



# Fossil woods of Detarioideae subfamily (Fabaceae) from El Palmar Formation (Late Pleistocene) in South America



R. Soledad Ramos <sup>a,\*</sup>, Mariana Brea <sup>a,b</sup>, Daniela M. Kröhlhling <sup>c</sup>

<sup>a</sup> Laboratorio de Paleobotánica, Centro de Investigaciones Científicas y Transferencia de Tecnología a La Producción (CICYTTP-CONICET), Dr. Materi y España SN, E3105BWA, Diamante, Entre Ríos, Argentina

<sup>b</sup> Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos, Sede Oro Verde Diamante, Ruta Nacional 11 Km 10,5 (3100), Oro Verde, Entre Ríos, Argentina

<sup>c</sup> CONICET and Universidad Nacional Del Litoral, Facultad de Ingeniería y Ciencias Hídricas CC 217, 3000 Santa Fe, Argentina

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## ABSTRACT

The main aim of the present paper is to describe the first Detarioideae fossil woods from El Palmar Formation (Late Pleistocene) in the Uruguay River Basin (Entre Ríos, Argentina). This study is based on five silicified wood specimens preserved in fluvial deposits, which were transported from their growth site. Two new genera and species are described: *Paraoxystigma concordiensis* gen. nov and sp. nov. has medium-sized vessels, paratracheal axial parenchyma, heterocellular and multiseriate rays, and diffuse axial canals similar in size and shape to vessels, and *Gossweilerodendroxylon palmariensis* gen. nov and sp. nov. has medium-sized vessels, alternate intervessel pits, paratracheal and apotracheal axial parenchyma, homocellular and uni to-multiseriate rays, and small diffuse axial canals. These Detarioideae fossil records in south-eastern South America support the existence of a very old relationship with the extant West African forests. Eco-anatomical features observed in these fossil woods, along with the climatic information available from the Nearest Living Relatives (NLRs) comparison, suggest warm and humid climatic conditions for the upper-middle basin of the Uruguay River during some periods of the Late Pleistocene.

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## 1. Introduction

Leguminosae or Fabaceae occurs in a wide variety of vegetation types, from rainforests and mangrove swamps to deserts and temperate or alpine zones. It is the most important angiosperm family of African and American tropical forests (Lebrun and Stork, 1998; Lewis et al., 2005; LPWG, 2017). Detarioideae is a new subfamily of Leguminosae with diversity much higher in Africa than in South America or Asia; and, this clade is sister to almost all other Leguminosae (LPWG, 2017).

Currently Detarioideae has 84 genera, ca. 760 species with pantropical distribution. The most of these genera occur in tropical Africa, with a less diverse representation in Asia (Barneby et al., 1998; Bruneau et al., 2001; Herendeen, 2000; Herendeen et al., 2003; Gasson et al., 2003). 23 genera live in South America, and

only four in Argentina: *Copaifera* L. *Cynometra* L. *Hymenaea* L. and *Peltogyne* Vogel (Melandri and Espinoza de Pernía, 2008; Ulibarri, 2008; LPWG, 2017). Many tree species belonging to this subfamily are the most dominant taxonomic group of flowering plants in lowland evergreen rainforest (Lewis et al., 2005; Moggi et al., 2015; De la Estrella et al., 2017).

Within forests in central-western Africa, Detarioideae members of this clade like *Oxystigma* Harms and *Gossweilerodendron* Harms are common components of the canopy, can tower above this layer as emergent species and can even form monodominant communities (Richter and Dallwitz, 2000; Langenheim, 2003; Pan et al., 2010; Couvreur et al., 2011; Couvreur, 2015).

*Oxystigma* was based on *Copeifera? mannii* Baill, from Central Africa to which Harms added *Oxystigma buchholzii* also from Central Africa and *Oxystigma msoo* from Tanzania (see revision of *Prioria* in Breteler, 1999).

The genus *Pterygopodium* was created by Harms and based on *P. oxyphyllum* from Cameroun. The type species was only known for fruits, but later he described the flowers and assigned them as possible Caesalpinioideae (currently Detarioideae subfamily,

\* Corresponding author.

E-mail addresses: [laresole@hotmail.com](mailto:laresole@hotmail.com) (R.S. Ramos), [cidmbrea@gmail.com](mailto:cidmbrea@gmail.com) (M. Brea), [dkrohling@santafe-conicet.gov.ar](mailto:dkrohling@santafe-conicet.gov.ar) (D.M. Kröhlhling).

LPWG, 2017). A second species of *Pterygopodium*, *P. balsamiferum* from Congo (Kinshasa), was added by Vermoesen in 1923. For the latter species, Harms in 1925 erected the genus *Gossweilerodendron* (Breteler, 1999).

*Gossweilerodendron*, as a genus separate from *Prioria* Griseb. comprises two West African species. One, *G. balsamiferum* (Verm.) Harms (basonym = *Pterygopodium balsamiferum*), is one of the largest rain forest trees in Africa and is common in southern Nigeria and Angola; and *G. joveri* Aubrev. which forms the canopy layer in semi-deciduous rain forest from Cameroun, Angola and Gabon (Cheek, 2004).

The first occurrence of the Detarioideae clade would be the *Sindora*-like pollen from the Upper Cretaceous (Maastrichtian) of Siberia, Canada and Colombia. However, their assignment, even to family level, has been questioned by many authors (Muller, 1981; Herendeen et al., 1992; Calvillo-Conadell et al., 2010). The unequivocal fossils evidence of Detarioideae is from the Paleocene of Nigeria (Adegoke et al., 1978), and in Central America occur near the Oligocene-Miocene boundary (Hueber and Langenheim, 1986; Poinar and Poinar, 1999; Poinar and Chambers, 2015). Calvillo-Conadell et al. (2010) have extensively documented the fossil record of Detarioideae.

The main goal of this paper is to describe in detail five new fossil woods that have the diagnostic features of the Detarioideae subfamily. They represent the first report of fossil wood with affinities to the Detarioideae subfamily recovered from the El Palmar Formation in eastern Entre Ríos province, northeastern Argentina. This report adds new information to the historical biogeography of the *Prioria* clade.

## 2. Material and methods

The fossils woods were collected in the Concordia, Arroyo Yuquerí and Punta Viracho localities (Concordia Department, Entre Ríos, Argentina) of the El Palmar Formation (Fig. 1). One specimen (CIDPALBO-MEG 106) was collected in the Concordia locality by one of the authors (R.S. Ramos), and four wood samples (CIDPALBO-MEG 119, 138, 153 and 156) were recovered by M. Brea and A. Zucol from the Punta Viracho and Arroyo Yuquerí localities (Fig. 1).

The fossil woods were permineralized by silica with excellent preservation of the secondary xylem. The specimen CIDPALBO-MEG 106 is 11 cm long and 7 cm in diameter; CIDPALBO-MEG 119 and 138 are 11 cm in length and 9 cm in diameter; CIDPALBO-MEG 153 is 8 cm long and 5 cm in diameter and CIDPALBO-MEG 156 is 10 cm in length and 5 cm in diameter. Standard petrographic techniques were used to make the transverse (TS), tangential (TS) and radial (RS) sections for each of the five studied specimens (c. 20–40 µm thick).

The anatomical terms used in this paper follow the recommendations of the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee, 1989). The bibliographic lists provided by Gregory (1994) and Gregory et al. (2009) were also used. To compare the samples to extant and fossil species, we used the InsideWood website (InsideWood, 2004-onwards; Wheeler, 2011) and descriptions by Metcalfe and Chalk (1950), Cozzo (1951), Tortorelli (1956), Banks and Gasson (2000), Gasson et al. (2003, 2009) and Evans et al. (2006). Systematic assignment follows APG IV (2016) and LPWG (2017). The names used are as found in The International Plant Names Index (The Plant List, 2010) and the Index Nominum Genericorum (ING) (Farr and Zijlstra, 1996).

The quantitative values in the anatomical description are averages of 35 measurements, in all cases the average is cited first, followed by the minimum and maximum values, which are given in parentheses. The material was studied with a Nikon Eclipse E200 light microscope, and photomicrographs were taken with a Nikon

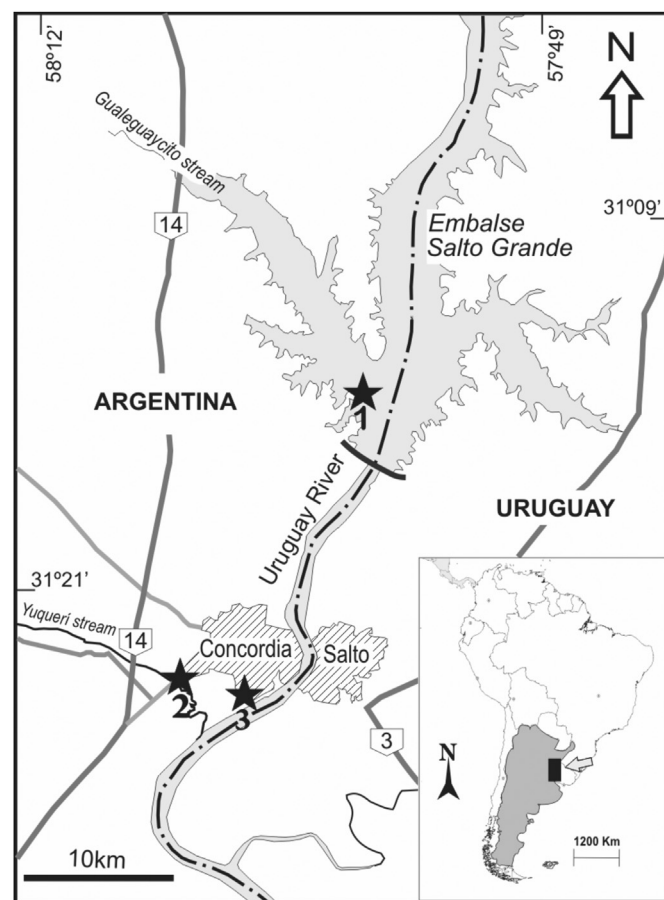


Fig. 1. Location map showing fossiliferous localities cited in the text. 1. Punta Viracho, 2. Arroyo Yuquerí and 3. Concordia.

Coolpix S4 digital camera. The fossil specimen and microscope slides are deposited in the Laboratorio de Paleobotánica (CICYTTP-CONICET), Diamante, Argentina, under the acronym CIDPALBO-MEG for wood specimens and CIDPALBO-MIC for slides.

The material was prepared for SEM by cutting a 2 cm<sup>3</sup> block of wood that was mounted on SEM stubs without coating and observed under low vacuum using a Phenom Pro Desktop SEM scanning electron microscope at the Laboratorio de Microscopía Electrónica (EMLAB), CICYTTP-CONICET, Diamante, Entre Ríos, Argentina.

The Vulnerability Index (V) and Mesomorphy ratios (M) were calculated using the equations developed by Carlquist (1977). The taxon independent approach (TIA) and Nearest Living Relatives (NLRs) were used to infer the past environmental conditions (Wheeler and Baas, 1992; Martínez-Cabrera et al., 2014).

## 3. Geological and palaeobotanical setting and age

The El Palmar Formation was defined by Iriondo (1980). It is a Late Pleistocene sedimentary unit generated by the Uruguay River in its middle basin (eastern Entre Ríos province and north-western Uruguay). This fluvial unit is composed of siliceous sands and gravels in a clayey-sandy matrix, red to yellowish brown in colour, with planar stratification. High energy channel deposits are represented by gravel and sandy strata; levee and splay deposits correspond to silty-clayey sands. This formation, 15–20 m thick, forms the upper fluvial terrace of the Uruguay, with a height of 10 m above the bottom of the valley tributaries. The unit is covered

by Holocene fluvial/swampy and aeolian deposits (Iriondo, 1980; Iriondo and Kröhling, 2008; Kröhling, 2009).

The El Palmar Formation was dated, in the type area, by thermoluminescence (TL) at  $80,670 \pm 13,420$  years BP (Federación locality; Argentina; Iriondo and Kröhling, 2008), while in Uruguay it was TL dated at  $88,370 \pm 35,680$  years BP (Salto locality; Iriondo and Kröhling, 2008). These ages in the upper part of the El Palmar Formation was probably developed during the Oxygen Isotopic Stage 5a (MIS 5a), which corresponds to a warm sub stage of the Late Pleistocene.

Recently, a new date of the upper part of the unit, outcropping in profiles located at El Palmar National Park and obtained by OSL (optical stimulated luminescence) resulted in an age of ca. 185 ka BP ( $184,491 \pm 13,946$  years BP; Lab Code L0090, Laboratório de Espectrometria Gama e Luminescência, USP, Brazil). This result would extend the age of the outcrop sequence of the El Palmar Formation to the penultimate interglacial (MIS 7; Middle Pleistocene).

The paleoflora of the El Palmar Formation has revealed a rich angiosperm flora (Lutz, 1979, 1980, 1984, 1986; Brea, 1998, 1999; Brea and Zucol, 2001a, b; 2011; Brea et al., 2001, 2010; Zucol et al., 2005; Ramos et al., 2012, 2014, 2015) with diverse and abundant legume fossils which are represented by *Menodoxylon arenensis*, *M. mesopotamiensis*, *M. piptadiensis*, *Mimosoxylon caccavariae*, *Prosopisinoxylon castroae*, *Piptadenioxylon chimeloi* and *Peltophoroxylon uruguayensis*, *Holocalyxylon cozzoi* and *Amburanoxylon tortorellii* (Lutz, 1979; Brea, 1999; Zucol et al., 2005; Brea et al., 2010; Ramos et al., 2012, 2014).

## 4. Results

### 4.1. Systematic palaeobotany

**Family Fabaceae** Lindley, 1836.

**Subfamily Detarioideae** Burmeister, 1837.

**Genus Paraoxystigma** gen. nov. Ramos, Brea et Kröhling.

**Type species Paraoxystigma concordiensis** sp. nov. Ramos, Brea et Kröhling.

*Genus and species diagnosis.* Diffuse-porous wood; short vessel elements; simple perforation plates; small to minute, alternate and vested intervessel pits; vessel-ray parenchyma pits similar in size and shape to intervessel pits; heterocellular rays (body ray cells procumbent with one row upright and/or square marginal cells); axial parenchyma scarce vasicentric, aliform to confluent and in narrow bands or lines up to three cells wide; 3–6 cells per parenchyma strand; diffuse axial canals similar in size and shape to the diameter of the vessels; crystals in ray cells.

*Derivatio nominis.* The generic name, *Paraoxystigma*, refers to its affinity with the genus.

*Oxystigma.* The specific name, *concordiensis*, refers to the geographic provenance where the fossil specimen was collected.

**Holotype.** CIDPALBO-MEG 106, CIDPALBO-MIC 1363 (three slides).

**Repository.** Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.

**Type Stratigraphic horizon and age.** El Palmar Formation, Late Pleistocene.

**Type Locality.** Concordia, Entre Ríos, Argentina ( $31^{\circ}19' S$ ,  $57^{\circ}59' W$ ).

**Search Criteria InsideWood:** 5p 13p 22p 25p 29p 30p 58p 66p 69p 79p 80p 81p 82p 83p 86p 89p 92p 97p 106p 129p 136p 138p 142p (see codification in InsideWood, 2004-onwards).

**Description.** Growth rings boundaries are distinctly marked by narrow-banded marginal axial parenchyma. The wood shows diffuse porosity (Fig. 2. a, f). Vessels are commonly solitary (50%), in

radial multiples of 2–4 vessels (43%), and rarely in clusters (7%) (Fig. 2 a, f, h; 5. a). The solitary vessels are circular to oval in outline in TS, with thin walls, 12 (8–20)  $\mu m$  thick. The mean tangential diameter of the vessels is 118 (73–170)  $\mu m$ , and the mean radial diameter is 112 (76–152)  $\mu m$ . The mean vessel density is 17 (15–19) per  $mm^2$ . Dark deposits occur in vessels (Fig. 2 a, h). The mean vessel element length is 277 (140–450)  $\mu m$  (Fig. 2 c). The perforation plates are simple, horizontal end walls (Fig. 2 l). The intervessel pits are small (3–5  $\mu m$ ), alternate, circular, and vested (Fig. 5 c, e).

The fibres are angular to oval in outline on TS, non-septate, with a mean diameter of 16 (13–23)  $\mu m$  and with a wall thickness of 4 (2–5)  $\mu m$ .

The axial parenchyma is scarce vasicentric, aliform to confluent, and in narrow bands or lines up to three cells wide (Fig. 2 a, f, h), and has strands of 3–6 cells (Fig. 2 e, g, k).

The rays are heterocellular, 1 to 3 cells wide (95%), and rarely 7 cells wide (5%). They are composed of procumbent body cells with one row of upright marginal cells (Fig. 2 d, e, g, i, k, m). The mean width of rays is 66 (58–75)  $\mu m$ . The mean height of rays is 327 (200–575)  $\mu m$  and 12 (6–21) cells high. The mean number of rays is 7 (7–8)/mm (Fig. 2 b, i, k).

The vessel-ray parenchyma pits with distinct borders and similar in size and shape to intervessel pits (Fig. 5 d). Ovoid and dark deposits are present in ray cells, have a mean diameter of 11 (10–13)  $\mu m$  (Fig. 2 m).

There are diffuse axial canals with similar diameter to vessels both in size and shape (Fig. 2 f, h; Fig. 5 b). The crystals [size mean 27 (20–29)  $\mu m$ ] are present in procumbent ray cells and in chambered axial parenchyma cells, with one crystal per chamber (Fig. 2 j).

**Genus Gossweilerodendroxylon** gen. nov. Ramos, Brea et Kröhling.

**Type species Gossweilerodendroxylon palmariensis** sp. nov. Ramos, Brea et Kröhling.

*Genus and species diagnosis.* Diffuse-porous wood; simple perforation plates; small to medium size, alternate and vested intervessel pits; vessel-ray parenchyma pits with distinct borders are similar to intervessel pits in size and shape; uniseriate and multiseriate rays, homocellular to heterocellular rays; axial parenchyma vasicentric, aliform to confluent and in marginal or in seemingly marginal bands; up to eight cells per parenchyma strand; non-septate fibres; axial canals small and diffuse; prismatic crystals in axial parenchyma cells.

*Derivatio nominis.* The generic name, *Gossweilerodendroxylon*, refers to the affinity with the genus *Gossweilerodendron*. The specific name, *palmariensis*, refers to the stratigraphic (El Palmar Formation) provenance of the type specimens.

**Holotype.** CIDPALBO-MEG 156, CIDPALBO-MIC 1679 (three slides).

**Paratype.** CIDPALBO-MEG 153, CIDPALBO-MIC 1576 (three slides).

**Type Locality.** Punta Viracho, Entre Ríos, Argentina ( $31^{\circ}12' S$ ,  $57^{\circ}55' W$ ).

**Paratype.** CIDPALBO-MEG 119, CIDPALBO-MIC 1542 (three slides); CIDPALBO-MEG 138, CIDPALBO-MIC 1561 (three slides).

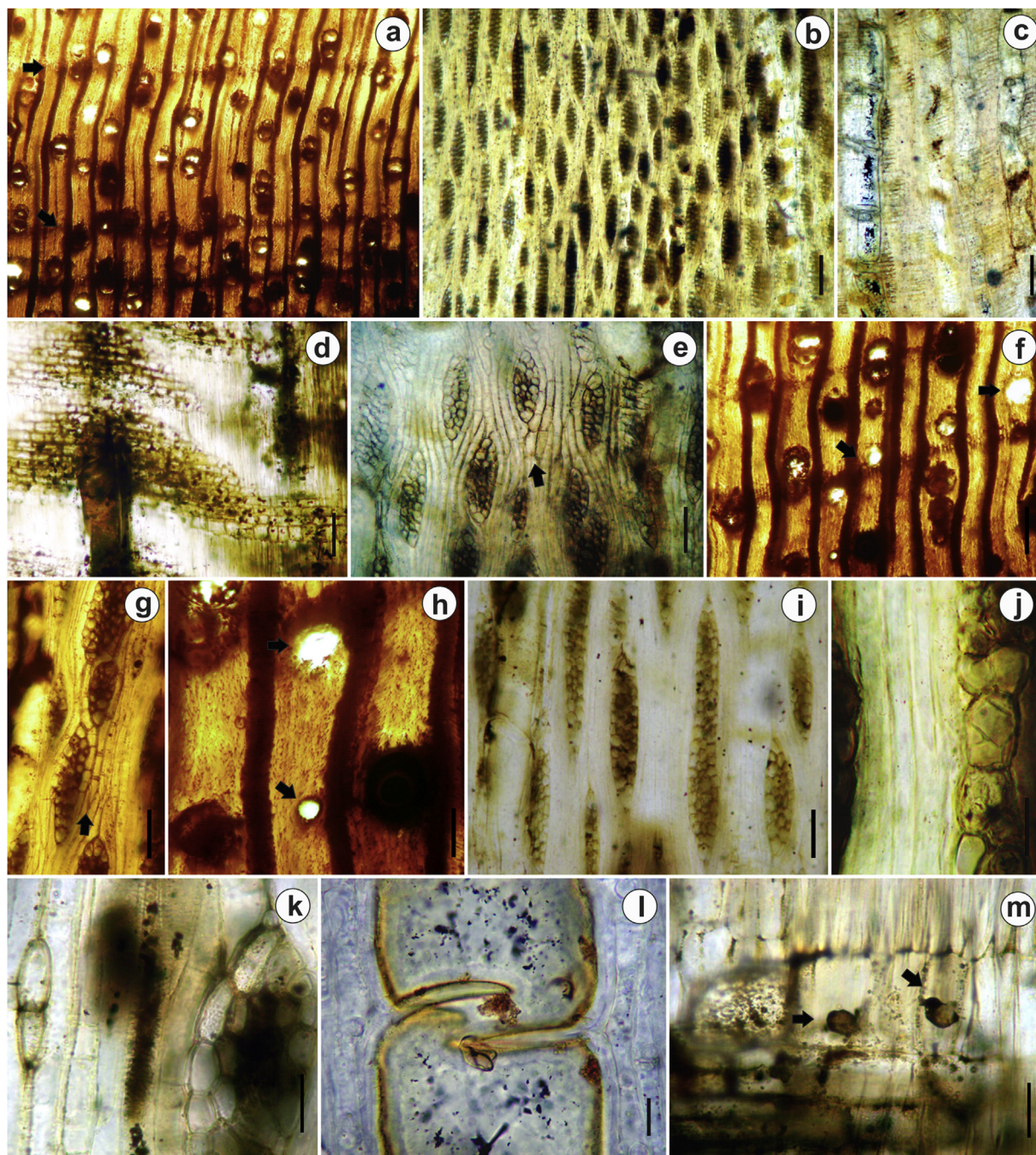
**Other locality.** Arroyo Yuquerí, Entre Ríos, Argentina ( $31^{\circ}22' S$ ,  $58^{\circ}04' W$ ).

**Repository.** Laboratorio de Paleobotánica, CICYTTP-CONICET, Diamante.

**Type Stratigraphic horizon and age.** El Palmar Formation, Late Pleistocene.

**Search Criteria InsideWood:** 13p 25p 29p 30p 66p 79p 80p 83p 89p 92p 97p 104p 129p 142p (see codification in InsideWood, 2004-onwards).





**Fig. 2.** *Paraoxystigma concordiensis* gen. nov. sp. nov. Ramos, Brea et Kröhlting (CIDPALBO-MIC 1363). a, general view diffuse porous and axial parenchyma in narrow bands or lines up to three cells wide (arrow) TS; b, multiseriate rays TLS; c, short element vessels RLS; d, heterocellular rays RLS; e, irregular storied rays and strands of axial parenchyma (arrow) TLS; f, irregularly scattered axial canals (arrows) TS; g, strands of axial parenchyma (arrow) TLS; h, axial canals (arrows) TS; i, multiseriate rays and vessels TLS; j, prismatic crystals in upright ray cells, non-septate fibres TLS; k, detail of axial parenchyma and ray cells TLS; l, simple perforation plates TLS; m, detail of upright cells rays with oval deposits (arrows) RLS. Scale bar: a, b = 250; c, f = 200  $\mu\text{m}$ ; d–i = 100  $\mu\text{m}$ ; k, l = 30  $\mu\text{m}$ ; j, m = 20  $\mu\text{m}$ .

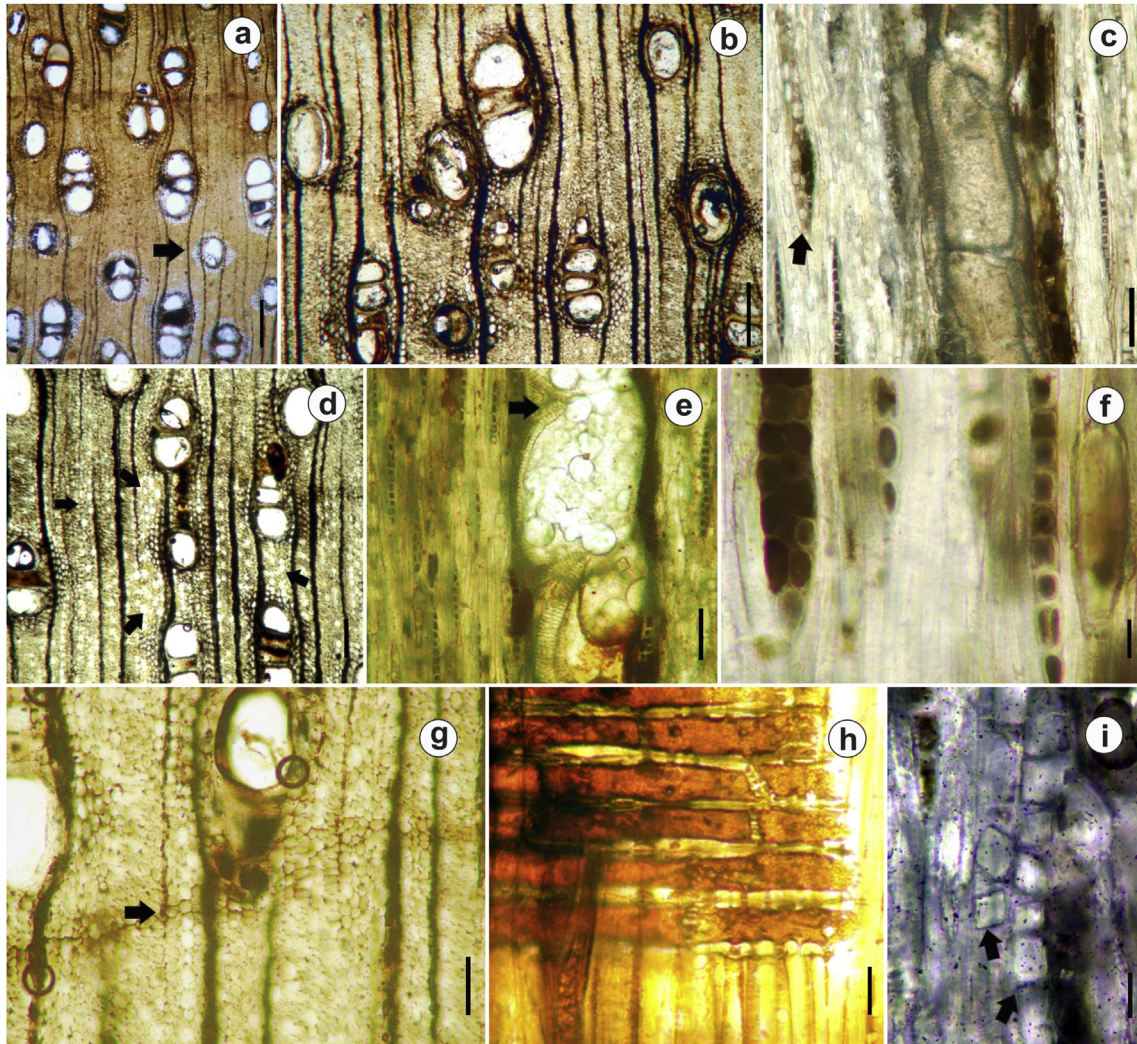
**Description.** Growth ring boundaries are distinctly marked by narrow bands of axial marginal parenchyma (Fig. 3 a, b, g). The wood shows diffuse porosity (Fig. 3 a, b, d) but in CIDPALBO-MEG 119 shows slight tendency to semi-ring-porous. The vessels are commonly solitary (68%), some in radial multiples of 2–5 elements (32%), with the mean tangential diameter of 145 (50–229)  $\mu\text{m}$ , and the mean radial diameter of 161 (25–305)  $\mu\text{m}$ . The vessels are circular to oval in outline in TS with thin walls of 16 (7–28)  $\mu\text{m}$  thick. The mean vessel density is 9 (4–12) per  $\text{mm}^2$ . The tyloses or/

and other deposits are present in vessels (Fig. 3 b; Fig. 4 b, c, e, g). The mean vessel element length is 280 (127–500)  $\mu\text{m}$ . The perforation plates are exclusively simple, with oblique end walls (Fig. 3 c, e). The intervessel pits are alternate and vestured, with a mean diameter of 7 (5–9)  $\mu\text{m}$  (Fig. 4 g; Fig. 5 g).

The fibres are circular to oval in outline in TS, non-septate with a mean diameter of 18 (10–28)  $\mu\text{m}$  and with a wall thickness of 4 (2–5)  $\mu\text{m}$  (Fig. 4 a, c, f, h).

The axial parenchyma is vasicentric, aliform to confluent,





**Fig. 3.** *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. (CIDPALBO-MIC 1679). a, vessels solitary and in radial multiples, vasicentric axial parenchyma (arrow) TS; b, vessels in radial multiples, vasicentric and confluent axial parenchyma TS; c, detail of axial canal (arrow), uniseriate rays, short vessel elements TLS; d, axial canals (arrows) TS; e, uniseriate rays, vessel element with oblique end walls (arrow) TLS; f, homocellular rays TLS; g, marginal axial parenchyma TS; h, homocellular rays composed of procumbent cells RLS i, prismatic crystals in chambered axial parenchyma cells (arrow) TLS. Scale bar: a = 500  $\mu$ m; b, d = 200  $\mu$ m; c, e, g = 100  $\mu$ m; f, h, i = 20  $\mu$ m.

unilateral and in marginal or in seemingly marginal bands; apotracheal diffuse; and has strands of 5–8 cells (Fig. 4 b, c, f; Fig. 5 f).

The rays are 1–3 cells wide and homocellular, composed exclusively of procumbent cells or with most cells procumbent and some square and upright. The mean width of the rays is 27 (18–46)  $\mu$ m. The mean height of the rays is 257 (38–450)  $\mu$ m and 14 (2–25) cells high. The mean number of rays per linear millimetre is 9 (7–14)/mm (Fig. 3 c, e, f, h; Fig. 4 c, d; Fig. 5 f). The vessel-ray parenchyma pits with distinct borders and similar in size and shape to intervessel pits (Fig. 4 d, i).

There are small diffuse axial canals with a diameter of 25–38  $\mu$ m (Fig. 3 d; Fig. 4 e, f, h). The crystals are present in chambered axial parenchyma cells, with one crystal per chamber (Fig. 3 i).

## 5. Discussion

### 5.1. Comparison with extant species

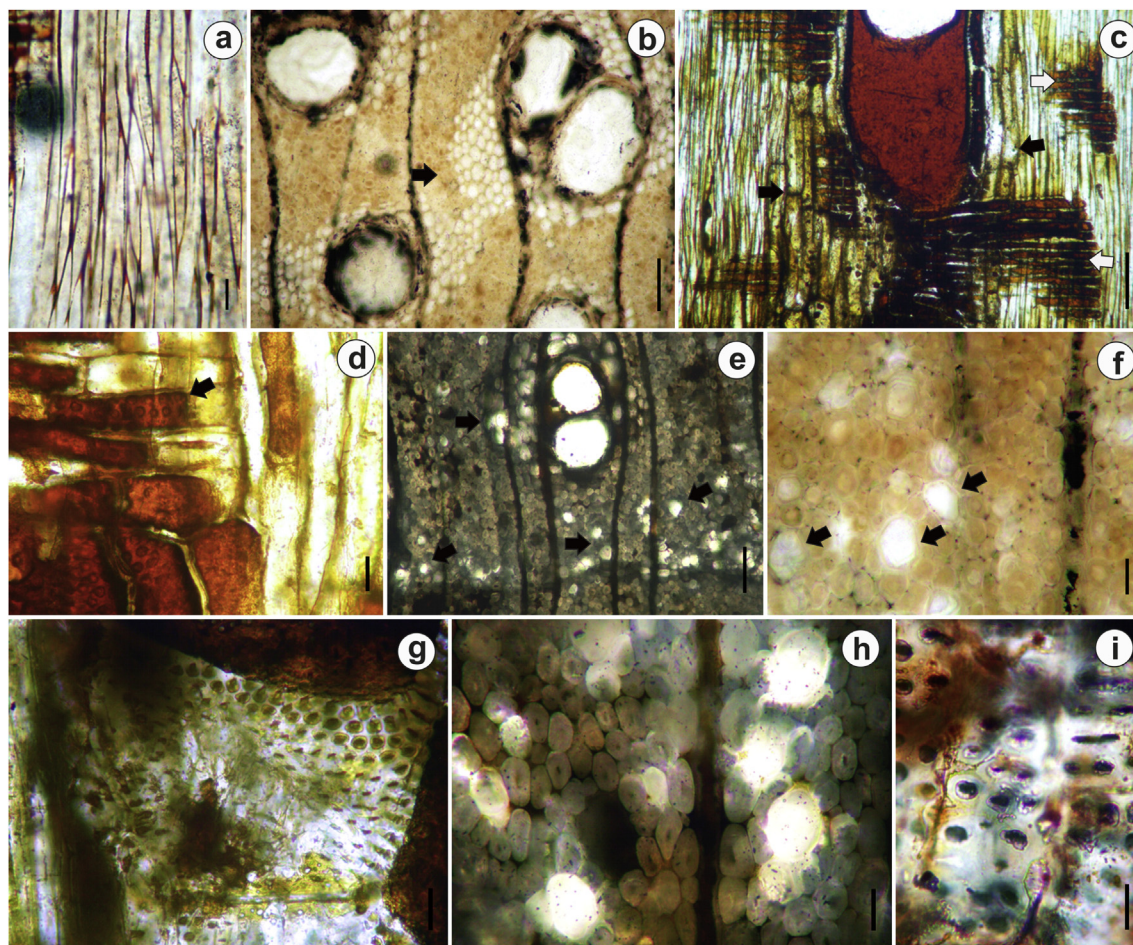
Some families, within the dicots, have intercellular axial canals and this is a useful diagnostic feature. These include the Connaraceae (*Connarus* L. and *Cnestidium* Planchon), Cornaceae

(*Mastixia* Blume), Vochysiaceae (*Qualea* L.), Dipterocarpaceae (all genera except *Marquesia* Gilg and *Monotes* de Candolle), and Fabaceae family, Detarioideae subfamily (*Copaifera* L. *Bikinia* Wieringa, *Brandzeia* Baillon, *Daniellia* Benth, *Detarium* Jussieu, *Eperua* Aublet, *Gossweilerodendron* Harms, *Kingiodendron* Harms, *Oxystigma* Harms, *Prioria* Griseb. *Pseudosindora* Symington, *Sindoropsis* J. Léonard and *Sindora* Miquel (Metcalf and Chalk, 1950; Baretta-Kuipers, 1981; Gasson, 1994; Banks and Gasson, 2000; Richter and Dallwitz, 2000—onwards; Carlquist, 2001; Melandri and Espinoza de Pernía, 2008; InsideWood, 2004—onwards).

The fossils materials studied here differ from the Connaraceae mainly in the absence or extremely rare axial parenchyma and uniseriate and heterocellular rays which allows the exclusion of this family (InsideWood, 2004—onwards). Within the Cornaceae only *Mastixia* has axial canals in long tangential lines; however it differs from the fossil material because it has scalariform perforation plates and rays of two distinct sizes that are heterocellular and composed exclusively of upright cells (Noshiro and Baas, 1998; Richter and Dallwitz, 2000—onwards).

Vochysiaceae (mainly *Qualea rosea* Aubl.) differ from the fossil woods because it has septate fibres, abundant apotracheal





**Fig. 4.** *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. a, (CIDPALBO-MIC 1576) non-septate fibres TLS; b, (CIDPALBO-MIC 1561) vasicentric and confluent axial parenchyma (arrow) TS; c, (CIDPALBO-MIC 1542) axial parenchyma strands surrounding the vessel (black arrows) and homocellular rays composed of procumbent cells (white arrows) RLS; d, (CIDPALBO-MIC 1542) vessel-ray pits (arrow) RLS; e, (CIDPALBO-MIC 1542) detail of diffuse axial canals (arrows) and radial multiples vessels TS; f, (CIDPALBO-MIC 1561) diffuse axial canals (arrows) TS; g, (CIDPALBO-MIC 1576) alternate intervessel pits TLS; h, (CIDPALBO-MIC 1542) fibres, diffuse and small axial canals TS; i, (CIDPALBO-MIC 1542) detail of vessel-ray pits with distinct borders are similar to intervessel pits in size and shape throughout the ray cell RLS. Scale bar: b, c, e = 100  $\mu$ m; a, d, f, g, h = 20  $\mu$ m; i = 10  $\mu$ m.

parenchyma axial and intercellular canals of traumatic origin (Detienne and Jacquet, 1983; InsideWood, 2004-onwards).

Dipterocarpaceae differ from the fossil woods studied here because has exclusively solitary vessels, rays mostly up to 4–8 cells wide and with occasional radial canals (Metcalf and Chalk, 1950; Richter and Dallwitz, 2000–onwards; InsideWood, 2004–onwards).

In addition to the radial canals the features that the El Palmar Formation fossil woods have in common with the Detarioideae subfamily are: vasicentric, aliform, confluent and marginal axial parenchyma, homocellular to heterocellular rays, with one row of square or upright marginal cells, prismatic crystals in chambered axial parenchyma cells and ray cells, vested intervessel pits and axial canals (Baretta-Kuipers, 1981; Wheeler and Baas, 1992; Herendeen, 2000; Gasson et al., 2003; Espinoza de Pernía and Melandri, 2006; Melandri and Espinoza de Pernía, 2008).

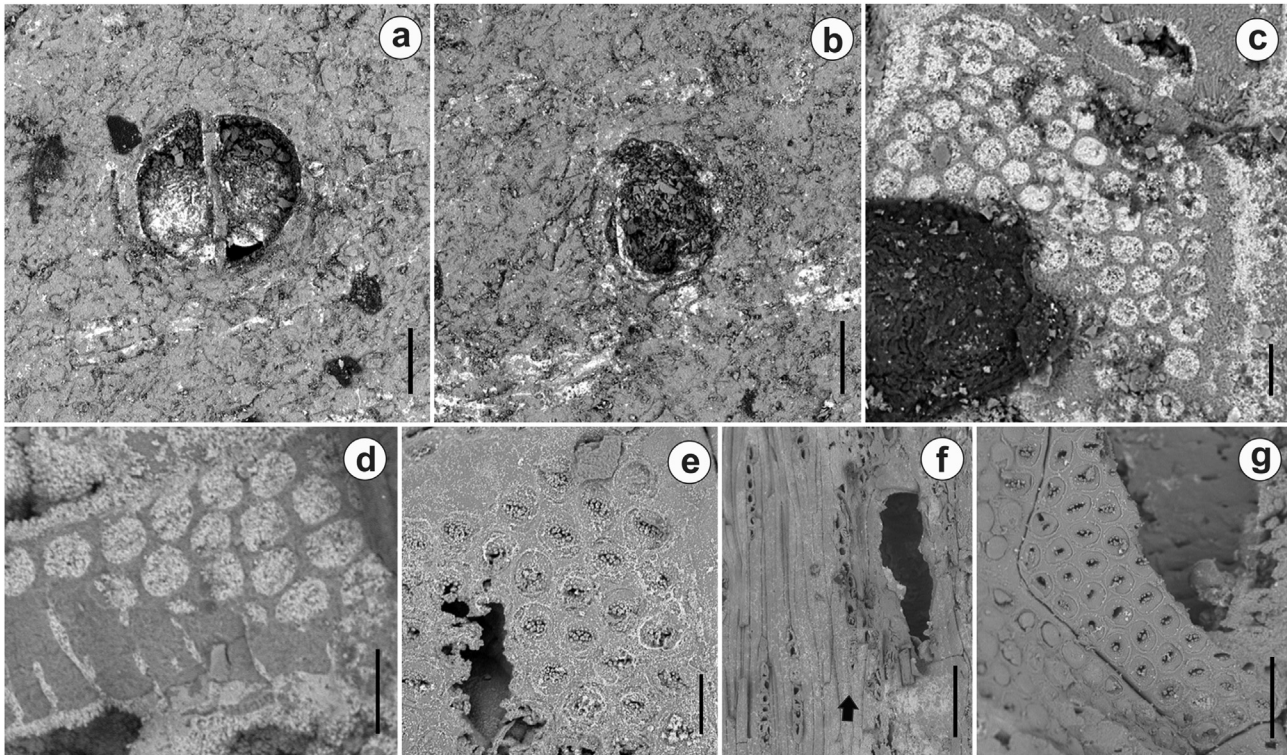
Reviewing the Insidewood search short list, *Bikinia* show normal axial canals in short tangential lines but not with the diffuse distribution, and *Sindora* show have intercellular canals of traumatic origin, different from the fossils (Quirk, 1983). *Daniellia* has large intervessel pits, fibres and axial parenchyma and/or vessel elements storied, a combination not observed in the fossils (Normand and Paquis, 1976) (see Table 1).

According to Fougère-Danezan et al. (2010), *Prioria* s.l. includes two taxonomic subgroups: *Prioria* sub-group (*Gossweilerodendron*,

*Oxystigma*, *Kingiodendron* Harms and *Prioria*) and the *Hardwickia* sub-group (*Colophospermum* (Benth.) and *Hardwickia* Roxb.). All species of the *Prioria* s.s. clade have diffuse axial canals except for *Prioria*, whose axial canals are in tangential lines (Gasson et al., 2003). The fossil materials studied here has normal diffuse axial canals (i.e. not traumatic in origin). These features are diagnostic of the *Prioria* group (Baretta-Kuipers, 1981; Cevallos-Ferriz and Barajas-Morales, 1994; Breteler, 1999; Fougère-Danezan et al., 2010). Table 1 shows the comparison with extant genera more related with the fossil woods described in this paper: *Oxystigma*, *Gossweilerodendron*, *Sindora*, *Bikinia*, *Daniellia*, *Kingiodendron* and *Prioria*.

*Kingiodendron* combines multiseriate and homocellular rays with abundant and banded axial parenchyma; *Prioria* shows abundant axial parenchyma and some species have irregularly storied elements (e.g. *Prioria copaifera*), all these features not seen in the fossil woods studied here (Normand and Paquis, 1976; Baretta-Kuipers, 1981; Quirk, 1983; Rodríguez-Reyes et al., 2017). *Gossweilerodendron* and *Oxystigma* generally have up to eight cells per parenchyma strand, while  $\leq 4$  cells have other genera (Pearson and Brown, 1932; Detienne and Jacquet, 1983; Gasson et al., 2003). Moreover, they have vasicentric, aliform and confluent paratracheal and diffuse axial parenchyma. In addition, small to minute intervessel pits are common in *Oxystigma* and *Gossweilerodendron*





**Fig. 5.** *P. concordiensis* gen. nov. sp. nov. (CIDPALBO-MIC 1363) a, detail of vessel with cell wall TS; b, detail of axial canal with similar diameter of vessels and without cell wall TS; c, detail of alternate intervessel pits TLS; d, detail of vessel-ray pits with distinct borders are similar to intervessel pits in size and shape throughout the ray cell RLS; e, detail of vestured intervessel pits TLS; *G. palmariensis* gen. nov. sp. nov. (CIDPALBO-MIC 1679) f, detail of axial parenchyma in strand of 5 cells (arrow) TLS; g, detail of alternate and vestured intervessel pits TLS. Scale bar: a, b = 50  $\mu\text{m}$ ; c, e = 10  $\mu\text{m}$ ; d = 5  $\mu\text{m}$ ; f = 100  $\mu\text{m}$ ; g = 20  $\mu\text{m}$ .

(Metcalf and Chalk, 1950; Kribs, 1968; Normand and Paquis, 1976).

CIDPALBO-MIC 1363 particularly resembles the genus *Oxystigma* which is characterized by the presence of axial canals with sizes similar to those of their vessels, mainly heterocellular rays and small to minute intervessel pits. CIDPALBO-MIC 1679, 1576, 1542, 1561 are assigned to *Gossweilerodendron* based on the presence of small diffuse axial canals, small to medium intervessel pits and commonly homocellular rays.

An InsideWood search used these features: 5p (wood diffuse-porous), 13p (simple perforation plates), 22p (intervessel pits alternate), 25p (small pits), 29p (vestured pits) 30p (vessel-ray pits with distinct borders), 58p (gum and other deposits in vessels), 66p (non-septate fibres), 79p (axial parenchyma vasicentric), 80p (axial parenchyma aliform), 89p (marginal axial parenchyma), 92p (3–4 cells per parenchyma strand), 97p (rays width 1 to 3 cells), 106p (body ray cells procumbent with one row upright and/or square marginal cells), 129p (axial canals diffuse), 136p (prismatic crystals present) and 138p (prismatic crystals in procumbent ray cells) with 0 allowable mismatches, they showed that the CIDPALBO-MIC 1363 fossil wood described here closely resembles *Oxystigma oxyphyllum* described by Normand and Paquis (1976).

*Oxystigma oxyphyllum* has thin-walled fibres, paratracheal axial parenchyma and indistinct bands up to 5 cells wide, including marginal bands (described as terminal in Kribs, 1959), axial parenchyma in strands of 2–4 cells, not storied, axial canals about the same diameter as vessels that are diffusely scattered and often present in tangential parenchyma bands (Banks and Gasson, 2000). These characters also occur in specimen CIDPALBO-MIC 1363.

*Oxystigma oxyphyllum* has axial parenchyma lozenge-aliform and rays with  $\leq 3$  cells wide (Normand and Paquis, 1976), features not observed in the fossil specimen. This fact suggests its new

assignment within the extant genus, but as a new species, *Para-oxystigma concordiensis* gen. nov. sp. nov.

*Gossweilerodendron* is the most closely related genus with the fossil specimens (CIDPALBO-MIC 1679, 1576, 1542, 1561) and shares numerous features, such as: size of vessels, type and size of intervessel pits, homocellular rays, non-septate fibres, mainly vasicentric axial parenchyma, presence of diffuse-small vertical canals and prismatic crystals in axial parenchyma (Metcalf and Chalk, 1950; Normand and Paquis, 1976; Baretta-Kuipers, 1981; Cevallos-Ferriz and Barajas-Morales, 1994; Richter and Dallwitz, 2000; Fougère-Danezan et al., 2010; Brea et al., 2012).

We did an InsideWood search using features present in the fossil specimens related to *Gossweilerodendron* such as: 25p (small intervessel pits), 29p (vestured pits), 30p (vessel-ray pits with distinct borders, similar to intervessel pits in size and shape throughout the ray cell), 66p (non-septate fibres), 79p (axial parenchyma vasicentric), 83p (axial parenchyma confluent), 89p (axial parenchyma in marginal or in seemingly marginal bands), 92p (four (3–8) cells per parenchyma strand), 97p (ray width 1 to 3 cells), 104p (all ray cells procumbent), 129p (axial canals diffuse) and 142p (prismatic crystals in chambered axial parenchyma cells) with 0 allowable mismatches. This search yielded *Gossweilerodendron balsamiferum* and *Oxystigma oxyphyllum* (Baretta-Kuipers, 1981; Léonard, 1950, 1999). However, the four specimens (CIDPALBO-MIC 1679, 1576, 1542 and 1561) are closer to *G. balsamiferum* because they have small axial canals, smaller than the diameter of the vessels, and homocellular rays.

*Gossweilerodendron joveri* (sensu Richter and Dallwitz, 2000) differs from the fossil material in the presence of vessels with two distinct diameter classes (very small to large) and heterocellular and multiseriate rays. *G. balsamiferum* differs only in the presence

**Table 1**

Comparison of wood anatomical characters of *Paraoxystigma concordiensis* gen. nov. sp. nov., *Gosseilerodendroxylon palmariensis* gen. nov. sp. nov. and extant genera of the Group Prioria s.s. (data taken from Metcalfe and Chalk, 1950; Normand and Paquis, 1976; Baretta-Kuipers, 1981; Quirk, 1983; Cevallos-Ferriz and Barajas-Morales, 1994; Fougère-Danezan et al., 2010; InsideWood, 2004-onwards).

Detarieae Clade o Group Prioria	<i>Gosseilerodendron</i>	<i>Kingiodendron</i>	<i>Prioria</i>	<i>Bikinia</i>	<i>Daniellia</i>	<i>Sindora</i>	<i>Oxystigma</i>	<i>Paraoxystigma</i> <i>concordiensis</i> gen. nov. sp. nov.	<i>Gosseilerodendroxylon</i> <i>palmariensis</i> gen. nov. sp. nov.
Porous	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Perforation plates	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple
Intervessel pits	Alternate, polygonal, small to-diminate, vestured	Alternate, polygonal, small to-medium, vestured	Alternate, polygonal, small, vestured	Alternate, small to medium, vestured	Alternate, large, vestured	Alternate, medium, vestured	Alternate, polygonal, small to- medium	Alternate, polygonal, minute to-small, vestured	Alternate, small to-minute, vestured
Vessels Groupings	Generally, in short radial multiples (2–3) vessels	?	Solitary and radial multiples	–	–	–	Solitary and radial multiples	Solitary and radial multiples	Solitary (68%) and radial multiples of 4 or more common
Tangential diameter (µm)	≤200	≤200	≤200	≤200	≤200	≤200	≤200	≤200	≤200
Per square millimetre	≤10	5–20	5–20	5–20	5–20	5–20	≤20	≤20	9 (4–12)
Mean vessel element length	≤350, o ≤ 800	≤800	≤350, o ≤ 800	–	–	≤350, o ≤ 800	≤350, o ≤ 800	≤450	280 (127–500)
Tyloses and/ or deposits	Present	Present	Absent	–	Present?	Present	Absent	Present	Present
Fibres	Non-septate	Non-septate	Non-septate	Non-septate	Non-septate	Non-septate	Non-septate	Non-septate	Non-septate
Axial parenchyma	D, V, A, C, B, M	V, A, C, B	V, M	V, A, M	V, M	V, C, M	A, C, BM, V	Scarce P, V, A, C; A, BM	Scarce M, V, U, A to-C, ≈ D
Rays	Type and N° width cells	Ho, 1–3 cells wide	He, 1–10 cells wide	He, 1 cells wide	He, 1 –10 cells wide	He, 1–10 cells wide	He, 1–8 cells wide	He, 1–10 cells wide	Ho, 1 to-2 cells wide
Per millimetre	7–12	4–12	4–12	4–12	4–12	–	5–20	7–8	9 (7–14)
Prismatic crystals	Axial parenchyma	Ray cells, axial parenchyma	Present	Axial parenchyma, fibres	Rays cells	Axial parenchyma	Axial parenchyma and ray cells	Ray cells and axial parenchyma	Axial parenchyma
Axial parenchyma cell strand	3–8 cells	3–4 cells	2–4 cells	2–4 cells	2–4 cells	3–8 cells	2–8 cells	2–8 cells	4–8 cells
Normal axial canals	Present	Present	Present?	Present	Present	Present	Present	Present	Present
Geographical distribution	South Asia and Pacific	South America	Africa	Africa	Africa	Africa	Africa	South America	South America

Axial parenchyma **D** = diffuse; **V** = vasicentric, **C** = confluent; **B** = banded, **M** = marginal, **BM** = marginal banded, **A** = aliform, **U** = unilateral.



of biseriate rays (Kribs, 1968; Richter and Dallwitz, 2000). *G. balsamiferum* (sensu Banks and Gasson, 2000) has mainly small diffuse axial canals and vasicentric, aliform to confluent axial parenchyma, two characters present in the specimens described here.

We also compared these fossils with the species *Sindora klaineana* Pierre, a species that arises by removing the 25p and 142p features from the InsideWood search. This taxon differs basically by having intervessel pits >10 µm, rays more than 4 cells wide and intercellular canals of traumatic origin (Kribs, 1968; Normand and Paquis, 1976).

Although specimens similar to the genus *Gossweilerodendron* do not completely coincide with the features present in *G. balsamiferum*, for example in the presence of axial parenchyma that is more than three cells wide (85p). That leads us to propose a new genus and new species *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. from the upper Pleistocene in the middle-east of South America.

In short, *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. are more akin to the African taxa, by combination of the anatomical characters like diffusely arranged, normal axial canals; uni to multiserial rays; crystals in rays and axial parenchyma; small intervessel pits.

## 5.2. Comparison with fossil species

The fossil woods were compared with fossil species that have axial canals. The InsideWood search using the above coding returned four family: Cornaceae, Combretaceae, Dipterocarpaceae and Leguminosae (InsideWood, 2004-onwards). *Mastixioxylon microporosum* Gottwald (Cornaceae) has axial canals but differs with the studied material because it has rays of two distinct sizes and sheath cells (Gottwald, 1992). *Terminalioxylon traumaticum* Ramanujam (Combretaceae) has uniseriate rays and banded axial parenchyma (Ramanujam, 1965). The fossil genera of Dipterocarpaceae differ because they have sheath cells (Trivedi and Ahuja, 1977; InsideWood, 2004-onwards).

Finally, the fossil woods described here were compared with fossil members of the Leguminosae. Eight fossil genera of this Detarioideae subfamily, which have axial canals and vasicentric, aliform and confluent axial parenchyma, are known from the Paleocene to the Pliocene (Kräusel, 1922; Navale, 1962 (1963); Müller-Stoll and Mädler, 1967; Gregory, 1971, [1973]; Louvet, 1973; Awasthi, 1975 [1977]; Koeniguer, 1975; Fessler-Vrolant, 1977; Awasthi and Prakash, 1986 [iss. 1987]; Crawley, 1988; Cevallos-Ferriz and Barajas-Morales, 1994; Privé-Gill et al., 1999; Gottwald, 1994; De Franceschi and De Ploëg, 2003; El-Saadawi et al., 2011; Brea et al., 2012; Rodríguez-Reyes et al., 2017). The taxa are from North Africa, South America, Central America and Asia (see Table 2).

The fossil genera mainly differ from the specimens under study in the co-occurrence of paratracheal and apotracheal axial parenchyma, the type of the rays, and the size and arrangement of the axial canals. Here we focus our comparison and discussion on woods in the Detarioideae subfamily, at species level: *Aulacoxylon sparnacense* Combes specimen described by De Franceschi and De Ploëg (2003) differs from the specimens under analysis in having banded axial parenchyma and storied rays, both *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. do not have these features.

*Hopeoxylon arcotense* Awasthi differs in having procumbent body ray cells with mostly 2–4 rows of upright and/or square marginal cells, and larger commonly 4-to 10 seriate rays (Awasthi, 1975).

*Copaiferoxylon migiurtinum* (Chiarugi) Müller-Stoll and Mädler, and *Copaiferoxylon matanzensis* Cevallos-Ferriz and Barajas-

Morales both have axial canals but differ from the new fossils in have banded axial parenchyma and tyloses in vessels (El-Saadawi et al., 2011; Cevallos-Ferriz and Barajas-Morales, 1994).

*Caesalpinioxylon palembangense* Kräusel differ due to the presence of sheath cells (Kräusel, 1922). *Detarioxylon*, mainly *Detarioxylon aegyptiacum* (Unger) Louvet and *Sindoroxylon aethiopicum* Lemoigne, Beauchamp and Samuel account with little information in InsideWood (2004-onwards) differs in the multiserial rays (>4 cells wide) and fibres septate not seen in our new fossils (Louvet, 1973; Lemoigne et al., 1974). *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. differ from *Enterrioxylon victoriensis*, a species from the Paraná Formation (Miocene) in the Paraná River basin (north-eastern Argentina and southern Brazil), since they lack vessels of two distinct diameter classes and vasicentric tracheids (Brea et al., 2012).

*Kingiodendron* and *Paraoxystigma concordiensis* gen. nov. sp. nov. differ from *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. due to the presence of heterocellular and multiserial rays (Harms, 1897). *Paraoxystigma concordiensis* gen. nov. sp. nov. also differs from *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. by the presence of small to minute intervessel pits, crystaliferous ray cells and axial canals with similar vessels size (Awasthi and Prakash, 1986; Brea et al., 2012; Guleria et al., 2001).

*Kingiodendron prepinnatum* Awasthi and Prakash differ from *Paraoxystigma concordiensis* gen. nov. sp. nov. by having large intervessel pits, homocellular rays and body ray cells procumbent with mostly 2–4 rows of upright and/or square marginal cells (Awasthi and Prakash, 1986; Guleria et al., 2001).

To summaries, according to the list of Features for Hardwood Identification and key literature (IAWA Committee, 1989), we confirmed the occurrence of the particular features in the fossil woods and members of the Detarioideae subfamily, *Prioria* clade (e.g., aliform, vasicentric parenchyma combined with marginal narrow bands, 3–8 cells per parenchyma strand, prismatic crystals presence in chambered parenchyma cells and diffuse axial canals). The fossil woods studied here are different from previously described Detarioideae and *Prioria* s.l. fossil woods (Fougère-Danezan et al., 2010), and consequently the nominations of two new species *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. is justified in this paper. However, the fact these fossils cannot be fully associated with any single extant taxon within *Prioria* clade is significant, since it as they may therefore be able to provide additional information about distribution patterns in America.

## 5.3. Palaeoecology and biogeographic implications of detarioideae

The Detarioideae fossil woods found in Argentina are closely related to the modern taxa from tropical Africa. This group has a restricted distribution in the tropics, arid and semiarid areas of Africa, Eurasia and the America during the Late Cretaceous. Subsequently, it surrounded the Tethys Sea by a rapid adaptive radiation. Other studies detected a decrease in their areas (north-eastern to south-western and centre of the Tethys Sea) during the late Miocene (Wheeler and Baas, 1992; Mackinder, 2005; Schrire et al., 2005a, b; Bruneau et al., 2008; Pan et al., 2010; Wang et al., 2014; De la Estrella et al., 2017). Our fossil record reflects a footprint of ancient South America is physical bonding with the Central-West of the African continent. The ancient junction between the African continents with South America has strong paleontological and geological support, including the phylogenetic relation of animal and plant species, and geological structures along the coasts of Brazil and southwest of South Africa e.g. presence of diamond and topographic similarities (Bueno et al., 1999). Probably successive

**Table 2**

Comparison of *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. with eight genera fossils (*Caesalpinioxylon* Kräusel, 1922, *Kingiodendron* Harms, 1897, *Hopeoxylon* Navale emend. Awasthi, 1975, *Sindoroxyton* Lemoigne, Beauchamp and Samuel, 1974, *Detarioxylon* Boureau and Louvet, 1970, *Copaiferoxylon* Lalitha and Prakash, 1980, *Entrerrioxylon* (Lutz) Brea et al., 2012), *Prioria* sp. Rodríguez-Reyes et al., 2017 of Detarioideae with axial canals and vasicentric, aliform and confluent axial parenchyma.

	<i>Paraoxystigma concordiensis</i> gen. nov. sp. nov.	<i>Gossweilerodendroxylon palmariensis</i> gen. nov. sp. nov.	<i>Caesalpinioxylon</i>	<i>Kingiodendron</i>	<i>Hopeoxylon</i>	<i>Sindoroxyton</i>	<i>Detarioxylon</i>	<i>Copaiferoxylon</i>	<i>Entrerrioxylon</i>	<i>Prioria</i>
Locality	Argentina	Argentina	South Asia	Asia	Asia	Africa	El Cairo	North Africa	South America	Panama
Age	Pleistocene	Pleistocene	Oligocene	Miocene	Miocene	Miocene	Eocene-Miocene	Oligocene	Miocene	Miocene
Porosity	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse	Diffuse
Perforation plate	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple	Simple
Intervessel pits	Alternate, polygonal, small, vestured	Alternate, small to-medium, vestured	Alternate	Alternate, medium to-large	Small to-medium, vestured	Alternate, medium to-large	Alternate	Alternate, medium to-small	Alternate and circular, small to medium	Alternate, small to medium
Vessels grouping	Solitary and radial multiples	Solitary (68%)	?	Solitary and radial multiples	Solitary and radial multiples	Solitary and radial multiples	?	Radial multiples and solitary	Solitary (75%), radial multiples	Solitary (49%), radial multiples
diameter (μm)	≤200	≤200	≥200		≤200	≤200	≤200	≤200	119 (65–155); 203 (169–312)	
per mm <sup>2</sup>	≤20	≤20	≤20	≤20	6–10	≤5	≤350 or ≤ 800	≤5	12 (8–16)	
length (μm)	≤450	≤500	≤350 or ≤ 800	≤350 or ≤ 800	170–300	≤350 or ≤ 800	≤350 or ≤ 800	≤350	124 (85–165)	
Fibres	Non-septate	Non-septate	?	?	?	?	?	?	Non-septate	Non-septate
Axial parenchyma	P, V, A, C; A, D in-aggregates, BM	M, V, U, A, C, ≈D	A, C, V, D, B	V, A, BM	V, A, C, B	A, V, C	V, A, C, BM	V, A, C, BM	V, A, C	A, D, M
Rays type, width	He, 1–10 width cells	Ho, 1 to-2 width cells	He, 1–10 width cells	He, 1–3 width cells	He–Ho, 1–4 width cells	He, 1–3 width cells	He, 4–10 width cells	He, 1–3 width cells	Ho, 1–3 width cells	He, 1–3 width cells
per mm	7–8	9 (4–14)	4–12	4–12	6–8	4–12	4–12	4–12	3–5	
Prismatic crystals	R, PA	A, PA?			PA	PA	PA	PA	R, PA	PA, R
Axial canals	Present	Present	Present	Present	Present, tangential	Present	Present, diffuse	Present	Present, diffuse	Present, diffuse and tangential line

Crystals in, **R** = rays cells, **PA** = axial parenchyma; Parenchyma axial: **D** = diffuse, **V** = vasicentric, **C** = confluent, **B** = banded, **M** = marginal, **BM** = banded marginal, **A** = aliform, **U** = unilateral; ? = no data.



vicariance events in this area, and long-distance dispersal episodes (perhaps mediated by birds) led to the colonization of flora and fauna in Africa and America, enhancing the exchange between them (Fritsch, 2001; Bruneau et al., 2008, 2014; Bryja et al., 2014).

Several features of the *Prioria* s.s. clade suggest pollen dispersal by wind dispersal (Breteler, 1999; Fougère-Danezan et al., 2010). Some extant species of Detarioideae are found in beach, mangrove and riparian forest communities and aquatic propagule dispersal has been noted in several of these species (Tomlinson, 1986; Clarke et al., 2001) which contributed to their survival in the world. Members of the *Afzelia* clade are well known as marine/aquatic propagule dispersers; *Intsia bijuga* (Colebr.) Kuntze, a mangrove, strand and riparian forest tree, is the most widespread species in the group, extending from East Africa to the western Pacific, and has fruits containing lightweight, durable, flat seeds with hard seed coats that float in and are resistant to seawater (Thaman et al., 2006). This also suggests high adaptation to environments with water.

Some authors suggest that several genera (e.g. *Styrax* L. *Afzelia* Sm. *Cynometra* L. *Anacardium* L.) were more widespread in the past, and that their modern distribution has been the result of regional resections, perhaps due to climate changes (Adegoke et al., 1978; Muller, 1981; Crawley, 1988; Pan et al., 2010; Moya et al., 2015).

Mesomorphic anatomical features of woods observed in *Paraoxystigma concordiensis* gen. nov. sp. nov. (V = 7, M = 1939); and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. (V = 16, M = 4480) support the idea that the fossil woods grew under warm and humid environmental conditions. The Vulnerability and Mesomorphy ratios indicate that these woods show evidence of mesomorphic features. According to Pan et al. (2010) and Donkpegan et al. (2017), some groups of legumes are more sensitive to intense climate changes, especially if the changes tend to be xeric. The quaternary climatic fluctuations could have affected the distribution of these taxon in South America and later, they become extinct at some time during the Pleistocene.

## 6. Concluding remarks

Two new genera of fossil Detarioideae subfamily have been recorded from the late Pleistocene in the northeast of Argentina, *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. These woods are the first fossils in the world closely related to *Oxystigma* and *Gossweilerodendron*.

The new fossil records related to the *Prioria* group provide important paleobiogeographical and climatic information. According to the extant distribution of the *Prioria* clade, the evidence presented here supports the arguments that *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. lived under warm and humid climate and were components of tropical forests.

These new records suggest that the flora of south-eastern South America sometime in the Late Pleistocene could be partially comparable to the current flora of central-western Africa. Preliminary paleobiogeographical studies also seem to indicate that the dispersal of Detarioideae subfamily occurred firstly across the Atlantic Ocean, from Africa to the northern parts of South America, and subsequently towards the south.

The origin and phytogeography of *Gossweilerodendron* and *Oxystigma* is hardly known, partly because of the very limited fossil record of the *Prioria* s.s. clade. Overall, our analysis suggests that the extant distribution of *Oxystigma* and *Gossweilerodendron* is the result of historical dispersal climatic events combined with biome fragmentation, followed by recent extinction events.

The fossil woods studied here increase our knowledge on the

record of the Detarioideae subfamily in South America and support the existence of a very old relationship with the Africa flora.

Comparison of *Paraoxystigma concordiensis* gen. nov. sp. nov. and *Gossweilerodendroxylon palmariensis* gen. nov. sp. nov. with eight genera fossils (*Caesalpinioxylon* Kräusel, 1922, *Kingiodendron* Harms, 1897, *Hopeoxylon* Navale emend. Awasthi, 1975, *Sindoroxylon* Lemoigne et al., 1974, *Detarioxylon* Boureau and Louvet, 1970, *Copaiferoxylon* Lalitha and Prakash, 1980, *Enterrioxylon* (Lutz) Brea et al., 2012), *Prioria* sp. Rodríguez-Reyes et al., 2017 of Detarioideae with axial canals and vasicentric, aliform and confluent axial parenchyma.

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