A new genus of Anacardiaceae based on wood from the Tepetate Formation (upper Eocene) of Baja California Sur, Mexico

Angelica J. Mejia-Roldan, Gerardo González-Barba, Oris Rodríguez-Reyes & Emilio Estrada-Ruiz



We describe a new fossil wood genus of Anacardiaceae with two species from the Tepetate Formation (upper Eocene), Baja California Sur State, Mexico. The first species has distinct growth ring boundaries, vessels solitary and in radial multiples; alternate intervessel pitting, and the vessel-ray parenchyma pits with reduced borders. Its other features are: non-septate and septate fibers, axial parenchyma rare, and rays mostly uniseriate except for those with radial canals. The second species has distinct growth ring boundaries, vessels solitary and in radial multiples (a higher percentage of solitary vessels than the first species), vessel-ray pits with a horizontal to round shape, all fibers nonseptate, vasicentric axial parenchyma, heterocellular rays and radial canals in some multiseriate rays. The diagnostic traits in both woods allow us to erect in a new fossil genus, *Pericuxylon* with two species in the Anacardiaceae family. The occurrence of Anacardiaceae in the late Eocene of southern Baja California Sur confirms its long geological history and importance in forests of northern Mexico. • Key words: Baja California Peninsula, eudicots, fossil woods, Sapindales.

MEJIA-ROLDAN, A.J., GONZÁLEZ-BARBA, G., RODRÍGUEZ-REYES, O. & ESTRADA-RUIZ, E. 2024. A new genus of Anacardiaceae based on wood from the Tepetate Formation (upper Eocene) of Baja California Sur, Mexico. *Bulletin of Geosciences 99*(1), 73–83 (3 figures, 2 tables). Czech Geological Survey, Prague. ISSN 1214-1119. Manuscript received September 20, 2023; accepted in revised form April 3, 2024; published online April 14, 2024; issued April 14, 2024.

Angelica J. Mejía-Roldan & Emilio Estrada-Ruiz, Departamento de Zoología, Laboratorio de Ecología, Escuela Nacional de Ciencias Biológicas – Instituto Politécnico Nacional, Prolongación de Carpio y Plan de Ayala s/n, 11340, Ciudad de México, México; emilkpaleobot@yahoo.com.mx • Gerardo González-Barba, Departamento Académico de Ciencias Marinas y Costeras, Museo de Historia Natural, Universidad Autónoma de Baja California Sur, Carretera al sur km. 5.5, El Mezquitito, 23080, La Paz, B.C.S., México • Oris Rodríguez-Reyes, Instituto de Ciencias Ambientales y Biodiversidad, Universidad de Panamá, Estafeta universitaria, 0824 Panamá, Panamá; Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancón Republic of Panamá, Panama

The Anacardiaceae family is represented by trees, shrubs and some woody climbers, with *circa* 79 genera and 900 species, with a wide distribution in tropical, subtropical, and warm temperate regions (Mabberley 2008, Pell *et al.* 2010). In Mexico, this family has ~62 species distributed in 20 genera with some species of food importance, e.g., *Spondias purpurea* L. (jocote or ciruela de Tierra Caliente), or for medicinal uses, e.g., *Cyrtocarpa procera* to treat stomach diseases (Martínez-Millán & Cevallos-Ferriz 2005, Martinez-Elizalde *et al.* 2015).

Anacardiaceae has an extensive fossil record worldwide, that includes flowers, fruits, pollen, leaves and woods of about 140 fossil species in over 35 genera. The records range from the Late Cretaceous to the Miocene, being very abundant during the Eocene; most of these records are from South America and Asia (Del Rio *et al.* 2023). Currently, there are approximately 80 fossil woods assigned to this family (*e.g.*, Kruse 1954, Selmeier 2000, Gregory *et al.* 2009, Estrada-Ruiz *et al.* 2010, Pérez-Lara *et al.* 2017, Woodcock *et al.* 2017, Rodríguez-Reyes *et al.* 2021).

The oldest known anacardiaceous woods are *Anacardiaceoxylon semecarpoides* (Prakash & Dayal 1964) and *Dracontomeloxylon palaeomangiferum* Prakash from the Upper Cretaceous to Paleocene of India (Bande & Khatri 1980, Wheeler *et al.* 2017). Estrada-Ruiz *et al.* (2010) described a fossil wood from the Olmos Formation Upper Cretaceous (Campanian) of Mexico, with a mosaic of characteristics that resemble the families Anacardiaceae and Burseraceae. The fossil record of Anacardiaceae in Mexico is represented by pollen, flowers, leaves or leaflets, and woods. The genus *Tapirira* Aubl. has been described based on a flower and some wood from the Oligocene-Miocene of Chiapas and Baja California Sur and a wood resembling *Loxopterygium* Hook. f. was described from the Oligocene of Coayuca de Andrade, Puebla, Mexico (Miranda 1963, Martínez-Cabrera & Cevallos-Ferriz 2004, Méndez-Cárdenas *et al.* 2014). There are also reports of leaves and/or leaflets ascribed to *Pseudosmodingium* Engl., *Haplorhus* Engl., *Rhus* L., *Comocladia* L., and *Pistacia* L., from the Oligocene Los Ahuehuetes locality, Tepexi de Rodríguez in Puebla (Ramírez *et al.* 2000, Ramírez & Cevallos-Ferriz 2002). More recently, Pérez-Lara *et al.* (2017) described the second oldest record of the family based on a fossil wood from the Bosque Formation (early Eocene) of Chiapas, Mexico.

In this work, we describe two new fossil species of Anacardiaceae from the Tepetate Formation (upper Eocene), Baja California Sur, Mexico. The occurrence of these two species in the Eocene of Baja California Sur adds to the notion that Anacardiaceae have long been a key element in Mexican floras. This finding enriches the fossil record of the family in the Neotropics, and it also contributes to a better understanding of its phytogeographic history.

Geological setting

The Tepetate Formation crops out in southwestern Baja California Sur, between the arroyos El Aguajito (in the south) and La Salada (in the north) streams (Fig. 1). The base of the Tepetate Formation is not exposed. A 37 m thick composite section of the Tepetate Formation in Arroyo San Hilario was published by González Barba et al. (2002), consisting of mudstones, siltstones and sandstones (see González Barba et al. 2002, p. 723). The fossil woods were collected at locality MHN-UABCS Te-5 in arroyo El Canelo, a tributary of Arroyo San Hilario, in a bed of orange-yellow siltstone. There are other sites with abundant fossil woods, but the fossil woods referred to as the El Cien Formation of Oligocene age have been argued for the fact that they are mostly transported materials or not collected in situ. There is evidence to consider whether some materials may correspond to the Comondú Formation, of Miocene age, due to the proximity to the outcrops corresponding to terrestrial or continental deposit environments. While the relationship with the El Cien Formation would correspond to terrestrial materials dragged and deposited in marine sediments of the continental shelf, that is allochthonous materials. Although in our experience fossil woods in the Cien Formation are scarce. In the case of the fossil woods from the Tepetate Formation of Eocene age, these have been collected directly from outcrops of marine sediments

of this formation, so they would also be allochthonous materials deposited in a continental shelf environment, as in the case of the woods of the El Cien Formation. We can also remark that the woods from the Tepetate Formation are generally darker than the ones from El Cien Formation. For the general and specific mapping of the referred formations, please see Hausback (1984), and Álvarez *et al.* (1999).

The most abundant fossils are macroforaminiferans, mollusks, crustaceans, echinoids and shark teeth. In general, the outcrops reflect a shallow marine shelf depositional environment. The available paleontological data indicate that the Tepetate Formation is latest Cretaceous to middle late Eocene in age. Based on foraminiferans, the beds exposed in the Arroyo San Hilario are early middle Eocene in age, but shark teeth collected at the same bed indicate an age of middle late Eocene (González Barba *et al.* 2002; Schweitzer *et al.* 2002, 2005, 2006; Morales-Ortega *et al.* 2015, 2018).

Materials and methods

The two fossil samples described in this study were found in the southern part of the Baja California Peninsula, approximately 100km northwest of La Paz, in the town of "El Cien". These woods were collected in 2017 and processed using the thin sections technique proposed by Hass & Rowe (1999). Specimens were cut to expose three planes: transverse section (TS), tangential longitudinal section (TLS) and radial longitudinal section (RLS). Each thin section was studied using an optical microscope, brand BX53 Trinocular Olympus (ENCB, IPN).

An Olympus SC100 camera with a 10.5 Mpix color CMOS sensor was used for imaging. Measurements of cell structures were compiled with the aid of the CellSens Entry program was used to get information on quantitative features. All the measurements were taken in 25 fields chosen at random, from which the average was obtained to avoid bias in the measurements. All this work was carried out in the Laboratorio de Ecología of the Departmento de Zoología at the Escuela Nacional de Ciencias Biológicas del Instituto Politécnico Nacional. Once all the anatomical data were obtained, we made a first approach toward identification using the Inside Wood Database (IWD) (Wheeler 2011, Wheeler et al. 2020) and followed the terminology proposed by the IAWA Hardwood List (1989), and Wheeler (1986). For the classification of ray types, we used the terminology proposed by Kribs (1935). The two fossil specimens described in this work are housed at the Colección de Paleontología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (IPN-PAL), located in Mexico City, Mexico.

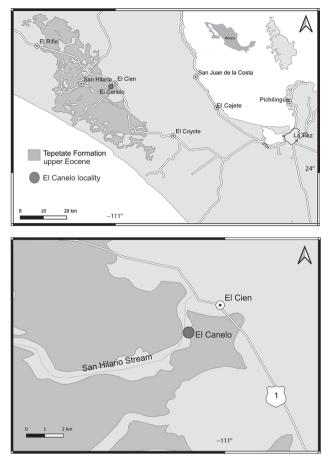


Figure 1. A – map of Mexico and Baja California Sur. B – location of the fossiliferous outcrop (circle), Cañada El Canelo.

Systematic paleontology

Order Sapindales Family Anacardiaceae

Genus *Pericuxylon* Mejia-Roldán, Rodríguez-Reyes et Estrada-Ruiz gen. nov.

Type species. – Pericuxylon ductifera.

Etymology. – The generic name honors the Pericú (Edués or Coras), the aboriginal inhabitants of Baja California Sur.

Diagnosis. – Growth ring with distinct boundaries marked by radially narrowed latewood fibers; vessels mostly solitary with occasional radial multiples; intervessel pitting alternate; vessel-ray parenchyma pits with reduced borders and round to horizontal shape; non-septate and septate fibers, 2–3 septa per fiber; axial parenchyma scanty paratracheal to vasicentric; heterocellular rays with bodies composed of procumbent cells, usually with one marginal row of erect or square cells; small radial canals, usually one per ray, located near the ray margins.

Pericuxylon ductifera Mejia-Roldán, Rodríguez-Reyes et Estrada-Ruiz sp. nov. Figure 2

Holotype. – IPN-PAL 17 (wood sample) with six thin sections. Colección de Paleontología, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico City, Mexico.

Type horizon and locality. – Tepetate Formation, upper Eocene; locality MHN-UABCS Te-5 in arroyo El Canelo, a tributary of Arroyo San Hilario, California Baja Sur, Mexico.

Etymology. – The specific epithet refers to the presence of radial canals.

Diagnosis. - As for the genus.

Description. – Description based on a single permineralized float wood sample with an estimated original diameter of ~ 60 cm.

Growth rings distinct, the rings marked by four to five rows of radially flattened latewood fibers. Diffuse-porous wood (Fig. 2A, B). Solitary vessels (82 %) and in radial multiples of 2 to 3, with 8 (range = 3-11) vessels per square millimeter; vessel elements round to oval in outline (Fig. 2A). Mean tangential vessel diameter 130 (range = 97-169) µm (Fig. 2B); simple perforation plates (Fig. 2C); intervessel pitting alternate, small, polygonal in outline, 4 to 6 µm in horizontal diameter; vessel-ray parenchyma pitting with reduced borders, round to horizontal shape (Fig. 2D). Mean vessel element length, 196 (range = 129-246) µm. Bubble-like tyloses common (Fig. 2C).

Fibers are mostly septate, but non-septate fibers commonly occur. 2–3 septa per fiber (Fig. 2, E - G), with thin to medium walls, pitting not observed.

Axial parenchyma scanty paratracheal (Fig. 2A, B).

Rays heterocellular, 1–2 (3) (Fig. 2H, I). Rays Kribs heterogeneous type IIA, with procumbent body cells and usually one marginal row with erect or square cells (Fig. 2I). Uniseriate rays are 7.5 (range = 3-12) cells and 188 (range = 128-265) µm high. Rays 8 (range 5-12) per tangential millimeter (Fig. 2E, G).

Radial canals in some multiseriate rays (Fig. 2E, G), one canal per ray, some radial canals are off-center (Fig. 2E, G); mean tangential diameter of 50 (range = 33-75) µm, one canal per ray delimited by a layer of 1–2 epithelial cells (Fig. 2G).

A few prismatic crystals were observed in procumbent ray cells (Fig. 2H).

Pericuxylon eocenicum Mejia-Roldán, Rodríguez-Reyes et Estrada-Ruiz sp. nov. Figure 3

Holotype. – IPN-PAL 18 (wood sample) with six thin sections.

Type horizon and locality. – Tepetate Formation, upper Eocene; locality MHN-UABCS Te-5 in arroyo El Canelo, a tributary of Arroyo San Hilario, California Baja Sur, Mexico.

Etymology. – The specific epithet refers to the age of the locality where the sample was collected.

Diagnosis. – Distinct growth ring boundaries marked by radially narrowed latewood fibers; vessels solitary and in radial multiples of 2 to 3; intervessel pitting alternate; vessel-ray and vessel parenchyma pits with reduced borders, elongated shape; non-septate fibers; axial parenchyma vasicentric; heterocellular rays; radial canals in some multiseriate rays.

Description. – Growth rings distinct, the rings marked by four rows of radially flattened latewood fibers. Diffuseporous wood (Fig. 3A–C). Mostly solitary vessels (>90%) and rarely in radial multiples of two (occasionally 3), 8 (range = 5–12) vessels per square millimeter. Vessel elements round to oval in outline (Fig. 3A, C). Mean tangential vessel diameter 120 (range = 92–173) µm, vessel walls in transverse sections of 7 (range = 5–10) µm thick (Fig. 3A–C); simple perforation plates (Fig. 3D, E); intervessel pitting alternate, polygonal in outline, 6 to 8 µm in horizontal diameter, with elliptical apertures of 3 µm (Fig. 3D); vessel-ray parenchyma pitting with reduced borders, round shape (Fig. 3E). Mean vessel element length 227 (range = 169–291) µm. Bubble-like tyloses common (Fig. 3F).

Nonseptate fibers (Fig. 3F–H), with thin to medium walls.

Axial parenchyma scanty paratracheal to scarce vasicentric (Fig. 3C).

Rays heterocellular, mostly uniseriate rays, occasionally 2–3-seriate rays (Fig. 3F–H). Rays heterogeneous, Kribs type IIA, with procumbent body cells and usually one marginal row with erect or square cells (Fig. 3I). Multiseriate rays mean 9 (range = 6-13) cells and 196 (range = 124-305) µm high. Rays 11 (range = 9-14) per tangential millimeter (Fig. 3F).

Radial canals in some multiseriate rays (Fig. 3G, H); mean tangential diameter of 41 (range = 20–91) μ m, one canal per ray delimited by a layer of one epithelial cell (Fig. 3G, H).

Discussion

The two new fossil woods described in this work share some traits, but with sufficient differences between them that enable us to propose a new fossil genus with two species, as follows: *Pericuxylon ductifera* has paratracheal axial parenchyma and mostly septate fibers, whereas *Pericuxylon eocenicum* has some vasicentric axial parenchyma in addition to scanty paratracheal, nonseptate fibers, and mostly solitary vessels (> 90%); Also, the position of the radial canals in the ray body differs. In *P. eocenicum* the radial canals are in the middle of the ray, whereas in *P. ductifera* the canals are off center (see Fig. 2G, Tab. 1).

These two fossil woods from the Tepetate Formation (upper Eocene) have a combination of features that occur in the Anacardiaceae and Burseraceae families (order Sapindales). Although these two families are difficult to distinguish, certain features allow us to separate them. Generally, Burseraceae do not have distinct growth ring boundaries, but have a higher percentage of uniseriate rays, less abundant axial parenchyma, and exclusively septate fibers, whereas Anacardiaceae generally have more abundant axial parenchyma, frequent nonseptate fibers, and fewer occurrences of radial canals (Terrazas 1994, Martínez-Cabrera et al. 2006, Bell et al. 2010, Pérez-Lara et al. 2017). The two fossil woods have the following set of characters: growth ring boundaries distinct and wood diffuse porous, vessels mostly solitary, perforation plates simple; intervessel pits alternate, small to medium, vessel-ray pits with much reduced borders, septate and nonseptate fibers, axial parenchyma scanty paratracheal to vasicentric, ray width 1 to 3 cells, radial canals.

We conducted several searches of the IWD. One search was for an exact match for these features: growth ring boundaries distinct (1p); wood diffuse porous (5p); perfor-

Figure 2. *Pericuxylon ducftifera* Mejia-Roldan, Rodríguez-Reyes et Estrada-Ruiz gen. et sp. nov., locality MHN-UABCS Te-5 in arroyo El Canelo, a tributary of Arroyo San Hilario, California Baja Sur, Mexico, IPN-PAL 17. A – transverse section (TS). Vessels solitary and in radial multiples of two to three, and growth ring boundary (arrows). Scale bar = 500 μ m. B – (TS) diffuse porous wood with growth ring marked by four tangentially flattened rows of latewood fibers (arrows). Scale bar = 100 μ m. C – tangential longitudinal section (TLS). Simple perforation plate (arrow). Scale bar = 50 μ m. D – radial Longitudinal Section (RLS). Vessel-ray parenchyma pits with reduced border, round shape (arrows). Scale bar = 20 μ m. E – (TLS) rays mostly uniseriate, some biseriate. Scale bar = 100 μ m. F – (TLS) biseriate rays and septate fibers (arrows). Scale bar = 20 μ m. G – (TLS) a radial canal near the ray margin (arrow). Scale bar = 50 μ m. H – (RLS) crystals on the ray (arrow). Scale bar = 20 μ m. I – (RLS) heterocellular rays with procumbent body cells and usually one marginal row with erect or square cells. Scale bar = 100 μ m.

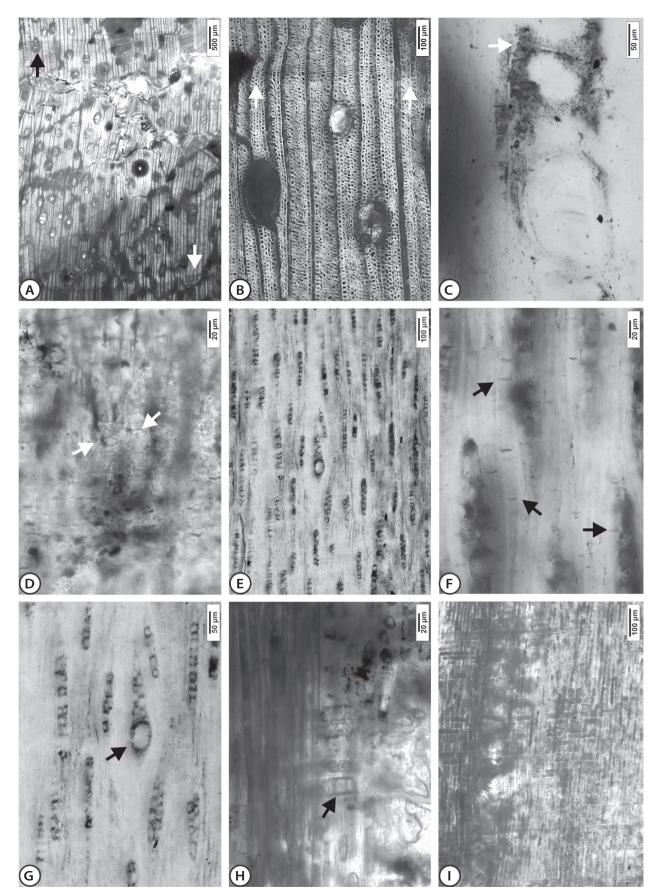


Table 1. Comparison anatomy among *Schinopsis, Tapirira peninsularis*, and the two fossil woods from Baja California Sur. Bold names = *Pericuxylon;* VEG = vessel element grouping; TVD = tangential diameter vessels; V/mm2 = number of vessel elements per square mm; Sp = scanty paratracheal; Vc = vasicentric; W-A = winged aliform.

Genera	VEG	TVD (μm)	V/MM ²	Septa per fibre	Axial parenchyma	Heterogeno us ray type	Radial canal (µm)	Layers of epithelial cells
Schinopsis	1–2	38–171	12–24	1–3	Sp, Vc, and weakly W-A	IIB	45-76	1–2
Tapirira peninsularis	2–4	110-230	7–13	1–3	Vc, and Sp	IIB	45–65	2–4
Pericuxylon ductifera	2–3	97–169	3–11	2–3	Sp	IIA	33–75	1–2
Pericuxylon eocenicum	1–2	92–173	5-10	Non septate	Sp and Vc	IIA	2w0–91	1

ation plates simple (13p); intervessel pits alternate (22p); intervessel pits, small (25p); vessel-ray pits with much reduced borders to apparently simple: pits horizontal (32p); septate fibers present (65p); non-septate fibers present (66p); axial paratracheal parenchyma scanty (78p); axial parenchyma vasicentric (79p); ray width 1 to 3 cells (97p); body ray cells procumbent with one row of upright and/or square marginal cells (106p); radial canals present (130p). This search yielded the fossil wood genera Anacardioxylon, Bosquesoxylon, Edenoxylon, and the extant genus Schinopsis (Tabs 1, 2). Species of Schinopsis have woods with a weak pattern of winged-aliform parenchyma and heterogeneous rays, Kribs type IIB (Tab. 1), these characters do not occur in the woods of Tepetate Formation, hence these are ruled out. We discuss Bosquesoxylon and Edenoxylon in the section about Eocene Anacardiaceae.

Both woods from Tepetate Formation have a distinct combination of characters that allows the erection of two new fossil species, especially because of a paratracheal to vasicentric axial parenchyma with septate and non-septate fibers combined; mostly uni to biseriate rays, and one radial canal per ray. We refer to Tables 1 and 2 for a more detailed discussion of the features to rule out these genera.

Previously, several fossil dicots wood have been described in Baja California Sur from El Cien Formation (Oligocene) (*e.g.*, Martínez-Cabrera & Cevallos-Ferriz 2004, Martínez-Cabrera *et al.* 2006). Among these woods, there is only a plant resembling to the Anacardiaceae, named *Tapirira peninsularis* Martínez-Cabrera *et* Cevallos-Ferriz. A few characters are shared between *T. peninsularis* and *P. ductifera*, however, we can distinguish them because *T. peninsularis* has wider vessels, larger intervascular pits (range $6-12 \mu m$), exclusively septate fibers, and higher rays in cells; more layers of epithelial cells of 2–4, as well as occasionally two canals per ray (Martínez-Cabrera & Cevallos-Ferriz 2004; Tab. 1).

Around 13 Eocene anacardiaceous fossil genera of woods have been described worldwide (InsideWood 2004, Pérez-Lara et al. 2017, Woodcock et al. 2017, Rodríguez-Reyes et al. 2020). Differences between these woods and the Pericuxylon woods follow. Kruse (1954) described Schinoxylon actinoporosum Kruse and Edenoxylon parviareolatum Kruse from the Eocene of Eden Valley, Wyoming (revised Boonchai & Manchester 2012) but both woods differ with Pericuxylon in having vesselray pits with distinct borders; Schinoxylon actinoporosum does not have axial parenchyma and Edenoxylon parviareolatum has indistinct growth ring as well as higher vessel frequency and more rays per mm. Brett (1966) described two fossil species of Edenoxylon from Herne Bay, England, E. aimulum has a higher vessel frequency, E. atkindoniae does not have distinct growth ring boundaries or radial canals. Wheeler et al. (1978) described Rhus crystallifera from the Eocene of Yellowstone National Park, Wyoming, USA, this wood is semiring-porous and lacks radial canals. Manchester (1977), and Wheeler & Manchester (2002) described three genera of woods with resemblance to Anacardiaceae from the middle Eocene Clarno Nut Beds, Oregon, USA. Maureroxylon has diffuse-in-aggregates axial parenchyma, and lacks radial canals; Tapirira sp. has wider vessels,

Figure 3. *Pericuxylon eocenicum* Mejia-Roldan, Rodríguez-Reyes et Estrada-Ruiz gen. et sp. nov., locality MHN-UABCS Te-5 in arroyo El Canelo, a tributary of Arroyo San Hilario, California Baja Sur, Mexico, IPN-PAL 18. A – (TS) mostly solitary vessels, wood diffuse-porous. Scale bar = $200 \mu m. B - (TS)$ growth ring boundary marked by radially narrow latewood fibres (arrows). Scale bar = $100 \mu m. C - (TS)$ vasicentric axial parenchyma (arrow). Scale bar = $50 \mu m. D - (TLS)$ simple perforation plate and Intervessel pitting alternate, and polygonal in outline (arrow). Scale bar = $50 \mu m. E - (RLS)$ vessel-ray parenchyma pits with reduced border, round and horizontally elongates (arrow). Scale bar = $20 \mu m. F - (TLS)$ non-septate fibers, bi and uniseriate rays, and bubble-like tyloses. Scale bar = $100 \mu m. G - (TLS)$ a radial canal in a multiseriate ray (arrow). Scale bar = $50 \mu m. H - (TLS)$ radial canal with a uniseriate layer of epithelial cells (arrow). Scale bar = $20 \mu m. I - (RLS)$ heterocellular rays (arrow). Scale bar = $50 \mu m.$

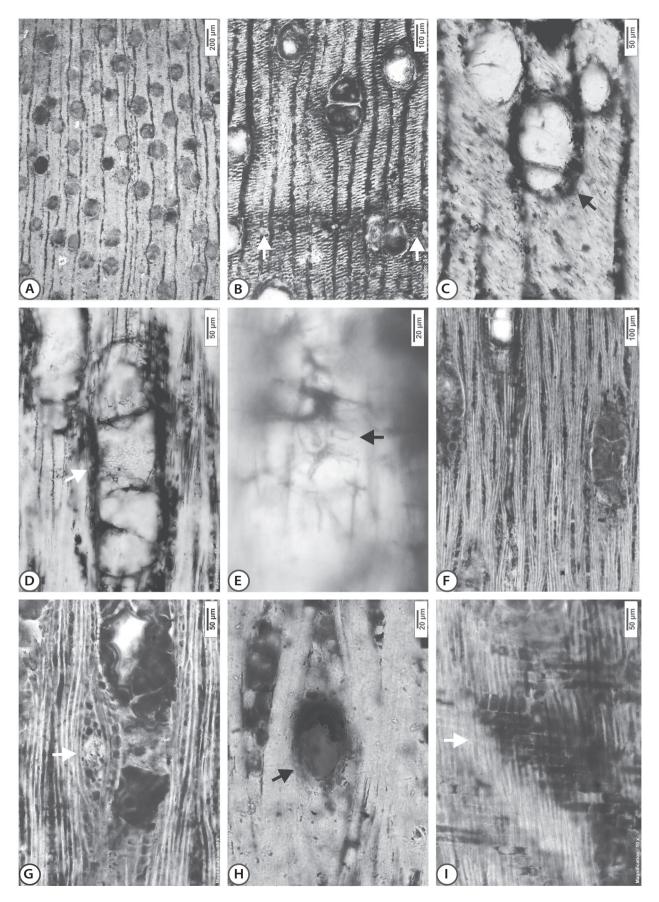


Table 2. Comparison between selected anacardiaceous fossil genera and the new two fossil woods from Baja California Sur (modified from Rodríguez-
Reyes <i>et al.</i> 2021).

Taxon	Distinct characteristics	Age	References
Anacardioxylon	Aliform axial parenchyma, rays 4-10 seriate	Cretaceous-Miocene	Wheeler et al. 2017
Astroniumxylon	Wider vessels diameter, vessel-ray pits with distinct borders	Pliocene	Franco 2009
Bouea	Growth rings indistinct, banded parenchyma, absent radial canals	Miocene	Agarwal 1988
Buchananioxylon	Growth rings indistinct, axial parenchyma aliform sometimes confluent	Miocene	Roy & Ghosh 1981
Dracontomeloxylon	Rays 4-10 seriate, radial canals absent	Cretaceous-Miocene	Wheeler et al. 2017
Dracontomelumoxylon	Growth rings indistinct, axial parenchyma aliform to confluent, rays 4–10 seriate	Cretaceous-Miocene	Ghosh & Roy 1979
Glutoxylon	Banded axial parenchyma, exclusively uniseriate rays	Miocene-Pliocene	Prakash & Tripathi 1969
Holigarnoxylon	Growth rings indistinct, axial parenchyma aliform to aliform confluent	Eocene-? Miocene	Prakash & Awasthi 1969
Lanneoxylon	Growth rings indistinct, rays 4-10 seriate	Miocene	Prakash & Tripathi 1969
Llanodelacruzoxylon	Growth rings indistinct, axial parenchyma slightly aliform, radial canals absent	Oligocene-Miocene	Rodríguez-Reyes et al. 2020
Loxopterygium	Wider vessels, sometimes two canals per ray, no crystals present	Oligocene	Méndez-Cárdenas et al. 2014
Mangiferoxylon	Aliform parenchyma, banded parenchyma, radial canals absent	Miocene-Pliocene	Awasthi 1966
Melanorrhoeoxylon	Banded parenchyma, homocellular rays	Miocene	Roy & Ghosh 1981
Parametopioxylon	Growth rings indistinct, intervessel pitting alternate to opposite, axial parenchyma sometimes confluent, lozenge-aliform	late Miocene?	Franco et al. 2020
Pistacioxylon	Latewood vessels in long radial multiples or clusters, vessels in diagonal pattern, helical thickenings	Miocene	Cheng et al. 2012
Resinaxylon	Vessels in diagonal pattern, higher vessel frequency (102–242 mm ²)	Oligocene	Pujana 2009
Schinopsixylon	Rays 4–10 seriate, non-septate fibres, sometimestwo canals per ray	Pliocene	Franco et al. 2020
Sclerocaryoxylon	Growth rings indistinct, higher vessel frequency, axial parenchyma absent	Miocene	Biondi 1981
Swintonioxylon	Growth ring indistinct, banded parenchyma	Miocene-Pliocene	Prakash & Tripathi 1969

solitary and in radial multiples of 2-5, larger intervascular pits, exclusively septate fibers, and more layers of epithelial cells of 2-4, as well as occasionally two canals per ray; Terrazoxylon ductifera Wheeler et Manchester has indistinct growth rings, vessels solitary and in radial multiples of 2-6, and higher vessel frequency, exclusively septate fibers. Woodcock et al. (2017) described two fossils from the Eocene of Peru that were assigned to extant genera: cf. Mangifera and Anacardium. Confer Mangifera axial parenchyma irregularly aliform with narrow wings, and radial canals are absent (Woodcock et al. 2017). Rodríguez-Reyes et al. (2021) reported the oldest Anacardium-like fossil based on a fossil wood, but this wood differs from our woods in having indistinct growth rings and lacking radial canals. Recently, Pérez-Lara et al. (2017) described a new fossil genus named Bosquesoxylon from the El Bosque Formation, Mexico. This wood has rays that are mostly 2- to 3-seriate (up to 4) and a few rays have two or three canals per ray. Bamford & Pickford (2021) described a wood that resembles to Sorindeia, named Sorindeioxylon from Mazamba Formation, Mozambique, it has banded and aliform axial parenchyma, and lacks radial canals. Finally, Wheeler & Manchester (2021) described a wood that resembles the genus Pistacia, from the lower part of John Day Formation, Post Hammer locality, Crook County, Oregon, USA. Pistacia terrazaseae has clusters common, helical thickenings in vessel elements, and non-septate fibers (Wheeler & Manchester 2021).

Several anacardiaceous fossil woods have been described from different geological epochs in the world. Some features such as the occurrence of distinct growth ring boundaries, axial parenchyma pattern or ray composition, and radial canals, differ the two woods reported herein (*e.g.*, Kruse 1954, Awasthi 1966, Poole & Davies 2001, Wheeler & Manchester 2002, Martínez-Cabrera & Cevallos-Ferriz 2004, Gregory *et al.* 2009, Rodríguez-Reyes *et al.* 2021). In Table 2 we compare the new genus fossil described herein with other selected taxa resulting from several searches in the IWD and a review of the wood anatomical literature.

The occurrence of this new genus of fossil wood from the upper Eocene of northern Mexico reinforces the hypothesis that during the middle-late Eocene several biological and geological events occurred, such as the migration of some groups of plants to the Neotropics via Boreotropical bridges between the continents, which facilitated the dispersal of various groups of plants (Week *et al.* 2014, Rodríguez-Reyes *et al.* 2021). This Eocene biotic exchange between North America, Europe and Asia is documented by the fossil record of different plant families, *e.g.*, Fabaceae (Martínez Millán 2000, Ramírez & Cevallos-Ferriz 2002, Estrada-Ruiz *et al.* 2010, Pérez-Lara *et al.* 2019). The diversity of the fossil record of the Anacardiaceae during the Eocene in North America (including Mexico) suggests that this area was one of the centers of diversification for the family.

Conclusions

The low latitudes of North America (Mexico and Central America) have been suggested to be an important area in the history and evolution of some anacardiaceous taxa (Martínez Millán 2000, Ramírez & Cevallos-Ferriz 2002), since several fossil taxa of Anacardiaceae have been reported in Mexican Neogene and Paleogene sediments based on leaves and wood (Ramírez Garduño 1996, Pérez-Lara et al. 2017). Furthermore, the fossil record of the family in the area extends back to the Cretaceous (Martínez Millán 2000, Estrada-Ruiz et al. 2010). The presence of these two new fossil species from the late Eocene of northern Mexico provides more evidence and reinforces the hypothesis that various biological, geological, and climatic events occurred during the middle-late Eocene. The occurrence of this family in the late Eocene of Baja California Sur confirms its long geological history and importance in forests of the north of Mexico.

Acknowledgments

This research was funded by Secretaria de Investigación y Posgrado – Instituto Politécnico Nacional (20230153) grant to E.E.R. This work was improved with the comments of Elisabeth Wheeler and Steve Manchester, thank you very much.

References

- AGARWAL, A. 1988. Occurrence of *Bouea* in the Neyveli Lignite Deposits, India. *Geophytology* 18, 166–168.
- ÁLVAREZ ARELLANO, A., SCHWENNICKE, T., ROJAS SORIANO, H., ROMERO ROJAS, S.A. & DE DE LA O BURROLA, F. 1999. *Carta Geológica-Minera La Paz G12-10-11 Baja California Sur*. Servicio Geológico Mexicano (SGM).
- AWASTHI, N. 1966. Fossil woods of Anacardiaceae from the Tertiary of South India. *The Palaeobotanist 14*, 131–143. DOI 10.54991/jop.1965.728
- BAMFORD, M. & PICKFORD, M. 2021. Stratigraphy, chronology and palaeontology of the Tertiary rocks of the Cheringoma Plateau, Mozambique. *Fossil Imprint* 77, 187–213. DOI 10.37520/fi.2021.014
- BANDE, M.B. & KHATRI, S.K. 1980. Some more fossil woods from the Deccan Intertrappean beds of Mandla District, Madhya Pradesh, India. *Palaeontographica Abt. B 173*, 147–165.
- BELL, C.D., SOLTIS, D.E. & SOLTIS, P.S. 2010. The age and diversification of the angiosperms re-revisited. *American Journal* of Botany 97, 1296–1303. DOI 10.3732/ajb.0900346

- BIONDI, E. 1981. Arganioxylon sardum n. gen., n. sp., et Sclerocaryoxylon chiarugii n. gen., n. sp.: bois fossiles de Miocène de la Sardaigne (Italie). Review of Palaeobotany and Palynology 34, 301–320. DOI 10.1016/0034-6667(81)90047-6
- BOONCHAI, N. & MANCHESTER, S.R. 2012. Systematic affinities of early Eocene petrified woods from Big Sandy Reservoir, southwestern Wyoming. *International Journal of Plant Sciences 173*, 209–227. DOI 10.1086/663161
- BRETT, D.W. 1966. Fossil wood of Anacardiaceae from the British Eocene. *Palaeontology 9*, 360–364.
- CHENG, Y-M, MEHROTRA, R.C., JIN, Y-G., YANG, W. & LI, C-S. 2012. A new species of *Pistacioxylon* (Anacardiaceae) from the Miocene of Yunnan, China. *IAWA Journal 33*, 197–204. DOI 10.1163/22941932-90000089
- DEL RIO, C., TOSAL, A., KARA, E., MANCHESTER, S.R., HERRERA, F., COLLINSON, M.E. & DE FRANCESCHI, D. 2023. Fruits of Anacardiaceae from the Paleogene of the Paris Basin, France. *International Journal of Plant Sciences 184*, 164–176. DOI 10.1086/723841
- ESTRADA-RUIZ, E., MARTÍNEZ-CABRERA, H.I. & CEVALLOS-FERRIZ, S.R.S. 2010. Upper Cretaceous woods from the Olmos Formation (Late Campanian-Early Maastrichtian), Coahuila, Mexico. *American Journal of Botany 97*, 1179–1194. DOI 10.3732/ajb.0900234
- FRANCO, M.J. 2009. Leños fósiles de Anacardiaceae en la Formación Ituzaingó (Plioceno-Pleistoceno), Toma Vieja, Paraná, Entre Ríos, Argentina. *Amerghiniana 46*, 587–604.
- FRANCO, M.J., MOYA, E., BREA, M. & MARTÍNEZ, C.M. 2020. Astroniumxylon, Schinopsixylon, and Parametopioxylon n. gen. fossil woods from the upper Cenozoic of Argentina: taxonomic revision, new taxon and new records. Journal of Paleontology 94, 185–201. DOI 10.1017/jpa.2019.97
- GHOSH, P.K. & ROY, S.K. 1979. Fossil wood of *Dracontomelum* from the Tertiary of West Bengal, India. *Current Science* 48, 362.
- GONZÁLEZ-BARBA, G., SCHWENNICKE, T., GOEDERT, J. & BARNES, L.G. 2002. Earliest record of the Pelagornithidae (Aves: Pelecaniformes) from the Pacific Basin. *Journal of Vertebrate Paleontology 23*, 722–725.
 - DOI 10.1671/0272-4634(2002)022[0722:EPBROT]2.0.CO;2
- GREGORY, M., POOLE, I. & WHEELER, E.A. 2009. Fossil dicot wood names: an annotated list with full bibliography. *IAWA Journal*, *Suppl.* 6, 220.
- HASS, H. & ROWE, N.P. 1999. Thin sections and wafering, 76–81. In JONES, T.P. & ROWE, N.P. (eds) Fossil Plants and Spores: Modern Techniques. Geological Society of London.
- HAUSBACK, B.P. 1984. Cenozoic volcanic and tectonic evolution of Baja California Sur, Mexico, 219–236. In FRIZELL, V.A. JR. (ed.) Geology of the Baja California Peninsula. Pacific Section, Society of Economic Paleontologists and Mineralogists, California.
- IAWA COMMITTEE. 1989. IAWA List of Microscopic Features for Hardwood Identification. IAWA Bulletin new series 10, 219–332.
- INSIDEWOOD 2004–onwards. *Biblioteca virtual*. Accessed January 10th 2020. *http://insidewood.lib.ncsu. edu/search*

KRIBS, D.A. 1935. Salient lines of structural specialization in the

wood rays of dicotyledons. *Botanical Gazette 96*, 547–557. DOI 10.1086/334500

- KRUSE, H.O. 1954. Some Eocene dicotyledonous woods from Eden Valley, Wyoming. *The Ohio Journal of Science 54*, 243–268.
- MABBERLEY, D.J. 2008. Mabberley's plant-book: a portable dictionary of plants, their classification and uses. 3rd Edition. 1040 pp. Cambridge University Press, Cambridge.
- MANCHESTER, S.R. 1977. Wood of *Tapirira* (Anacardiaceae) from the Paleogene Clarno Formation of Oregon. *Review of Palaeobotany and Palynology 23*, 119–127. DOI 10.1016/0034-6667(77)90020-3
- MARTÍNEZ-CABRERA, H.I. & CEVALLOS-FERRIZ, S.R.S. 2004. A new species of *Tapirira* from Early Miocene sediments of the El Cien Formation, Baja California. *IAWA Journal 25*, 103–117. DOI 10.1163/22941932-90000353
- MARTÍNEZ-CABRERA, H.I., CEVALLOS-FERRIZ, S.R. & POOLE, I. 2006. Fossil woods from early Miocene sediments of the El Cien Formation, Baja California Sur, Mexico. *Review of Palaeobotany and Palynology 138(3–4)*, 141–163. DOI 10.1016/j.revpalbo.2006.01.001
- MARTINEZ-ELIZALDE, K.S., JIMENEZ-ESTRADA, M., FLORES, C.M., HERNANDEZ, L.B., ROSAS-LOPEZ, R., DURAN-DIAZ, A., NIETO-YAÑEZ, O.J., BARBOSA, E., RODRIGUEZ-MONROY, M.A.
 & CANALES-MARTINEZ, M. 2015. Evaluation of the medicinal properties of *Cyrtocarpa procera* Kunth fruit extracts. *BMC Complementary and Alternative Medicine 15*, 1–7. DOI 10.1186/s12906-015-0602-y
- MARTÍNEZ MILLÁN, M. 2000. *Biogeografia historica (Terciario* y Cuaternario) de Anacardiaceae con base en caracteres anatómicos de la madera. 72 pp. Bachelor thesis, Universidad Nacional Autónoma de México, Facultad de Ciencias, México.
- MARTÍNEZ-MILLÁN, M. & CEVALLOS-FERRIZ, S.R.S. 2005. Arquitectura foliar de Anacardiaceae. Revista Mexicana de Biodiversidad 76, 137–190. DOI 10.22201/ib.20078706e.2005.002.308
- MÉNDEZ-CÁRDENAS, J.P., CEVALLOS-FERRIZ, S.R.S., CALVILLO-CANADELL, L., RODRÍGUEZ-YAMA, G.A., BORJA, A.M. & MARTÍNEZ-CABRERA, H.I. 2014. Loxopterygium wood in Coayuca de Andrade, Oligocene of Puebla, Mexico. Review of Palaeobotany and Palynology 207, 38–43. DOI 10.1016/j.revpalbo.2014.04.004
- MIRANDA, F. 1963. Two plants from the amber of Simojovel, Chiapas, Mexico, area. *Journal of Paleontology* 37, 611–614.
- MORALES-ORTEGA, P. & GONZÁLEZ-BARBA, G. 2018. Gasterópodos marinos de la Formación Tepetate, Baja California Sur, México. *Paleontología Mexicana* 7, 101–117.
- MORALES-ORTEGA, P., GONZÁLEZ BARBA, G., NAVA SANCHES, E. & VERA DIMAS, D. 2015. New early Eocene echinoids from Baja California Sur, Mexico. *Paleontologia Mexicana 4*, 43–54.
- PELL, S.K., MITCHELL, J.D., LOBOVA, T. & MILLER, A.J. 2010. Anacardiaceae, 7–50. In KUBITZKI, K. (ed.) Flowering Plants. Eudicots. The Families and Genera of Vascular Plants, vol. 10. Springer, New York. DOI 10.1007/978-3-642-14397-7 3
- PÉREZ-LARA, D.K., CASTAÑEDA-POSADAS, C. & ESTRADA-RUIZ, E.

2017. A new genus of Anacardiaceae fossil wood from El Bosque Formation (Eocene), Chiapas, Mexico. *IAWA Journal 38*, 543–552. DOI 10.1163/22941932-20170179

- PÉREZ-LARA, D.K., ESTRADA-RUIZ, E. & CASTANEDA-POSADAS, C. 2019. New fossil woods of Fabaceae from El Bosque Formation (Eocene), Chiapas, Mexico. Journal of South American Earth Sciences 94, 102202. DOI 10.1016/j.jsames.2019.05.018
- POOLE, I. & DAVIES, C. 2001. *Glutoxylon* Chowdhury (Anacardiaceae): the first record of fossil wood from Bangladesh. *Review of Palaeobotany and Palynology 113*, 261–272. DOI 10.1016/S0034-6667(00)00063-4
- PRAKASH, U. & AWASTHI, N. 1969. Fossil woods from the Tertiary of eastern India 1. *The Palaeobotanist 18*, 32–44. DOI 10.54991/jop.1969.816
- PRAKASH, U. & DAYAL, R. 1964. Fossil wood resembling Semecarpus from the Deccan Intertrappean beds of Mahurzari near Nagpur. *The Palaeobotanist 13*, 158–162. DOI 10.54991/jop.1964.693
- PRAKASH, U. & TRIPATHI, P.P. 1969. On *Glutoxylon burmense* from Hailakandi in Assam with critical remarks on the fossil woods of *Glutoxylon* Chowdhury. *The Palaeobotanist 17*, 59–64. DOI 10.54991/jop.1968.780
- PUJANA, R. 2009. Fossil woods from the Oligocene of southwestern Patagonia (Río Leona Formation). Atherospermataceae, Myrtaceae, Leguminosae and Anacardiaceae. *Ameghiniana* 46, 523–535.
- RAMÍREZ-GARDUÑO, J.L. 1996. Análisis foliar de plantas del Terciario, Tepexi de Rodríguez, Puebla: Pseudosmodingium (Anacardiaceae). Master thesis, Universidad Nacional Autónoma de México, FES Zaragoza, México.
- RAMÍREZ, J.L. & CEVALLOS-FERRIZ, S.R.S. 2002. A diverse assemblage of Anacardiaceae from Oligocene sediments, Tepexi de Rodríguez, Puebla, Mexico. *American Journal of Botany 89*, 535–545. DOI 10.3732/ajb.89.3.535
- RAMÍREZ, J.L., CEVALLOS-FERRIZ, S.R.S. & SILVA PINEDA, A. 2000. Reconstruction of the leaves of two new species of *Pseudosmodingium* from Oligocene strata of Puebla, Mexico. *International Journal of Plant Sciences* 161, 509–519. DOI 10.1086/314261
- RODRÍGUEZ-REYES, O.J. & ESTRADA-RUIZ, E. 2020. Two new reports of ancient rainforest trees from the Azuero Peninsula, Panama. *Ameghiniana* 57, 209–218. DOI 10.5710/AMGH.22.02.2020.3299
- RODRÍGUEZ-REYES, O.J., ESTRADA-RUIZ, E. & GASSON, P. 2020. Evidence of large Anacardiaceae trees from the Oligocene– early Miocene Santiago Formation, Azuero, Panama. *Boletín de la Sociedad Geológica Mexicana 72(2)*, a300719. DOI 10.18268/BSGM2020v72n2a300719
- RODRÍGUEZ-REYES, O., ESTRADA-RUIZ, E., MONJE DUSSÁN, C., BRITO, L.A. & TERRAZAS, T. 2021. A new Oligocene-Miocene tree from Panama and historical *Anacardium* migration patterns. *PLoS ONE 16(6)*, e0250721. DOI 10.1371/journal.pone.0250721
- Roy, S.K. & GHOSH, P.K. 1981. Fossil woods of Anacardiaceae from the Tertiary of west Bengal, India: *The Palaeobotanist* 28, 338–352. DOI 10.54991/jop.1981.1422

- SCHWEITZER, C.E., FELDMANN, R.M., GONZÁLEZ-BARBA, G. & VEGA, F.J. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *Journal of Paleontology 76*, 1–43. DOI 10.1666/0022-3360(2002)76[1:NCFTEA]2.0.CO;2
- SCHWEITZER, C.E., GONZÁLEZ-BARBA, G., FELDMANN, R.M. & WAUGH, D.A. 2005. Decapoda (Thalassinidae, Paguroidea) from the Eocene Bateque and Tepetate Formations, Baja California Sur, México: Systematics, cuticle microstructure, and Paleoecology. *Annals of the Carnegie Museum 74*, 275–293.
 - DOI 10.2992/0097-4463(2005)74[275:DTAPFT]2.0.CO;2
- SCHWEITZER, C.E., FELDMANN, R.M., GONZÁLEZ-BARBA, G. & ĆOSOVIC, V. 2006. New Decapoda (Anomura, Brachyura) from the Eocene Bateque and Tepetate Formations, Baja California Sur, México. Bulletin of the Mizunami Fossil Museum 33, 21–45.
- SELMEIER, A. 2000. A silicified Pistacia wood, Anacardiaceae, from the Upper Miocene of southern Franconian Alb, Germany. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie 40*, 201–212.
- TERRAZAS, T. 1994. Wood anatomy of the Anacardiaceae: ecological and phylogenetic interpretation. Ph.D. thesis, Department of Biology, University of North Carolina, Chapel Hill, N.C.
- WEEK, A., ZAPATA, F., PELL, S.K., DALY, D.C., MITCHELL, J.D. & FINE, P.V.A. 2014. To move or to evolve: contrasting patterns of intercontinental connectivity and climatic niche evolution in "Terebinthaceae" (Anacardiaceae and Burseraceae). *Frontiers in Genetics* 5, 409. DOI 10.3389/fgene.2014.00409
- WHEELER, E.A. 1986. Vessels Per Square Millimetre or Vessel Groups Per Square Millimetre? *IAWA Journal* 7, 73–74. DOI 10.1163/22941932-90000444
- WHEELER, E.A. 2011. InsideWood a web resource for hardwood anatomy. *IAWA Journal 32(2)*,199–211. DOI 10.1163/22941932-90000051
- WHEELER, E.A. & MANCHESTER S.R. 2002. Woods of the Eocene Nut Beds flora, Clarno Formation, Oregon, USA. *IAWA Journal*, *Suppl.* 3.
- WHEELER, E.A. & MANCHESTER, S.R. 2021. A diverse assemblage of Late Eocene woods from Oregon, western USA. *Fossil Imprint* 77, 299–329. DOI 10.37520/fi.2021.022
- WHEELER, E.A., SCOTT, R.A. & BARGHOORN, E.S. 1978. Fossil dicotyledonous woods from Yellowstone National Park. II. *Journal of the Arnold Arboretum 59*, 1–26. DOI 10.5962/p.185868
- WHEELER, E.A. SRIVASTAVA, R. MANCHESTER, S.R. & BAAS, P. 2017. Surprisingly modern. Latest Cretaceous–earliest Paleocene woods of India. *IAWA Journal 38*, 456–542. DOI 10.1163/22941932-20170174
- WHEELER, E.A., GASSON, P.E. & BAAS, P. 2020. Using the InsideWood web site: Potentials and pitfalls. *IAWA Journal* 41(4), 412–462. DOI 10.1163/22941932-bja10032
- WOODCOCK, D.W., MEYER, H.W. & PRADO, Y. 2017. The Piedra Chamana fossil woods (Eocene, Peru). *IAWA Journal 38*, 313–365. DOI 10.1163/22941932-20170175