

Fruits and wood of *Parinari* from the early Miocene of Panama and the fossil record of Chrysobalanaceae¹

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PREMISE OF THE STUDY: Chrysobalanaceae are woody plants with over 500 species in 20 genera. They are among the most common trees in tropical forests, but a sparse fossil record has limited our ability to test evolutionary and biogeographic hypotheses, and several previous reports of Chrysobalanaceae megafossils are doubtful.

METHODS: We prepared fossil endocarps and wood collected from the lower Miocene beds along the Panama Canal using the cellulose acetate peel technique and examined them using light microscopy. We compared the fossil endocarps with previously published fossils and with fruits from herbarium specimens. We compared the fossil wood with photographs and descriptions of extant species.

KEY RESULTS: *Parinari* endocarps can be distinguished from other genera within Chrysobalanaceae by a suite of features, i.e., thick wall, a secondary septum, seminal cavities lined with dense, woolly trichomes, and two ovate to lingulate basal germination plugs. Fossil endocarps from the Cucaracha, Culebra, and La Boca Formations confirm that *Parinari* was present in the neotropics by the early Miocene.

CONCLUSIONS: The earliest unequivocal evidence of crown-group Chrysobalanaceae is late Oligocene–early Miocene, and the genus *Parinari* was distinct by at least 19 million years ago. *Parinari* and other Chrysobalanaceae likely reached the neotropics via long-distance dispersal rather than vicariance. The presence of *Parinari* in the Cucaracha flora supports the interpretation of a riparian, moist tropical forest environment. *Parinari* was probably a canopy-dominant tree in the Cucaracha forest and took advantage of the local megafauna for seed dispersal.

KEY WORDS Chrysobalanaceae; fossils; fruits; Miocene; neotropics; Panama; *Parinari*; wood

Chrysobalanaceae comprises 20 genera and over 500 species of trees and shrubs. The family is pantropical and among the most common trees in tropical forests (Prance and White, 1988; Gentry, 1993; Burnham and Johnson, 2004). Molecular phylogenetic studies and flower anatomy indicate that Chrysobalanaceae is closely related to Euphroniaceae, Dichapetalaceae, and Trigonaceae within the large order Malpighiales (Soltis et al., 2011; Xi et al., 2012; Endress et al., 2013), and several reproductive synapomorphies support the monophyly of the family (Yakandawala et al., 2010). A Late Cretaceous origin has been inferred from molecular divergence estimates (Davis et al., 2005; Wang et al., 2009; Bardon et al., 2013), but fossil evidence is key to testing hypotheses about the diversification and biogeographic history of the family.

Fossil pollen attributed to Chrysobalanaceae is known from the late Oligocene–Miocene of South America, Panama, and Africa (Salard-Chebouldaef, 1978; Jaramillo et al., 2006, 2014; Eisawi and Schrank, 2008; Hoorn et al., 2010), and phytoliths produced by Chrysobalanaceae dominate some tropical fossil assemblages (Piperno, 2006), but the published megafossil record of Chrysobalanaceae is sparse (Table 1). The first report of fossil Chrysobalanaceae was permineralized wood described by Pfeiffer and Van Heurn (1928) from the Pliocene of Southeast Asia. Several woods have since been attributed to the family from the Miocene of India. Only seven fossil fruits have been reported (Table 1) even though the endocarps of many genera are hard and have high preservation potential (Tiffney et al., 1994; Wijninga, 1996; Lott et al., 2011). The paucity of studies on fruit morphology in Chrysobalanaceae may be the reason more fossils have not been recognized.

Here we describe exquisitely preserved and abundant permineralized endocarps attributable to *Parinari* Aubl. and wood attributable to Chrysobalanaceae. The fossils come from three sites in lower Miocene deposits along the Panama Canal and we hypothesize that the same plants produced the endocarp and wood remains. These

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TABLE 1. Fossil record of Chrysobalanaceae. Summary of the Paleogene and Neogene megafossils that have been attributed to Chrysobalanaceae with our evaluation of their reliability.

Taxon	Organ(s)	Age	Country	Citation	Familial status
<i>Chrysobalanus coloradensis</i> Knowlton	leaves	Mio-Pliocene	United States	Knowlton, 1930	
<i>C. ellipticus</i> (non Solander) Chaney et Sandborn	leaves and fruit	Eocene	United States	Chaney and Sanborn, 1933	
<i>C. eoiaco</i> MacGinitie	leaves	Eocene	United States	MacGinitie, 1941	
<i>C. inaequalis</i> Berry	leaves	Eocene	United States	Berry, 1916	
<i>C. lacustris</i> Brown	leaves	Eocene	United States	Brown, 1929	
<i>C. pollardianus</i> Knowlton	leaves	Miocene	United States	Knowlton, 1900	
<i>C. praecuspidatus</i> Hollick et Berry	leaves	Late Cenozoic	Brazil	Berry and Hollick, 1924	
<i>C. praecaco</i> Ettingshausen	leaves	Mio-Pliocene	Brazil	Krasser, 1903	
<i>C. miocenicus</i> Ettingshausen	leaves	Miocene	Brazil	Ettingshausen, 1870	
<i>C. venezuelanus</i> Berry	leaves	Miocene	Venezuela	Berry, 1936	
<i>Hirtella hussakii</i> Ettingshausen	leaves	Mio-Pliocene	Brazil	Krasser, 1903	
<i>H. lojana</i> Berry	leaves	Miocene	Brazil	Berry 1945; Duarte, 1972	
<i>H. perfecta</i> Duarte et Mello Filha	leaves	Eocene?	Brazil	Duarte and Mello Filha, 1980	
<i>Licania pliocenica</i> Ettingshausen	leaves	Mio-Pliocene	Brazil	Krasser, 1903	
<i>L. angustata</i> Duarte et Mello Filha	leaves	Eocene?	Brazil	Duarte and Mello Filha, 1980	
<i>L. gandarelensis</i> Duarte et Mello Filha	leaves	Eocene?	Brazil	Duarte and Mello Filha, 1980	
<i>Parinari</i> sp.	leaves	Pleistocene	Costa Rica	Horn, 2003; Lott et al., 2011	confirmed
<i>Parinari kathogodamense</i> Prasad	leaves	Miocene	India	Prasad, 1994	
<i>"Magnistipula" butayei</i> De Wild.	wood	Pliocene	Congo	Dechamps and Meas, 1990	confirmed
<i>Parinarioxylon cuddalorese</i> Awasthi	wood	late Miocene	India	Awasthi, 1969	confirmed
<i>P. cuddalorese</i>	wood	middle Miocene	India	Srivastava and Awasthi, 1996	confirmed
<i>P. itersonii</i> Pfeiffer et Van Heurn	wood	Pliocene	Java	Pfeiffer and Van Heurn, 1928	confirmed
<i>P. itersonii</i>	wood	Miocene	Ethiopia	Lemoigne, 1978	
<i>P. neyveliense</i> Awasthi et Agarwal	wood	Miocene	India	Awasthi and Agarwal, 1986	confirmed
<i>P. panamensis</i> sp. nov.	wood	early Miocene	Panama	this study	confirmed
<i>P. splendidum</i> Trivedi et Ahuja	wood	Miocene	India	Trivedi and Ahuja, 1979	confirmed
<i>Chrysobalanus eocenica</i> Berry	endocarps	Eocene	United States	Berry, 1916, 1930	
<i>Colombicarpon biloculare</i> Reid	endocarps	Oligocene?	Colombia	Reid, 1933	tentative
<i>Parinari</i> sp.	endocarps	Pleistocene	Costa Rica	Lott et al., 2011	confirmed
<i>Parinari</i> sp.	endocarps	Pliocene	Colombia	Wijninga and Kuhry, 1990	
<i>Parinari</i> sp.	endocarps	middle Miocene	Colombia	Wijninga, 1996	tentative
<i>P. antiquum</i> Tiffney, Fleagle, et Brown	endocarps	early Miocene	Ethiopia	Tiffney et al., 1994	confirmed
<i>P. panamensis</i>	endocarps	early Miocene	Panama	this study	confirmed
<i>Licania dominicensis</i> (Poinar, Chambers et Brown) Chambers et Poinar	flowers & fruit	Oligo-Miocene	Dominican Republic	Chambers and Poinar, 2010	confirmed

fossils provide new data for interpreting the paleo-environment of southern Central America. Finally, we review the status of the megafossil record of Chrysobalanaceae to clarify what is known about the biogeographic history of the family.

MATERIALS AND METHODS

Comparative material—We examined fruits of extant Chrysobalanaceae using the collections at the University of Florida Herbarium (FLAS) in Gainesville, Florida; the Missouri Botanical Garden Herbarium (MO); and the New York Botanical Garden Herbarium (NY) (Table 2). We made transverse sections of the living fruits using a Microslice 2 annular saw and examined the cut faces. In some cases, we made thin (20–30 μm) sections and stained them with 0.5% w/v methylene blue in alcohol to make the fibers and vascular tissue more visible. We compared the fossil wood with available descriptions and images in Metcalfe and Chalk (1950) and the InsideWood Database (InsideWood, 2004 onward; Wheeler, 2011), and we wrote our description using the IAWA List of Features for Hardwood Identification (IAWA Committee, 1989).

Geologic setting—The wood and most of the fossil endocarps described here were collected from the northern Lirio East exposure in the Culebra Cut (Gaillard Cut) section of the southeastern part of the Panama Canal (Fig. 1). This locality is in the lower part of the Cucaracha Formation. The fossil assemblage includes at least 61 morphotypes of fossil fruits and seeds dated to approximately ~19 million years ago (Ma) (Herrera et al., 2010, 2014; MacFadden et al., 2014). Lithofacies, sedimentary structures, fossils, and ichnofossils support the inference that the 100–140 m thick formation was deposited in a coastal delta-plain setting (Kirby et al., 2008; Herrera et al., 2010). The fossils are preserved as calcareous cellular permineralizations in poorly sorted volcanoclastic sandstones. The plant fossils probably represent a local assemblage based on the exceptional preservation of delicate plant parts (e.g., flowers) that would not survive extensive transport. Three additional endocarps were collected from two other localities. One was collected from the uppermost Culebra Formation at the Empire site, across the Canal from the northern Lirio East exposure. The other two endocarps were collected from the Gold Hill site, southeast of the northern Lirio East exposure along the canal. The La Boca Formation is exposed at Gold Hill. Woodring (1964) considered La Boca younger than the Cucaracha Formation; however, Kirby et al. (2008)

TABLE 2. List of examined comparative material from extant Chrysobalanaceae. FLAS: Florida Agricultural Station; MO: Missouri Botanical Garden Herbarium; NYBG: New York Botanic Garden Herbarium.

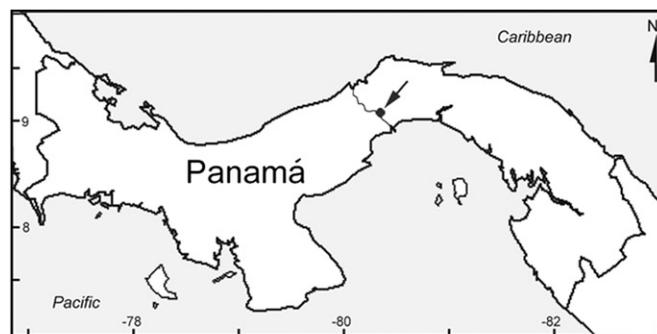
Species	Herbarium accession
<i>Acioa schulesii</i> Maguire	MO 2787220
<i>Acioa whytei</i> Stapf	MO 2130129
<i>Atuna excels</i> (Jack) Kosterm.	MO 933985
<i>Bafodeya benna</i> (Sc. Ell.) Prance	MO 1652308
<i>Chrysobalanus icaco</i> L.	FLAS 163564
<i>Chrysobalanus icaco</i> L.	FLAS 1939
<i>Couepia guianensis</i> Aubl.	FLAS 215778
<i>Dactyladenia bellayana</i> (Baill.) Prance et F. White	MO 5724447
<i>Dactyladenia chevalieri</i> (De Wild.)	NYBG 2393
<i>Exellodendron barbatum</i> (Ducke) Prance	MO 5945818
<i>Exellodendron coriaceum</i> (Benth.) Prance	MO 2468609
<i>Exellodendron coriaceum</i>	NYBG 1700
<i>Grangeria porosa</i> Boivin ex Baill.	MO 6472361
<i>Hunga rhamnoides</i> (Guillaumin) Prance	MO 5993660
<i>Hunga</i> sp.	MO 3132019
<i>Kostermanthus heteropetalus</i> (King ex Scort.) Prance	FLAS 567904
<i>Licania hypoleuca</i> Benth.	FLAS 131113
<i>Licania parviflora</i> Benth.	FLAS 110863
<i>Magnistipula cerebriformis</i> (R. Cap.) F. White	MO 5744021
<i>Magnistipula tessmannii</i> (Engl.) Prance	MO 2749A
<i>Maranthes corymbosa</i> Blume	FLAS 2066082
<i>Maranthes robusta</i> (Oliv.) Prance, in F. White	MO 1829083
<i>Neocarya macrophylla</i> (Sabine) Prance, in F. White	MO 5657564
<i>Parastemon urophyllus</i> (Wall. ex A.D.C.) A.D.C.	NYBG 3613
<i>Parastemon versteeghii</i> Merrill et Perry	NYBG 25062
<i>Parinari campestris</i> Aubl.	FLAS 1710267
<i>Parinari choacoensis</i> Prance	MO 05054889
<i>Parinari excelsa</i> Sabine	MO 5944082
<i>Parinari pachyphylla</i> Rusby	NYBG 3383a
<i>Parinari pachyphylla</i>	NYBG 3383b
<i>Parinari parvifolia</i> Sandw.	MO 2028906
<i>Parinari sprucei</i> Hook	FLAS 9945

concluded that the La Boca Formation is older and was deposited 20.62–23.07 Ma. If Kirby et al. (2008) are correct, then the Gold Hill *Parinari* specimens are ~1–4 million years (Myr) older than the specimens from the Cucaracha and Culebra Formations.

Fossil preparation—We examined more than 145 *Parinari* specimens (at least 143 endocarps and 1 wood fragment). Several endocarps were cut along either a longitudinal or transverse plane and then serially sectioned using the cellulose acetate peel technique (Joy et al., 1956). The peels were mounted on microscope slides with Canada Balsam mounting medium. Images of macroscopic features were captured with a Canon EOS digital camera and a 100 mm EF macro lens, and microscopic features were captured with the camera mounted on a Nikon compound microscope. We processed the images with Adobe Photoshop (San Jose, California, USA). The specimens, peels, and microscope slides are curated at Florida Museum of Natural History Paleobotanical Collections, Gainesville, Florida, United States.

RESULTS

Our comparison of all the extant genera of Chrysobalanaceae showed that *Parinari* and *Neocarya* Prance are easily distinguished from the others (Table 3). A secondary septum divides the locule into two seminal cavities in 8 of 20 genera (*Atuna* Rafin., *Bafodeya*



Lirio East (North)

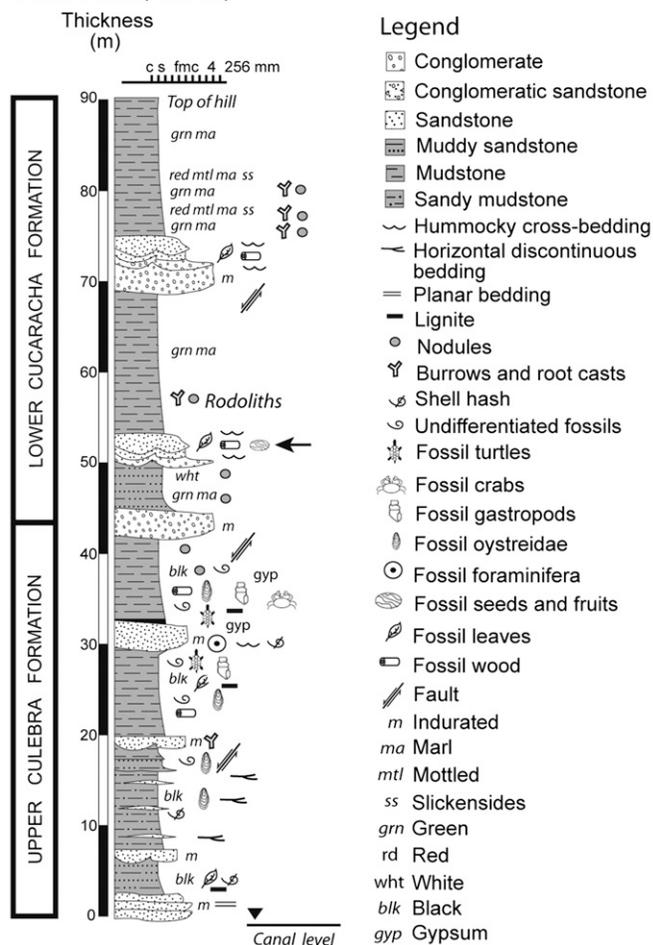


FIGURE 1 Map of Panama and stratigraphy of the northern Lirio East exposure. The locality where the fossils were collected is marked by arrow on both map and stratigraphic section. The fossil-bearing layers discussed here occur in a transitional zone between the shallow marine Culebra Formation and the primarily terrestrial Cucaracha Formation.

Prance, *Exellodendron* Prance, *Hunga* Pancher ex Prance, *Magnistipula* Engl. sg. *Pelligriniella*, *Maranthes* Blume, *Neocarya*, and *Parinari*). In *Parinari* and *Neocarya*, seedlings emerge from the endocarp via basal germination plugs, whereas in other six genera there are lateral germination plates (e.g., *Maranthes*), longitudinal lines of fracture (e.g., *Hunga* L.) that separate and allow the seedling to emerge, or seedlings may emerge via irregular fracture of the

TABLE 3. Morphological characters distinguishing *Parinari* endocarps from those of related genera. Character states in boldface are shared with *P. panamensis*. In very thick-walled endocarps, the ratio of diameter of the seminal cavity to the thickness of the wall in equatorial section is ≥ 1 .

Taxon	Secondary septum	Endocarp wall thickness	Germination mechanism	Seminal cavity lining
<i>Parinari</i> Aubl.	present	thick to very thick	2 ovate-lingulate basal plugs	dense woolly
<i>Acioa</i> Aubl.	absent	thin to thick	irregular fracture	glabrous; hispid
<i>Afrolicania</i> Mildibr.	absent	very thin	irregular fracture	sparsely pubescent
<i>Angelesia</i> Korth.	absent	not examined	irregular fracture	not examined
<i>Atuna</i> Raf.	absent	thick	irregular fracture	sparsely pubescent
<i>Bafodeya</i> Prance ex F. White	present	thick	irregular fracture	hispid
<i>Chrysobalanus</i> L.	absent	thin	4–8 longitudinal lines	sparsely pubescent
<i>Couepia</i> Aubl.	absent	thin to thick	irregular fracture	sparsely pubescent
<i>Dactyladenia</i> Welw.	present	thin	irregular fracture	hispid
<i>Exellodendron</i> Prance	absent	thin to thick	1 line of dehiscence	sparsely woolly
<i>Gaulettia</i> Sothers et Prance	absent	thin to thick	irregular fracture	sparsely pubescent
<i>Grangeria</i> Comm. ex Juss.	absent	thin	2 lateral plates	sparsely woolly
<i>Hirtella</i> L.	absent	thin	4–7 longitudinal lines	sparsely woolly
<i>Hunga</i> Prance	present	thin	4–6 longitudinal lines	dense woolly
<i>Kostermanthus</i> Prance	absent	thick	irregular fracture	sparsely pubescent
<i>Licania</i> Aubl.	absent	very thin	irregular fracture	sparsely pubescent
<i>Magnistipula cerebriiformis</i> (Capuron) F. White	absent	thin	irregular fracture	sparsely pubescent
<i>Magnistipula butayei</i> De Wild.	absent	thin	irregular fracture	hispid
<i>Magnistipula tessmannii</i> (Engl.) Prance	present	thick	irregular fracture	hispid
<i>Maranthes</i> Blume	present	thick to very thick	2 lateral plates	dense woolly
<i>Neocarya</i> (DC.) Prance ex F. White	present	very thick	2 circular basal plugs	dense woolly
<i>Parastemon</i> A.DC.	absent	thin	2 lateral plates	sparsely pubescent

endocarp wall (e.g., *Exellodendron*). Our observations also suggest that the trichomes lining the seminal cavities and the histology of the endocarp wall may also be useful for distinguishing between the genera, and these will be explored in a forthcoming study. The endocarps of *Neocarya macrophylla* (Sabine) Prance may be distinguished from those of *Parinari* by their wide, dorsoventrally flattened shape, their small, nearly circular basal germination plugs, and by a prominent beak at the base of the endocarp (Hill, 1937; Tiffney et al., 1994). Our examination of all the extant genera has given us confidence in placing the new Panamanian fossil endocarps in *Parinari*; next we provide additional developmental and morphological features of the extant fruits that are useful for its recognition in the fossil record.

Fruit structure and anatomy in extant *Parinari*—The gynoecium is initially tricarpeolate, but normally only the anterior carpel is functional. As the flower matures, the single functional carpel bulges outward and upward, resulting in a pseudomonomerous ovary with a gynobasic style and a basal, axile placenta that is translated to a topographically dorsal position (Juel, 1915; Matthews and Endress, 2008). At the same time, a secondary septum develops that longitudinally divides the locule into two collateral seminal cavities except at the placenta (Juel, 1915; Matthews and Endress, 2008). A single seed may develop in each seminal cavity; however, there is commonly only one mature seed per fruit.

The fruit is a fleshy drupe with a lenticellate epicarp, a thin, fleshy mesocarp, and a thick-walled, hard endocarp. The endocarp is typically prolate-ellipsoid to oblong with a rough, verrucous, and fibrous surface that may be channelled (Fig. 2A). Two germination plugs are located ventrolaterally near the base of the endocarp, and each is associated with one of the two seminal cavities (Fig. 2A–C; also note the secondary septum). The plugs are ovate to lingulate, about twice as long as wide, and they extend one-quarter to one-third the length of the endocarp.

The endocarp wall consists of several layers. The innermost layer is made up of dense sclerenchymatous tissue and is only present

near the base of the endocarp where it surrounds the germination plugs and interrupts the secondary septum (Fig. 2D). This layer ranges from less than one half to several millimeters wide, extends through the endocarp wall at the base and is sometimes visible on the exterior surface as a line connecting the two germination plugs near where the fruit was attached to the pedicel. Two vascular bundles (Fig. 2D, E) run through this layer from the point of fruit attachment to each of the two seminal cavities.

The second layer of tissue is typically less than 0.5 mm wide and lines the seminal cavities. Near the base of the endocarp, it envelops the innermost layer (Fig. 2F). The inner surface of this layer bears trichomes that give the wall of the seminal cavities a woolly texture; the other side is lined with large spherical to subspherical idioblasts (Fig. 2F).

The third and outermost layer of the endocarp, called the mesocarp by Kostermans (1965), is thick, tough, and has a marmorate appearance in transverse section. It is composed of convoluted bundles of very thick-walled fibers (here termed fiber tracts), thick-walled sclereids, and longitudinal fiber bundles. The fiber tracts (Fig. 2F–H) are irregularly shaped and range from one quarter to several millimeters across. They appear homogenous under a hand lens, but their fibrous composition is readily apparent in thin sections, especially when stained with methylene blue. The individual fibers are ~10–15 μm in diameter and have almost no lumen. These fiber tracts provide the endocarp wall with its marmorate appearance (Kostermans, 1965). The sclereids surrounding the fiber nests are ~65 μm long by 35 μm wide and have larger lumina than the fibers (Fig. 2H). The longitudinal fiber bundles are positioned on the endocarp surface where they may run the length of the fruit (Fig. 2A). Cavities may or may not be present in the outer part of the endocarp wall.

Systematics—

Order—Malpighiales C. Martius

Family—Chrysobalanaceae R. Brown

Genus—*Parinari* Aublet

Species—*Parinari panamensis* sp. nov. Jud, Nelson, et Herrera (Fig. 3A–I)

Specific Diagnosis: Plants producing drupes with thick, tough, endocarps. Endocarps prolate-ellipsoid to oblong, usually about 3 cm long by 2 cm wide. Surface with irregular, shallow longitudinal grooves. Two ventrolateral ovate to lingulate germination plugs (L:W ratio \approx 2) located near endocarp base; plugs extend 1/4–3/8 the length of the endocarp. Locule divided into two lateral seminal cavities by secondary septum. Inner walls of the seminal cavities woolly. Endocarp wall thick, multilayered. Innermost layer thin, composed of small, thick-walled cells lining the germination plugs at base of endocarp. Two small vascular bundles running through this layer from base of endocarp to each of two seminal cavities. Second layer thin, forming the lining of the seminal cavities and enveloping the innermost layer near the base of the endocarp. Outer margin of this layer marked by narrow zone of large idioblasts. Outermost endocarp layer thick, without cavities, and composed primarily of both sclereids and fiber tracts.

Holotype here designated. UF063001 (Fig. 3B–F, H)

Paratypes: UF063005 (Fig. 3G); UF063006 (Fig. 3I). UF060854; UF060857; UF060856; UF060858; UF060855; UF060853; UF063201; UF063250

Localities: Panama; northern Lirio East site Panama Canal (N 9.051375°, W 79.649027°); Empire site, Panama Canal (N 9.05769°, W 79.66185°); Gold Hill, Panama Canal (N 9.04545°, W 79.644167°)

Stratigraphic position and age: Uppermost Culebra Formation and Lower Cucaracha Formation; early Miocene; 19 Ma. La Boca Formation; early Miocene

Etiymology: named for the country in which it was discovered

Detailed Description: Endocarps ellipsoid to oblong, 21–40 mm long and 15–27 mm wide (we measured the smallest and largest specimens); surface smooth to shallowly pitted, abraded, with shallow, irregular, longitudinal grooves (Fig. 3A). Locule divided into two seminal cavities by a longitudinal secondary septum (1.1–1.6 mm wide in transverse sections taken above germination plugs, $n = 10$), which is almost entirely continuous with the outer endocarp wall, except near the base of the endocarp where it is interrupted by the innermost tissue layer (Fig. 3D). Two ventrolateral, ovate to lingulate germination plugs present in the endocarp wall near the base (Fig. 3A, C). Endocarp wall made up of three distinct layers of tissue. Innermost layer composed of dense sclerenchyma, typically <0.5 mm thick, only present near the base of the endocarp where it surrounds the germination plugs and meets the secondary septum (Fig. 3D); visible on the surface of the endocarp as a line connecting the two germination plugs; contains two vascular bundles which run along it from the base of the endocarp to the seminal cavities; vascular bundles \sim 350 μ m in diameter, composed of xylem cells \sim 10 μ m in diameter; phloem either lacking or not preserved (Fig. 3E). Second layer typically <0.5 mm thick; lines the seminal cavities with trichomes to the inside; contains subspherical idioblasts (\sim 25 μ m in diameter) to the outside (Fig. 3F, G); also envelops the innermost layer near the base of the endocarp. Third and outermost layer 1.0–5.4 mm thick ($n = 10$) and marmorate, composed of isodiametric thick-walled sclereids and convoluted bundles of poorly preserved very-thick-walled fibers (fiber tracts); tracts up to \sim 1 mm across (Fig. 3H).

Remarks: Several other specimens of *Parinari* have been described from fossilized endocarp material. *Parinari antiquum* Tiffney et al. (1994) was described from the lower Miocene of

Ethiopia, but several features distinguish *P. panamensis* from *P. antiquum* including the narrower shape, the absence of cavities in the endocarp wall, and the presence of a woolly, rather than papillate lining of the seminal cavities. The absence of trichomes lining the seminal cavities in *P. antiquum* is surprising because trichomes were present in all of the herbarium specimens that we examined. It is possible that they were not preserved rather than truly absent.

Parinari endocarps were also described by Wijninga (1996) from the Miocene of Colombia and by Lott et al. (2011) from the Pleistocene of Costa Rica. Wijninga (1996) documented the bilocular endocarp and distinctive basal germination plugs in the Colombian specimens, but the internal anatomy was not described. Unfortunately, to our knowledge, those Colombian specimens collected by Wijninga (1996) have been lost, and the fossil locality remains unexplored. We reexamined the specimens from Costa Rica and confirmed that the histology of endocarp wall matches *Parinari*. The specimens from Costa Rica are similar to *P. panamensis* because they share the characteristic germination plugs, the marmorate endocarp wall composed of sclereids and fiber tracts, the endocarp wall lacking cavities, and the woolly trichomes lining the seminal cavities; however, they are typically smoother, often with a narrower septum (less than 1 mm), and can exceed *P. panamensis* in length (up to 53 mm reported by Lott et al. [2011]) because the endocarps have a more pronounced, beak-like tapered base.

Wijninga (1996) compared fossils of *Colombicarpon biloculare* Reid with *Parinari* endocarps based on size, shape, the presence of two asymmetrical seminal cavities, two germination plugs, and a wall composed of tortuous strands of woody fibers. In the original description, Reid (1933, p. 213) noted the presence of a groove that lies “in the plane which bisects the two plugs, [and] is aligned towards the apex of the fruit.” This groove may correspond to the innermost layer in extant *Parinari* (Figs. 2D, 3D). While we agree that the specimens of *C. biloculare* may in fact be *Parinari* endocarps, they are consistently smaller than *P. panamensis* and more strongly asymmetrical. Similar to *P. antiquum*, the locules are said to be lined with digitate cells (Reid, 1933), not woolly trichomes as in extant *Parinari* and *P. panamensis*. The age of *C. biloculare* is unknown; Reid suggested an Oligocene age based only on the degree of carbonization.

Berry (1916) described “*Chrysobalanus eocenica* Berry (fruits) and *C. inaequalis* Berry (leaves) from the Eocene of North America (see also Dilcher, 1965). The leaves were assigned to *Chrysobalanus* based on shape and pattern of the major veins, and the fruits were assigned to *Chrysobalanus* based on the shape and presence of longitudinal ridges similar to those in *Chrysobalanus icaco* L. We reexamined these specimens and we do not consider these fossils reliable occurrences of Chrysobalanaceae because they do not preserve diagnostic characters.

Genus—*Parinariosylon* Pfeiffer et Van Heurn

Species—*Parinariosylon panamensis* sp. nov. Jud, Nelson et Herrera (Fig. 4)

Specific Diagnosis: Tree-sized plant producing diffuse-porous wood without growth rings. Vessels almost exclusively solitary, irregularly arranged; with simple perforation plates. Mean tangential diameter of vessels 100–200 μ m; 5–20 mm⁻². Vessel-ray pits large, apparently simple. Tyloses common. Fibers nonseptate, medium to thick-walled, with distinctly bordered pits. Axial parenchyma exclusively apotracheal; in narrow, irregularly spaced bands 1–4 cells wide, approximately 2 mm⁻¹. Rays nonstoried, almost

exclusively uniseriate (rarely biserate) and homocellular to weakly heterocellular.

Holotype: UF063032 (Fig. 4)

Locality: Panama; Lirio East (North) exposure of the Panama Canal (N 9.051375°, W 79.649027°)

Stratigraphic position and age: Lower Cucaracha Formation; early Miocene; 19 Ma

Etymology: named for the country in which it was discovered

Detailed Description: Fragment of mature wood. Growth rings absent; wood diffuse porous. Vessels exclusively solitary, irregularly arranged, round in transection; mean tangential diameter 158 μm (SD 26.7; range 65–204 μm), frequency 7.55 mm^{-2} (range 6.91–7.95 mm^{-2}). Perforation plates exclusively simple. Intervessel pitting not observed; vessel-ray pits large, vertically elongate, with much reduced borders. Helical thickenings not observed. Vessel element length obscured by poor preservation and abundant tyloses. Tyloses not sclerotic. Fibers medium- to thick-walled, with distinctly bordered pits; septa not observed. Axial parenchyma in narrow bands 1–4 cells wide; band frequency $\sim 2 \text{ mm}^{-1}$. Paratracheal parenchyma scanty to absent. Rays uniseriate, rarely with biseriate portions; weakly heterocellular with predominantly square cells. Rays 19.6 cells tall (range 6–36 cells; $n = 18$); frequency 15.3 mm^{-1} (range 13.3–17.3). Crystals not observed. Secretory structures and storied structure not observed.

Remarks. The diagnosis of the type species, *Parinarioxylon itersonii* Pfeiffer and Van Heurn (1928), is based on diffuse porous wood with indistinct growth rings and large, mostly solitary vessels, and a vessel frequency of 1–2 mm^{-2} , narrow parenchyma bands, and almost exclusively uniseriate rays. The combination of randomly arranged, exclusively solitary vessels, common tyloses, exclusively uniseriate rays, fibers with distinctly bordered pits, paratracheal parenchyma absent, and narrow parenchyma bands is found only in Chrysobalanaceae, and the wood of most of the extant genera conforms to *Parinarioxylon* (see InsideWood Database, 2004 onward). The differences between the fossil species *P. panamensis* and *P. itersonii* include the presence of tyloses in our species and a few quantitative differences such as higher vessel frequency and smaller mean vessel diameter.

Summary: *Parinari* endocarps are easily recognized and distinguished from those of other genera of Chrysobalanaceae because they have a thick wall, a secondary septum, seminal cavities lined with dense, woolly trichomes, and two ovate to lingulate basal germination plugs (Table 3). The diagnosis of *Parinarioxylon panamensis* wood is based on two fragments of diffuse-porous mature secondary xylem with large, exclusively solitary vessels, simple perforation plates, large ray-vessel pits, fibers with distinctly bordered pits, little to no paratracheal parenchyma, narrow parenchyma bands, diffuse apotracheal parenchyma, and almost exclusively uniseriate, weakly heterocellular rays. This com-

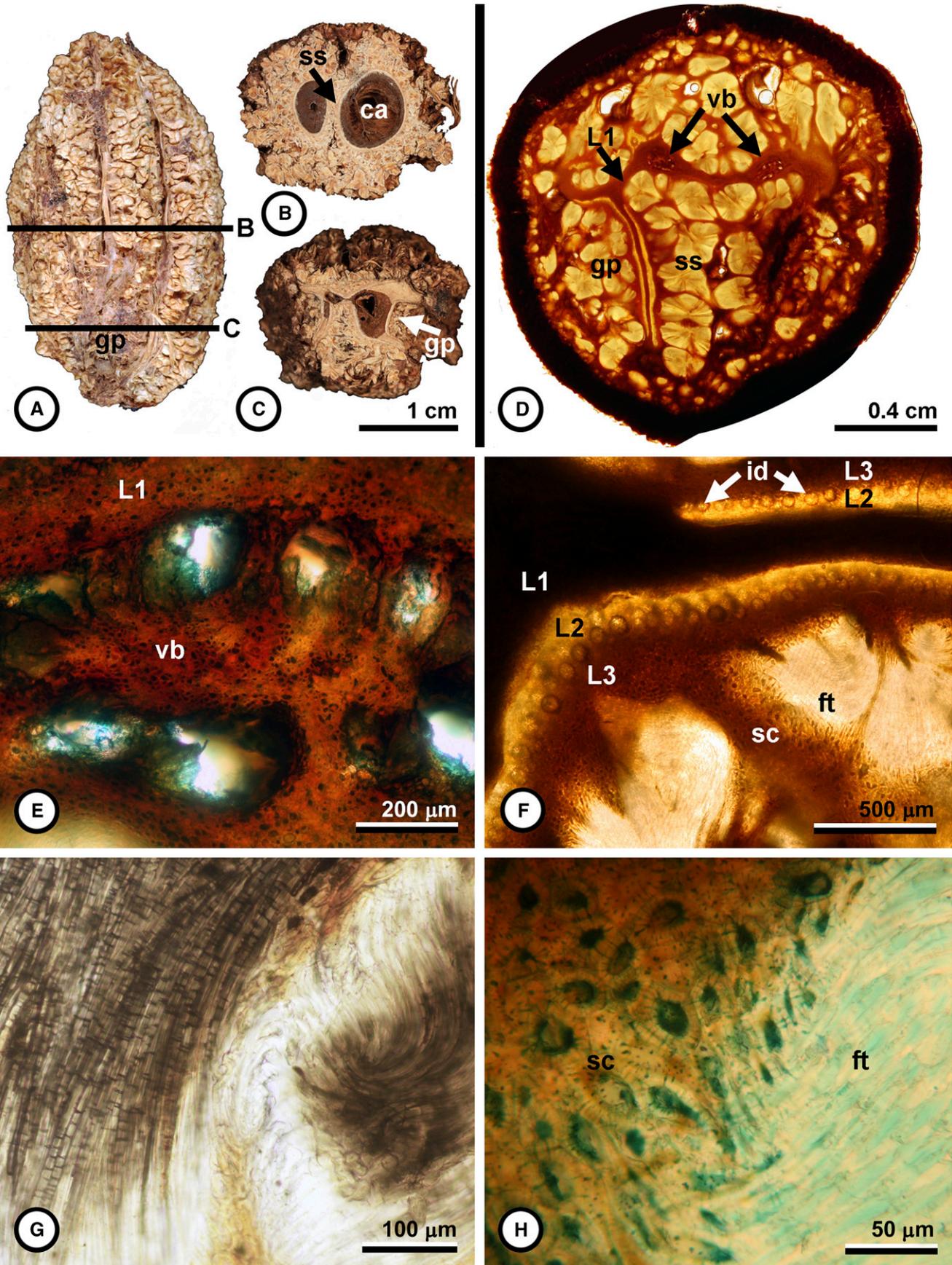
bination of features is diagnostic of Chrysobalanaceae (Metcalf and Chalk, 1950; Prance and White, 1988) and is used to assign chrysobalanaceous fossil wood to the genus *Parinarioxylon*. Characters that define specific genera are unfortunately few (e.g., rare spiral thickenings; Ter Welle, 1975), so until clear combinations of xylem characters are identified for each genus, assigning fossil woods to extant genera of Chrysobalanaceae should be avoided without other evidence linking the wood to more diagnostic plant parts.

DISCUSSION

Fossil record of *Parinari*—*Parinari* endocarps are anatomically distinctive and have high preservation potential because of their thick-walled fibers and sclereids, but there are few published fossil occurrences. At 19 Myr old, the occurrence of *Parinari panamensis* in the lower Cucaracha Formation is among the oldest and best documented of the genus, although the La Boca specimens also described here may be slightly older (~ 21 Ma). Tiffney et al. (1994) described several permineralized endocarps from the lower Miocene of Ethiopia that match the distinctive morphology of *Parinari*, and a radiometrically dated tuff indicates that the fossils are ~ 16 Myr old. Reid (1933) described *Colombicarpum biloculare* from the Cenozoic of Colombia, which she compared with Anacardiaceae but could also be *Parinari* (Wijninga, 1996). The fossils have two seminal cavities and two germination plugs, but examination of the histology of the endocarp wall and the lining of the seminal cavities are needed to confirm its affinity. Other specimens of *Parinari* described by Wijninga (1996) from the middle-late Miocene of Colombia are ovoid to ellipsoid bilocular endocarps with two basal germination plugs and therefore are likely *Parinari*; however, examination of the of the endocarp wall and the trichomes lining the seminal cavities could again confirm the presence of the genus in the Colombian Andes. The fossils described by Wijninga and Kuhry (1990) are probably not *Parinari* because they have large lateral germination valves rather than basal germination plugs. The specimen figured by Lott et al. (2011) from the Pleistocene of Costa Rica clearly shows a thick, hard endocarp wall, two seminal cavities, and two basal germination plugs. Further examination revealed sclereids, fiber tracts, and woolly trichomes lining the seminal cavities (N. A. Jud, personal observations), also supporting a *Parinari* identification.

Woods assigned to *Parinarioxylon* share features that are typical of Chrysobalanaceae in general and therefore do not necessarily represent occurrences of *Parinari*. Reports of *Parinarioxylon* indicate that the family was also present in Miocene and younger deposits in Southeast Asia (Pfeiffer and Van Heurn, 1928) and India (Awasthi, 1969; Trivedi and Ahuja, 1979; Awasthi and Agarwal, 1986; Srivastava and Awasthi, 1996). Lemoigne (1978) reported

FIGURE 2 Endocarp anatomy of extant *Parinari* spp. *P. campestris* Aubl. (A–C), *P. parvifolia* Sandwith (D), *P. congensis* F. Didr. (E–H). (A) External longitudinal view of endocarp showing fibrous texture, longitudinal fiber bundles running along the endocarp, and the location of one germination plug (gp). (B) Transverse section (TS) of the endocarp showing seminal cavities (ca) and secondary septum (ss). (C) TS showing germination plug (gp) near the base of the endocarp. (D) Thin TS near base of endocarp showing two vascular bundles (vb), germination plug (gp), and secondary septum (ss) meeting the dense sclerenchymatous innermost layer (L1). (E) Stained TS showing vascular bundle (vb) in the innermost layer (L1). (F) TS showing three tissue layers: dense, sclerenchymatous innermost layer (L1), second layer (L2) with idioblasts (id), and outermost layer (L3) with sclereids (sc) and fiber tracts (ft). (G) TS showing fiber tracts with fibers at various angles. (H) TS stained with methylene blue showing sclereids with dark lumina (sc) and a fiber tract (ft).



a *Parinarioxylon* from the Miocene of Ethiopia; however, the description of this specimen includes vasicentric paratracheal parenchyma and therefore does not match the diagnosis for *Parinarioxylon*. The wood described here is the first occurrence of *Parinarioxylon* in the neotropics.

The leaves of most Chrysobalanaceae are coriaceous, simple, and pinnate; with entire margins and eucamptodromous to brochidodromous secondary venation (Prance and White, 1988). Thus, identifying the leaves to genus-level can be challenging and is further complicated by convergence in general leaf architecture between Chrysobalanaceae and many other tropically distributed angiosperm families (Prance, 1972; Prance and White, 1988; Corrêa et al., 2015). Fossil leaves assigned to Chrysobalanaceae only by their shape and major venation characters should be treated with extreme caution (Table 1). More reliable fossil identifications will be based on diagnostic features such as glands on the lamina or petiole, trichomes, phytoliths, or cuticle. The only leaf fossils meeting these criteria that we are aware of are those described by Lott et al. (2011) assigned to *Parinari*.

Chrysobalanaceous pollen is distinctive, but the genera are difficult to distinguish (Patel et al., 1983; Prance and White, 1988). Chrysobalanaceous pollen has been reported in late Oligocene–Miocene and younger samples from low latitudes in Panama, South America, and Africa (Anderson and Muller, 1975; Salard-Cheboldaëff, 1978; Hoorn, 1993; Hoorn et al., 2010; Jaramillo et al., 2006, 2010). Chrysobalanaceae also produce abundant and distinctive phytoliths that can dominate sediment samples (Ter Welle, 1976; Piperno, 1991, 2006). Phytoliths from Neogene and older deposits have the potential to further reveal the history of Chrysobalanaceae (Strömberg, 2004), but assigning pollen and phytoliths to particular genera should be done cautiously.

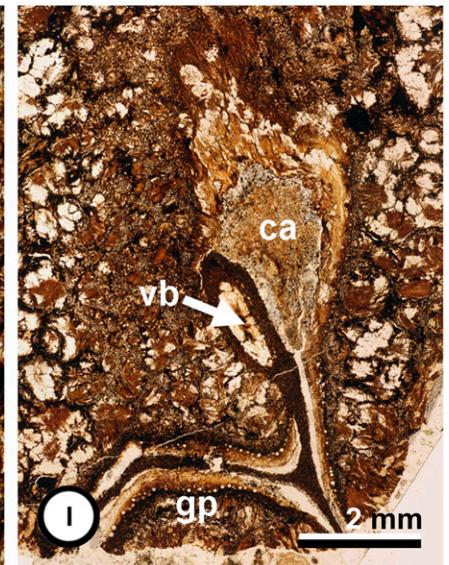
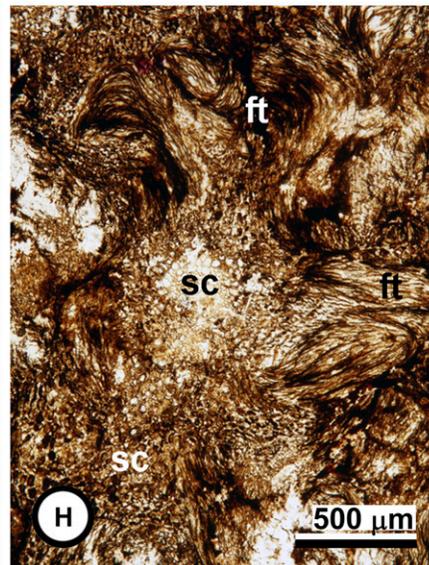
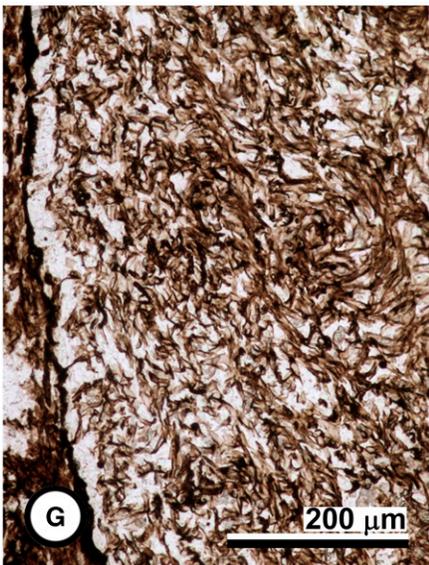
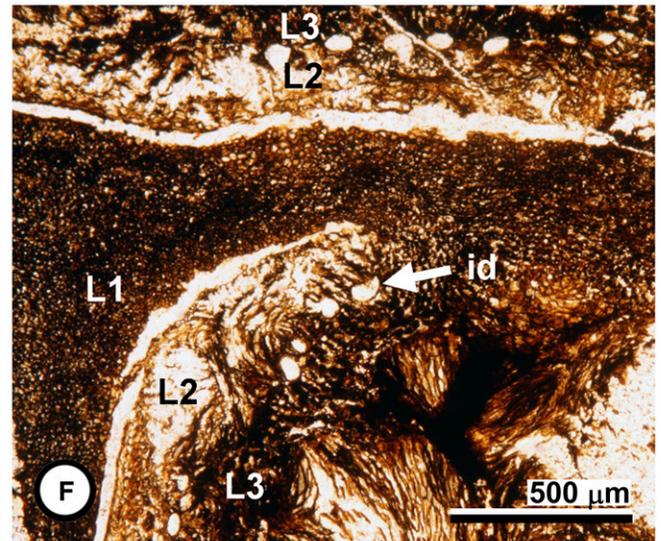
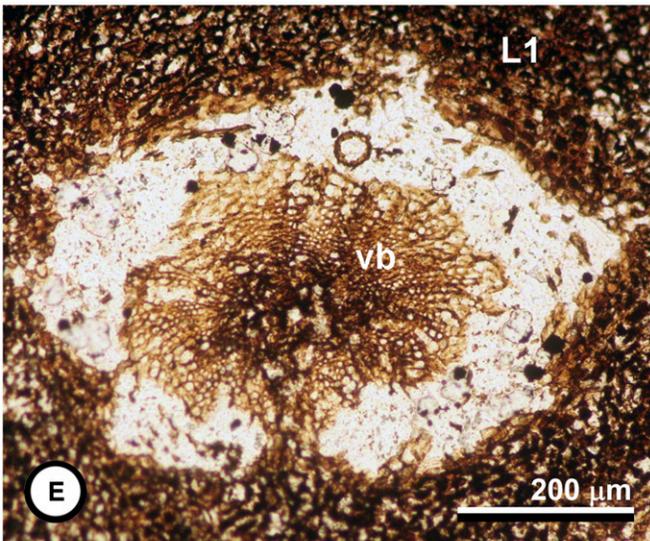
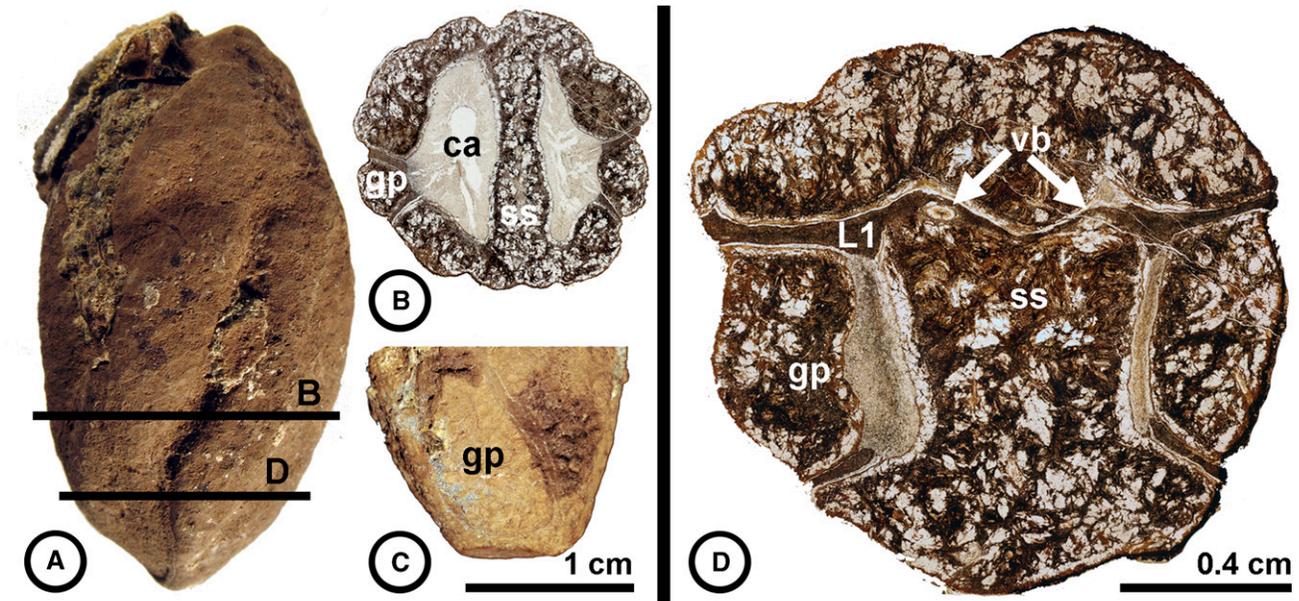
Biogeography—Although the Chrysobalanaceae are pantropical with the highest species richness in neotropical forests (Prance and Sothers, 2003), the phylogenetic relationships among the living genera favor an Old-World origin for the family sometime during the Late Cretaceous to Eocene (Raven and Axelrod, 1974; Bardon et al., 2013). Given the presence of extant Chrysobalanaceae (including *Parinari*, *Chrysobalanus*, *Licania* Aubl.) on islands and the buoyancy of the fruits, transoceanic dispersal events appear to be the most likely explanation for the modern distribution (White, 1983; Prance and White, 1988). The importance of long-distance dispersal across the Atlantic is known in several other tropical plant families as well (Dick et al., 2003; Doyle et al., 2004; Givnish and Renner, 2004; Pennington and Dick, 2004; Antunes Carvalho and Renner, 2012). The asymmetry in species richness between the neotropics and the Old-World tropics may have been generated

by elevated diversification rates in the neotropics, higher extinction rate in the Old-World tropics, or both (Bardon et al., 2013).

Davis et al. (2005) and Bardon et al. (2013) cited Wodehouse (1932), as the earliest occurrence of Chrysobalanaceae pollen, but that occurrence actually was based on a fossil leaf from the Green River Formation in North America. Wodehouse compiled a list of families and genera in the Green River flora based on previously identified megafossils, including a fossil leaf identified by Brown (1929) who compared the leaf with *Chrysobalanus*. The leaf does not have basilar glands nor other distinctive features for Chrysobalanaceae and should not be considered reliable evidence of the family. This misinterpreted fossil was also used to constrain the tree dating of Chrysobalanaceae (Bardon et al., 2013). More recent treatments of the Green River Formation palynoflora do not include Chrysobalanaceae (e.g., Nichols 2010). Other Eocene leaf fossils from North America have also been attributed to Chrysobalanaceae, but none of these determinations are convincing (Table 1). The earliest reliable evidence for the family is from pollen assigned to the species *Psilatricolporites undulates* Salard-Cheboldaëff, which is reported from the Oligocene–lower Miocene of Africa (Salard-Cheboldaëff, 1978; Eisawi and Schrank, 2008) and South America (Jaramillo et al., 2006; Hoorn et al., 2010), and Panama (Jaramillo et al., 2014). These fossils indicate that the family was widespread by the earliest Miocene. Furthermore, Chambers and Poinar (2010) described *Licania* based on flowers and fruits from the Dominican Amber which may be of similar age. The fossil *Licania* also supports the hypothesis that many of the modern genera of the family were established by the early Miocene, and that at least one dispersal of crown-group Chrysobalanaceae from Africa or Eurasia had already taken place.

Parinari, like Chrysobalanaceae as a whole, are pantropical, richest in tropical South America, and likely originated in the Old-World tropics (Bardon et al., 2013). A tropical African origin for *Parinari* is most likely because the neotropical species form a clade nested within the Old-World species and because the sister genus, *Neocarya*, is native to Africa. Transoceanic dispersal is the most likely mechanism by which *Parinari* colonized the neotropics given that the genus has colonized oceanic islands in the Pacific as well (Keppel et al., 2011); however, an alternative hypothesis is a boreotropical route from Asia or Europe during warm climatic intervals (Givnish and Renner, 2004). The discovery of *Parinari* in the Cucaracha Formation confirms that the genus was present in the neotropics by 19 Ma, and if the fossils from the middle Miocene of Colombia are also *Parinari* (Wijninga, 1996), they indicate either that *Parinari* was able to cross the Central American Seaway before its final closure (Montes et al., 2015) or that there was more than one dispersal into the neotropics.

FIGURE 3 Holotype *Parinari panamensis* sp. nov. Jud, Nelson, et Herrera. Specimens UF063001 (A, B, D, E, F, H), UF060854 (C), UF063005 (G), UF063006 (I). (A) External longitudinal view of endocarp showing irregular, shallow, longitudinal grooves (specimen has since been serially sectioned, see UF060854). (B) Transverse peel of the endocarp showing seminal cavities (ca), secondary septum (ss), and germination plugs (gp); slide A6. (C) External view of basal end of endocarp showing ovate shape of germination plug (gp). (D) Transverse peel of the endocarp showing two vascular bundles (vb), secondary septum (ss), germination plugs (gp), and dense sclerenchymatous innermost layer (L1); slide B85. (E) Transverse peel showing vascular bundle (vb) composed of radially aligned xylem cells nested in innermost layer (L1); slide B69. (F) Transverse peel showing three tissue layers: dense, sclerenchymatous innermost layer (L1), second layer (L2) with idioblasts (id), and outermost layer (L3); slide B98. (G) Longitudinal peel showing trichomes lining the interior of a seminal cavity; slide A12. (H) Transverse peel showing details of the outermost tissue layer, composed of sclereids (sc) and fiber tracts (ft); slide B90. (I) Longitudinal peel showing the distal end of a germination plug (gp), and a vascular bundle (vb) nested within the innermost tissue layer entering a seminal cavity (ca); slide 17.



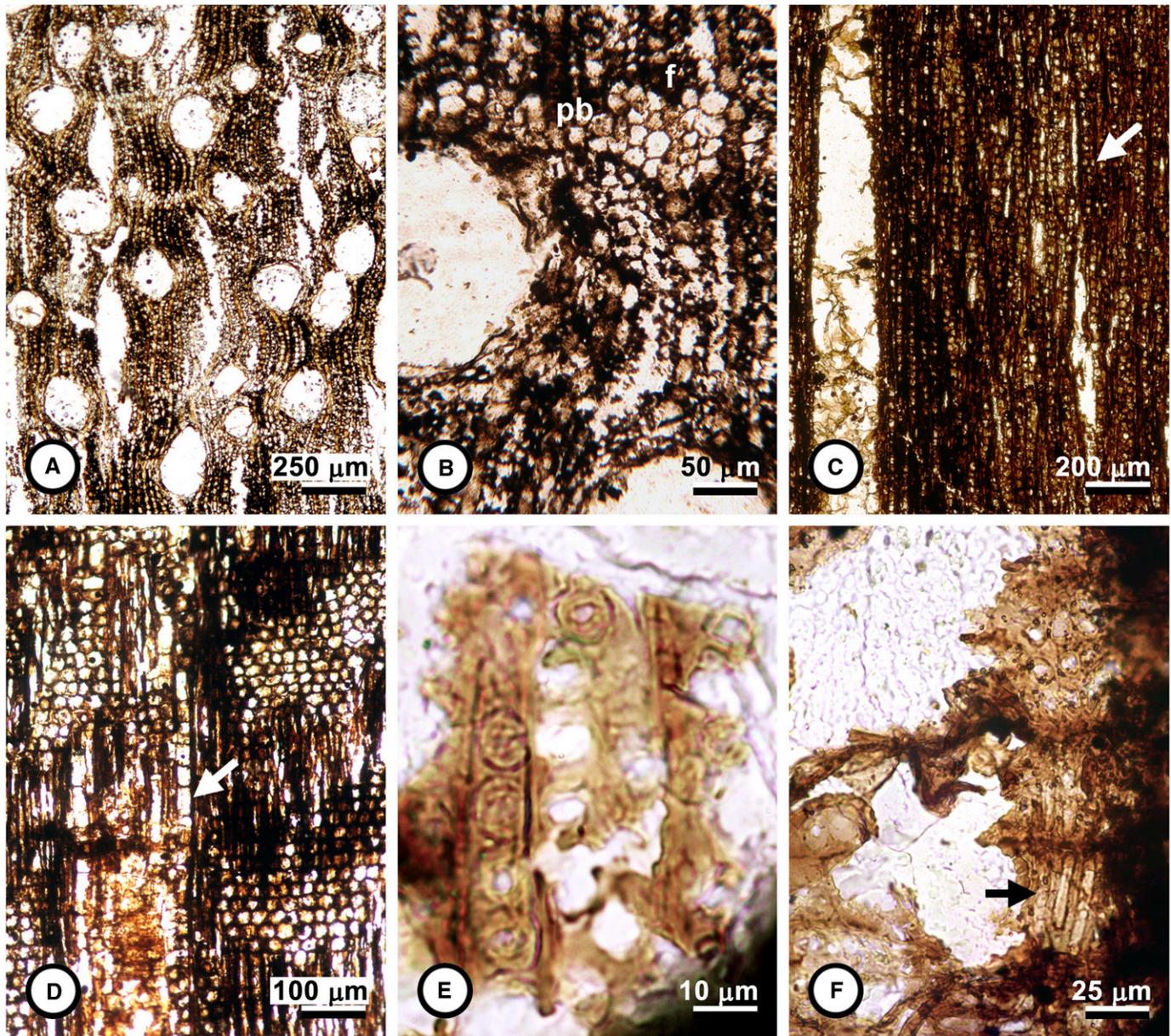


FIGURE 4 Holotype of *Parinarioxylon panamensis* sp. nov. Jud, Nelson, et Herrera. Specimen UF063032. (A) Transverse peel showing diffuse porous xylem with medium-sized solitary vessels. (B) Transverse peel showing a narrow band of axial parenchyma (pb) among the fibers (f) and vessels. (C) Tangential longitudinal peel showing numerous uniseriate rays with a few biseriate portions (arrow). (D) Radial longitudinal peel showing weakly heterocellular rays with predominantly square cells and a strand of axial parenchyma (arrow) among the fibers. (E) Tangential longitudinal peel showing distinctly bordered fiber pits. (F) Radial longitudinal peel showing large, subvertical vessel-ray pits with reduced borders (arrow).

Paleoecology—*Parinari* endocarps are among the most common fruit types in the Lirio East fossil assemblage. Extant *Parinari* is common in lowland rainforests throughout the tropics, but species also occur in montane forest and in dry evergreen forests to savannahs (Whitmore, 1974; White, 1976; Keppel et al., 2011). In tropical South America, *Parinari* is a species-rich and widespread component of the canopy in terra firma forests (Prance, 1972; Gentry, 1993). Some species are typically found along river margins or in open cerrado habitats (Prance, 1972). Only *Parinari choacoensis* ranges into Panama today, where it occurs along high riverbanks. Other common plants known from fruits at the Lirio East locality

include *Sacoglottis* Walp. (Humiriaceae) (Herrera et al., 2010) and *Oreomunnea* Oerst. (Juglandaceae) (Herrera et al., 2014). Wood attributable to Malvaceae and Fabaceae is among the most common found at Lirio East and other lower Cucaracha localities (Rodríguez-Reyes et al., 2014; N. A. Jud, personal observation), and Berry (1918) described a fossil palm stem from the Cucaracha Formation. The distributions of modern relatives of these taxa, along with the palynoflora reported by Jaramillo et al. (2014), are consistent with a forested, moist, tropical, riparian environment. As studies of plant fossils from Lirio East continue, we expect to expand our understanding of the community to which *P. panamensis* belonged.

Plant–animal interactions are common in extant *Parinari*. The flowers are pollinated by bees (Prance and White, 1988), and vertebrate-mediated seed dispersal is important. Primates (Peres and van Roosmalen, 2002), foxes (Alves-Costa and Eterovick, 2007), squirrels, bats, birds, and fish (Prance and White, 1988) are known seed dispersers in modern neotropical communities. However, Altrichter et al. (2000) found that *Parinari* fruits consumed by pecararies are not viable. In Africa, elephants are also effective dispersal vectors (Campos-Arceiz and Blake, 2011). Various extinct animals may have dispersed *Parinari* fruits over land such as squirrels, protoceratids, oreodonts, rhinoceroses, or equids, all of which are known from the early Miocene of Panama (MacFadden et al., 2014).

CONCLUSIONS

Despite the richness and ecological importance of *Parinari* and other Chrysobalanaceae in modern tropical forests, the fossil record of this family is not well known. Many of the Paleogene and Neogene macrofossils that have been attributed to the family are unreliable, including all Eocene occurrences. Pollen attributed to Chrysobalanaceae first occurs in Oligocene sites, and megafossils attributable to the family with good age control are early Miocene or younger. The lack of reliable Eocene occurrences of Chrysobalanaceae has important implications for estimating diversification rate because one of the rejected Eocene occurrences was used in two studies as a calibration point for age of the family. The new fossils of *Parinari* described here constitute the oldest evidence of the genus and provide a minimum date for when the genus was established in the neotropics. Colonization of the neotropics likely occurred via long-distance dispersal rather than vicariance. During the early Miocene, *Parinari* fruits were probably dispersed by vertebrate frugivores throughout what is now southern Central America.

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