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Research paper

Redescription and reassignment of *Entrerrioxylon victoriensis* from the Upper Miocene, Paraná Formation, South AmericaMariana Brea^{a,*}, María Jimena Franco^a, Alicia I. Lutz^b^a Laboratorio de Paleobotánica, Centro de Investigaciones Científicas, Diamante (CICYTP-Diamante, Consejo Nacional de Investigaciones Científicas y Técnicas), Dr. Materi y España SN, E3105BWA Diamante, Entre Ríos, Argentina^b Centro de Ecología Aplicada del Litoral-Área de Paleontología-Consejo Nacional de Investigaciones Científicas y Técnicas y Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste. Casilla de Correo 128, 3400 Corrientes, Argentina

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ABSTRACT

A new study of *Entrerrioxylon victoriensis* Lutz, 1981 has revealed that this taxon possesses many anatomical characteristics associated with the Caesalpinioideae, especially with the tribe Detarieae s.l. This paper redescibes and reassigns this specimen recovered from the upper Miocene Paraná Formation in the province of Entre Ríos, Argentina. The combined presence of intercellular axial canals, crystals in ray cells, partially storied rays and fiber walls with similar thicknesses was the diagnostic characteristics that support its transfer to the tribe Detarieae s.l. The discovery of this legume wood in southern South America also supports the existence of an old relationship with the African flora and close links with Central America and tropical South America. Also, many of the characteristics observed in *Entrerrioxylon victoriensis* could be used as indicators of wet tropical conditions.

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1. Introduction

Entrerrioxylon victoriensis had been assigned by Lutz (1981) to Fabaceae (Faboideae) with close relations to *Cytisus* L. and *Genista* L., two genera within the Genisteae Tribe. However, Lutz also concluded that this taxon's suprageneric systematic position had to remain uncertain (Lutz, 1981). Here, this fossil species is reviewed and redescibed, and a new affiliation is proposed. This reassignment of *E. victoriensis* is based upon a redescription of the CTES-PB 4859 holotype, using new thin section slides.

The material described was recovered from the Paraná Formation in the Cantera Municipal of Victoria, Entre Ríos, Argentina (Fig. 1) by one of the authors (AIL). The Paraná Formation was deposited during a shallow introgression with deltaic influences, and is characterized by massive light-green and gray mudstones and green and white sandstones (Iriondo, 1973; Chebli et al., 1989; Del Río, 2000; Aceñolaza, 2007). This ancient sea is known as the 'Entrerriense Sea' or 'Paranense Sea', and the corresponding geological units were deposited from the middle Miocene to the late Miocene (Tortonian), probably without the existence of a connection with the western Caribbean Sea forming an intracontinental seaway (Hernández et al., 2005; Cozzuol, 2006; Latruesse et al., 2007). But more recently, invertebrate fossil assemblages were recovered from the Paraná Formation in the Entre Ríos

province and studied by Pérez and Griffin (2010), who reconsider the hypothesis of an intracontinental seaway (Fig. 1). These authors suggest at least an intermittent passage of faunal elements during the Tortonian period (ca. 11 to 7 Ma) (Pérez and Griffin, 2010). This connection has been subject of much controversy. Also, the relatively scarce knowledge of Miocene paleobotanical records represents a serious obstacle for taking firm positions regarding the presence or absence of an intracontinental seaway (Brea and Zucol, 2011).

Paleobotanical studies of the Paraná Formation have revealed a rich angiosperm flora. This unit contains fossil palynomorphs (Gammero, 1981; Anzótegui and Garralla, 1982, 1986; Garralla, 1989; Anzótegui, 1990), phytoliths (Zucol and Brea, 2000a, 2000b), leaf compressions (Aceñolaza and Aceñolaza, 1996; Anzótegui and Aceñolaza, 2008) and permineralized woods (Lutz, 1981; Brea et al., 2001; Franco and Brea, 2008). The paleobotanical evidence supports the argument that the Miocene floral communities developed under tropical-subtropical and arid-to-humid environmental conditions (Brea and Zucol, 2011 and reference therein).

South America has an extensive and diverse fossil record, and woods with affinities to the Fabaceae and all of its subfamilies (Mimosoideae, Caesalpinioideae and Faboideae) are represented throughout an extensive temporal record from the Paleocene to the Pleistocene. This family's fossil record also has an extensive geographical range, from northern Colombia to southernmost Patagonia (Pujana et al., 2011). In particular, the fossil wood of the Caesalpinioideae, a group which is present from the Miocene to the Pliocene and includes *Crudioxylon pinalense*

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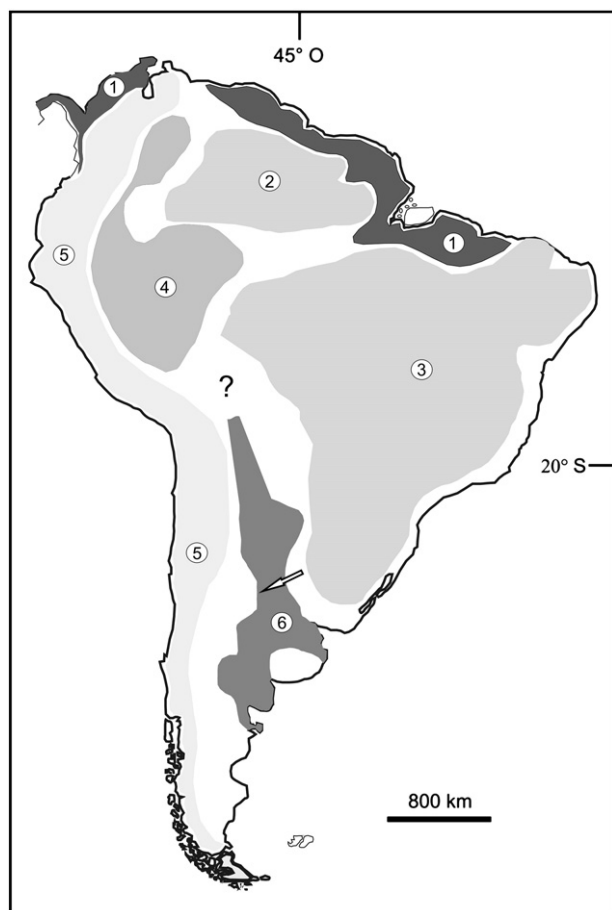


Fig. 1. Paleogeography of South America during Middle Miocene. 1. Marginal marine transgressions; 2. Guyana Shield; 3. Brazilian Shield; 4. Solimões/Pebas Formation; 5. Andes; 6. Paraná Formation. Arrow shows the fossil locality. The interrogation shows the probable connection of the Caribbean Sea with the south Atlantic trough the Venezuelan/Colombian Llanos Basin, western Amazonia, the Beni-Chaco plain, and the Parana Basin in Argentina. Taken and modified from Cozzuol (2006) and Latrubesse et al. (2007).

Pons (Boureau and Salard, 1962; Pons, 1980) from the Pliocene of Colombia; *Crudioxylon brasiliense* Selmeier from the Cenozoic? Rio Paranaíba, Maranhão, Brazil (Selmeier, 2004) and *Gleditsioxylon riojana* Martínez and Rodríguez Brizuela from the Miocene Toro Negro Formation (Martínez and Rodríguez Brizuela, 2011).

In this contribution, we report on a restudy of *Entrerrioxylon victoriensis*, which allows the reassignment of this taxon to the Caesalpinoideae subfamily and a more accurate placement within the tribe Detarieae s.l. (Fig. 2) (Baretta-Kuipers, 1981; Gasson, 1994; Banks and Gasson, 2000; Fougère-Danezan et al., 2007, 2010; Melandri and Espinoza de Pernía, 2009).

The South American extant flora includes 65 genera of Caesalpinoideae. This subfamily is represented by four tribes (Caesalpinoideae, Cassieae, Cercideae and Detarieae) and 23 genera which belong to the Detarieae. The South American Caesalpinoideae inhabits in tropical and subtropical areas. All of them grow in diverse habitats — from rainforests, evergreen or deciduous forests, to savannas, semi-deserts and high mountains (Ulibarri, 2008).

Finally, preliminary paleobiogeographic and paleoecology interpretations are presented and discussed.

2. Material and methods

The examined wood material was preserved by permineralization and new thin sections were made using techniques typically employed

for rock specimens. Three characteristic sections (transverse, tangential longitudinal and radial longitudinal section) were prepared.

The description follows the IAWA Committee (1989) guide for hardwoods. The identification of fossil woods was performed by using the wood atlases and descriptions by Baretta-Kuipers (1981), Gasson (1994), Banks and Gasson (2000), Melandri and Espinoza de Pernía (2009) and Richter and Dallwitz (2000–onwards) as well as the InsideWood (2004–onwards). Systematic assignment follows the Apg (2009).

The Vulnerability Index (V) and Mesomorphy ratios (M) were calculated using the equations developed by Carlquist (1977). A diverse set of anatomical characteristics of wood were also analyzed in terms of their associated paleoecological requirements, including vessel diameter, vessels density, percentage of solitary vessels, vessel arrangement, length of vessel elements, perforation plate types, porosity, presence of vasicentric tracheids, axial parenchyma distributions, presence of crystalliferous parenchyma, storied structure and growth rings (Carlquist and Hoekman, 1985; Wheeler and Baas, 1991, 1993; Lindorff, 1994).

The quantitative values provided in the anatomical description are averages of 25 measurements. The average is cited first, followed by the minimum and maximum values, which are given in parentheses.

The fossil wood was studied with a Nikon Eclipse E200 light microscope, and the photomicrographs were taken with a Nikon Coolpix S4 digital camera.

The studied fossil wood and microscope slides have been deposited in the Colección Paleobotánica, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes, under the acronym CTES-PB for wood specimen and CTES-PMP for slides.

3. Results

3.1. Systematic paleobotany

Family FABACEAE Lindley, 1836

Subfamily CAESALPINIOIDEAE Candolle, 1825

Genus *Entrerrioxylon* Lutz, 1981 emend. Brea, Franco and Lutz

Emend. generic diagnosis: Growth rings indistinct or absent; diffuse porous; vessels commonly solitary and in radial multiples of 2–4; vessels of two distinct diameter classes; simple perforation plates; intervessel pits alternate and circular; vasicentric tracheids abundant; rays uniseriate and multiseriate; rays homocellular and partially storied; axial parenchyma vasicentric, aliform to confluent; fibers non-septate and thick walled; axial canals diffuse and small; crystals in procumbent ray cells and in parenchyma strands.

Note: The generic diagnosis was emend. to include diffuse and small axial canals, crystals in procumbent ray cells and crystals in parenchyma strands, and to remove heterocellular rays.

Type species: *Entrerrioxylon victoriensis* Lutz, 1981 emend. Brea, Franco and Lutz

Entrerrioxylon victoriensis Lutz, 1981 emend. Brea, Franco and Lutz (Plates I, II and III)

Holotype: CTES-PB 4859; CTES-PMP 1252–1256 and CTE-PMP 3052–3054.

Repository: Colección Paleobotánica, Facultad de Ciencias Exactas y Naturales y Agrimensura, Universidad Nacional del Nordeste, Corrientes (CTES-PB) and slides (CTES-PMP).

Stratigraphic horizon and age: Paraná Formation, late Miocene

Locality: Cantera Municipal de Victoria, Entre Ríos, Argentina

Emend. Specific diagnosis: Growth rings indistinct or absent; diffuse porous; vessels commonly solitary and in radial multiples of 2–4, few clusters; vessels of two distinct diameter classes, very small to large and few; short vessel elements; simple perforation plates; intervessel pits alternate and circular; vasicentric tracheids abundant;

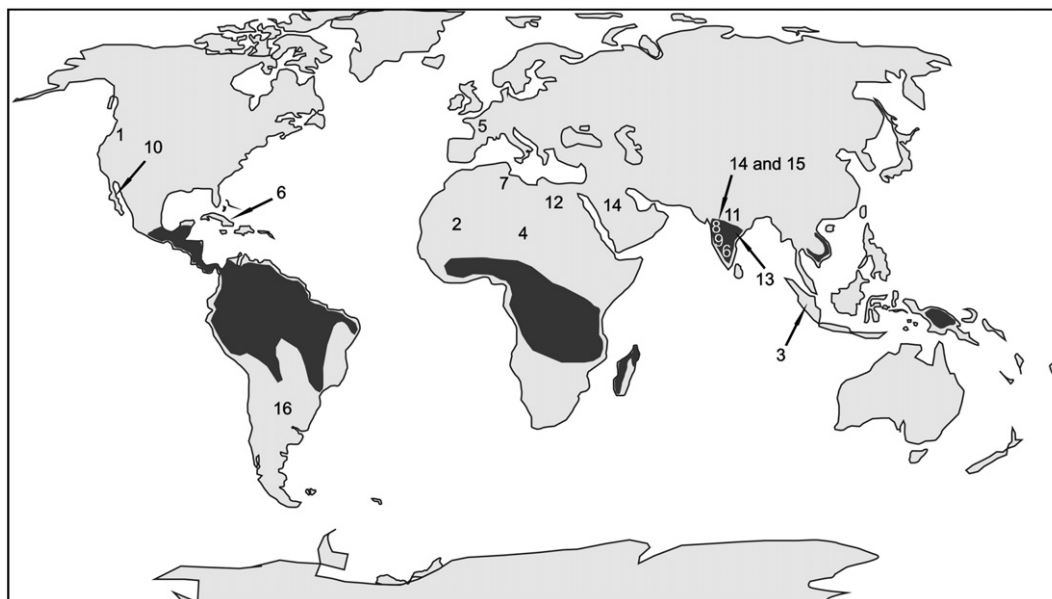


Fig. 2. Biogeography distribution of extant genera from tribe Detarieae s.l. sensu Fougère-Danezan et al., 2010 (dark gray shading) closely related with *Entrerrioxylon victoriensis*, taken of Tropics. Missouri Botanical Garden. 5 Oct. 2011 [<http://www.tropics.org>]. Localities of fossil woods that have axial canals in the anatomical structure: 1. *Acacia gregorii*; 2. *Caesalpinioxylon moragionesiae*; 3. *Caesalpinioxylon palembangense*; 4. *Caesalpinioxylon tchadense*; 5. *Aulacoxylon sparnacense*; 6. *Erythrophloeoxylon scholleri*; 7. *Copaiferoxylon copaiferoides*; 8. *Copaiferoxylon assamicum*; 9. *Copaiferoxylon eosiamensis*; 10. *Copaiferoxylon matanzensis*; 11. *Kingiodendron prepinnatum*; 12. *Detarioxylon aegyphacum*; 13. *Hopeoxylon arcotense*; 14. *Hopeoxylon indicum*; 15. *Hopeoxylon speciosum*; 16. *Entrerrioxylon victoriensis*.

rays uniseriate and multiseriate; rays homocellular and partially storied; rays narrow, low and few; axial parenchyma vasicentric, aliform to confluent; fibers polygonal in outline, abundant, non-septate and thick walled; diffuse and small axial canals; crystals in procumbent ray cells and in parenchyma strands.

Note: The specific diagnosis was emend. to include diffuse and small axial canals, crystals in procumbent ray cells and crystals in parenchyma strand cells, and to remove vessel diameter, vessel density and length values of vessel elements, as well as width and length values of rays and number of rays per linear mm.

Description: Growth ring boundaries indistinct or absent. Diffuse porous and with diagonal and/or radial pattering in the vessels (Plate I, 1). Vessels are commonly solitary (75%) (Plate I, 1–4, 5), some in radial multiples of 2–4 (24%) and rarely in clusters (1%) (Plate I, 1–4, 6). The solitary vessels are circular to oval in outline with thin walls (Plate II, 1). Although wood is not ring porous, vessels are of two distinct diameter classes: a) very small to medium size, with a mean radial diameter of 115 (45–175) μm and a mean tangential diameter of 119 (65–155) μm ; and b) medium to large size, with a mean radial diameter of 239 (187–312) μm and a mean tangential diameter of 203 (169–312) μm . The mean vessel density is 12 (8–16)/ mm^2 . The mean vessel element length is 124 (85–165) μm (Plate I, 7–8, 12; Plate III, 3). Perforation plates are exclusively simple, with oblique end walls (Plate I, 11, 14; Plate III, 2). Intervessel pits are small to medium, bordered, alternate, circular and probably vested (Plate I, 7; Plate II, 16; Plate III, 8, 9). They are 5 (4–10) μm in diameter, with circular apertures.

Vasicentric tracheids are present around the vessels and are irregularly shaped and partially storied (Plate I, 7–8, 12; Plate II, 5–6, 12). Their mean diameter is 35 (15–48) μm . The vasicentric tracheids have bordered pits ca. 3–5 μm in diameter (Plate II, 5–6; Plate III, 7, 8). There are grooves interconnecting pit apertures, but there is no helical thickening on the walls of vessels and vasicentric tracheids (Plate II, 7).

Fibers are polygonal in outline, abundant and non-septate (Plate II, 1–3; Plate III, 1), with a mean diameter of 18 (13–23) μm and with a wall thickness of 5 (3–8) μm . The axial parenchyma is vasicentric, aliform to confluent (Plate I, 1–6) and occurs in strands of two to eight cells. The rays are uniseriate and also multiseriate,

2–3 cells wide (Plate I, 9, 13; Plate II, 9–10; Plate III, 5, 6). The mean number of rays per linear mm is 4 (3–5 per linear mm). They are homocellular and composed exclusively of procumbent cells (Plate I, 15; Plate II, 15; Plate III, 4). The mean width of rays is 54 (20–95) μm . The mean height of rays is 79 (38–157) μm and 5 (3–8) cells high. They are Kribs' Homogeneous Type I and are partially storied (Plate I, 13). There are small diffuse axial canals (Plate I, 1–4, 10, 16; Plate II, 4, 8), with a mean diameter of 11 (5–15) μm , sometimes in small groups of 3–5. In tangential longitudinal section, epithelial cells around axial canals are observed (Plate II, 7). The canals are normal (i.e. not traumatic in origin) (Plate I, 1–4, 10, 16; Plate II, 4, 8). Crystals are present in procumbent ray cells, usually one crystal per chamber (Plate II, 9–10, 13–14), as well as in parenchyma strands, with one crystal per cell (Plate I, 14; Plate II, 11, 14).

Vessel-ray pits with distinct borders are similar to intervessel pits in size and shape throughout the ray cell (Plate III, 4).

4. Discussion

4.1. Comparison with extant families

Normal vertical canals represent secretory canals that occur in axial parenchyma and run parallel to it (Carlquist, 2001). The following listing of families with these characteristic vertical canals is based on a compilation by Metcalfe and Chalk (1950, p. 1353); Baretta-Kuipers (1981); Gasson (1994); Banks and Gasson (2000); Richter and Dallwitz (2000–onwards); Carlquist (2001, p. 270), Melandri and Espinoza de Pernía (2009) and the InsideWood (2004–onwards): Connaraceae (*Connarus* L. and *Cnestidium* Planchon), Cornaceae (*Mastixia* Blume), Dipterocarpaceae (all genera except *Marquesia* Gilg and *Monotes* Alphonse de Candolle), and Caesalpinoideae, tribe Detarieae s.l. sensu Fougère-Danezan et al., 2010 (*Copaifera* L., *Brandzeia* Baillon, *Daniellia* Benth, *Detarium* Jussieu, *Eperua* Aublet, *Gossweilerodendron* Harms, *Kingiodendron* Harms, *Oxystigma* Harms, *Prioria* Grisebach, *Pseudosindora* Symington, *Sindoropsis* Jean Léonard and *Sindora* Miquel, see Table 1).

The fossil material studied here differs from Connaraceae in various characteristics (absent or extremely rare axial parenchyma, exclusively uniseriate and heterocellular rays) which allows the exclusion of this

family (InsideWood database, 2004–onwards). Only *Mastixia*, one genus of Cornaceae, has intercellular canals in long tangential lines, but it differs from the studied material in the number of vessels/mm², scalariform perforation plates, scalariform and opposite intervessel pits, apotracheal axial parenchyma and rays of two distinct sizes that are heterocellular and composed exclusively of upright cells (Richter and Dallwitz, 2000–onwards).

The combination of vessels exclusively solitary, apotracheal and paratracheal parenchyma, rays which is mostly up to 4–8 cells wide and occasional radial canals are characteristic of Dipterocarpaceae. All these features differ from the fossil wood studied here (Metcalfe and Chalk, 1950; Richter and Dallwitz, 2000–onwards; InsideWood database, 2004–onwards).

The woody Fabaceae are characterized by the presence of diffuse porous wood, vessels with simple perforation plates, vestured alternate intervessel pitting (except in some caesalpinoid species), vessel elements from medium to short length, solitary vessels, or in radial multiples and clusters. Diagonal–tangential arrangement is occasional in Caesalpinoideae. Rays are usually low and made up primarily or entirely of procumbent cells. The parenchyma is commonly abundant and paratracheal. The vessel-ray pits are similar to the intervessel pits. Storied structure is present in most Papilionoideae, many Caesalpinoideae but hardly any Mimosoideae and crystals in chambered axial parenchyma cells are usually present (Baretta-Kuipers, 1981; Wheeler and Baas, 1992).

The species of the Caesalpinoideae subfamily have medium to thick fiber walls, aliform, confluent and marginal axial parenchyma, homocellular rays or rays with a row of square or upright marginal cells, non-storied biseriate rays and prismatic crystals in chambered axial parenchyma cells (Baretta-Kuipers, 1981; Espinoza de Pernía and Melandri, 2006; Melandri and Espinoza de Pernía, 2009).

There are two characteristics – axial canals with epithelial cells and crystals in ray cells – which are restricted to the tribe Detarieae

s.l. in the Caesalpinoideae (Baretta-Kuipers, 1981; Gasson, 1994; Melandri and Espinoza de Pernía, 2009).

Diagnostic features for reliable identification within the tribe Detarieae s.l. include fiber wall thickness, ray composition, ray width, irregular storied structure, intercellular axial canals, axial parenchyma type, and prismatic crystals in ray cells. The presence and distribution of axial canals are a good diagnostic and systematic character in Detarieae (Melandri and Espinoza de Pernía, 2009).

4.2. Comparison with extant genera of the tribe Detarieae s.l.

The tribe Detarieae s.l. contains many genera that produce resins, but which had been previously placed in different generic groups of the tribe Detarieae sensu Cowan and Polhill (1981) (see for more details in Fougère-Danezan et al., 2007). The resin-producing Detarieae are not resolved as monophyletic in analyses realized by Fougère-Danezan et al. (2007). Morphology appears to be more in agreement with molecular data than was previously thought on the basis of traditional classifications (Cowan and Polhill, 1981). According to Fougère-Danezan et al. (2010), despite the fact that the tribe Detarieae has a high level of homoplasy, several characters are useful for reconstructing phylogenetic relationships.

Although some of the relationships within Detarieae remain poorly resolved, Fougère-Danezan et al. (2010) propose a new informal classification of the tribe Detarieae s.l. in which 5 new groupings (Sub-tribe Detariinae: 1, *Daniellia* group, 2, *Prioria* group, 3, *Hymenaea* group, 4, *Eperua* group and 5, *Detarium* group) are recognized. However, these authors argued that some groups may need further modifications (see Table 2, p. 316 in Fougère-Danezan et al., 2010).

The wood anatomy of the tribe Detarieae s.l. sensu Fougère-Danezan et al. (2010) is mainly heterogeneous (Banks and Gasson, 2000; Richter and Dallwitz, 2000–onwards; Melandri and Espinoza de Pernía, 2009). According to Melandri and Espinoza de Pernía (2009) the presence

Plate I. *Entrerrioxylon victoriensis* Lutz, 1981 emend. Brea, Franco and Lutz. Holotype CTES-PB 4859.

1. Transverse section, general view showing vessels in diagonal and/or radial pattern, fibers distribution, vasicentric, aliform to confluent axial parenchyma and small diffuse normal axial canals (white arrows).
2. Transverse section, showing small diffuse normal axial canals (white arrows).
3. Transverse section, detail of small diffuse axial canals (white arrows) and confluent axial parenchyma (black arrow).
4. Transverse section, detail of solitary and radial multiples vessels with aliform and confluent axial parenchyma and axial canals (white arrows).
5. Transverse section, detail of solitary vessel with aliform axial parenchyma.
6. Transverse section, detail of radial multiple vessels with vasicentric axial parenchyma.
7. Tangential longitudinal section, showing vessels with intervessel pits (black arrow) and vasicentric tracheids around the vessels with irregular shape (white arrows).
8. Tangential longitudinal section, general view showing short vessels (black arrows) and vasicentric tracheids (white arrows).
9. Tangential longitudinal section, general view showing uniseriate and 2–3 seriate rays.
10. Transverse section, detail of normal axial canals (white arrows).
11. Radial longitudinal section, detail of simple perforation plate (black arrow) and vasicentric tracheids (white arrows).
12. Tangential longitudinal section, detail of vessels (black arrows) and vasicentric tracheids (white arrows).
13. Tangential longitudinal section, general view showing partially storied rays.
14. Radial longitudinal section, detail of simple perforation plate and prismatic crystals in chambered axial parenchyma (white arrow).
15. Radial longitudinal section, detail of homocellular ray composed exclusively of procumbent cells (white arrow).
16. Transverse section, detail of fibers distribution, confluent axial parenchyma (black arrow) and axial canals (white arrow). (Scale bar in 1 = 1000 µm; in 2 = 500 µm; in 3–16 = 300 µm).

Plate II. *Entrerrioxylon victoriensis* Lutz, 1981 emend. Brea, Franco and Lutz. Holotype CTES-PB 4859. (see on page 6)

1. Transverse section, detail of solitary vessel, vasicentric parenchyma axial (black arrow) and fibers distribution (white arrow).
2. Transverse section, detail of parenchyma cells (black arrow) and fiber cells (white arrow).
3. Transverse section, detail of polygonal, non-septate and very thin-walled to thin-to thick-walled fibers.
4. Transverse section, detail of two axial canals.
5. Tangential longitudinal section, details of vasicentric tracheid with bordered pits and irregular shape (black arrow).
6. Tangential longitudinal section, showing vasicentric tracheid (black arrow).
7. Tangential longitudinal section, showing epithelial cells of axial canals (black arrow).
8. Transverse section, showing normal axial canals.
- 9–10. Tangential longitudinal section, detail of a ray with large prismatic crystals (white arrows).
11. Tangential longitudinal section, parenchyma with strand of six chambers with prismatic crystals (white arrow).
12. Tangential longitudinal section, detail of vasicentric tracheids with bordered pits and irregular shape.
13. Radial longitudinal section, detail of prismatic crystals (white arrow) in procumbent ray cell.
14. Radial longitudinal section, showing prismatic crystals in chambered axial parenchyma (white arrows) and crystal in procumbent ray cell (black arrow).
15. Radial longitudinal section, detail of homocellular rays composed exclusively of procumbent cells (black arrow).
16. Tangential longitudinal section, detail of small, bordered, alternate, circular and probably vestured intervessel pits (black arrow). (Scale bars in 1–7, 10–12, 14–15 = 100 µm; in 8–9, 13, 16 = 25 µm).

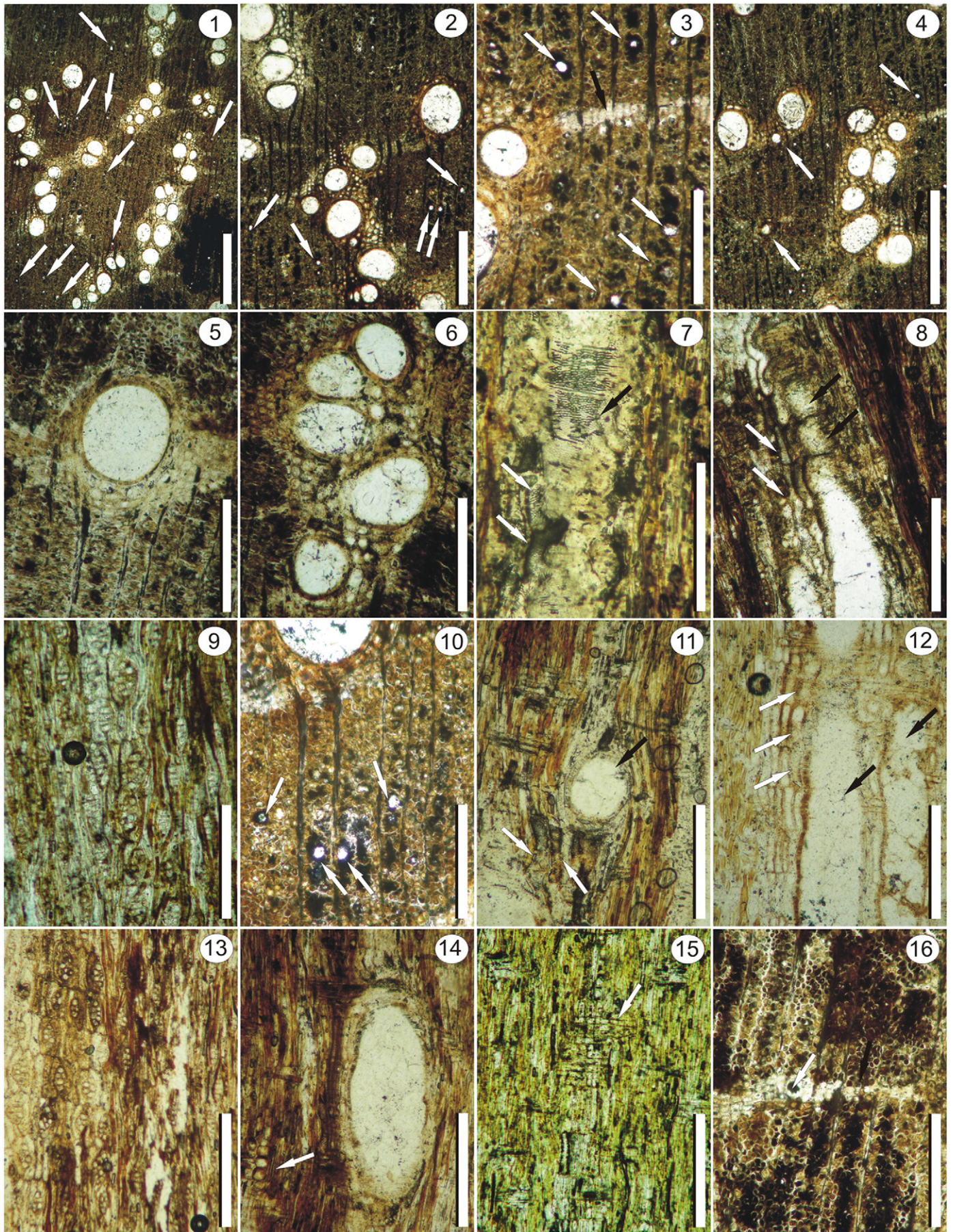


Plate I.

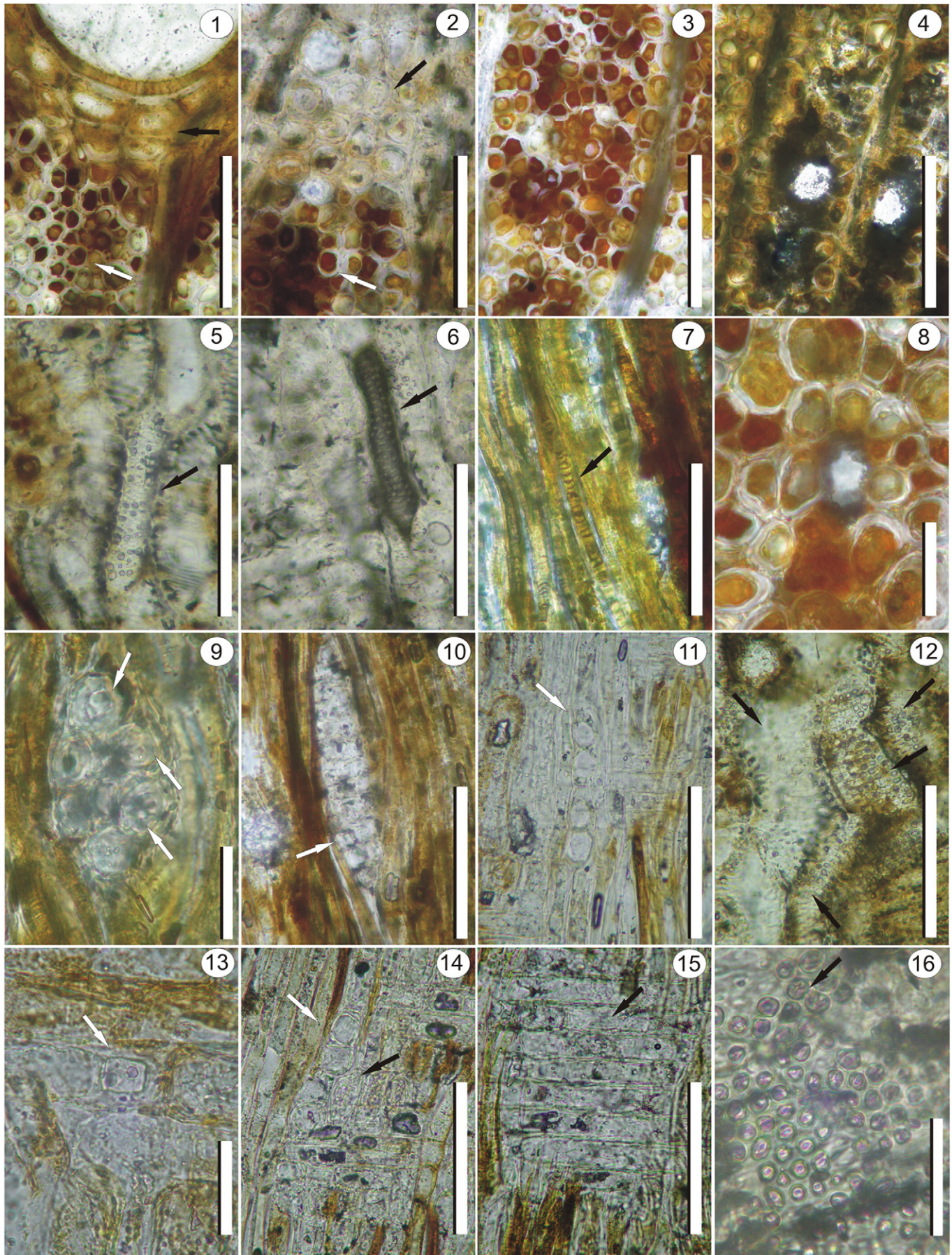


Plate II (caption on page 4).

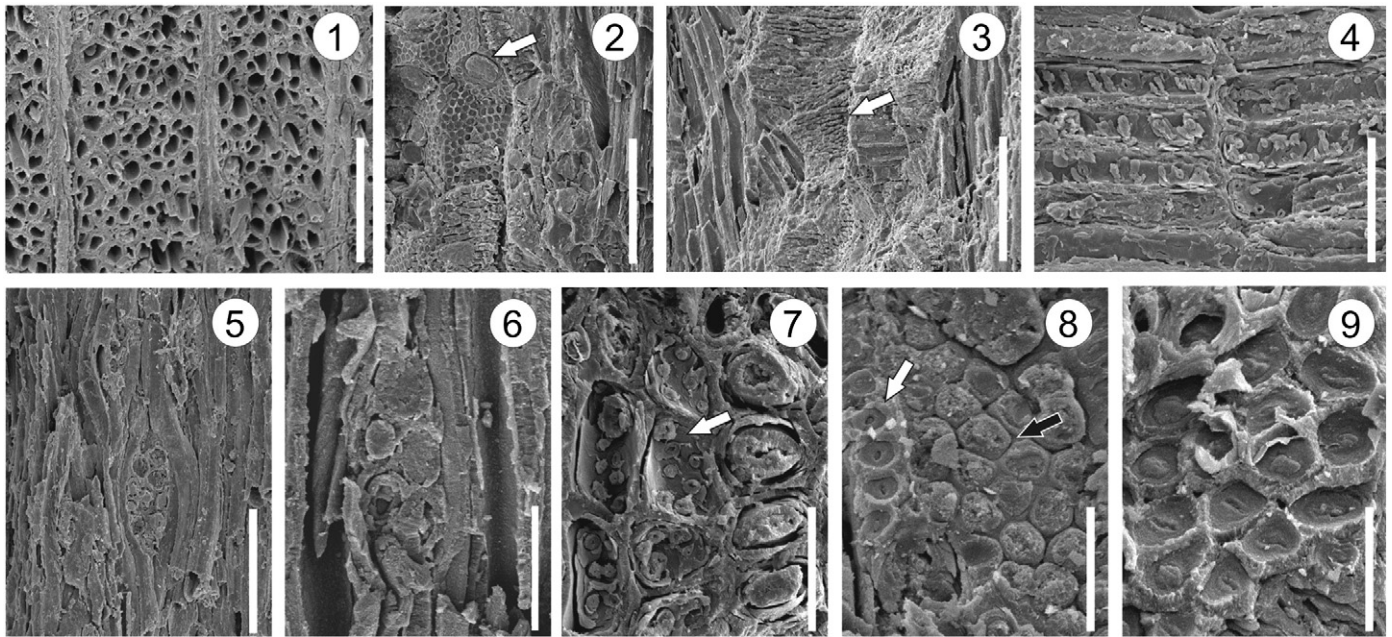


Plate III. *Entrerrioxylon victoriensis* Lutz, 1981 emend. Brea, Franco and Lutz. Holotype CTES-PB 4859.

1. Transverse section, general view showing rays and fibers.
2. Tangential longitudinal section, showing a simple perforation plate (white arrow) and intervessel pits.
3. Tangential longitudinal section, showing short vessels (white arrow).
4. Radial longitudinal section, detail of procumbent cells and vessel-ray pits.
5. Tangential longitudinal section, general view showing a ray.
6. Tangential longitudinal section, detail of ray cells.
7. Transverse section, showing detail of pits tracheids (white arrow) and parenchyma cells (black arrow).
8. Tangential longitudinal section, showing detail of tracheids pits (white arrow) and vessel pits (black arrow).
9. Tangential longitudinal section, detail of small, bordered, alternate, circular and probably vested intervessel pits. (Scale bar in 1 = 72 μ m; in 2 = 290 μ m; in 3 = 200 μ m; in 4 = 43 μ m; in 5, 7 = 47 μ m; in 8 = 19 μ m and 9 = 13 μ m).

and distribution of axial canals are a good diagnostic and systematic characteristic in Detarieae. Many genera, such as *Daniellia*, *Prioria*, *Oxystigma*, *Gossweilerodendron* and *Kingiodendron*, have diffusely arranged axial canals (Banks and Gasson, 2000). The axial canals are small in *Daniellia*, *Gossweilerodendron*, *Oxystigma* and *Kingiodendron* but much larger in *Prioria* (Baretta-Kuipers, 1981; Höhn, 1999, see Table 1). The size of the axial canals of *Entrerrioxylon victoriensis* is similar to the Tw 4838 specimens of *Daniellia klainei* Pierre ex A. Chevalier, JRw 13746 of *Daniellia thurifera* Bennett (see InsideWood database, 2004–onwards) and *Gossweilerodendron balsamiferum* (Vermoesen) Harms (see fig. 61 and 63, p37 in Banks and Gasson, 2000). In addition, *Detarioxylon aegyptiacum* (Unger) Louvet from the El Cairo Petrified Forest (Eocene–Miocene), Egypt, has a similar size to the normal axial canals (see Plate II, fig. 3 in EL-Saadawi et al., 2011).

Brandzeia Baillon has tangential bands of small axial canals and slightly wider rays, but is otherwise similar to the above genera (Table 1). On the other hand, *Copaifera*, *Prioria*, *Detarium*, *Pseudosindora*, *Sindora*, *Sindoropsis* and *Eperua* have tangential bands of axial canals (Brazier, 1959; Melandri and Espinoza de Pernía, 2009, see Table 1).

Most genera of the tribe Detarieae s.l. (*Neoapaloxyton* Rauschert, *Colophospermum* Kirk ex J. Léonard, *Hardwickia* Roxburgh, *Guibourtia* Bennett, *Stemonocoleus* Harms and *Baikiaea* Benth) lack normal axial canals (Banks and Gasson, 2000; Richter and Dallwitz, 2000–onwards), although one specimen of *Guibourtia* Bennett has traumatic axial canals (Banks and Gasson, 2000). Furthermore, traumatic canals are present in *Hymenaea* L., *Peltogyne* Vogel and *Tessmannia* Harms (Table 1).

The storied structure is present in *Daniellia*, *Neoapaloxyton*, *Prioria*, *Peltogyne* and *Baikiaea* (Table 1). *Daniellia* has all rays, axial parenchyma, fiber or vessel elements storied. *Neoapaloxyton*, *Prioria* and *Peltogyne* have axial parenchyma and/or vessel elements storied. Axial

parenchyma and/or vessel elements storied and rays and/or axial elements irregularly storied are present in *Baikiaea*. The type rays and rays irregular storied of *Entrerrioxylon victoriensis* are very similar to the Kw 6856 specimen of *Baikiaea eminii* Taubert (see InsideWood database, 2004–onwards).

Oxystigma and *Baikiaea* as well as the Miocene fossil wood (Richter and Dallwitz, 2000–onwards) have vascular tracheids. *Entrerrioxylon victoriensis* has crystals in rays and so do *Daniellia* and *Kingiodendron*. Homocellular rays are present in *Gossweilerodendron*, *Oxystigma* and *Kingiodendron*, which is a character shared with the Miocene fossil wood (Table 1).

The presence of axial canals and crystals in ray cells are rare characters, restricted to tribe Detarieae. Both anatomy characters are present in *Entrerrioxylon victoriensis*. The combination of fossil wood features is closely related to several genera within the tribe Detarieae s.l.

The slightly diagonal and/or radial arrangement of vessels in the fossil wood is not found in any extant genera of the tribe Detarieae, according to the available references (see Table 1). However, in the InsideWood database, some specimens of *Daniellia oliveri* (Rolfe) Hutchinson and Dalziel (specimen Kw1580), *Daniellia thurifera* Bennett (specimen SJRW 13745), *Prioria copaifera* Grisebach (specimens FPAw 21494 and Tw 53024), and *Baikiaea eminii* (specimen Kw 6856) show a tendency of diagonal or radial arrangement in their pictures (see InsideWood database, 2004–onwards).

The significance of diagonal or tangential arrangement lies in being a form of vessel redundancy and, therefore, conductive safety in taxa that have either vasicentric tracheids or very narrow vessels (plus an occasional vasicentric tracheid) mixed with wider vessels. All of the vessels in a stem are potentially linked with each other in a single group with intermixed narrow vessels and vasicentric tracheids forming a safeguarding subsidiary conductive system for the

Table 1
Comparison of selected wood anatomical characters of *Entrerrioxylon victoriensis* and extant genera of the tribe Detarieae s.l. (data taken from Baretta-Kuipers, 1981; Gasson, 1994; Banks and Gasson, 2000; Espinoza de Pernía and Melandri 2006; Richter and Dallwitz, 2000–onwards InsideWood, 2004–onwards; Melandri and Espinoza de Pernía, 2009).

	Distribution	Growth rings	Vasicentric Tracheids	Vessels				Rays				Septate Fibres	Fibre wall thickness	Storied structure	Axial canals	Parenchyma	Crystals
				Diameter (µm)	Length (µm)	Frequency (mm ²)	Pitting	Type	Height (µm)	Width (cells)	Frequency (mm linear)						
<i>Entrerrioxylon victoriensis</i>	Sa	I	P	65–318	85–165	4–16	S, M, A, V	Ho	38–157	1–3	3–5	N	1,2	P	D	V, A, C	R, P
<i>Brandzea</i>	Af/M	I	A	100–200	<350, 350–800	<=5	S, M, A, V	He	–	4–10	4–12	N	2	A	T	V, A, C, M	P, F
<i>Daniellia</i>	Af	D	A	115–380	<350, 350–800	3–6	A	He	<1000	1–4	4–12	N	2	P	D	V, A, C	R, P
<i>Neopaloxylon</i>	Af/M	I	A	100–200	<350, 350–>800	<=5	M, A, V	He	–	4–10	4–12	P	–	P	A	A, C, B	P
<i>Gossweilerodendron</i>	Af/As	D	A	90–155	–	6–15	S, A	Ho	<1000	1–3	5–7	N	2	A	D	B, M, D, A, C	P
<i>Kingiodendron</i>	As	I	A	100–200	<350, 350–800	<5, 5–20	S, M, A, V	Ho, He	<1000	1–3	4–12	N	2	A	D	V, A, C, M, B	R, P
<i>Oxystigma</i>	Af	I	P, A	150–250	<350, 350–800	2–4	S, A, V	Ho, He	<500	1–5	6–8	N	1,2	A	D	B, V, A, M	P
<i>Prioria</i>	Sa	I	A	100–200	>=800	5–20	S	He	–	1–3	4–12	N	1,2	P	T	S, V, A, C, B	P
<i>Colophospermum</i>	Af	D	A	50–200	>=350	5–40	S, A, V	Ho	–	1–3	4–12	N	3	A	A	V, A, C	P
<i>Hardwickia</i>	As	I, D	A	50–200	>=350	5–20	S, A, V	Ho	–	4–10	4–12	N	2	A	A	V, A, B	P
<i>Guibouria</i>	Af	I	A	60–220	<350, 350–>800	5–20	S, A, V	Ho	–	1–6	4–8	N	2	A	A, R	V, A, C	P, F
<i>Hymenaea</i>	Sa	I, D	A	100–200	350–800	5–20	M, L, A, V	Ho	–	4–10	6–9	N	2,3	A	A, R	V, A, C	P
<i>Peltogyne</i>	Sa	I, D	A	100–>200	350–800	5–20	S, A, V	Ho	–	4–10	4–12	N	2,3	P	A, R	A, C, U	P
<i>Eperua</i>	Sa	D	A	70–300	200–600	2–13	S, M, A	He	180–750	1–4	5–8	N	2	A	T	S, DA, V, M	P
<i>Eurypetalum</i>	Af	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Augouardia</i>	Af	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Stemonocoleus</i>	Af	I, D	A	100–200	<350, 350–>800	5–20	M, A, V	Ho	–	1–3	4–12	N	2,3	A	A	V	P
<i>Baikiaea</i>	Af	D	P	40–90	250–400	17–30	A, V	Ho-He	–	2–4	7–11	N	2	P	A	V, C, U	P
<i>Copaifera</i>	Sa/Af	D	A	90–210	100–480	3–8	S, M, A	Ho-He	220–1050	1–4	6–8	N	1,2	A	T	V, A, C, M	P
<i>Detarium</i>	Af	D	A	145–360	<350	2	A, V	Ho-He	<1000	1–6	3–4	N	2,3	A	T	B, D, V, A	P
<i>Gilletiodendron</i>	Af	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Hylodendron</i>	Af	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pseudosindora</i>	As	D	A	>=200	350–800	<=5	M, L, A, V	He	>1000	1–3	4–12	N	2	A	T	V, M	P
<i>Sindora</i>	As	D	A	100–220	<350, 350–800	3–9	A, V	He	<1000	2–3	6–11	S	2,3	A	T	B, M, V, A, C	P
<i>Sindoropsis</i>	Af	D	A	>=200	<350, 350–800	5–20	M, A, V	Ho	–	1–3	4–12	N	2	A	T	V, A, M	P
<i>Tessmannia</i>	Af	D	A	100–220	<350, 350–800	5–20	M, A, V	Ho	–	4–10	4–12	N	3	A	R	V, A, M	P

Key to abbreviations used:

Distribution: Af = Africa; Sa = Tropical South America; M = Madagascar; As = Asia.

Growth rings: D = distinct; I = indistinct.

Vascular tracheids: P = present, A = absent.

Vessel arrangement: D = vessels in dendritic pattern; A = without vessel arrangement.

Vessels grouping: S = solitary; M = radial multiples; C = clusters.

Vessel pitting: S = small (4–7 µm); M = medium (7–10 µm); L = large (≥10 µm); A = alternate; V = vested.

Rays type: Ho = homocellular; He = heterocellular.

Septate fibers: P = present; N = not present.

Fibre wall thickness: 1 = very thin-walled; 2 = thin- to thick-walled; 3 = very thick-walled.

Storied structure: P = present; A = absent.

Axial canals: D = diffuse; T = tangential lines; R = traumatic; A = absent.

Parenchyma: S = scanty; V = vasicentric; A = aliform; C = confluent; M = marginal; B = banded; U = unilateral; DA = Diffuse-in-aggregates; D = diffuse.

Crystals: P = parenchyma; R = rays; F = fibers.

Table 2
Comparison of *Enterrrioxylon victoriensis* with 15 fossil wood species of Caesalpinoideae with axial canals and vasicentric, aliform and confluent axial parenchyma.

	Region	Age	Growth rings	Vascular Tracheids	Arrangement	Vessels			Frequency (mm ⁻²)	Pitting	Fibres		Rays				Axial canals	Parenchyma	Crystals
						Diameter (µm)	Length (µm)	Groupings			Septate	Diameter (µm)	Type	Height (µm)	Width (cells)	Frequency (mm linear)			
<i>Enterrrioxylon victoriensis</i>	Sa	Mi	I	P	D	65–318	85–165	S, RM, C	4–16	A, V, S	N	13–23	Ho	38–157	1–3	3–5	D, N	V, A, C	R, P
<i>Acacia gregorii</i> Gregory	Na	Eo	I	–	WD	?	200–400	S, RM, C	4–11	A, S, O, S, L	N	?	Ho	?	1–2	ca. 5	T, Tr	V, A, C; M	R, P
<i>Caesalpinioxylon moragionesiae</i> Crawley	Af	Pa	I	–	WD	100–200	350–800	?	5–20	A	P	?	He	?	1–3	4–12	N	V, A, B	P
<i>Caesalpinioxylon palembangense</i> Kräusel	Sp	Ol, Mi	I	–	WD	100–200, ≤ 200	≤ 350–800	?	5–20	A, S, L	N	?	He	?	4–10	≤ 12	N	V, A, C, B, D	A
<i>Caesalpinioxylon tchadense</i> Koeniguer	Af	Pl	I	–	WD	100–200	≤ 350	?	5–20	A, L	P	?	Ho	?	1	4–12	N	C, B	P
<i>Aulacoxylon sparnacense</i> Combes emend. De Francheschi and De Ploëg	Eu	Eo	I	–	WD	100–170	150–400	S, RM	9–10 (5–16)	O	N	?	He	150–350	1–2 (3)	9–15	T, Tr	V, B	R
<i>Erythrophloeoxylon scholleri</i> Boureau	Eu	Ol	D	–	WD	100–200	≤ 350	?	≤ 5	A	N	?	He	?	1–3	4–12	N	V, C, B, D, M	R, P
<i>Copaiferoxylon copaiferoides</i> Fessler-Vrolant	Eu	Ol	D	–	WD	100–200	≤ 350	?	≤ 5	A	N	?	He	?	1–3	4–12	N	V, C, A, B	P
<i>Copaiferoxylon assamicum</i> Gottwald	As	Mi	I	–	WD	165–200	≤ 350, 350–800	?	≤ 5, 5–20	A	N	?	He	?	2–3	4–12, ≥ 12	N, T	A, B	P
<i>Copaiferoxylon eosiamensis</i> Gottwald	As	Mi	I	–	WD	200–260	≤ 350, 350–800	?	≤ 5	A	N	?	He	400–500	4–10	4–12, ≥ 12	N	A, B	P
<i>Copaiferoxylon matanzensis</i> Cevallos-Ferriz and Barajas-Morales	Na	Ol, Mi	D	–	WD	87–128	178–321	S, RM, C	2–6	A, V	N	5–20	He	325–978	2–3	5–9	N, T	A, C, M, D	F
<i>Kingiodendron prepinnatum</i> Awasthi and Prakash	As	Mi	D	–	WD	> 250	150–175	S, RM	6–12	A, M, L, V	N	32	Ho, He	?	1–4	7–9	N, T	A, V, D	
<i>Detarioxylon aegyptiacum</i> (Unger) Louvet	Af	Ol, Mi	I	–	WD	100–200	≤ 350, 350–800	?	≤ 5	A	N	?	He, Ho	?	4–10	4–12, ≥ 12	N	A, V, C, B	–
<i>Hopeoxylon arcotense</i> Awasthi	As	Mi, Pl	I	–	WD	120–270	150–400	S, RM	8–18	A, L, V	N	?	He	?	1–5		N, T	A, V, D	A
<i>Hopeoxylon indicum</i> Navale	As	Mi, Pl	I	–	WD	60–165	?	S, RM	10–20	A, L, V	N	?	He	?	1–3	?	N, T	V, A, C, D	A
<i>Hopeoxylon speciosum</i> (Navale) Awasthi	As	Mi, Pl	D	–	WD	75–300	?	S, RM		A, L, V	N	?	He	?	3–6		N, T	V, A, C, D	P

Key to abbreviations used:

Distribution: Af = Africa; Sa = South America; Na = North America; Eu = Europe; As = Asia; Sp = Southeast Asia and Pacific.

Age: Pa = Paleocene; Eo = Eocene; Ol = Oligocene; Mi = Miocene; Pl = Pliocene.

Growth rings: D = distinct; I = indistinct.

Vascular tracheids: P = present.

Vessel arrangement: D = vessels in dendritic pattern, WD = without vessel arrangement.

Vessels grouping: S = solitary; RM = radial multiples, C = clusters.

Vessels pitting: S = small; M = medium, L = large; A = alternate, O = opposite; Sc = scalariform; V = vested.

Septate fibers: P = present; N = non present.

Rays type: Ho = homocellular; He = heterocellular.

Parenchyma: V = vasicentric; A = aliform; C = confluent; M = marginal; D = diffuse; B = banded, M = marginal banded.

Axial canals: D = diffuse, T = tangential; N = normal, Tr = Traumatic.

Crystals: P = parenchyma; R = rays; F = fibers; A = absent.

entirety (Carlquist, 2001). The presence of this feature in the fossil wood is interpreted here as an ecological adaptation.

Entrerrioxylon victoriensis differs more from American taxa than the African taxa. The combination of the anatomy characters (small, diffusely arranged, normal axial canals; homocellular rays; crystals in rays; vasicentric tracheids and storied structure) in *E. victoriensis* has a close relationship with *Daniellia*, *Prioria*, *Oxystigma*, *Gossweilerodendron*, *Kingiodendron* and *Baikiaea*. The presence of these characters in this fossil wood allows to establish a close relationship with the African taxa.

The fact that this fossil cannot be fully associated with any single extant taxon is significant, since it may therefore be able to contribute substantially to phylogenetic studies and provide new information about distribution patterns.

4.3. Comparison with fossil wood of the Caesalpinoideae

Seven fossil genera and 15 fossil wood species of Caesalpinoideae 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 Mädel, 1967; Gregory, 1971, [1973]; Louvet, 1973; Awasthi, 1975 [1977]; Koeniguer, 1975; Fessler-Vrolant, 1977; Awasthi and Prakash, 1986 [iss. 1987]; Crawley, 1988; Awasthi, 1992; Cevallos-Ferriz and Barajas-Morales, 1994; Privé-Gill et al., 1999; Gottwald, 1994; De Franceschi and De Ploëg, 2003; El-Saadawi et al., 2011).

The fossil species are: *Acacia gregorii* Gregory, *Caesalpinioxylon morajonesiae* Crawley, *Caesalpinioxylon palembangense* Kräusel, *Caesalpinioxylon tchadense* Koeniguer, *Aulacoxylon sparnacense* Combes emend. De Franceschi and De Ploëg, *Erythrophloemoxylon scholleri* Boureau, *Copaiferoxylon copaiferoides* Fessler-Vrolant, *Copaiferoxylon assamicum* Gottwald, *Copaiferoxylon eosiamensis* Gottwald, *Copaiferoxylon matanzensis* Cevallos-Ferriz and Barajas-Morales, *Kingiodendron prepinnatum* Awasthi and Prakash, *Detarioxylon aegyptiacum* (Unger) Louvet, *Hopeoxylon arcotense* Awasthi, *Hopeoxylon indicum* Navale, and *Hopeoxylon speciosum* (Navale) Awasthi (Table 2).

Acacia gregorii differs from the fossil wood studied here by the presence of axial parenchyma in marginal or seemingly marginal bands, larger rays that are commonly 4–10 seriate and axial canals of the traumatic type arranged fairly frequently in tangential rows (Gregory, 1971 [1973]).

Caesalpinioxylon morajonesiae and *Caesalpinioxylon palembangense* have heterocellular rays and axial parenchyma bands, while *Caesalpinioxylon tchadense* differs in having exclusively uniseriate rays, axial parenchyma and/or vessels with storied structure and septate fibers (Kräusel, 1922; Koeniguer, 1975; Crawley, 1988).

Entrerrioxylon victoriensis differs from *Aulacoxylon sparnacense* by its possession of heterocellular rays and axial canals that are of traumatic origin, arranged in tangential bands (De Franceschi and De Ploëg, 2003), while *Erythrophloemoxylon scholleri* differs by having marginal and diffuse axial parenchyma, oil and/or mucilage cells associated with ray, axial parenchyma and fibers types and is also characterized by the presence of axial canals associated with axial parenchyma cells and ray cells (Müller-Stoll and Mädel, 1967).

The *Copaiferoxylon*, *Detarioxylon*, and *Kingiodendron* genera have heterocellular rays composed of procumbent body ray cells with 1–4 rows of upright and/or square marginal cells, while *Entrerrioxylon victoriensis* has exclusively homocellular rays composed of procumbent cells (Louvet, 1973; Fessler-Vrolant, 1977; Awasthi and Prakash, 1986 [1987]; Cevallos-Ferriz and Barajas-Morales, 1994; Gottwald, 1994). Only some specimens of *Detarioxylon aegyptiacum* from El Cairo (Egypt) have homocellular rays, but they also present axial canals in long tangential lines (El-Saadawi et al., 2011). *Kingiodendron* has abundant axial, vertical and singly occurring canals, in pairs sometimes tangentially aligned in small groups of 3–5 and surrounded by 3–6 layers of parenchyma tissue. Also, axial canals that are of normal origin (Awasthi and Prakash, 1986 [1987]) are present.

Hopeoxylon differs from *Entrerrioxylon* by the presence of apotracheal parenchyma lines or bands containing vertical gum canals, 1–5 seriate heterocellular rays consisting of procumbent cells and 1–2 rows of marginal upright cells (Navale, 1962 (1963); Privé-Gill et al., 1999).

4.4. Fossil record, paleoecology and biogeographic implications

The basally branching clades of the Leguminosae (e.g., Cercideae, Detarieae and Cassieae) have more species in the Old World (Schrire et al., 2005a). The pantropical distribution of the Detarieae s.l. is very wide, as species occur in tropical America, Africa and Asia. However, there are no extant genera in Australia (Fougère-Danezan et al., 2003, 2010).

The Detarieae s.l., includes five groups within the informal classification proposed by Fougère-Danezan et al. (2010); 1) the *Daniellia* group with *Brandzeia*, *Daniellia* and *Neopaloxylon*; 2) the *Prioria* group that is made up of *Colophospermum*, *Hardwickia* from the *Hardwickia* sub-group, and *Gossweilerodendron*, *Oxystigma*, *Kingiodendron*, and *Prioria* from the *Prioria* sub-group; 3) the *Hymenaeae* group composed of *Guibourtia*, *Hymenaea* and *Peltogyne*; 4) the *Eperua* group with two sub-groups (*Eperua* sub-group with *Eperua* and *Eurypetalum* and *Stemonocoleus* sub-groups with *Augouardia* and *Stemonocoleus*); and finally 5) the *Detarium* group composed of *Baikiaea*, *Copaifera*, *Detarium*, *Gilletiodendron*, *Hylodendron*, *Pseudosindora*, *Sindora*, *Sindoropsis* and *Tessmannia* (Fougère-Danezan et al., 2007, 2010).

Fossil records of pollen interpreted as belonging to the *Sindora*-like forms from the Upper Cretaceous of Siberia, Canada and Colombia may correspond with an earlier appearance of Caesalpinoideae in the fossil record; however, their assignment, even to the family level, has been questioned by many authors (Muller, 1981; Herendeen et al., 1992; Calvillo-Comadell et al., 2010 and references therein). The unequivocal pollen record of *Crudia* was found in sediments from the Paleocene of Nigeria (Adegoke et al., 1978). The genus was subsequently reported from the United States, where fruits and leaves were found in the middle Eocene (Herendeen and Dilcher, 1990). The fossil record with Detarieae affinity is extensively documented in Calvillo-Comadell et al. (2010).

Flowers of *Prioria* and *Peltogyne* and petals of *Hymenaea* included in amber have been described from the Oligocene/Miocene Dominican amber (Poinar and Poinar, 1999). Recently, flower organs similar to those of extant *Hymenaea* included in the Simojovel de Allende amber of the early Miocene were recorded in Chiapas, Mexico (Calvillo-Comadell et al., 2010). This record and the fossil wood records referred to above (see Introduction), support the occurrence of Detarieae in North and South America.

Many of the anatomical characters observed in *Entrerrioxylon victoriensis* support that idea that the fossil wood studied here would have lived under warm and humid environmental conditions, including indistinct growth rings, diffuse porosity, relatively abundant axial parenchyma and mostly solitary (>70%), low-density, medium-sized to large diameter vessels with very thin to thin walls (Carlquist and Hoekman, 1985; Wheeler and Baas, 1991, 1993; Lindorft, 1994). In addition, there is a higher incidence of woods with a combination of chambered crystalliferous parenchyma, storied structure and short vessel elements in tropical legumes than temperate ones (Wheeler and Baas, 1992). The Vulnerability Index (V) and Mesomorphy ratios (M) show values of 13.42 and 1664 respectively. These values demonstrate that *E. victoriensis* shows mesomorphic features (Carlquist, 1977).

Lavin and Luckow (1991) have provided evidence for a biogeographic and evolutionary relationship between the extant legume flora of Africa (Madagascar) and tropical America. Such a relationship suggests that dispersal between Africa and tropical America occurred in the early history of the family (Herendeen et al., 1992) and the

fossil wood described here may provide some evidence for floristic exchange between these regions.

The boreotropics hypothesis proposed by Lavin and Luckow (1993) postulates a preferential tropical interchange between North America and Eurasia during the early Cenozoic that was directed by the Eocene Thermal Maximum (ETM) and the close proximity of these two continental plates. Furthermore, this preferential interchange occurred at a time when South America was geologically and biotically isolated. This hypothesis suggests that many tropical elements in North America could be descendants of northern tropical progenitors.

Recently, Schrire et al. (2005a, b) provide a hypothesis for the origination and diversification of Fabaceae along the margin of the Tethys Seaway during the early Cenozoic. The hypothesis is based on the likelihood that legumes originated in seasonally dry environments. Four global legumes biomes were delimited by Schrire et al. (2005a, b) and called Succulent (S), Grass (G), Rainforest (R) and Temperate (T). Lineages confined to the S biome gave rise to sublineages occupying all other biomes and the R biome taxa are primarily derived from dry S and G biome taxa. The Detarieae group, Diallineae and Basal Papilionoideae contains the highest proportions of taxa in the R biome. Lineages occupying R and G biome have been less persistent—a result of the predictable water requirement of these biomes affected by climatic fluctuations (Schrire et al., 2005a).

A dry origin for legumes is in accordance with key morphological synapomorphies and a high nitrogen metabolism in the family. The S biome largely overlaps with the seasonally dry to arid-tropical climate belt proposed by Scotese (2001). This paleoclimatic belt also coincides with the known spatial and temporal distribution of legume fossils (Herendeen et al., 1992).

A molecular biogeographic study in legumes (Lavin et al., 2000) suggests that diversification occurred during the Cenozoic in seasonally dry tropical vegetation (Pennington et al., 2004). The presence of semi-arid to arid environments around the Paleogene Tethys Seaway allowed a widespread distribution of Fabaceae and the nearly instantaneous pervasiveness over a large global area shortly after their earliest occurrence in the fossil record (Schrire et al., 2005a; Pan et al., 2010). According to Pan et al. (2010) the Tethys Seaway may have been an ideal corridor for such dispersal, but there does not appear to be enough definitive data to pinpoint the landmass which was the place of legume origins.

The record of legume fossils in Africa, South America, North America and Britain in the Paleocene indicates that the Fabaceae was already widely distributed at that time and suggests either a Late Cretaceous origin or a rapid initial diversification and dispersal in the Paleocene (Pan et al., 2010).

The fossil record for genera that have intercellular axial canals demonstrates that this legume group was more widespread in the past than today. The past widespread distribution is connected with a past warmer climate at higher latitude.

The presence of *Enterrrioxylon victoriensis* in the Miocene Paraná Formation in South America suggests closer links with Central America and tropical South America, and a very old relationship with Africa's tropical flora. Although further information and a more complete study of the Detarieae s.l. fossil record are needed to create models of dispersal routes and the directionality of dispersal events in the Fabaceae, the evidence from *E. victoriensis* seems to indicate that the dispersal occurred across the Atlantic Ocean from Africa towards the northern parts of South America, and then towards the south.

5. Conclusions

Enterrrioxylon victoriensis has been redescribed and emended, and a new suprageneric affinity has been proposed. This taxon has been transferred to tribe Detarieae s.l. by the presence and combination of intercellular axial canals, crystals in ray cells, partially storied

rays and similar fibre wall thickness. *Daniellia*, *Prioria*, *Oxystigma*, *Gossweilerodendron*, *Kingiodendron* and *Baikiaea* are the extant genera most closely related to *E. victoriensis*.

The evidence presented here supports the arguments that *Enterrrioxylon victoriensis* lived in a warm and humid climate and was a component of tropical forests that were developing in coastal landscapes near the Entrerriense Sea.

Enterrrioxylon victoriensis supports the existence of a very old relationship with the African flora, as well as close links to Central America and tropical South America. Preliminary paleobiogeographical studies also seem to indicate that dispersion of the tribe Detarieae occurred first across the Atlantic Ocean from Africa towards the northern parts of South America, and later dispersing towards the south. This model is supported by the new fossil evidence presented here for *E. victoriensis*.

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