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19-MILLION-YEAR-OLD SPONDIOID FRUITS FROM PANAMA REVEAL A DYNAMIC DISPERSAL HISTORY FOR ANACARDIACEAE

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Premise of research. Recent classifications of Anacardiaceae recognize two subfamilies, Anacardioideae and Spondioideae. Most genera within Spondioideae are still recognized for having drupes with sclerified stones that vary in locule number and germination mechanisms. Spondioid fruits have been recognized in the Cenozoic fossil record of Europe, Asia, and North America. However, they have remained elusive in the Neotropics, where today they are an important component of tropical rain forests and seasonally dry tropical forests. Here, we describe three new species of fossil endocarps related to *Spondias*, *Dracontomelon*, and *Antrocaryon*.

Methodology. Fossil endocarps were collected from the 19–18.5 Ma (early Miocene) Cucaracha Formation, Panama Canal. The fossils were studied by physical sections, acetate peels, and X-ray microtomography. The fossil endocarps were exhaustively compared with all extant genera of Spondioideae.

Pivotal results. *Spondias rothwellii* sp. nov. and *Antrocaryon panamaensis* sp. nov. are so far the earliest and best evidence of these genera in the Neotropics. *Dracontomelon montesii* sp. nov. extends the occurrence of this genus to the early Miocene in Central America.

Conclusions. The new Cucaracha fossils reveal that Spondioideae were a significant part of the early Miocene forests in Panama. The extant natural habitats and occurrences of the newly recognized genera suggest multistratified rain forests and active biogeographical patterns for Spondioideae approximately 19 million years ago in southern Central America.

Keywords: *Antrocaryon*, *Dracontomelon*, endocarps, fossils, long-distance dispersal, Miocene, Neotropics, Panamanian Seaway, *Spondias*.

Online enhancements: videos.

Introduction

Anacardiaceae are a mostly tropical family of trees, shrubs, and lianas within the Sapindales with ~800 species in 82 recognized genera (Pell et al. 2011). Although some genera extend into warm temperate regions, Anacardiaceae are widely distributed in the New and Old World tropics and are a common element of tropical rain forests and seasonally dry tropical forests. Recent classifications of Anacardiaceae recognize two subfamilies, Anacardioideae and Spondioideae (Pell 2004; Mitchell et al. 2006; Pell et al. 2011); however, both subfamilies appear to be polyphyletic (Weeks et al. 2014). In the analyses of Weeks et al. (2014), the Spondioideae fall into two unrelated clades (named informally Spondioideae I and II). Anacardiaceae have been previously interpreted as having a Gondwanan origin (Raven and Axelrod 1974; Gentry 1982) based on their extensive tropical distribution and diversity. Nonetheless, recent phylogenetic reconstructions have shown that the widespread distribution of the family (and of numerous individual genera within) may be attributed to a more complex combination of mechanisms (e.g., variety of fruit morphologies, dispersal, and ecological strategies) and their ability to diversify into new niches (Weeks et al. 2014).

Fruits of many Anacardiaceae, and in particular most of the genera of Spondioideae, are distinctive for having drupes with sclerified stones that vary in locule number and germination mechanisms (e.g., simple pluglike opercula, recessed bilabiate germination valves, apical flaps, pores, or simple slits). The fruit morphology of all extant genera of Spondioideae has recently been comprehensively reviewed (Herrera et al. 2018). The main characters that can be potentially recognized in fossil endocarps and that are useful for the identification of genera include locule number; type, position, and shape of the germination mechanism and lacunae; type of endocarp ornamentation; and presence of apertures (Herrera et al. 2018).

Divergence time estimates indicate early to late Cretaceous radiations of Anacardiaceae (Weeks et al. 2014; Muellner-Riehl et al. 2016). A recent examination of fossils from the Deccan Intertrappean beds of central India indicates the presence of

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anacardiaceous wood during the latest Cretaceous to the earliest Paleocene (Wheeler et al. 2017). However, fossil fruits attributable to stem and crown group Anacardiaceae have not been found in the Cretaceous record. The earliest well-documented fossils of extant genera of the family range from the Eocene to the Miocene (e.g., Reid and Chandler 1933; Tiffney et al. 1994; Ramírez and Cevallos-Ferriz 2002; Burnham and Carranco 2004; Manchester et al. 2007, 2009; Collinson et al. 2012; Fu et al. 2017).

A few reliable fossils of Anacardiaceae have been described previously from the Neotropics. Burnham and Carrasco (2004) described winged fruits of *Loxopterygium* from the Miocene of the Ecuadorian Andes, and today this genus is endemic to Caatinga of northeastern Brazil. Ramírez and Cevallos-Ferriz (2002) reported a diverse assemblage of anacardiaceous leaves from the Oligocene of Mexico. Herrera et al. (2012) relocated the historical Tonosi locality of Berry (1918) and studied new fruit collections, in addition to those of Berry, resulting in the reassignment of *Diospyros macdonaldii* Berry to the Asian genus *Dracontomelon*. Fossil wood and pollen have also been described from the Neotropics (e.g., Graham 1985, 1988*a*, 1988*b*; Jaramillo et al. 2014; Pérez-Lara et al. 2017). On the other hand, other traditionally accepted anacardiaceous fossils have proven to be unreliable records of the family. For example, the Oligocene silicified cashews described as *Anacardium peruvianum* by Berry (1924, 1927) were reexamined based on new collections and placed into the extinct genus *Pseudoanacardium*, of uncertain familial affinity (Manchester and Balmaki 2018). Although Anacardiaceae are an important element of lowland to montane forests and seasonally dry to rain forests in the Neotropics, the fossil record of this family remains remarkably scarce in the region.

Here we report abundant and well-preserved permineralized endocarps of Spondioideae (Anacardiaceae) from the early Miocene Cucaracha flora of Panama. The fossils are assigned to the extant genera *Spondias* (Pantropical in distribution), *Dracontomelon* (now native to tropical Asia), and *Antrocaryon* (now endemic to tropical Africa and the Amazon), and all likely grew as canopy trees. The new species of *Spondias* and *Antrocaryon* are the best and earliest record of these genera in the Neotropics, whereas the new *Dracontomelon* species extends the occurrence of this genus in southern Central America. The new fossils also suggest dynamic biogeographical scenarios of Spondioideae during the early Miocene, a time when the Panamanian Seaway was still active.

Material and Methods

Geological Setting, Fossil Locality, and Repository

The fossil fruits reported in this study were collected from the Gaillard Cut (Lirio East outcrop) of the southeastern part of the Panama Canal (UF locality 19391; GPS: lat. 9°3′20″N, long. 79° 39′40″W) and are deposited in the Paleobotanical Collection of the Florida Museum of Natural History University of Florida (UF), Gainesville.

The site was found while exploring new temporary exposures created during the expansion of the Panama Canal (Herrera et al. 2010). The fruit-bearing stratum is in the lowermost part of the Cucaracha Formation (see stratigraphic section in Jud et al. 2016). The age of this formation has been deduced from mammals, pollen, marine invertebrates, magnetostratigraphy, and radiometric dating (Woodring 1957–1982; Bold 1973; Graham 1988*a*, 1988*b*; MacFadden and Higgins 2004; Johnson and Kirby 2006; MacFadden 2006; Kirby et al. 2008; Montes et al. 2012*a*, 2012*b*; Jaramillo et al. 2014; MacFadden et al. 2014; Buchs et al. 2019). These sources indicate an age of ca. 19–18.5 Ma for the Cucaracha Formation.

The Cucaracha Formation was deposited in a succession grading from nearshore shallow marine environments at the base to terrestrial facies in upper levels, and it is reconstructed as a coastal delta plain consisting of abundant paleosols, channels, levees, floodplains, marshes, and volcanic deposits (Retallack and Kirby 2007; Kirby et al. 2008; Buchs et al. 2019). The fossil assemblage at the Lirio East locality includes at least 61 morphotypes of fossil fruits, seeds, flowers, and fungi (Herrera 2014), 52 pollen types (Jaramillo et al. 2014), and wood (Jud and Nelson 2017). The fruits are preserved as calcareous three-dimensional permineralizations in poorly sorted volcaniclastic sandstones and conglomerates.

Comparative Material

Fruit characters of all genera and most species of spondioid Anacardiaceae were recently studied by Herrera et al. (2018); the information on voucher specimens is provided in their article. Comparative data for extant Anacardiaceae were also obtained from available descriptions (e.g., Von Teichman 1987, 1990, 1992; Wannan and Quinn 1990; Mitchell et al. 2006; Pell et al. 2011; Mitchell and Daly 2015).

Fossil Preparation, Tomography, and Imaging

The internal fossil fruit structure was revealed by physical sections made with a Microslice II annular diamond saw with minimal kerf loss of about 30 μm from the path of the blade. Anatomical details of the fossil fruits were obtained by preparing acetate peels after etching the slices in 5%–10% hydrochloric acid for 5–10 s using the technique of Joy et al. (1956). We also obtained X-ray data sets for key fossil specimens using a GE Phoenix V|tome|xm240 CT Scanner at the University of Florida College of Engineering Nanoscale Research Facility (NRF). Voltages, current, and timing were varied according to the resolution desired. We used a tungsten reflection target and 0.5-mm copper filter, at 210 kV and 270 μA, respectively, with 1900 images of a single specimen, for voxel size of 65 μm. Data sets from nano-CT were analyzed with Avizo 9.0 Lite (FEI Visualization Science Group, Bordeaux, France) to provide volume renderings, isosurface renderings, and virtual sections in transverse and longitudinal orientations. The original CT scan data sets are available online and also archived at the Morphobank website (http://morphobank.org/permalink/?P3460). Macrophotographs of the fossils with reflected light were captured using a Canon Rebel camera with a 100-mm macrolens attached to a StackShot system (Cognisys, Traverse City, MI), and successive digital images were merged using Helicon Focus software (Helicon Soft).

Systematics

Order—Sapindales Berchtold & J. Presl

Family—Anacardiaceae R. Brown, nom. cons.

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Subfamily—Spondioideae

Genus—Spondias *L.*

Species—Spondias rothwellii *Herrera, Carvalho, Jaramillo et Manchester sp. nov.*

Specific diagnosis. Prolate drupes composed of a conspicuous central vascular bundle, surrounded by an endocarp that contains five locules and five lacunae. Endocarp conspicuously ornamented, appearing star shaped, T shaped, and with radiating ribs and spines, forming deer antler–like outlines in transverse and/or longitudinal sections. Mesocarp thick and composed of thin-walled parenchyma and sporadic sclereids. Locules single seeded, radially arranged near the center of the drupe, elliptical in transverse section and elongated, straight to curved as seen in longitudinal section. Each locule surrounded by a locular envelope. Lacunae alternating with the locules, radially arranged and variously shaped as seen in transverse section; lacunae open distally, not fully enclosed by endocarp tissue. Each lacuna with a ventral longitudinal row of minute orbicules. Drupes with recessed internal bilabiate germination (i.e., valves hidden within the spongy tissue) in which the locular envelope opens along an apical keel that is recessed within a pore of the endocarp wall.

Holotype. UF60773 (fig. 1*A*, 1*B*).

Other material. UF60774 (figs. 1*C*, 1*I*–1*L*, 4*A*, 4*B*), UF60775 (fig. 1*D*, 1*E*), UF60776 (fig. 1*F*), UF60784 (fig. 1*G*), UF60777 (fig. 1*H*), UF60778–UF60783.

Repository. Paleobotany collections of the Florida Museum of Natural History, University of Florida.

Stratigraphic position and age. Lower Cucaracha Formation; early Miocene; 19–18.5 Ma.

Localities. Gaillard Cut section (Lirio East outcrop) of the southeastern part of the Panama Canal (GPS: lat. 9°3′20″N, long. 79°39′40″W).

Etymology. This species is named in honor of Gar W. Rothwell for his research contributions to the study of fossil plants.

Detailed description. Drupes, prolate, ca. 12.8–23.9 mm high and 8.4–16.5 mm wide (measured at the equator; $n = 12$). When the specimens are found isolated from the matrix or are manually extracted, a corrugated to verrucate surface is exposed (fig. 1*G*). Structurally, the drupes are composed of a conspicuous central vascular bundle that contains five locules (pentalocular) and five lacunae (figs. 1*A*–1*H*, 4*A*–4*E*). The endocarp is preserved brown to black in our material (fig. 1*B*) and appears variably ornamented (fig. 1*B*, 1*C*, 1*G*, 1*H*). The endocarp, including the locular envelopes, is enclosed by a pinkish light-colored mesocarp (up to 4.7 mm thick in transverse section; fig. 1*B*, 1*C*, 1*H*); no exocarp is preserved in our specimens, but it may be presumed to have been fleshy, as in modern species of *Spondias*.

The central vascular bundle appears circular in transverse sections, ca. 0.9–1.1 mm in diameter (fig. 1*B*, 1*C*, 1*H*). The vascular bundle is composed of radial files of late vessels (toward the periphery of the bundle; ca. 29–50 μm in diameter) and early vessels (toward the center of the bundle; ca. 15–25 μm in tangential diameter), which are separated by thin fiber files, one or two cells thick (fig. 1*I*); fibers are ca. 5 μm in diameter. Phloem is either lacking or not preserved in our samples.

In transverse section, the endocarp appears completely fused and circular near the base, encircling five locules and five lacunae (figs. 1*B*, 1*C*, 1*G*, 1*H*, 4*B*). Near the center and toward the apical end, the endocarp appears star shaped, with radiating ribs that, in transverse section, give the appearance of spines or deer antlers (figs. 1*B*, 1*C*, 1*G*, 1*H*, 4*B*, 4*E*). The deer antler–like outlines are formed when the external regions of the lacunae are open to the mesocarp, rather than closed with endocarp tissue in the manner of the proximal lacunae. In longitudinal section, the locular envelope and the endocarp appear more or less amorphous, sometimes with projecting spines to riblike structures (up to 1.9–4.5 mm long; figs. 1*A*, 1*D*, 1*F*, 4*E*). The endocarp consistently forms a distal horizontal T-like structure (as seen in longitudinal section) above the locules and the germination pores (figs. 1*D*, 1*F*, 4*D*).

The locules are single seeded, radially arranged near the center of the drupe, elliptical in transverse section (ca. 1.6–3.2 mm long and ca. 0.5–1.3 mm wide; figs. 1*B*, 1*C*, 1*H*, 4*A*, 4*B*) and straight to curved in outline in longitudinal section (ca. 7.6–10.8 mm long and ca. 0.5–1.2 mm wide; figs. 1*A*, 1*D*, 4*D*, 4*E*). Five radially arranged lacunae alternate with the locules; these are closed and variously shaped near the basal end of the drupe (rounded-triangular, nearly circular, four- or five-sided polygons; figs. 1*B* [*far left*], 1*C*, 1*H* [*left*], 4*B*) to poorly defined and open near the center and apical end of the fruits (as seen in transverse sections; i.e., not enclosed by endocarp tissue; fig. 1*B* [*far right*], 1*H* [*right*]). Within each lacuna there is a ventral, longitudinal row of five to nine orbicules (ca. 0.4–1.2 mm in diameter; figs. 1*A*, 1*D*–1*F*, 4*D*). The orbicules are rounded cavities that may be seen singly in successive transverse sections (fig. 1*B*), but the longitudinal rows of them are best documented in longitudinal sections (figs. 1*A*, 1*D*–1*F*, 4*D*). As the CT scan images reveal, each locule is supplied with an internal bilabiate dehiscence mechanism in which the locular envelope opens along its apical keel, which is recessed within a pore of the endocarp wall (fig. 4*A*, 4*C*–4*E*).

The locular envelope is composed of horizontal encircling fibers forming a layer ca. 50–320 μm thick (fig. 1*C*, 1*H*). Between adjacent locular envelopes, the septum tissue is formed by isodiametric brachysclereids (ca. 47–74 μm in diameter; fig. 1*J*) and parenchyma (ca. 28–45 μm in diameter; fig. 1*K*). The endocarp tissue is largely formed by an intricate layer of fiber tracts (ca. 140–230 μm long; fig. 1*K*) and thick-walled sclereids (ca. 40–77 μm in diameter; fig. 1*L*). The mesocarp is predominantly composed of thin-walled parenchyma (ca. 20–60 μm in diameter) and sporadic sclereids.

Systematic placement. Fruits of *S. rothwellii* are indistinguishable from some extant species of *Spondias*. Endocarps of both are prolate and remarkably ornamented, typically pentalocular with recessed internal bilabiate germination (i.e., cryptic, hidden within the spongy tissue) in which the locular envelope opens along its apical keel (figs. 1, 4*A*–4*E*, 5*A*–5*G*). More strikingly, some living *Spondias* species and the Miocene *S. rothwellii* are unique within Spondioideae in having endocarps with a deer antler–like outline as seen in transverse section (figs. 1*B*, 1*C*, 1*H*, 5*C*–5*E*) and also by possessing ventral rows of orbicules within the lacunae (figs. 1*B*–1*F*, 5*D*–5*G*). So far, these two characters have been observed only in Neotropical species of the genus such as *S. globosa*, *S. macrocarpa*, *S. mombin*, *S. purpurea*, *S. radlkoferi*, and *S. tuberosa* (Herrera et al. 2018; figs. 5*C*–5*G*, 6*B*), while they appear to be absent from Old World species such as *S. bipinnata*, *S. dulcis*, and *S. pinnata* (Herrera et al. 2018).

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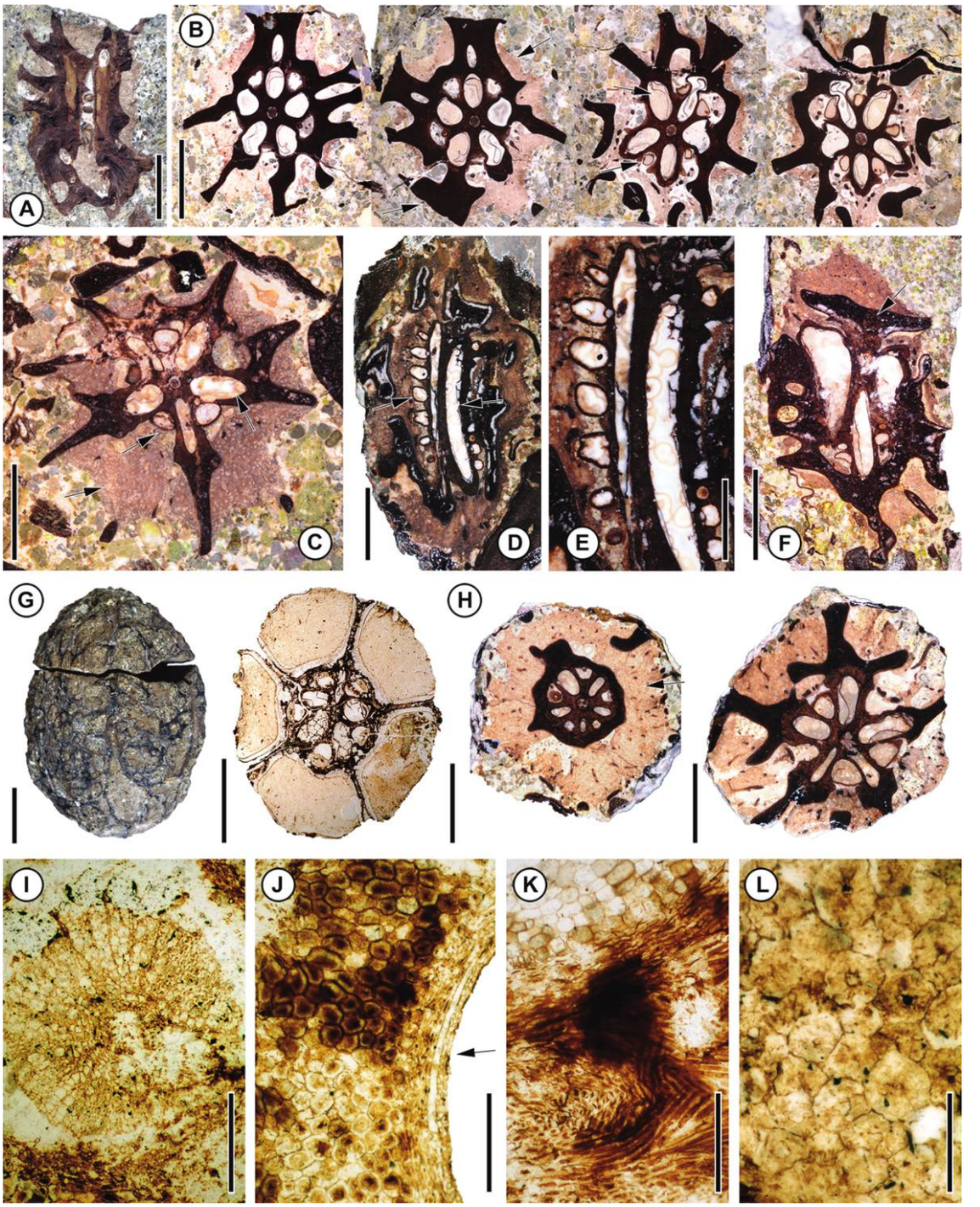

Fig. 1 *Spondias rothwellii* sp. nov. *A*, *B*, Holotype (UF60773). *A*, Drupe exposed in longitudinal section showing ornamented endocarp. *B*, Serial transverse sections of drupe from *A* showing a central vascular bundle and the endocarp containing five locules and five lacunae. Second image from left showing mesocarp tissue (upper arrow) and riblike ornamentation of endocarp (lower arrow); third image from left showing single-seeded locule (upper arrow) and minute orbicule within open lacuna (lower arrow). *C*, Transverse section near equator showing deer antler–like ornamentation of endocarp, with lacuna (middle arrow) and locule (upper arrow) and faintly preserved mesocarp (lower arrow; UF60774). *D*, Longitudinal section showing long and curved locule (right arrow) and one ventral row of seven orbicules (left arrow; UF60775). *E*, Detail from *D*; note two locules and two ventral rows of orbicules. *F*, Obliquely longitudinal section showing three locules and T-shaped apical end of the endocarp (arrow; UF60776). *G*, Isolated specimen showing eroded, verrucate surface on lateral view (*left*); equatorial transverse section showing conspicuous mesocarp and central locules and lacunae (UF60784). *H*, Transverse section near the distal end of fruit showing thick mesocarp (arrow) and endocarp including locular envelopes (*left*); section above equator showing conspicuously deer antler–like ornamentation of endocarp and five radially arranged locules and alternating with lacunae (*right*; UF60777). *I*–*L*, Acetate peels from specimen in *C* showing anatomy. *I*, Detail of central vascular bundle composed of radial files of xylem. *J*, Detail of septum showing isodiametric brachysclereids and locule lining (arrow). *K*, Detail of septum composed of parenchyma (upper zone) and fibrous endocarp. *L*, Detail of thick-walled sclereids of endocarp. Scale bars = 5 mm (*A*–*H*), 400 μm (*I*), 200 μm (*J*, *K*), 50 μm (*L*).

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Hence, the fossil is most similar morphologically to the extant New World representatives.

Genus—Dracontomelon *Blume*

Species—Dracontomelon montesii *Herrera, Carvalho, Jaramillo et Manchester sp. nov.*

Specific diagnosis. Asymmetrically oblate to mushroom-shaped drupes composed of five radially arranged locules and five lacunae. Endocarp star shaped to pentagonal as seen in transverse section, with a small central vascular bundle; in longitudinal section, more or less mushroom shaped; outer surface of endocarp ornamented with up to 10 equatorial depressions. Locules single seeded, reaching nearly to the periphery of the endocarp, usually unevenly developed, elliptical to circular in outline as seen in transverse section and reniform/phalloid as seen in longitudinal section. Lacunae radially arranged, alternating with locules, mostly triangular shaped as seen in transverse section; empty or filled with loose fibers. Lacunae connected to the equatorial external depressions by a pair of channels. Each locule topped by a distally placed simple operculum (apical stopper-like plug) that reaches the periphery of the endocarp.

Holotype. UF60827 (figs. 2*A*, 4*F*–4*K*).

Other material. UF60828 (fig. 2*B*), UF060832 (fig. 2*C*, 2*H*–2*L*), UF60829 (fig. 2*D*, 2*E*), UF60830 (fig. 2*F*), UF060834 (fig. 2*G*), UF060831, UF060833, UF060835, UF060836, UF060837.

Repository. Paleobotany collections of the Florida Museum of Natural History, University of Florida.

Stratigraphic position and age. Lower Cucaracha Formation; early Miocene; 19–18.5 Ma.

Localities. Gaillard Cut section (Lirio East outcrop) of the southeastern part of the Panama Canal (GPS: lat. 9°3′20″N, long. 79°39′40″W).

Etymology. This species is named in honor of Camilo Montes for his research contributions to the study of the geological evolution of Panama.

Detailed description. Drupes, asymmetrically oblate, mushroom shaped in lateral view (figs. 2*A*, 2*E*, 4*F*–4*H*), ca. 4.2–7.5 mm high and ca. 5.8–12 mm wide (measured at the widest point; $n = 11$). When the specimens are found isolated from the matrix or manually dissected, a smooth to slightly verrucate surface is exposed (fig. 2*A*–2*C*). Structurally, the drupes are composed of stone with a small central vascular bundle and five locules (pentalocular) and five well-developed lacunae (figs. 2*A*–2*G*, 4*H*–4*K*); adjacent to the locular envelope is a dark endocarp (preserved brown to black in our material); no mesocarp or exocarp is preserved in our specimens.

The central vascular bundle appears circular in transverse sections, ca. 0.2–0.5 mm in diameter (fig. 2*C*, 2*F*). The vascular bundle is composed of xylem with radial files of vessels, ca. 1–4 μm in diameter (fig. 2*K*). Phloem is either lacking or not preserved in our samples.

In transverse section, the locular envelope and the endocarp appear completely fused and circular to pentagonal in outline near the basal end of the drupes, encircling five locules and five lacunae (figs. 2*C*, 4*J*). Near the center and the apical end of the fruits, the locular envelope and the endocarp appear star shaped (fig. 2*C* [*far right*], 2*F*). In longitudinal section, the stone appears more or less mushroom shaped (figs. 2*E*, 4*H*, 4*K*).

The locules are single seeded, radially arranged near the center of the drupe, and almost reaching the periphery of the endocarp, usually unevenly developed, elliptical to circular in transverse section (ca. 2.4–3 mm long and ca. 1–1.4 mm wide; figs. 2*C*, 2*F*, 4*J*); each locule is straight to reniform, with a phalloid distal portion in outline in longitudinal section (ca. 2.8–3.4 mm long and ca. 0.9–1.4 mm wide; figs. 2*E*, 2*G*, 4*H*, 4*K*). Five radially arranged lacunae alternate with the locules (ca. 1.6–2.3 mm long and 1.4–2.2 mm wide); these are almost triangularly shaped in transverse section and often appear filled with fibers (figs. 2*C*, 4*J*). The outer surface of the endocarp is ornamented with up to 10 equatorial depressions (figs. 1*B*, 4*F*, 4*G*). The lacunae are connected to the equatorial external depressions by a pair of channels (figs. 1*C*, 4*J*). No apertures are observed at the base of the endocarp, but sometimes a deep and single depression can be seen at the point of fruit attachment (figs. 2*A* [*right*], 4*G*). Each locule is topped by a distally placed simple operculum (apical stopper-like plugs; figs. 2*A* [*left*], 2*B*, 2*D*, 2*G*, 4*F*, 4*I*, 4*K*). The opercula are radially arranged, elliptical, ca. 1.8–5 mm long (measured along the longest axis) and ca. 0.8–2.2 mm wide (measured along the narrow axis) and reach the periphery of the endocarp (figs. 2*A* [*left*], 4*F*, 4*I*). The opercula are similar in thickness and cellular composition to the surrounding endocarp wall (fig. 2*G*).

The locular envelope is ca. 270–300 μm thick and 6–12 seriate (fig. 2*H*, 2*I*), consisting mainly of periclinal fibers and thick-walled cells, ca. 13–18 μm in diameter (fig. 2*I*). The surrounding septal portion of the endocarp is formed almost entirely of brachysclereids (fig. 2*L*), ca. 14–23 μm in diameter. The remaining endocarp is composed of variously oriented tracts of tortuous fibers, ca. 90–130 μm long (fig. 2*J*).

Systematic placement. These fossils conform to Spondioideae in the radial arrangement of single-seeded locules alternating with lacunae and in the apically positioned germination valves. Compared to the fruits of all living Spondioideae (Herrera et al 2018), the petrified stones compare most favorably with extant *Dracontomelon* (endemic to India to Myanmar, Indo-China, tropical China, Malesia, and Fiji; figs. 5*H*–5*K*, 6*C*) in shape, configuration of the locules and lacunae, simple germination opercula (apical stopper-like plugs), and the pair of channels leading from each lacuna to the central equatorial depressions. They were also compared with the extinct genus *Pentoperculum* (known from the Eocene of Oregon and England; Manchester 1994) but are distinguished by the simple, rather than bipartite, germination valves.

Genus—Antrocaryon *Pierre*

Species—Antrocaryon panamaensis *Herrera, Carvalho, Jaramillo et Manchester sp. nov.*

Specific diagnosis. Subglobose to globose stone composed of a central vascular bundle, five locules, and five large lacunae. Endocarp prominently star shaped as seen in transverse section. Five prominent lacunae alternate in position with the locules; lacunae larger than the locules and more or less triangularly shaped in equatorial section. Each locule topped by a distally placed simple operculum (apical stopper-like plugs). A whorl of five depressions occurs at the base of the endocarp, alternating in position with the locules.

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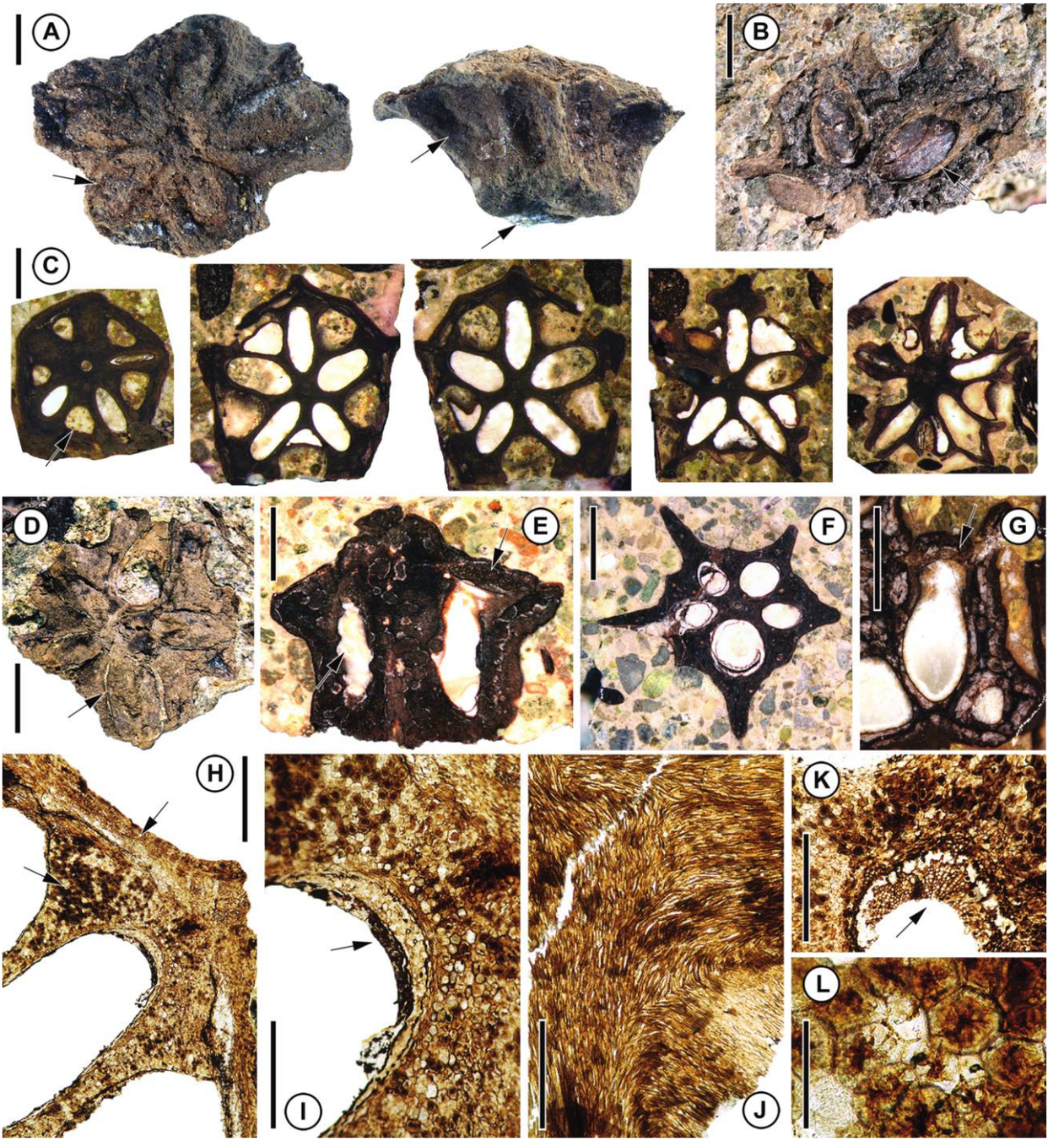

Fig. 2 *Dracontomelon montesii* sp. nov. *A*, Holotype (UF60827). *Left*, apical view of asymmetrical endocarp showing five well-developed simple opercula (stopper-like plugs; arrow). *Right*, lateral view showing mushroom-like shape of endocarp, equatorial depression (upper arrow), and basal depression at fruit attachment (lower arrow). *B*, Apical view of endocarp showing three exposed locule casts (arrow; UF60828). *C*, Serial transverse sections of endocarp from base (*left*) to apex (*right*) showing a central vascular bundle, five locules, and five lacunae (arrow; UF60832). *D*, Apical view of endocarp showing five simple opercula (stopper-like plugs; arrow; UF60829). *E*, Longitudinal section of endocarp from *D* showing two locules (left arrow) and operculum (right arrow). *F*, Transverse section near equator showing star-shaped endocarp and five locules (UF60830). *G*, Detail of longitudinal section of endocarp showing locules and one operculum (arrow; UF60834). *H–L*, Acetate peels from specimen in *C* showing anatomy. *H*, Detail of endocarp showing locular envelopes and endocarp (arrow). *I*, Detail of septum from *H* showing six- to 12-seriate locular envelope and locule lining (arrow); note periclinal fibers and thick-walled cells. *J*, Detail of endocarp showing variously oriented tracts of tortuous fibers. *K*, Detail of central vascular bundle composed of radial files of xylem (arrow). *L*, Detail of septal brachysclereids. Scale bars = 2 mm (*A–G*), 400 μm (*H*), 200 μm (*I*, *J*), 20 μm (*K*, *L*).

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Holotype. UF60957 (figs. 3*A*, 3*B*, 4*L*–4*N*).

Other material. UF60958 (fig. 3*C*, 3*F*–3*J*), UF60962 (fig. 3*D*), UF60959 (fig. 3*E*), UF60961.

Repository. Paleobotany collections of the Florida Museum of Natural History, University of Florida.

Stratigraphic position and age. Lower Cucaracha Formation; early Miocene; 19–18.5 Ma.

Localities. Gaillard Cut section (Lirio East outcrop) of the southeastern part of the Panama Canal (GPS: lat. 9°3′20″N, long. 79°39′40″W).

Etymology. The specific epithet refers to Panama, where the fossils were found.

Detailed description. Stone subglobose to globose, ca. 9.2–13.1 mm high and ca. 12.5–16.3 mm wide (measured at the widest point; $n = 4$). Structurally, the stones are composed of a central vascular bundle, surrounded by five locules (pentalocular) and five well-developed lacunae (figs. 3*A*–3*E*, 4*L*–4*N*); no mesocarp or exocarp is preserved in our specimens.

In transverse section, the endocarp appears more or less circular to pentagonal in outline with a prominent star-shaped structure formed by the radiating locular envelopes (fig. 3*A*–3*C*). The drupes possess five radially arranged locules and five conspicuous lacunae (fig. 3*A*–3*C*). The locules are elliptical to circular in transverse section (ca. 2.3–4.6 mm long and ca. 0.8–2.5 mm wide; figs. 3*A*–3*C*, 4*L*) and more or less reniform in sagittal section with a phalloid apical portion (ca. 7–9.7 mm long and ca. 2.6–4.2 mm wide; figs. 3*E*, 4*N*). The five prominent lacunae alternate in position with the locules; these lacunae are larger than the locules (up to ca. 6–8 mm in diameter) and are more or less triangularly shaped in equatorial section (fig. 3*B*, 3*C*). The lacunae were likely empty at maturity; some appeared broken and filled with sediment (fig. 3*A*–3*C*). Each locule is topped by a distally placed simple operculum as revealed by the CT scan images (apical stopper-like plugs; fig. 4*L*, 4*M*). These opercula are arranged in a circle on the apical surface midway between apex and equator of the stone, ca. 2.7–6 mm long (measured along the longest axis) and ca. 3.1–4.1 mm wide (measured along the widest axis). The opercula are similar in thickness and cellular composition to the surrounding endocarp wall (fig. 3*D*). A whorl of five depressions occurs at the base of the endocarp, alternating in position with the locules (fig. 4*L*).

The central vascular bundle is ca. 0.6–1.2 mm in diameter (fig. 3*A*–3*C*). The locular envelope is ca. 0.3–0.4 mm thick (fig. 3*F*), consists of a locule lining a few cell layers thick of brachysclereids (cells ca. 5–10 μm in diameter; fig. 3*J*), surrounded by a dense tissue of interwoven tracts of fibers (individual fibers ca. 10–15 μm thick; fig. 3*G*, 3*I*). The remaining endocarp is composed mainly of tortuous fibers grading from obliquely periclinal near the center to mostly anticlinal near the periphery. Probable resin canals (ca. 320 μm in diameter) are present in the endocarp tissue (fig. 3*H*).

Systematic placement. These fruits correspond to Spondioideae in the radial arrangement of single-seeded locules, alternating with lacunae, and in the apically positioned germination valves. Compared to the stones of all living Spondioideae (Herrera et al 2018), the permineralized specimens fit most favorably with extant *Antrocaryon* (endemic to tropical Africa and tropical South America; figs. 5*L*–5*N*, 6*D*) in shape, size, configuration of the locules and lacunae, and the simple germination opercula (apical stopper-like plugs). Some extant *Poupartia* species show a close similarity to *A. panamaensis* for having globose to subglobose pentalocular endocarps. At least three morphological types of endocarps were recognized for *Poupartia* in Herrera et al. (2018). The first two endocarp types, *Poupartia* type 1 and *Poupartia* type 2, are normally bisymmetrical and bilocular, unlike *A. panamaensis* (figs. 3*A*–3*E*, 4*L*–4*N*). *Poupartia* type 3, including *P. minor*, *P. orientalis*, and *P. silvatica* (Herrera et al. 2018), has pentalocular, prolate to subglobose endocarps comparable to *A. panamaensis*. However, *A. panamaensis* can be distinguished from *Poupartia* type 3 endocarps mainly by having a thicker locular envelope (ca. 0.3–0.4 mm vs. 0.1 mm) and more consistent star-shaped endocarps as seen in transverse section.

Discussion

Comparison with Other Extant Genera of Spondioideae

The morphology of the three new Panamanian species unequivocally supports a relationship with extant members of the Anacardiaceae and in particular with the subfamily Spondioideae (Pell et al. 2011; Herrera et al. 2018; fig. 6). The fossils can be assigned to this subfamily based on the occurrence of drupes with endocarps that are more or less woody, structurally composed of a central vascular bundle, surrounded by a stone that contains radially arranged locules (i.e., pentalocular) and lacunae, and the presence of specialized structures for germination, such as stopper-like opercula and pores (see review of extant Spondioideae in Herrera et al. 2018). Among angiosperms, we do not recognize any other families with fruits having the same set of characters seen in Spondioideae.

Drupes of *Spondias rothwellii*, *Dracontomelon montesii*, and *Antrocaryon panamaensis* differ from each other in size, symmetry, shape, the ornamentation of the endocarp, presence or absence of orbicules, and details of the germination mechanism (figs. 1–4). *Spondias rothwellii* is identical to extant Neotropical *Spondias* species; this is supported by the presence of ornamented endocarps with a deer antler–like outline (as seen in transverse section) and by the occurrence of ventral rows of orbicules within the lacunae. The pentalocular drupes of *D. montesii* and *A. panamaensis* are characterized by having conspicuous and distally placed simple opercula (apical stopper-like plugs) that top the locules (figs. 2*A*, 2*B*, 3*D*, 4*F*, 4*I*, 4*L*, 4*M*). Simple opercula are also present in the extant Spondioideae genera *Cyrtocarpa* (endemic to the Neotropics), *Lannea* (endemic to sub-Saharan Africa, South and Southeast Asia, and Socotra), *Operculicarya* (endemic to Madagascar and the Comoros and Aldabra Islands), *Poupartia* (endemic to Mascarene Islands and Madagascar), and *Sclerocarya* (endemic to Madagascar and sub-Saharan Africa; see detailed comparisons, figures, and descriptions in Herrera et al. 2018). *Cyrtocarpa* is distinguishable from *D. montesii*, *A. panamaensis*, and all other Spondioideae genera by having an irregular and variable position of the opercula. *Lannea* and *Operculicarya* drupes are bisymmetrical and typically unilocular, rarely bilocular in the latter. *Dracontomelon montesii* and *A. panamaensis* differ from *Sclerocarya* drupes because of their typically pentalocular endocarps with large lacunae versus the bilocular to tetralocular endocarps with crescent-shaped lacunae, respectively.

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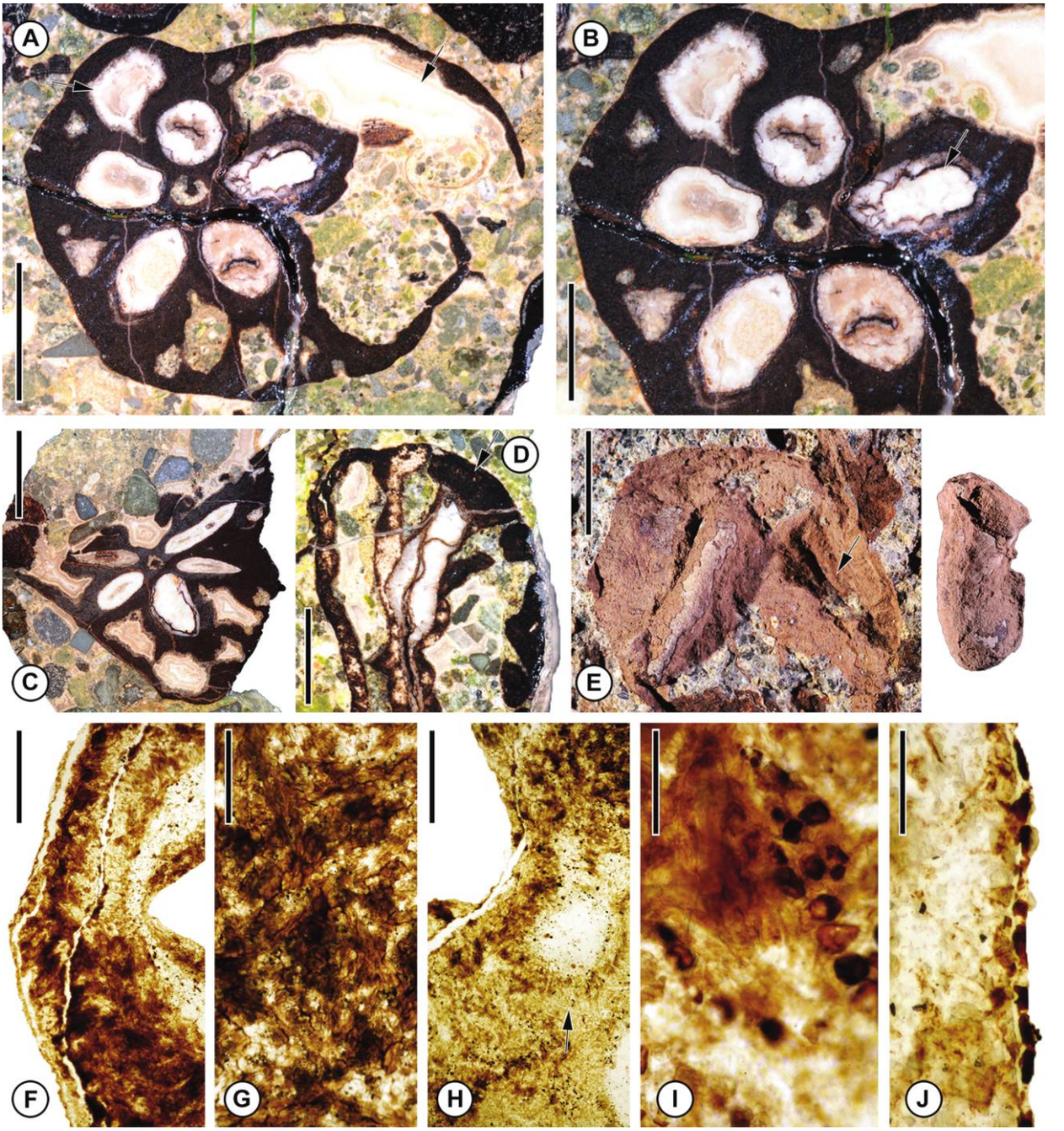

Fig. 3 *Antrocaryon panamaensis* sp. nov. *A*, *B*, Holotype (UF60957). *A*, Endocarp in nearly transverse equatorial section showing a central vascular bundle, five locules, and five lacunae (arrows); note broken lacuna (right arrow). *B*, Detail from *A* showing central vascular bundle and radially arranged locules (arrow). *C*, Transverse section of endocarp showing star-shaped endocarp and radially arranged locules (UF60958). *D*, Detail of longitudinal section of endocarp showing locules, lacunae, and stopper-like plug (arrow; UF60962). *E*, Endocarp in more or less longitudinal section showing locule casts (*left*); arrow indicates cavity in endocarp left by dislodged locule cast (*right*). Note phalloid distal portion of locule cast in right-side image (UF60959). *H–L*, Acetate peels from specimen in *C* showing anatomy. *F*, Detail of endocarp showing locular envelope and endocarp. *G*, Detail of endocarp showing dense tissue of interwoven tracts of fibers. *H*, Detail of endocarp showing possible resin canal (arrow). *I*, Detail of endocarp showing dark brachysclereids. *J*, Detail of locule lining showing cell with dark contents. Scale bars = 5 mm (*A–E*), 400 μm (*F*), 200 μm (*G*, *H*), 50 μm (*I*, *J*).

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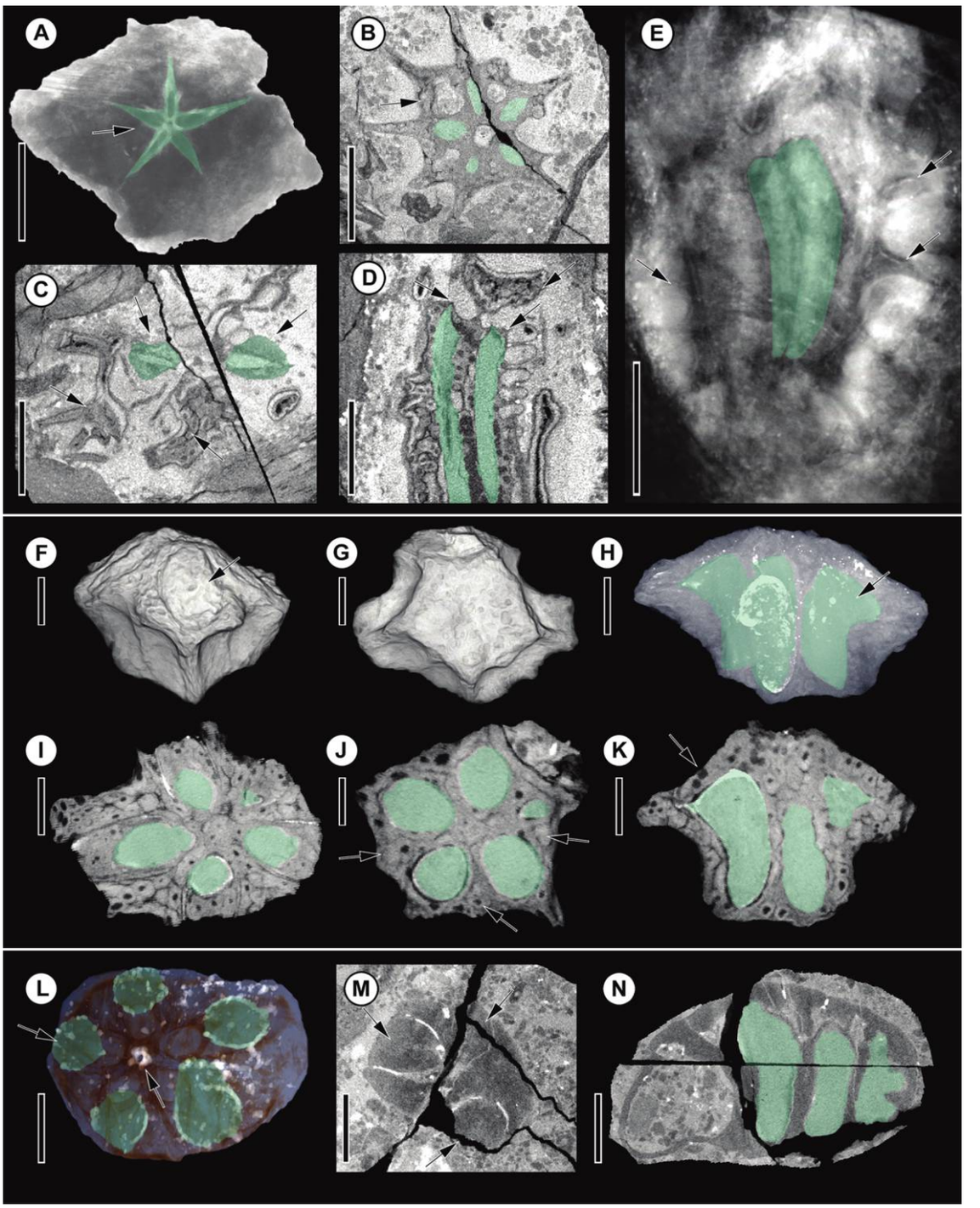

Fig. 4 Digital and volume rendering (VR) and sectional images of early Miocene fruits with locules or opercula highlighted in green. *A–E*, *Spondias rothwellii* sp. nov. (UF60774). *A*, VR of endocarp showing five radially arranged locules (arrow). *B*, Digital equatorial transverse section of endocarp showing ornamentation, five locules, and five lacunae (arrow). *C*, Digital transverse section showing endocarp ornamentation (lower arrows) and internal bilabiate dehiscence mechanism with two open locular envelopes (upper arrows). *D*, Digital longitudinal section showing two locules, pores in the endocarp wall (lower arrows), and (T-shaped) apical plate of endocarp located above pores. Note longitudinal row of orbicules. *E*, Translucent VR of endocarp showing elongate locules and projecting spinelike ornamentation (arrows). *F–K*, *Dracontomelon montesii* sp. nov., holotype (UF60827). *F*, VR in lateral view showing apical operculum (arrow). *G*, VR in basal view showing depression. *H*, VR showing four out of five reniform locule casts (arrow). *I*, Digital transverse section at level of opercula showing locules. *J*, Digital equatorial section showing five locules and filled lacunae (arrows). *K*, Digital longitudinal section showing locules and operculum (arrow). *L–N*, *Antrocaryon panamaensis* sp. nov., holotype (UF60957). *L*, VR of endocarp showing five apical opercula (left arrow) and a whorl of five depressions (right arrow). *M*, Digital transverse/oblique section at level of opercula (arrows). *N*, Digital longitudinal section showing three locules and large lacuna on left side of endocarp. Scale bars = 5 mm (*A–E*, *L–N*), 2 mm (*F–K*).

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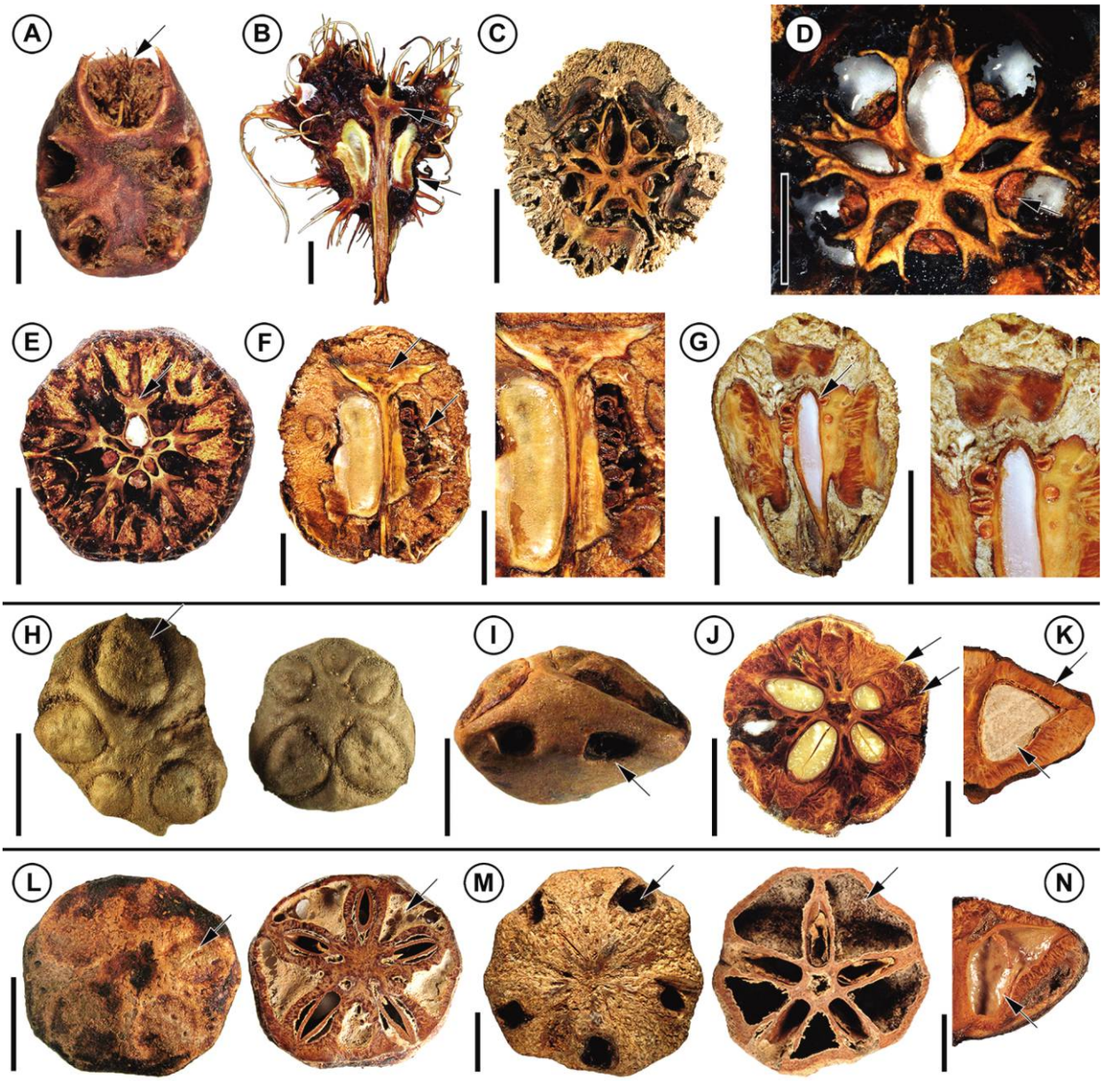

Fig. 5 Extant Anacardiaceae fruits. *A*, *Spondias tuberosa* (US 2701812: G. Eiten & L.T. Eiten; Maranhao, Brazil) in apical view showing apical pores; note unclosed pore (arrow). *B*, *Spondias dulcis* (UF 163: P Grote; Thailand) in longitudinal section showing endocarp denuded of spongy tissue; note locule (lower arrow), T-like structure (upper arrow), and conspicuous spinelike ornamentation. *C*, *Spondias globosa* (NY: Gentry 68,896; Tambopata, Peru) endocarp in transverse section showing central vascular bundle, five locules, and fine lacunae. *D*, Detail from *C* showing deer antler–like ornamentation and orbicules (arrow). *E*, *F*, *Spondias purpurea* (UF 1435: S. Pell s.n.; Costa Rica). *E*, Transverse section; note ornamentation (arrow). *F*, Longitudinal section (*left*) showing locule with seed, T-like structure (upper arrow), and ventral row of orbicules (lower arrow). Right showing detail from left image; note orbicules. *G*, *Spondias mombin* (UF 38: Dilcher s.n.; Guanacaste, Costa Rica) in longitudinal section (*left*) showing locule with seed and ventral rows of orbicules (arrow). Right showing detail from left image; note orbicules. *H*, *Dracontomelon duperreanum* (UF 2497: Xiaoyan Liu s.n.; Guangzhou Botanical Garden, Guangdong, China); two specimens in apical view showing asymmetrical endocarps and opercula (arrow). *I*, *Dracontomelon dao* (NY: Soejarto et al. 7822; Luzon, Philippines) in lateral view showing apical opercula and conspicuous equatorial depressions (arrow). *J*, *K*, *Dracontomelon dao* (NY: M. Ramos Edano 75,781; Catanuones, Philippines). *J*, Transverse section showing five locules and pair of channels connecting equatorial external depressions with lacunae (arrows). *K*, Longitudinal section showing operculum (upper arrow) and locule with seed (lower arrow). *L*, *Antrocaryon klaineanum* (NY: J.M. Reitsma 1978; Gabon); *left*, endocarp in apical view showing five opercula (arrow); *right*, transverse section showing five locules arranged in a star pattern and five large lacunae (arrow). *M*, *Antrocaryon amazonicum* (US 2439182: Lemos Fróes 20,295; Pará, Brazil); *left*, endocarp in apical view with five shed opercula (arrow); *right*, transverse section showing five locules arranged in a star pattern and five large lacunae (arrow). *N*, *Antrocaryon amazonicum* (US 3017984: T. Plowman et al. 8823; Pará, Brazil) in longitudinal view showing reniform locule (arrow). Scale bars = 1 cm (*A*–*C*, *E*–*N*), 5 mm (*D*).

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Comparison with Anacardiaceae Fossils

Spondias. To our knowledge, only one other fossil endocarp has been assigned to *Spondias* in the Neotropical region, that is, *S. lutea* L., described from the Pleistocene of Cuba (Berry 1934; Iturralde-Vinent et al. 2000); living *S. lutea* is a synonym of *S. mombin*. The fossil endocarps appear to have at least two locules and very long lingulate germination valves; unlike any Spondioideae, there is no clear evidence of lacunae or orbicules. It is very likely that the Pleistocene Cuban fossils belong to another angiosperm family (e.g., Humiriaceae), but this needs to be verified with further study. Miki (1941) reported several fossil occurrences as the extant species *S. axillaris* based on endocarps from the Miocene of Japan; since then, this species was transferred from *Spondias* to its own genus, *Choerospondias* (see also Fu et al. 2017). Several Pliocene fossil leaves from Brazil have also been assigned to *Spondias*, including *S. prae-laurifloria* (Krasser 1903), for which neither a description nor a photograph was presented, and the modern species *S. mirifica* (Hollick and Berry 1924). In our opinion, the affinity of these fossil leaves remains unclear, and a closer examination is needed. Quaternary pollen referred to *Spondias* is very common in quaternary deposits from the Caribbean islands and Central and tropical South America (e.g., Salgado-Labouriau 1980; Leyden 1985; Ferrera et al. 1990; Islebe et al. 1996). From Panama, *Spondias* pollen type (*Anacardiaceae* "*morenensis*") has been observed from the Gatún, Cayo Agua, and Tuira Formations (~9.6 Ma and younger; Jaramillo et al. 2014). The new Miocene species from the Cucaracha flora, *S. rothwellii* (figs. 1, 4*A*–4*E*), is the earliest and best-documented fossil evidence of this Pantropical genus described so far.

Dracontomelon. Endocarps of this genus have been reported from the early Eocene London Clay flora (Reid and Chandler 1933). However, those specimens that Reid and Chandler (1933) described as *D. minimus* were later transferred to the extinct genus *Pentoperculum* because of the presence of bipartite germination valves (Manchester 1994). Other specimens attributed by Reid and Chandler (1933) to the fossil genus *Pseudoscleroc arya* appear to actually represent *Dracontomelon* (M. E. Collinson and S. R. Manchester, unpublished manuscript; see also Collinson et al. 2016); however, more details are necessary to compare the London Clay specimens with the new Cucaracha fossils. Abundant and well-preserved permineralized calcareous endocarps from the late Eocene of Panama (Búcaro Formation; Tonosi flora) were recently described as *D. macdonaldii* (Herrera et al. 2012). These late Eocene fossils are predominantly subglobose, symmetrical, and large (ca. 6.0–12.1 mm high and ca. 9.0–19.2 mm wide), while fruits of the Miocene *D. montesii* (figs. 2, 4*A*–4*K*) are oblate to mushroom shaped, asymmetrical, and relatively small (ca. 4.2–7.5 mm high and ca. 5.8–12 mm wide).

Antrocaryon. Three permineralized *Antrocaryon* fossils have been reported from the Miocene (Tiffney et al. 1994) and Pliocene (Bonnefille and Letouzey 1976) of Ethiopia and from the Miocene of Kenya (Chesters 1957). The endocarps of *A. paramicraster* (Miocene) and *A.* aff. *micraster* (Pliocene) from Ethiopia are much larger than *A. panamaensis* (ca. 19–29 mm high, 23–38 mm wide vs. ca. 9.2–13.1 mm high, 12.5–16.3 mm wide) and also vary from having five or six locules, unlike the exclusively pentalocular Panamanian fossils. Endocarps of *A. pulchrum* from the Miocene of Kenya are always pentalocular and are similar in size to the new species; however, this fossil differs mainly from *A. panamaensis* by having scattered punctae on the endocarp surface, a feature seen in several extant *Antrocaryon* species from Africa (see Herrera et al. 2018).

Paleoecological and Paleobiogeographic Implications

These early Miocene Cucaracha fossils, *S. rothwellii*, *D. montesii*, and *A. panamaensis*, from the Panama Canal, together with previously described late Eocene fossils from the Búcaro Formation in western Panama, *D. macdonaldii* (Herrera et al. 2012), represent the oldest-known reliable evidence of the Spondioideae in the Neotropics. The natural affinities of the spondioid Cucaracha fossils are also consistent with previous paleoecological interpretations of moist lowland to premontane tropical forests existing during the early Miocene of Panama (e.g., Herrera et al. 2010, 2014; Herrera 2014; Jaramillo et al. 2014). Most extant species of *Spondias* and all species of *Dracontomelon* and *Antrocaryon* are trees of lowland tropical moist/rain forests (Pell et al. 2011; Mitchell and Daly 2015). Only *S. purpurea* and *S. tuberosa* occur naturally in Neotropical deciduous and semiarid forests (i.e., Caatinga arborea in Brazil; Miller and Schaal 2006; Mitchell and Daly 2015), where these species remain leafless during the dry season. Species-specific structures in the roots of *S. tuberosa* and the stems of *S. purpurea* provide water-storing abilities (Borchert 1994) and enable their occurrence in semiarid and seasonally dry environments. Given that drought-adaptive traits are not widespread across *Spondias* and that most species are restricted to tropical lowland moist forests (Mitchell and Daly 2015), as are all species of *Dracontomelon* and *Antrocaryon* (Pell et al. 2011), we infer that the Cucaracha spondioid endocarps are likely to represent moist/rain forest species of canopy trees.

The occurrence of rain forest spondioids in the Cucaracha flora adds new woody elements to the early Miocene forests of Panama. Previously described macrofossils have been identified from permineralized wood, fruits, or seed remains. These fossils reveal a complex forest structure that includes canopy-dominant trees such as those of spondioids (this study), *Oreomunnea* (Juglandaceae; Herrera et al. 2014), and *Parinari* (Chrysobalanaceae; Jud et al. 2016); woody species of *Mammea* (Calophyllaceae; Nelson and Jud 2017), Detarioideae (Fabaceae), Myristicaceae, Meliaceae, and Sapotaceae (Rodríguez-Reyes 2014; Rodriguez-Reyes et al. 2017); lianas, including *Rourea* (Connaraceae; Jud and Nelson 2017), Vitaceae, Icacinaceae, and Passifloraceae (Herrera 2014); and palms, zingiberales (Herrera 2014), and other mid/understory elements such as some members of Malvaceae (Byttnerioideae and Malvoideae) and Eleocarpaceae (Rodríguez-Reyes 2014; Rodríguez-Reyes et al. 2014). Paleodiets of co-occurring mammals based on $\delta^{13}C$ of tooth enamel indicate that early Miocene herbivores fed on C_3 plants (MacFadden and Higgins 2004), in agreement with the composition of the Cucaracha flora.

The spondioid fossil fruits from Panama, with their well-preserved morphology and anatomy, and diagnostic characters provide strong evidence for recognizing modern genera and establish a minimum age of 19–18.5 Ma for the appearance of *Spondias* and *Antrocaryon*. Molecular clock-based analyses suggested early

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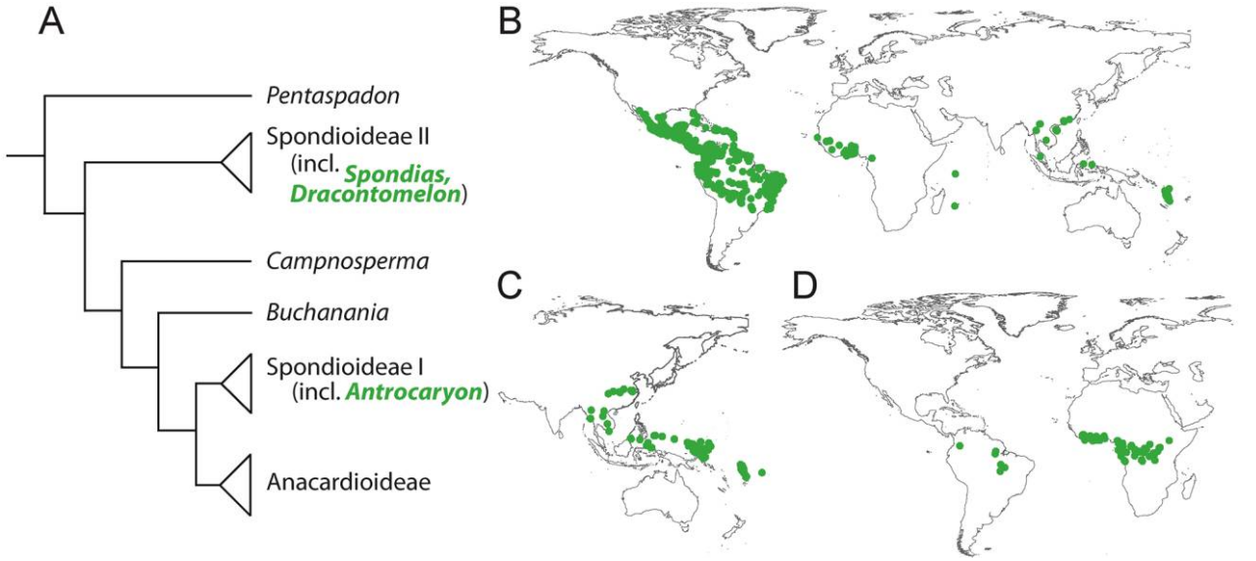

Fig. 6 *A*, Phylogenetic relationships of Anacardiaceae indicating placement of identified genera in the early Miocene Cucaracha flora (i.e., *Spondias*, *Dracontomelon*, and *Antrocaryon*; modified from Weeks et al. 2014). *B*, Occurrence of extant *Spondias*. *C*, Occurrence of extant *Dracontomelon*. *D*, Occurrence of extant *Antrocaryon*. Distribution data accessed through GBIF Data Portal, Global Biodiversity Information Facility (http://data.gbif.org).

to middle Miocene divergences of these two genera (Weeks et al. 2014). Given that these estimates are similar to the age of the Panamanian fossils, it is likely that molecular-clock approaches are underestimating the true divergence times of *Spondias* and *Antrocaryon* from each of their respective sister taxa. The age and occurrence of the spondioid Cucaracha fossils (*S. rothwellii*, *D. montesii*, and *A. panamaensis*) together with the previously described older endocarps from Tonosi (*D. macdonaldii*; Herrera et al. 2012) corroborate other lines of evidence indicating that long-distance dispersal and local extinctions explain the extant distribution patterns of the family (e.g., Weeks et al. 2014). *Spondias* includes 18 living species, 10 of which are endemic to Neotropical forests (fig. 6*B*). *Spondias rothwellii* is the earliest-confirmed record of *Spondias* in the Neotropics and indicates that this genus has been in tropical America at least since the early Miocene. Species of *Dracontomelon* are currently restricted to tropical rain forests of Indochina, Southeast Asia, and east Pacific Islands (fig. 6*C*), but their fossil records show a much wider distribution during the Neogene. *Antrocaryon panamensis* is the first and only record of this genus in the Neotropics so far. Most species of *Antrocaryon* live in tropical rain forests of west/central Africa, and a single species, *A. amazonicum*, grows in the Amazon (fig. 6*D*). Fossil *Antrocaryon* fruits have also been reported from early Miocene to Pliocene deposits in Ethiopia and Kenya (Chesters 1957; Bonnefille and Letouzey 1976; Tiffney et al. 1994), indicating a long presence of the genus in the African tropics. The occurrence of *A. panamensis* and *A. amazonicum* in the Neotropics indicates one or more instances of long-distance dispersal from Africa into and within the New World forests.

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Literature Cited

Berry EW 1918 The fossil higher plants from the Canal Zone. Bull US Natl Mus 103:15–44.

——— 1924 An Oligocene cashew nut from South America. Am J Sci 8:123–126.

——— 1927 Petrified fruits and seeds from the Oligocene of Peru. Pan-Am Geol 47:121–132.

——— 1934 Pleistocene plants from Cuba. Bull Torrey Bot Club 1:237–240.

Bold WA 1973 Ostracoda of the La Boca Formation, Panama Canal Zone. Micropaleontology 18:410–442.

Bonnefille R, R Letouzey 1976 Fruits Fossiles D'*Antrocaryon* dans la Vallée de L'Omo (Éthiopie). Adansonia 16:65–82.

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Borchert R 1994 Soil and stem water storage determine phenology and distribution of tropical dry forest trees. Ecology 75:1437–1449.

Buchs DM, D Irving, H Coombs, R Miranda, J Wang, M Coronado, R Arrocha, et al 2019 Volcanic contribution to emergence of Central Panama in the Early Miocene. Sci Rep 9:1417. doi:10.1038/s41598-018-37790-2.

Burnham RJ, NL Carranco 2004 Miocene winged fruits of *Loxopterygium* (Anacardiaceae) from the Ecuadorian Andes. Am J Bot 91:1767–1773. doi:10.3732/ajb.91.11.1767.

Chesters K 1957 The Miocene Flora of Rusinga Island, Lake Victoria, Kenya. Palaeontogr Abt B 101:30–71.

Collinson ME, NF Adams, SR Manchester, GW Stull, F Herrera, SY Smith, MJ Andrew, P Kenrick, D Sykes 2016 X-ray micro-computed tomography (micro-CT) of pyrite-permineralized fruits and seeds from the London Clay Formation (Ypresian) conserved in silicone oil: a critical evaluation. Botany 94:697–711. doi:10.1139/cjb-2016-0078.

Collinson ME, SR Manchester, V Wilde 2012 Fossil fruits and seeds of the middle Eocene Messel biota, Germany. Abh Senckenberg Ges Naturforsch 570:1–251.

Ferrera MM, E Hernández-Fuentes, M Cabrera-Castellanos 1990 Análisis polínico de sedimentos marinos del occidente de la Isla de la Juventud (Cuba). Acta Bot Hung 36:145–161.

Fu Q-Y, L Li, J-H Jin, X-Y Liu, C Quan 2017 Mummified fruits of *Choerospondias nanningensis* sp. nov. (Anacardiaceae) from the Upper Oligocene of a low latitude site in East Asia. J Syst Evol 55:477–483. doi:10.1111/jse.12255.

Gentry AH 1982 Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? Ann Mo Bot Gard 69:557–593.

Graham A 1985 Studies in Neotropical paleobotany. IV. The Eocene communities of Panama. Ann Mo Bot Gard 72:504–534.

——— 1988*a* Studies in Neotropical paleobotany. V. The lower Miocene communities of Panama: the Culebra Formation. Ann Mo Bot Gard 75:1440–1466.

——— 1988*b* Studies in Neotropical paleobotany. VI. The lower Miocene communities of Panama: the Cucaracha Formation. Ann Mo Bot Gard 75:1467–1479.

Herrera F 2014 Revealing the floristic and biogeographic composition of Paleocene to Miocene Neotropical forests. PhD diss. University of Florida, Gainesville.

Herrera F, SR Manchester, C Jaramillo 2012 Permineralized fruits from the late Eocene of Panama give clues of the composition of forests established early in the uplift of Central America. Rev Palaeobot Palynol 175:10–24. doi:10.1016/j.revpalbo.2012.02.007.

Herrera F, SR Manchester, C Jaramillo, B MacFadden, SA da Silva-Caminha 2010 Phytogeographic history and phylogeny of the Humiriaceae. Int J Plant Sci 171:392–408. doi:10.1086/651229.

Herrera F, SR Manchester, R Koll, CA Jaramillo 2014 Fruits of *Oreomunnea* (Juglandaceae) in the early Miocene of Panama. Pages 124–133 *in* Paleobotany and biogeography: a Festschrift for Alan Graham in his 80th year. Missouri Botanical Garden, St. Louis.

Herrera F, JD Mitchell, SK Pell, ME Collinson, DC Daly, SR Manchester 2018 Fruit morphology and anatomy of the spondioid Anacardiaceae. Bot Rev 84:315–393. doi:10.1007/s12229-018-9201-1.

Hollick A, EW Berry 1924 A Late Tertiary flora from Bahía, Brazil. Johns Hopkins Univ Stud Geol 5:11–137.

Islebe GA, H Hooghiemstra, M Brenner, JH Curtis, DA Hodell 1996 A Holocene vegetation history from lowland Guatemala. Holocene 6:265–271. doi:10.1177/095968369600600302.

Iturralde-Vinent MA, RD MacPhee, SD Franco, R Rojas-Consuegra, W Suárez, A Lomba 2000 Las Breas de San Felipe, a Quaternary fossiliferous asphalt seep near Martí (Matanzas Province, Cuba). Caribb J Sci 36:300–313.

Jaramillo CA, E Moreno, VO Ramírez, SAF Silva-Caminha, A de la Barrera, A de la Barrera S Moron, F Herrera, J Escobar, R Koll, SR Manchester 2014 Palynological record of the last 20 million years in Panama. Pages 134–251 *in* Paleobotany and biogeography: a Festschrift for Alan Graham in his 80th year. Missouri Botanical Garden, St. Louis.

Johnson KG, MX Kirby 2006 The Emperador limestone rediscovered: early Miocene corals from the Culebra Formation, Panama. J Paleontol 80:283–293. doi:10.1666/0022-3360(2006)080[0283:TELREM]2.0.CO;2.

Joy KW, AJ Willis, WS Lacey 1956 A rapid cellulose peel technique in palaeobotany. Ann Bot 20:635–637.

Jud NA, CW Nelson 2017 A liana from the lower Miocene of Panama and the fossil record of Connaraceae. Am J Bot 104:685–693. doi:10.3732/ajb.1700080.

Jud NA, CW Nelson, F Herrera 2016 Fruits and wood of *Parinari* from the early Miocene of Panama and the fossil record of Chrysobalanaceae. Am J Bot 103:277–289. doi:10.3732/ajb.1500425.

Kirby MX, DS Jones, BJ MacFadden 2008 Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American peninsula. PLoS ONE 3:e2791. doi:10.1371/journal.pone.0002791.

Krasser F 1903 Konstantin von Ettingshausen's studien uber die fossile flora von Ouricanga in Brasilien. Sitz Kais Akad Wiss Math-Nat Kl 112:852–860.

Leyden BW 1985 Late Quaternary aridity and Holocene moisture fluctuations in the Lake Valencia basin, Venezuela. Ecology 66:1279–1295.

MacFadden BJ 2006 North American Miocene land mammals from Panama. J Vertebr Paleontol 26:720–734. doi:10.1671/0272-4634(2006)26[720:NAMLMF]2.0.CO;2.

MacFadden BJ, JI Bloch, H Evans, DA Foster, GS Morgan, A Rincon, AR Wood 2014 Temporal calibration and biochronology of the Centenario Fauna, early Miocene of Panama. J Geol 122:113–135. doi:10.1086/675244.

MacFadden BJ, P Higgins 2004 Ancient ecology of 15-million-year old browsing mammals within C_3 communities from Panama. Oecologia 140:169–182. doi:10.1007/s00442-004-1571-x.

Manchester SR 1994 Fruits and seeds of the middle Eocene Nut Beds flora, Clarno Formation, Oregon. Palaeontogr Am 58:1–205.

Manchester SR, B Balmaki 2018 Spiny fruits revealed by nano-CT scanning: *Pseudoanacardium peruvianum* (Berry) gen. et comb. nov. from the early Oligocene Belén flora of Peru. Acta Palaeobot 58:41–48. doi:10.2478/acpa-2018-0005.

Manchester SR, Z-D Chen, A-M Lu, K Uemura 2009 Eastern Asian endemic seed plant genera and their paleogeographic history throughout the Northern Hemisphere. J Syst Evol 47:1–42. doi:10.1111/j.1759-6831.2009.00001.x.

Manchester SR, V Wilde, ME Collinson 2007 Fossil cashew nuts from the Eocene of Europe: biogeographic links between Africa and South America. Int J Plant Sci 168:1199–1206. doi:10.1086/520728.

Miki S 1941 On the change of flora in Eastern Asia since Tertiary period. 1. The clay or lignite beds flora in Japan with special reference to the *Pinus trifolia* beds in central Hondo. Jpn J Bot 11:237–303.

Miller AJ, B Schaal 2006 Domestication and the distribution of genetic variation in wild and cultivated populations of the Mesoamerican fruit tree *Spondias purpurea* L. (Anacardiaceae). Mol Ecol 15:1467–1480. doi:10.1111/j.1365-294X.2006.02834.x.

Mitchell JD, DC Daly 2015 A revision of *Spondias* L. (Anacardiaceae) in the Neotropics. Phytokeys 55:1–92. doi:10.3897/phytokeys.55.8489.

Mitchell JD, DC Daly, SK Pell, A Randrianasolo 2006 *Poupartiopsis* gen. nov. and its context in Anacardiaceae classification. Syst Bot 31:337–348. doi:10.1600/036364406777585757.

Montes C, G Bayona, A Cardona, DM Buchs, CA Silva, SE Morón, N Hoyos, DA Ramírez, C Jaramillo, V Valencia 2012*a* Arc-continent

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collision and orocline formation: closing of the Central American seaway. J Geophys Res 117:B04105. doi:10.1029/2011JB008959.

Montes C, A Cardona, RR McFadden, S Morón, CA Silva, S Restrepo-Moreno, DA Ramírez, et al 2012*b* Evidence for Middle Eocene and younger emergence in Central Panama: implications for Isthmus closure. Geol Soc Am Bull 124:780–799. doi:10.1130/B30528.1.

Muellner-Riehl AN, A Weeks, JW Clayton, S Buerki, L Nauheimer, YC Chiang, S Cody, SK Pell 2016 Molecular phylogenetics and molecular clock dating of Sapindales based on plastid *rbcL*, *atpB* and *trnL-trnF* DNA sequences. Taxon 65:1019–1036. doi:10.12705/655.5.

Nelson CW, NA Jud 2017 Biogeographic implications of *Mammea paramericana* sp. nov. from the Lower Miocene of Panama and the evolution of Calophyllaceae. Int J Plant Sci 178:241–257. doi:10.1086/689618.

Pell SK 2004 Molecular systematics of the cashew family (Anacardiaceae). PhD thesis. Louisiana State University, Baton Rouge.

Pell SK, JD Mitchell, T Lobova, AJ Miller 2011 Anacardiaceae. Pages 7–50 *in* K Kubitzki, ed. The families and genera of vascular plants. Vol 10. Springer, New York.

Pérez-Lara DK, C Castañeda-Posadas, E Estrada-Ruiz 2017 A new genus of Anacardiaceae fossil wood from El Bosque Formation (Eocene), Chiapas, Mexico. IAWA J 38:543–552. doi:10.1163/22941932-20170179.

Ramírez JL, SRS Cevallos-Ferriz 2002 A diverse assemblage of Anacardiaceae from Oligocene sediments, Tepexi de Rodríguez, Puebla, Mexico. Am J Bot 89:535–545. doi:10.3732/ajb.89.3.535.

Raven PH, DI Axelrod 1974 Angiosperm biogeography and past continental movements. Ann Mo Bot Gard 61:539–673.

Reid EM, MEJ Chandler 1933 The London Clay flora. British Museum (Natural History), London.

Retallack GJ, MX Kirby 2007 Middle Miocene global change and paleogeography of Panama. Palaios 22:667–679. doi:10.2110/palo.2006.p06-130r.

Rodríguez-Reyes O 2014 Systematics of Miocene angiosperm woods from the Panama Canal, and their palaeoenvironmental implications. PhD diss. University of London, Royal Holloway.

Rodríguez-Reyes O, HJ Falcon-Lang, P Gasson, ME Collinson, C Jaramillo 2014 Fossil woods (Malvaceae) from the lower Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama (Central America) and their biogeographic implications. Rev Palaeobot Palynol 209:11–34. doi:10.1016/j.revpalbo.2014.05.006.

Rodríguez-Reyes O, P Gasson, HJ Falcon-Lang, ME Collinson 2017 Fossil legume woods of the Prioria-clade (subfamily Detarioideae) from the lower Miocene (early to mid-Burdigalian) part of the Cucaracha Formation of Panama (Central America) and their systematic and palaeoecological implications. Rev Palaeobot Palynol 246:44–61. doi:10.1016/j.revpalbo.2017.06.005.

Salgado-Labouriau ML 1980 A pollen diagram of the Pleistocene-Holocene boundary of Lake Valencia, Venezuela. Rev Palaeobot Palynol 30:297–312.

Tiffney BH, JG Fleagle, TM Bown 1994 Early to middle Miocene angiosperm fruits and seeds from Fejej, Ethiopia. Tert Res 15:25–42.

Von Teichman IV 1987 Development and structure of the pericarp of *Lannea discolor* (Sonder) Engl. (Anacardiaceae). Bot J Linn Soc 95:125–135.

——— 1990 Pericarp and seed structure in *Tapirira guianensis* (Spondiadeae: Anacardiaceae). S Afr J Bot 56:435–439.

——— 1992 Notes on the ovule and partially pachychalazal seed of *Operculicarya decaryi* H. Perrier (Anacardiaceae) from Madagascar. Bot Bull Acad Sin 33:289–293.

Wannan BS, CJ Quinn 1990 Pericarp structure and generic affinities in the Anacardiaceae. Bot J Linn Soc 102:225–252.

Weeks A, F Zapata, SK Pell, DC Daly, JD Mitchell, PVA Fine 2014 To move or to evolve: contrasting patterns of intercontinental connectivity and climatic niche evolution in "Terebinthaceae" (Anacardiaceae and Burseraceae). Front Genet 409:1–20. doi:10.3389/fgene.2014.00409.

Wheeler EA, R Srivastava, SR Manchester, P Baas 2017 Surprisingly modern Latest Cretaceous–earliest Paleocene woods of India. IAWA J 38:456–542. doi:10.1163/22941932-20170174.

Woodring WP 1957–1982 Geology and paleontology of Canal Zone and adjoining parts of Panama. US Geol Surv Prof Pap 306.

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