

**NEW SPECIES OF *ESCHWEILERA*
AND A FIRST RECORD OF *CARINIANA* (LECYTHIDACEAE) FROM PANAMA**

JUVENAL E. BATISTA G.

Santa Inés Neighborhood, Santiago City
Veraguas, Republic of Panamá
batistajuvenal29@gmail.com

SCOTT A. MORI

Institute of Systematic Botany,
The New York Botanical Garden
Bronx, New York 10458–5126

JERRY S. HARRISON

PTY 9617, 2250 NW 114th Ave., Unit 1P
Miami, Florida 33192

ABSTRACT

Eschweilera jefensis J.E. Bat. & S.A. Mori, **sp. nov.**, and *E. roseocalyx* J.E. Bat., S.A. Mori, & J.S. Harrison, **sp. nov.**, from the cloud forests of Central Panama are described and illustrated. Information on distribution, ecology, phenology, pollination, dispersal, and conservation status is provided. *Eschweilera jefensis* is morphologically similar to *E. sessilis*, with which it has been confused. *Eschweilera roseocalyx* is only known by a single tree from which both flowers, fruits, and seeds have been collected. Both species are known from the Cerro Jefe area but *E. jefensis* is very common there and has also been recorded at lower elevation along the El Llano-Carti Road. *Cariniana pyriformis*, formerly documented only from South America, is reported as the first species of the genus documented by a herbarium collection from Central America. A key to the Central American genera of Lecythidaceae is presented.

The Lecythidaceae are ecologically important members of Neotropical forests, where they are especially abundant in lowland, non-flooded forests of Amazonia (Mori et al. 2001; Mori et al. 2017). Central American Lecythidaceae are also common in lowlands but recent collections from higher elevations indicate that more species of *Eschweilera* occur in premontane or cloud forests than anticipated. *Eschweilera* is the most diverse and widely distributed genus of the Lecythidaceae with 77 species (not including the 7 species of the *E. tetrapetala* clade, which do not possess the morphological features of *Eschweilera* [Huang et al. 2015]). This genus ranges from Veracruz, Mexico, to southern Brazil (Mori et al. 2017).

Eschweilera was divided into the following four sections by Mori & Prance (1990) based on morphological data: (1) sect. *Bracteosa* S.A. Mori; (2) sect. *Jugastrum* Prance & S.A. Mori; (3) sect. *Tetrapetala* S.A. Mori; and (4) sect. *Eschweilera*. Studies based on molecular data (Mori et al. 2007; Huang et al. 2015) found no evidence for recognizing the first two sections and suggested that the *E. tetrapetala* clade merits recognition as a separate genus. Huang et al. (2015) hypothesized that *Eschweilera sensu stricto* consists of the *E. integrifolia* and *E. parvifolia* clades, which are both distributed in Mesoamerica and South America. The *E. parvifolia* clade is widely distributed over the New World tropics whereas the *E. integrifolia* clade has two species east of the Andes (*E. andina* (Rusby) J.F. MacBr. and *E. ovalifolia* (DC.) Nied.) and approximately 17 other species associated with Andean and Central American cloud and lowland forests throughout the range of the clade from Costa Rica to Ecuador (Mori et al. 2017). In Panama, there are approximately 17 described species of *Eschweilera*, with about one-third of them belonging to the *E. integrifolia* clade.

The two new species of *Eschweilera* described in this paper are from the Cerro Jefe region of Panama. This relatively low cloud forest area, located in the Chagres National Park, has 1016 species of flowering plants reported of which 181 (18%) have been collected only from this region (de Sedas et al. 2009). Of the 1260 endemic species of vascular plants of Panama, 222 (almost 18%) are in the Cerro Jefe area, and 66 (almost 5.2%) are unique to this cloud forest (de Sedas et al. 2009). The great endemism of the area may be due to the combination of two factors: (1) the relative isolation of the Cerro Jefe summit and (2) that it was one of the first areas to emerge before the formation of the Isthmus of Panama (Lewis 1971; de Sedas et al. 2009).

The new record of *Cariniana pyriformis* for Panama was collected from lowland rainforests in the vicinity of the Marraganti River in the Province of Darién near the border with Colombia. These forests have not been well explored so we expect that additional species of trees already documented in adjacent Colombia will eventually be discovered in Panama.

ESCHWEILERA JEFENSIS J.E. Bat. & S.A. Mori, **sp. nov.** **TYPE:** Panamá. Provincia de Panamá, Parque Nacional Chagres, Alrededores de Cerro Jefe, 9°12' N 79°22' W, altura 900 m, 24 Ene 1996, *C. Galdames et al. 2414* (holotype: PMA; isotypes: MO, NY, SCZ). Figures 1–3, 8.

Trees of the understory 5–15 (–20) m tall. **Bark** fissured, the outer surface gray, the outer bark laminated. **Leaves:** petioles 2–11 mm long, canaliculate adaxially, blackish when dry; blades usually elliptic, infrequently ovate, 3.2–14.5 x 1.5–7.5 cm, coriaceous, glabrous, blackish punctuations, abundant and conspicuous abaxially (even without magnification), the base acute to obtuse, the margins entire, the apex acute to acuminate; secondary veins in 8–12 pairs, plane abaxially. **Inflorescences:** from branches below leaves (ramiflorous), axillary, or terminal (suprafoliar), once branched paniculate arrangement of racemes, often scarcely branched or infrequently unbranched, the principal rachis 2.5–16.5 cm long, rough, with white lenticels; pedicel/hypanthium 2–10 mm long, slightly tapered to articulation, puberulous, slightly to markedly lenticellate, the lenticels white. **Flowers:** 2.5–4 cm diam.; hypanthium puberulous; calyx-lobes 6, ovate, 1.5–3 x 2–3 mm, horizontally oriented at anthesis, the bases not imbricate; petals 6, 15–20 x 15–12 mm, pink of various intensity, speckled with white; stamens with clavate filaments; androecial hood triple-coiled, yellow, especially near opening into flower); style narrowly obconical. **Fruits:** globose to depressed globose, 2.5–7 (including operculum) x 2.5–7.5 cm; calycine ring conspicuous, the infracalycine zone dark-brown, rounded to pedicel/hypanthium, lenticels white when fruits dry; the supracalycine zone erect, dark-brown, lenticellate, the operculum convex, sometimes umbo slightly developed, lenticellate. **Seeds** 1–7 per fruit, globose, 2.5–4.5 x 2–4.5 cm; aril spreading, white.

Ecology and Distribution. *Eschweilera jefensis* is endemic to the central and eastern parts of Panama Province, Panama (Fig. 8) where it is small trees most commonly found in cloud forest between 800 and 1000 meters. *Colpothrinax aphanopetala* R. Evans (Arecaceae) is a conspicuous co-dominant with this species (Fig. 7). In addition, specimens have been collected between 350 to 400 m from the lowland moist forests along the El Llano-Carti Road (e.g., *Dressler et al. 3543* and *S. A. Mori et al. 7728*).

Phenology. Flowers have been collected in April to August and infrequently in January (*Galdames 2414*) and fruiting has been documented from March (*Hernández 209, Galdames et al. 3769*) to July (*Batista et al. 1076, 1077*).

Pollination and dispersal. There are no observations of pollinators visiting the flowers of this species. However, other species of *Eschweilera* have been reported to be pollinated by bees

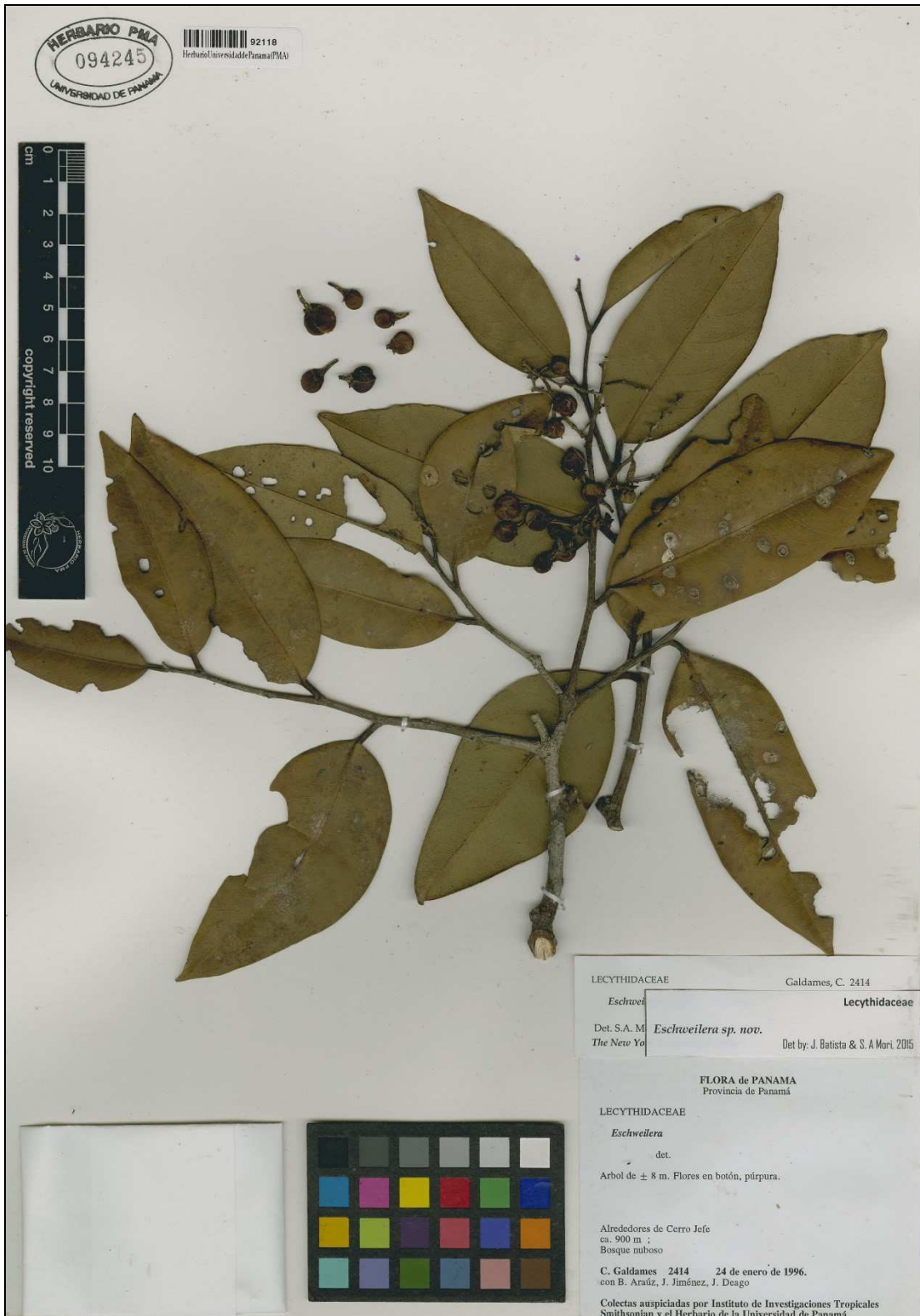


Figure 1. Holotype of *Eschweilera jefensis* archived at the University of Panama Herbarium (PMA). Photo by the University of Panama Herbarium.



Figure 2. *Eschweilera jefensis*. **A.** Bark Irregularly fissured, grayish, the slash thick, laminated. **B.** Leaf blades usually elliptic, less commonly slightly ovate. **C.** Abaxial view of blade surface showing black punctations (visible without magnification). **D.** Close-up of black punctations on abaxial leaf blade surface. **E.** Four mature fruits with conspicuous calyx rings. **F.** Lateral view of immature and mature fruits. **G.** Open fruit showing white aril beginning to surround seeds. **H.** Seeds showing spreading aril completely surrounding seeds. Vouchered by *Batista et al.* 1076 [A, B, D], 1077 [E, G], and *F. Hernández et al.* 209 [C, F, H]. Photos by J. Batista [A, B, D, E, G], and R. Carranza [C, F, H].

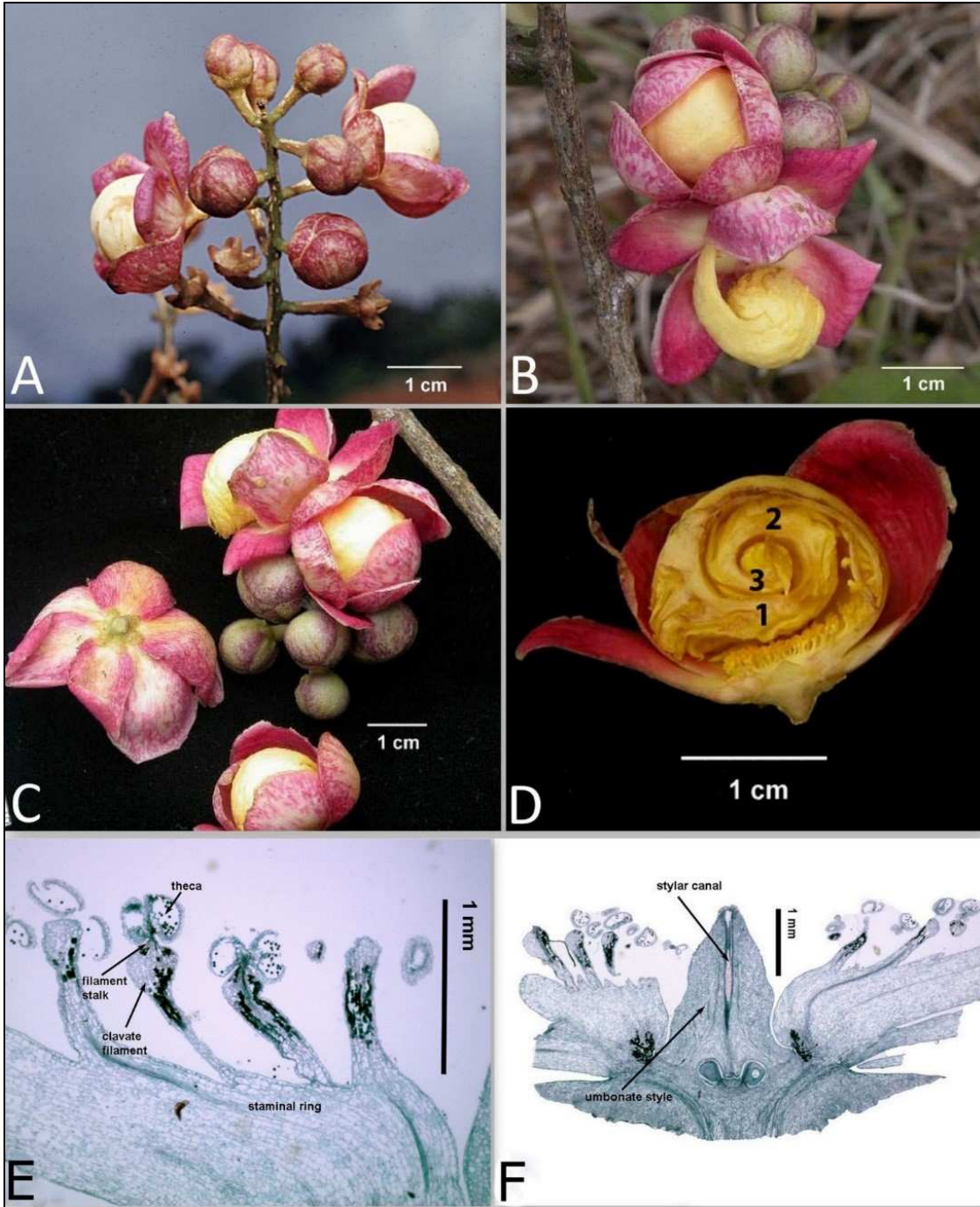


Figure 3. *Eschweilera jefensis*. **A.** Upper part of an inflorescence. The pedicel/hypanthium is elongate and slightly tapered to the articulation. **B.** Flowers are sometimes congested. **C.** Flowers and buds showing small, non-imbricate calyx-lobes in the basal view of the flower on the left. **D.** Medial longitudinal section of an androecial hood showing three coils. **E.** A stamen showing a clavate filament. The anther is attached to the filament on a constricted stalk. **F.** Pistil showing the obconical style and the stylar canal. This type of ovary is sometimes called half-inferior but we consider it as inferior because it is only the expanded style that protrudes beyond the ovary. Note that the ovules are in a single row, a feature only found in *Eschweilera*. Vouchered by S.A. Mori et al. 8077 [A], 7728 [E, F], F. Hernández et al. 209 [B], C. Galdames et al 5779 [C, D]. Photos by S.A. Mori [A], R. Carranza [B], C. Galdames [C, D], and C. Carollo Matos [E, F].

(Gamboa-Gaitán 1997; Mori & Boeke 1987). Likewise, there are no observations of dispersal agents dispersing the seeds. However, it is likely that the spreading aril surrounding the seeds attracts animals that carry away the seeds.

Etymology. The epithet refers to Cerro Jefe where it is a common tree in cloud forest.

Conservation Status. *Eschweilera jefensis* is known from four localities, three in the Chagres National Park and another located along the Llano-Carti Road. Some localities in the Chagres National Park are threatened by housing developments and the Llano-Carti area, which falls outside of the national park, is converted to pasture for livestock grazing. These localities have an Extent of Occurrence (EOO) 199.2 km² and Area of Occupation (AOO) 36 km². According to the IUCN (2012) criteria, *E. jefensis* is considered Endangered [EN B1ab(i,ii,iii,iv,v)+2ab(i,ii,iii,iv,v)].

Discussion. This species is characterized by its small stature; usually elliptic, medium-sized, coriaceous leaf blades with abundant black punctations abaxially; a pedicel/hypanthium tapered from the hypanthium to articulation (not truncate); medium-sized flowers; calyx-lobes ovate, small, not imbricate; petals pink, often with patches of white; androecium triple-coiled, the hood is light yellow; style thick, narrowly obconical; fruits globose to depressed globose, the operculum convex or infrequently with slightly developed umbo; and the arils spread over seeds when mature.

The Panamanian populations of *Eschweilera jefensis* have been misidentified as *E. sessilis* A.C. Sm. (Mori & Prance 1990). The type of *E. sessilis* (A.E. Lawrence 239 NY) was collected from cloud forest at 2100 m elevation in Andean Colombia. *Eschweilera jefensis* differs from the type of *E. sessilis* in its coriaceous leaf texture (vs. chartaceous leaf texture), very high density of dark punctuations on the abaxial leaf blade surface (vs. few punctuations), and plane tertiary veins abaxially (vs. salient tertiary veins abaxially). The new species belongs to the *E. integrifolia* clade (Huang et al. 2015) because it possesses a triple-coiled androecial hood and a spreading aril common to this clade.

Additional specimens examined. PANAMA. Provincia de Panamá, Corregimiento de la 24 de Diciembre, Cerro Jefe, La Eneida, 12 Jul 1968, *Dressler 3543* (NY, PMA); una milla después de la Eneida, región de Cerro Jefe, 9°11'19" N, 79°23'01" W, ca. 700 m, 8 de Ago 1968, *Correa & Dressler 956* (F, MO, NY, PMA, SCZ); premontane wet forest along new El Llano-Carti Road, 8–12 km N of El Llano, 400–450 m, 12 Dec 1973, *Nee et al. 8748* (MO, NY, PMA); El Llano-Carti Road, 12.5 km from inter-American hwy, ca. 350 m, 25 May 1975, *Mori & Kallunki 6358* (MO, NY, PMA); El Llano-Carti Road, 8–11 km from Inter-American hwy, tropical moist forest, 9°16' N, 79°00' W, 392 m, 13 Aug 1975, *Mori 7728* (MO, NY, PMA); cloud forest dominated by *Clusia* spp. and *Colpothrinax aphanopetala*, premontane rain forest, ca. 1000 m alt, 29 Aug 1975, *S. Mori 8007* (MO, NY, PMA); forested slopes near radio tower 9°15' N, 79°30' W, 950 m, 11 Oct 1985, *McPherson 7142* (MO, NY, PMA); vicinity of Cerro Jefe, forest slopes, 9°15' N, 79°30' W., ca. 650 m, 27 Aug 1986, *McPherson 9996* (MO, NY, PMA); near Summit, along road to east about a quarter mile below tower, 9°15' N, 79°30' W, 794 m, 8 Jul 1987, *McPherson 11170* (MO, NY, PMA); road to right about 0.5 mi below tower, 9°15' N, 79°30' W, 864 m, 13 Apr 1988, *McPherson 12446* (MO, NY, PMA); along Summit road and trail into Chagres Valley, forested slopes, 9°15' N, 79°30' W, 900 m, 10 May 1991, *McPherson & Hensold 15294* (MO, NY, PMA); Altos de Pacora, 09°14' N, 079°21' W, altura 805 m, 21 Mar 1997, *Galdames et al. 3769* (MO, PMA, SCZ); a orillas de la carretera en Altos de Pacora, cerca del caserío, 9°14'33" N, 79°21'10" W, 825 m, 29 Mar 2007, *Hernández et al. 209* (MO, NY, SCZ); en la entrada de la calle que va hacia Altos de Pacora, propiedad privada, 9°11'51" N, 79°24'16" W, 996 m, 2 May 2007, (DNA Voucher), *Hernández et al. 317* (NY, PMA, SCZ); entrando por Altos de Cerro Azul, 9°11'51" N, 79°24'16" W, altura 996 m, 2 May 2007, *Hernández et al. 331* (PMA); finca privada al lado del camino, 9°11'51" N, 79°24'16" W, 950 m, 17 Jul 2014, *Batista &*

Montenegro 1076 (NY, PMA); bosque achaparrado, 9°13'38.6" N, 79°22'24.7" W, 901 m, 17 Jul 2014, *Batista & Montenegro 1077*, (PMA).

ESCHWEILERA ROSEOCALYX J.E. Bat., S.A. Mori, & J.S. Harrison, **sp. nov.** **TYPE: Panamá.**

Provincia de Panamá, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, bosque achaparrado dominado por *Colpothrinax aphanopetala* R. Evans (Arecaceae), 9°13'39" N 79°23'20" W, altura 970 m, 28 Mayo 2016, *J. Batista et al. 1680* (holotype: PMA; isotypes: MO, NY, SCZ, UCH, US). Figures 4–6, 8).

Trees of the understory, 10–12 m tall. **Bark:** outer surface scalloped, grayish-brown, peeling in longitudinal plates, the slash with outer bark thicker than inner bark, the outer bark slash reddish-brown. **Leaves:** petioles 9–20 x 2–6 mm, canaliculate adaxially, blackish when dry; blades elliptic to widely elliptic, sometimes oblong, 20.0–28.2 x 7–13 cm, coriaceous, glabrous, without conspicuous punctuations abaxially, the base rounded, the margins entire, the apex short acuminate; secondary veins in 14–18 pairs, salient abaxially, prominulous adaxially. **Inflorescences:** usually from branches below leaves (ramiflorous), axillary, or terminal (suprafoliar), unbranched to once-branched racemes, the principal rachis 4–8 cm, strongly lenticellate, rough, glabrous; pedicel/hypanthium 5–8 x 3–5 mm, slightly tapered to articulation, lenticellate, glabrous. **Flowers:** 3.5–4.5 cm diam.; hypanthium pinkish, glabrous; calyx lobes 6, widely triangular, 1–4 x 2–5 mm, horizontally oriented at anthesis, the bases not imbricate, fused to one another, pinkish to pinkish-yellow; petals 6, white, 22–40 x 14–24 mm; androecium with ligule 14–25 x 12–23 mm, the hood double-coiled, 15–24 x 16–23 mm, pale yellow; ovary 2-locular, 3–4 ovules per locule. **Fruits:** base conical, 5.7 (including operculum) x 4.5 cm, the pericarp 8–9 mm thick, the calycine ring conspicuous, the infracalycine zone conical, brown, thickened to pedicel/hypanthium the supracalycine zone erect, brown; operculum obconical 2.1 x 4.3 cm. **Seeds:** 3 per fruit, globose, 2–2.3 x 1.3–2 cm; aril spreading (especially along major veins), white.

Ecology and distribution. Understory tree found in cloud forest dominated by *Colpothrinax aphanopetala* R. Evans (Arecaceae) (Fig. 7). It is known from a single tree on Cerro Jefe at 900 to 1000 m in the Chagres National Park (Fig. 8).

Phenology. One collection of flowers has been made in May (*Batista et al. 1680*), and fruiting has been documented in July (*Batista et al. 1682*).

Pollination and dispersal. There are no observations of pollinators visiting the flowers of this species. However, other species of *Eschweilera* have been reported to be pollinated by bees (Gamboa-Gaitán 1997; Mori & Boeke 1987). Likewise, there are no observations of seed dispersal. However, it is likely that the spreading aril surrounding the seeds attracts animals that carry away the seeds to eat the arils.

Etymology. The species epithet refers to the pinkish color of the calyx.

Conservation Status. *Eschweilera roseocalyx* is known from one locality, near the summit of Cerro Jefe. According to IUCN (2012) criteria *E. roseocalyx* is considered Data Deficient (DD).

Discussion. This species is characterized by its small stature; cloud forest habitat; large leaf blade width (over 10 cm wide) which is rounded at the base and short acuminate at the apex; at least some inflorescences ramiflorous; a pinkish hypanthium; broadly triangular calyx-lobes fused to one another at their bases, and pinkish-yellow color when fresh; a double-coiled androecial hood; and an aril that spreads over the entire seed.

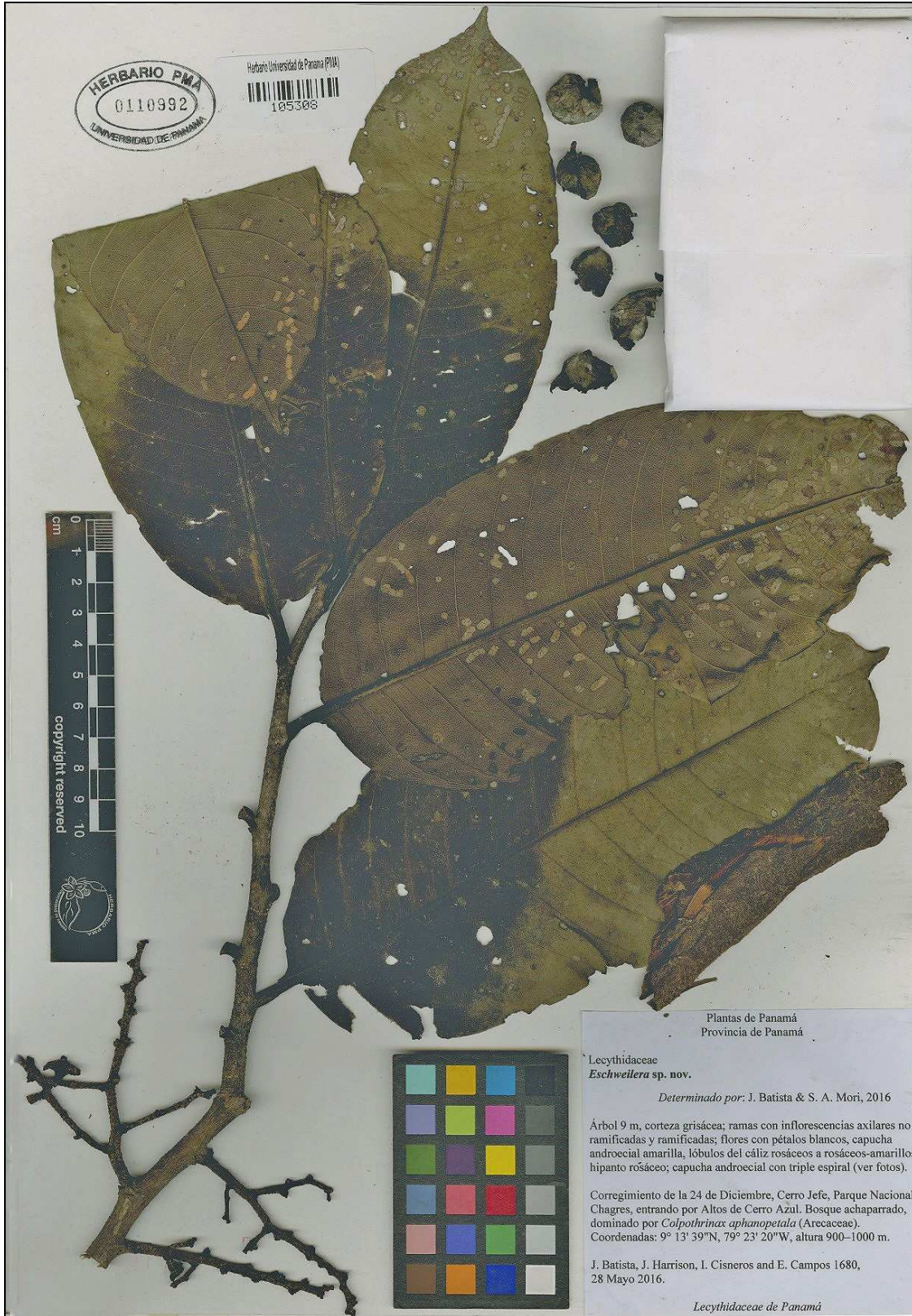


Figure 4. Holotype of *Eschweilera roseocalyx* archived at the University of Panama Herbarium (PMA). Photo by the University of Panama Herbarium.

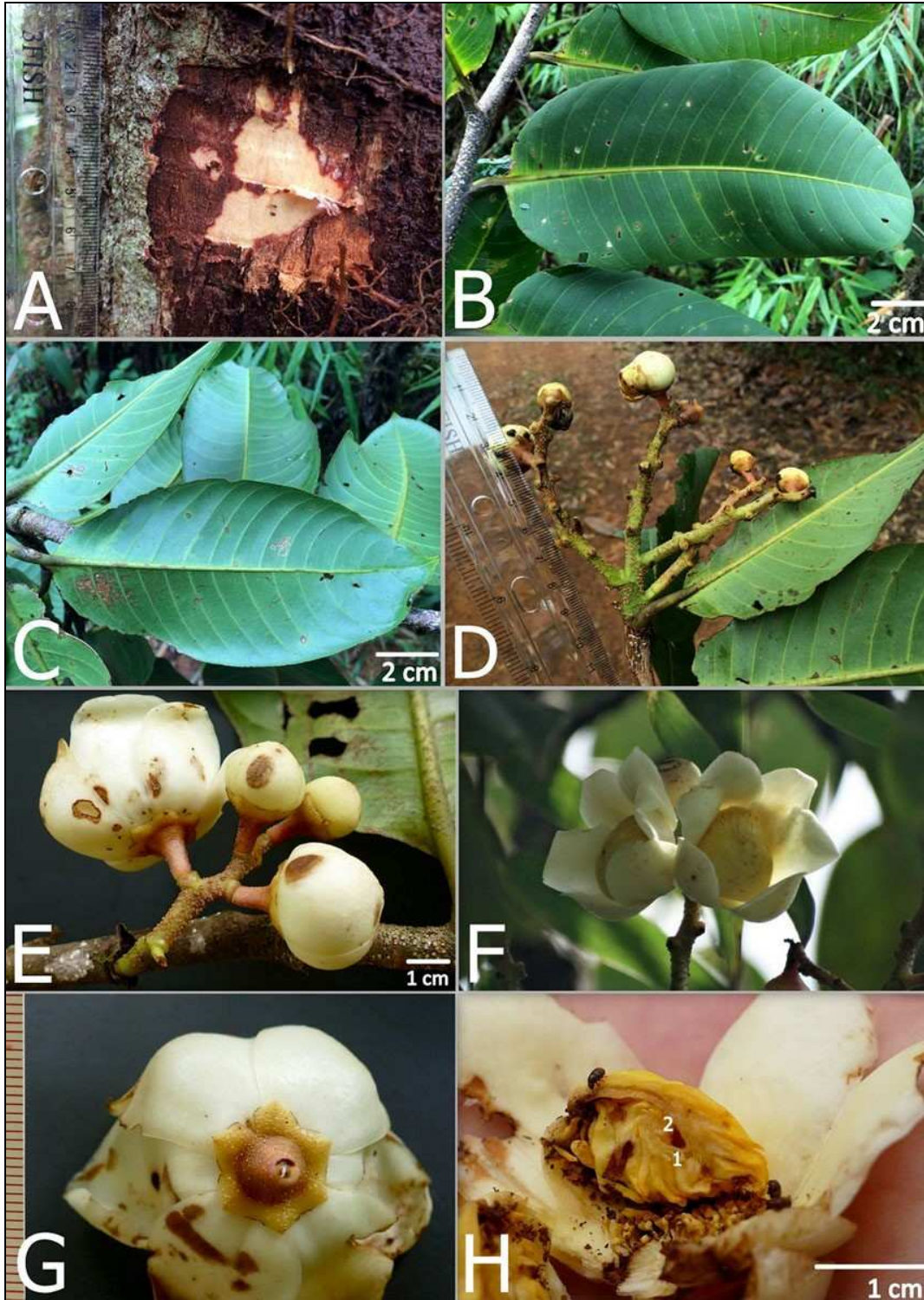


Figure 5. *Eschweilera roseocalyx*. **A.** Grayish-brown outer bark surface and dark reddish-brown slash. **B.** Leaf blade showing adaxial surface. **C.** Leaf blade showing abaxial surface. **D.** Branched inflorescence in bud. **E.** Unbranched inflorescence showing buds and an open flower. **F.** Apical and lateral views of mature flowers. **G.** Basal view of a flower showing white petals, yellow calyx-lobes, and hypanthium. **H.** Medial longitudinal section of an androecial hood showing two coils. Vouchered by J. Batista 1680 [A–H]. Photos by J. Batista [A–D, H] and J. Harrison [E–G].

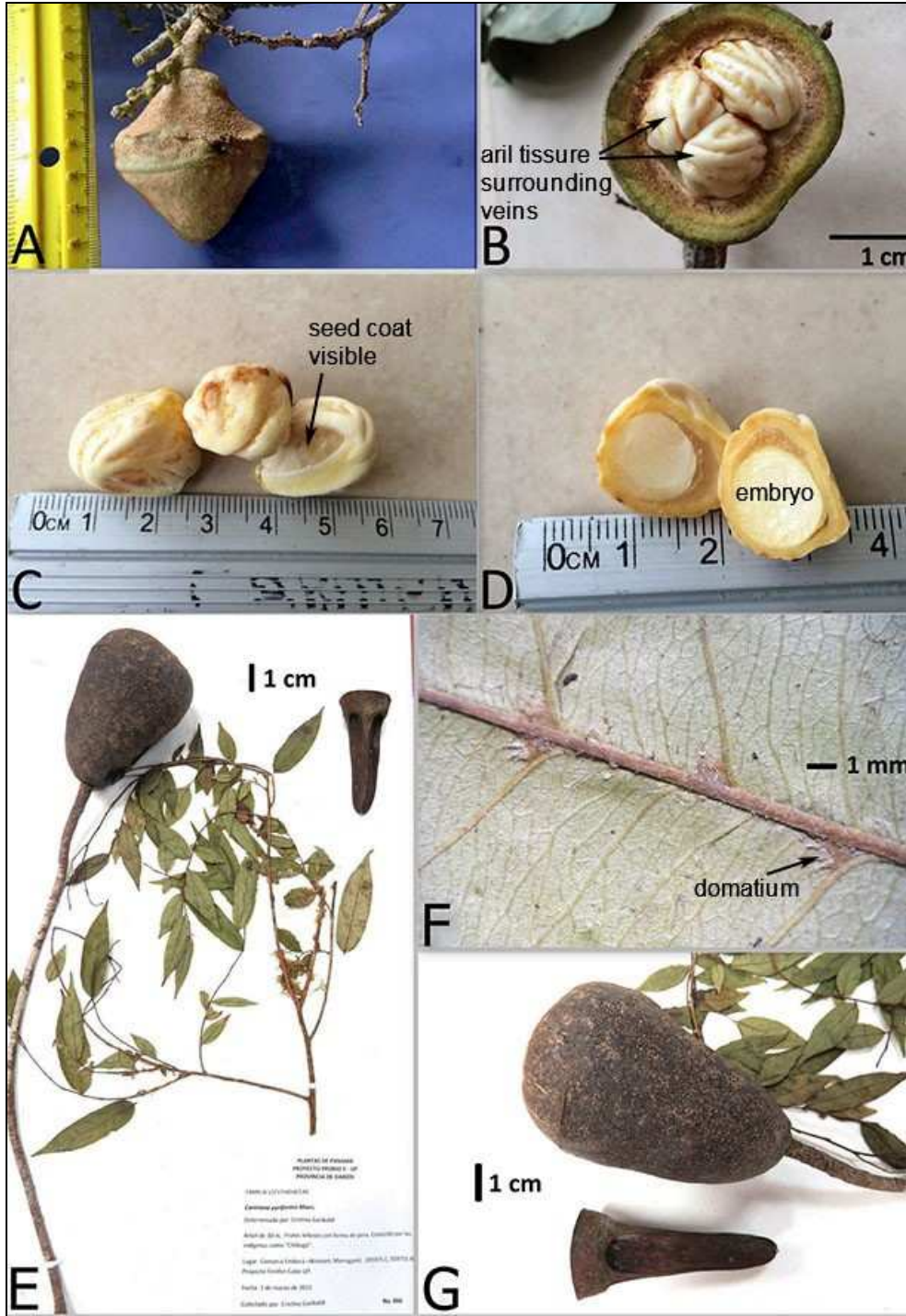


Figure 6. *Eschweilera roseocalyx*. **A.** Immature fruit showing obconical operculum. **B.** Open fruit showing 3 seeds. **C.** Seeds showing aril tissue covering major veins but parts of seed coat between the veins not yet covered by the aril. **D.** Cross-section of a seed showing immature white embryo. Vouchered by *J. Batista et al.* 1682 [A–D]. Photos by J. Harrison [A] and J. Batista [B–D]. *Cariniana pyriformis*. **E.** Fruit collection of *C. pyriformis* at the Universidad de Panamá Herbarium (PMA). **F.** Close-up showing domatia in the axils between the midrib and secondary veins abaxially, note the long, white trichomes along the margin of the domatia. **G.** Pyxidium (fruit) and operculum showing the extended triangular columella. Vouchered by *Garibaldi & Yuleman* 866. Photos by J. Batista.

The *Eschweilera parvifolia* (type of the genus) and *E. integrifolia* clades share the characters of two or three coiled androecial hoods, the presence of vestigial stamen nectaries (also found in species of *Couratari*), ovules in a single row, and lateral arils. They differ, however, in the double-coiled androecial hood of the *E. parvifolia* clade (vs. triple-coiled androecial hood of the *E. integrifolia* clade), and the lateral aril of the *E. parvifolia* clade (vs. the spreading aril of the *E. integrifolia* clade). This species is the first we have seen with a double-coiled androecial hood as found in the *E. parvifolia* clade (Fig. 5H) and a spreading aril as found in the *E. integrifolia* clade (Fig. 6B–D). In short, *E. roseocalyx* could be placed in either clade but this is not surprising because the hood coils are adaptations selected for by pollinators and the aril types are adaptations selected for by dispersal agents (Huang et al. 2015).

The characters that distinguish the *Eschweilera parvifolia* and *E. integrifolia* clades are difficult to score. In the first place, the androecial hood coils are only revealed when the hood is cut in a medial longitudinal section. For example, if a section is not cut through the middle a triple-coiled hood might look like a double-coiled hood but that does not appear to be the case in our section of the androecial hood of *E. roseocalyx* (Fig. 5H), i.e., it is double-coiled. Another problem is that it is difficult to determine when a character state changes enough to be called another character state. In both of these characters the more complicated character states most likely evolved through a continuum of changes. For example, a double-coiled androecial hood and a lateral aril precede the evolution of a triple-coiled androecial hood and a spreading aril, respectively. In *E. roseocalyx* the double-coiled androecial hood (Fig. 5H) and in *E. jefensis* the triple-coiled androecial hood (Fig. 3D) are well defined but it is not always as easy as this to determine the number of coils of some individual. In our definition of androecial hood coils, we do not count vestigial stamen nectaries as a coil.

In the *Eschweilera parvifolia* and *E. integrifolia* clades the funicle is surrounded by an aril. In the least complex type the aril runs laterally along the length of the seed and does not completely cover the seed coat (Type 1). This type of aril is found in the *E. parvifolia* clade (Huang et al. 2015). In a Type 2 aril, tissue spreads from a lateral aril and eventually covers the entire seed coat. Spreading arils do not develop until late in seed development (Fig. 2GH). Thus, in order to describe a spreading aril, the seeds need to be ripe. In addition, the seeds should not be dried until they are studied and photographed because spreading arils dry up and cannot be seen in herbarium specimens. In *E. roseocalyx*, the vascularization of the seed is more complex (Type 3). In this species, the lateral aril splits at the chalazal end of the seed and the proliferation of aril tissue covers all of the major seed veins. The seed coat is mostly covered by aril tissue but some areas of it may not be covered (Fig. 6B–D).

We suggest that *Eschweilera roseocalyx* belongs to the *E. parvifolia* clade because it has a double-coiled, androecial hood. The petals are white and the androecial hood is yellow, a combination of colors that dominates the *E. parvifolia* clade. Nevertheless, some species of the *E. integrifolia* clade have the same flower color (e.g., *E. awaensis* S.A. Mori & Cornejo & *E. collinsii* Pittier). The occurrence of a spreading aril (Type 2) supports the placement of this species in the *E. integrifolia* clade but the Type 3 aril may be different than the Type 2 aril of the *E. integrifolia* clade. Adding this species to a phylogeny based on molecular data should provide insight into the placement of this species.

Additional specimen examined. PANAMA. Provincia de Panamá, Parque Nacional Chagres, entrando por Altos de Cerro Azul, Cerro Jefe, 9°13'39" N, 79°23'20" W, altura 970 m, 26 Jul 2016, *Batista et al.* 1682 (NY, PMA, SCZ, UCH).

CARINIANA PYRIFORMIS Miers, Trans. Linn. Soc. London 30: 290, t. 63, figs. 11–13. 1874. **TYPE: Colombia.** Córdoba, Plato Bolivia, Rio Sinu, *Anthoine*, *s.n. no date* (holotype: K). Miers (1874) interpreted the collecting locality to mean “some small river [called] Betanie flowing into the Magdalena [River] near Plato” in Colombia not Bolivia.

Distribution and Ecology. The nine known species of *Cariniana* (Huang et al. 2008) are found in lowland forests or savanna habitats on well-drained soils. The overall distribution of this clade (see Map 11 in Mori et al. 2017) includes central and southwestern Amazonia, the savanna habitats of central Brazil, and the Atlantic Forest of eastern Brazil. The genus is not known from northern Amazonia and the Guianas. Two species (*C. estrellensis* (Raddi) Kuntze and *C. ianeirensis* R. Knuth) are disjunct between southwestern Amazonia and the Atlantic Forest of eastern Brazil and one species (*C. pyriformis*) is found in lowlands west and north of the Andes in eastern Panama, northern Colombia, and the Maracaibo Basin of Venezuela. Species of *Cariniana* do not occur in dry thorn scrub (= *caatinga*) of northeastern Brazil or in cloud forests.

Conservation status. The World Conservation Monitoring Centre of the IUCN (1998) first classified this species as Lower Risk/Near Threatened (NT) but the IUCN (2001) upgraded the species to Critically Endangered CR A2cd+4cd because of overexploitation of timber and the opening of land for agricultural plantings and for making extensive pastures for livestock grazing (Calderón et al. 2002; Cárdenas & Salinas 2007; Cárdenas et al. 2015).

Cariniana pyriformis is cultivated in botanical gardens in Trinidad, Jamaica, and Singapore (Prance & Mori 1979). Species of *Cariniana* have the best timbers found in Lecythidaceae and wood of *Cariniana pyriformis* has been exported to the United States and Europe under the names of *abarco* (Prance & Mori 1979), *chibugá* (Cárdenas & Salinas 2007), and *Colombian mahagaony* (IUCN 1998) and large stands of this species have been observed in northern Colombia (Record & Hess 1943). Betancur and Raigosa (1973) report that *C. pyriformis* trees are used for reforestation projects in northern Colombia. Because this species is cultivated in plantations and used for forest reclamation projects, it is difficult to determine with certainty if voucher specimens are from native or cultivated trees.

Discussion. Although *Cariniana pyriformis* was suspected to appear in Panama (Mori & Prance 2009) because it has been known from adjacent similar habitats in Colombia since at least 1916 (*H.M. Curran 353*), it was not documented with a herbarium voucher in Panama until 2011 (*Garibaldi & Yalman 866*).

Specimen examined. Panamá. Provincia de Darién, Comarca Emberá-Wounaan, Marragantí, 8°20'32" N, 77°40'49" W, ca. 66 m, 1 Marzo 2011, *Garibaldi & Yalman 866* (NY, PMA) (Fig. 6EG).

KEY TO CENTRAL AMERICAN GENERA OF LECYTHIDACEAE SUBFAM. LECYTHIDOIDEAE

Neotropical Lecythidaceae have flowers and fruits so different from other plant families that special terminology is needed to describe them. In order to understand the terminology consult the online glossary for Lecythidaceae at "The Lecythidaceae Pages" (Mori et al. 2010).

1. Androecium actinomorphic, staminal tube present, androecial hood absent.
2. Petals 6–8 (–18); stamens 500–1200, the anthers linear, dehiscence poricidal. Fruits usually with 2 or more seeds **Gustavia**
2. Petals 4; stamens 85–210, the anthers globose, dehiscence lateral. Fruits with a single seed **Grias cauliflora**
1. Androecium zygomorphic, staminal tube absent (slightly developed in *Cariniana*), androecial hood present (slightly developed in *Cariniana*).
3. Flower diam. 10 mm or less; androecium forming thin-walled staminal tube, one side of tube slightly elongated. Fruits conical, the pericarp greater than 10 mm thick; seeds with a unilateral wing **Cariniana pyriformis**
3. Flower diam. 10 mm or more; androecial hood well-developed, arising from staminal ring (staminal tube absent). Fruits not conical; seeds without unilateral wings (*Couratari* has circumferential wings).
4. Inflorescences arising from large tree trunks. Ovaries 6-locular. Fruits cannon-ball shaped, indehiscent; seeds immersed in pulp, the seed coat covered with trichomes **Couroupita**
4. Inflorescences not arising from large tree trunks (a few smaller stature species have cauline inflorescences). Ovaries not consistently 6-locular. Fruits not cannon-ball shaped, usually dehiscent; seeds not immersed in pulp, the seed coats always glabrous.
5. Androecial hood with external flap, ovary 3-locular. Fruits cylindrical; seeds flattened, with wing encircling margins; cotyledons leaf-like **Couratari**
5. Androecial hood without external flap; ovary usually 2- or 4-locular. Fruits not cylindrical; seeds not flattened; cotyledons absent.
6. Androecial hoods plane or arched (= not coiled), without vestigial stamen nectaries; ovary usually 4-locular, the ovules in more than 1 row. Seeds with basal arils **Lecythis**
6. Androecial hoods double- or triple-coiled, with vestigial stamen nectaries at the apices of coils; ovary usually 2-locular, the ovules in a single row. Seeds with lateral or spreading arils **Eschweilera**

With the exceptions of *Lecythis* and *Eschweilera*, the Central American genera of Lecythidaceae are monophyletic and will probably retain their current generic status (Huang et al. 2015; Mori et al. 2015). On the other hand, *Lecythis* is not monophyletic. It consists of five clades with three of them native to Central America — the *Lecythis pisonis* clade (only *L. ampla* Miers), the *L. ollaria* clade (only *L. turyana* Pittier), and *L. chartacea* (only *L. mesophylla* S.A. Mori). It is possible that the *L. pisonis* clade will be segregated as a separate genus in the future (Huang et al. 2015; Mori et al. 2017). If that happens, a new generic name for the species of the *Lecythis pisonis* clade will have to be selected, because *Lecythis* Loefl. (Loefling 1758) applies to the *L. ollaria* not the *L. pisonis* clade.

Eschweilera is also not monophyletic. It consists of three clades with two of them, the *Eschweilera parvifolia* and *E. integrifolia* clades, found in both Central and South America. The *E. tetrapetala* clade (Huang et al. 2015; Mori et al. 2017) is limited to the Atlantic Forest and adjacent *cerrado* of Brazil (= savannah). The *E. parvifolia* and *E. integrifolia* clades are morphologically similar clades that have not been retrieved as sister taxa based on molecular data (Huang et al. 2015; Mori et al. 2017). If further molecular study does not show a sister relationship between these two clades then the *E. integrifolia* clade may have to be given a new generic name. If study shows that they are sister to one another, then it would be more appropriate to treat them as subgenera of *Eschweilera*.



Figure 7. Cloud forest habitat of *Eschweilera jefensis* and *Eschweilera roseocalyx* dominated by *Colpothrinax aphanopstala* (Arecaceae). Photo by J. Batista.

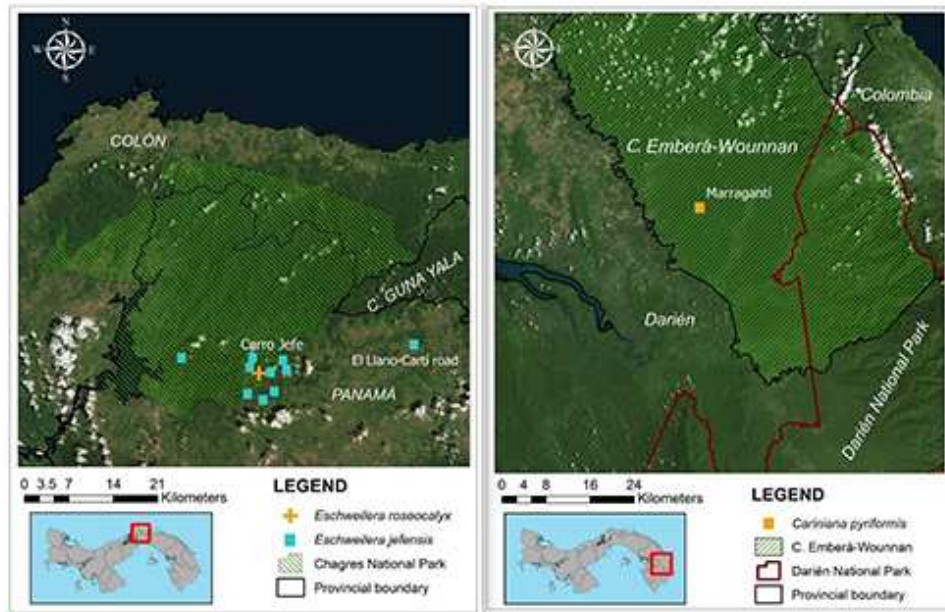


Figure 8. Maps of the Panamanian distributions of *Eschweilera jefensis*, *E. roseocalyx*, and *Cariniana pyriformis*. See Mori et al. (2017) for the overall distribution of *C. pyriformis* in Panama, Colombia, and Venezuela.

ACKNOWLEDGEMENTS

We are grateful to the National Geographic Society Committee for a Research and Exploration Grant (no. 8432-08) for support of field work; Jonathan Montenegro, Iliana Cisneros, Ernesto Campos, and Linda Harrison for assistance with fieldwork; the herbarium staffs of the Universidad de Panama (PMA), Smithsonian Tropical Research Institute (SCZ), and The New York

Botanical Garden (NY) for facilitating study of specimens in their herbaria; and Carmen Galdames, Reyes Carranza, Carol Carollo Matos, and the PMA herbarium for allowing use of their images. We thank Carlos Seixas of the Universidad de Panamá, Centro Regional de Veraguas for allowing use of the facilities of their botanical laboratory; Vayron De Gracia for producing the ArcGIS distribution map; the Dirección Nacional de Áreas Protegidas y Vida Silvestre of the Ministerio de Ambiente (MIAMBIENTE) for providing collecting and exporting permits; and Orlando Ortiz for help in the evaluation of conservation status (IUCN criteria) of the new species.

LITERATURE CITED

- ArgGIS Pro 10.3. 2014. Environmental Systems Research Institute, Inc. (ESRI), California-New York, United States. Download software: <<http://www.esri.com/en/arcgis/products/arcgis-pro/Overview>>
- Betancur, P.G. & E.J. Raigosa. 1973. Características y propiedades germinativas de las semillas de abarco (*Cariniana pyriformis* Miers). Rev. Fac. Agron. Medellín 28: 36–56.
- Calderón, E., G. Galeano & N. Garcia. 2002. Lecythidaceae, in Libro Rojo de Plantas Fanerógamas de Colombia 1: 141–202.
- Cárdenas, L.D., A.N. Castaño, T.S. Sua, & B.L. Quintero et. al. 2015. Planes de Manejo para la Conservación de Abarco, Caoba, Cedro, Palorosa y Canelo de los Andaquíes. Primera edición. Bogotá, Colombia: Instituto Amazónico de Investigaciones Científicas – SINCHI. ISBN 978-958-8317-90-8. 201 pp.
- Cárdenas, L.D. & N.R. Salinas (eds.). 2007. Lecythidaceae in Libro Rojo de Plantas de Colombia, Especies Maderables Amenazadas 4: 63–67.
- de Sedas, A., L. Martínez, M.N. de Stapf, & M. Correa. 2009. Guía Fotográfica de Plantas Vasculares del Cerro Jefe, Panamá. Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica.
- Gamboa-Gaitán, M.A. 1997. Biología reproductiva de *Eschweilera bogotensis* (Lecythidaceae) en la Cordillera Occidental de Colombia. Caldasia 19: 479–485.
- Huang, Y.Y.; S.A. Mori, & L.M. Kelly. 2015. Toward a phylogenetic-based generic classification of Neotropical Lecythidaceae - I. Status of *Bertholletia*, *Corythophora*, *Eschweilera* and *Lecythis*. Phytotaxa 203: 085–121.
- IUCN. 2001. The IUCN Red List Categories and Criteria, version 3.1, first edition. IUCN Species Survival Commission. Gland, Switzerland and Cambridge, U. K.
- IUCN. 2012. The IUCN Red List Categories and Criteria, version 3.1, second edition. IUCN Species Survival Commission. Gland, Switzerland and Cambridge, U. K.
- Lewis, W.H. 1971. High floristic endemism in low cloud forests of Panama. Biotropica 3: 78–80.
- Loefling, P. 1758. *Ilex hispanicum*. Stockholm: Lars Salvius.
- Miers, J. 1874. On the Lecythidaceae. Trans. Linn. Soc. Lond. 30(2): 157–318.
- Mori, S.A. & J.D. Boeke. 1987. Chapter XII. Pollination. In S.A. Mori & collaborators. The Lecythidaceae of La Fumée Mountain, French Guiana. Mem. New York Bot. Gard. 44: 137–155.
- Mori, S.A. & G.T. Prance. 1990. Lecythidaceae–Part II. The zygomorphic-flowered New World genera (*Couropita*, *Corythophora*, *Bertholletia*, *Couratari*, *Eschweilera* & *Lecythis*). Fl. Neotrop. Monogr. 21(II): 1–376.
- Mori, S.A., P. Becker, & D. Kincaid. 2001. Lecythidaceae of a central Amazonian lowland forest. Implications for conservation. Pp. 54–67, in R.O. Bierregaard, Jr., C. Gascon, T.E. Lovejoy, & R.C.G. Mesquita (eds.). Lessons from Amazonia. The Ecology and Conservation of a Fragmented Forest. Yale Univ. Press, New Haven, Connecticut.
- Mori, S.A., C.-H. Tsou, C.-C. Wu, B. Cronholm, & A. Anderberg. 2007. Evolution of Lecythidaceae with an emphasis on the circumscription of Neotropical genera: Information from combined ndhF and trnL-F sequence data. Amer. J. Bot. 94: 289–301.

- Mori, S.A., N.P. Smith, X. Cornejo & G.T. Prance. 2010. The Lecythidaceae Pages. The New York Botanical Garden, Bronx. <<http://sweetgum.nybg.org/lp/index.php>>
- Mori, S.A., E.A. Kiernan, N.P. Smith, L.M. Kelley, Y-Y. Huang, G.T. Prance & B. Thiers. 2017. Observations on the phylogeography of the Lecythidaceae clade (Brazil nut family). *Phytoneuron* 2017-30: 1–85.
- Prance, G. T. & S.A. Mori. 1979. Lecythidaceae–Part I. The actinomorphic-flowered New World Lecythidaceae (*Asteranthos*, *Gustavia*, *Grias*, *Allantoma* & *Cariniana*). *Fl. Neotrop. Monogr.* 21: 1–277.
- Record, S.J. & R.W. Hess. 1943. *Timbers of the New World*. Yale Univ. Press, New Haven, Connecticut.
- World Conservation Monitoring Centre. 1998. *Cariniana pyriformis*. The IUCN Red List of Threatened Species 1998: e.T33961A9824874. Available from <<http://dx.doi.org/10.2305/IUCN.UK.1998.RLTS.T33961A9824874.en>>