Palaeobio Palaeoenv (2009) 89:95–109
DOI 10.1007/s12549-009-0005-5

ORIGINAL PAPER

Gymnospermous woods (Coniferales, Taxales, and Ginkgoales) from the Upper Permian Tacuary Formation, Eastern Paraguay

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Received: 12 March 2009 / Revised: 20 May 2009 / Accepted: 20 May 2009 / Published online: 29 July 2009

Abstract Six gymnosperm woods from the Upper Permian Tacuary Formation from Eastern Paraguay are described. *Protophyllocladoxylon dolianitii* Mussa, has been recorded in the Lower Permian Rio Bonito Formation from Brazil and the Mount Glossopteris Formation of Antarctica; *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant Mackie is similar to this species from the Lower Triassic Arawi Formation of New Zealand and the Upper Triassic Laguna Colorada Formation (El Tranquilo Group) from Santa Cruz province (Argentina); *Austaloxylon teixeirae* Marguerier has been recorded from the Raniganj Formation (India), the Karroo System (Mozambique), and the Yaguary Formation (Uruguay) all of Upper Permian age; *Bageopitys herbstii* Crisafulli, from the Yaguarí Formation of Uruguay; and *Prototaxoxylon brasilianum* Kräusel and Dolianiti, a wood assigned to the Taxales, has been recorded in the Upper Permian Estrada Nova Formation of Brazil. Wood with affinities to the order Ginkgoales is represented by *Baieroxylon cicatricum* Prasad and Lele recorded from the Triassic Tiki Formation from India and the Yaguarí Formation of Uruguay. All the woods show well-marked growth rings which reflect favorable climatic conditions. An analysis of the anatomical characters shows evolutionary intermediate stages between the more primitive (araucarioid) Paleozoic and the more advanced (mixed to abietoid) Mesozoic wood taxa. Except for the numerous species of *Podocarpoxylon*, *Protophyllocladoxylon, Prototaxoxylon* and *Baieroxylon* which have more extended biochrons, *Australoxylon* and *Bageopitys* are exclusive Upper Paleozoic (Permian) taxa.

Keywords Gymnosperms · Anatomy · Upper Permian · Paraguay

Introduction

Fossil plants from the Permian of the Paraná Basin in Paraguay are poorly known in contrast to the more or less abundant records from Brazil and Uruguay. The first paper was the description of an osmundaceous fern ("*Osmundites carnieri*") by Schuster (1913) which was considered "… Jurassic or Tertiary" but is now known to be Permian (Herbst 1975, 1981c). Herbst (1972, 1981a, 1987) described some impressions of Sphenopsids and Lycopsids, as well as anatomically well-preserved specimens of the marattiaceous ferns *Tuvichapteris* and *Tietea* and the osmundacean fern *Guairea* (formerly "*Osmundites*" from Schuster). The impression fossils are poorly preserved; From the locality Siraty (close to San Estanislao), 130 km north of Arroyo Vino, they have been assigned to undetermined stems of "Lycopodopsidaceae" and *cf. Phyllotheca* sp. (Herbst 1981a) and to *Cyclodendron cf. leslii* (Seward) Kräusel (Herbst 1986), and from Arroyo Vino "Lycopsidae *incertae sedis* (Sigillariaceae ?)" (Herbst 1972). Herbst and Gutiérrez (1995) considered

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that these specimens could be assimilated to a new species from the Upper Permian Yaguarí Formation of Uruguay, viz., *Cyclodendron andreisii* Herbst and Gutierrez. Finally, Herbst (1981b) described some charophytes, *Leonardosia langei* with wide distribution in Brazil. In several papers (Harrington 1950; Eckel 1959), the presence of picnoxylic wood was stated, mainly as "*Dadoxylon*", but it was Crisafulli (2000, 2004) who described them in detail. Collections at different localities of eastern Paraguay (Fig. 1) from the Upper Permian Tacuary Formation have been made since the 1980s and here we present the first part of this paleoxiloflora, which is included in her unpublished PhD thesis (Crisafulli 2004).

Geological setting

The Permian in Paraguay was first described in some detail by Harrington (1950) followed by Eckel (1959) who referred to it as "Serie Independencia". These sediments are now included in the Independencia Group ("Mapa Geológico Paraguay", 1986 based on the "Mapa Geológico de Paraguay" by The Anschutz Co., 1981, unpublished), with two outcroping units, viz., San Miguel and Tacuary Formations. Wiens (1982) added two units, viz., the Tapytá and Cabacuá Formations but they are not well known nor widely accepted. According to the "Mapa Geológico Paraguay" (1986), these latter two units belong to the Triassic–Jurassic succession. Muff et al. (1999, Fig. 4) refer to them as "undifferentiated sequence" placed in the Tatarian or eventually as part of the overlying Mesozoic formations. The two outcropping Permian units have an extended distribution in the southern part of eastern Paraguay, but their outcrops are small and discontinuous. The distinction between the San Miguel and Tacuary Formations is not easy to establish as they are from a transitional succession. The lithology of the San Miguel Formation indicates deposition mainly of a braided river system. The Tacuary Formation is a succession of shales, siltstones, sandstones and minor limestone lenses. They represent deposition in a fluvio-lacustrine system or "…locally restricted, partially open or closed lagoonal estuaries or lagoons" (Muff et al. 1999). Jalfin (1986) stated that they represent "…sediments laid down in near-shore lakes which were periodically connected to the open sea". The upper part of the Tacuary Formation certainly represents a large fresh water body (lake), as shown by the well known "*Pinzonella* fauna", composed of an assemblage of molluscs, ostracods and the presence of charophytes (Herbst 1981b) with wide distribution in Paraguay, Brazil and Uruguay (Herbst et al. 1987). These units are correlated with the Upper Permian Estrada Nova Formation of Brazil and the Yaguarí Formation of Uruguay. All the known woods (inclusive the above mentioned ferns) are from the Tacuary Formation, from levels below those containing the mollusc fauna. According to Filippi and Báez (2002) the strata with woods could be included in the uppermost San Miguel Formation while Báez Presser et al. (2004) accept them as Tacuary Formation. In any case, there would be no appreciable difference in age, as both are considered Upper Permian.

Material and methods

The specimens studied are decorticated trunks of various sizes, well preserved as silicifications and do not show signs of mechanical distortion because cells have retained their sizes and forms, a fact that could be of taphonomical interest. They were prepared with standard procedures, i.e., thin sections of the transverse, longitudinal radial and tangential surfaces, as well as polished surfaces studied under reflected light. The peel method with acetate films, gave good results in several cases. The terminology used for descriptions is that from the list of microscopic features for softwood identification, (IAWA 2004); anatomical elements were measured based on the biometric values established by García Esteban et al. (2002) and García Esteban et al. (2003); a minimun of 25 measuments were made quoting the median and, in parentheses, minimun and maximun values.

All the specimens here described were collected at Arroyo Vino, a small creek close to the village of Melgarejo, a few kilometres north-west of Colonia Independencia (Fig. 1). A stratigraphical section of this locality was given by Herbst and Leguizamón (1984).

Specimens are housed in the Paleobotanical Collection of the Facultad de Ciencias Exactas, y Naturales y Agrimensura (Universidad Nacional del Nordeste) under acronym CTES-PB and thin sections under CTES-PMP.

Systematic Palaeontology

Division Gymnospermophyta
Class Coniferopsida
Order Coniferales
Genus *Bageopitys* Dohms, 1976

Bageopitys herbstii Crisafulli, 2001
Figures 3 a–e

2001 *Bageopitys herbstii* Crisafulli, Ameghiniana 38: 61–72 Figs. 7 D, 8A–B, 9

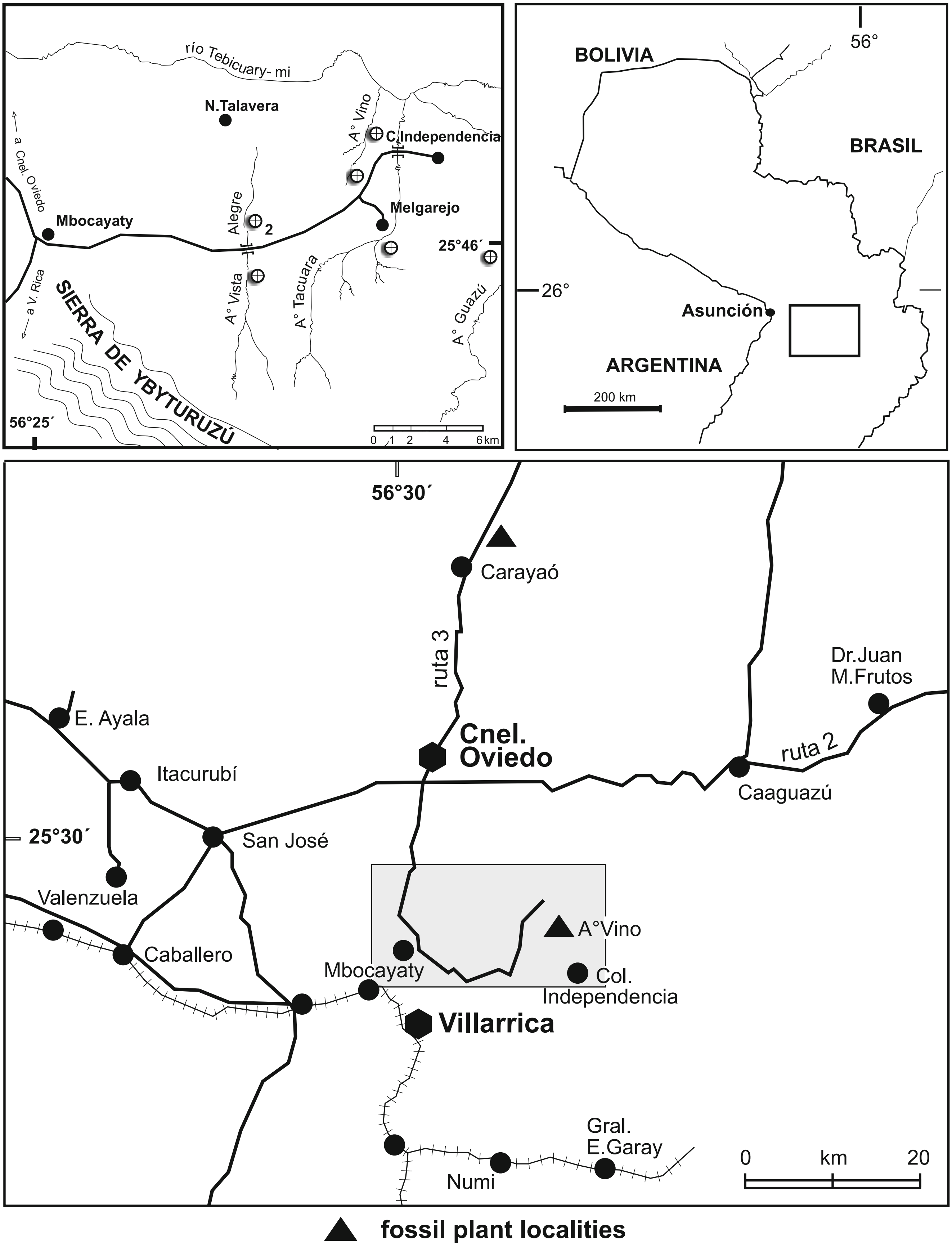


Fig. 1 Location map

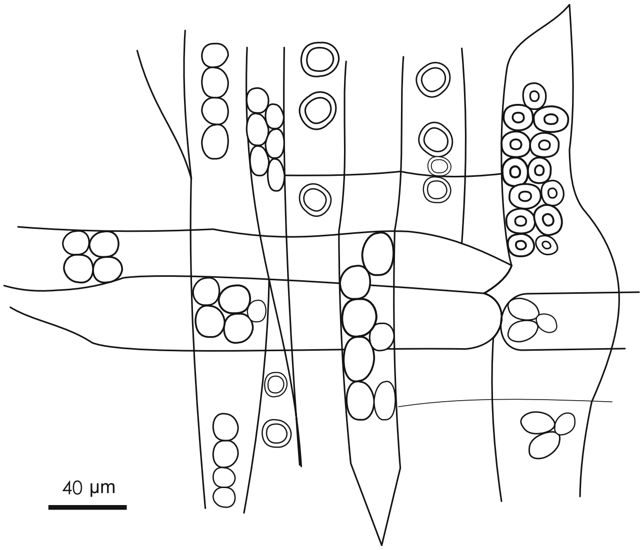


Fig. 2 *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant Mackie, 1996: sketch of pits and cross fields (Lra) (Pmp 2645). *Lra* Longitudinal radial surface

Type species

Bageopitys articulata Dohms, 1976

Description

Wood fragment 8 cm long × 9–12 cm wide, with pith, primary and secondary xylem and marked growth rings well preserved (Fig. 3a). Homogeneous pith, composed of parenchymatic rounded cells, undifferentiated in size between centre and periphery. They measure 28 µm (15–30) radially and 29 µm (15–48) tangentially. Primary xylem endarch, with wedge-shaped projections. In transverse section, the metaxylem tracheids are irregularly disposed, polygonal in shape, 45 µm radially and 37 µm tangentially. Secondary xylem homoxylic, pycnoxylic (Fig. 3b). The tracheids are quadrangular in transverse section. Few intercellular spaces throughout the wood in transverse section (Fig. 3c); shearing zones sensu Erasmus have been observed. The transition from early to late wood is gradual (feature 43, IAWA 2004: 18). In longitudinal radial section, araucarioid uniseriate, predominantly biseriate and triseriate pits on the tracheidal walls (Fig. 3d). The arrangment of two or three seriate tracheid pitting in radial walls are opposite, sometimes alternate; they are circular and average 7.5 µm; the uniseriate pits measure 9 µm. The cross fields are araucarioid. The average number per cross- ield is 2–4 pits. Tracheids are short, with an average length of 900 µm. The end walls and the horizontal walls of ray parenchyma cells are smooth (unpitted). In longitudinal tangential section rays are homogeneous. The average ray height is low, 4 cells (8–2). The rays are uniseriate. Uniseriate and ovals pits on the tangential tracheidal walls are present (Fig. 3e).

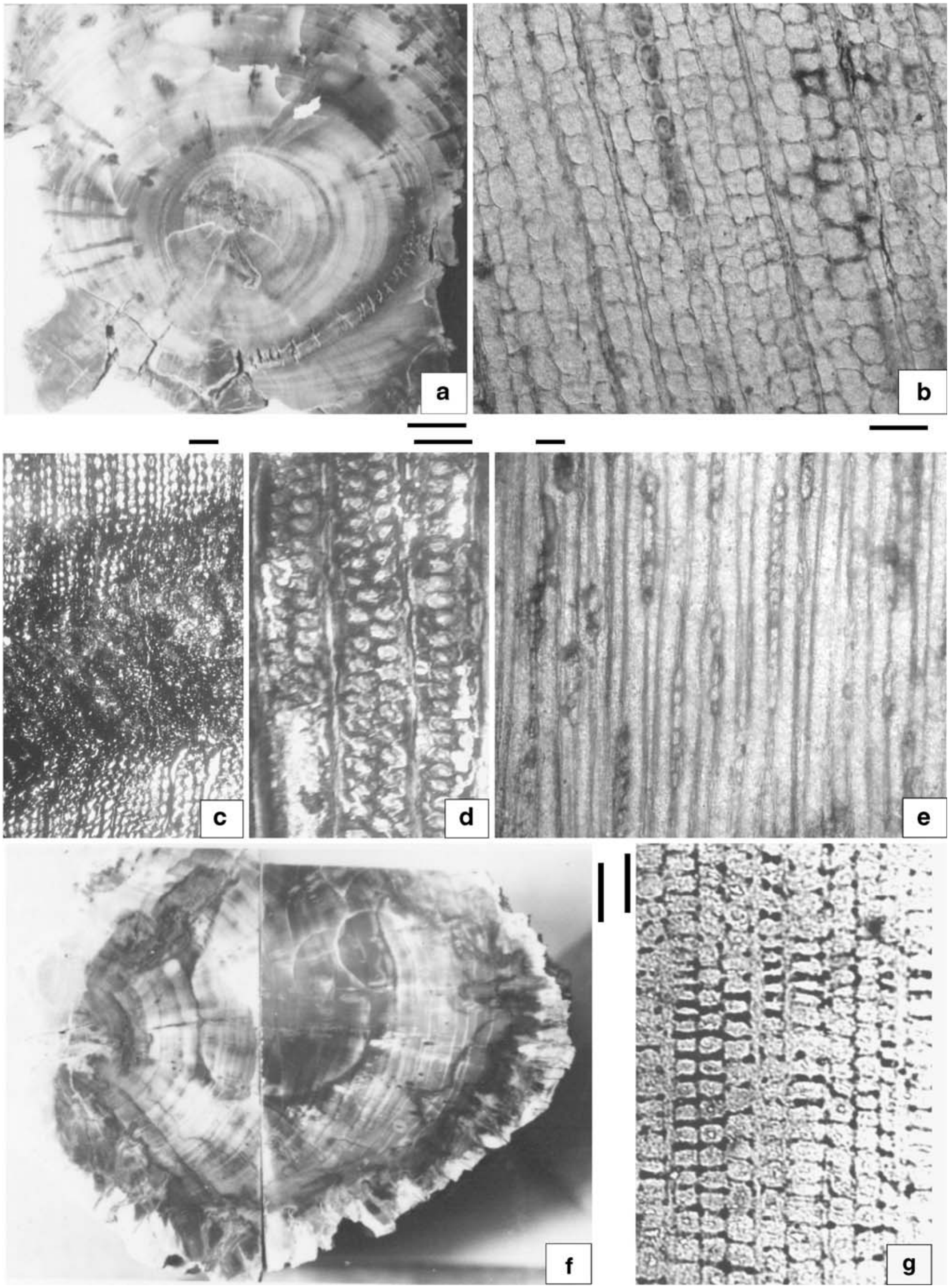
Fig. 3 **a**–**e** *Bageopitys herbstii* Crisafulli. **a** Stem (Tra) (Pb 12338). **b** Tracheids secondary xylem (Tra) (Pmp 2650). **c** Shearing zones (Tra) (Pmp 2650). **d** Detail of uni- and biseriate pits on tracheid walls (Lra) (Pmp 2651). **e** Uniseriate radii (Ltg) (Pmp 2652). (**f**–**g** *Australoxylon teixeirae* Marguerier. **f** Stem. The concentric rings in the centre reflect the upright position of the tree. The eccentric phase with the compression wood (right zone) indicates mechanical stress (Tra) (Pb 12339). **g** Detail of secondary xylem tracheids (Tra) (Pmp 2653). *Scale bars* **a**, **f** 1 cm; **b**, **e**, **g** 60 µm; **c** 90 µm; **d** 30 µm. *Tra* Transverse surface, *Lra* longitudinal radial surface, *Ltg* longitudinal tangential surface ▶

Studied material

CTES-PB 12338; CTES-PMP 2650, 2651, 2652

Discussion

The described anatomical characters show very clearly that it belongs to the genus *Bageopitys* Dohms (1976) from the Permian Iratí Formation of Brazil. There are only a few Permian Gondwana wood taxa known with homogeneous pith. Mussa (1982) does not accept Dohms' genus, placing the species in *Abietopitys articulata* (Dohms). This view is not shared here because one of the differential characters of this genus are the thickenings of their radii (referring to the layer S3 of the tertiary walls), which are clearly abietinoid. Archangelsky (1960) described two species of *Abietopitys* from the Permian of Argentina which clearly show this character. The *sensu stricto* abietinoid type is not found in *Bageopitys* as described by Dohms (1976). The present specimen can be determined as *B. herbstii* Crisafulli (2001) and differs from *B. articulata* Dohms, for it lacks the bi- and triseriate rays, the latter without the crossed lumens as the type species, and the articulation between cells (according to Dohms (1976) there usually is a small amount of lignin between the parenchymatic cells). This species has been found in the Upper Permian Yaguarí Formation of Uruguay (Crisafulli 2001) while the genus, with an undefined species, is also present in the Lower Permian Melo Formation from Uruguay (Crisafulli 1998). The present specimen does not show externally the numerous leaf scars as the uruguayan one. The growth rings of this species are characteristic for many trees from the temperate boreal regions, at palaeolatitudes supposedly similar to those of the Tacuary Formation. However, this character has limited diagnostic value as both gradual and abrupt transition may be observed in a given specimen. The transitions may also be caused by wood compression or false growth rings.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Genus *Australoxylon* Marguerier, 1973

Australoxylon teixeirae Marguerier, 1973
Figures 3 f–g; 4 a–d
1973 *Australoxylon teixeirae* Marguerier, Palaeontologia africana 16: 37–58, 7 fig., 6 pl. 2 tab 1
1986 *Australoxylon teixeirae* Marguerier in Bajpai and Maheshwari, The Palaeobotanist 35 (1): 39–47, 4-fig, pl. 2
1987 *Australoxylon teixeirae* Marguerier in Pant & Singh, Palaeontographica 203B: 19
1999 *Australoxylon teixeirae* Marguerier in Bamford, Palaeontologia africana 35: 25–40, figs. 13–16
2002 *Australoxylon teixeirae* Marguerier in Crisafulli Revista. Museo Argentino Ciencias Naturales, n.s. 4: 45–54 fig. 2 A–D fig. 3 A

Type species

Australoxylon teixeirae Marguerier, 1973

Description

Secondary pycnoxylic wood 6–9 cm long x 7–10 cm wide, with marked growth rings (Fig. 3f). The tracheids are quadrangular to rectangular in transverse section, arranged end to end in regular rows. Thickness of tracheidal walls 8 µm average (7 –11 µm). The transition from early to late wood is gradual (feature 43, in IAWA 2004: 18). Early wood tracheids measure 53 µm (30 – 60 µm) radially and 36 µm (30 – 45 µm) tangentially (Fig. 3g) while late wood tracheids are 23 µm (15 – 30 µm) radially and 36 µm (23 – 45 µm) tangentially. Xylem rays are separated by 5 (2 – 8) tracheid cell wide radial bands. In longitudinal radial section a variety of types and arrangements of the pits on the tracheidal walls are observed. They are mostly uniseriate, separate, circular with abietinoid tendency or contiguous. There also are biseriate, circular, opposite and separate, occasionally hexagonal, alternate, contiguous arrangements. Very often are 3-seriate opposite pits clustered in groups of low numbers of 3–4 cells (Fig. 4a–c). Cross-fields with simple and bordered pits, 2–6 (3–4) in number, are arranged in 2–3 series, 8 µm in diameter (Figure 11). In longitudinal tangential section xylem rays are homogeneous, uniseriate and with only three cells in a row (2–9 cells high) occasionally partially biseriate and low numbers of cells. Ray widths range approximately between 15 and 23 µm. Ray central cells are ovoidal but elliptical at the end. Uniseriate and oval pits on the three tangential tracheidal walls are observed (Fig. 4d).

Studied material

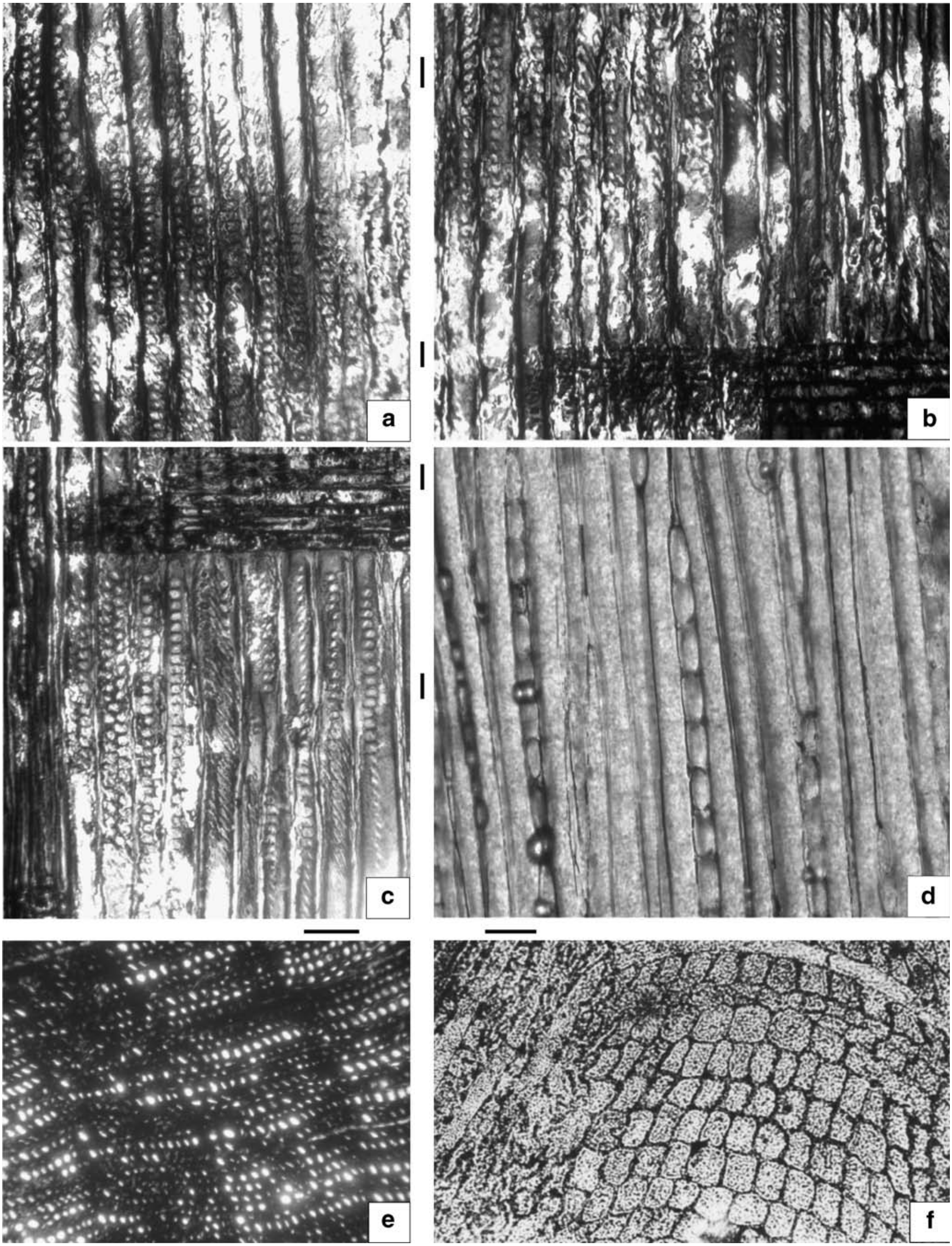
CTES-PB 12339; CTES-PMP 2653, 2654, 2655

Fig. 4 **a**–**d** *Australoxylon teixeirae* Marguerier. **a**–**c** Detail of uni-biseriate pits on tracheidal walls (Lra) (Pmp 2654). **d** Small, slender, parallel rays are characteristic of the xylem of straight, upright-growing stems (Ltg) (Pmp 2655). **e**–**f** *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant Mackie. **e** Growth-rings. **f** Tracheids and rays of secondary xylem (Tra) (Pmp 2644). *Scale bars* **a**–**d** 15 µm; **e** 120 µm; **f** 80 µm. *Tra* Transverse surface, *Lra* longitudinal radial surface, *Ltg* longitudinal tangential surface ▶

Discussion

These specimens are clearly assigned to *A. teixeirae* which is characterized mainly by the variety of their pits on the radial walls of the tracheids and the cross fields. This species has been found in the Ecca Formation, Karroo System (Marguerier 1973), the Abrahamskraal and Teekloof Formations (Middle and Upper Beaufort Group) of Mozambique (Bamford 1999), the Raniganj Formation of India (Bajpai and Maheshwari 1986) and the Yaguarí Formation of Uruguay (Crisafulli 2002). All these units are Upper Permian in age. It can be distinguished from the other species of the genus: *A. nicoli* Bamford (1999) and *A. zambesiensis* Bamford (1999) (Karroo System in Mozambique), *A. natalense* Marguerier (1973) (Ecca Formation, South Africa), *A. mondi* Weaver et al. (1997) and *A. bainii* Weaver et al. (1997) (Mount Glossopteris Formation of Antarctica), *A. duartei* (Japiassu) Marguerier (1973) (Morro Pelado Formation, Brazil) Yaguarí Formation Crisafulli, (2002) and *A. catarinensis* Merlotti and Kurzawe (2006); and from India: *A. ranaense* Pant and Singh (1987) (Raniganj Formation), *A. longicellularis* Prasad and Chandra, (1981) Kamthi Formation, *A. khanhargaoense,* Prasad and Chandra (1978) (Kamthi Formation), *A. kharkhariense (*Barakar Formation) Pant and Singh (1987) and *A. barakarense* (Barakar Formation.) Pant and Singh (1987). All these units are Permian.

The stratigraphic extension of *Australoxylon* is limited as it appears in the Middle Permian and diversifies in the Upper Permian. Up to now, it has not been found in younger strata and, for this reason, and its particular anatomical structure (i.e., grouped pits: triads) on their radial tracheidal walls (Vozenin-Serra and Grant-Mackie 1996), it becomes a characteristic wood for the Permian of the Gondwana realm. We agree with Bajpai and Maheshari's opinion (1986) that most Gondwana Paleozoic woods would have to be referred to the genus *Australoxylon.* However, we prefer not to transfer woods with pith and primary xylem to this genus (Giraud 1991). Marguerier (1973) relates it to the "Cordaitophyta", but it lacks the typical diafragmated pith and other anatomical characters of the secondary xylem (cordaitalean pits, dimensions, section, etc.), as proposed by Scott and Maslen (1910), Emberger (1968), Taylor and Taylor (1993), among others. A more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conservative position is considered here and thus the genus is included among the Coniferales.

Family Podocarpaceae *sensu* Page, 1990

Podocarpoidean type woods

Many gondwanic species included in the large “complex” of specimens assigned to *Dadoxylon–Araucarioxylon–Agathoxylon* show anatomical characters closely allied to the Podocarpaceae. This type of secondary wood is found in several of the extant genera of the family. Here, we are not analyzing the phylogeny but only comparing these features and considering their relevance for the Permian xilofloras. Mussa (1982) described podocarpoidean wood types characterized by alternate pits on the radial tracheidal walls and the characteristic pits in the cross-fields, some araucarioid mixed with podocarpoid ones and species with phyllocladoid type pits. She named this type as “subpodocarpoid” and recognized three gondwanan types:

1) Sub-podocarpoid I: radial tracheidal pits with combined alternate or opposite arrangement, araucarioid type cross-fields.
2) Sub-podocarpoid II: radial tracheidal pits similar to type I, cross fields with one podocarpoid pit per cross field, sometimes two, rarely three; they are areolate, of similar size to radial tracheidal walls and different from araucarioid pits.
3) Sub-phyllocladoide: radial tracheidal generalized arrangement; cross field with large and oval pores, generally in the centre of cross field with features close to phyllocladoid ones.

The extant genera with the subpodocarpoid types closest to the Gondwana taxa are *Phyllocladus* and *Podocarpus.*

Genus *Podocarpoxylon* Gothan, 1905

Podocarpoxylon paralatifolium Vozenin-Serra & Grant Mackie, 1996
Figures 2, 4e–f; 5a–c

1996 *Podocarpoxylon paralatifolium* Vozenin-Serra & Grant-Mackie, Paleontographica 241B: 102–108, lam. 1–3

Type species

Podocarpoxylon juniperoides Gothan, 1905

Description

Secondary pycnoxylic wood with marked growth rings. Externally with ovoidal leaf scars (Fig. 4e). Tracheids polygonal in transverse section, 30 µm (22–53 µm) radially and 29 µm (25–48 µm) tangentially (Fig. 4f). Thickness of tracheidal walls 7 µm average. The transition from early to late wood is gradual (feature 43, in IAWA 2004: 18). The specimen shows “false” growth rings probably due to unusual climatic extremes or traumatic events (IAWA 2004). Xylem rays are separated 5 (2–9) tracheids of wide radial bands. In longitudinal radial section, mostly uniseriate, contiguous and spaced, circular pits on the tracheidal walls. Very often there are biseriate pits with abietinoid tendency. Scarce mixed pits are also present. Cross fields are podocarpoid, generally one pit per field, sometimes two and excepcionally three (Fig. 2; Fig. 5a–b). Axial parenchyma scarce. In longitudinal tangential section, xylem rays are homogeneous, homocellular and low (2–3 cells). The average height is 73 µm. Parenchyma cells in this section have been observed. The rays are uniseriate, sometimes partially biseriate (Fig. 5c), ranging between 21 µm and 23 µm.

Fig. 5 **a**–**c** *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant Mackie. **a** Cross field. **b** Detail of uniseriate pits on the tracheidal walls (Lra) (Pmp 2645). **c** Irregularly arranged large and short rays indicate irregular flow forces. Note the uniseriate and partially biseriate rays (Ltg) (Pmp 2646). **d**–**g** *Protophyllocladoxylon dolianitii* Mussa: D. Stem (Tra) (Pb 12337). **e** Secondary xylem (Tra) (Pb 2647). **f** Low and uniseriate rays (Ltg) (Pb 2649). **g** Uni-biseriate and mixed pits on the tracheidal walls (Lra) (Pmp 2648). **h** *Baieroxylon cicatricum* Prasad and Lele. Stem with helical distribution of leaf traces (Pb 12340). *Scale bars* **a**, **b** 40 µm ; **c** 120 µm ; **d** 0.5 cm; **e**, **f** 80 µm; **g** 60 µm; **h** 0.2 cm. *Tra* Transverse surface, *Lra* longitudinal radial surface, *Ltg* longitudinal tangential surface ▶

Studied material

CTES-PB 12336; CTES-PMP 2644–2646

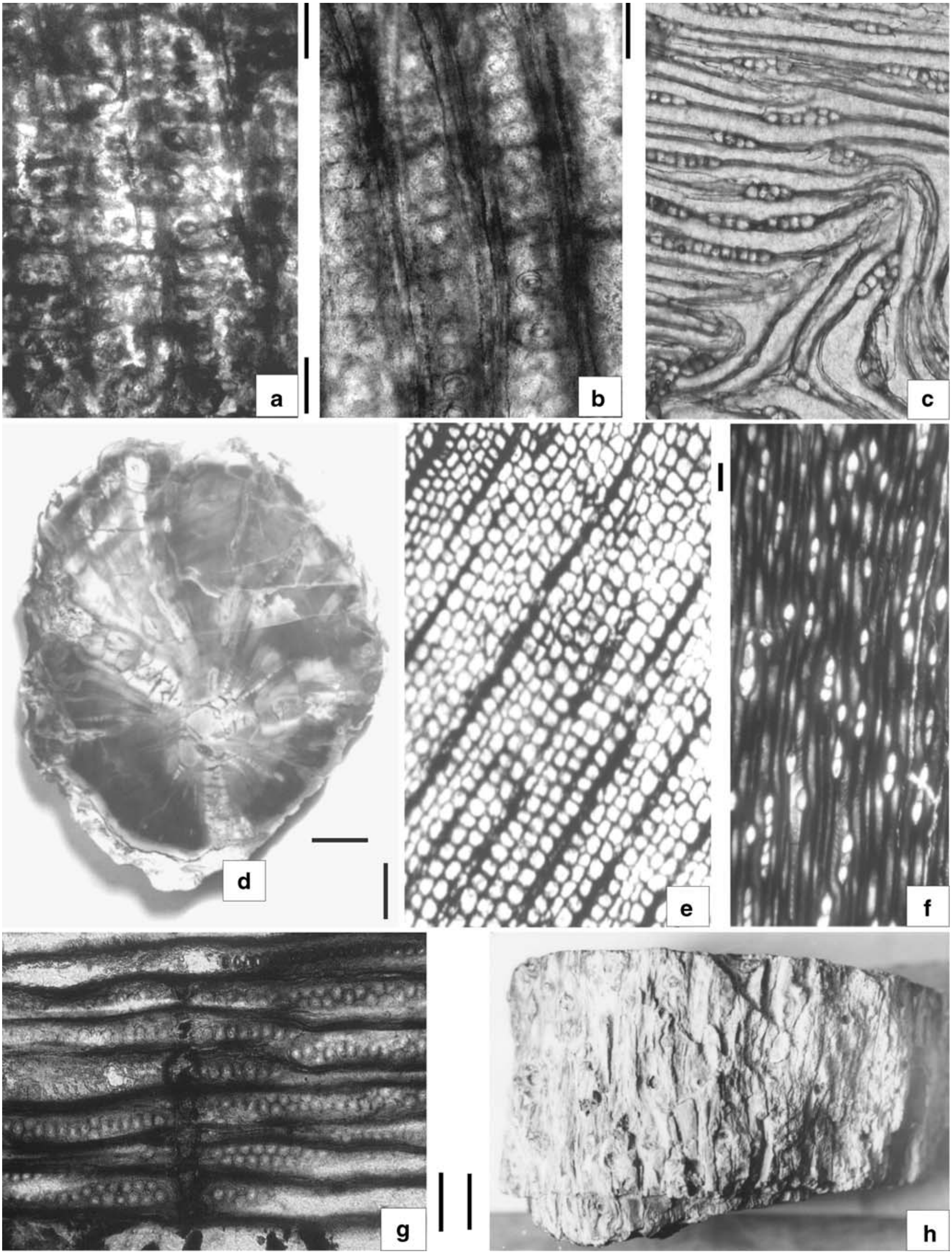
Discussion

These specimens share all characters with *P. paralatifolium* Vozenin-Serra and Grant-Mackie (1996) from the Lower Triassic Arawi Formation of New Zealand. There are numerous species of Podocarpaceae in the Gondwana realm, from Permian to Cenozoic, *P. paralatifolium* being one of the most primitive for its araucarioid characters, i.e., the mixed pits, scarce radial parenchyma and their typical cross fields.

However, the material from Tacuary Formation does not present pits on the tangential tracheidal walls like those from the Arawi Formation, but sometimes this character may appear or not depending on the way the wood section has been cut.

Genus *Protophyllocladoxylon* Kräusel, 1939

Protophyllocladoxylon dolianitii Mussa, 1958
Figures 5d–g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1958 *Protophyllocladoxylon dolianitii* Mussa, Boletim Servicio Gráfico do Instituto Brasileiro de Geografia e Estatistica 182:7–23, 4 pl., 8 figs.

1958 *Protophyllocladoxylon dolianitii* Mussa, in Kräusel & Dolianiti, Paleontographica 104 B: 126–128

1972 *Protophyllocladoxylon dolianitii* Mussa, in Maheshwari, Paleontographica 138B: 126, textfigs. 11–12, plate 6 figs. 1–6, plate 7 figs. 1–7, plate 9 fig. 1

Type species

Protophyllocladoxylon leuchsii Kräusel, 1939

Description

Specimen 19 cm long × 5–9 cm wide with marked growth rings (Fig. 5d). Tracheids quadrangular or rectangular in transverse section, measuring 36 µm (30–42) radially and 48 µm (39–57) tangentially. Thickness of tracheidal walls 5 µm on average (4–10 µm). There are xylem rays about 6 (4–8) tracheids wide forming radial bands (Fig. 5f). The transition from early to late wood is gradual (feature 43 in IAWA 2004: 18). In transverse section, the intercellular spaces throughout the wood are few. In longitudinal radial section uniseriate, circular, bordered, contiguous or spaciate pits occur, mostly uniseriate, circular, contiguous or separate, circular with an abietinoid tendency. Often there are mixed pits with circular pores (Fig. 5g). Cross fields with simple and bordered pits, with a central pore of sub-phyllocladoid type, 10 µm diameter. Xylem rays in longitudinal tangential section are homogeneous, uniseriate and low in number, 4 (2–8) cells height (Fig. 5f).

Studied material

CTES-PB 12337; CTES-PMP 2647–2649

Discussion

Protophyllocladoxylon is a cosmopolitan genus characterized by the type of its cross fields. Its ca. 18–20 species are distributed widely in both hemispheres, from the Permian to the Cretaceous, with its most primitive representatives in Gondwana. We share Mussa's (1958) opinion to include this genus within the Podocarpaceae because of its affinities with the living genera of the family. Our specimen is clearly identified as *P. dolianitii* Mussa (1958) recorded from the Lower Permian Rio Bonito Formation of Brazil and from the Mount Glossopteris Formación of Antarctica (Maheshwari 1972). Mussa (1982, unpublished PhD thesis) also described *Solidoxylon mafrense* from another locality of the Permian in Brazil with pith characters and secondary xylem of the *Protophyllocladoxylon dolianitii* type.

Fig. 6 **a**–**e** *Baieroxylon cicatricum* Prasad and Lele. **a** Transversal section of leaf-trace (Ltg) (Pmp 2673). **b** Secondary xylem. **c** Detail of fungal hyphae on the tracheids of secondary xylem (Tra) (Pmp 2671). **d** Contiguous uniseriate pits on the tracheidal walls with thin helical thickenings (Lra) (Pmp 2672). **e** Uniseriate rays (Ltg) (Pmp2673). **f**–**g** *Prototaxoxylon brasilianum* Kräusel and Dolianiti. **f** Uniseriate rays (Ltg) (Pmp 2682). **g** Secondary xylem (Tra) (Pmp 2680). *Scale bars* **a**1 mm; **b**, **g** 90 µm; **c**, **d** 30 µm; **e**, **f** 45 µm. *Tra* Transverse surface, *Lra* longitudinal radial surface, *Ltg* longitudinal tangential surface

Order Ginkgoales

Genus *Baieroxylon* Greguss, 1961

Baieroxylon cicatricum Prasad & Lele, 1981

Figures 5h; 6 a–e

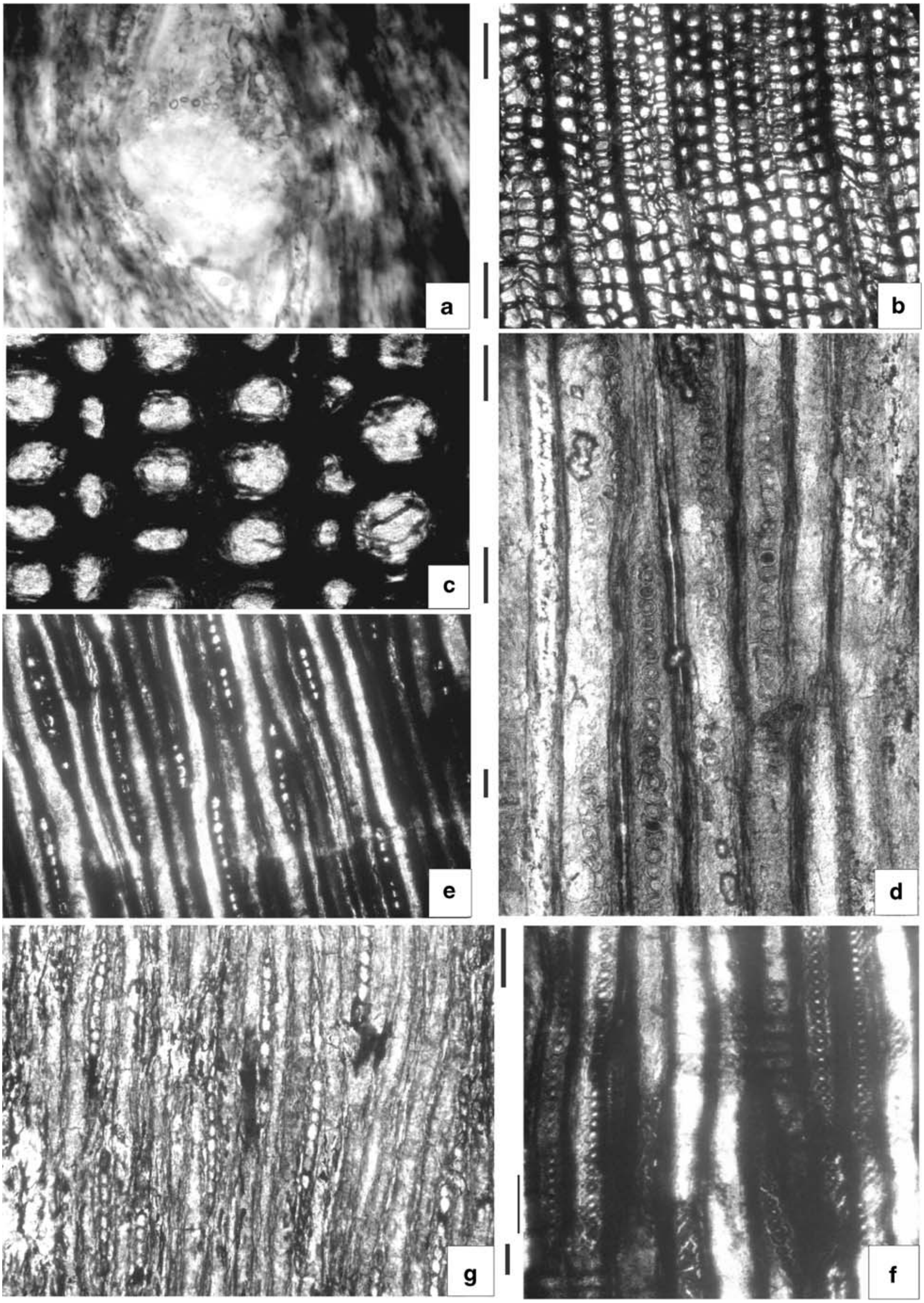
2001 *Baieroxylon cicatricum* Prasad & Lele, in Crisafulli, Ameghiniana 38: 62, fig. 2 A–G, fig. 4 a–c

Type species

Baieroxylon implexum Greguss, 1961

Description

Decorticated wood 15 cm long x 8–9 cm wide, with marked growth rings (Fig. 5h). Externally, several helically arranged scar traces are present. Scars in longitudinal tangential section show a homogeneous parenchymatous pith with ovoidal or circular cells 20 µm (12–27) in diameter (Fig. 6a). Primary xylem not preserved in scars. Secondary xylem pycnoxylic, homogeneous; in transversal section, tracheidal cells are quadrangular to ovoidal, measuring 37 µm (30–55) and 42 µm (38–66) tangentially. The presence of smaller tracheids and variously shaped and sized intercellular spaces give an unorganized appearance in some sectors. Tracheid cell walls are 11 µm thick (Fig. 6b); an average of 7 (4–11) tracheids separate radial bands. Fungal hyphae are present on their walls. On their radial walls tracheids show 1–2 seriate pits; when uniseriate pits are araucarioid, spaced, rounded, ca. 10 µm, while when biseriate they are rounded, alternate and opposite, ca. 7.5 µm in diameter; mixed pits are also present (Fig. 6d). Helical tickenings are present on both radial and tangential walls. Cross fields average 4 circular pits, with 5-µm-wide pores. On tangential walls, tracheids have uniseriate, 6-µm-diameter, pits. Xylem rays are homogeneous, uniseriate, homocellulary rays. Ray height usually 4 (3–12) cells, 190 µm and


a
b
c
d
e
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g

38 µm wide; individual cells 45 µm high x 30 µm wide (Fig. 6e).

Studied material

CTES-PB 10421; CTES-PMP 2187. 2188, 2189

Discussion

Lepekhina and Yatsenko-Khemelevsky (1966) proposed a classification for Paleozoic woods without pith nor primary xylem, establishing five main types of secondary xylem: *Araucarioxylon* (Kraus 1870), *Protophyllocladoxylon* (Kraus 1870), *Prototaxoxylon* (Kräusel and Dolianiti 1958), *Platyspiroxylon* (Greguss 1961) and *Baieroxylon* (Greguss 1961). The last three types have secondary xylem with helical thickenings on their tracheidal walls as in the present specimen. *Baieroxylon* has the closest affinities as it also shares the mixed pit type, simple pits in cross fields and homocellular rays. There are several species of this genus but we assign our material to *B. cicatricum* Prasad and Lele (1984), a species present in the Permian Yaguarí Formation of Uruguay (Crisafulli 2001), the Upper Triassic Tiki Formation (India) (Prasad and Lele 1984), and the Cretaceous Gangapur Formation (India) (Muralidhar-Rao and Ramanujam, 1986). It shares several characters (helical thickenings on radial and tangential walls of the tracheids, the pit arrangement in cross fields, uniseriate rays) but mainly those of the "eye-shaped" foliar scars (Prasad and Lele 1984) present in both the specimens from Tiki and Yaguarí Formations. A detailed explanation of the inclusion by different authors (Prasad and Lele 1984; Greguss 1961, Giraud and Hankel 1986) of *Baieroxylon* within the Ginkgoales was given by Crisafulli (2001). Here, Greguss' (1955) opinion is followed because of the normal possession of certain characters of the secondary xylem of trees of this order, like the absence of secretary canals, the arrangement of small tracheids in unorganized radial series, the frequent presence of intercellular spaces of varied shape and size and the uniseriate rays with low number of cells, these with orbicularly shaped cells and elongated marginal at ends. The presence of *Baieroxylon* in the Tacuary Formation widens its geographical distribution in South American Gondwana; together with the Yaguarí specimens they represent the oldest findings in this region; in Chile and Argentina their species are all Mesozoic.

Order Taxales
Genus *Prototaxoxylon* Kräusel & Dolianiti, 1958

Prototaxoxylon brasilianum Kräusel & Dolianiti, 1958
Figures 6f, g

1958 *Prototaxoxylon brasilianum* Kräusel & Dolianiti, Paleontographica 104B: 121

Type species

Prototaxoxylon africanum (Walton) Kräusel & Dolianiti, 1958

Description

Secondary pycnoxylic wood with marked growth rings. Tracheids quadrangular to rectangular in transverse section, radially averaging 33 µm (27–37 µm) and 56 µm (48–60 µm) tangentially. There are xylem rays 7 (4–8) tracheids wide. Transition from early to late wood is gradual (feature 43, in IAWA 2004: 18) (Fig. 6g). In longitudinal radial section usually uniseriate, rarely biseriate subalternate, circular pits are present on tracheidal walls; tertiary spirals, running over or between pits, clock- or anti-clockwise. Cross field pits 1–4, bordered, araucarioid. Xylem rays are homogeneous, uniseriate and low; their average height is 6 (2–8) cells (Fig. 6f).

Studied material

CTES-PB 12343; CTES-PMP 2680-2682; CTES-PB 12342; CTES-PMP 2677– 2679; CTES-PB 12341; CTES-PMP 2674–2678

Discussion

According to the anatomical characters described, (helicoidal thickenings on the xylem, araucarioid pits and the type of cross fields), the present specimens can be included in the genus *Prototaxoxylon* Kräusel and Dolianiti (1958). There exist some other types of Gondwanan wood with the same general secondary wood such as T*axopitys* Kräusel, *Taxoxylon*, Unger and *Taxaxeoxylon* Kräusel and Jain, but these have a higher percentage of pits with abietinoid tendencies on the radial walls, while *Prototaxoxylon* has a combination of araucarioid and cordaitoid features.

Prototaxoxylon has an extended biochron from the Upper Carboniferous to the Cenozoic (Prasad 1982) with many species worldwide. The closest ones to our specimen are *Prototaxoxylon africanum* (Walton) Kräusel and Dolianiti 1958, from the Tsarabis Formation in Namibia (SW África), *P. indicum* (Mehta) Prakash and Srivastava 1961, from India and P. br*asilianum* Kräusel and Dolianiti 1958, from the Estrada Nova Formation of Brasil; all of them are Upper Permian in age. With the latter, it shares all the important characters, like the number of pits in cross fields, the pit type on tracheidal walls, rays mostly uniseriate with cells low in number. The other species differ from this one in the spiral type of thickenings and the pit numbers in cross fields.

Final comments

A few considerations can be drawn from this Upper Permian wood assemblage from Paraguay:

1) An analysis of the anatomical characters shows these genera exhibit an intermediate stage between the more primitive Paleozoic forms and the more advanced Mesozoic ones (Césari et al. 2007, Herbst et al. 2007). Thus, characters like (1) the presence of secretory canals in the pith, considered primitive by Van Thieghem (1908), Mussa (1982) and Greguss (1955) are absent; (2) medullary rays are short and rarely partially biseriate, which according to Greguss (1955) are more or less modern characters shared by the Mesozoic conifers and the extant Araucariaceae; and (3) the presence of at least two podocarpacean genera, with mixed and abietinoid pits, which are typical Mesozoic coniferous features. All these characteristics are considered advanced conditions.
2) The Late Permian age of the Tacuary Formation is reinforced by: (1) the similitudes of the wood associations in the Paraná Basin in Brazil (3 species in common: *Protophyllocladoxylon dolianitii*, *Prototaxoxylon brasilianum* and *Australoxylon teixeirae)* and Uruguay (3 species in common: *Australoxylon teixeirae, Bageopitys herbstii* and *Baieroxylon cicatricum*); (2) the same "*Pinzonella* fauna" (Herbst et al. 1987); and (3) the more or less advanced anatomical characters (see 1, above).
3) This is the second locality/formation with Ginkgoales in the Permian of South America, the first being the Yaguarí Formation with *Baieroxylon cicatricum* Prasad and Lele and *Ginkgophytoxylon lucasii* Tidwell and Munzing.
4) The accompanying impression flora (Herbst 1972, 1986; Herbst and Leguizamón 1984) of poorly preserved Lycopsida and Sphenopsida and the well preserved arborescent ferns (Herbst 1981a, 1981c, 1987) are very similar to the floras from the Yaguarí (Uruguay) and the Rio Bonito and Estrada Nova floras from Brazil. They indicate hygromesophytic to mesoxerophytic paleocommunities.
5) All species have marked growth rings, which suggest favorable climatic conditions. The ring boundaries are clear cut which would indicate that their growth ended abruptly with the appearance of the cold season. According to Agashe and Prasad (1989), during the Gondwana Permian the dominating groups of plants belonging to coniferous families like Araucariaceae and Podocarpaceae and the Taxales indicate more or less hot and humid paleoclimates.
6) These gymnospermous taxa also show a great uniformity with contemporaneous xylopaleofloras in the Nothoafroamerican and Indogondwanoaustralian provinces, i.e., South Africa, India, Antarctica and New Zealand.
7) The presence of Podocarpacean genera (*Protophyllocladoxylon and Podocarpoxylon)* implies an extension of the geographic and temporal boundaries for this group as defined by Mussa (1958, 1974).
8) From the five Paleozoic Gondwanian wood types of Pant and Singh (1987), four of them, types I, II, III, and V, are present in this Paraguayan wood flora.

Acknowledgements We are indebted to Mr. Osvaldo Revuelta (Resistencia, Argentina) who very kindly helped with the photographic work. The present study was partially financed by the Agencia Nacional P Cientificos y Tecnología, (Project PICT 2005–33497) of Argentina. Part of the collections were made in the 1980s with financial help of the National Geographic Society (USA). We also would like to thank two anonymous reviewers for comments on the manuscript.

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