

Pleistocene flora of Rio Puerto Viejo, Costa Rica

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ABSTRACT

The Puerto Viejo Pleistocene megafossil flora presented here is based on fossil leaves, fruits, and seeds from the banks of Río Puerto Viejo, Costa Rica. Eleven types of plant megafossils are described in this study, including *Laurophyllum*, *Oxandra*, *Piperites*, *Ingeae*, *Parinari*, *Sacoglottis*, *Byrsonima*, and *Pouteria*. Detailed morphological and anatomical data are provided for each taxon. Although the Puerto Viejo site is situated in the Atlantic Lowland Tropical Wet Forest today, the fossil flora suggests a relationship with nearby modern forests at slightly higher elevation, and cooler paleotemperatures than at present.

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INTRODUCTION

The lowland neotropical flora of La Selva Biological Station in Costa Rica (10°26'N, 84°00'W) is predominately that of an undisturbed tropical wet forest. The station also includes some secondary forest, along with areas of swamp, riparian, disturbed, and managed vegetation (McDade et al. 1994). Research at La Selva has included numer-

ous studies of the extant flora (Hartshorn and Hammel 1994; Wilbur 1994), along with some paleoecological research focused on pollen and charcoal evidence of Late Quaternary vegetation and fire history (Horn and Sanford 1992; Kennedy and Horn 1997, 2008; Horn and Kennedy 2001; Titiz and Sanford 2007). The plant fossil record for this area is relatively scarce, and records from Quaternary deposits of Costa Rica overall are pre-

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dominately from plant microfossils. A few plant macrofossils have been found in the Miocene (Uscari sequence; Berry 1921a) and Tertiary of Costa Rica (Puntarenas Province; Gómez 1971, 1972), but some determinations have been shown to be incorrect (Graham 1987b, 1988).

In this paper we present systematic descriptions of plant megafossils from a Pleistocene deposit along the banks of Río Puerto Viejo, on the northeastern edge of La Selva Biological Station in the canton of Sarapiquí, Heredia Province, Costa Rica. The plant fossil assemblage is based on leaves, cuticle, fruits, seeds, wood, pollen, and spores, and provides information on the composition of a lowland Atlantic flora during the Pleistocene of Costa Rica. Preliminary leaf identification, along with wood, pollen, and spore identifications were presented in Horn et al. (2003) but without systematic descriptions.

MATERIAL AND METHODS

The fossils presented here were collected from exposed vertical banks of the Puerto Viejo river, on the northeastern edge of the La Selva Biological Station. The specific locality is called Site PV1 and was under clay-rich volcanic tephra up to 1.4 m thick overlain by 11.8 m of alluvium, colluvium, and modern soil. Radiocarbon analyses of wood from the deposit, and $^{40}\text{Ar}/^{39}\text{Ar}$ analysis of plagioclase in the tephra, indicate that the flora is Pleistocene in age (older than 46 ka but younger than 915 ka; Horn et al. 2003). Sally Horn and Robert Sanford collected fossils and bulk clay samples in August 1992 from which the fossils were isolated. The sedimentology and dating of this site is presented in Horn et al. (2003), along with initial macrofossil and microfossil determinations. The present physiognomy of the site is a tropical wet forest in the Atlantic lowlands, about 35 m above sea level.

The bulk clay samples were washed at the Paleobotany and Palynology Laboratory, Florida Museum of Natural History, University of Florida using commercial detergent to separate the leaves and remove debris. The isolated organic material was soaked in hydrofluoric acid (HF) to remove silicates, and then thoroughly washed with filtered water. Specimens include fragmentary leaves, cuticle, wood, fruits, and seeds. They were photographed with a Nikon 35 mm (Melville, New York, USA) and a Zeiss 35 mm camera (Thornwood, New York, USA). Specimens were also imaged using a Nikon Coolpix990 and Zeiss AxioCam camera. Square sections (1.0 cm x 1.0 cm) were

cut from the middle of the leaves, and these sections were soaked in Jeffrey's solution (50% Nitric acid/ 50% of 10% Chromic acid) to remove the mesophyll. An insect pin mounted in a wooden probe was used to tease apart the upper and lower cuticle, and then a small paint brush with 2-3 bristles was used to gently clean away the mesophyll. The cuticle then went through an alcohol dehydration series of 50%, 95%, and 100% ethanol, stained with 1% Safranin-O in 100% ethanol, then through a series of 100% ethanol, 10% EtOH/90% HemoDe (or Citrisolv), and then 100% HemoDe (or Citrisolv [Fisher Scientific, Pittsburgh, Pennsylvania]). The cuticle was then mounted in a drop of HSR (synthetic resin) in HemoDe (or Citrisolv) on a microscope slide, placed on a slide warmer with a lead weight over the cover slip, and later sealed with fingernail polish. Over 100 cuticle and mesofossil slides were prepared, and the cuticle of over 100 modern leaf species were also prepared and examined. All cuticle parameters were determined using the Zeiss KS400, Version 3.0, 1999 imaging system. Five different and randomized areas within the alveoles were measured for epidermal cell density (ED [n/mm^2]) and stomatal density (SD [n/mm^2]). The stomatal density was then calculated using the Stomatal Index formula of $\text{SI} = [\text{stomatal density}/(\text{stomatal density} + \text{epidermal cell density})] \times 100$ (Salisbury 1927).

The fossil material is numbered with the University of Florida acronym (UF) followed by the locality number and then the specimen number (e.g., UF18882-32685). Modern leaves used for comparisons are numbered in the University of Florida Modern Leaf Reference Collection according to a consecutive numbering system (e.g., UF5437). Modern leaf specimens were examined from the herbaria of the University of Florida (FLAS), Smithsonian Institution (SI), Missouri Botanical Garden (MO), and the Modern Reference Collection of the Paleobotany and Palynology Laboratory (prepared cuticle slides of nearly 5,000 species). All sorted and unsorted fossil samples are stored in the Florida Museum of Natural History Paleobotany/Palynology Collection. Systematic description and terminology follows Dilcher (1974) and Ellis et al. (2009), and classification follows APG III (2009) and Judd et al. (2002). Terminology for stomates is as follows: the term stomata includes stomatal aperture plus guard cells, while stomatal complex includes stomatal aperture plus guard cells plus subsidiary cells (Dilcher 1974; Ellis et al. 2009).

SYSTEMATICS

Order PIPERALES Berchtold and Presl, 1820

Family PIPERACEAE Giseke, 1792

Genus PIPERITES Goepfert, 1854

Piperites sp.

Figure 1.1–3, 1.5–7

Material: Puerto Viejo – UF18882–33585a,b, 33586, 53699

Description: Leaves petiolate. Lamina incomplete, ovate, unlobed, > 4.8 cm long by 2.5 cm wide. Apex missing, base and margin fragmented. Petiole marginal, 1 cm long with scattered trichomes (Figure 1.3). Venation basal actinodromous, consisting of 5–7 primary veins, and two secondary veins. Interior secondaries chevron, diverging from primaries at 60–80° (Figure 1.1–1.2). Simple agrophic veins, minor secondaries simple brochidodromous. Tertiary and quaternary veins irregular reticulate (Figure 1.2). Adaxial surface glabrous; epidermal cells mostly pentagonal with some tetragonal (average size ca. 23 x 32.9 µm), surface is smooth, and cell walls mostly arcuate, some sinuate to sinuous, or rarely sinuate (Figure 1.5). Abaxial surface with numerous basal cells (average size ca. 15.8 x 22.3 µm), and occasional minute glandular cells; epidermal cells smooth (average size ca. 24.9 x 33.6 µm) (Figure 1.6–1.7). Stomata sunken, barley visible, and tetracytic (average size ca. 31.4 x 31.6 µm) (Figure 1.7).

Comments: Characters such as palmate venation and interconnecting secondary veins suggest the families Piperaceae, Malvaceae, Cecropiaceae, Urticaceae, and Menispermaceae. Within Urticaceae, genera such as *Cecropia* (Judd and Olmstead 2004; Systma et al. 2002), and Cecropiaceae, genera such as *Pourouma*, venation is similar, but the petiolar attachment is peltate in *Cecropia* (Burger 1977; Hammel 1986), and the deeply lobed lamina of *Pourouma* (Burger 1977; Berg et al. 1990) do not match the fossil specimen. Within the Malvaceae, genera such as *Sterculia* and *Theobroma* are basal plinerved, with glandular cells and epidermal cell features that are similar to the fossils, but the predominance of stellate trichomes are lacking in the fossil specimens (Robyns 1964; Hussin and Sani 1998). The numerous basal cells and some glandular cells, and stomatal shapes appear most similar to those found in the Piperaceae (Pant and Banerji 1965; Bornstein 1989) and Malvaceae, but Malvaceae contain stomatal ledges. In Menispermaceae, the presence of basal and glandular cells is similar to the fossil but

Menispermaceae have stomatal ledges and stomatal shape is not tetracytic (Krukoff and Moldenke 1938, 1941, 1942, 1943; Krukoff and Barneby 1970; Barneby and Krukoff 1971; Wilkinson 1989; Hong et al. 2001). Characters such as venation (Figure 1.1–1.3), basal cells (Figure 1.6), epidermal and stomatal shape (Figure 1.5, 1.7) suggest a relationship to Piperaceae, near *Piper rosei* C.DC. and *P. novogalicianum* A.J. Bornstein (Figure 1.4) (Burger 1971; Bornstein 1989).

The family Piperaceae are tropical trees, shrubs, lianas, herbs, and sometimes epiphytic, with five genera and ca. 3000 species, with *Piper* having around 1000 species. Due to the lack of an apex, fragmented base, and poorly defined stomata, assignment of the fossil to any one species of Piperaceae is not advisable and is referred to the fossil genus *Piperites*. Piperaceae pollen has been found in the Pleistocene and Holocene of Costa Rica (Kesel 1974; Horn 1985, 1992; Hooghiemstra et al. 1992; Northrop and Horn 1996; Arford 2001; Clement and Horn 2001; Anchukaitis and Horn 2005; Kennedy and Horn 2008). Leaves of *Piperites* have been reported from the Miocene of Costa Rica (Berry 1921a), and the Tertiary of Venezuela (Berry 1936) and Indonesia (van Konijnenburg-van Cittert et al. 2004).

Order LAURALES Jussieu ex Berchtold and Presl, 1820

Family LAURACEAE Jussieu, 1789

Genus LAUROPHYLLUM Goepfert emend Hill, 1986

Laurophyllum sp.

Figure 1.8–1.12

Material: Puerto Viejo – UF18882–32687, 32688, 32689, 32690, 32692, 32693.

Description: Leaves petiolate. Lamina incomplete, elliptic, unlobed, 6.0 cm long and 2–4.7 cm wide at the middle. Apex angle acute (Figure 1.10), with straight flanks, base angle acute, with cuneate flanks (Figure 1.8). Margin entire. The petiole marginal, 4.0 mm long by 2.0 mm wide. Primary venation pinnate, secondary venation eucamptodromous (Figure 1.9), secondary vein angle of divergence near the base 30–40° (Figure 1.8), middle 35–60°, and apex 30–90°. Basal veins are subopposite, remaining veins alternate; basal secondaries arch laterally and upward extending out to the margin, middle and upper secondaries arching slightly or straight from the midvein outward to near margin, then an abrupt upward curve to the superadjacent vein. Intersecondary veins 1–3 per intercosta, traversing more than ½ distance

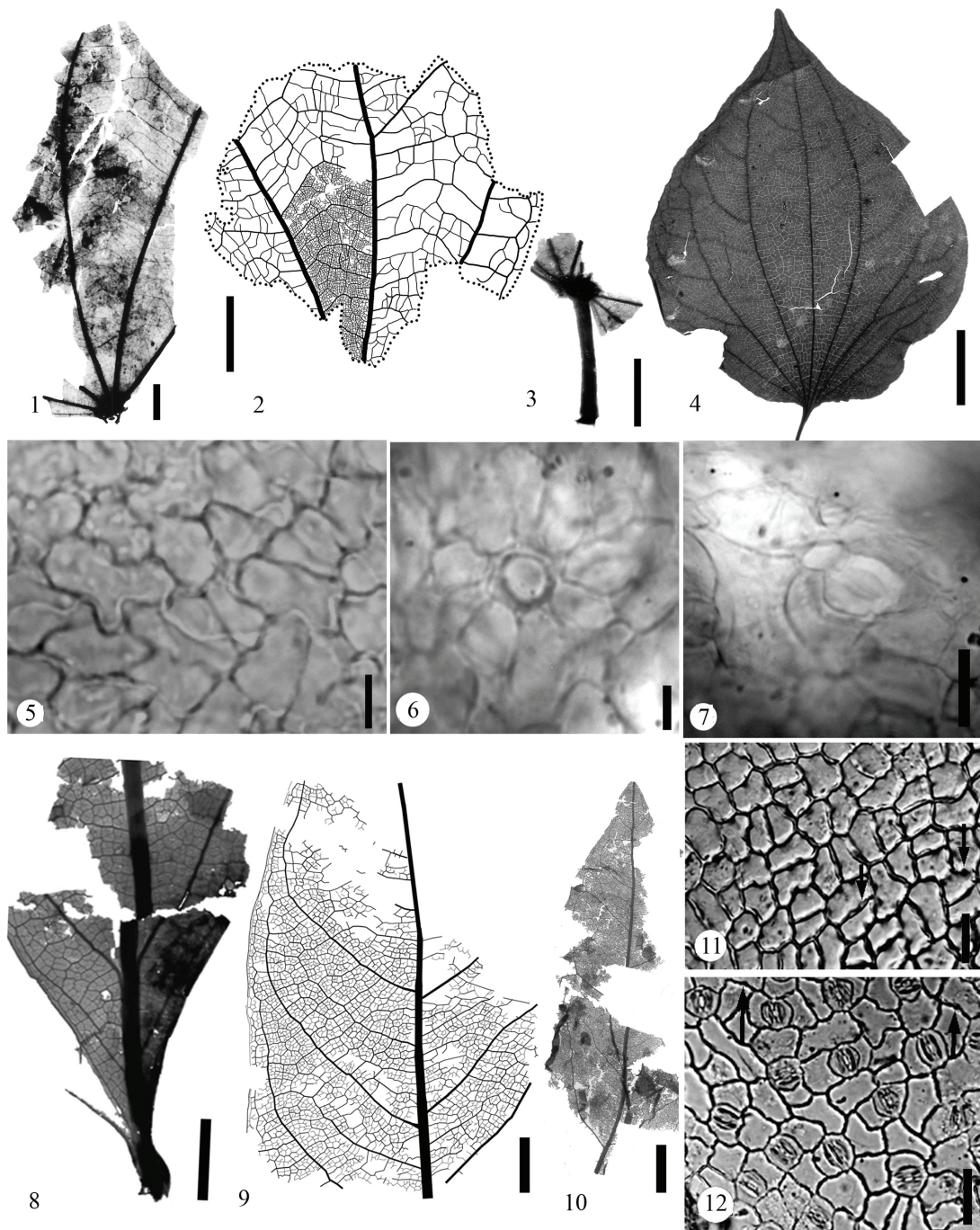


FIGURE 1. 1–3, 5–7, *Piperites*. 1, 5–7, UF18882-33585a. 1. Partial leaf with basal actinodromous venation. 2. Line drawing of partial leaf showing chevron interior secondaries, and irregular reticulate tertiary veins, UF18882-53699. 3. Petiole and basal venation, UF18882-33585b. 4. Extant leaf of *Piper rosei*, UF6048. 5. Adaxial surface with mostly arched epidermal cell walls. 6. Abaxial trichome base with numerous basal cells. 7. Abaxial sunken stomata. 8–12, *Laurophyllum*. 9, 11, 12, UF18882-32689. 8. Partial leaf with basal straight margins, UF18882-32687. 9. Line drawing of partial leaf with eucamptodromous secondary venation. 10. Partial leaf with acute apex, UF18882-32688. 11. Adaxial surface with epidermal cell walls with thin sections or knobby projections (arrows). 12. Abaxial epidermal cells also with thin sections or knobby projections (arrows). Stomates with inner ridge on the guard cell. Ridge presented as a thick black line in the stomate. Scale bar for 1–3, 8, and 10 equals 5 mm; 4 equals 1 cm; 5, 11, and 12 equals 20 μ m; 6 equals 15 μ m; 7 equals 30 μ m; 9 equals 10 mm.

to the margin before forking into two branches, one joining the superadjacent secondary, and one joining the subadjacent secondary (Figure 1.9). Tertiary venation reticulate and tertiary vein angle obtuse. Marginal vein present. Adaxial surface glabrous; epidermal cells tetragonal to pentagonal with some hexagonal (average size ca. 8.7 x 15.5 μm), surface smooth, cell walls straight, slightly curved to slightly sinuate with thin sections or knobby projections along anticlinal walls (Figure 1.11, arrow). Abaxial surface glabrous but with a few trichome bases; epidermal cells pentagonal to tetragonal (average size ca. 7.5 x 15.1 μm), surface smooth, cell walls straight, slightly curved or slightly sinuate with thin sections or knobby projections along the anticlinal walls (Figure 1.12, arrow). Stomatal complex is random, brachyparacytic, and hemiparacytic (stomata average size ca. 9.1 x 13.6 μm) with an inner rim scale on the guard cell, trapezoid in shape, and cutinized inner walls of the subsidiary cells adjacent to the guard cell scales. Stomatal pore is flat to round topped to slightly flared, opening slit-like, stomatal index ca. 13.5–16.3, and subsidiary cell size ca. 4.6–6.3 x 9.2–16.3 μm .

Comments: Extant species of Lauraceae have predominately simple, entire-margined leaves with acrodromous, brochidodromous, and camptodromous venation (Wolfe 1977; Christophel and Rowett 1996; Carpenter et al. 2007). Thus, the character of fossil leaf venation alone is not reliable for placement within Lauraceae. A cuticular character unique to Lauraceae is paracytic stomata with cuticular scales between the small embedded guard cells and overaching subsidiary cells (Bandulksa 1926; Dilcher 1963; Hill 1986). The presence of entire leaves with the above mention stomatal character provides a stable placement of the fossils with Lauraceae. The fossils provide numerous characters that are similar to extant species of *Ocotea*, *Nectandra*, and *Beilschmiedia* such as overall leaf shape, size, venation (Figure 1.8–1.10), epidermal shape, size, and stomatal type. The trapezoid-shaped inner rim scale of the guard cells (Figure 1.12) is characteristic of *Ocotea* (Dilcher 1963), *Nectandra*, and pan-tropical species *Beilschmiedia* (Nishida and Christophel 1999) but in *Beilschmiedia* the epidermal cells are highly sinuate or knobby (buttressed) (Christophel and Rowett 1996).

Due to the difficulty of distinguishing between *Ocotea* and *Nectandra* based on leaf morphology, placement within either genus is not advisable. Here, we follow Hill's (1986) advice and place our

specimens in the organ genus *Laurophyllum* based on characters of entire-margined leaves, cuticular scales mentioned above, and slit like stomatal openings on the outer abaxial surface. Cuticular characters of our specimens are similar to the dispersed fossil cuticle organ species *Piliparicutis hradekensis* except the stomatal size is twice the size in *P. hradekensis* (Schneider 2005). Venation and cuticular specimen UF18882-32689 is unique with trichome bases limited to the abaxial surface and the stomatal index is higher. Thus, there is the possibility of more than one species of *Laurophyllum*.

Lauraceae are a subtropical to tropical family of woody plants, with over 50 genera and 2500–3000 species (Rohwer 1993). *Ocotea*, with over 300 species, are found in subtropical to tropical Central America to South America, Madagascar, Africa, and the Canary Islands. *Nectandra*, with about 120 species, are found in subtropical to tropical Central to South America (Rohwer 1993). Fossil leaves and reproductive structures of Lauraceae are known from mid- and Late Cretaceous localities in the Northern Hemisphere, and well-preserved leaves of Lauraceae are commonly found in Cenozoic floras of Europe, North America, and Australia (Hill 1986; Carpenter et al. 2007). Within the neotropics, fossil leaves of *Laurophyllum* are found in the Miocene of Argentina (Anzótegui and Aceñolaza 2008), and *Nectandra* leaves in the Cenozoic of Central America, and South America (Engelhardt 1895; Berry 1921a, 1923, 1929, 1936; Anzótegui and Aceñolaza 2008). The presence of *Ocotea* leaves in the Pleistocene of Costa Rica (Horn et al. 2003) is now in question due to leaf similarities of *Ocotea* and *Nectandra*.

Order MAGNOLIALES Jussieu ex Berchtold and Presl, 1820

Family ANNONACEAE Jussieu, 1789

Genus OXANDRA Richard ex Sagra, 1841

Oxandra sp.

Figure 2.1–2.3.

Material: Puerto Viejo – UF18882–33609, 33610, 33611.

Description: Dispersed carpels of a berry, ellipsoid, 2.4 cm long, 1.3 cm wide, and 0.8 cm high. Surface finely verrucose and glabrous, apex rounded and base narrows to 0.5 cm wide. Carpel wall is woody, 1–1.3 mm thick, black, and the pulp is spongy (Figure 2.1–2.3).

Comments: Carpel characters (Figure 2.1–2.3) of the fossil are very similar to Annonaceae, and in particular *Oxandra xylopioides* Diels (Figure 2.4)

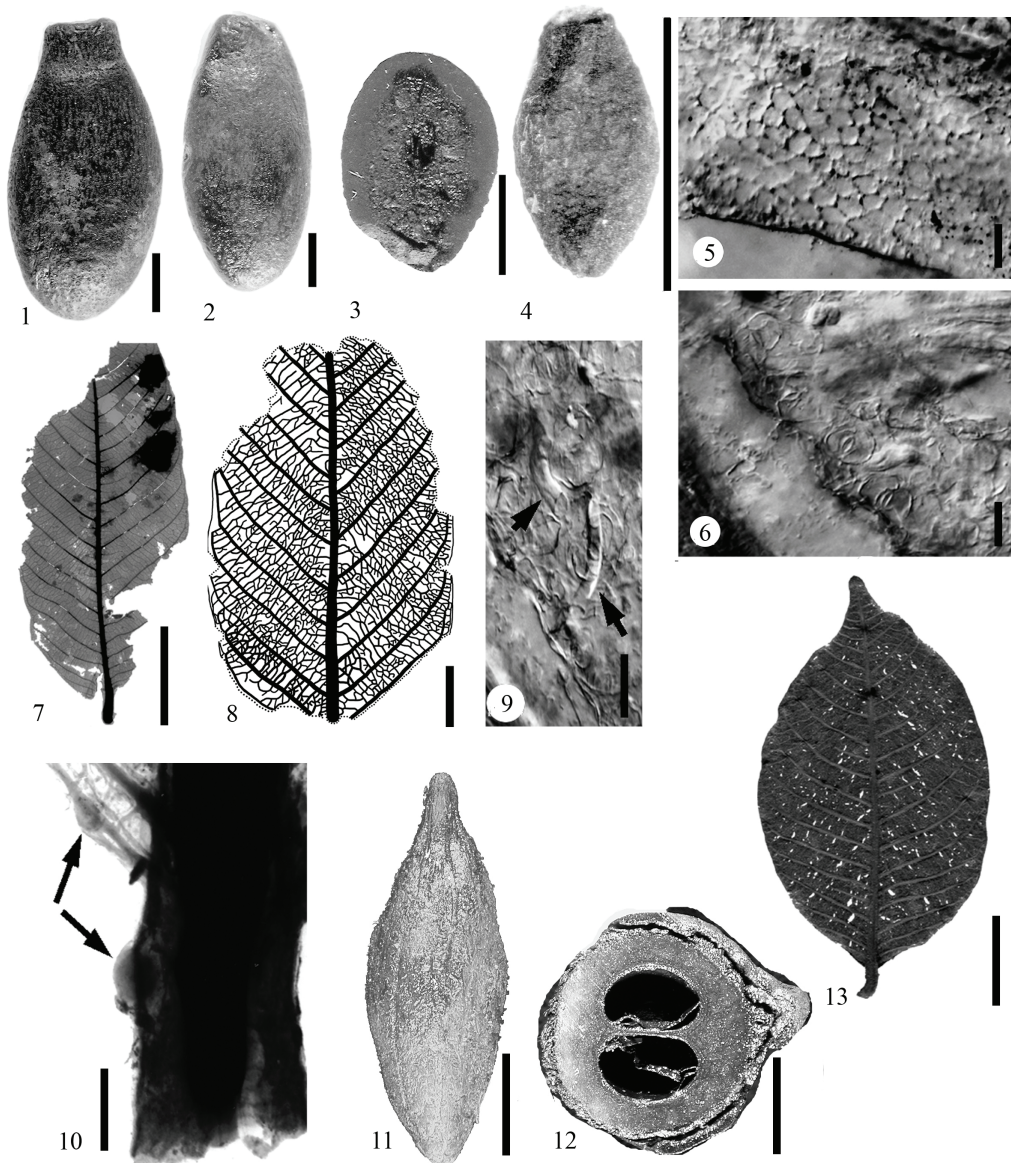


FIGURE 2. 1–3, carpels of *Oxandra*. 1. Side view, UF18882-33609. 2. Side view, UF18882-33610. 3. Sectional view showing woody wall and spongy pulp, UF18882-33611. 4. Immature carpel of extant *Oxandra xylopioides*, UF1152. 5–10, *Parinari* sp. 1. 5–7, 9, UF18882-32685. 5. Adaxial surface with epidermal cell walls that are straight to slightly curved. 6. Abaxial epidermal cells and “butterfly-shape” stomates. 7. Partial leaf with numerous regular spaced secondary veins. 8. Line drawing of partial leaf with alternate percurrent tertiary venation, UF18882-53698. 9. Abaxial surface with simple single-celled trichome (arrows). 10. Laminar and petiolar glands (arrows), UF18882-32686. 11, 12, *Parinari* sp. 2. 11. Side view of elliptical fruit, UF18882-33067. 12. Sectional view of fruit showing thick and bony endocarp with two locules, UF18882-33066. 13. Extant leaf of *Parinari excelsa*, UF5437. Scale bar for 1–4, and 8 equals 5 mm; 5, 6 equals 20 μ m; 7 equals 2 cm; 9 equals 15 μ m; 10 equals 0.5 mm; 11–13 equals 1 cm.

(Diels 1927; van Setten and Koek-Noorman, 1992).

Annonaceae are a pantropical family of trees, shrubs, rarely subshrubs, or climbers, with 128 genera and ca. 2300 species (Kessler 1993). *Oxandra* are trees to shrubs, with around 22 species, and are found in the West Indies and Panama to South Brazil (Kessler 1993). Fossil seeds of Annonaceae are known from the Maastrichtian of Nigeria, and then diversify in the Eocene London Clay flora (Doyle and Thomas 1997). Based on the phylogenetic analyses of Annonaceae using *rbcl* and *trnL-F* plastid DNA sequences, *Oxandra* may have originated within the Miocene (Richardson et al. 2004). Leaves of *Annona* have been reported in the Tertiary of Venezuela (Berry 1921b, 1936), Panama (Berry 1918), and in the Miocene of Mexico (Berry 1923) and Costa Rica (Berry 1921a). Leaves of *Guatteria* are published from the Tertiary of Panama (Berry 1918). Annonaceous pollen has been reported in the Pleistocene of Costa Rica (Kesel 1974). In this report, we correct the previous identification of *Xylopi*a (Horn et al. 2003) to *Oxandra*.

Order MALPIGHIALES Jussieu ex Berchtold and Presl, 1820
 Family CHRYSOBALANACEAE Brown ex Tuckey, 1818
 Genus PARINARI Aublet, 1775
Parinari sp. 1
 Figure 2.5–2.10 (leaf)

Material: Puerto Viejo – UF18882–32684, 32685, 32686, 32694, 32695, 32696, 32697, 33596, 33597, 53698.

Description: Leaves petiolate. Lamina incomplete, elliptic to oblong, unlobed, symmetrical, 3.3–7.4 cm long by 1.2–3.5 cm wide, laminar ratio 2.1:1–2.8:1 (Figure 2.7–2.8). Apex missing, base angle acute to obtuse, with cuneate to rounded flanks; 1–2 basilaminar sessile glands present (Figure 2.7, 2.10). Margin entire. Petiole marginal, 6 mm long and 1–2 mm wide, bearing 1–3 sessile glands and simple single-celled trichomes (Figure 2.9). Primary venation pinnate; secondary venation eucamptodromous. More than 21 secondary veins per side, alternate to opposite, spacing regular, angle of divergence 50–60°, arching slightly from midvein outward to near margin, then arching abruptly towards apex, unbranched (Figure 2.7, 2.8). Tertiary venation alternate percurrent, tertiary vein angle obtuse (Figure 2.8). Adaxial surface glabrous; epidermal cells mostly pentagonal, some tetragonal (average size ca. 6.6 x 9.6 µm), surface

smooth, cell walls straight to slightly curved (Figure 2.5). Abaxial surface with simple single celled trichomes around sunken stomata; epidermal cells mostly pentagonal with some tetragonal (average size ca. 5.1 x 6.7 µm), surface smooth, cell walls straight to slightly curved (Figure 2.6). Stomatal complex with cells crowded against each other and stomata brachyparacytic (stomata average size ca. 9.5 x 11.6 µm). Subsidiary cells form a circular shape with each guard cell distinctly arching outward into the center of its adjacent subsidiary cell (sometimes referred to as “butterfly-shape” Prance 1972); subsidiary cell size ca. 6.7 x 10.7 µm (Figure 2.6).

Comments: Morphological characters of the fossil such as leaf entire, elliptic to oblong shape, basilaminar and petiolar glands, simple trichomes, and pinnate venation are similar to Euphorbiaceae (*Tetrorchiduim*), Malpighiaceae (*Bunchosia*, *Byrsonima* [elliptic form], *Heteropteris*, *Lophopteris*, and *Mascagnia*), and Chrysobalanaceae (*Parinari* and *Licania*). In *Tetrorchiduim* (Burger and Huft 1995), the placement of the laminar glands, and low number of secondary vein pairs do not match the fossil leaf. In *Bunchosia*, *Byrsonima* [elliptic form], *Heteropteris*, *Lophopteris*, and *Mascagnia* (Anderson 1982, 1999, 2001; Amorim 2001; Anderson and Davis 2001), the low number of secondary vein pairs does not match the fossil. The venation and anatomy of the fossil leaves do suggest a close affiliation with *Parinari* or *Licania* (Prance 1972). The basilaminar and petiolar glands are characteristic for both *Parinari* (Figure 2.13) and *Licania*, along with single celled trichomes on the petiole. Both genera have characteristic sunken stomatal regions (Prance 1972). Whole leaf sizes tend to be smaller than *Licania* but in the range of *Parinari* (Figure 2.7–2.8, 2.13). The secondary vein angle of divergence resembles *Licania*, but the number and spacing of secondary veins per side resemble *Parinari* (Figure 2.7–2.8). Adaxial and abaxial epidermal characteristics are similar between the fossil, *Parinari* and *Licania* but abaxial cell surfaces in *Licania* have some striations while *Parinari* tend to be smooth. Abaxial trichomes are similar to *Parinari*. The stomata for both *Parinari* and *Licania* are brachyparacytic and the lateral subsidiary cells extend out in a butterfly wing shape, but stomatal and subsidiary size tends to be larger than observed for *Licania* and is in the size range observed for *Parinari*. When all the characters are considered, the fossils are best placed in the genus *Parinari*.

Chrysobalanaceae are a lowland pantropical family of trees and shrubs, with 17 genera and 494 species (Prance and White 1988). *Parinari* is also pantropical with 49 species (Prance and White 1988). The fossil history of Chrysobalanaceae is limited, with pollen found in the Oligocene (Muller 1981) and phytoliths in the Pleistocene of Panama (Piperno and Jones 2003).

Parinari sp. 2

Figure 2.11–2.12 (fruit)

Material: Puerto Viejo – UF18882–33066, 33067.

Description: An elliptic drupe, 3.7–5.3 cm long by 1.3–2.0 cm wide; tapered apically, base rounded; bilocular, each single seeded (Figure 2.11–2.12). Exocarp smooth, 1 mm thick; mesocarp spongy/fibrous, 1 mm thick; endocarp thick and bony, 3–5 mm thick. Locules 9 mm long by 6 mm wide, smooth interior. Fibrous strands near attenuate end.

Comments: Characters of the fossil (Figure 2.11–2.12) fit well with *Parinari* (Prance 1972; van Roosmalen 1985; Roth 1987) except extant *Parinari* has densely pubescent locules while the locules of the fossil lacks pubescence. The subgenus *Licania*, section *Pulverulenta*, has similar endocarp characters but the exocarp is wrinkled to ridged, and is densely pubescent in the locules. *Parinari* fruits have been reported in the Miocene of Ethiopia (Tiffney et al. 1994), Pliocene of Colombia (Wijninga and Kuhry, 1990; Wijninga, 1996) and the Holocene of Zambia (Phillipson 1976).

Family HUMIRIACEAE Jussieu ex St. Hilaire et al., 1829

Genus SACOGLOTTIS Martius, 1827

Sacoglottis tertiaria Berry

Figure 3.1–3.2.

Material: Puerto Viejo – UF18882–33581, 33582, 33583, 33584, 33600, 33601.

Description: Fruit an elliptical drupe of five valves, 2.2–3.2 cm in length by 1.5–2.5 cm in diameter (Figure 3.1–3.2) with rounded apex and truncate base. Endocarp woody, five carpels radially arranged. Five valves with surface irregularly warty and dotted with surface pits representing collapsed lacunae or resin ducts, five septa with smooth surfaces united at the apex and base.

Comments: Characters of the fossil such as shape, size, woody endocarp with irregular warts and collapsed lacunae, and carpel arrangement are similar to Humiriaceae and in particular *Sacoglottis* and *Schistostemon* (Cuatrecasas 1961;

Burger and Zamora 1991). A recent review of Humiriaceae has determined that *Schistostemon* should be a subgenus of *Sacoglottis* (Herrera et al. 2010).

Humiriaceae are trees and shrubs with eight genera and 49 species, found in the tropics of Central America, South America, and Western Africa. *Sacoglottis*, with eight species, are found in Central America, South America, and Western Africa while *Schistostemon*, with seven species, are found in South America (Cuatrecasas 1961). Fossil fruits of *Sacoglottis* have been reported from the Oligocene and Pliocene of Colombia (Reid 1933; Cuatrecasas 1961; Wijninga and Kuhry 1990; Wijninga 1996), and the Pliocene of Bolivia (Berry 1922). Our specimens are very similar to *Sacoglottis tertiaria* Berry (1922) of Bolivia.

Family MALPIGHIACEAE Jussieu, 1789

Genus BYRSONIMA Richard ex Humboldt, Bonpland, Kunth, 1821

Byrsonima sp.

Figure 3.3–3.5.

Material: Puerto Viejo – UF18882–33602, 33603, 33604, 33605, 33606, 33607.

Description: Fruit with endocarp preserved, non-dehiscent. Shape is globose, apex rounded, and base with a shallow indentation (Figure 3.3). Average length 7.6 mm, average equatorial diameter 7.0 mm. Endocarp woody with rugose surface (Figure 3.4), trilocular with a single seed per locule, and vascular bundle down center of the fruit. Locules are dorsally depressed ovate and symmetrically arranged about the long axis of the fruit (Figure 3.5).

Comments: Fossil fruit characters of shape, three woody carpels, and each carpel with a single locule are similar to the families Euphorbiaceae, Violaceae, and Malpighiaceae. Violaceae fruits are predominately capsular, dehiscent into three valves (van Roosmalen 1985), while in the fossil specimen there is no trace of longitudinal grooves indicative of capsules. In Euphorbiaceae, drupaceous fruits that are non-dehiscent, and trilocular with a single seed per locule is found in *Drypetes*, although the endocarp is hard but brittle, not evident in the fossil specimen that includes a thick endocarp (Berry et al. 1999). Within Malpighiaceae, morphological characters of an endocarp with a rugose surface, a shallow basal indentation, and locule shape and arrangement place the fossil within *Byrsonima* (Figure 3.6–3.7) (Robertson 1972, figure 1h, i; Anderson 1982, 1999, 2001; van Roosmalen 1985).

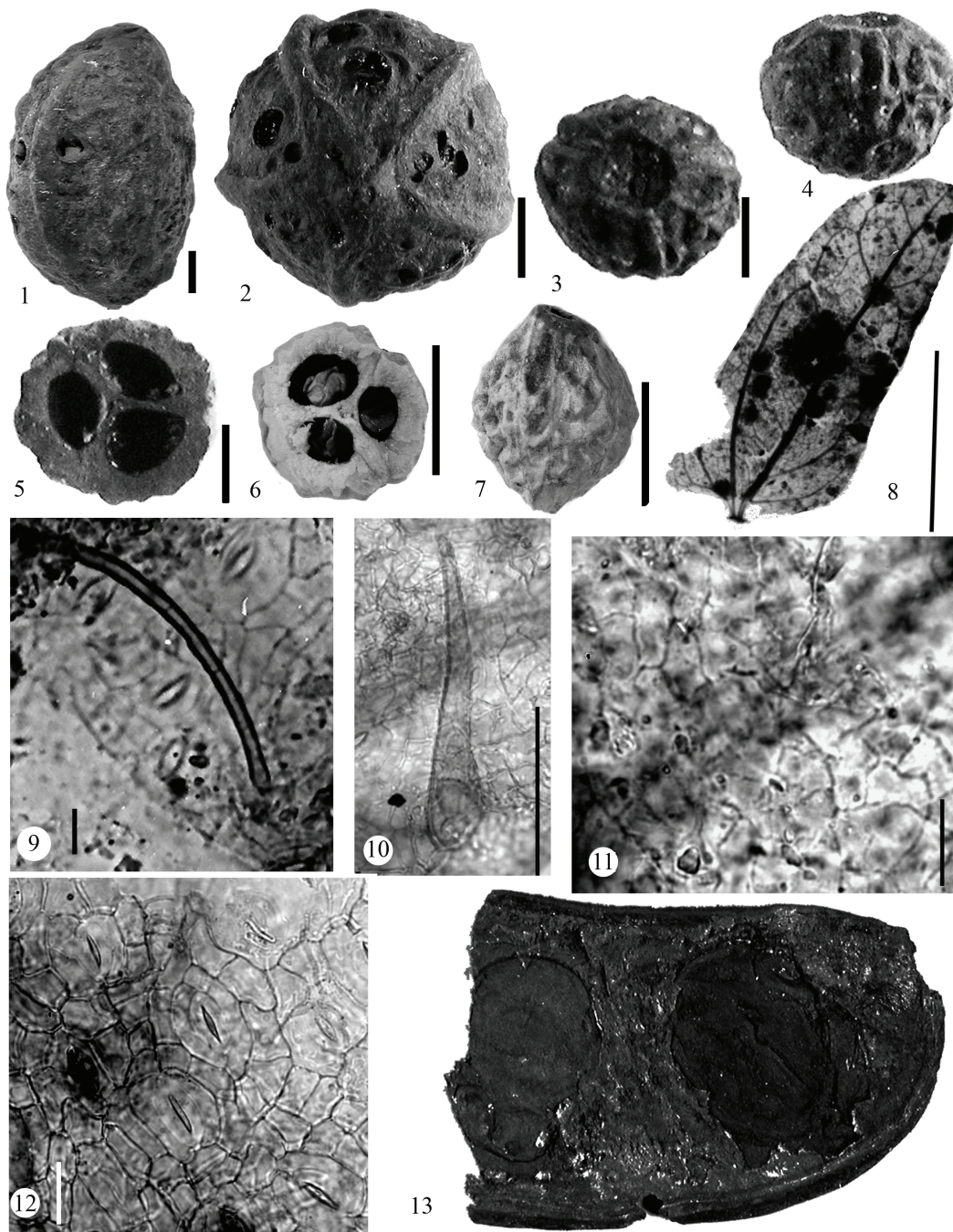


FIGURE 3. 1–2, fruits of *Sacoglottis tertiaris* Berry. 1. Side view, UF18882-33584. 2. Apical view showing five valves with surface irregularly warty and dotted with pits representing collapsed lacunae or resin ducts, UF18882-33582. 3–5, fruits of *Byrsonima*. 3. Basal view with a shallow indentation, UF18882-33603. 4. Side view of Figure 3.3 with rugose surface. 5. Transverse section of 3 locular, single seeded fruit, UF18882-33602. 6. Transverse section of 3 locular, single seeded fruit of extant *Byrsonima lucida*, UF1151. 7. Side view of Figure 3.6 before sectioned. 8–12, Ingeae leaflet, UF18882-33578. 8. Complete oblong leaflet. 9. Abaxial short trichome. 10. Marginal trichome that is unicellular and conical. 11. Adaxial surface, epidermal cell walls straight to slightly curved. 12. Abaxial epidermal cells and stomates. 13. *Leguminocarpon* with wall peeled away to reveal ovate seeds perpendicular to fruit length, UF18882-33577. Scale bar for 1, 2, 6, and 7 equals 5 mm; 3–5 and 8 equals 3 mm; 9–12 equals 15 μ m; 13 equals 1 cm.

Malpighiaceae are pantropical to subtropical trees, shrubs, subshrubs, or lianas, with 66 genera and 1200 species (Anderson 1990). *Byrsonima* are trees, shrubs, or subshrubs with 135 species, found in S.E. Florida, the Caribbean, and from Mexico to South America. Fossil pollen of Malpighiaceae are found in the Miocene of Costa Rica (Graham 1987a, b) and leaves in the Tertiary of Panama (Berry 1918). Fossil pollen of *Byrsonima* occurs in the Quaternary of Costa Rica (Kesel 1974; Horn 1985; Graham and Dilcher 1995).

Order FABALES Bromhead, 1838

Family FABACEAE Lindley, 1836

Subfamily MIMOSOIDEAE de Candolle, 1825

Tribe INGEAE Benth and Hooker, 1865

Morphotype PV1-28

Figure 3.8–3.12 (Leaflet)

Material: Puerto Viejo – UF18882–33578.

Description: Leaflet complete, oblong, asymmetrical, unlobed, 7–8 mm long by 2.5–3.0 mm wide, lamina ratio 2.6:1–2.8:1 (Figure 3.8). Apex angle acute and mucronate, with convex flanks, base angle obtuse, with concavo-convex flanks. Margin entire. Petiole missing. Primary venation pinnate; secondary venation brochidodromous, basal secondary veins present and arching upward to mid-section of leaflet. Secondary vein spacing increasing toward base. Adaxial surface with short unicellular trichomes (average size ca. 2 x 25 µm) with an acute apex (usually broken off) and thickened base; epidermal cells mostly tetragonal, some pentagonal (average size ca. 7.4 x 13.6 µm), surface smooth, cell walls straight to slightly curved (Figure 3.11). Abaxial surface with short trichomes (average size ca. 3 x 40 µm) with an acute apex (usually broken off) and slightly thickened base (Figure 3.9); epidermal cells mostly tetragonal, some pentagonal (average size ca. 8 x 19.2 µm), surface smooth, cell walls straight to arcuate (Figure 3.9). Marginal trichomes present, unicellular, and conical (average size ca. 15 x 90 µm) (Figure 3.10). Stomatal complex random and hypostomatic, paracytic to anisocytic (stomata average size ca. 7.5 x 17 µm) with thin inner rim, stomatal index 9.7; in paracytic stomata, subsidiary cells equal to unequal in size, (average size ca. 4.7 x 26.1 µm) (Figure 3.12).

Comments: Overall shape and size of the fossil leaflet is similar to Zygophyllaceae except in Zygophyllaceae there are more basal secondary veins, and the leaflets are amphistomatic. The leaflet architecture, prominent basal secondary veins, and trichomes of the fossil (Figure 3.8–3.9) are similar

to the tribes Mimoseae (*Acacia*) and Ingeae (*Albizia*, *Pithecellobium*, *Calliandra*, and *Zapoteca*) (Woodson and Schery 1950; Leelavathi and Ramayya 1982; Ghosh and Roy 1986; Grosso et al. 1994; Ogundipe and Akinrinlade 1998). *Acacia* and *Pithecellobium* tend to be amphistomatic while *Calliandra* and *Zapoteca* are hypostomatic. *Albizia* shows both amphistomatic and hypostomatic condition, although when amphistomatic, the adaxial stomata are very sparse. *Acacia*, *Albizia*, *Pithecellobium*, and *Calliandra* tend to have both paracytic and anisocytic stomata with equal to unequal subsidiary cells and unicellular hairs. *Calliandra* and *Zapoteca* epidermal cell walls are sinuate. Although no one genus contains all the characters noted in the fossil, Ingeae seems closer in character traits to the fossil. More than one specimen is needed for character variability, allowing for a more precise placement within a recognized taxa, so a temporary Morphotype category (Johnson 1989) will be used.

The tribe Ingeae are trees, shrubs, or rarely climbers, found in the pantropical to subtropical regions, with 17 genera and ~1000 species (Nielsen 1981; Herendeen et al. 1992). Ingeae pollen is known from the Eocene of Egypt (Herendeen et al. 1992), and possible leaflets from the Eocene of Kentucky (Herendeen and Dilcher 1987) and the Tertiary of Costa Rica (Berry 1921a, Graham 1992).

Genus LEGUMINOCARPON Goeppert, 1855

Leguminocarpum sp. 1

Figures 3.13, 4.1–4.2 (fruit)

Material: Puerto Viejo – UF18882–33575, 33576, 33577.

Description: Pod fragmented, > 5.5 cm long by 1–1.9 cm wide, linear to slightly curved, straight; rounded to short tapered apex and oblique with longitudinal axis of fruit; curved tapered base aligned with longitudinal axis of the fruit (Figures 3.13, 4.1–4.2). Marginal sutures 1 mm thick, medial along entire length of fruit, possibly dehiscence along one suture. Fruit non-winged, and surface with small papilla. Seeds 9–10 mm long by 5–6 mm wide, ovate, perpendicular to fruit length; funiculus 3 mm long by 0.5 mm wide.

Comments: The fragmented nature of the pods makes it difficult to place this fossil within a subfamily status, although the papillose nature of the fruit wall is not usually found in the subfamily Caesalpinioideae (Cowan 1981). Although a fruit that is dehiscent along one suture can be found in all three subfamilies, the general shape of the pod,

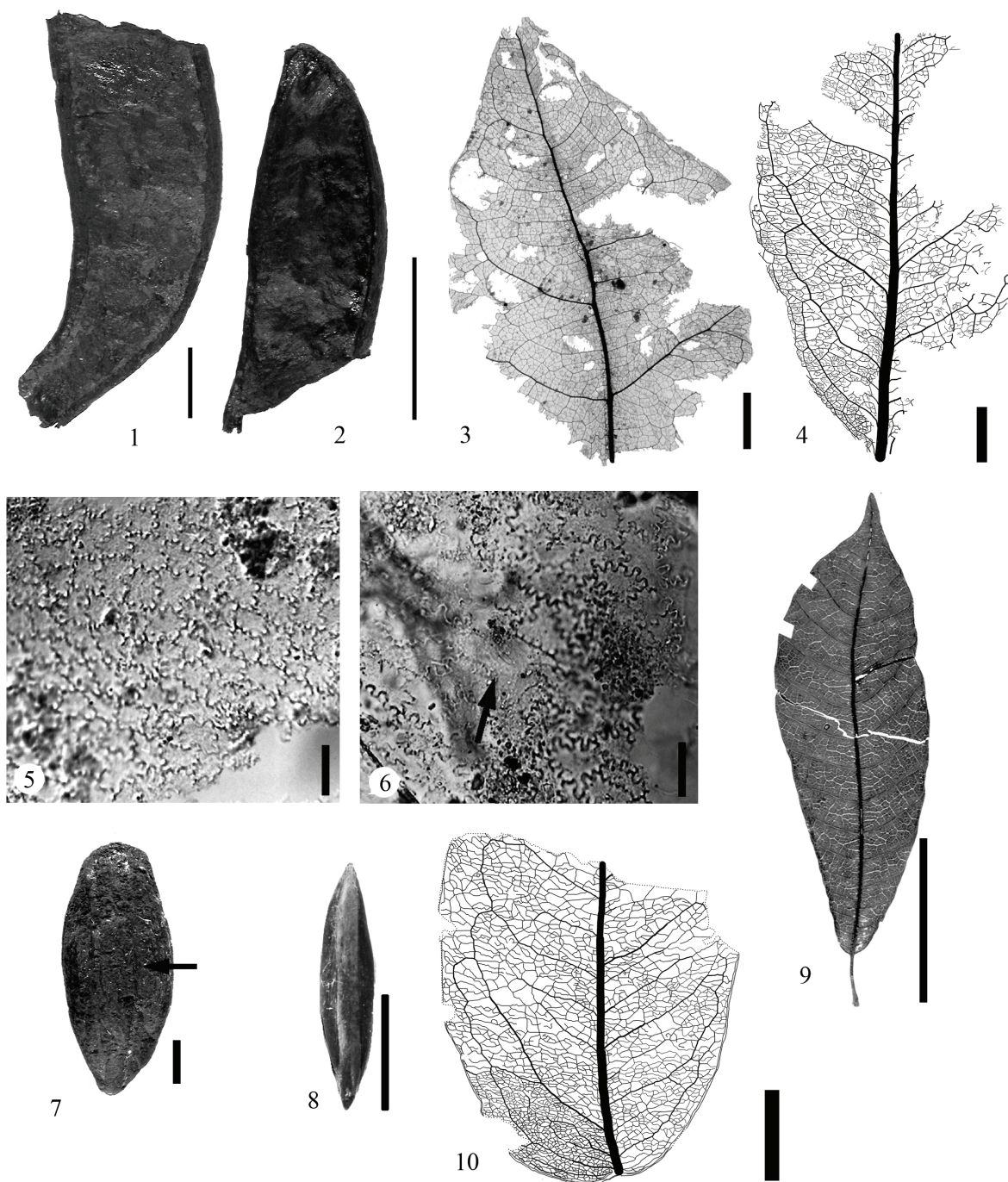


FIGURE 4. 1, 2, *Leguminocarpon*. 1. Basal section with curved tapered base, UF18882-33576. 2. Apical section with rounded apex oblique to longitudinal axis, UF18882-33575. 3–6, partial leaves, and cuticle of *Pouteria*. 3. Apical section with short attenuate, rounded end apex, UF18882-45285. 4. Line drawing of partial leaf with festooned brochidodromous venation, UF18882-53697. 5. Adaxial surface with sinuate epidermal cell walls, UF18882-32803. 6. Abaxial surface with sinuate epidermal cell walls, and stomata (arrow), UF18882-32803. 7. Ellipsoid seed of *Pouteria* with hilum covering full length of seed, UF18882-32825. 8. Extant seed of *Pouteria*, UF1153. 9. Extant leaf of *Pouteria torta*, UF5208. 10. Line drawing of Incertae Sedis leaf with festooned brochidodromous secondary venation, and two series of unorganized exmedial loops, UF18882-53700. Scale bar for 1–3 equals 1 cm; 4, 7, 8, and 10 equals 5 mm; 5, 6 equals 20 μ m; 9 equals 2.5 cm.

base, and apex of the fossil fruits (Figures 3.13, 4.1–4.2) are close to *Albizia* and *Havardia* (Mimosodidae: Nielsen 1981; Kirkbridge et al. 1999). The fossil fruits share characters with *Albizia* such as apex oblique to longitudinal axis and margin with thickened sutural area, but again the fragmentary nature of the fossils preclude placement within *Albizia*. *Mimosites* has been used for fossil legume fruits and leaves but this name should be restricted to the tribe Mimoseae (Herendeen and Dilcher 1990).

Calliandra pollen has been found in the Quaternary of Panama (Barlett and Barghoorn 1973) and the Pliocene of Colombia (Caccavari 1996) while *Calliandra* and *Acacia* pollen are found in the Pleistocene of Costa Rica (Kesel 1974).

Order ERICALES Berchtold and Presl, 1820
 Family SAPOTACEAE Jussieu, 1789
 Genus POUTERIA Aublet, 1775

Morphotype PV1-12
 Figure 4.3–4.6 (leaf)

Material: Puerto Viejo – UF18882–32803, 32804, 33598, 33599, 45285, 53697.

Description: Lamina incomplete, elliptic, unlobed. Apex short attenuate, rounded end (Figure 4.3) and micro aristate, base fragmented but tending convex. Margin entire. Primary venation pinnate, secondary venation festooned brochidodromous with two-three series of exmedial loops, last series close against the margin (Figure 4.4). Secondary veins alternate, spacing irregular, angle of divergence 50–60°. Secondaries gently curving upward and out toward the margin. Secondary attachment decurrent. Intersecondary veins 1–3 per intercosta, traversing more or less one half the distance to the margin then forking into two branches and joining adjacent intersecondaries or secondaries. Tertiary and quaternary veins irregular reticulate, marginal vein lacking, midrib flat. Adaxial surface glabrous; epidermal cells mostly tetragonal (average size ca. 12.9 x 17.6 µm), surface smooth, cell walls sinuate to sinuate (Figure 4.5). Abaxial surface glabrous; epidermal cells mostly tetragonal (average size ca. 12.1 x 17.0 µm), surface smooth, cell walls sinuous to sinuate (Figure 4.6). Stomata paracytic to anocytic (average size ca. 8.5 x 11.5 µm), stomatal index 10.8.

Comments: The form and venation of the fossil leaves are very similar to *Pouteria* (Sapotaceae) (Figure 4.9) and *Macrolobium* (Leguminosae). The adaxial and abaxial sinuate cell walls of the fossil are very similar to *Pouteria* while in *Macrolobium*,

abaxial cell walls are straight to slightly undulating (UF5127, 5131, 5212; Watson and Dallwitz 1983, 1993). Although characters such as attenuate apex, festooned brochidodromous venation, lack of a marginal vein, and a flat midrib (Pennington 1990) place the fossil leaf close to *Pouteria*, the fragmentary nature of the leaves prevent a precise affiliation to any one species, so we place the fossil into the morphotype designation.

Sapotaceae are pantropical trees, shrubs, or lianas, with 53 genera and 1100 species. *Pouteria* are pantropical with 325 species and are confined to lowland rainforest below 1000 m altitude (Pennington 2004). Fossil pollen of Sapotaceae are found worldwide through the Cenozoic (Harley 1990) and more specifically of *Pouteria* in the Pliocene and Pleistocene of Costa Rica (Kesel 1974; Graham and Dilcher 1998). Fossil Sapotaceous leaves are found in the Eocene/Miocene of Argentina (Berry 1938).

Morphotype PV1-27
 Figure 4.7 (seed)

Material: Puerto Viejo – UF18882–32825.

Description: Seed ellipsoid, 3.3 cm long by 1.4 cm wide, hilum adaxial covering full length of seed, scar 2 mm wide at base, 8.0 mm wide at apex (Figure 4.7).

Comments: Fossil seed characters of shape, and hilum position and extent fits well in Sapotaceae, and in particular *Pouteria* (Figure 4.8).

INCERTAE SEDIS

Morphotype PV1-16
 Figure 4.10

Material: Puerto Viejo – UF18882–53700.

Description: Lamina incomplete, elliptic, unlobed, > 2 cm long by 1.7 cm wide. Apex missing, base slightly cordate with rounded flanks (Figure 4.10). Margin entire. Primary venation pinnate, secondary venation festooned brochidodromous with two series of unorganized exmedial loops. Secondary veins alternate, spacing irregular, angle of divergence 52–86°. Ascendence of secondaries unequal, one side with two secondary loops reaching middle of lamina, other side with three secondary loops reaching middle of lamina. Intersecondaries 1–2 per intercosta, traversing less than or more than one half the distance to margin then joining tertiary veins. Tertiary and quaternary veins irregular reticulate, marginal vein present.

TABLE 1. Megafossil abundance for site PV1, Rio Puerto Viejo, Costa Rica.

Taxon	Organ	Leaf abundance	Reproductive abundance
<i>Byrsonima</i>	Fruit		9.8%
<i>Ingeae</i>	Leaflet	0.4%	
<i>Leguminocarpon</i>	Legume		2.7%
<i>Laurophyllum</i>	Leaf	1.6%	
<i>Oxandra</i>	Carpels		10.7%
<i>Parinari</i>	Leaf	50.3%	
<i>Parinari</i>	Fruit		32.1%
<i>Piperites</i>	Leaf	0.4%	
<i>Pouteria</i>	Leaf	31.3%	
<i>Pouteria</i>	Seed		5.3%
<i>Sacoglottis</i>	Fruit		9.8%

DISCUSSION

The Pleistocene fossil flora collected along the Río Puerto Viejo contains fragmentary leaves, cuticle, wood, fruits, and seeds, adequately preserved to allow detailed morphological and anatomical observations. This fossil flora sits within a gray layer of clay-rich volcanic material, which, in turn, is overlain by sedimentary deposits and modern soil horizon at the top of the riverbank (Horn et al. 2003). The depositional soil near Puerto Viejo is classified as old alluvial terraces, Pleistocene River terraces (Sollins et al. 1994). The fossiliferous gray layer was initially described as a fluvially reworked volcanic deposit (Alvarado 1990), but subsequent lab analyses of feldspar grains and detritus in this gray sediment indicated a primary airfall deposit (Horn et al. 2003). Except for a single leaflet, all the fossil leaves examined from this layer are fragmentary, and the sizes are under 8 cm long. The size range for extant species that are related to the fossil leaves include *Pouteria*, up to 45 cm long (Pennington 1990), *Parinari* up to 17 cm long (Prance 1972), *Piper* (multi-nerved species, Bornstein 1989) up to 20 cm long, and Costa Rica species of *Ocotea/Nectandra* up to 55 cm long (Burger and Werff 1990). The lack of large leaves may be due in part to the collection methods, which involved cutting out blocks of material that would fit in plastic bags ca. 20 cm x 20 cm in size. The condition of the leaves in the flora may also reflect the fact that larger leaves tend to become fragmented and destroyed in turbulent conditions (Wolfe 1971), and they do not travel very far via air currents (Roth and Dilcher 1978). In comparison, small leaves may be

an overrepresentation of streamside plants, or differential aerial transport of more distant species (MacGinitie 1953; Wolfe 1971; Spicer 1981). The fact that almost all the fossil leaves are small and fragmentary suggests mechanical fragmentation of streamside plants in a fluvial setting. Further field examination needs to be done for a proper taphonomic analysis of the leaves, such as the direction of the midvein to explore if the leaves were oriented in the same direction and comparing the deposit with modern leaf deposits in similar environments along the Rio Puerto Viejo.

The Puerto Viejo Pleistocene sediments contain macrofossils of leaves, fruits, and seeds of 43 morphotypes, 11 of which have been determined to the Tribe, Family, Genus, or Species level (see Horn et al. 2003 for identifications of fossil wood, pollen, and spores). Of the undetermined morphotypes, most have an abundance of less than 0.4%. Of the 11 identified taxa, five are fragmentary leaf/cuticle types, and six are whole fruit/seed types. Leaves that dominate the paleoflora are *Parinari* (50.3%) and *Pouteria* (31.3%). Other leaves are *Laurophyllum* (1.6%), *Piperites* (0.4%), and *Ingeae* (0.4%). Reproductive units that dominate the flora are *Parinari* (32.1%), followed by *Oxandra* (10.7%), *Sacoglottis* and *Byrsonima* (9.8% respectively), *Pouteria* (5.3%), and *Leguminocarpon* (2.7%) (Table 1). Fossil *Parinari* represents half of the leaves and nearly one-third of the fruits recovered, with an extant distribution in the lowland tropics. Although *Parinari* is lacking in the modern flora of La Selva, it is present at nearby higher elevations of 500 m (Horn et al. 2003). Another extant lowland tropical species is *Pouteria*, with a high percentage of fossil

Pouteria leaves in the fossil flora. *Pouteria*, which grows at La Selva today, increases in abundance from 300–600 m (Pringle et al. 1984; Lieberman et al. 1996). *Sacoglottis* and *Byrsonima* can be found living at La Selva and up to 500–1000 m (Burger and Zamora 1991). The close relatives of *Laurophyllum* are found in La Selva (*Nectandra*) and in higher elevations of 2300–2600 m (*Ocotea*) (Wilbur 1994; Lieberman et al. 1996). *Oxandra* seems to be lacking in La Selva and higher elevations near La Selva. *Pentaclethra macroleoba* dominates the extant primary lowland forest of La Selva (35–150 m), is not dominant at 300 m (Pringle et al. 1984) and is lacking in the fossil flora. The preceding distributions suggest that the fossil flora has some connection to a slightly higher elevation tropical forest of present-day Braulio Carrillo National Park (Hartshorn and Hammel 1994; Lieberman et al. 1996), just south of La Selva. The Quaternary period included 18–20 glacial-interglacial cycles (Johnson 1982; Davis 1983). In the mountains of Costa Rica, cooling during Quaternary glacial intervals resulted in altitudinal shifts downward in species ranges and vegetation belts (Martin 1964; Hooghiemstra et al. 1992; Islebe et al. 1995; Islebe and Hooghiemstra 1997). Extrapolating from modern ranges of the preceding species and surface temperature lapse rates (Horn et al. 2003), the macrofossil flora of La Selva suggests paleotemperatures 2.5–3.1°C cooler than at present, which may coincide with fluctuations in the Quaternary climate. The fossil flora is similar to the modern Costa Rican tropical forest, which has a biogeographic connection with tropical forest of Northern South America (Gentry 1990). This biogeographic connection shows up in the fossil record of Central and Northern South America (Burnham and Graham 1999). Genera and families in common with previous reports of the fossil flora of Costa Rica and Northern South America include *Parinari*, *Sacoglottis*, Piperaceae, and Annonaceae (Engelhardt 1895; Berry 1921a, b, 1922, 1923, 1936; Wijninga and Kuhry 1990; Wijninga 1996).

CONCLUSIONS

Plant species identified in the Rio Puerto Viejo deposit lived in a lowland neotropical forest of Northeastern Costa Rica during the Pleistocene (younger than 915 ka), with cooler paleotemperatures than at present. Sedimentary analysis of the gray layer from which the fossils were found suggests a fluviually reworked volcanic or primary airfall deposit. Except for a single leaflet, all the leaves

are fragmented suggesting a fluvial deposit but further taphonomic analysis is required to confirm this assessment. The fossil flora is similar to modern Costa Rica tropical forest and shows a biogeographic connection with northern South America.

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