Permineralized fruits from the late Eocene of Panama give clues of the composition of forests established early in the uplift of Central America

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1. Introduction

Central American rainforests are noted for their extraordinary plant diversity, family composition, and climate (Phillips et al., 2002). Except for few reports of pollen assemblages (Germeraad et al., 1968; Graham, 1985) and one species of endocarp (Berry, 1918) from the Eocene of Panama; few data have been available on the plants that inhabited the earliest terranes of Central America during the Paleogene. When did rainforests first become established in Central America? What families first colonized the emergent land in the Panamanian seaway? These questions are difficult to address without a sufficient paleobotanical record.

The rise of the southern part of Central America (from Nicaragua to Panama) has been hypothesized as a result of a volcanic arc that started no earlier than the middle Miocene (~17 Ma) (see review in Molnar, 2008). Nevertheless, new and abundant field, geochronological, and thermochronological data from Central Panama suggest the presence of large volcanic terranes above sea level at least since the Eocene (Fig. 1; Iturralde-Vinent, 2006; Buchs et al., 2011; Montes et al., 2012). Given the complex geological history of Central America and especially in Panama (Wegner et al., 2011), it may be inferred that the earliest forests in those Eocene terranes evolved in parallel to the tectonics of the region, where long-distance dispersal, island-hopping, and vicariance might have played an important role for the colonization of the new land.

Recent discoveries of macrofloras from the middle to upper Paleocene of Colombia (Doria et al., 2008; Herrera et al., 2008, 2011; Gómez-Navarro et al., 2009; Wing et al., 2009; Carvalho et al., 2011) have provided evidence of the earliest Neotropical rainforests, similar to biomes from this region in leaf morphology, family composition, and inferred climatic conditions. However, the Paleocene plant diversity was much lower than in modern tropical counterparts. Plant diversity similar to or even higher than extant Neotropical levels is first observed during the warmest periods of the Cenozoic in northern South America: the Paleocene–Eocene boundary and the early-middle Eocene (Jaramillo et al., 2006, 2010). High temperatures and wet conditions, in correlation with high levels of atmospheric CO2, seem to be some of the main reasons for the elevated levels of plant diversity recorded globally in the Eocene (Graham, 1994; Zachos et al., 2001). New localities from the Paleogene of Central America are important for the understanding of the evolution, diversity, and composition of the earliest forests in the region before the final closing of the Panamanian seaway during the Neogene (Coates et al., 2004).

Here, we report new permineralized fossil endocarps and seeds from an upper Eocene locality from the Pacific coast of Panama near Tonosi. A fossil layer first reported by Berry (1918) was relocated and seven of the eight taxa reported here are new fossil species. These fossils provide insight into the families and genera typical of lowland rainforests in the earliest terranes of Central America. Also, two of the new fossil species belong to modern genera that today grow only in lowland rainforests of Africa, Southeast Asia, and Australasia.

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2. Materials and methods

The newly recovered disseminules are from the mouth of the Tonosí River at the fishing village of Punta Búcaro of Los Santos State, Azuero Peninsula, Panama. All specimens were found at locality 1: 7°20′52.8″N, 80°21′12.1″W (this plant locality outcrops directly behind the local school–church building. Smithsonian Tropical Research Institute (STRI) database locality #090014), except for the specimens UF608-56168 to 56170 which were found at locality 2: 7°20′833″N, 80°21′12.111″W, the locality outcrops at the beach. Also, the specimen UF610-56167 was found at locality 3: 7°20′870″N, 80°35′347″W, the locality is uphill from the school-church building, about 10 m up in the stratigraphic section.

The paleobotanical potential of the Tonosí area was first recognized by Berry (1918) with the publication of a single plant species that he assigned to the modern genus Diospyros. The type specimen, originally collected by D.F. MacDonald, contains several conspecific permineralized fruits. A visit to the mouth of the Tonosí River in the summer of 2007 allowed us to relocate the fossiliferous layer. After two more visits in the summers of 2010 and 2011 more than 70 specimens of calcium carbonate-permineralized endocarps and seeds have been collected.

The plant remains come from the Búcaro Formation, and are found in blue-green calcareous fine-grained sandstone and siltstones with abundant muscovite fossils. The stratigraphy of the Tonosí area shows an intercalation of widespread basalts, calcareous sandstones, conglomerates, and shales, many of these beds also containing abundant invertebrate faunas and carbonized and calcified wood.

The Tonosi strata have been suggested to be among the oldest sedimentary sequences in Panama (Vaughan, 1919); several historical studies of the invertebrate faunas (mollusk and foraminifera) propose an early late Eocene age for this sequence (Miller and Furnish, 1939; Olsson, 1942) based on correlations with the Eocene Talara Formation from Peru. A more recent study based on foraminifera from the Azuero Peninsula corroborates a late Eocene age for the shallow sedimentary sequences from Tonosí (Baumgartner-Mora et al., 2008).

Transverse (cut perpendicular to longest axis of the specimen) and longitudinal (cut parallel to the longest axis of the specimen) sections were cut through the center of the fossils with a thin-bladed diamond saw; subsequently the specimens were photographed while immersed in xylene or low-viscosity resin (Opticon No. 224) to highlight their internal anatomy. Acetate peels of the fossil plants were prepared using the technique of Joy et al. (1956). Sectioned specimens were first polished with an aqueous slurry of silicon carbide grit (600) on a glass plate and then etched in 5% HCl for five seconds. After etching, the specimens were carefully washed with tap water and allowed to dry. Then, the etched surface was flooded with acetone and a strip of cellulose acetate was placed over it. The peels were air-dried for about 20 min and then the acetate was gently peeled away by hand, trimmed with scissors, and mounted on a glass slide with Canada balsam mounting medium.

For comparison with the fossils we studied extant genera of angiosperms with materials from the herbaria of the University of Florida (FLAS), the United States National Herbarium (US) in Washington, D.C, STRI in Panama, the New York Botanical Garden (NY), and the modern fruit and seed bank of the Paleobotanical collection of the Florida Museum of Natural History, Gainesville, Florida. Collection information of fruit taxa in plate captions is presented as: (herbarium abbreviation, collector information, country). Fruit characters among extant genera of the Spondioideae subfamily (Anacardiaceae) were investigated in cooperation with J.D. Mitchell, D.C. Daly, and S.K. Pell (unpublished data) and from previous studies by Grote (1989) and Mitchell et al. (2006). Seed characters among extant genera of Vitaceae were inspected in cooperation with Iju Chen.

3. Systematics

Family—Arecales Schultz
Fossil genus—Ruminosemen Herrera, Manchester et Jaramillo gen. nov.
Generic diagnosis—Seed with abundant and longitudinal striations on the exterior part of the seed coat. Circular embryo scar. Seed coat very thick.
Derivation of generic name—From the Latin words “rumino” for ruminate and “semen” for seed.
Type species—Ruminosemen panamensis Herrera, Manchester et Jaramillo sp. nov.
Specific diagnosis—Seed subglobose to ovoid in shape. Seed coat with inward intrusions accommodating a strongly ruminate endosperm.
Holotype hic designatus—UF618-56164 (STRI-15661). Plate I, 1–3
Paratype—UF618-56165 (STRI-15676).
Description—Seeds subglobose, ~10 to 17.6 mm in length and ~9.6 to 13.1 mm in width. Outer surface covered with longitudinal striations (Plate I, 2). One end of seed with a circular depression corresponding to the embryo scar (Plate I, 1). Seed coat thick (>2.6 mm); transverse and longitudinal sections show irregular and deep intrusions of seed coat indicating a strongly ruminate endosperm (Plate I, 3, 4).

Derivation of specific epithet—From Panama, where the fossil was found.

Systematic affinity—Ruminosemen panamensis resembles disseminules found in some genera of palms. The combination of characters such as longitudinal striations, the embryo scar, a thick seed coat, and a strongly ruminate endosperm support the placement of this fossil taxon within the Arecaceae (Dransfield et al., 2008). Ruminate seeds are also found in other families (Bayer and Appel, 1996), for example in Annonaceae, however its seeds are bisymmetrical unlike the Panamanian fossil. Another example is Myristicaceae, however, the ruminate endosperm in seeds of that family extends radially inward nearly to the center of the seed (Doyle et al., 2008); in our fossil the ruminations are only superficial intrusions of the seed coat and lack the radial pattern seen in Myristicaceae.

A survey of extant seeds in the Arecaceae shows that the combination of characters present in this fossil occurs in several genera, including for example Bismarckia, Ptychococcus, Roystonea, and Tahina. This occurrence

Plate I. Ruminosemen panamensis Herrera, Manchester et Jaramillo sp. nov. 1–3 Holotype UF618-56164. 1. Apical view of the seed, arrow indicating the embryo scar. 2. Lateral view showing longitudinal striations (arrow) of the seed coat. 3. Transverse section showing very thick seed coat and strongly ruminate endosperm. 4. Paratype UF618-56165, longitudinal section showing ruminate endosperm. Scale bar 2 mm.
Plate II. 1–6. cf. *Leea*, specimen UF618-56163. 1. Lateral view of the seed showing series of rugae; arrow shows basal ruga, scale bar 2 mm. 2. SEM, the arrow shows a vascular strand that runs along the ruga, scale bar 750 μm. 3. Transverse section, upper arrow indicates possible base of the Y-shaped dorsal infold; lower arrows show longitudinal ruga, scale bar 2 mm. 4. Detail from 3, arrow possible Y-shaped dorsal infold, scale bar 0.5 mm. 5. Lower transverse section, arrow indicates possible base of the Y-shaped dorsal infold, scale bar 1 mm. 6. Detail from 5, upper arrow shows possible apical notch, lower arrows Y-shaped dorsal infolds, scale bar 0.5 mm. 7–9. *Leea* philippinensis Merrill [A. C. Frake 56725, Philippines], arrow shows basal ruga, scale bar 2 mm. 8. Transverse section from 7 showing Y-shaped dorsal infold (arrow), scale 2 mm. 9. *Leea* guineensis Descoings [TAIF, I. Chen 44, Taiwan], upper arrow shows Y-shaped dorsal infold, lower arrow a lateral ruga, scale bar 1 mm. Photos of extant *Leea* were provided by Iju Chen.
of rumination seems to be highly homoplasious as it appears in several unrelated clades of the family (Dransfield et al., 2008); therefore, we cannot attribute this fossil to a particular genus or tribe. No other fossil previously related to Arecaceae (see review in Harley, 2006) preserves all the characters observed in the Panamanian specimens.

Family—Vitaceae Juss.
Genus—cf. Leea L.


Description—Half of a seed preserved in lateral view (Plate II, 1). Length ~6.9 mm and width ~5.7 mm. Seed coat very thin, ~80 μm in thickness. The seed coat covers a corrugated surface with a series of ridges that correspond to the rugae. From these rugae, a lateral, c-shaped ruga runs basally, more or less parallel to the dorsal side of the seed and several rugae depart from it at approximately right and obtuse angles and bifurcate (Plate II, 1). The seed also preserves vascular strands that run along the crests of rugae (Plate II, 2). The transverse sections of the specimen (Plate II, 3–6) reveal that the seed was filled with sediment; however, internal remains of what appears to be the dorsal infold and the longitudinally arranged rugae are still preserved (Plate II, 3–6). On the dorsal side there are two intrusions of the seed coat; they appear broken, but might represent the bases of the Y-shaped dorsal infold. Other remains of the longitudinal grooves are also preserved, supporting the branching pattern observed on the lateral view (Plate II, 3–6).

Systematic affinity—the genus Leea of the grape family (Vitaceae) shows the closest similarity to this fossil. Extant species of Leea (Plate II, 7–9) are recognized by seeds with a long chalaza on the dorsal side, a Y-shaped dorsal infold (seen in transverse section), a pair of ventral infolds, and a pair of longitudinally arranged rugae on each of the lateral faces (representing lateral infolds) (Chen and Manchester, 2011). This fossil is an incomplete cast (infilling of the seed coat), with some patches of remaining seed coat, interpreted to represent a seed that had split open in the plane of bisymmetry. Important characters, including the chalaza and ventral infolds, cannot be seen due to the fragmentary, incomplete nature of the single specimen, but the portion preserved closely resembles the ornamentation seen in some species of Leea, e.g., L. philippinensis Merrill (Plate II, 7) and L. heterodoxa Schumann and Lauterbach. The fossil shows a series of highly branched furrows, developed from the longitudinally arranged ruga and internal remains of what appear to be the Y-shaped dorsal infold (Plate II, 3–6); these two characters are distinctive for extant Leea (Plate II, 8, 9) and set the genus apart from other Vitaceae (Chen and Manchester, 2011). Thus, based on the presence of these characters, we support the placement of the Panamanian fossil within this Paleotropical and Australasian genus. However, we hope to find more complete specimens as collecting efforts at the Tonosí locality continue, to fully observe the chalaza and ventral infolds.

Modern Leea grows mostly in lowland to montane forests from Malaysia, Indochina, South and Southwest China, and India, extending to Micronesia, Melanesia, Australia, and tropical Africa (Wen, 2007). Given this exclusively Old World distribution of its extant species, the occurrence of Leea fossils in Central America might seem unexpected. However, fossil seeds of the same genus have also been recognized on the basis of better-preserved and more complete specimens from the Paleogene Belén flora of Peru. The specimens from Belén described as Carpolithus olissoni Berry (1927) were identified as Leea by Chen and Manchester (2007). The age of the Belén locality was formerly considered to be Eocene; however a recent visit to the original site recovered diatoms from the seed-bearing layer that lead us to infer a younger, latest early Oligocene age (~30–28.5 Ma; Manchester et al., in press).

Fossil genus—Saxuva Herrera, Manchester et Jaramillo gen. nov.

Generic diagnosis—Chalaza long and linear. Ventral infolds two, each with a short surface slit, and a broad, deep cavity. These openings form caverns extending apically beyond the surface slits. Seed cavity in transverse section m-shaped. Transverse sections of seed cavity in the apical ¼ (above the ventral slits), distinctively lemniscate (=shaped).

In transverse sections the raphe appears sharply pointed to bulbous. Endotesta thickness variable. Raphe strand enveloped within the endotesta.

Derivation of generic name—from the Latin words “sax” for rock and “uva” for grape.

Type species—Saxuva draculoidea Herrera, Manchester et Jaramillo sp. nov.

Specific diagnosis—Seed obovate in dorsal view and subtriangular to approximately circular in transverse sections. Dorsal surface smooth. Seed cavity with limbs directed ventrally; sharply ridged or bilobed towards the raphe area. Endotesta thick at the chalaza-raphe areas and the sharp lateral edges of the ventral cavities but thin on the ventral faces. The endotesta is formed by three layers of isodiametric and anisodiametric cells.

Holotype hic designatus—UF610-56166. Plate III, 1.

Paratypes—UF608-56168, UF608-56169, UF608-56170, UF618-56151.

Description—Seed obovate in dorsal view and subtriangular to approximately circular in transverse sections (Plate III, 1–15). Maximum length and width ~7.8 mm and ~5.7 mm respectively (measured from the dorsal side); in transverse sections the three seeds measured range from the base at ~4.2 mm long and 4.0 mm wide, at the equator ~7.8 mm long and 5.2 mm wide; and at the apex ~3.2 mm long and 4.6 mm wide. Ventral infolds two, each with a short surface slit, and a broad, deep cavity (Plate III, 4, 5, 11). These openings become cavities now filled with sediment; observed in transverse sections only: extending apically beyond the surface slits (Plate III, 6–9, 13). Ventral cavities at the equator of the seed are bordered by thin and sharply pointed lateral edges, with a maximum width of 1.3 mm; these ventral cavities appear in two successive transverse sections (Plate III, 4, 5), thus we estimate a maximum vertical length of 4.0 mm. Beak angle ~50° (measured dorsally). Dorsal surface smooth (Plate III, 1). Chalaza long and linear, terminated near beak (Plate III, 1); chalaza surface angle (measured in transverse section) ranging from ~90° basally to 105° apically; chalazal depression angle from ~143° basally to 96° apically. In transverse section the raphe appears sharply pointed (Plate III, 4–10) to bulbous (Plate III, 11, 12, 15). Seed cavity (=endospore area) in cross section m-shaped with limbs directed ventrally (Plate III, 3–7, 11), sharply pointed (Plate III, 3–7) or bilobed towards the raphe area (Plate III, 11, 12). Transverse sections near the apex of the seed, beyond the ventral infolds, show a lemniscate (=shaped) configuration of the seed cavity (Plate III, 8, 9, 13). Consistently near the sunken chalaza (Plate III, 3–9, 11, 13, 17) and sometimes in the raphe area (observed only in two apical cuts; Plate III, 9, 13) the endospore area protrudes the endotesta. Endotesta is variable in thickness—very thick at the chalaza-raphe areas (0.4–2.0 mm) and at the sharp lateral edges of the ventral cavities (1.5–2.3 mm; Plate III, 4, 5, 11), but very thin endotesta on the ventral faces of the seed (0.03–0.08 mm; Plate III, 3–9, 11–13, 17, 19–20). The endotesta is formed by three layers of isodiametric and anisodiametric cells (Plate III, 18–20); these layers are usually well preserved in the ventral, raphe and chalaza areas. By the ventral faces the endotesta is very thin and shows only two layers of parenchyma cells; the outermost layer shows square parenchyma cells ~27 to 23 μm (Plate III, 19), the innermost layer (in contact with the endospore cavity) is formed by columnar cells ~68 μm in length and ~16 μm in width, this layer is not well preserved in the raphe, chalaza and lateral edges of the ventral cavities (Plate III, 20). A third, almost undefined layer of thick-walled anisodiamic cells (ranging from 25 to 117 μm in diameter) is present in the borders of the raphe and chalaza areas only (Plate III, 16–18). A circular canal, 227 μm in diameter, interpreted as the raphe, passes through the endotesta along the median ventral crest (Plate III, 2, 3, 12, 16, 18).
Derivation of specific epithet—From the fictional character Count Dracula, making reference to the vampire/bat shape of the seed as viewed in transverse sections (Plate III, 4–5, 11).

Systematic affinity—Saxuva draculoida presents a dorsal chalaza and paired ventral infolds, two characters diagnostic of the grape family–Vitaceae (Chen and Manchester, 2007, 2011). Other characters consistent with Vitaceae that are preserved in these fossils include the basal beak, the ruminate and m-shaped endosperm cavity (seen in transverse sections), and the lignified endostele (Plate III, 1–20). Within Vitaceae, S. draculoida resembles modern taxa within the genera that possess a long, linear chalaza, correlating mostly with the clade having tetratermous flowers (Wen et al., 2007; Chen and Manchester, 2011; Ren et al., 2011). It is readily distinguished from most members the pentameral clade including Vitis, Ampelopsis, Ampelocissus, and Parthenocissus, by the linear, rather than circular to oval, chalazal scar. Although some species within the tetratermous clade vary by having oval chalazas instead, its presence may be a derived condition (Chen, 2009). The new fossil taxon exhibits characters seen in the modern genera Cissus, Cayratia, and Cyphostemma.

Cissus is the largest genus in the family, with ca. 350 species (Lombardi, 2007; Chen, 2009). Its seeds can be smooth (Plate III, 1, 21) or rugose, the opening of the ventral infolds on the seed surface are linear or wide (Plate III, 11, 24), and occasionally the endostele appears exceptionally thickened near the chalaza, (Plate III, 11, 17, 22, 23), raphe (Plate III, 16, 27), and lateral edges (Plate III, 4, 11, 25) (Chen and Manchester, 2011). Also, we observe in the endostele of the fossil and several extant species of Cissus, an undefined, outermost layer of thick-walled anisodiamicotan tissue toward the raphe and chalaza (Plate III, 16, 17, 23, 27). Transverse sections above the opening of the ventral infold slits in extant Cissus also show the lemniscate-shaped structure (=) formed by the endosperm cavity (Plate III, 8, 9, 13, 26); nevertheless, this character seems to be common across some other genera in the family, including Cayratia and Cyphostemma as well. Saxuva draculoida fits partially within the natural morphological variation observed in Cissus (Plate III, 21–27). However, Saxuva preserves what appears to be a circular vascular strand wrapped inside the endostele (Plate III, 12, 16, 18), this character has been observed only in species of Cyphostemma so far (Plate III, 29, 30) (Chen and Manchester, 2011). Significant morphological differences between Saxuva and Cyphostemma lie in the presence of closed ventral infolds and a strongly rugulate surface seed in the extant genus (Chen and Manchester, 2011). Cayratia also has some seeds that resemble S. draculoida (i.e. long and linear chalaza, wide opening of the ventral infolds, thick endostele, and a smooth dorsal surface) (Plate III, 28). Cayratia seeds display more morphological variation compared to Cissus, but that morphological range does not seem to include the form exhibited by this fossil species. Due to the notable differences between S. draculoida and the mentioned extant genera, we consider this genus to be of uncertain placement within the tetratermous flower clades in Vitaceae. No other fossil assigned to Vitaceae shows all the characters observed in S. draculoida.

Extant Cissus has a Pantropical distribution and Cayratia, and Cyphostemma are restricted to the Old World (Wen et al., 2007; Ren et al., 2011). In the Neotropics, three other genera also co-occur today with Cissus: Ampelocissus, Ampelopsis, and Vitis, ranging from lowland to high mountain forests (Lombardi, 2007). Although Ampelocissus and Leea are known from the Oligocene of Belén, Peru (Chen and Manchester, 2007), the antiquity of Ampelopsis and Vitis in Central and South America remains unknown. The new fossil genus Saxuva and the above-described specimen of cf. Leea (Plate II, 1–6) are the earliest evidence of the grape family in the Neotropics. Vitaceae are of interest for their basal position within Rosids, one of the largest clades in flowering plants (Wang et al., 2009).

Family–Humiriaceae Jussieu
Fossil genus—Lacunofructus Herrera, Manchester et Jaramillo gen. nov.
Generic diagnosis—Penta to hexa-carpellate with five to six valves or septa. Valves conspicuous. Seeds one per locule. Small cavities abundant within valves and sepa.

Description of generic name—from the Latin “lacuna”: hole, pit, cavity and “fructus” for fruit.

Type species—Lacunofructus cuatrecasana Herrera, Manchester et Jaramillo sp. nov.

Specific diagnosis—Endocarp elliptic to globose. Valves lingulate in shape, running lengthwise and without a median furrow on the surface. Seeds pentagonal as seen in ventral section. Small cavities abundant within valves and sepa.

Holotype hic designatus—UF618-56157 (STRI–15663). Plate IV, 1, 2.

Description—Endocarp elliptic to globose (Plate IV, 1, 3). Length ~19 to 12.3 mm, width 11.3 to 7.9 mm (n = 5). Surface smooth. Apex acute to rounded (Plate IV, 4), base elliptic. Septa and valves five to six, radially arranged. Septa enlarging outward, as seen in transverse section (Plate IV, 2, 5, 6). Valves conspicuous, apparently without a median furrow on the surface, lingulate, running lengthwise, but never reaching fully to the apex or the base of the endocarp (Plate IV, 1, 3, 4). Seeds one per locule. Up to three locules per fruit; trigonal as viewed in transverse section (Plate IV, 2, 5–7). Endocarp without apical foramina. Small ellipsoidal cavities present and

Plate III, 1–20. Saxuva draculoida Herrera, Manchester et Jaramillo sp. nov. 1. Holotype UF610-56166; upper arrow shows thick, long, and linear chalaza, lower arrow indicates beak, scale bar 2 mm. 2–9. Paratype UF608-56168, successive transverse sections; scale bars 2 mm. 2. Lowermost transverse section of the seed, upper arrow indicates chalaza, lower arrow shows vascular strand. 3. Arrow shows opening of one of the ventral cavities. 4. Upper arrow shows pronounced chalaza, lower arrows indicates wide ventral cavities. 5. Notice broad and deep ventral infolds bordered by thin and sharply pointed lateral edges, arrow indicates raphe. 6. Notice closing of ventral cavities. 7. Arrow shows m-shaped endosperm cavity toward the chalaza area. 8. Left arrow indicates cavern (now filled with sediment) located above the ventral infold slits, right arrow lemniscate-shaped structure (=) formed by the endosperm cavity. 9. Upper most transverse section, top arrow shows chalaza, lower arrow shows raphe. 10–19. Paratype UF608-56169, successive transverse sections, scale bars 2 mm, except where noted after description. 10. Lowermost transverse section, arrow shows thick raphe. 11. Notice broad and deep ventral infolds (black arrow) bordered by thin and sharply pointed lateral edges, white arrow shows endosperm cavity protruding the endostele. 12. Detail from 11, notice the bilobed endosperm cavity near the raphe; arrow shows vascular strand wrapped in the endostele, scale bar 1 mm. 13. Notice lemniscate-shaped structure (=) formed by the endosperm cavity; upper arrow shows protruding endosperm near chalaza, lower arrow shows cavern. 14. Upper most transverse section. 15–19. Acetate peel of a transverse section (from 11). 15. Notice variability of the thickness of the endostele. 16. Arrow shows vascular strand wrapped by endostele, notice undefined layer of thick-walled anisodiamicotan cells by the edge of the raphe, scale bar 0.5 mm. 17. Upper arrow shows thick-walled anisodiamicotan cells near chalaza, lower arrow indicates protruding endosperm, scale bar 0.5 mm. 18. Detail from 16, near raphe showing vascular strand and thick-walled cells of the endostele, scale bar 250 μm. 19. Thin endostele on the ventral face of the seed, arrow shows the outer most layer composed of square parenchyma cells, the inner most layer (in contact with the endosperm) is formed by columnar cells, scale bar 100 μm. 20. Paratype UF608-56170, notice two layers of the endostele, thin layer indicated by the arrow, scale bar 100 μm. 21–30. Extant Vitaceae. 21. Cissus verticillatus (L.) Nicolson and C.E. Jarvis [TAIF, Nicolson and Jarvis, Taiwan], dorsal view, arrow shows long, linear, and thick chalaza, scale bar 22–23. C. paulinifolia Veloso [US, R.K 1770, Brazil]. 22. Transverse section, arrow shows pronounced chalaza, scale bar 2 mm. 23. Detail from 22, notice thick-walled anisodiamicotan cells in chalaza, scale bar 0.5 mm. 24, C. juliginea Kunth [US, PHA 5450, Costa Rica], notice broad and deep ventral infolds and wide ventral cavities (arrows), scale bar 1 mm. 25. C. producta Azzelius [US, A.H. 2051, Gabon], arrow shows thick endostele near lateral edges, scale bar 1 mm. 26–27. C. repens L. [TAIF, Austria], arrow shows ventral cavity slits, arrow shows lemniscate-shaped structure (=) formed by the endosperm, scale bar 1 mm. 27. Detail from 26 showing thick-walled cells of the endostele near raphe (arrow), scale bar 0.5 mm. 28. Cayratia trifolia (L.) D Donini [TAIF, Chen 110, China], arrow shows ventral cavity, notice endostele, scale bar 1 mm. 29–30. Cyphostemma cyphopetalum (Fresenius) Descoins ex Wild and R.B. Drummond [US, R.L.P 22, Kenya]. 29. Arrow shows closed ventral cavity, scale bar 1 cm. 30. Detail from 29, arrow indicates vascular strand wrapped by endostele, scale bar 1 mm. Photos of extant Vitaceae were provided by Jiu Chen, except for those in 26 and 27.
abundant in the endocarp wall and septa, ranging from 0.1 to 0.5 mm in diameter (Plate IV, 2, 5–7). Vascular strand at the central axis of the endocarp (Plate IV, 2, 5).

Derivation of specific epithet—In honor of the botanist Jose Cuatrecasas (1903–1996) who studied Humiriaceae intensively.

Systematic affinity—Fruits of Humiriaceae have woody endocarps with a central vascular axis, up to 10 carpels, mostly one seed per locule, and are readily recognizable by their distinctive germination valves (Plate IV, 8–12; Herrera et al., 2010). Several genera in the family, of which Sacoglottis is perhaps the best-known example (Plate IV, 11, 12), also have cavities in the wall that have been referred to in the literature as resin or oil cavities (Cuatrecasas, 1961). Lacunofructus cuatrecasana presents a set of characters diagnostic for the family; however, the combination of characters does not coincide with that of any single modern genus. In most of its morphological characters, this fossil species conforms most closely to the modern genus Vantanea, except for one conspicuous difference—the absence of wall cavities in extant species of the genus (Plate IV, 8–10; Herrera et al., 2010). Such cavities within the endocarp wall and septa are hypothesized to have evolved independently several times in the family (Herrera et al., 2010). It is possible that ancestral Vantanea species retained or developed these cavities and subsequently lost them (in which case our fossil could be attributed to the genus), but we consider it more likely that their presence in the Panamanian fossil indicates an extinct genus, convergent in other endocarp characters with Vantanea.

The only fossil species of Humiriaceae that resembles Lacunofructus cuatrecasana is Vantanea cipaconensis (Berry) Herrera comb. nov.
from the middle Miocene of Colombia and Oligocene of Belén, Peru (Herrera et al., 2010); however, this fossil taxon has a median furrow on the surface of the valves and lacks the wall cavities observed in L. cuatrecasana.

Family—Anacardiaceae L.
Genus—Dracontomelon L.
Species—Dracontomelon macdonaldii (Berry) Herrera, Manchester et Jaramillo comb. nov.


Emended specific diagnosis—Endocarp subglobose, lensoidal, and obovoid. Base with a depression representing the area of pedicel attachment, from which several ornamental furrows in the endocarp wall radiate. Pentacarpellate. Locules five, single seeded, radially arranged. Each locule is associated with a convex, elliptical, dorsal-apical, germination valve without a median longitudinal slit. Seed outline conforming in shape to the locule or sometimes with more or less an irregular course. Large lacunae usually alternating in position with the locules. Endocarp exterior wall perforated with ten apertures that are located at the equator and connected with the lacunae. Endocarp wall and septa composed of anisodiametric parenchyma cells.

Lectotype—USNM 35316b, Plate V, 1.

Additional specimens—UF618-56133, UF618-56134, UF618-56135, UF618-56136, UF618-56137, UF618-56138, UF618-56139, UF618-56140, UF618-56141, UF618-56142, UF618-56143, UF618-56144, UF618-56145, UF618-56146, UF618-56147, UF618-56148, UF618-56149, UF618-56150.

Description—Endocarp subglobose, lensoidal, and obovoid (Plate V, 4, 10, 17); apex rounded and more or less smooth; base with a depression representing the area of pedicel attachment from which several ornamental furrows in the endocarp wall radiate (Plate V, 3, 9), reaching the equator; apical side of the endocarp with fewer furrows than the basal side. Maximum length ~6–12.1 mm, maximum width ~9–19.2 mm (n = 43). Shape in transverse section circular, elliptic and pentagonal (Plate V, 5–7, 11–13, 18). Endocarp pentacarpellate. Locules five, single-seeded, radially arranged; shape and size grading

Plate V. 1–18. Dracontomelon macdonaldii (Berry) Herrera, Manchester et Jaramillo comb. nov. 1. Lectotype (b) and syntypes (a, c) USNM 35316; the arrows indicate three endocarps, scale bar 1 cm. 2–18. New specimens collected from Tonosí. 2–7. Specimen UF618-56133. 2. Apical view of endocarp showing the arrangement of the five convex, dorsal germination valves (without a median longitudinal slit), one of them indicated by the arrow. 3. Basal view showing a depression where several ornamental furrows (arrow) in the endocarp wall radiate. 4. Lateral view of endocarp showing a specimen with a lensoidal shape, arrow shows one of the ten exterior apertures. 5–7. Transverse sections of the endocarp starting above, then near, and below the equator; note variation in the shape and size of the seeds and lacunae from apex to base; in 7, upper arrow shows the connection of the lacunae and the exterior aperture, middle arrow shows one the five seeds, and lower arrow indicates one of the five big lacunae. 8–14. Specimen UF618-56135. 8. Apical view of endocarp showing dorsal germination valves. 9. Basal view showing depression. 10. Lateral-basal view showing the obovate shape of the endocarp, four of the ten exterior apertures near the equator, and pedicel attachment (arrow). 11–13. Transverse sections of the endocarp starting above, then near, and below the equator; note variation in the shape and size of the seeds and lacunae from apex to base. 14. Acetate peel of a transverse section (from 12) showing anisodiametric parenchyma cells of the endocarp wall, scale bar 1 mm. 15–18. Specimen UF618-56138. 15. Apical view showing a more or less pentagonal shaped endocarp. 16. Basal view of endocarp. 17. Lateral view of endocarp showing a more or less lenticular shape and three of the ten exterior apertures near the equator. 18. Transverse section at the equator showing five locules and five seeds. 19–21. Extant Anacardiaceae. 19–20. D. cumingiana Baillion [NY, A. Elmer, Philippines]. 19. Apical view showing five convex, dorsal germination valves (without a median longitudinal slit), one of them indicated by the arrow. 20. Lateral view showing several exterior apertures (arrow) and lenticular shape of the endocarp. 21. D. edule (Blanco) Skeels [NY, M. Ramos, Philippines]; transverse section of endocarp showing five locules, five lacunae (arrow) and four seeds. Scale bar 2 mm, except where otherwise indicated.
from base to apex from elliptic/oblong to obovate (thickest part exmedially; Plate V, 5–7, 11–13), up to 4.2 mm in length (measured in transverse section at the equator), locule wall ~0.2 mm thick. Each carpel with a convex, dorsal-apical, germination valve, resulting in five elliptical or tongue-like bulges at the surface of the endocarp, extending from above the equator but never reaching the apex (Plate V, 2, 8, 16); germination valves up to 3.6 mm in length (measured on the surface of the endocarp), 1 mm in width and 0.5 mm in thickness, without a median longitudinal slit. Seed outline conforming in shape to the locule or sometimes with more or less an irregular course (as seen in transverse section; Plate V, 7, 13), embryo forming in shape to the locule or sometimes with more or less an irregular course (as seen in transverse section; Plate V, 7), embryo apparently straight. Lacunae typically five to four and alternating with the locules, corresponding in position to the exterior angles of the endocarp (Plate V, 7), lacunae grading in shape and size from base to apex, basally up to 1.3 mm in radial dimension and, 1.6 mm in width (as measured in transverse section), and more or less rounded or elliptic in shape; apically the lacunae are up to 4.6 mm in radial dimension, 2.9 mm in width, and the apical shape is concave towards the center of the endocarp. Endocarp exterior wall is perforated with ten apertures that are located at the equator or slightly on the apical side (Plate V, 4, 10, 17), their size varies from ~1 to 1.9 mm in diameter, there is one aperture on each side of the five lacunae; a transverse section through these apertures show that they connect with the lacunae (Plate V, 7). An axile vascular strand extends from base to apex of the endocarp, up to 1.1 mm in diameter. Endocarp wall and septa composed of anisodiametric parenchyma cells 256–458 μm in diameter (Plate V, 14).

Systematic affinity—Berry (1918) originally reported three specimens (Plate V, 1) of this taxon that he assigned to Diospyros of the family Ebenaceae. Reexamination and sectioning of Berry’s type material and of the newly collected specimens allowed us to describe this taxon in more detail and also to reassess its taxonomic affinity. Although in Ebenaceae there are drupes with valvate endocarps (although not in Diospyros), the affinity with this family can be ruled out based on the absence of lacunae, endocarp wall apertures, and the valve morphology observed in modern Anacardiaceae.

Within Anacardiaceae the fossil endocarps resemble most genera of the Spondioideae subfamily (Plate V, 19–21), i.e., fibrous endocarps with a relatively thick exocarp, often multilocular with single seeded locules, radially arranged, typically having elliptical germination pores near the apex of each locule, and sometimes with specialized opercula (Grote, 1989; Mitchell et al., 2006; Mitchell, J.D., Daly, D.C., and Pell, S.K., unpublished data).

Within Spondioideae, the Panamanian fossil taxon closely resembles the extant genus Dracontomelon (Plate V, 19–21) in the presence of endocarps with five, single seeded locules, and radially arranged, convex-dorsal-apical germination valves without median longitudinal slits, five lacunae, ten peripheral equatorial apertures that are connected to the lacunae, and the organization of tissues making up the endocarp. The combination of these characters is unique to Dracontomelon. The connection between the lacunae and the external apertures of the endocarp, together with plug-like opercula without median longitudinal slits, distinguish this fossil from the otherwise similar extinct genus Pentoperculum (Manchester, 1994), and are the most significant characters for the placement of the Panamanian fossil within the modern genus.

Two fossil species based on endocarps from the Eocene London Clay flora were placed within Dracontomelon (Reid and Chandler, 1933), however, both species have bipartite valves presumed to have opened like shutters and the lacunae do not appear connected to the exterior apertures. One of the London Clay fossil species (D. minimum Reid and Chandler) was transferred to the genus Pentoperculum also known from the Nut Beds flora of the Clarno Formation (Manchester, 1994). Although the second species (D. subglobosum Reid and Chandler) was not formally transferred to Pentoperculum, new transverse sections of one of the paratypes (Manchester, personal observation) support its placement within Pentoperculum as well.

No other fossil shows the combination of characters present in Dracontomelon macdonaldii, and this is the first recognition of this extant Old World genus in the American fossil record. Modern Dracontomelon consists of eight species of trees, found almost entirely in lowland rainforests of India to Myanmar, tropical China, Malaysia, and Fiji (Pell et al., 2011).

Order—Lamiales Bromhead Family—Indet.

Fossil genus—Cruxfructus Herrera, Manchester et Jaramillo gen. nov. Generic diagnosis—Fruits with four single-seeded locules separated by sepa intersecting at 90°, forming a cross-like structure. Seeds longitudinally elongate, conforming more or less in shape to the locule, asymmetrically lenticular in transverse section, with a pair of blade-like edges extending into the plane of locule dehiscence.

Derivation of generic name—From the Latin words “crux” for cross (making reference to the cross-shaped sepa) and “fructus” for fruit.

Type species—Cruxfructus ecocinus Herrera, Manchester et Jaramillo sp. nov.

Specific diagnosis—Fruit globose to subglobose. Apex with a circular scar, base rounded. Mesocarp very thick and composed of isodiametric parenchyma cells. Endocarp very thin (<1 mm). Placentation axile. Fruit surface fibrous. Well-defined planes of weakness aligned with sepa, likely for splitting at germination.


Description—Fruit globose to subglobose (Plate VI, 1, 2), smoothly rounded basally and apically, rounded to quadrangular-rounded in transverse section. Length from 11.3 to ~21 mm, width from ~15 to 20 mm (n = 3). Apex of the fruit with a circular scar (Plate VI, 1), 3.5 mm in diameter. Surface with longitudinal furrows and fiber-like cells (Plate VI, 2). Mesocarp wall thickness from 7.2 to 7.6 mm; endocarp wall very thin (~1 mm). Four-carpellate (Plate VI, 3, 5, 7). Locule number three to four (in one case one of the locules is small and poorly developed, Plate VI, 9); each locule single-seeded, radially arranged, shape more or less elliptic in transverse and longitudinal sections, and located at the inner part of the mesocarp/endocarp (Plate VI, 4). Septa intersecting at 90°, forming a cross-like structure (Plate VI, 3–5), very thick at the center of the fruit (up to ~2 mm) and thinning distally; these sepa either reach the wall of the mesocarp or appear undeveloped exmedially; the lateral edges of the sepa coincide with planes of weakness along which loculval edges apparently opened at dehiscence or germination. Seeds longitudinally elongate, conforming more or less in shape to the locule (Plate VI, 6), with a pair of sharp ridges that run into the locule edges (as seen in transverse and longitudinal sections, Plate VI, 4, 6); seed depth and width measured in transverse section from 1.1 to 0.5 mm and 4.5 to 1.4 mm respectively, seed length in longitudinal section up to 8.9 mm; embryo straight, placentation axile. Mesocarp composed of isodiametric parenchyma cells ~34–69 μm in diameter (Plate VI, 8). Well-defined planes of weakness aligned with sepa, likely for splitting at dehiscence or germination are visible on the surface of the fruit.

Derivation of specific epithet—“ecocinus” denoting the age of the locality.

Systematic affinity—Cruxfructus shows strong similarity with the fruits observed in two closely related families of the Lamiales, i.e., Verbenaceae and Lamiaceae. In these families there are two connate carpels which develop false sepa giving the appearance of four independent locules, usually forming a schizocarp that splits into four nutlets (Judd et al., 2007). Several features suggest to us an affinity of Cruxfructus ecocinus with Verbenaceae or Lamiaceae: the constant appearance of four locules, cross-shaped sepa; two of the sepa are generally undeveloped (which may correspond to the two false carpels), but form a splitting plane that reaches the surface of...
the fruit, placenta
tion axile, one seed per locule, seeds elliptic in
transverse and longitudinal sections, and mesocarp wall composed of
isodiametric parenchyma cells. All these characters are observed
in fruits of these families, but we did not observe all of them together
in any single extant genus or species. We have not conducted a com-
plete survey of the fruits of these families, but based on detailed com-
parison with several genera (e.g. Aegiphila, Clerodendrum, Tectona,
Vitex), we consider it likely that the Panamanian fossil represents an
extinct genus within Verbenaceae or Lamiaceae.

Lamiaceae has an almost world wide distribution, except for the
Saharan, Mongolian, and the Arabian deserts. Verbenaceae has a more
restricted distribution than Lamiaceae, being absent from Eastern
Europe and Northern Asia.

Incertae sedis
Fossil genus—Loculifructus Herrera, Manchester et Jaramillo gen. nov.

Generic diagnosis—Loculicidal capsule. Fruit radially divided by
thick septae that are not continuous toward the axes of the fruit.
Seeds one per locule and attached to the ventral margin. Each locule
and its seed are accompanied by a splitting plane that runs from the
most exmedial point of the locule to the exocarp wall. Seed coat thick.

Derivation of generic name—Making reference to the probable
loculicidal dehiscence type and the Latin word “fructus” for fruit.

Type species—Loculifructus tonosiense Herrera, Manchester et Jaramillo sp. nov.

Specific diagnosis—Fruit shape subglobose. Exocarp thin. Meso-
carp composed of aggregates of fibers and polygonal cells of variable
size. Seven radially arranged carpels. Placenta
tion axile. Locules ellip-
soidal. Seed outlines elliptic to—rounded, sometimes with wavy pro-
jections into the locule wall. Seed coat composed of three layers.
Embryo straight with two cotyledons.

Holotype hic designatus—UF618-56163 (STRI-15673). Plate VII.

Description—Fruit a subglobose syncarpous loculicidal capsule,
~13 mm in length and 10.2 mm in width (Plate VII, 1). Exocarp thin.
Surface with longitudinal ribs corresponding with the septa and the
splitting planes along the locules. Seven radially arranged carpels
(two of them being abortive) including five well developed locules
(Plate VII, 2, 3), each with a single seed. The thick septa (from 0.2 to
0.7 mm) are not continuous toward the central vascular bundle. Loc-
ule outline elliptic as seen in transverse section at the equator (Plate
VII, 3). Each locule and its seed are accompanied with a splitting plane
oriented in the radial plane of the fruit; it runs from the most exme-
sial point of the locule to the exocarp wall (Plate VII, 4). Mesocarp
composed of aggregates of fibers and polygonal cells of variable size
(Plate VII, 3). Placenta
tion axile with seeds attached to the ventral
margin of the locule. Seeds 1.5 to 4.1 mm in diameter (as seen in
transverse section), seed outlines as seen in transverse section vary
from elliptic—to—rounded, sometimes with wavy projections that pro-
trude into the locule wall (Plate VII, 4). Seed coat thick, composed of
three layers: the outer one black in color, ~30 μm in thickness, and
formed by palisade cells; the middle layer thick (~490 μm) composed
of parenchyma cells up to ~120 μm in diameter; the inner layer
(~60 μm in thickness) forming a ring of columnar sclerenchyma
cells. The embryo is straight, with a pair of large cotyledons divided
by a radial plane (Plate VII, 4).

Derivation of specific epithet—From Tonosí River, the mouth of
which cuts into the strata bearing these fossils.

Systematic affinity—Loculifructus tonosiense resembles, at least
superficially, the Eocene fossil fruit genera Melicarya (Reid and
Chandler, 1933) from the London Clay flora and Tiffneyarpca
(Manchester, 1994) from the Nut Beds flora of the Clarno Formation,
Oregon. According to recent observations these two fossil genera ap-
pear to be synonyms (Manchester, S.R, personal examination). The
Panamanian fossil is similar to Melicarya and Tiffneyarpca in general
morphology, it is within the range of the number of carpels and loc-
ules, presents the same locule and seed shape as seen in transverse
section, and probably similar dehiscence type, characterized by a lon-
gitudinal plane of weakness extending from each locule to the fruit
periphery. However, several differences support the placement of
this fossil within a separate genus. In L. tonosiense the septa are
thicker and do not continue to the axis of the fruit as seen in the
endocarps of the London Clay and Nut Bed floras; the new fossil also
lacks the ten vascular bundles and the expanded apical cavity of the central axis. Despite these differences it is likely that *L. tonosiense* could have been related to the northern hemisphere taxa during the Eocene.

*Melicarya* was classified as an extinct genus of the family Meliaceae (Reid and Chandler, 1933) and for *Tiffneyecarpa* no affinity was suggested. We have not observed yet any fruit within Meliaceae that supports the placement of *Loculifructus* within this family.

The fruit morphology of *Loculifructus* excludes placement among extant monocots and its syncarpy suggests that it belongs to Eudicots. Within this large angiosperm clade, Ericaceae (e.g. modern genera such as *Planocarpa*, *Leptecophylla*, and *Styphelia*) has capsules that resemble the fossil taxon in several characters: size and general morphology, carpel number, seed shape in transverse section, and locules accompanied by a longitudinal splitting plane that runs from the most exmedial point of the locule to the exocarp wall, this character appears related to the dehiscence of the fruit. However, we have not observed in extant Ericaceae the thick septa and seed anatomy as seen in *Loculifructus*. Therefore we refrain from assigning these fossils to this family until a more detailed survey of extant representatives of this and other ericalean families is conducted.

Fossil genus—*Carpolithus* sp. 1
Specimen—UF618-56152 (STRI-1567). Plate VIII.
Description—Disseminule ~7 mm in length and 7.1 mm in width, more or less pear-shaped in lateral view and pointed apically (Plate
VIII, 1, 2); in transverse section its shape appears compressed and fractured (Plate VIII, 3); however, it was probably elliptic in transverse section. A thick wall is present (Plate VIII, 4), ~0.5 mm in thickness, and composed of two layers, the exterior one made up of anisodiamic cells, up to ~40 μm in size; the interior layer presents high degree of recrystallization making difficult to determine the shape of the cells in transverse section, however this layer leaves the impression of overlapping isodiametric cells that are circular to elliptic in shape and that range from ~43 to 64 μm (Plate VIII, 5). The interior anatomy of the disseminule is obscured by recrystallization.

Systematic affinity—Uncertain.

4. Discussion

The Tonosí fruit and seed flora constitute the only macrofossil palaeobotanical record so far known for the Eocene in southern Central America. This flora, together with the pollen and spore flora of lignite from the Gatuncillo Formation from Central Panama (Graham, 1985, 1994), coincides with the Eocene uplift of terranes above sea level from the volcanic arc that gave origin to southern Central America (Wegner et al., 2011; Buchs et al., 2011; Montes et al., 2012; Fig. 1). The sedimentology of the Tonosí locality, the co-occurring invertebrate fauna, and the stratigraphic sequence in Azuero Peninsula, suggest that the fruits and seeds were deposited in a shallow coastal setting supplied with sandy and muddy terrestrial sediments. Therefore, it is probable that the fossil disseminules grew in nearby forests. Two fossil taxa, *Dracontomelon* and *Lacunofructus* (Plates IV-V), seem to exhibit a full size range, from very small to large specimens, indicating that their provenance may have been local. Given the sedimentary conditions where the fossils are found, it is also likely that some of the disseminules were transported by sea currents to the final site of deposition. The relatively low plant diversity observed from Tonosí (eight taxa among ~70 specimens) could be the product of taphonomic filtering, from the sedimentary environment and perhaps to the ecological stress and/or reduced area caused by the complex geological history of the volcanic arc in the region (Coates et al., 2004; Iturralde-Vinent, 2006; Buchs et al., 2011; Montes et al., 2012). We interpret the Tonosí macroflora as a record of the vegetation that colonized (maybe with some mixture of ocean-carried debris) the new
landscape produced by the onset of the emergence of the volcanic arc in southern Central America, that started during the middle to late Eocene.

The tectonic event that led to the uplift of the volcanic arc in Tonosi area seems to be the same that uplifted the Gatuncillo area (190 km northeast of Tonosi) (Montes et al., 2012). From the late Eocene Gatuncillo Formation, Graham (1985, 1994) reported 87 polynomorphs, with their floristic affinities including Selaginellaceae, Bromeliaceae, Anacardiaceae, Bignoniaceae, Fabaceae, Malvaeeae, Malpighiaceae, Moraceae, Myrtaceae, Polygonaceae, Rubiaceae, and Sapotaceae. Graham (1985, 1994) reconstructed this Eocene flora as a tropical rainforest fringed by mangrove vegetation. The new fossils from Tonosi augment the list of typical tropical families found in the Eocene rainforests in Central America, e.g. Arecaceae, Humiriaceae, and Vitaceae.

The identification of *Dracontomelon* (Anacardiaceae) and cf. *Leea* (Vitaceae) (Plates II and V) in the Tonosi locality provides interesting paleobiogeographic implications. These two genera are currently restricted only to the Old World tropical rainforests (*Dracontomelon* in Australasia; *Leea* in southern Asia and Malaysia, Africa, and Madagascar). The Tonosi fossils are the oldest record for these two genera so far, so it is possible that they reached the growing terranes of Central America from nearby rainforests of South or North America, although no other confirmed older fossils of *Dracontomelon* and *Leea* have been reported elsewhere. It is still unknown when *Dracontomelon* and *Leea* became extinct in the Neotropics. However, their absence from a new collected assemblage of abundant permineralized fruits and seeds, from sedimentological similar beds of the lower to middle Miocene Cucaracha Formation, along the Panama Canal (Herrera et al., 2010; Herrera and Manchester personal observation), may suggest local extinction in Central America sometime prior to ~20–15 million years ago. Fossil endocarps of Menispermaceae recently found in the Paleocene Cerrejón and Bogota formations in Colombia (Herrera et al., 2011) also show affinity with extant African and Australasian genera, suggesting that long-distance dispersal events between New and Old World forests were common in the Paleogene.

*Saxuva* (Plate III), the new extinct genus belonging to the tetramerosclerous clade of the grape family (Vitaceae), also has biogeographic significance. This fossil and the abovementioned specimen of cf. *Leea* constitute the earliest records of Vitaceae in the Neotropics. The fossil leaf taxon, *Cissites patagonicus* Berry, from the Paleocene of Argentina was assigned to Vitaceae (Berry, 1937), however, examination of the published photos leads us to question the familial assignment. So far, the Vitaceae seem to be absent from well-collected Paleocene strata of Colombia, but it is possible that the diagnostic, but small seeds have been overlooked by investigators concentrating on leaf remains. Vitaceae seem to be absent up to now from Upper Cretaceous and Paleocene collections in South America. Accordingly, it is possible that Vitaceae may have entered the Neotropical region via the earliest Central American terranes. Later, during the early Oligocene Vitaceae flourished in extinct Pacific rainforests of Peru, this is supported by four taxa, based on well-preserved seeds from the Belén flora (Berry, 1927; Chen and Manchester, 2007; Herrera and Manchester, personal observation).

*Dracomontelon* and the subfamily Spondioideae, to which it belongs, have been considered to be basal within the Anacardiaceae (Pell, 2004). Nevertheless, recent studies suggest that the Spondioideae may be polyphyletic (Pell et al., 2011). The new species from Panama adds to the rich Eocene record of fruits of Anacardiaceae; *Choeospondias*, *Lannea*, and *Pentoperculum* from the London Clay flora (Reid and Chandler, 1993; Collinson and Cleal, 2001), *Anacardium* from Messel, Germany (Manchester et al., 2007), and *Rhus* from the Eocene of Oregon (Manchester, 1994). The anacardiaceous fruit fossil species confirmed so far expand vastly the range of distribution observed today for these genera.

The new genus *Lacunofructus cuatrecasana* (Plate IV) supports a previous study of the dominantly Neotropical Humiriaceae that suggested that this family likely originated in tropical America (Herrera et al., 2010). This is based on confirmed and abundant fossil endocarps and pollen from South and Central America, together with discreditation of former reports from Europe. *L. cuatrecasana* is the oldest record for the family, although molecular divergence time estimates suggest a pre-Cenozoic origin (Davis et al., 2005).

Although no fruit or seed from Tonosi was placed within any fossil genera recognized from the Eocene localities of the London Clay flora (Collinson and Cleal, 2001), or the Nut Beds flora of the Clarno Formation (Manchester, 1994), two taxa (i.e. *Dracontomelon* and *Loculifruitus*; Plates IV and VI) seem to show close affinity with those Laurasian floras (Fig. 1), however, we are unable to assess their relatedness until cladistic analyses are conducted.

### 5. Conclusions

The new Eocene fossil fruits from Panama are a record of the early vegetation in the emergent Eocene volcanic arc of southern Central America. Whether these fossil taxa reached the terranes from nearby forests from South or North America, as a result of transoceanic long-distance dispersal, or as a combination of both sources is still unknown. It could be proposed that the plant taxa from Tonosi have evolved *in situ* with previous arrival of the stem lineages, but this hypothesis would require that the taxa that gave origin to the Panamanian fossils reached this region before the late Eocene. However, the Tonosi sequences, as well as Gatuncillo lignite, are the oldest evidence of subaerial deposition in southern Central America (Montes et al., 2012), so favoring a late Eocene colonizing scenario.

The affinity of the fossil disseminules from the Tonosi locality also suggest families and genera typical of extant tropical rainforests, in accordance with a previous pollen record from the Eocene Gatuncillo Formation (Graham, 1985). Some of the new families/orders from the Tonosi locality include Arecaceae, Vitaceae, Humiriaceae, Anacardiaceae, and Lamiales. Biogeographically, two of the Tonosi fossil taxa, *Dracontomelon* and *Leea*, are interesting because they occur today only in lowland rainforests of the Old World. The Tonosi fossils offer a unique opportunity to understand the composition of the earliest plant communities in southern Central America, a period when no land connection with South (and probably North) America existed yet.

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