Fossil woods from the Cenozoic of Panama (Azuero Peninsula) reveal an ancient neotropical rainforest

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Author contributions: NAJ described and identified the fossil woods, and carried out the analysis of anatomy and paleoclimate. JID designed, carried out, and interpreted the REE analysis.

ABSTRACT

Silicified woods from near the town of Ocú on the Azuero Peninsula, Panama were first reported by Stern and Eyde in 1963; however, the significance of these fossils has been largely overlooked. Well-characterized fossil floras from Central America can be used to test hypotheses related to the historical biogeography and paleoclimate of the Neotropics. We describe 10 new wood types and one palm based on 22 samples from Oligo-Miocene deposits. Affinities at the family/order level include Fabaceae, Lauraceae, Moraceae, Sapotaceae, Euphorbiaceae, Arecaceae, Sapindales, Ericales, and Humiriaceae. The fossil woods are fragmentary and have not been found in-place, but the size and angularity of the specimens suggests minimal transport from the site of growth. We compared these woods with calcareous woods from the Lower Miocene Cucaracha Formation and silicified woods from the upper Miocene Alajuela Formation using Rare Earth Element (REE) analysis to test the hypothesis that the Ocú woods were preserved under uniform conditions and not reworked. Although the results were ambiguous with respect to the original hypothesis, we note that the REE concentrations in silicified woods are much lower than in calcareous woods. We used comparative analysis of wood anatomical features to draw conclusions about the paleoclimate from the fossil flora. All the dicot woods are diffuse porous and none have distinct growth rings; some have very wide vessels at low frequencies. These features are typical of canopy trees in tropical lowland forests. Nonmetric multidimensional scaling of wood anatomical characters from a variety of communities and ecological categories showed that the anatomy of the Ocú woods is most similar to that found in tropical rainforests. Based on the combination of taxonomic identity and functional anatomy, we interpret these fossils as evidence for humid to perhumid megathermal climate in Panama during the late Paleogene-early Neogene.

Keywords: Central America, fossil wood anatomy, Rare Earth Elements, tropical rainforest, Lauraceae; Moraceae; Ficus.
INTRODUCTION

The tropical forests of Panama boast exceptionally high biodiversity in a relatively small and geologically young area (Myers et al. 2000; Phillips et al. 2002; Francis & Currie 2003). Recent studies indicate the presence of an island arc between North and South America since at least the Eocene until the final closure of the Central American seaway during the Pliocene (Iturralde-Vinent 2006; Buchs et al. 2011; Montes et al. 2012; Ramírez et al. 2016). Paleobotanical data indicate that these islands were colonized via long-distance dispersal primarily from South America, with little input from Asia and North America (Berry 1918; Graham 1985; Kolarsky et al. 1995; Graham 1999, 2010; Herrera et al. 2012). Fossils from the Panama Canal area indicate that by the early Miocene much of Panama was part of a peninsula connected to North America, but the flora was already dominated by primarily South American tropical plants (Graham 2010; Farris et al. 2011; Jaramillo et al. 2014; MacFadden et al. 2014; Bloch et al. 2016).

In 1963, Stern and Eyde called attention to the abundance of silicified wood fossils in the northern part of the Azuero Peninsula, Panama. They noted the excellent quality of preservation and provided preliminary identifications for three of the wood types: Vantanea Aubl. (Humiriaceae), Tetrathyllum Poepp. & Endl. (formerly Flacourtia-ceae, now Salicaceae), and Hernandia L. (Hernandiaceae). The Vantanea-like wood was recently described as *Humiriaceoxylon ocuense* Herrera, Manchester, Vélez-Juarbe et Jaramillo (2014). The rest of this remarkable wood assemblage has remained undescribed and the potential significance of these fossils for understanding both Central American floristic diversity and Central American paleoclimate has been largely overlooked.

The purpose of this work is to describe the diversity of plants from the fossil wood assemblage reported by Stern and Eyde, discuss what is known of the geological context of the fossils, and to draw conclusions about the paleoclimate based on wood anatomy and systematics. First, we describe and identify ten dicot wood types and one palm from two collections. Several of these identifications are first occurrences in Panama that may be important for researchers tracing the history of extant angiosperm families or genera. Two undetermined wood types are included here because they contribute to the richness of the collection and provide paleoclimate information. They may be identifiable in the future with additional research and we suggest possible affinities. We also used rare earth element analysis to test the hypothesis that the woods were not extensively transported or reworked. Finally, we assert that these plants grew under tropical wet to perhumid conditions and thus represent one of Panama’s earliest rainforests based on wood physiognomy, geography, and paleoclimate evidence.

MATERIALS AND METHODS

**Geologic setting**

The woods are preserved as silica permineralizations. They commonly occur as float in pastures and gullies in the northern part of the Azuero Peninsula, north of the Ocú-Parita Fault Zone (Fig. 1). Five of the specimens examined here were collected from the topsoil at the edge of a plowed farm field without evidence of the parental rock (UF
locality 606), and the other 17 are part of a collection purchased from a nearby shop that sells building stone (UF locality 604), but they were all collected from the same area (Herrera et al. 2014). Locality details available from the Museum of Natural History at the University of Florida (UF). The co-occurrence of large (up to 50 cm diameter) and small woods, as well as their angularity, suggest autochthonous to parautochthonous preservation; the assemblage is likely dominated by local plants.

The fossil woods come from either the Tonosí Formation (Fm.) or the Santiago Fm. (sometimes referred to as the Macaracas Fm.) and fieldwork to address this question is ongoing. The Tonosí Fm. consists of widespread marine and non-marine sedimentary rocks thought to be of Middle Eocene-early Miocene age (Terry 1956; Kolarsky et al. 1995; Buchs et al. 2011). It crops out in the northern part of the Azuero Peninsula near the towns of Ocú and Macaracas, and in the southern part of the peninsula northeast of the Azuero-Zona fault. Kolarsky et al. (1995) subdivided the Tonosí into a lower unit (LTF) and an upper unit (UTF). The LTF is comprised of conglomerates and sandstones partly intercalated with minor coal seams and reefal limestone and was considered Middle Eocene to Upper Oligocene. The UTF consists of interbedded sandstone, siltstone, shale and calcarenites and was considered Upper Oligocene to Lower Miocene (Kolarsky et al. 1995; Krawinkel et al. 1999). In the central and northern parts of the Azuero peninsula, near the towns of Santiago and Macaracas, the Santiago Fm. overlies the Tonosí Fm. and is thought to be Miocene (Kolarsky et al. 1995; Krawinkel et al. 1999; Buchs et al. 2011). Kolarsky et al. (1995) reported samples of pollen, foraminifera, and nanofossils from the Santiago Fm. in central Azuero and concluded that they support a late Oligocene to early Miocene age. Stern and Eyde (1963) reported that the Ocú woods are associated with tuffs, which may be the source of the silica (Murata 1940) that were mapped as Eocene-Oligocene by Terry (1956).

**Fossil preparation**

The wood types (including the palm) described below were identified from 22 hand samples. Thin sections of the silicified woods were prepared using standard thin-sectioning techniques (Haas & Rowe 1999). Minimum axis diameter estimates were obtained from radius estimates taken from the fossil specimens viewed in transverse section. Polished transverse, radial, and tangential faces of the fossils were mounted onto slides using epoxy, which were then ground down to ~30 μm thick wafers. Canada Balsam and cover slips were applied and the slides were examined using light microscopy. The descriptions, measurements and terminology follow the guidelines
described in the IAWA Hardwood List (IAWA Committee 1989), with quantitative features based on 25 measurements unless otherwise noted. Images of microscopic features were captured with a Canon EOS digital camera mounted on a Nikon compound microscope and were processed with Adobe Photoshop (San Jose, California, USA). The specimens and slides are housed at the Florida Museum of Natural History Paleobotanical Collections, Gainesville, FL, USA. The fossil woods were first compared with the available descriptions and images in Metcalfe & Chalk (1950) and InsideWood (InsideWood 2004-onwards; Wheeler 2011). Once the woods were identified to order or family, additional literature was used to examine differences in the wood anatomy within those groups. When a fossil wood has a suite of anatomical features characteristic of an extant genus, we assign it to that genus with the knowledge that this approach could underestimate the number of extinct genera because the other parts of the plant might not correspond to an extant genus. In the two cases where we were unable to determine the ordinal or familial affinities of the wood, we describe the woods using an informal designation following the approach of Page (1979, 1980, 1981). Systematic descriptions are organized following a linear sequence of angiosperm families (Haston et al. 2009).

**Rare Earth Element analysis**

Rare Earth Element (REE) signatures obtained from fossils are thought to be controlled by the early diagenetic environment (Trueman 1999). If this holds for woods, then fossil woods mineralized in different early diagenetic environments may be distinguished by their REE signatures. Similarly, assemblages composed of fossils from a variety of early diagenetic environments should have more variation in REE signatures than autochthonous to paraautochthonous assemblages that have not been reworked. However, we note that whereas the rare earth element profiles of vertebrate and invertebrate fossils have been the subject of many studies, fossil woods have seldom been subject to this method (Sigleo 1979; MacFadden et al. 2017). Nonetheless, to test the hypothesis that REE signatures can be used to distinguish groups of fossil woods from the Miocene of Panama based on early diagenetic environmental conditions, we drilled samples of woods to obtain ~0.1 g of powder each using a heavy-duty flex shaft grinder. Fossil wood samples were selected from the Miocene Cucaracha and Alajuela Formations in the Panama Canal area. The fossil woods from the Cucaracha Fm. are calcareous and considered paraautochthonous, whereas those from the Alajuela Fm. are silicified and considered allochthonous and likely reworked (MacFadden et al. 2017). We used a carbide bit for the calcareous permineralizations from the Cucaracha Fm.; for the silicified woods from Ocú and Alajuela we used sintered diamond bits and ran the drill at low velocities to minimize contamination from the bit material. For each sample, we drilled ~0.1 g of fine powder. All collected powders were weighed out and digested in Teflon vials for preparation. Different acids were used according to the sample compositions. Cucaracha woods were digested using 8M HNO₃ (50%), whereas silica-bearing samples (i.e. Alajuela and Ocú woods) required 50% HF + HNO₃ for digestion. 30% H₂O₂ was used in conjunction with HNO₃ to remove heavy organic content found in Cucaracha woods. All vials were then capped and heated at 120 °C for
24 hours to reflux, and then again for another 24 hours uncapped until dried. Samples were then spiked with acid (5% HNO\textsubscript{3} + 8 ppm Re-Rh + 150 ppm HF) and placed uncapped on a hotplate to be reheated at 120 °C for another 24-hour period. Samples were brought to 2000 ppm ± 200 ppm for the final dilution using 3 mL of 5% HNO\textsubscript{3} Re-Rh spike solution and the appropriate volume of sample before analysis. A Thermo Scientific Element Inductively Coupled Plasma-Mass Spectrometer (ICP-MS) at the Department of Geological Sciences of the University of Florida (UF) was used to carry out the analysis.

**Nonmetric multidimensional scaling**

Martínez-Cabrera and Cevallos-Ferriz (2008) used Principle Components Analysis (PCA) to identify modern analogs for fossil wood assemblages and drew conclusions about paleoclimate. This approach depends on the assumption that plants growing in similar environments exhibit more anatomical similarity than plants growing in different environments, but does not distinguish between similarity from convergent evolution or shared ancestry. This assumption of similarity may be met through shared ancestry, environmental filtering, evolutionary convergence, or a combination of these factors. We elected to analyze the same data using Nonmetric Multidimensional Scaling (NMDS) in two dimensions rather than regression equations (e.g. Wiemann et al. 1999) to estimate paleoclimate because variation in wood anatomical characters is not independent of phylogeny. We chose NMDS, which maximizes rank-order correlation, rather than PCA because some of the response variables have null values. The analysis was run on a natural-log transformed matrix of eight wood anatomical characters and 17 floras: six tropical mesic communities from Central America, 10 ecological categories from the Southern California flora (Carlquist & Hoekman 1985; Martínez-Cabrera & Cevallos-Ferriz 2008), and the Ocú assemblage. We omitted the ‘mean mesomorphy’ variable used by Martínez-Cabrera & Cevallos-Ferriz (2008) because it is calculated from variables already included in the data (vessel diameter, vessel frequency, and vessel element length). We used RStudio Version 0.99.902 for the data analyses (RStudio Team 2015), and carried out the NMDS analysis using the R package vegan version 2.4-0 (Oksanen et al. 2008).

**RESULTS**

**Systematics**

Family – Lauraceae Jussieu, 1789.

Genus – *Beilschmiedia* Nees, 1831.

Species – *Beilschmiedia oleifera* Jud, sp. nov. (Fig. 2).

Specific diagnosis – Growth rings indistinct, marked by narrow bands of parenchyma, wood diffuse porous; vessels solitary and in multiple radials of 2–3, perforation plates simple, vessel elements short; intervessel pitting alternate, vessel-parenchyma pits large with reduced borders; rays 1–4-seriate, composed of procumbent body cells and one row of marginal upright cells; fibers thin- to thick-walled; oil cells among the fibers and axial parenchyma; axial parenchyma paratracheal, winged aliform to confluent.
Figure 2. *Beilschmiedia oleifera* Jud, *sp. nov.* (UF604-54272). – A: Diffuse porous wood with vessels solitary and in short radial multiples, winged-aliform axial parenchyma, and an indistinct growth ring boundary marked by a marginal parenchyma band, transverse section (XS). – B: Idioblasts associated with paratracheal parenchyma (at arrow), XS. – C: Alternate, polygonal intervessel pitting, tangential longitudinal section (TLS). – D: Vessel-axial parenchyma pits with reduced borders (at arrows), radial longitudinal section (RLS). – E: Ray with procumbent body cells and rows of upright marginal cells (at arrows), RLS. – F: Elongate idioblasts with dark contents, RLS. – G: Vessel elements with simple perforation plates at left and narrow rays, TLS. – H: 1–3-seriate rays, TLS. – I: Elongate idioblast with dark contents in tangential section, TLS. — Scale bars: A, G = 200 µm; B, H = 100 µm; C, D, F, I = 40 µm; E = 120 µm.
Holotype – UF604-54272.

Etymology – The specific epithet oleifera refers to the high frequency of diffuse idioblasts interpreted as oil cells throughout the fossil wood.

Description – Fragment of mature wood with nearly parallel rays and diameter of ≥ 20 cm. The wood is diffuse porous (Fig. 2A). Growth rings are indistinct, marked by narrow bands of parenchyma (Fig. 2A,B). Vessels are solitary (74%) and in radial multiples of 2–3 (Fig. 2A,B). Solitary vessels are oval in outline (Fig. 2A,B). Tangential vessel diameters are narrow to medium: 80–170 µm (mean = 116 µm; SD = 25), vessel frequency is very low: 2.8–4.1 mm⁻² (mean = 3.6; SD = 0.55; n = 5), and vessel element length short: 144–369 µm (mean = 258; SD = 54). Perforation plates are simple and oblique (Fig. 2C,G). Intervessel pits are alternate, polygonal, and medium to large: 8–12 µm (Fig. 2C). Vessel-parenchyma pits large, with reduced borders, and rounded (Fig. 2D). Thin-walled tyloses are present but rare. Fibers are thin- to thick-walled (Fig. 2B), pitting not observed, septae not clear. Axial parenchyma is paratracheal winged-aliform to confluent (Fig. 2A,B) with four cells per strand. Rays are 1–4-seriate (mean = 2.7) (Fig. 2H) and composed of predominantly procumbent body cells with 1 row of taller procumbent or upright marginal cells (Fig. 2E). Ray frequency is medium: 6–11 mm⁻¹ (mean = 8; SD = 2.0; n = 5) and ray height is generally less than 1 mm (range = 132–1009 µm; mean = 381 µm; SD = 184) (Fig. 2H). Elongate, ovoid idioblasts with dark contents are present in the axial system among fibers and axial parenchyma, at a frequency of ~16.5 mm⁻² (Fig. 2A,B,F,I). Enlarged idioblasts 51 µm (35–70 µm) in tangential diameter, 74 µm (45–115 µm) in radial diameter, and 272 µm (170–375 µm) high (n = 10). Unambiguous crystals or silica deposits were not observed, but small silica particles may be present in the ray cells. Storied structure is absent.

Remarks – The idioblasts among the fibers and axial parenchyma that typically have dark contents are likely oil cells. Oil cells in the wood is a common feature among the magnoliid angiosperms. In combination with large alternate intervessel pits, vessel-ray parenchyma pits with reduced borders, aliform to winged-aliform paratracheal parenchyma, and multisierate heterocellular rays, the oil cells suggest an affinity with Lauraceae or Hernandia L. (Hernandiaceae) (Metcalfe & Chalk 1950; Stern 1954; Shutts 1960). However, an affinity with Hernandia is unlikely for this fossil because in Hernandia the rays are composed of exclusively procumbent ray cells (although occasionally with taller, but still procumbent cells at the ray margins), and the fibers are generally thin-walled. By contrast, the rays in the fossil are heterocellular with upright marginal cells and the fibers are moderately thick-walled, as in many Lauraceae.

Among the Lauraceae Aniba Aubl., Beilschmiedia, Cinnamomum Schaeff., and Eusideroxylon Teijsm & Binn. (Stern 1954; Richter 1981; Dupéron-Laudoueneix & Dupéron 2005) have wood anatomy like this fossil; however, Cinnamomum species lack marginal parenchyma bands and frequently have scalariform perforation plates in addition to simple perforation plates, Aniba often has idioblasts at the ray margins, and Eusideroxylon is endemic to Borneo and has idioblasts only associated with the axial parenchyma and generally at a lower frequency. We searched InsideWood with 0 allowable mismatches for the characters diffuse porous; evenly dispersed vessels solitary and in short radial multiples; perforation plates exclusively simple; alternate
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pits not minute-small; vessel ray pits not similar to intervessel pits; less than 20 vessels mm⁻²; fibers with simple pits and thin to medium thick walls, winged aliform axial parenchyma; rays narrow multiseriate, less than 1 mm high, and with one marginal row of upright cells, storied structure absent, oil cells present with axial parenchyma and amongst fibers (5p 6a 7a 8a 9a 10a 11a 12a 13p 14a 22p 24a 25a 30a 48a 49a 50a 61p 69p 80p 82p 96a 99a 102a 106p 118a 120a 125p 126p). This search yielded only the genus *Beilschmiedia*.

Woods assigned to the Lauraceae are common in the fossil record. Several genera have been established for lauraceous fossil woods, and we accept nine of the names that have been proposed (Jud et al. 2017). The fossil wood described here is most like *Beilschmiedioxylon* Dupéron-Laudoueneix & Dupéron, but can be distinguished from the type by the presence of rays with only one row of upright cells at the ray margins, the abundance of aliform axial parenchyma, a higher proportion of solitary vessels (74% vs. 57%), and somewhat more frequent idioblasts (10–13 mm⁻² vs. 4–9 mm⁻²). The features of both woods fall within the range of variation seen in extant *Beilschmiedia* (Richter 1981; Dupéron-Laudoueneix & Dupéron 2005). There may be some other species of *Laurinoxylon* that conform to the morphology of *Beilschmiedia* or *Beilschmiedioxylon*, but a review of that fossil genus is beyond the scope of this work. Dupéron-Laudoueneix and Dupéron (2005) noted that some of the differences between *Beilschmiedia* and *Ocotea* are subtle and that the genera may be difficult to distinguish in some cases; however, this Ocú wood is more like *Beilschmiedia* than *Ocotea* in oil cell distribution and the presence of marginal parenchyma bands (Dupéron-Laudoueneix & Dupéron 2005). Although the Ocú wood could be considered a new species of *Beilschmiedioxylon*, we have assigned the fossil to the extant genus because the features in the fossil fall within the range of variation known for *Beilschmiedia* and not, to our knowledge, within the range of variation for other lauraceous genera.

Despite the thickness of the fiber walls and presence of upright marginal ray cells, this wood type may be the same as the one identified as *Hernandia* by Stern and Eyde (1963). Unfortunately, they did not designate a type or exemplar specimen and we were unable to locate the material on which the identification was based. Therefore, we were unable to evaluate this hypothesis at this time.

Family – Lauraceae Jussieu, 1789.


Species – *Laurinoxylon elongatum* Jud, sp. nov. (Fig. 3).

Specific diagnosis – Growth rings absent, wood diffuse porous; vessels solitary and in multiple radials of 2–4, perforation plates mixed–simple and scalariform with fewer than 10 bars, vessel elements very long, > 500 µm; intervessel pitting alternate, vessel-ray parenchyma pits large with reduced borders; rays 1–3-seriate, heterocellular, with oil cells in the rays; axial parenchyma scanty paratracheal.

Holotype – UF604-54275.

Etymology – This species is named for its long vessel elements.

Description – Fragment of mature wood with an estimated diameter of 12.6 cm.
The wood is diffuse porous (Fig. 3A). Growth rings are indistinct (Fig. 3A). Vessels are solitary (69%) and in radial multiples of 2–3. Solitary vessels are oval in transverse section (Fig. 3A). Vessel tangential diameters are medium: 103–188 μm (mean = 148 μm, SD = 23), vessel frequency is low to very low: 5.6–7.2 mm⁻² (mean = 6.3; SD = 0.6; n = 5), and vessel elements are long: 612–1090 μm (mean = 879; SD = 158; n = 12) (Fig. 3G). Both simple and scalariform perforation plates (4–6 bars) are present and oblique (Fig. 3E,F,G). Intervessel pits are alternate, polygonal, and medium (~6–10 μm) (Fig. 3C). Vessel-parenchyma pits are horizontally elongate and with reduced borders (Fig. 3D). Thin-walled tyloses are rare. Fibers are very thin- to thick-walled (Fig. 3B) and fiber septa likely present, but unclear (not figured); pitting not observed.

Figure 3. *Laurinoxylon elongatum* Jud, sp. nov. (UF604-54275). – A: Diffuse porous wood with vessels solitary and in short radial multiples, scanty paratracheal parenchyma, XS. – B: Thin-walled fibers and a radial multiple of three vessel elements, XS. – C: Alternate intervessel pitting, TLS. – D: Elongate vessel-parenchyma pits with reduced borders (upper arrow) and a single strand of axial parenchyma (lower arrowhead), RLS. – E: Simple perforation plate, RLS. – F: Scalariform perforation plate with four bars (at arrow), RLS. – G: Vessel elements (950 μm long) and idioblasts with dark contents (at arrow) in the rays, RLS. – H: Multiseriate heterocellular ray with large idioblasts in body of the ray (at arrow), TLS. — Scale bars: A = 400 μm; B, E, H = 100 μm, C = 25 μm, D = 40 μm; F = 25 μm; G = 250 μm.
on fiber walls. Axial parenchyma is scanty paratracheal (Fig. 3A). Rays are 1–3-seriate, heterocellular with procumbent and upright cells mixed throughout (either along the margins or in files in line with idioblasts), and with enlarged idioblasts (100 µm tall by 90 µm wide in RLS by 50 µm wide in TLS; n = 10) present in the ray bodies (Fig. 3G,H). Uniseriate rays are rare. Ray frequency is 6.3–8.1 mm⁻¹ (mean = 7.3 mm⁻¹; SD = 0.8; n = 5). Ray height is 304–1149 µm (mean = 635; SD = 25). Prismatic crystals were not observed. Storied structure is absent.

Remarks – The combination of diffuse porosity, both simple and scalariform perforation plates, large, alternate intervessel pits, vessel-ray parenchyma pits with reduced borders, scanty paratracheal parenchyma, narrow multisieriate heterocellular rays, and oil cells in the rays is diagnostic of Lauraceae (Metcalfe & Chalk 1950; Stern 1954; Richter & Metcalfe 1987; Dupérnon-Laudoueneix & Dupéron 2005). Although it is relatively easy to identify woods as Lauraceae, many genera have similar combinations of features (Edwards 1931; Metcalfe & Chalk 1950; Stern 1954; Richter 1981; Ogata et al. 2008; Boonchai & Manchester 2012).

Only a few of the lauraceous genera known from fossil woods include species with both simple and scalariform perforation plates (Dupéron-Laudoueneix & Dupéron 2005; Jud et al. 2017). These are Cinnamomoxylon Gottwald, Laurinoxylon Felix emend. Dupéron, Dupéron-Laudoueneix, Sakala & Franceschi, Paraperseoxylon Wheeler & Manchester and Sassafrasoxylon Brezinova & Süss (a genus of uncertain status, but certainly belonging to Lauraceae) (Dupéron-Laudoueneix & Dupéron 2005; Jud et al. 2017). The Ocú wood differs conspicuously from Paraperseoxylon because it has larger intervessel pits (6–10 vs. ~5 µm) and lacks idioblasts among the fibers, from Cinnamomoxylon because it has only scanty paratracheal parenchyma, and from Sassafrasoxylon because it is diffuse porous rather than ring-porous. The fossil most closely matches Laurinoxylon based on the combination of simple and scalariform perforation plates, heterocellular rays 1–5 cells wide, elongate vessel-ray parenchyma pits with reduced borders, scanty paratracheal parenchyma, and idioblasts (oil cells) among the ray cells (Unger 1847; Felix 1884; Dupéron et al. 2008).

Mantzouka et al. (2016) suggest a restricted definition of Laurinoxylon that excludes those species with elaborate conformations of axial parenchyma such as marginal or confluent axial parenchyma, with rays > 1 mm high, and those with ring porosity. Even in this restricted sense, this specimen conforms to Laurinoxylon. They also propose a system for grouping species of Laurinoxylon based on the distribution of oil cells. The Ocú wood has idioblasts only associated with the ray parenchyma cells and therefore belongs to the Laurinoxylon Type 1 group (Mantzouka et al. 2016). In comparison with other Laurinoxylon spp. assigned to this group, L. elongatum lacks growth rings and has wider vessels, lower vessel frequency, longer vessel elements, and larger idioblasts in the rays (Table 1). Extant genera with anatomy like Type 1 Laurinoxylon include Dicypellium Nees, Laurus L., Litsea Lam., Persea Mill., Systemonodaphne Mez, and Urbanodendron Mez (Mantzouka et al. 2016) which are common in the Americas.
### Table 1. Comparison of *Laurinoxylon* species with idioblasts primarily in the rays.

| Species            | Reference                  | GR | VG               | MTD    | VF | BAR | AP | RW | RH   | SF | Id   | GR = growth rings, + = present/distinct, - = absent/indistinct; VG = vessel grouping, Sol = solitary, rms = radial multiples, clus. = vessels in clusters; MTD = mean tangential diameter of vessels in micrometers, ranges in parenthesis; VF = vessel frequency per square millimeter; BAR = bars per perforation plate; AP = paratracheal axial parenchyma, 1 = scanty paratracheal, 2 = vasicentric, 3 = aliform, 4 = confluent; RW = ray width in cells; RH = ray height in micrometers unless otherwise indicated; SF = septate fibers; Id = Mean idioblast dimensions in micrometers, R = radial width, T = tangential width, Ht = height. |
|--------------------|----------------------------|----|-----------------|--------|----|-----|----|-----|------|----|------|
| *L. intermedium*   | Huard 1967                 | +/-| Sol (48%) & rms of 2–5 | (70–130) | 15–27 | 10–20 | 7  | 1–5 | 120–700 | -  | ?    |
| *L. litseoides*    | Süß & Mädel 1958          | +  | Sol & rms of 2–6 & clus.| 70 (30–125) | 35  | 0   | 1,2 | 1–4 | 100–470 | +  | R: 45 T: 28 Ht: 75 |
| *L. microtracheale*| Süß & Mädel 1958          | +  | Sol & rms of 2–6      | 45 (35–60) | 35  | 0   | 2   | 1–5 | 50–320 | +  | R: 35 T: 21 Ht: 65 |
| *L. oligocenicum*  | Prakash et al. 1974        | +  | Sol & rms of 2–4      | (70–190) | 10–14 | 0   | 1,2,3 | 1–3 | ?    | ?    |
| *L. nansangense*   | Lakhanpal et al. 1981      | -  | Sol & rms of 2–5      | 75–300 | 8–10 | unk | 1   | 1–3 | 5–22 cells | +  | ?    |
| *L. mueller-stolli*| Süß & Mädel 1958          | +/-| Sol & rms of 2–3     | ?    | ?   | 0/0 | 1   | 1–3 | NA    | +  | ?    |
| *L. elongatum sp. nov.* | this study               | -  | Sol (69%) & rms of 2–3 | 103–188 | 5.6–7.2 | 0/4–6 | 1   | 1–3 | 304–1149 | +  | R: 90 T: 50 Ht: 100 |

### Table 2. Comparison of *Andiroxylon* species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>GR</th>
<th>MTD</th>
<th>VF</th>
<th>PAP</th>
<th>BAP</th>
<th>RW</th>
<th>RH</th>
<th>MU</th>
<th>SF</th>
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<tbody>
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<td><em>A. thanobolensis</em></td>
<td>Khan et al. 2016</td>
<td>–</td>
<td>185–224</td>
<td>3–4</td>
<td>3,4,6</td>
<td>2</td>
<td>1–4</td>
<td>6–12</td>
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<td><em>A. cinnamoneus</em></td>
<td>Martínez-Cabrera et al. 2006</td>
<td>–</td>
<td>158 (120–225)</td>
<td>0–6</td>
<td>3,4,6</td>
<td>2</td>
<td>1–4</td>
<td>9–20</td>
<td>0–3</td>
<td>–</td>
<td>t, vt</td>
<td></td>
</tr>
<tr>
<td><em>A. barghornii sp. nov.</em></td>
<td>This study</td>
<td>–</td>
<td>207 (68–317)</td>
<td>3–6</td>
<td>3,4,6</td>
<td>2</td>
<td>1–2</td>
<td>10–32</td>
<td>1</td>
<td>?</td>
<td>vt</td>
<td></td>
</tr>
</tbody>
</table>

GR = growth rings, + = present/distinct, - = absent/indistinct; MTD = mean tangential diameter of vessels in micrometers, ranges in parenthesis; VF = vessel frequency per square millimeter; PAP = paratracheal axial parenchyma, 1 = scanty paratracheal, 2 = vasicentric, 3 = aliform, 4 = confluent; BAP = banded axial parenchyma, 1 = narrow bands (≤3 cells), 2 = wide bands (≥4 cells); RW = ray width in cells; RH = ray height in cells; MU = number of rows of marginal upright cells in multiseriate rays; SF = septate fibers; FW = fiber wall thickness, t = thick, vt = very thick.
Figure 4. *Palmoxylon* sp. (UF604-54282) – A: Cocos-type fibrovascular bundles and fibrous ground tissue. Note the fibrovascular bundles with cordata-type dorsal caps, two metaxylem elements, and occasional scalariform bars visible in the elements (at arrow), XS. – B: Elongate fibrovascular bundles toward the periphery of the stem. Note that one bundle is oriented opposite to the rest, XS. – C: Detail of smaller fibrovascular bundles near the stem center, XS. – D: Single fibrovascular bundle from near the central zone of the stem, XS. – E: Single fibrovascular bundle from the peripheral zone of the stem. Note the unusual state of three metaxylem elements, XS. – F: Oblique perforation plate with ~10 bars (at arrow), LS. – G: Scalariform thickenings on the metaxylem elements (at arrows), LS. — Scale bars: A = 1000 µm; B, C = 500 µm, D, E = 200 µm, F, G = 40 µm.
Family – Arecaceae Bercht. & J. Presl, 1820.
Genus – *Palmoxylon* Schenk, 1883.
Species – *Palmoxylon* sp. (Fig. 4).
Exemplar specimen – UF604-54282.
Other material – UF604-54277, UF606-56059.

Description – Fragment of a palm stem at least 14 cm diameter consisting of central zone and subcortical zone. The general pattern of fibrovascular bundles is *Cocos*-type (Fig. 4A–E). Non-vascular fibrous bundles in the central cylinder not present. The fibrovascular bundle (fvb) frequency increases from 33 cm⁻² in the central zone to 42 cm⁻² in the subcortical zone (Fig. 4B). Fvb size ranges from short and squat ($H_{\text{max}}$ 1.02 mm, $L_{\text{max}}$ 0.94 mm, $H_{\text{vasc}}$ 0.53 mm, $L_{\text{vasc}}$ 0.67 mm) to weakly radially elongate ($H_{\text{max}}$ 2.12 mm, $L_{\text{max}}$ 1.15 mm, $H_{\text{vasc}}$ 1.55 mm, $L_{\text{vasc}}$ 0.48 mm). The dorsal cap is cordata-type and the ratio of the area of the fibrous zone to the vascular zone in each bundle ranges from 1.3 near the center to 2.6 near the subcortical zone. The vascular zone is excluded from the fibrous zone and the auricular sinus is rounded. Vascular zones have two (rarely 3) metaxylem elements each; mean metaxylem element diameter is 134.5 µm (SD = 21.4) (Fig. 4E). Perforation plates are oblique and scalariform with ~10 bars (Fig. 4F). Metaxylem elements with scalariform thickenings (Fig. 4G). One phloem strand is present per fvb. Tabular, radiating and paravascular parenchyma present around the vascular zone of fvb’s. Thin ventral fiber cap present. The ground parenchyma is well preserved in the central zone and comprises compact isodiametric to triangular cells that are 192.2 µm (SD = 45.4) in transverse section.

Remarks – This plant most likely belongs to the tribe Sabaleae (Coryphoideae) based on the combination of *Cocos*-type anatomy (the low ratio of fibrous area to vascular area in in fvb’s, modest radial increase in fvb frequency, and absence of fibrous part centrifugal differentiation), 2 (rarely 3) metaxylem elements with oblique end-walls per fvb bundle, the reniforma to cordata shape of the fibrous part of each fvb, and the presence of only one phloem strand per fvb (Thomas 2011; Tomlinson *et al.* 2011; Thomas & De Franceschi 2013; Thomas & Boura 2015). A complete review of *Palmoxylon* species is beyond the scope of this study; however, these specimens differ from the only other fossil palm stem known from Panama, a specimen of *Palmoxylon pulmacites* (Sprengel) Stenzel identified by Berry (1918) from the lower Miocene Cucaracha Formation. That specimen has smaller and more tightly packed fibrovascular bundles with lunaria-type dorsal caps, and may represent tribe Borasseae (Coryphoideae) but needs more detailed re-evaluation.

Family – Fabaceae Lindl., 1836 (Leguminosae Juss. 1789).
Species – *Andiroxylon barghoornii* Jud, *sp. nov.* (Fig. 5).

Specific diagnosis – Diffuse porous wood with indistinct growth rings; vessels mostly solitary and in radial pairs, sporadically in multiples of three or four; perforation plates simple; intervessel pits alternate, medium, oval to polygonal in outline; vessel-ray parenchyma pits and vessel-axial parenchyma pits similar to intervessel pits; fibers non-septate, very thick walled; axial parenchyma aliform to banded, mostly confluent; paren-
chyma strands typically of 4 (3–6) cells; axial parenchyma, rays, and vessel elements vary from regularly storied to irregularly storied; rays heterocellular, predominantly 2–3 cells wide, uniseriate rays rare, ray body composed primarily of procumbent cells, but often with one row of marginal upright cells; axial canals absent.

Holotype – UF604-54270.

Additional material – UF604-54263, UF604-54266, UF604-54279, UF606-56056, UF606-56060.

Etymology – Named for Dr. Elso Barghoorn who identified some of the Ocú woods as legumes during a trip to Panama in 1963–1964 (Graham 1992).

Figure 5. *Andiroxylon barghoornii* Jud, sp. nov. (UF604-54263; 54266; 54270) – A: Diffuse porous wood with aliform-confluent paratracheal parenchyma. Note vessels solitary and in short radial multiples, XS (54270). – B: Aliform-confluent axial parenchyma, XS (54266). – C: Storied rays, axial parenchyma, vessel elements, and fibers, TLS (54270). – D: Alternate inter-vessel pitting, TLS (54263). – E: Axial parenchyma strands of four cells and 2–3-seriate rays, TLS (54263). – F: Ray with procumbent body cells and upright marginal cells (at arrows), RLS (54263). – G: Very thick-walled fibers at the top (at arrow), thin-walled parenchyma cells at the bottom, part of vessel in lower left, XS (54263). — Scale bars: A = 500 µm; B, C = 250 µm; D = 75 µm; E = 125 µm; F = 100 µm; G = 25 µm.
Description – This description is based on the holotype and five additional fragments of mature wood. The largest specimens come from trees with diameters of no less than 30 cm. Growth rings are indistinct, and the wood is diffuse porous (Fig. 5A). Vessels are mostly solitary (59%) and in radial pairs, sporadically in multiples of three or four. The solitary vessels are nearly circular or tangentially elongate rather than radially elongate (Fig. 5A, B). Vessel diameters are mostly wide to very wide: 68–317 µm (mean = 207 µm, SD = 54), vessel frequency is very low: 3.0–6.3 mm⁻² (mean = 4.6 mm⁻²), and vessel element length is short to medium: 132–580 µm (mean = 350; SD = 69.4) (Fig. 5C). Perforation plates are simple and only slightly oblique (almost transverse). Intervessel pitting alternate, polygonal, and small to medium (5–8 µm) (Fig. 5D). Vessel-parenchyma pits are similar. Thin-walled tyloses are present but rare. Fibers are very thick-walled (Fig. 5G), pits not observed on fiber walls. Axial parenchyma is aliform confluent, forming wide bands (Fig. 5A, B). Axial parenchyma strands are typically 4 cells high, but range from 3–6 cells (Fig. 5E). Rays are 1–3-seriate and heterocellular with procumbent body cells and 1 row of marginal upright cells (Fig. 5F). Ray frequency is 7.2 to 8.8 mm⁻¹ (mean = 7.6 mm⁻¹) and ray height is less than 1 mm: 138–570 µm (mean = 318; SD = 9.2). The vessel elements, rays, fibers, and axial parenchyma are irregularly to regularly storied (Fig. 5E).

Remarks – The combination of diffuse porosity, simple perforation plates, similar intervessel and ray-vessel pits, low rays composed of mostly procumbent cells, storied structure, and abundant confluent axial parenchyma support the assignment of this wood type to Fabaceae (Metcalfe & Chalk 1950; Baretta-Kuipers 1981; Wheeler & Baas 1992). The combination of rays with upright marginal cells, abundant axial parenchyma, storied structure of all elements (rays, vessel elements, axial parenchyma and fibers), and all fibers non-septate excludes Mimosoideae and supports assignment to Caesalpinioideae or Faboideae/Papilionoideae (Baretta-Kuipers 1981; Evans et al. 2006).

This specimen conforms to the anatomy of *Andira* Juss. summarized by Pennington (2003), but a comparison between these fossils and extant species available on the InsideWood database (InsideWood 2004-onwards) revealed similarity with several other genera including *Dalbergia* L.f. (Faboideae/Papilionoideae) and *Dicorynia* Benth., *Koompassia* Maingay ex Benth., *Microberlinia* A. Chev., and *Bauhinia* L. (Caesalpinioideae) depending on whether the fibers and axial parenchyma are scored as storied or irregularly storied. The fossils differ from available specimens of *Dalbergia* in having more irregular banding and confluent axial parenchyma, and they lack the diffuse-in-aggregates axial parenchyma present in some species of *Dalbergia*. The Ocu fossils also differ from *Dicoryna* because they have wider bands of parenchyma and because the storied structure in the axial parenchyma is more organized in the Ocu fossils than in extant *Dicorynia* specimens that we examined. Although we consider the fossil most similar to *Andira* among extant genera, we note that many legume genera are notoriously difficult to distinguish based on wood anatomy alone, and that the wood anatomy of many genera is incompletely known.

There are dozens of names that have been used for fossil legume woods, most of which have not been evaluated in a phylogenetic context and many of which are probably in need of revision. We did not conduct an exhaustive search of all genera used
for fossil legume woods; however, the fossils conform to the diagnosis of the genus *Andiroxylon* Müller-Stoll & Mädel (1967), and they are only subtly different from previously described species of *Andiroxylon* in combining very wide vessels with dominantly confluent axial parenchyma rather than dominantly banded or aliform axial parenchyma, and very thick-walled fibers (Table 2). Together, these features allow the recognition of a new species based on the Ocú material.

Family – Moraceae Gaudich., 1835.
Genus – *Ficus* L., 1754.
Species – *Ficus koek-noormaniae* Jud, sp. nov. (Fig. 6).

Specific diagnosis – Diffuse porous wood with indistinct growth rings; vessels solitary and in short radial multiples; perforation plates simple; intervessel pits alternate, polygonal in outline and medium to large, vessel-parenchyma pits with reduced borders and scalariform to gash-like; axial parenchyma banded; parenchyma bands wide, regularly spaced; rays narrow (1–3-seriate), heterocellular with procumbent body cells and 1–2 (4) rows of upright marginal cells; narrow laticifers common in the rays.

Holotype – UF604-54284.
Additional material – UF604-54269; UF604-54285.

Etymology – Named for Jifke Koek-Noorman in recognition of her work on the systematic wood anatomy of the Moraceae.

Description – Two fragments of mature wood with estimated minimum diameters of 30 cm. Growth rings are indistinct, and the wood is diffuse porous (Fig. 6A). Vessels are solitary (69%) and in radial multiples of 2–3 (Fig. 6A,B). The solitary vessels are oval in transverse section (Fig. 6A,B). Vessel diameters are medium to wide: 126–288 μm (mean = 208; SD = 35), vessel frequency is very low: 1.3–2.2 mm⁻² (mean = 1.7) and vessel element length short to medium: 311 μm (SD = 63.6; n =17). Perforation plates are simple and only slightly oblique (almost transverse). Intervessel pits are alternate, polygonal, and medium: 5–9 μm (Fig. 6D). Vessel-parenchyma pits are large and scalariform to gash-like, with reduced borders (Fig. 6E). Thin-walled tyloses are present but rare. Fibers are moderately thin-walled (Fig. 6B) and often septate (Fig. 6F), pits not observed. Axial parenchyma banded. The bands are 4–6 cells wide and regularly spaced ~1.67 mm⁻¹ (Fig. 6A,B). Rays are mostly 1–3-seriate, but up to 5-seriate in rays with laticifers (mean = 2.6) (Fig. 6F,H). Multiseriate rays are composed of predominantly procumbent body cells and 1–2 (4) rows of marginal upright cells (Fig. 6F,G). Sheath cells are occasionally present but only weakly differentiated. Uniseriate rays may be composed entirely of upright cells (Fig. 6F). Ray frequency is 3.4–6.4 mm⁻¹ and ray height ranges from 144–708 μm (mean = 422 μm; SD = 150). Narrow (8–15 μm in diameter), radial latex tubes (laticifers) are present in some rays, 0–3 tubes per ray (Fig. 6H). Crystals were not observed.

Remarks – The combination of diffuse porous wood, simple perforation plates, alternate intervessel pits, large scalariform vessel-ray parenchyma pits with reduced borders, regularly spaced wide bands of axial parenchyma, narrow rays with procumbent body cells and 1–2 rows of marginal upright cells, and laticifers in the rays is found only in *Ficus* (Moraceae) (Metcalfe & Chalk 1950; Koek-Noorman et al. 1984).
Fossil evidence of the genus is sparse (Collinson 1989), but the earliest unequivocal evidence of the genus is fossil fruits from the Eocene and Oligocene of Europe (Givulescu 1984; Mai & Walther 2000; Bernabei et al. 2010). Fig wasps with fig pollen have also been found in Oligocene deposits in Europe, supporting the hypothesis that the fig-fig wasp mutualism was established by that time (Compton et al. 2010).

Fossil woods that are anatomically like *Ficus* have been assigned to the genus *Ficoxylon* Kaiser. Several species have been described from deposits in Africa (Dupéron-Laudoueneix & Dupéron 1995; Kamal El-Din 2003; Gregory et al. 2009; Jolly-Saad et al. 2010) and Eurasia (Prakash 1965; Bande & Prakash 1986; Gregory et al. 2009; Licht et al. 2014). By contrast, few occurrences are known from the Americas (Table 3).

Table 3. Comparison of the fossil *Ficoxylon/Ficus* woods.

<table>
<thead>
<tr>
<th>Neotropical <em>Ficoxylon/Ficus</em></th>
<th>Reference</th>
<th>GR</th>
<th>MTD</th>
<th>VF</th>
<th>VEL</th>
<th>IVP</th>
<th>BF</th>
<th>BW</th>
<th>RW</th>
<th>RH</th>
<th>RF</th>
<th>MU</th>
<th>SC</th>
<th>Cry</th>
<th>Lat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>F. koek-noormanii</em> sp. nov.</td>
<td>This study</td>
<td>–</td>
<td>208</td>
<td>1.6</td>
<td>312</td>
<td>4–7</td>
<td>1.67</td>
<td>4–6</td>
<td>1–3</td>
<td>379</td>
<td>~7</td>
<td>1–7</td>
<td>occ.</td>
<td>n.o.</td>
<td>+</td>
</tr>
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</table>

Table 4. Comparison of *Burseroxylon* woods.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reference</th>
<th>GR</th>
<th>VG</th>
<th>MTD</th>
<th>VF</th>
<th>VEL</th>
<th>Ty</th>
<th>IVP</th>
<th>RVP</th>
<th>PAP</th>
<th>1-r</th>
<th>MRW</th>
<th>MU</th>
<th>RH</th>
<th>SF</th>
<th>Cry</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. preserratum</td>
<td>Prakash &amp; Tripathi 1973</td>
<td>–</td>
<td>Sol &amp; rms 1–4</td>
<td>(80–200)</td>
<td>12–18</td>
<td>(300–640)</td>
<td>n.o.</td>
<td>lrg (8–10)</td>
<td>31</td>
<td>1,2</td>
<td>h.u.</td>
<td>2–4</td>
<td>1</td>
<td>160–480</td>
<td>+</td>
<td>in u.r.c.</td>
</tr>
<tr>
<td>B. panamense</td>
<td>this study</td>
<td>–</td>
<td>Sol (63 %) &amp; rms of 2–3</td>
<td>233 (173–266)</td>
<td>1.6</td>
<td>(1.3–1.9)</td>
<td>437 (280–700)</td>
<td>n.o.</td>
<td>med-lrg (6–10)</td>
<td>31</td>
<td>1,2</td>
<td>h.u.</td>
<td>2–3</td>
<td>1–3</td>
<td>238–1141</td>
<td>+</td>
</tr>
</tbody>
</table>
Ficoxylon helictoxyloides Platen was described from the Miocene of California (Platen 1908). Ficoxylon bajacaliforniense Martínez-Cabrera, Cevallos-Ferriz et Poole was described from the early Miocene El Cien Fm. of Mexico (Martínez-Cabrera et al. 2006). Ficoxylon cretaceum Schenk was identified from what was thought to be the Cretaceous of Colombia (Boureau & Salard 1962; Pons 1969; Martínez-Cabrera et al. 2009); however, Pons (1980) showed that the wood is Miocene in age and likely a legume (Crudioxylon Pons) based on the presence of storied structure. Ficoxylon bajacaliforniense has wider rays (up to 8 cells) and wider parenchyma bands (5–12 cells) than the fossil described here, and F. helictoxyloides has much wider rays (up to 12 cells).

The Ocú specimens also differ from the old-world species of Ficoxylon. Ray width, band width, and quantitative vessel features in the fossils described here fall within the range of values reported for various old-world specimens of F. cretaceum (Kamal El-Din 2003); however, there are two important differences between the Ocú specimens and previous descriptions for F. cretaceum. The Ocú specimens have 1–2 rows of upright marginal cells in the rays, and commonly 1–3 laticifers per ray. Upright marginal ray cells are reported in a few specimens of Ficoxylon reported from old-world localities, including an unidentified species reported by Jolly-Saad et al. (2010) from the Pliocene of Ethiopia and in Ficoxylon mogaungense from the Eocene of Myanmar (Licht et al. 2014). The Ocú specimens differ from F. mogaungense in having parallel, rather than anastomosing, bands of axial parenchyma and in the presence of distinct laticifers in the rays.

Ficus koek-noormaniae is a fossil species known only from wood anatomy, but nevertheless possesses a combination of characters that allows assignment to the extant genus Ficus. Many species of Ficoxylon likely represent valid occurrences of Ficus, and could probably be transferred to the genus Ficus upon re-examination and updated comparative work. For now, we show that the new species is distinct from the type species of Ficoxylon and from other species assigned to the genus (Table 3). This is the first fossil evidence of Ficus from Panama.

Family – Euphorbiaceae Jussieu, 1789
Species – Euphorbioxylon crotonoides Jud, sp. nov. (Fig. 7).
Specific diagnosis – Diffuse porous wood with indistinct growth rings; vessels solitary and in groups of 2–6; radial multiples often dumbbell-shaped; perforation plates simple; vessel diameters medium to wide, vessel frequency low; vessel element length short to medium; intervessel pits alternate, polygonal, medium; vessel-ray-parenchyma pits similar to intervessel pits; axial parenchyma diffuse-in-aggregates, strands of > 8 cells; rays exclusively uniseriate, short to very tall (> 1 mm), very frequent (13–22 mm⁻¹), heterocellular with several rows of upright marginal rows.
Holotype – UF604-54281.
Etymology – The specific epithet crotonoides comes from Crotonoideae, a subfamily in the Euphorbiaceae that includes many species with wood anatomy like the fossil (Metcalfe & Chalk 1950).
Description – Fragment of mature wood with estimated minimum diameter of 30 cm. Growth rings are indistinct and the wood is diffuse porous (Fig. 7A). Vessels are solitary (42.3%) and in radial multiples of 2–3, rarely up to 6. The solitary vessels are nearly circular in transverse section (Fig. 7A, B) and the radial multiples are often composed of wide end-members with smaller diameter vessels in between (Fig 7B). Vessel diameters are medium to wide: 142–246 µm (mean = 195 µm; SD = 28), vessel frequency is very low: 2.0–3.1 (mean = 2.6 mm⁻²), and vessel element length is short to medium: 220–700 µm (mean = 420; SD = 157; n = 10) (Fig. 7E). Perforation plates are simple and oblique. Intervessel pitting alternate, polygonal, and medium: 6.3–8.8 µm, vessel-ray parenchyma pits similar (Fig. 7C). Thin-walled tyloses are rare. Fiber wall thickness medium, pits not observed, septa not observed (Fig. 7G). Axial parenchyma is
apotracheal, diffuse-in-aggregates to short uniseriate, discontinuous bands (Fig. 7B,D). Axial parenchyma strands are commonly > 8 cells high. Rays are exclusively uniseriate; heterocellular, with upright, square and procumbent cells mixed throughout the ray body (Fig. 7F–H). Ray frequency is high: 13–22 mm⁻¹. It was not possible to take a representative sample of ray heights in this specimen because of poor preservation; however, ray height ranges from 25 to 1780 µm.

Remarks – The combination of solitary vessels and vessels in dumbbell-shaped radial multiples, low vessel frequency (often below 5 mm⁻²), simple perforation plates, medium to large alternate intervessel pits, abundant apotracheal axial parenchyma either diffuse-in-aggregates or in short uniseriate bands, and narrow heterocellular rays that are 1–2- (rarely 3-)seriate with biseriate portions as wide as the uniseriate portions is typical of Euphorbiaceae (Metcalfe & Chalk 1950; Hayden & Hayden 2000; Mennega 2005). The absence of laticifers in the samples we examined suggests an affinity either with Crotonoideae and/or Acalyphoideae rather than Euphorbioideae (Mennega 2005).

We searched the online InsideWood database (InsideWood 2004-onwards) for diffuse porous wood, with vessels evenly distributed and in radial multiples with up to four or more common, vessel outline rounded, simple perforation plates, intervessel pits alternate and medium, fibers medium- to thin-walled, axial parenchyma diffuse-in-aggregates to narrow interrupted lines and uniseriate rays composed of procumbent and upright cells and rays >12 mm⁻¹, storied structure absent with 0 allowable mismatches (5p 6a 7a 8a 9a 11a 12a 13p 22p 26p 70a 77r 78a 79a 80a 83a 84a 85a 96p 104a 116p 118a 120a). This search yielded 17 genera in Euphorbiaceae and in Crypteroniaceae, but an affinity with Crypteroniaceae is unlikely because that family is characterized by bordered fiber pits, and the vessels do not occur in dumbbell-shaped radial multiples (van Vliet 1975; van Vliet & Baas 1975).

Only a handful of genera have been used for fossil woods thought to be Euphorbiaceae, including Euphorbioxylon, Bridelioxylon Ramanujam, Aleuritoxylon Mädel, Mallotoxylon Lakhanpal & Dayal, Piranheoxylon Grambast, Pseudolachnostyloxylon Gottwald, and Securinegoxylon Mädel, and some species attributed to Paraphyllanthoxylon Bailey (Gregory et al. 2009). Mädel (1962) reviewed fossil woods of the Euphorbiaceae and grouped the genera at that time into five groups. This wood belongs to her fifth group, the Crotonoideae-group, because of the combination of diffuse porosity, simple perforation plates, and tall, narrow heterocellular rays. In addition to Euphorbioxylon speciosum Felix, Heveoxylon microporosum Kruse and Aleurites miocenica Watari, this group should also include Mallotoxylon (Lakhanpal & Dayal 1964). Within this group, the present fossil is most like Euphorbioxylon; however, it differs from the type species in having vessels in long radial multiples, axial parenchyma forming short uniseriate bands (two features typical of many other euphorbiaceous woods), narrower rays, and abundant very tall rays (> 1 mm). Thus, in the tradition of using Euphorbioxylon for euphorbiaceous woods that cannot be assigned to modern genera (Mädel 1962), we have elected to treat this fossil wood as a new fossil species of Euphorbioxylon.
Family – Humiriaceae Jussieu, 1789
Holotype – USNM 312574.
Other specimens – UF604-54267; UF604-54271.
Etymology – From Ocú, Panama (Herrera *et al.* 2010).
Remarks – The generic name ends in -on and is therefore neuter. The specific epithet should agree in gender with the genus, but *ocuensis* is masculine. We consider this ending an orthographic error and hereby correct it.

Family – Uncertain; cf. Anacardiaceae/Burseraceae.
Species – *Burseroxylon panamense* Jud (Fig. 8).
Specific diagnosis – Diffuse porous wood with indistinct growth rings; vessels solitary and in groups of 2–4; perforation plates simple; mean vessel diameter wide to very wide (> 200 µm), intervessel pits alternate, polygonal, large; vessel-ray-parenchyma pits with reduced borders; septate fibers present; axial parenchyma scanty paratracheal to narrow vasicentric; rays uniseriate and narrow multiseriate, mostly biseriate, heterocellular with several rows of upright marginal rows.
Holotype – UF606-56058.
Description – Fragment of mature wood with an estimated minimum diameter of 20 cm. The wood is diffuse porous with indistinct growth rings. Vessels are solitary (63%) and in radial multiples of 2–4 (Fig. 8A,B). Solitary vessels are roughly circular in outline, with simple perforation plates (Fig. 8D). Vessel diameters are wide: 173–366 µm (mean = 233; SD = 45), vessel frequency very low: 1.3–1.9 mm-2 (mean = 1.6), and vessel element length medium: 282–700 µm (mean = 437 µm; SD = 115; n = 17). Intervessel pits are alternate, polygonal, large (10–12 µm) (Fig. 8C,E). Vessel-ray parenchyma pits are rounded with reduced borders (Fig. 8F); tyloses were not observed. Fibers thin- to thick-walled (Fig. 8B), septate fibers present (Fig. 8I). Axial parenchyma is scanty paratracheal to narrow vasicentric (Fig. 8A,B). Rays are 1–3-seriate, primarily biseriate, and heterocellular with procumbent body cells and commonly 1–4 rows of marginal upright cells (Fig. 8C,H,I). Ray height is 238–1141 µm (mean = 599; SD = 226). Ray frequency is 5.7–9.1 mm-1 (mean = 6.9 mm-1). Crystals were not observed. Radial canals were not observed.
Remarks – We searched the online InsideWood database (InsideWood 2004-onswards) for diffuse porous wood, with vessels evenly distributed and in short radial multiples, vessel outline rounded, simple perforation plates, intervessel pits alternate and large, vessel-ray parenchyma pits elongate and with much reduced borders, septate fibers present, axial parenchyma scanty paratracheal, 1–3-seriate, heterocellular rays with fewer than four rows of marginal upright cells, without oil or mucilage cells, nor
Figure 8. *Burseroxylon panamense* Jud, sp. nov. (UF606-56058). – A: Diffuse porous wood; vessels solitary and in radial pairs, XS. – B: Thin-walled fibers, wide vessels, and scanty paratracheal axial parenchyma, XS. – C: Alternate intervessel pitting, TLS. – D: Simple perforation plates at arrows, RLS. – E: Polygonal intervessel pitting (at arrow), TLS. – F: Vessel-axial parenchyma pits with reduced borders (at arrow), TLS. – G: Procumbent and upright ray cells, RLS. – H: 1–2-seriate rays, TLS. – I: 1–2-seriate rays and septate fiber (at arrow), TLS. – Scale bars: A = 525 µm; B, G = 250 µm; C, D, I = 100 µm; E = 40 µm; F = 25 µm; H = 200 µm.
cambial variants, and with 0 allowable mismatches (5p 6a 7a 8a 9a 10a 11a 12a 13p 14a 22p 27p 32p 65p 78p 80a 83a 84a 85a 86a 89a 97p 104a 105a 108a 124a 125a 126a 133a, 134a). This search yielded 20 genera of Anacardiaceae and 11 genera of Burseraceae.

Metcalfe and Chalk (1950) noted that the woods of Anacardiaceae and Burseraceae share a combination of features that distinguish them from other families, but that distinguishing among the genera of these families based on wood anatomy is difficult. We compiled a list of fossil woods attributed to Anacardiaceae or Burseraceae that lack distinct growth rings, radial or axial canals, and elaborate conformations of axial parenchyma (e.g. aliform, confluent, or banded). This list included only *Dracontomeloxylon* Prakash, *Edenoxylon atkinsoniae* Brett emend. Crawley, *Coahuiloxylon terrazasiae* Estrada-Ruiz, Martínez-Cabrera & Cevallos-Ferriz, *Burseroxylon* Prakash & Tripathi, and *Canarioxylon* Prakash, Brezinová & Awasthi. There is independent evidence for the presence of *Dracontomelon* in Panama in the past (Herrera et al. 2012); however, wood of *Dracontomelon* typically has vasicentric to aliform paratracheal parenchyma and *Dracontomeloxylon* has wider rays, 2–4 (5) cells and commonly narrow-aliform axial parenchyma (Prakash 1979), which is unlike the fossil. *Edenoxylon atkinsoniae* has higher vessel frequency (20–28 mm⁻²), narrower vessels (63–105 µm), longer vessel elements (410–470 µm) and primarily biseriate rays with multiseriate portions no wider than the uniseriate portions (Crawley 2001). *Coahuiloxylon terrazasiae* was described from the Upper Cretaceous of Mexico and has much narrower vessels (mean = 96 µm) and wider rays (1–5 cells) despite being known from smaller axes. *Canarioxylon* differs from the material described here in that it generally has only one row of upright marginal cells in the rays. The fossil conforms to the genus *Burseroxylon*, which is characterized by simple perforation plates, scanty to narrow vasicentric axial parenchyma, large intervessel pits with linear to lenticular apertures, narrow 1–5-seriate heterocellular rays with procumbent body cells and one to few rows of upright marginal cells, radial canals generally absent, and septate fibers (Prakash & Tripathi 1973; Lakhanpal et al. 1981). This genus is also characterized by crystals in the upright ray cells, a feature not observed in the Ocú material so far. We also note that the original and emended diagnoses did not include a description or photographs of the vessel-ray parenchyma pits, but the photographs available on the InsideWood database show that the vessel-ray parenchyma pits in *Burseroxylon* are rounded and have reduced borders.

This is the third species assigned to the genus *Burseroxylon*. Silicified wood of *B. preserratum* Prakash & Tripathi was described from the upper Miocene beds of the Tipam Sandstone Formation in the upper Assam Valley, India (Prakash & Tripathi 1973), and *B. garugoides* Lakhanpal, Prakash & Awasthi was described from the Miocene beds of Namsing near Deomali, India (Lakhanpal et al. 1981). *Burseroxylon panamense* differs from these species based on the combination of very large vessel diameters, very low vessel frequency, vessel-parenchyma pits with reduced borders, and narrow rays up to 3 cells wide and up to three rows of marginal upright cells (Table 4).
Figure 9. *Sapotaceoxylon penningtonii* Jud, gen. et sp. nov. (UF604–54268). – A: Diffuse porous wood with narrow bands of axial parenchyma and vessels in long radial multiples, XS. – B: Narrow bands of axial parenchyma and a radial multiple of six vessels, XS. – C: Vessels with segmenting tyloses, TLS. – D: Minute alternate intervessel pitting, TLS. – E: Thin-walled fibers, XS. – F: Portion of an axial strand (center, at arrow), vessel (at left), and ray (at right), TLS. – G: Narrow rays with short biseriate zones (at arrow), TLS. – H: Procumbent body cells and upright marginal cells, RLS. – I: Intervessel pits at the upper arrow, and larger, elongate vessel-ray parenchyma pits with reduced borders at the lower arrow, TLS. – Scale bars: A = 300 µm; B, C = 100 µm; D–F = 30 µm; G, H = 50 µm; I = 40 µm.
Family – Sapotaceae Jussieu, 1789


Generic diagnosis – Diffuse porous wood with indistinct growth rings; vessels solitary and in radial multiples commonly of more than 3 vessels, in radial to oblique pattern, perforation plates simple, intervessel pits alternate; vessel-ray parenchyma pits with reduced borders; axial parenchyma in closely-spaced narrow or uniserate bands; rays 1–2-seriate, heterocellular, with procumbent body cells and long uniseriate margins composed of upright cells.

Derivation of generic name – *Sapotaceoxylon* comes from Sapotaceae and the Greek root “xyl” for wood.

Type species – *Sapotaceoxylon penningtonii* Jud, *gen. et sp. nov.* (Fig. 9).

Holotype – UF604-54268.

Additional material – UF606-56057.

Specific diagnosis – Vessels solitary and in radial multiples of 2–7, arranged in a radial pattern; intervessel pits minute; axial parenchyma in closely-spaced uniserate bands composed of strands of > 8 cells; rays 1–2-seriate, heterocellular, with short sections of procumbent body cells and commonly with more than four rows of uniseriate upright marginal cells; ray height < 1 mm.

Etymology – The specific epithet *penningtonii* honors T.D. Pennington for his work on the morphology of extant Sapotaceae.

Description – Fragment of mature wood with a minimum diameter of 18 cm. The wood is diffuse porous with indistinct growth rings (Fig. 9A). Vessels are generally evenly dispersed, tending to a radial/diagonal arrangement; solitary (16%) and in radial multiples of 2–7 (Fig. 9A,B). The solitary vessels are oval in transverse section (Fig. 9A). Vessels are narrow: 57–115 µm (mean = 88 µm; SD = 14), vessel frequency is medium: 8.6–17.2 mm⁻² (mean = 12.7). Vessel element length could not be determined with certainty because of segmenting tyloses (Fig. 9C). Perforation plates are simple. Intervessel pitting is minute and alternate (Fig. 9D). Vessel-ray parenchyma pits are large with reduced borders (Fig. 9I). Fibers are medium thick to thick-walled (Fig. 9B), pits on fiber walls were not observed, septa were not observed. Axial parenchyma in uniseriate bands (8 mm⁻¹), with more than 8 cells per strand. Rays are 1–2-seriate and composed of short groups of procumbent body cells with long, uniseriate marginal extensions of upright cells (Fig. 9G,H). Ray height is generally < 1 mm, but is obscured by poor preservation of the marginal extensions. Ray frequency is medium to high: 11.0–17.7 mm⁻¹. Crystals were not observed.

Remarks – The combination of diffuse porous wood with vessels in long radial multiples (> 4), simple perforation plates, minute alternate intervessel pits, enlarged vessel-ray parenchyma pits, uniseriate bands of axial parenchyma, narrow heterocellular rays with procumbent body cells and long uniseriate margins of upright cells suggests affinities with the Sapotaceae (Metcalfe & Chalk 1950; InsideWood 2004-onwards). Similar woods are found in Apocynaceae, Ebenaceae, Olacaceae, and Rubiaceae, but this wood may be excluded from Ebenaceae because that family is characterized by primarily uniseriate rays with occasional biseriate rays (Metcalfe & Chalk 1950),
from Catheda Miers (Olacaceae) because the axial parenchyma is in regular bands, rather than diffuse-in-aggregates, and from Rubiaceae and Apocynaceae because the vessel-ray pits in those families are small and similar to the intervessel pits (Metcalfe & Chalk 1950). Woods of Juglandaceae may also be convergent with some Sapotaceae (Müller-Stoll & Mädel-Angeliw 1983), but Sapotaceae may be distinguished from Juglandaceae by the presence of very narrow vessels, and long (> 4) radial multiples of vessels (Metcalfe & Chalk 1950). Neotropical Juglandaceae (Engelhardioideae) also typically have scalariform perforation plates in the narrower vessels (Manchester 1983; Blokhina 2007).

This wood differs from most genera used for fossil woods in Sapotaceae (Gregory et al. 2009) because it has narrow uniseriate bands of axial parenchyma, whereas others have multiseriate bands and/or axial parenchyma diffuse or diffuse-in-aggregates. It is most like some woods that have been assigned to Sapotoxylon Felix because it has vessels in long radial multiples, uniseriate banded axial parenchyma, and narrow rays with procumbent body cells and with long uniseriate margins composed of upright cells. However, the genus Sapotoxylon has a complicated history. The first use was by Felix (1882) when he established the genus with the type species S. taeniatum; however, species established in these are not generally valid under the current code of botanical nomenclature. One year later, Felix published a study of fossil wood where he again established the genus Sapotoxylon and this time included two species, S. guembellii and S. taeniatum (Felix 1883). Sapotoxylon guembellii should be considered the type species because it appears before the first valid publication of S. taeniatum. Later, S. guembellii was transferred to the genus Annonoxylon Boureau (Annonaceae) by Boureau (1954) and later to Eucaryoxylon Müller-Stoll & Mädel (Juglandaceae) by Müller-Stoll & Mädel-Angeliw (1983). Even if S. taeniatum were accepted as the type, Müller-Stoll & Mädel-Angeliw (1983,1984) showed that it is also unlikely that S. taeniatum belongs to Sapotaceae based on the combination of diffuse, vasicentric, and narrow-banded axial parenchyma along with low, homocellular rays. Instead, they suggested affinities with Meliaceae (Müller-Stoll & Mädel-Angeliw 1983, 1984). Most subsequently published fossil species assigned to Sapotoxylon and with Sapotaceae-like anatomy differ significantly from the type and therefore need a new generic assignment. Several of these possess the diagnostic features of Sapotaceoxylon, and we hereby make the following generic reassignments:


Species – *Symplocoxylon panamense* Jud, sp. nov. (Fig. 10).

Specific diagnosis – Wood diffuse porous with indistinct growth rings; vessels narrow to medium, exclusively solitary; perforation plates scalariform with many bars (> 20), fibers with distinctly bordered pits on the tangential walls, radial pits obscured by frequent rays; axial parenchyma diffuse; rays 1–3 cells wide, heterocellular with upright and procumbent cells mixed throughout, with weakly developed sheath cells, and with one to several rows of upright marginal cells.

Holotype – UF604-54264.

Etymology – The specific epithet *panamense* is derived from Panama, the country where the wood was collected.

Description – Fragment of mature wood with an estimated minimum diameter of 21 cm. The wood is diffuse porous with indistinct growth rings (Fig. 10A). Vessels are evenly dispersed and almost exclusively solitary (96%), with rare radial pairs (Fig. 10A, B). The solitary vessels are oval in transverse section (Fig. 10A, B). Vessel diameter is narrow to medium: 50–141 µm (mean = 116 µm; SD = 18), vessel frequency is low to medium, 19.3–22.4 mm⁻² (mean = 21.1), and vessel element length is long 800–1220 µm (mean = 975; SD = 205; n = 5). Perforation plates are scalariform, very oblique, and with over 40 bars (Fig. 10C). Intervessel pits not observed, likely minute. Vessel-ray parenchyma pits not observed. Tyloses not observed. Fibers are moderately thick-walled (Fig. 10B) with distinctly bordered pits on tangential walls, radial walls obscured by rays (Fig. 10H, I), septa not observed, possibly obscured by poor preservation. Axial parenchyma is diffuse, and the cells are ~300 µm high in strands of > 4 cells. Rays are uniseriate and narrow multiseriate (2–3). Ray cellular composition is heterocellular with rows of procumbent, square, and upright body cells mixed throughout, and one to many rows of upright marginal cells (Fig. 10D, E). Upright cells in triseriate rays are often along the edge of the ray (Fig. 10F–H). Ray frequency is 5.9–6.7 mm⁻¹. Ray height is less than 1 mm (mean = 390.6 µm; SD = 166.4; n = 9). Crystals were not observed.

Remarks – We searched the InsideWood database for diffuse porous wood with vessels evenly distributed and exclusively solitary, scalariform perforation plates with over 20–40 bars or > 40 bars, vessels narrow and with moderately high frequency, fibers with distinctly bordered pits and thin to thick walls, axial parenchyma diffuse, and narrow rays composed of procumbent and upright cells, storied structure, oil cells, and axial canals absent (5p 6a 7a 8a 9p 13a 14p 17p 18p 46a 50a 62p 69p 76p 79a 80a 83a 84a 85a 86a 97p 98a 104a 105a 118a 120a 124a 125a 126a 127a 128a 129a 130a with 0 allowable mismatches). This search yielded *Clethra* (Clethraceae), *Cornus* (Cornaceae), several genera in Dilleniaceae, *Dicoryphe* (Hamamelidaceae), *Apodytes* (Icacinaceae), *Gordonia* (Theaceae), and several genera in Pentaphylacaceae (including former Ternstroemioidae), and *Symplocos* (Symplocaceae).

Members of Dilleniaceae usually have rays of two distinct sizes, with the larger rays 8–10 cells wide or more, but a few old-world genera have exclusively narrow rays (*Acrotrema* Jack, *Hibbertia* Andrews, *Pachynema* R. Br. ex DC.) (Metcalf & Chalk
Figure 10. *Symplocoxylon panamense* Jud, *sp. nov.* (UF604–54264). – A: Diffuse-porous wood with mostly solitary vessels and rare radial pairs, XS. – B: Fibers and vessels, axial parenchyma rare to absent, XS. – C: Very oblique scalariform perforation plates with thin bars (lower arrow); narrow multiseriate and uniseriate (upper arrow) rays, TLS. – D, E: Upright and procumbent ray cells, RLS. – F: Rays commonly tri-seriate, TLS. – G: Tri-seriate ray with procumbent and upright cells; scalariform perforation plate, TLS. – H: Short cells at the ray center and the taller cells along the edges, TLS. – I: Fiber pits, at the arrow, TLS. – Scale bars: A = 500 µm; B, C, G = 100 µm; D, F = 250 µm; E, H = 50 µm; F = 250 µm; I = 25 µm.
A relationship to *Dicoryphe* is unlikely because that genus is restricted to Madagascar, and *Clethra* is unlikely because it includes mostly shrubs and small trees. We were not able to rule out a relationship with *Apodytes* given the available characters (Lens et al. 2008), but that genus is only found in the Old World. *Gordonia*, Pentaphylacaceae, Symplocaceae, are all widespread groups that include Neotropical trees and belong to a monophyletic group of families in Ericales that are characterized by a suite of wood anatomical characters including scalariform perforation plates, narrower vessels, and often helical thickenings as well (van den Oever et al. 1981; Liang & Baas 1991; Lens et al. 2007).

We know of no fossil woods assigned to Pentaphylacaceae, and only two have been compared with *Gordonia* (Beck 1945; Spackman 1949); however, several woods have been identified to Symplocaceae (Burgh 1964, 1973; Shibuya & Hayashi 1997; Dolezych & Estrada 2012). The Ocú specimen is anatomically very like extant *Sym- plocos* (van den Oever et al. 1981) except that scalariform intervessel pitting was not observed. The fossil conforms to the generic diagnosis for *Symplocoxylon* given by Burgh (1964), but it differs from the other species assigned to *Symplocoxylon* in lacking paratracheal axial parenchyma and having scalariform perforation plates with 40–50 bars (Table 5). Unfortunately, intervessel and vessel-parenchyma pits were not observed and clarification of those characters with additional specimens in the future may enable more precise conclusions about affinity of this fossil.

**Indet. Ocú wood type I.**

**Family – Unknown.**

**Exemplar specimen – UF604-54273 (Fig. 11).**

**Description –** Fragment of mature wood with an estimated minimum diameter of 12 cm. The wood is diffuse porous with indistinct growth rings (Fig. 11A). Vessels are evenly dispersed; they are solitary (40%) and in radial multiples of 2–3 (4), rarely in clusters (Fig. 11A,B). The solitary vessels are oval in transverse section (Fig. 11A). Vessels are narrow: 50–121 µm (mean = 87 µm; SD = 16), vessel frequency is 23–28 mm⁻² (mean = 26), and vessel element length ranges from 45–301 µm (mean = 188; SD = 61). Perforation plates are simple and oblique (Fig. 11H). Intervessel pitting alternate and minute (Fig. 11C). Ray-vessel pits are like intervessel pits (Fig. 11D). Tyloses were not observed. Fibers are thin- to thick-walled (Fig. 11B) and septate fibers are present (Fig. 11G). Axial parenchyma is diffuse but rare (Fig. 11F). Rays are 1–2-seriate and composed predominantly of procumbent body cells with 1 row of marginal upright cells (Fig. 11E,G,I); short uniseriate rays composed of predominantly upright cells. Ray frequency is 11–18 mm⁻¹ and ray height is < 1 mm (50–494 µm; mean = 262; SD = 110). Crystals were not observed.

**Remarks –** The combination of vessels solitary and in short radial multiples, simple perforation plates, minute to small alternate intervessel pits and similar vessel-ray parenchyma pits, narrow non-storied rays composed of procumbent body cells and 1–2 rows of marginal upright cells, and rare apotracheal parenchyma (diffuse to diffuse-in-aggregates), and without storied structure or canals occurs in a wide variety of families. A search for these characters on InsideWood (5p 6a 7a 8a 9a 10a
Fig. 11. Wood Type I (UF604–54273). – A: Diffuse porous wood with vessels solitary and in short radial multiples, XS. – B: Medium thick-walled fibers and a radial multiple of three vessels, XS. – C: Minute, alternate intervessel pitting, TLS. – D: Minute vessel-ray parenchyma pits, like the intervessel pits (arrow), RLS. – E: Additional vessel-ray parenchyma pitting, also note rows of procumbent and upright ray cells, RLS. – F: Diffuse axial parenchyma cell (arrow); medium thick-walled fibers, XS. – G: Uniseriate rays, vessel elements, and septate fibers (at arrow), TLS. – H: Ray cellular composition, vessel elements, note the simple perforation plate (at arrow), RLS. – I: Ray with procumbent body cells and 1–2 rows of upright marginal cells, RLS. – Scale bars: A = 300 µm; B, G = 100 µm; C, F = 25 µm; D, E, I = 50 µm; H = 250 µm.
Indet. Ocú wood type II.

Family – Unknown; cf. Salicaceae/Rubiaceae.

Exemplar specimen – UF604-54265 (Fig. 12).

Additional material – UF604-54283.

Description – Fragment of mature wood with a minimum diameter of 10 cm. The wood is diffuse porous with indistinct growth rings marked by narrow zones of radially
flattened fibers (Fig. 12A). Vessels are solitary (35.5%) and in radial multiples of 2–3 (Fig. 12A,B). The solitary vessels are oval in transverse section (Fig. 12B). Vessels are narrow: 47–103 µm (mean = 76 µm; SD = 12), vessel frequency is 30.6–43.0 mm⁻² (mean = 35.6) and vessel element length is obscured, but perforation plates appear to be simple and oblique at least in some cases. Intervessel pitting alternate-opposite, polygonal, and small (Fig. 12C). Vessel-parenchyma pits were not observed. Thin-walled tyloses are present but rare. Fibers are moderately thin-walled (Fig. 12B) and often apparently septate. Axial parenchyma is scanty paratracheal. Rays are 1–5-seriate (mean = 3.6) and ray height is 309–1129 µm (mean = 607; SD = 20). Rays are heterocellular and composed of predominantly procumbent body cells and two to several rows of marginal upright cells (Fig. 12E,F). Ray frequency is 11.4–14.5 mm⁻¹ (mean = 12.9). Crystals not observed.

Remarks – A search for families with members that combine diffuse porous wood with vessels solitary and in short radial multiples, simple perforation plates, small and alternate intervessel pitting, separtate fibers, rare or scanty paratracheal axial parenchyma, and rays that are 1–5-seriate with procumbent body cells and one to many rows of upright marginal cells. InsideWood (1a 5p 9a 10a 11a 13p 14a 22p 65p 78p 80a 85a 86a 97p 98p 108p) yielded Achariaceae, Anacardiaceae, Elaeocarpaceae, Lamiaceae, Malpighiaceae, Ochnaceae, Phyllanthaceae, Rubiaceae, and Salicaceae. Our inability to find reasonably well-preserved vessel-ray parenchyma pits makes identifying of this wood type difficult; however, in browsing the photos of the families listed above, available in InsideWood, we note similarity between the ray structure in the fossil and some Neotropical Rubiaceae and Salicaceae (e.g. Psychotria, Homalium). Although both wood type I and wood type II are both compared with Salicaceae/Rubiaceae, the two woods are easily distinguished in tangential section. Whereas wood type I is characterized by 1–2-seriate rays with procumbent body cells and one marginal row of upright cells, wood type II is characterized by 1–4-seriate rays with procumbent body cells and 2–4+ marginal rows of upright cells.

**Rare Earth Element analysis**

We analyzed the Rare Earth Element patterns of woods from the Ocú area and compared them with the Alajuela and Cucaracha Formations. The results are summarized in Figure 13. Typically, when taphonomically mixed fossils form during different sedimentary cycles, they have different (heterogeneous) REE patterns (Trueman & Benton 1997) that allow temporal discrimination. Conversely, fossils preserved under similar conditions at the same time generally are expected to have homogeneous REE patterns. Although the Alajuela woods are likely reworked (Macfadden et al. in press) and the Cucaracha woods are minimally transported, the REE pattern of the woods from Ocú is indistinguishable from the pattern of the woods from both the Alajuela and the Cucaracha Formations, except that the Cucaracha woods showed higher total REE concentrations (Fig. 13).
Figure 13. Plot of log-transformed rare earth element (REE) concentrations for wood specimens from Panama. Samples are grouped into box and whisker plots by locality. Lines follow group mean values, boxplots indicated group median values. The PAAS-normalized data are presented in the Supplementary table.

Figure 14. Results of Nonmetric Multidimensional Scaling analysis. – A: Stress plot showing the goodness of fit between the observed Bray dissimilarity between floras and the observed distance between floras in the two-dimensional configuration. – B: Two-dimensional configuration data presented in Table 7 following natural-log transformation. Note that the Ocú flora occurs on the far right side of the plot closest to the tropical forest communities (marked with an asterisk). GR = proportion of species with distinct growth rings, VG = mean vessel grouping, VF = vessel frequency, SE = proportion of species with helical sculpture, T = proportion of species with tracheids, BAR = mean number of bars per perforation plates, VEL = vessel element length, MTD = mean vessel diameter.
Nonmetric Multidimensional Scaling

We used Nonmetric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarity (Cox & Cox 2001; McCune & Grace 2002). The stress is 0.045 and therefore the plot provides good representation of the data in two dimensions (Fig. 14A). Although we excluded the mesomorphy index used by Martínez-Cabrera and Cevallos-Ferriz (2008) and projected the data using NMDS rather than PCA, our results were comparable. On average, the wood anatomy of the tropical rainforest species has larger vessel diameters (MVD), lower vessel frequencies (VF), longer vessel elements (VEL), smaller vessel groups (VG), fewer incidences of tracheids (T), and fewer incidences of helical sculpture (SE) than the woods from other communities and ecological categories. The modern tropical rainforest communities are on the right side of the plot, and the Ocú flora plots to the right of the modern rainforests (Fig. 14B).

DISCUSSION

Stern and Eyde (1963) reported silicified wood of *Vantanea* (Humiriaceae), *Tetrathylocladium* (formerly Flacourtiaceae, now Salicaceae), and *Hernandia* (Hernandiaceae) from the near Ocú on the Azuero Peninsula; however, they did not provide detailed justification for the generic identifications. Herrera et al. (2014) confirmed the humiriaceous affinity of the specimen identified as *Vantanea* and described *Humiriaceoxylon ocuense* based on the original thin sections from Stern & Eyde and new material from the same collection as the woods described here. The *Vantanea* assignment was rejected because no one genus within Humiriaceae has a unique combination of wood anatomical characteristics, and both *Sacoglottis* and *Vantanea* are known from the Miocene of Panama based on fossilized fruits (Herrera et al. 2010, 2014). Unfortunately, we were unable to track down the specimens identified as *Tetrathylocladium* and *Hernandia* at Harvard or at the Smithsonian Institution (where the type specimen of *Humiriaceoxylon ocuense* is stored).

Among the woods described herein are ones assigned to *Ficus* and Lauraceae, which have not been recognized previously in the fossil record of Panama. The other families identified here were already known from fossil pollen, fruits, or leaves collected elsewhere in Panama (Berry 1918; Graham 1985, 1991; Jaramillo et al. 2014).

All the taxa identified here occur in tropical forests of Central America today (Gentry 1982; Jaramillo et al. 2014), but some are more broadly distributed than others. For example, Lauraceae in general, and *Beilschmiedia* in particular, are associated with a variety of tropical and temperate forests, and the same is true for Arecaceae, Fabaceae, Euphorbiaceae, and Anacardiaceae/Burseraceae. *Ficus* and Sapotaceae are both pantropical and associated with a variety of tropical, subtropical and temperate habitats, but in the Neotropics they are primarily associated with humid tropical lowland vegetation (Berg 1989; Pennington 1990). Humiriaceae are primarily Neotropical trees associated with lowland and montane rainforests (Herrera et al. 2010). Pentaphyllacaceae (including Ternstroemioidae) are pantropical, but in the Neotropics they are associated with premontane or montane tropical forests (Weitzman et al. 2004). If it can be demonstrated that *Symplocoxylon panamense* instead belongs to
Table 5. Comparison of *Symplocoxylon* species.

GR = growth rings, + = present/distinct, − = absent/indistinct; MTD = mean tangential diameter of vessels in micrometers, ranges in parenthesis; BAR = number of bars per perforation plate; VRP = vessel-ray parenchyma pits, 32 = horizontally elongate with reduced borders; PAP = paratracheal axial parenchyma, 1 = scanty paratracheal, 2 = vasicentric; AAP = apotracheal axial parenchyma, 1 = diffuse; 1-r = uniseriate rays, h.u. = homocellular ray composed of upright cells; MRW = multiseriate ray width in cells; SC = sheath cells; MU = number of rows of marginal upright cells in multiseriate rays.

<table>
<thead>
<tr>
<th>Species</th>
<th>Citation</th>
<th>GR</th>
<th>MTD</th>
<th>BAR</th>
<th>VRP</th>
<th>PAP</th>
<th>AAP</th>
<th>1-r</th>
<th>MRW</th>
<th>SC</th>
<th>MU</th>
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<tr>
<td><em>S. latiporosum</em></td>
<td>Burgh 1964</td>
<td>–</td>
<td>25–100</td>
<td></td>
<td>32</td>
<td>0</td>
<td>1</td>
<td>h.u.</td>
<td>2–3</td>
<td>+</td>
<td>1–4+</td>
</tr>
<tr>
<td><em>S. krausellii</em></td>
<td>Burgh 1973</td>
<td>+</td>
<td>40–100</td>
<td>18–25</td>
<td>32</td>
<td>1</td>
<td>1</td>
<td>?</td>
<td>2–5</td>
<td>+</td>
<td>–</td>
</tr>
<tr>
<td><em>S. eschweilerense</em></td>
<td>Burgh 1973</td>
<td>–</td>
<td>40–80</td>
<td>40–60</td>
<td>32</td>
<td>2</td>
<td>1</td>
<td>h.u.</td>
<td>2–5</td>
<td>–</td>
<td>1–4</td>
</tr>
<tr>
<td><em>S. panamense sp. nov.</em></td>
<td>this study</td>
<td>–</td>
<td>(57–115)</td>
<td>40–50+</td>
<td>?</td>
<td>0</td>
<td>1</td>
<td>h.u.</td>
<td>2–3</td>
<td>+</td>
<td>1–4+</td>
</tr>
</tbody>
</table>

Table 6. Summary of the climatically informative characters in the Ocú woods.

GR = growth rings, + = present/distinct, − = absent/indistinct; MTD = mean tangential diameter of vessels in micrometers, ranges in parenthesis; VF = vessel frequency per square millimeter; VEL = vessel element length in micrometers; VG = vessel grouping index; BAR = mean number of bars per perforation plate; VI = vulnerability index; AAP = apotracheal axial parenchyma, 1 = diffuse, 2 = diffuse-in-aggregates; PAP = paratracheal axial parenchyma, 1 = scanty paratracheal, 2 = vasicentric, 3 = aliform, 4 = confluent; BAP = banded axial parenchyma, 1 = narrow bands (≤3 cells), 2 = wide bands (≥4 cells); %AP = percent of cross-sectional area occupied by axial parenchyma.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>GR</th>
<th>MTD</th>
<th>VF</th>
<th>VEL</th>
<th>VG</th>
<th>BAR</th>
<th>VI</th>
<th>AAP</th>
<th>PAP</th>
<th>BAP</th>
<th>%AP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Beilschmiedia oleifera sp. nov.</td>
<td>–</td>
<td>116</td>
<td>3.6</td>
<td>258</td>
<td>1</td>
<td>0</td>
<td>32.2</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>6%</td>
</tr>
<tr>
<td>Laurinxylon elongatum sp. nov.</td>
<td>–</td>
<td>148</td>
<td>6.3</td>
<td>879</td>
<td>2</td>
<td>0/5</td>
<td>23.5</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2%</td>
</tr>
<tr>
<td>Andiroxylon barghoornii sp. nov.</td>
<td>–</td>
<td>207</td>
<td>4.6</td>
<td>350</td>
<td>2</td>
<td>0</td>
<td>45</td>
<td>0</td>
<td>3,4</td>
<td>2</td>
<td>40%</td>
</tr>
<tr>
<td>Ficus koek-noomianiae sp. nov.</td>
<td>–</td>
<td>207</td>
<td>1.7</td>
<td>311</td>
<td>1</td>
<td>0</td>
<td>122</td>
<td>0</td>
<td>6</td>
<td>2</td>
<td>18%</td>
</tr>
<tr>
<td>Euphorbioxylon crotonoides sp. nov.</td>
<td>–</td>
<td>195</td>
<td>2.6</td>
<td>420</td>
<td>2</td>
<td>0</td>
<td>75</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>18%</td>
</tr>
<tr>
<td>Burseroxylon panamense sp. nov.</td>
<td>–</td>
<td>233</td>
<td>1.6</td>
<td>437</td>
<td>1</td>
<td>0</td>
<td>146</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>2%</td>
</tr>
<tr>
<td>Sapotaceoxylon penningtonii gen. et sp. nov.</td>
<td>–</td>
<td>88</td>
<td>12.7</td>
<td>NA</td>
<td>3</td>
<td>0</td>
<td>6.9</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>12%</td>
</tr>
<tr>
<td>Symplocoxylon panamense sp. nov.</td>
<td>–</td>
<td>116</td>
<td>21.1</td>
<td>975</td>
<td>1</td>
<td>38</td>
<td>5.5</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>~1%</td>
</tr>
<tr>
<td>WT I</td>
<td>–</td>
<td>87</td>
<td>25.5</td>
<td>210</td>
<td>2</td>
<td>0</td>
<td>3.4</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>~0%</td>
</tr>
<tr>
<td>WT II</td>
<td>–</td>
<td>76</td>
<td>35.6</td>
<td>NA</td>
<td>1</td>
<td>0</td>
<td>2.1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>~1%</td>
</tr>
<tr>
<td><em>Humiriaceoxylon ocuense</em> Herrera et al. 2012</td>
<td>–</td>
<td>154</td>
<td>5.7</td>
<td>1082</td>
<td>1</td>
<td>8</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>~0%</td>
</tr>
</tbody>
</table>
Symplocos (Symplocaceae), then the detailed work of van den Oever et al. (1981) on ecomorphic gradients in Symplocos may be used to support the conclusion that S. panamense was an understory tree growing at low elevation in everwet rainforest, a conclusion that would be consistent with what is known of the depositional environment and co-occurring taxa.

All the woods that were examined for this study are diffuse porous and growth rings are generally absent or indistinct, suggesting minimal seasonality and continuous water availability. The assemblage exhibits a broad range of vessel diameters, including several with mean values greater than 200 µm. These features are typical of trees in tropical forests where soil moisture is maintained year-round (Détienne 1989; Worbes 1999, 2002; Wheeler et al. 2007a; Fichtler & Worbes 2012). The samples described above are generally small, with minimum stem diameters of 30 cm or less, but larger specimens (up to 50 cm) are common in Ocú and in the collections at Harvard. In modern tropical forests, trees 30–50 cm in diameter at breast height are typically 21–27 m tall on average (Feldpausch et al. 2011). Because the stem diameters of the fossils are not necessarily taken at breast height and because the fossil woods are decorticated, 21–27 m is a minimum canopy height estimate for the fossil flora.

The Vulnerability Index (VI) was developed by Carlquist (1975) as a means of assessing the relative vulnerability of woods to cavitation. VI values are calculated by dividing the mean vessel diameter by the vessel frequency; high VI values (> 2–3) together with rare growth rings are considered indicative of tropical rainforest communities (Wheeler 1991; Burnham & Johnson 2004). For the Ocú wood assemblage, VI values range from 2.1–146, supporting a tropical rainforest interpretation (Table 6). However, a review of data from modern tropical forests shows that trees with high VI values and indistinct growth rings are also found in tropical forests with long and short dry seasons (den Outer & van Veenendaal 1976; Barajas-Morales 1985; Lindorf 1994), and so this combination of features alone may not be sufficient for demonstrating tropical rainforest conditions.

Many wood anatomical features vary predictably with climate (Baas 1986; Baas & Schweingruber 1987; Carlquist 1988; Wheeler & Baas 1991, 1993; Woodcock & Ignas 1994; Wiemann et al. 1999; Fichtler & Worbes 2012) and those relationships are thought to have been consistent at least during the Cenozoic (Wheeler & Baas 1991). The stability of these relationships through time permits paleoclimate inferences based on fossil woods; however, taxon-independent methods for quantitative estimates of paleoclimate using fossil woods are not well developed for the tropics where formation of growth rings can result from a variety of environmental factors that may or may not be annual (Worbes 2002). For example, using data obtained from stem disks, Fichtler and Worbes (2012) showed that mean vessel diameter is positively correlated with mean annual precipitation and negatively correlated with mean duration of the stress period (i.e., dry season or flooding season). Vessel diameter also varies with stem length (Wheeler et al. 2007a; Fichtler & Worbes 2012; Olson & Rosell 2013; Rosell & Olson 2014) and therefore the relationships found by Fichtler and Worbes (2012) include variation from canopy structure and canopy height. Fichtler and Worbes (2012) also showed that the cross-sectional area of the stem occupied by parenchyma is not related to tree
height, but is significantly correlated with mean annual precipitation and mean duration of the stress period. Woods with > 30% of cross-sectional area occupied by axial parenchyma are rare outside the tropics (Morris et al. 2016). Within the tropics wetter habitats tend to have trees with a lower cross-sectional area of parenchyma, whereas dryer habitats tend to have trees with a higher cross-sectional area of parenchyma (Fichtler & Worbes 2012). The inverse is true for cross-sectional area occupied by fibers (Fichtler & Worbes 2012). The Azuero woods exhibit a wide range of values for cross-sectional area of axial parenchyma < 1–40% and of parenchyma conformation, but most have very low values (Table 6). This is consistent with the hypothesis that that they grew under tropical moist to tropical wet conditions with a short dry interval.

Nonmetric Multidimensional Scaling of wood anatomical characters from a variety of communities and ecological categories shows that the anatomy of the Azuero woods is most like that of modern tropical rainforests (Fig. 15). We concur with Martínez-Cabrera & Cevallos-Ferriz (2008) that the arrangement of communities and ecological categories along the first axis could be interpreted as a mesomorphy gradient. Position along the second axis is closely related to average number bars per perforation plate and may reflect humidity or light availability. The communities on the right are characterized by features that confer highly efficient water conduction but high vulnerability to cavitation such as simple perforation plates, wide vessels, and low vessel frequency. On average, the woods from Ocú are very efficient and vulnerable, and plot closest to other tropical forests and rainforests. Whereas high incidences of simple perforation plates are associated with plants that experience high evapotranspirative demand such as rainforest canopy trees or desert plants, scalariform plates are common in plants that experience lower demand such as rainforest understory trees or in cloud forests (e.g. Baas 1986; Christman & Sperry 2010). We suggest that the presence of several woods with scalariform perforation plates among an assemblage dominated by wood types with simple perforation plates and very wide vessels indicates the co-occurrence of shade-adapted understory trees and canopy-dominant trees in a multistoried tropical rainforest.

The paleogeographic setting of Panama during the late Paleogene to Miocene provides another source of information about the environment of the Ocú woods. Paleogeographic reconstructions show that Central America has been near the equator since its emergence in the Eocene (Iturralde-Vinent 2006; Buchs et al. 2011; Farris et al. 2011; Ramírez et al. 2016), and estimated mean annual sea surface temperatures are more than 26°C from the late Eocene (Tripati & Zachos 2002) to late Miocene (LaRiviere et al. 2012). These temperatures would have supported megathermal conditions on land in Panama during the late Eocene to Miocene.

We expected the Rare Earth Element analysis to show that the relative concentrations of rare earth elements in the Ocú woods was more similar to either the calcareous, parautochthonous woods from the Cucaracha Fm. or the allochthonous silicified woods from the Alajuela Fm. We also hypothesized that the variation in REE profiles within the Alajuela assemblage might be higher than in the Cucaracha Fm., if the Alajuela woods were reworked from an older unit. In this case, the REE profiles were not use-
ful for discriminating the groups of fossil woods based on transport regime, but the REE concentrations were useful for discriminating the groups of fossil woods based on mineralization type. We speculate that the REE environment was broadly similar across depositional basins in Panama during the Miocene because it was controlled by the regional erosion regime (Trueman & Benton 1997). Therefore, the differences in time and space between the three populations were not large enough to detect differences between the groups apart from mineralization environment, which appears to influence concentration.

CONCLUSIONS

This work contributes to our knowledge of the history of Panama’s extraordinary biodiversity, and builds on the initial work of Stern and Eyde (1963). At least ten taxa are recognized. These occurrences include the first records of Ficus (Moraceae) and Lauraceae from Panama, and the first macrofossil evidence of Sapotaceae and either Symplocos or Pentaphylacaceae from Panama. This study emphasizes the importance of fossil wood as a source of information about the history of plant groups that are rare or difficult to identify based on fossil leaves, fruit, or pollen (e.g. Ficus), as well as a source of information about paleoenvironment. Taken together, the taxonomic affinities, wood functional traits, and paleogeography all support the conclusion that these trees were part of a tropical rainforest (MAT > 18 °C and MAP > 2000 mm yr⁻¹). The full significance of the discovery of a tropical rainforest community based on the fossil woods from the Azuero Peninsula, Panama, rests on determining the precise age of the fossils and additional fieldwork to identify the source(s) of the wood is ongoing.

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