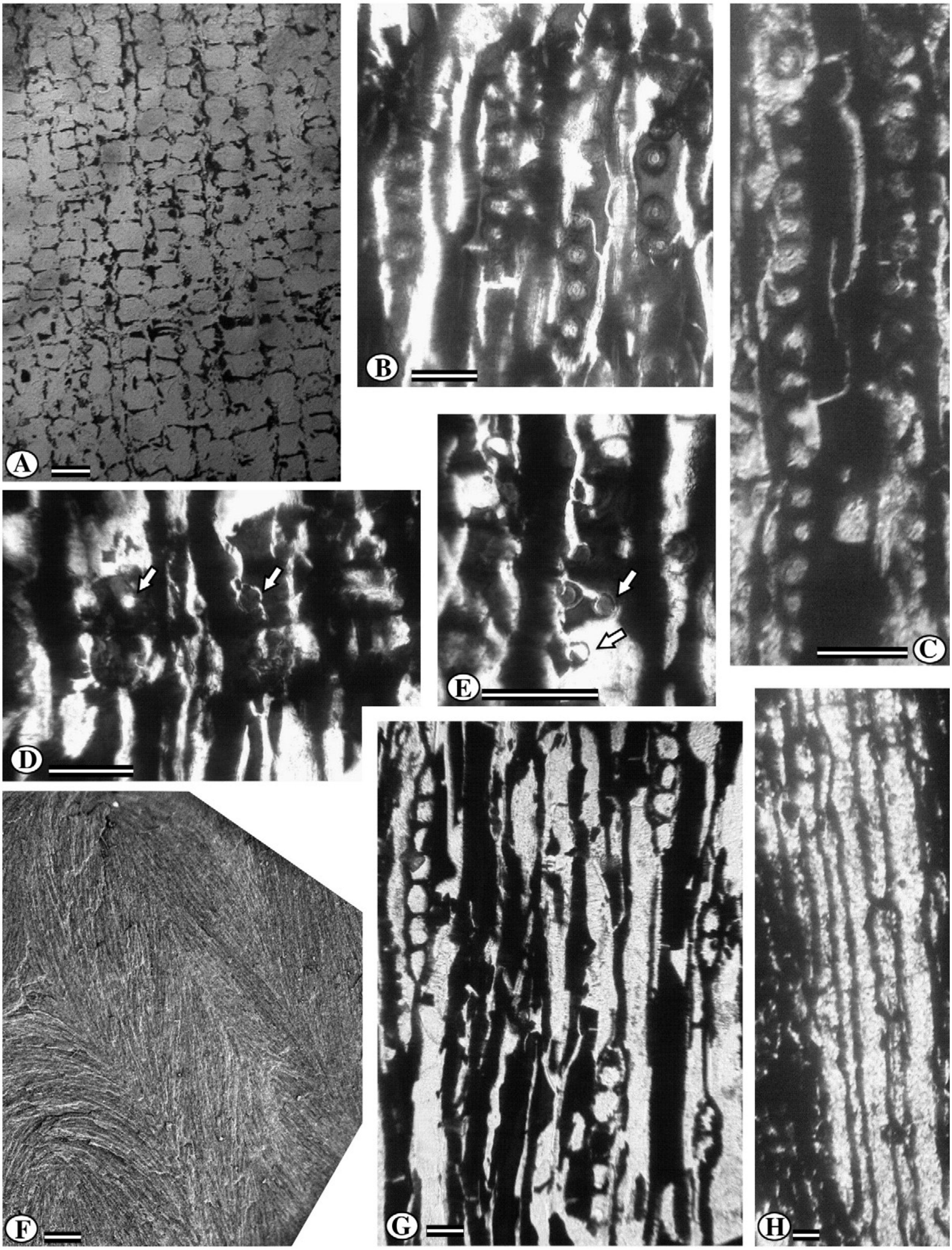
The transversal section shows distinct growth rings. In some regions, this specimen presents distortion caused during the preservation, that is to say the vascular elements arranged in "S-shaped linear rows" (*sensu* Maheshwari, 1972) (Plate IIIA). Tracheids have a rectangular–quadrangular shape. The tracheid mean radial diameter of the early wood is 43 μm (30–60 μm) and the tangential diameter is 35 μm (22–52 μm). The mean number of tracheids that separate rays is 4, varying between 2–6 tracheids.

In radial longitudinal section, tracheid pitting is of the abietinoid type. Pits are circular, spaced or rarely contiguous; mostly uniseriate, some uniseriate with portions opposite–subopposite biseriate. (Fig. 2A; Plate III, B–C). The size of pits is 11–13 μm. Pits show a circular aperture of 4–6 μm and their flattening coefficient is 0.6. Cross-fields show 1–2 (3–4) circopore type pits, with circular, rarely oval shape of 8–9 μm size (Fig. 2B; Plate III, D–E).

Plate II. *Podocarpoxylon austroamericanum* Gnaedinger nov. sp. All LM, except D, F = SEM. Scale bar. A = 60 μm, B–H = 30 μm.

A. TS, detail of the tracheids and growth ring (arrow);
B–D. RLS, pits on tracheid radial walls (arrow: cross fields pits);
E–F. RLS, detail of cross fields pits;
G. TSL, rays;
H. TSL, axial parenchyma. (CTES-PB 12016, CTES-PMP 2437).

In tangential longitudinal section, the radial system is homogeneous; rays are homocellular, uniseriate, some of them partially biseriate, in portions of 1–4 cells. The mean height of rays is 6 cells, with a range of 2–15 cells. In this section, rays and tracheids show a "V" or "U" distribution that could correspond to protuberances of



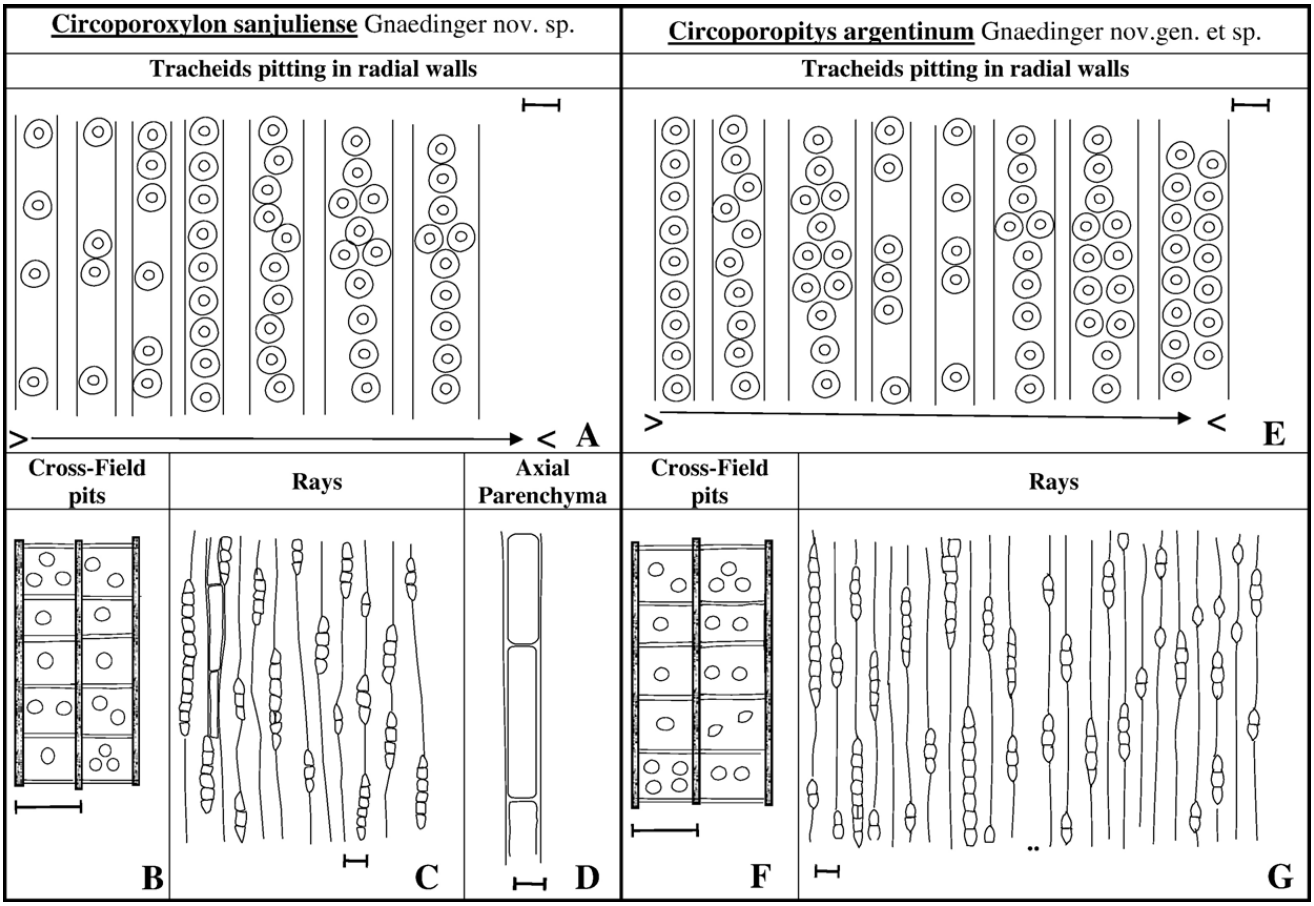


Fig. 2. Schematic diagram of the anatomical features. A–D. *Circoporoxylon sanjuliense* Gnaedinger nov. sp.; E–G. *Circoporopitys argentinum* Gnaedinger nov. gen. et. sp.; A, E. RLS, pits on the radial tracheid walls (the arrow indicates a gradient percentage of the uniseriate–biseriate pits types presence); B, F. RLS, detail of cross fields; C, G. TLS, rays; D. TLS, axial parenchyma. Scale bar. A, E = 13 µm, B, F–C, G = 45 µm, D = 22 µm.

rameal traces or nodes (Fig. 2C; Plate III, F–G). Axial parenchyma is observed, with cells measuring 120–150 µm high and 22 µm wide (Fig. 2G; Plate III, H).

Comparison: The structure of this wood corresponds most closely to that of *Circoporoxylon* Kräusel which is characterized by simple circular (or oval) pits in the cross-fields. The present woods are compared with the species described from Gondwana and Laurasia, but they differ in one or another character (Table 2). For this reason, specimens described in this study are assigned to a new species: *Circoporoxylon sanjuliense.*

The new species from the La Matilde Formation is more closely comparable to *Circoporoxylon amarjolense* Kräusel and Jain of the Early Cretaceous from India in most of the features. Specimens from Patagonia differ in the presence of axial parenchyma and in the arrangement of pits in the radial tracheid walls. Also, it is comparable with the species studied from the Cretaceous of the Argentina, *C. gregusii* Del Fueyo, 1998 (Rio Negro Province) and *C. krauselli* Martinez and Lutz (in press) (Neuquen Province). Both species differ because they have uni–triserate rays and different numbers of cross-field pits (1–2) (Table 2).

Moreover, these specimens are similar to the secondary wood of *Circoporopitys argentinum* Gnaedinger, but they differ in that the latter lacks an axial parenchyma and presents biseriate, alternate pits in the radial tracheid walls (Fig. 2, Table 2).

Plate III. A–H. *Circoporoxylon sanjuliense* Gnaedinger nov. sp. All LM, except F = SEM. Scale bar. A = 89 µm, B–C = 43 µm, F = 720 µm.

A. TS, detail of the tracheids and growth ring;
B–C. RLS, pits on tracheid radial walls;
D–E. RLS, detail of cross fields pits (arrows);
F–G. TLS, rays and tracheids show a "V" or "U" distribution;
H. RLS, axial parenchyma. (CTES-PB 12017, CTES-PMP 2438).

Table 2
Comparison among *Circoporoxylon* Kräusel species and *Circoporopitys* Gnaedinger nov. gen. (partially adapted from Kräusel and Jain, 1964)

Species	Age	Locality/ country	Characters					
			Radial walls pits	Axial parenchyma	Resin plates	Cross-Fields	Rays	
			Arrangement				Width	Height in cells
Circoporoxylon sewardi (Sahni) Kräusel and Jain, 1964	Jurassic	Australia	Uniseriate Separate	Present	Present	1	Uniseriate	1–4
C. sanjuliense Gnaedinger[a]	Middle Jurassic	Santa Cruz Province/ Argentina	Uniseriate, partially biseriate Separate (some contiguous). Opposite	Present	Absent	1–2 (3)	Uniseriate (partially biseriate)	1–15
C. macGeei (Knowlton) Kräusel and Jain, 1964	Jurassic or Cretaceous	North America	Uniseriate or multiseriate Separate or opposite	Absent	Present	1–2	Uniseriate	1–49
C. amarjolense Kräusel and Jain, 1964	Early Cretaceous	Rajmahal Hills, Jharkhand/India	Uniseriate or multiseriate Separate or contiguous. Opposite or alternate	Absent	Absent	1–2	Uniseriate (biseriate)	1–15
C. krauselli Martinez and Lutz, in press	Early Cretaceous	Neuquen Province/ Argentina	Uniseriate or biseriate Contiguous or separate Alternate or opposite	Absent	Present	1	Uni–bi–triseriate	1–13
C. gregusii Del Fueyo, 1998	Early Cretaceous	Río Negro Province/ Argentina	Uniseriate or multiseriate Separate or opposite	Present	Present	1–2	Uni–biseriate (triseriate)	1–50
C. goepperti (Conwentz) Andrews, 1955	Oligocene	Argentina	Uniseriate Contiguous	Absent	Absent	1	Uniseriate	1–25
C. priscum (Prill) Kräusel and Jain, 1964	Tertiary	Europe	Uniseriate or multiseriate Separate or contiguous. Opposite or alternate	Present	Present	1–4	Uniseriate	1–2
C. glyptostrobinum (Schmalhausen) Kräusel and Jain, 1964	Tertiary	Europe	Uniseriate or multiseriate Separate. Opposite	Absent	Present	1–2	Biseriate	…
Circoporopitys shanense (Shani) Gnaedinger nov. comb.[a]	Jurassic	Asia	Uniseriate. Separate	Absent	Absent	1 (2)	Uniseriate	1–2 ,4
Circoporopitys argentinum Gnaedinger nov. gen et sp.[a]	Middle Jurassic	Santa Cruz Province/ Argentina	Uniseriate or biseriate Contiguous or separate. Opposite, subopposite or occasionally alternate	Absent	Absent	1–2 (3–4)	Uniseriate (biseriate)	1–18

[a] This paper.

Circoporopitys **Gnaedinger nov. gen**

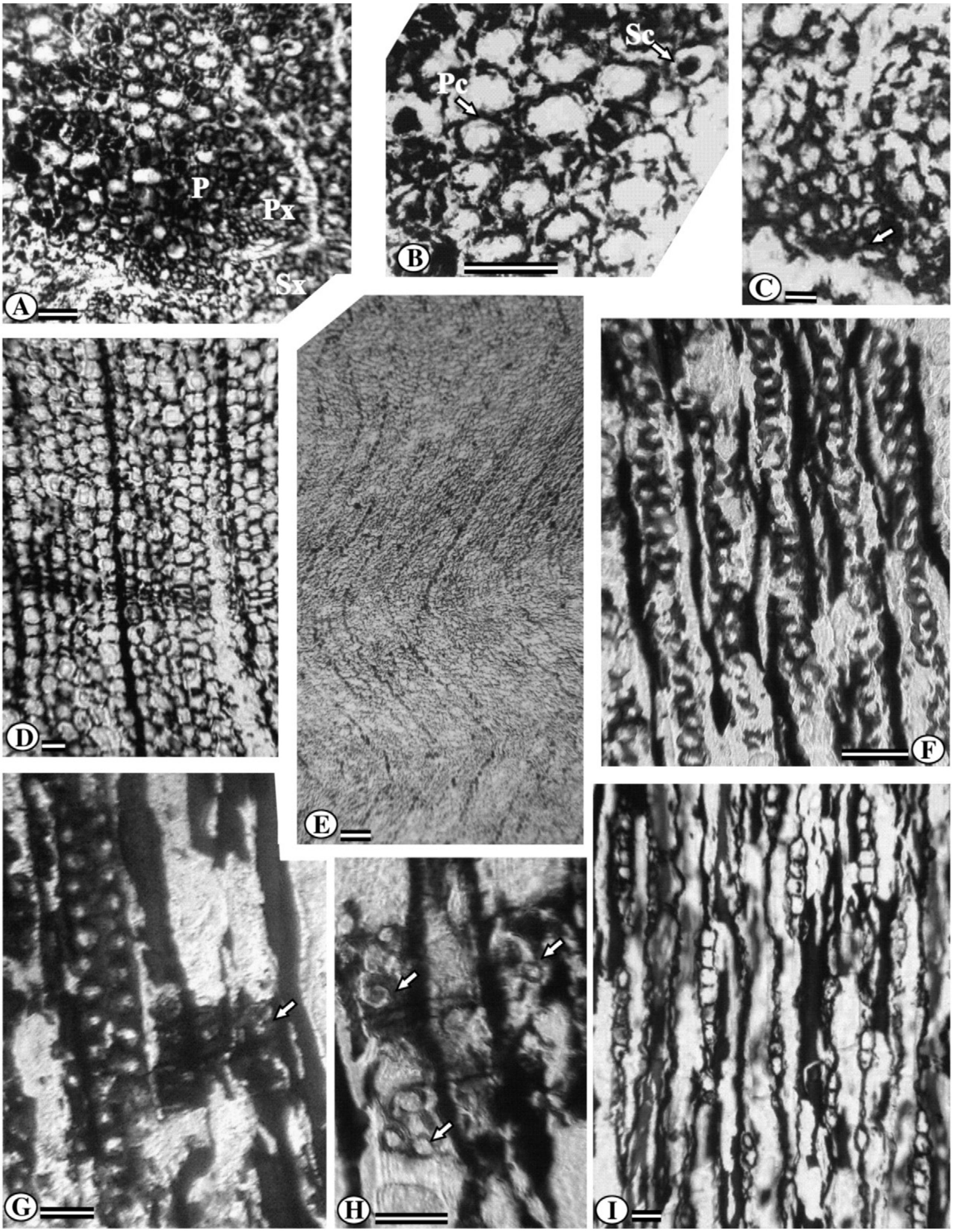
Type species: Circoporopitys argentinum Gnaedinger (this paper)

In the literature, there are two systematic series of morphogenera to classify petrified woods of gymnosperms. One of them refers to morphogenera diagnosed on the basis of characteristics of the pith, primary and secondary xylem. The other series refers to wood that only show a secondary structure. This double system is useful since a type of secondary wood can be found combined to different types of pith and primary xylem

Plate IV. A–I. *Circoporopitys argentinum* Gnaedinger nov. gen. et. sp. All LM. Scale bar. A–C=50 μm, D=68 μm, E=160 μm, F–I=43 μm.

A. Pith (P), primary (Px) and secondary xylem (Sx);
B. Detail of the pith with parenchyma (Pc) and sclerenchyma cells (Ps);
C. Primary xylem (arrow);
D. TS, detail of tracheids and growth ring (arrow);
E. TS, secondary xylem are arranged in “s-shaped linear rows”;
F–G. RLS, pits on tracheid radial walls (arrow: cross fields pits);
H. RLS, detail of cross fields pits (arrows);
I. TLS, rays. (CTES-PB 10691, A–E: CTES-PMP 2375, F–I: CTES-PMP 2376).

and *vice versa* (Lepekhina and Yatsenko Khmelevsky, 1966). According to this criterium, in this study, a new genus, *Circoporopitys*, is established and described on the basis of characteristics of the pith and primary xylem features and on the "*Circoporoxylon* type" of secondary xylem. Specimens from the La Matilde



Formation described in this study are designated as *Circoporopitys argentinum* Gnaedinger nov. sp. Moreover, a new combination: *Circoporopitys shanense* (Sahni) Gnaedinger nov. comb. (= *Mesembrioxylon shanense* Sahni), is here proposed.
Diagnosis: Heterogeneous pith, constituted by parenchymatic and sclerenchymatic cells. Endarch wedge shaped primary xylem. Secondary xylem of the "*Circoporoxylon* type".
Derivatio nominis: The name of the genus refers to the genus *Circoporoxylon* Kräusel, created on the basis of the secondary xylem because of the presence of circopores in the cross-fields.

Circoporopitys argentinum Gnaedinger nov. sp.

Diagnosis: Pith heterogeneous, with parenchymatic and sclerenchymatic cells. Endarch wedge shaped primary xylem. Secondary xylem of the "*Circoporoxylon* type". Growth rings distinct. Tracheid pitting of the abietinoid type. Pits are areolate, circular, mainly uniseriate, spaced (30%), others contiguous (16%); some uniseriate with biseriate portions, opposite (28%) subopposite (16%) and occasionally alternate, biseriate. Cross-fields with 1–2 (3–4) simple circopore type. Pits circular, rarely oval. Radial system homogeneous. Rays homocellular, uniseriate, some partially biseriate in 1–2 cells. Height varies between 1–18 cells, with a mean of 4 cells.
Holotype: CTES-PB 10691 (CTES-PMP 2375–2376)
Locality: Cerro Conito, Gran Bajo de San Julián area, Santa Cruz province, Argentina.
Additional material: Localities: **Cerro Conito:** CTES-PB 10692 (CTES-PMP 2379–2380); **Mina de Pareja:** CTES-PB 12025 (CTES-PMP 2444–2445); **Laguna del Carbón**: CTES-PB 12018 (CTES-PMP 2439)
Stratigraphic position. La Matilde Formation, Middle Jurassic.
Derivatio nominis. The name of the species refers to the country where the studied material comes from.
Description. Wood fragments are 8–10 cm long and 9–14 cm wide. Heterogeneous pith, constituted by subcircular–irregular parenchymatic cells, measuring 45–75 μm, and polygonal sclerenchymatic cells, measuring 22–30 μm diameter. Endarch primary xylem; protoxylem tracheids measure 7.5 μm and metaxylem elements measure 15 μm (Plate IV, A–C).

The transverse section shows the secondary xylem with well marked growth rings (Plate IV, D); in some zones, false rings are observed, and in others, vascular elements are arranged in "S-shaped linear rows" (*sensu* Maheshwari, 1972) (Plate IV, E) or present "shearing zones" (*sensu* Erasmus, 1976). The description is based on the specimen CTES-PB 10691, but it also characterizes the rest of the specimens. Tracheids have a rectangular–quadrangular (some polygonal) shape. The tracheid radial diameter of the early wood is 34 μm (22–45 μm) and the tangential diameter is 37 μm (30–52 μm). Tracheids of the late wood measure 7.5–15 μm by 22 μm. The mean number of tracheids that separate the rays is 5, with a range of 2–8 tracheids.

In radial longitudinal section, tracheid pitting of the abietinoid type. Pits are areolate, circular, mainly uniseriate, spaced (30%), others contiguous (16%); some uniseriate with biseriate portions, opposite (28%) subopposite (16%) and occasionally alternate, biseriate (Fig. 2E; Plate IV, F–G). The size of pits is 11 to 15 μm diameter; they show a circular pore of 4–7.5 μm, and their flattening coefficient is 0.5. Cross-fields show 1–2 (3–4) circopore (oopore) type pits; in some cases, they are oval in shape of 6–9 μm size (Fig. 2F; Plate IV, G–H).

In tangential longitudinal section, the radial system is homogeneous, constituted by homocellular, uniseriate rays, some of them partially biseriate in 1–2 cell states. Height varies between 1–18 cells, with a mean of 4 cells. Extreme cells are ovoid and central cells are rectangular. They measure 15–22 μm height by 15 μm width. In some zones the height of most rays is very low, predominantly 1–4 cells height, while in others there is a combination of rays of up to 4 cells height with rays of a greater height (Fig. 2G; Plate IV, I).

In this specimen, there are parenchymatic–xylematic structures produced in response to wounds, constituting a callose tissue (Kuroda and Shimaji, 1984; Schweingruber et al., 1990). Rameal and/or foliar traces. Different states of development of rameal and/or foliar traces are recognized, *i.e.*, some of them with pith and primary xylem only, others with these two elements and secondary xylem.
Comparisons. Considering the secondary xylem features of the species described as *Circoporoxylon* Kräusel, the specimen from Patagonia is more closely comparable with the species *C. amarjolense* Kräusel and Jain. The difference is given by the number of pits in the cross-fields and by the seriation of rays. It differs from *C. shanense* on the type of tracheid pitting, the number of pits in the cross-fields and their height of rays (Table 2).

Circoporopitys shanense (Sahni) Gnaedinger nov. comb.

Basionym
1938 *Mesembrioxylon shanense* Sahni, pp. 380–389, figs. 1–3, plate 31.

Following the approach of using two systematic series of morphogenera to classify petrified woods of gymnosperms (mentioned above), the new combination *Circoporopitys shanense* (Sahni) Gnaedinger Is proposed. This specimen was described by Sahni (1938) with the name *Mesembrioxylon*, (genus considered invalid) and diagnosed on the basis of pith and primary and secondary xylem characteristics.

Diagnosis: Pith heterogeneous with parenchymatic and sclerenchymatic cells. Primary xylem endarch cuneiform. Secondary xylem of the "Circoporoxylon" type Distinct growth rings. Tracheid pitting of the Abietinoid type. Pits uniseriate and spaced. Cross-fields with 1, sometimes 2 circopores. Rays low, generally 1–2 or 4 cell height (Sahni, 1938).

4. Concluding remarks

The findings in the La Matilde Formation of leaves and branch impressions and silicified seed and pollen cones indicate that the "Jaramillo Petrified Forest" was mainly composed of Coniferales belong to the families Araucariaceae, Podocarpaceae and Taxodiaceae?. According to the xylological analysis carried out in this study, the presence of the family Podocarpaceae in the forests of the La Matilde Formation is corroborated.

The presence of callose tissue in some of the analyzed specimens points to the idea of an active plant/animal interaction, eventually with insects; on the other hand it could also indicate the presence of late frosts during the growing season.

Growth rings of trees give information on climatic conditions under which they grew. Taking into account the growth rings information provided by fossil and living trees (Fritts, 1976; Creber and Chaloner, 1984), and comparing the graphs proposed by Brison et al. (2001) with these of the Patagonian specimens it can be concluded that they correspond to supertype II, that comprises growth rings types D and E (categorized by Creber and Chaloner, 1984). Both types of growth rings indicate relatively uniform growth seasons, but each one has a terminal event representing a stop or retardation in cambial activity. In type D, the ring limit is more marked (Plate I.A), while in type E it is so weak that sometimes it is not perceived (Plate II.A, 3.A, 4.D). For this reason, a continuous growth, interrupted by variations in temperature and with a relatively uniform provision of water, although variable from 1 yr to the other. This information tends to point out that the wood of the Formation La Matilde corresponds to trees that grew under very favorable environmental conditions, with a warm and humid paleoclimate, what agrees with previous paleoclimatic data provided by Volkheimer (1970) for that part of the Patagonia *Podocarpoxylon* and *Circoporoxylon*, two typical Jurassic–Cretaceous genera from other areas of Gondwana, are described for the first time for the Argentine Jurassic. These species were compared with taxa of Podocarpaceae of the Gondwana (Tables 1 and 2) and are more closely comparable with species described from the Jurassic–Cretaceous from India.

According to the distribution of wood morphogenera into five climatic zones analyzed by Philippe et al. (2004), *Podocarpoxylon* is found in the warm temperate zone since Early Jurassic and winter wet zone since Early Cretaceous (11 sp.) being a dominant genus in the last one. On the other hand *Circoporoxylon* was only recorded in the warm temperate zone. The data from fossil wood here recorded shows the presence of both genera since Middle Jurassic in the winter wet zone and points out that Patagonia played an important role in the biogeographic distribution of the family Podocarpaceae through the geologic time.

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