

A NEW SPECIES OF *CARPOTROCHE* (ACHARIACEAE) FROM HONDURAS AND NICARAGUA

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Abstract. *Carpotroche caceresiae*, a newly delimited species from the Caribbean drainage of Honduras and Nicaragua, is described and illustrated and its extinction threat assessed as Near Threatened (NT) according to IUCN criteria. *Carpotroche caceresiae* has previously been confused with *C. platyptera*, a species characterized by a densely pubescent lower leaf surface and red fruits lacking crests between the wings; in contrast, *C. caceresiae* has sparsely pubescent lower leaf surface and green fruits with crests between the wings. *Carpotroche crassiramea* and *C. glaucescens*, typified with Costa Rican material, and hitherto included in the synonymy of *C. platyptera*, are treated here as distinct morphological identities; a list of the specimens examined and referred to these names are provided.

Keywords: *Carpotroche platyptera*, Flacourtiaceae, Herbaria, Malpighiales, Mesoamerica, Taxonomy, Ecuador

Prior to phylogenetic analyses of DNA sequence data, the core eudicot Rosid I family Achariaceae Harms. were considered to comprise small shrubs, acaulescent and creeping herbs of the monospecific genera *Acharia* Thunb., *Ceratiosticyos* Nees and *Guthriea* Bolus (Hutchison, 1969; Chant, 1985; Goldberg, 1986), restricted to South Africa. Phylogenetic analyses of DNA sequence data, however, led to a radical re-circumscription of several genera traditionally placed in Flacourtiaceae and suggested that Achariaceae should be expanded to include several genera of trees and shrubs of tropical and subtropical Africa, Australia, Asia, and the Americas.

Chase et al. (2002) classified Achariaceae into four tribes and 30 genera: Acharieae (three genera), Pangieae (11 genera), Erythrospermeae (five genera), and Lindackerieae (11 genera). Of these, *Chiangiodendron* T. Wendt (Pangieae tribe), *Carpotroche* Endl., *Kuhlmanniodendron* Fiaschi & Groppo, *Lindackeria* C. Presl and *Mayna* Aubl. have been documented from the Neotropics, all of which are in the Lindackerieae (Chase et al., 2002; Sosa et al., 2003; Fiaschi and Groppo, 2008; Groppo et al., 2010). Lindackerieae are recognized by the following combination of morphological characters: segments of the perianth organized asymmetrically; sepals usually imbricate and separated from the petals; petals lacking an adaxial basal scale and, greater

in number and longer, than the sepals; a floral disc lacking glands; numerous stamens with more or less linear anthers; a unilocular ovary with parietal placentation; and fruits that are usually winged, with spines or slight ribs (Chase et al., 2002; Fiaschi and Groppo, 2008; Groppo et al., 2010).

Carpotroche is notable for its winged, usually cauliflorous fruits that can be green, white, orange, red or a combination thereof (Fig. 1). As a relatively charismatic component of the forest understory, *Carpotroche* is well represented in herbarium collections (especially with fruits). Diagnostic morphological characters for *Carpotroche* include, stipulate leaves that lack translucent dots or lines and that are usually clustered towards the branch tips; petiole including a pulvinus at both ends; odoriferous, unisexual, polygamo-monoecious or -dioecious flowers with more petals than the sepals; numerous stamens; pubescent filaments; a pistil with 4–8 (–10) capitate or lacerated stylodes and late dehiscent capsular fruits with smooth, vertical or winged ridges (Sleumer, 1980; Alford, 2003, 2009; Fiaschi and Groppo, 2008; Groppo et al., 2013).

The current taxonomy of *Carpotroche* is based on Sleumer's Flora Neotropica treatment of Flacourtiaceae (1980) according to which the genus comprises 11 species, nine of which occur in South America and two in Central America [*C. longifolia* (Poepp.) Benth. and *C. platyptera*

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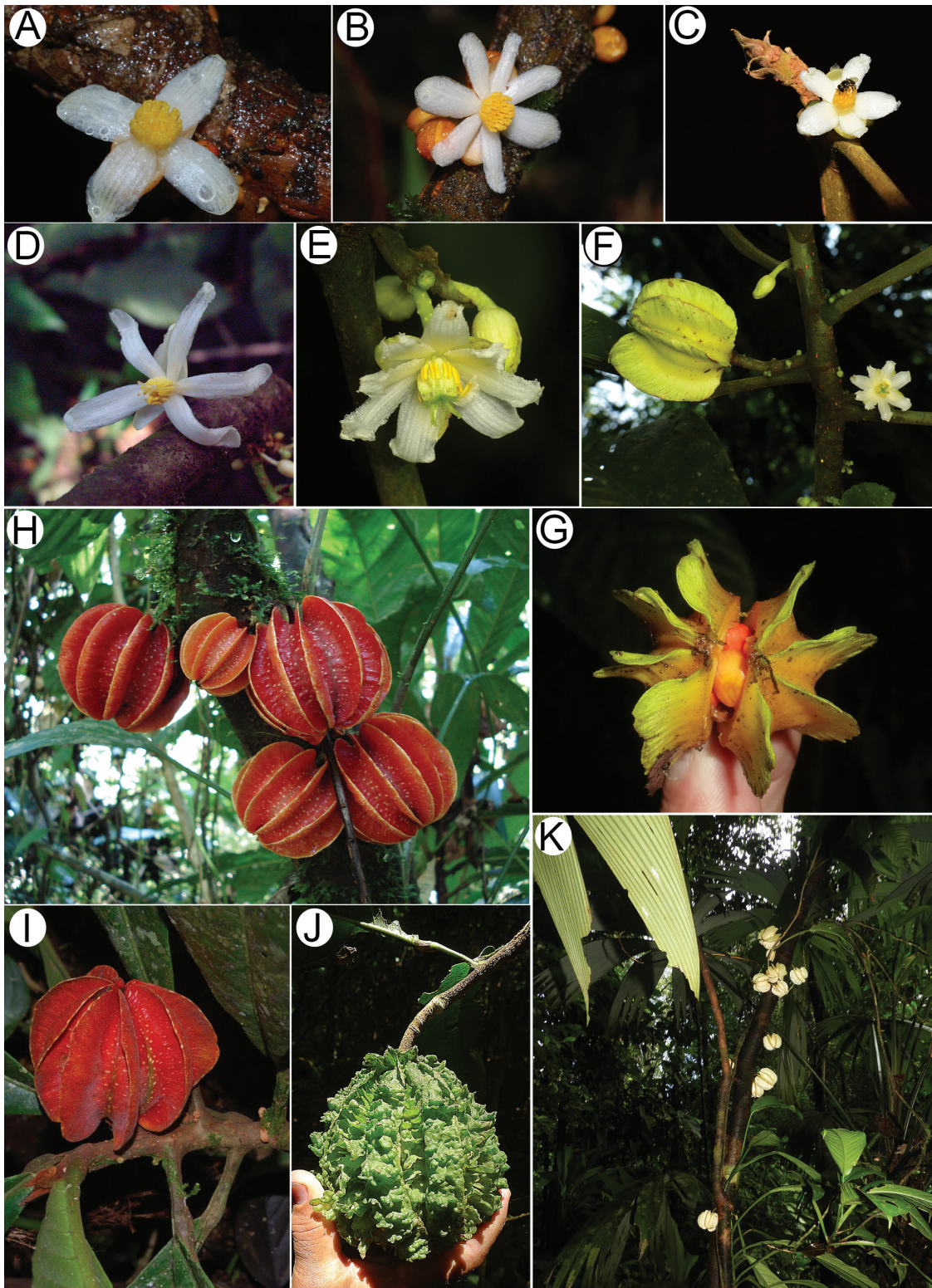


FIGURE 1. Some morphological character of flowers and fruits in *Carpotroche* Endl. **A**, *Carpotroche* sp. from Caribbean slope of Costa Rica (A. K. Monro et al. 6538); **B**, *Carpotroche crassiramea* (N. Zamora et al. 4864). **C**, *Carpotroche* sp. from Península de Osa, Pacific slope of Costa Rica (not herbarium specimens seen for these photographs, but taken in that region); **D**, *Carpotroche caceresiae* D. Santam. (I. Coronado et al. 4408); **E–G**, *Carpotroche ramosii* (Cuatrec.) Cuatrec. (not herbarium specimens seen for these photographs, but taken in Ecuador); **H–I**, *Carpotroche* sp. from Caribbean slope of Costa Rica, probably correspond with *C. crassiramea* Pittier (not herbarium specimens seen for these photographs, but taken in Veragua, Liverpool, Limón). **J**, *Carpotroche brasiliensis* (Raddi) Endl.; **I**, *Carpotroche crassiramea* (not herbarium specimens seen for these photographs). Images by Alex K. Monro (A–B, I), Reinaldo Aguilar (C, K), Indiana Coronado (D), Andreas Kay (E–G), Juan Mata-Lorenzen (H), Alex Popovkin (J).

Pittier]. *Carpotroche longifolia* is known from Panama (and South America), and *C. platyptera* Pittier from Guatemala (collections were not examined), Honduras, Nicaragua, Costa Rica, and Panama. *Carpotroche longifolia* and *C. platyptera* usually grow below 1000 m elevation, in humid or submontane forests (Sleumer, 1980). Sleumer (1980) described *Carpotroche froesina* Sleumer, endemic to Brazil and excluded *C. apterocarpa* Kuhlmann, the latter currently considered a species of *Kuhlmanniodendron* (Groppo et al., 2013).

Sleumer also placed two names in synonymy with *C. platyptera*: *C. crassiramea* Pittier and *C. glaucescens* Pittier (Pittier, 1909), all three of which are typified with Costa

Rican material. Sleumer's of *Carpotroche* was adopted by several flora treatments. For example, *Flora de Nicaragua* (Pool, 2001), *Manual de Plantas de Costa Rica* (González, 2010), and *Árboles de Costa Rica* (Zamora Villalobos et al., 2017). We, however, consider them distinct taxa. In addition, our own field and herbarium observations suggest that several specimens from the Pacific slope (Fila Costeña, Península de Osa, Tarrazú) and Caribbean slopes of Costa Rica (e.g., Hitoy-Cerere, Uatsi, Suretka) and Panama (El Llano-Cartí road) require further study (D. Santamaría-Aguilar et al. in prep.). With the proposal of this new species and the reestablishment of two names, the genus is composed by 14 species.

MATERIALS AND METHODS

Approximately 500 physical and digital herbarium specimens of *Carpotroche* were examined from BM, CR (including ex INB), GH, HULE, K, LSCR, LSU, MO, and NO (acronyms follow Thiers 2021 [continuously updated]). All type specimens were consulted. Of these, specimens from CR and MO comprised the majority of the material examined for this study. The following digital collections or virtual herbaria were used: F (<https://collections-botany.fieldmuseum.org/>), JSTOR Global Plants (<http://plants.jstor.org>), P (<http://www.mnhn.fr>), MEXU (<https://datosabierto.unam.mx/biodiversidad/>), INCT (<http://inct.splink.org.br>). Images of specimens not available online were provided by: EAP and HUH. Label information of specimens studied and housed at CR and MO are available online via the ECOBIOSIS (<http://ecobiosis.museocostarica.go.cr/index.aspx>), HERBARIO (<https://biodiversidad.museocostarica.go.cr/>) and TROPICOS (<http://www.tropicos.org/>). When

the coordinates and/or elevation were not included on the herbarium label, but were present in the TROPICOS database, the values from TROPICOS are included in brackets. Dot-distribution maps were compiled from studied specimens and generated with SimpleMappr (Shorthouse, 2010).

Species descriptions are based primarily on herbarium specimens. When necessary, flowers from herbarium specimens were rehydrated before measurement. A ruler was used to measure all morphological parts and trichomes were measured with a micrometer calibration tool (1div = 1mm) under a dissecting stereoscope (Bausch & Lomb). Colour of flowers and fruits, phenology, elevation, vernacular names and uses were observed from herbarium specimens. Field observations by the first author were made in the Osa Peninsula, Fila Matama, and La Selva Biological Stations of Costa Rica.

TAXONOMY

Carpotroche caceresiae D. Santam., *sp. nov.*

TYPE: NICARAGUA. Jinotega: Mpio. [Municipio] del Cua Bocay, Reserva de Bosawas, comunidad de San Andrés, Caño Susumwas, 180 m, 14°22'N, 085°03'W, 30 June 2005 (imm. fr.), *I. Coronado, M. Barrios, G. Pérez and M. Mercado* 1953 (Holotype: MO [5989394] [barcode MO-1690017]; Isotypes: HULE [23576], P [barcode P04782022; image]). Fig. 2, 3, 4A–B, 5A.

This new species is morphologically similar to *Carpotroche longifolia* (Poepp.) Benth. with respect to its whitish to greenish fruits that are longitudinally winged and possessing numerous crests between the wings, and the leaves, whose abaxial surface is short-pubescent. *Carpotroche caceresiae* can be distinguished from *C. longifolia* by the wings of the fruit having an entire or weakly sinuate margin (vs. deeply lacerate).

Shrub or small *tree*, 1.5–8 (–15) m high; *bark* smooth, brown-grey (*S. Blackmore* and *M. Chorley* 4184). *Young branches* 0.4–0.6 (–1.2) cm diameter, terete, sparsely lenticellate, the distal portions pubescent, trichomes of two classes, 0.2–0.3 (–0.5) mm, straight or apically uncinat, whitish or red-brown, the other a sparse to dense underlayer of smaller brown trichomes; stipules (0.15–) 0.4–0.9 × (0.1–) 0.15–0.3 cm, usually deltoid, both surfaces densely pubescent, trichomes brown, paler on the adaxial surface. *Leaves* spirally arranged; petioles (1.5–) 3–6.1

(–8.5) cm, occasionally fistulate, with a pulvinus towards the apex, pubescent as young branches, flattened, the adaxial surface occasionally weakly corrugated, abaxially rounded; laminae 19–48.5 × 5.8–13.3 cm, oblanceolate to obovate or obovate-elliptic; upper surface usually glabrous but occasionally with whitish trichomes on the midrib and lateral nerves; lower surface sparsely pubescent, trichomes 0.1–0.3 mm, whitish or red-brown; midrib flattened on the upper surface and raised on the lower surface, pubescent with two classes of trichomes, major trichomes whitish, minor trichomes brown; lateral veins (12–) 16–23 pairs, flat to weakly raised on the upper surface, raised on the abaxial surface, weakly curved, ascending; tertiary veins parallel, raised on the abaxial surface; quaternary veins reticulate; base cuneate; apex acuminate; margin usually serrate, with 19–40 teeth, the teeth (1–) 1.5 (–2) mm, each tooth bearing a small gland, the gland glabrous or pubescent. *Staminate inflorescences* in leaf axils, fasciculate, bearing 1–5 flowers, few of which are well developed at any one time; flowers bisexual, solitary, apparently cauliflorous. *Staminate flowers* pedicellate, pedicel 1.5–2.5 mm in bud, pubescent; sepals 2, white when fresh, ca. 6 × 4 mm, ovate; abaxial surface pubescent, occasionally glabrous towards the margins, with two classes of trichomes, one widespread, whitish, adpressed or erect and uncinat (at their apex), the other sparse to dense, brown; adaxial surface glabrous; petals

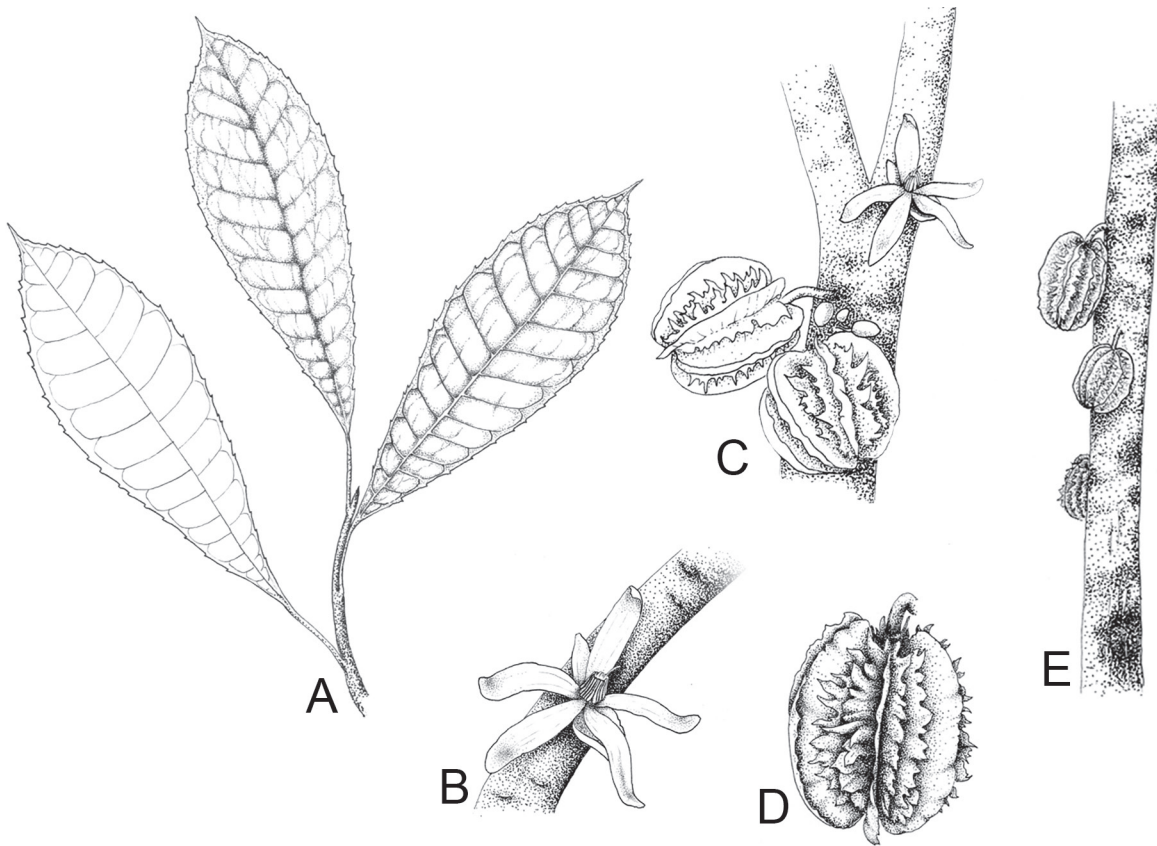


FIGURE 2. *Carpotroche caceresiae* D. Santam. **A**, leaves; **B**, hermaphrodite flowers; **C**, hermaphrodite flowers and fruits; **D**, stem with fruits; **E**, fruit detail showing wings and crests. Illustration by Alex Mauricio Campos, A from *I. Coronado et al.* 1953 (MO); B and C of the photographs *I. Coronado and A. Fernández* 4408; D of photography *I. Coronado and A. Fernández* 4736-A.

5 or 6, 4–11 mm in length, white, oblong-elliptic; abaxial surface sparsely pubescent, the trichomes concentrated on the central portion for almost all its length, whitish to transparent; adaxial surface glabrous or sparsely pubescent; stamens 18–21; filaments ca. 0.5 mm, densely pubescent; anthers ca. 3 mm in length, yellow, locellate, densely pubescent, the trichomes whitish yellow; gynoecium absent. *Hermaphrodite flowers* pedicellate, pedicel ca. 6 mm at anthesis, pubescent; sepals 2, white, ca. 10 × 4.5 mm, oblong-elliptic; petals 5, ca. 10 mm in length, white, oblong-elliptic, indument as in staminate flowers; stamens 18–21, yellow; filaments ca. 2 mm in length, densely pubescent; anthers ca. 5 mm in length, locellate, densely pubescent, trichomes whitish-pale yellow; gynoecium ca. 5 × 2.5 mm, ovoid, pubescent, trichomes whitish, with a sparse to dense under layer of smaller brown trichomes, 6-costate; styles 4, ca. 2.5 mm in length, glabrous; stigma glabrous, subcapitate, not lacerated. *Fruiting* pedicel 8–17 mm long; fruit (0.9–) 1.7–3.7 × 0.7–3.3 cm, ellipsoid to subglobose, longitudinally winged, yellowish, cream or lime-green when fresh, usually cauliflorous, pubescent throughout, two classes of indument, one of sparsely distributed larger, whitish, apically uncinatate trichomes, the other of densely distributed, smaller, brown trichomes; crests numerous, more or less triangular, distributed in the depressions

between wings, the crests 0.2–0.9 cm high depending on the degree of fruit maturity; styles occasionally persistent, glabrous or pubescent; the wings 6–8, spaced 0.5–1.4 cm apart, 0.8–1.3 cm high at their midpoint, erect, chartaceous, margin entire to weakly sinuate; pericarp 0.1–0.2 cm thick; seeds ca. 36 per fruit, ca. 1 × 0.6–0.7 cm, the fresh pulp described as being orange; testa yellowish to cream when dry, weakly rugose, sparsely pubescent, trichomes whitish.

Phenology: *Carpotroche caceresiae* flowering material has been collected from January to April; immature fruit have been collected January to February and May to July; mature fruits have been collected April to July and October.

Distribution and habitat: *Carpotroche caceresiae* has been collected in very wet undisturbed forest on the Caribbean coast of Honduras (Atlántida, Gracias a Dios, Yoro) and Nicaragua (Atlántico Norte, Jinotega) at altitudes of 0–600 m (Fig. 6). Based on this habitat and distribution it may be that this species also occurs in the Honduran departments of Olancho and Colón, the Guatemalan departments of Izabal and the Belizean District of Toledo.

Extinction threat assessment: We document 28 gatherings from 15 localities below. The associated locality data allows us to assess the species under criterion B of the IUCN Red List system. The EOO based on these gatherings

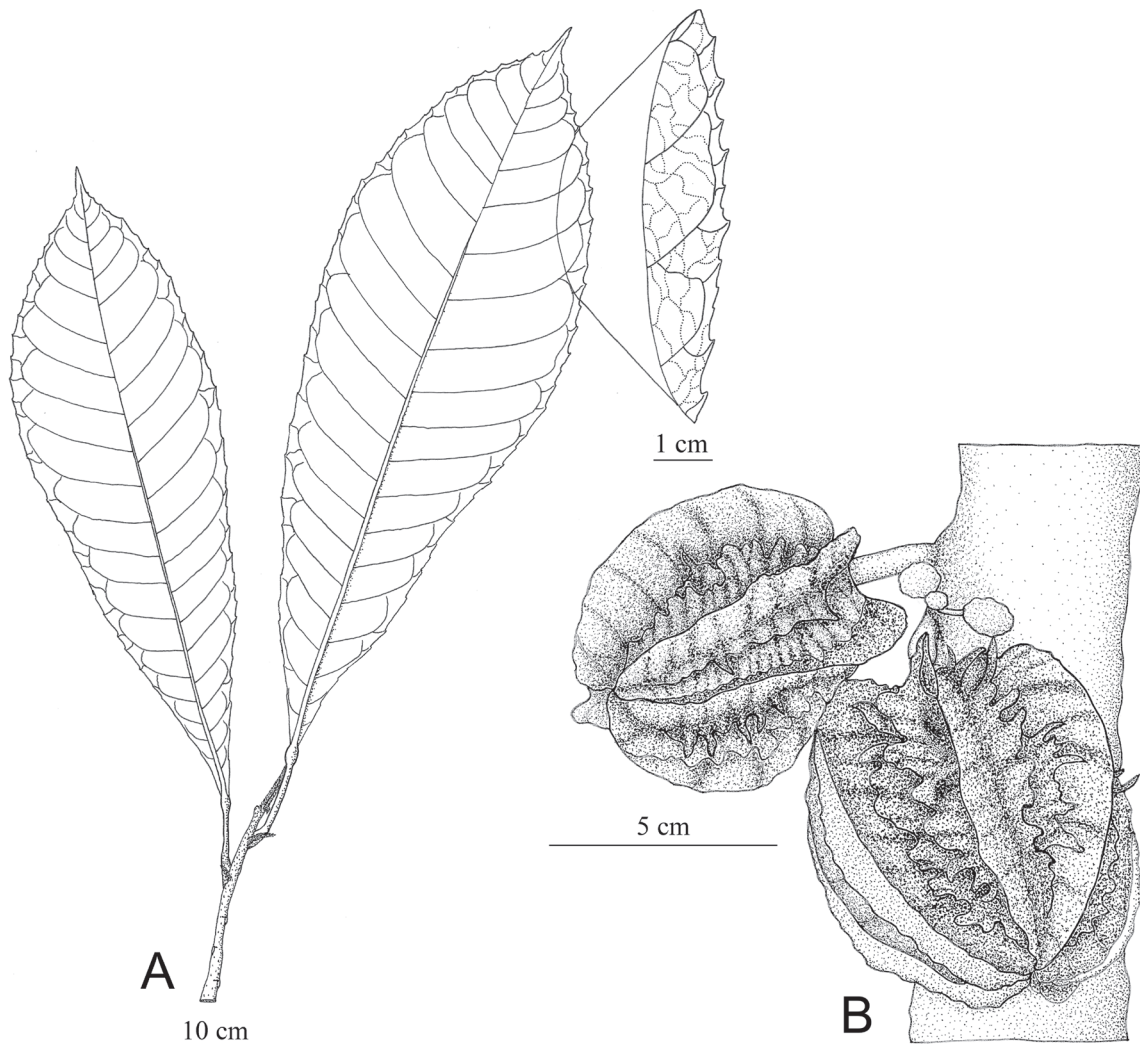


FIGURE 3. *Carpotroche caceresiae* D. Santam. **A**, leaf and margin detail; **B**, fruits. Illustration by Isler. F. Chinchilla, A from a image of the specimen *I. Coronado et al.* 1953 (MO); B of photography *I. Coronado et al.* 4636.

is 35,134 km², which is above the threshold of 20,000 km² for Endangered (EN). The corresponding AOO is 60 km², with a cell width of 2 km as recommended by IUCN (2012). This is also below the threshold for EN (<500 km²). Using the ProtectPlanet layer in GeoCAT (Bachman et al., 2011) we estimate that ca 40% of the EOO falls within the protected areas, Reserva Biológica Río Plátano, Reserva Biológica Tawahka, Parque Nacional Patuca and Reserva Natural Bosawas. The Global Forest Watch (2014) interactive map suggests that between 2001 and 2015, 8.6% of the EOO was deforested which suggests an active threat of deforestation (Criteria B, subcriteria C). Within the protected areas, however, there has been negligible deforestation.

Whilst the AOO is <500 km², only one subcriteria (C) applies and so *Carpotroche caceresiae* cannot be considered Endangered. We therefore assess this species as Near Threatened (NT) based on the number of known localities and a decline in the EOO as a result of active deforestation that will lead to a risk of extinction in the future.

Eponymy: This species is named in memory and recognition of the bravery of Berta Isabel Cáceres Flores (1971–2016), one of 123 environmental activists assassinated in retaliation for their opposition to environmental destruction and loss of indigenous land in Honduras, between 2009 and 2016 (Global Witness, 2017). Berta Cáceres (Fig. 7), in particular, was murdered because of her opposition to the Agua Zarcas hydroelectric project. She won the Goldman Environmental Prize in 2015.

Additional specimens examined: HONDURAS. Atlántida: Cordillera Nombre de Dios, Quebrada Grande on lower north slope of Pico Bonito, 25 May 1985 (imm. fr.), *S. Blackmore and M. Chorley* 4184 (BM); Tela, Lancetilla, 03 August 1929 (fr.), *W. N. Bangham* 233 (A-image); Lancetilla, 22 June–27 July 1929 (fr.), *A. M. Chickering* 89 (F-image); base of N slope of Pico Bonito, E of new CURLA (Centro Universitario Regional del Litoral Atlántico) camp building on the Quebrada Grande, ca. 1/3 km above its confluence with the río Bonito, ca. 10 km southwest of La



FIGURE 4. *Carpotroche caceresiae* D. Santam. **A**, hermaphrodite flowers; **B**, branch with hermaphrodite flower and fruits, insert stem and fruits). *Carpotroche longifolia* Benth. **C**, hermaphrodite flowers; **D**, flowers on the stem; **E**, fruits showing conspicuously lacerated wings. Images by Indiana Coronado (A–B, from I. Coronado and A. Fernández 4408, B inset from I. Coronado and A. Fernández 4736-A); and Robin Foster (C–E).

Ceiba, Parque Nacional Pico Bonito, 15°42'N, 086°51'W, 160 m, 03 February 1993 (♂ fl., fr.), *R. Evans 1047* (EAP-image, MO); *ibid*, 140 m, 08 February 1993 (fr.), *R. Evans 1565* (EAP-image, MO); La Ceiba, río Bonito, [15°42'00"N, 086°51'00"W], 15 January 1978 (st.), *C. Perry 38* (MO); montaña Lancetilla, cerca de El Portillo, 3 km al sur de Lancetilla, 500 m, 19 March 1962 (fr.), *A. Molina 10460* (EAP-image, F-image); Lancetilla Valley, 03 August 1929 (fr.), *F. M. Salvoza 817* (A-image); Tela, Lancetilla, [15°44'00"N, 087°27'00"W], 30 m, 18 August 1979 (fr.), *C. Soto 1* (MO); at base of hills south vicinity of San Alejo near río San Alejo, 150–270 m, 22–27 April 1947 (imm. fr.), *P. C. Standley 7608* (EAP-image); Lancetilla Valley, near Tela, 20–600 m, 06 December 1927–20 March 1928, *P. C. Standley 52627* (fr.), *53096* (fl. bud), *55539* (fl. bud) (A-image, US-

image); Lancetilla, 200 m, 26 April 1947 (imm. fr.), *L. O. Williams and A. Molina 13063* (EAP-image); hills back of Lancetilla, 1000 ft [305 m], 15 July 1934 (fr.), *T. G. Yuncker 4584* (A-image, NY); La Ceiba, Puente Alto, [15°37'39"N, 086°24'24"W], 800–1000 ft [265–335 m], 19 July 1938 (fr.), *T. G. Yuncker et al. 8522* (BM, GH-image, MO, NY-2 sheets). Gracias a Dios: [Brus Laguna], alrededores del río Plátano, 15°30'55"N, 084°43'00"W, [0–5 m], 17–23 May 1973 (fr.), *A. F. Clewell and G. Cruz 4083* (EAP-image, MO, U-image); [Brus Laguna], quebrada El Sargento, 80 m, 15°03'00"N, 084°50'00"W, 26 January 1994 (♂ fl.), *P. R. House 1823* (BM, MO); Cabecera de Unawas, 1 km al sureste de Krausirpe, pie de montaña de Wimpi, 15°03'N, 084°50'W, 90 m, 19 March 1994 (fl. bud), *P. R. House 1891* (BM-2 sheets); al norte de Krausirpe, 15°03'N, 084°50'W, 90 m,

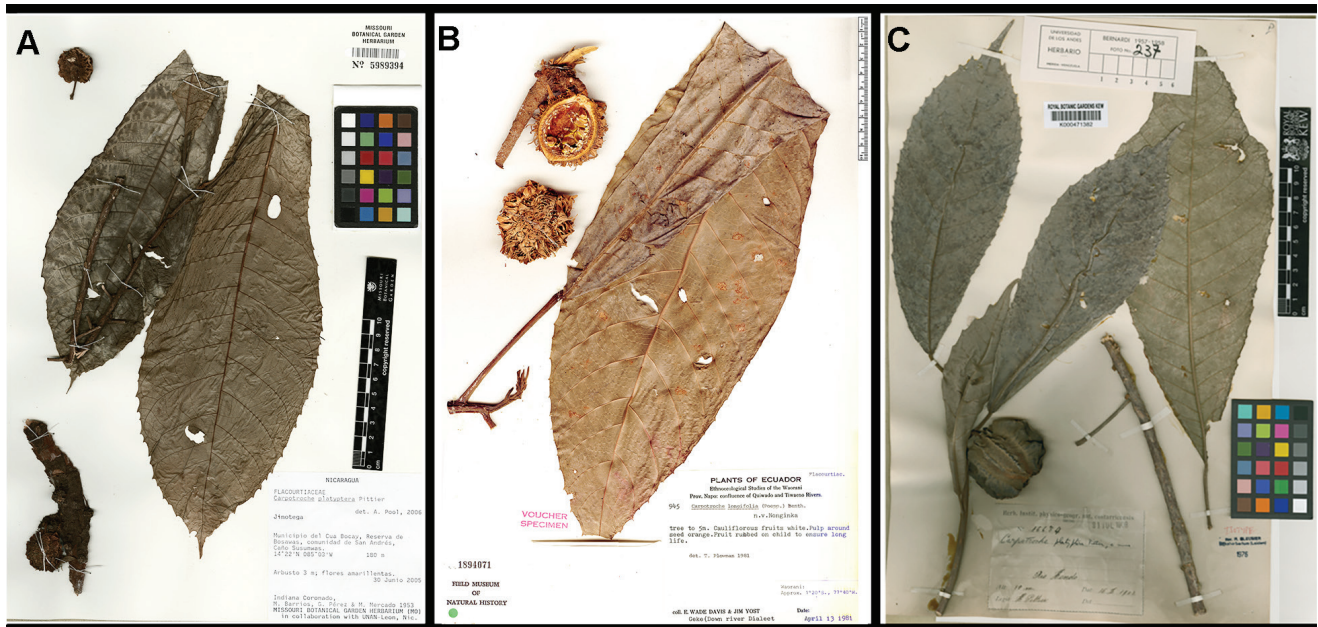


FIGURE 5. Comparison of herbarium specimens. **A**, *Carpotroche caceresiae* D. Santam. (*I. Coronado et al. 1953*); **B**, *C. longifolia* Benth. (*E. W. Davis and J. Yost 945*); **C**, *C. platyptera* Pittier (*C. H. F. Pittier 16634*). Photographs courtesy of Missouri Botanical Garden (A), Field Museum (B), and Royal Botanic Gardens, Kew (C).

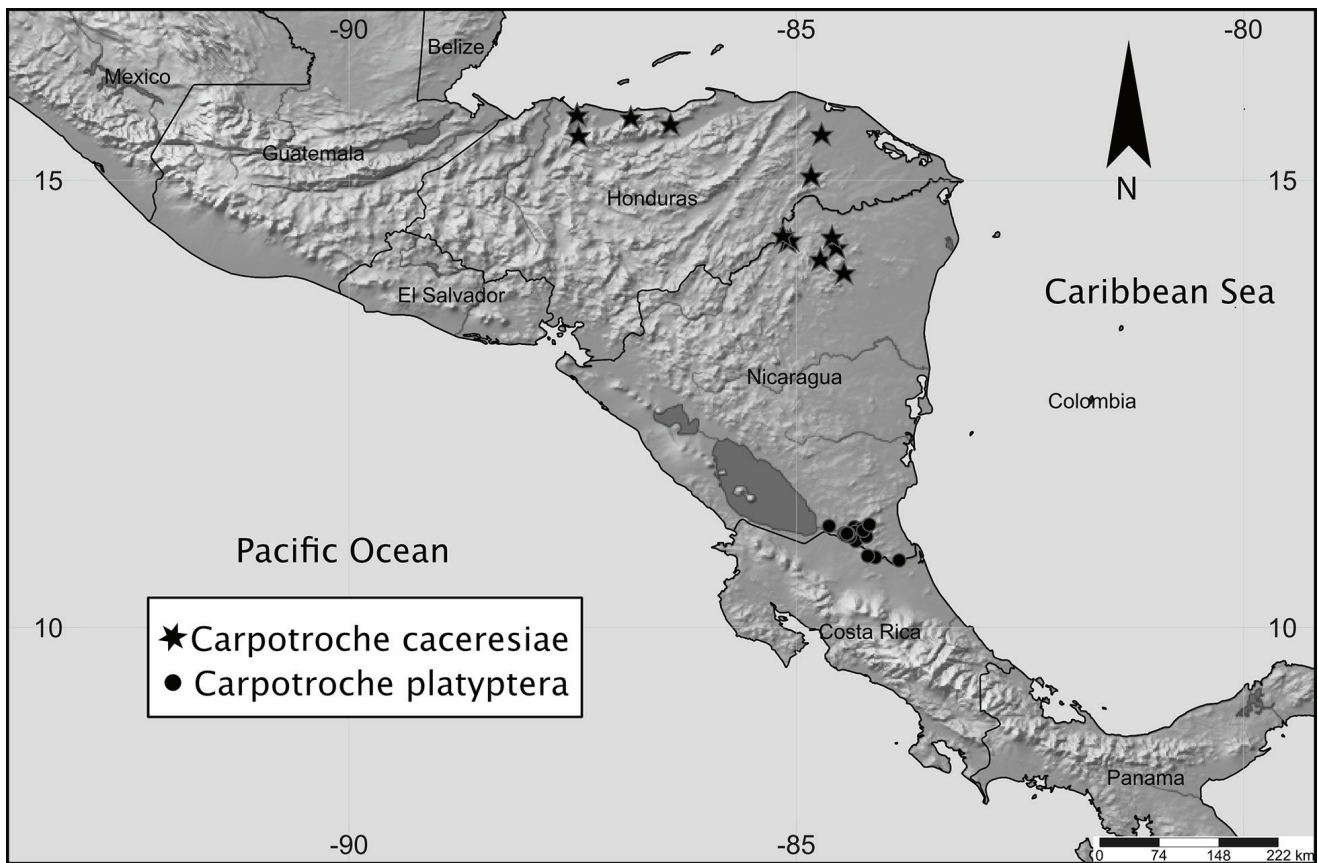


FIGURE 6. Distribution of *Carpotroche caceresiae* D. Santam. and *C. platyptera* Pittier in Nicaragua.



FIGURE 7. Berta Isabel Cáceres Flores (1971–2016). Courtesy by Michelle Meola.

07 March 1995 (fl. bud), *P. R. House 2272* (BM, MO). Yoro: Foot hills of the Cordillera Nombre de Dios, S of San José de Texiguat and the western side of the canyon of río Texiguat, 250–350 m, 15°30'00"N, 087°26'00"W, 15 May 1991 (fr.), *G. Davidse et al. 34409* (MO); margen E de río Guam-Guam, 2 km S de San José de Texiguat, 290 m, 05 August 1991 (fr.), *R. Zuñiga 1508* (EAP-2-sheets [imagen], K-2 sheets). NICARAGUA. Atlántico Norte [Zelaya]: Mpio. [Municipio] de Bonanza, Territorio Mayangna Sauni-As-Musawas, 14°06'59"N, 084°43'49"W, 50–150 m, 07 March 2003 (♂ bud. fl.), *C. Aker et al. 862* (MO); 7 km NW of Rosita, near a copper mine, [13°58'N, 084°28'W, 175 m], 17 August 1977 (fr.), *A. Danin 77-17-3* (MO); Mpio. [Municipio] Rosita, 15 km al NE del Poblado de Sahsa, 14°12'N, 084°09'W, 50–100 m, 23 May 1994 (imm. fr.), *R. Rueda and A. Grijalva 1467* (HULE, MO); Cerro Banacruz, 13°48'N, 084°24'W, 200–350 m, 10 July 1997 (fr.), *R. Rueda and I. Coronado 6654* (HULE, MO); Mpio. [Municipio] de Waspan, Reserva Bosawas, entre el cerro la Francia y la cima del Hill Tara (Asang, nuhni), 14°15'N, 084°33'W, 300 m, 20 January 1996 (imm. fr.), *R. Rueda et al. 3966* (HULE, MO); Reserva Bosawas, sobre el río Waspuk, 300 m después del rápido Wavla Kumbas, luego oeste hasta el cerro Suyakno Tuná Azan, 14°22'N, 084°36'W, 130–562 m, 02 October 1996 (fr.), *R. Rueda et al. 5037* (HULE, MO). Jinotega: Mpio. [Municipio] de Wiwilí, Reserva de Bosawas, comunidad de San Andrés, Caño Pilawas, 162 m, 14°19'00"N, 085°06'00"W, 03 April 2005 (st.), *I. Coronado et al. 1276* (MO); zona de conservación de Bosawas, comunidad de San Andrés, entre el transecto Yulu y caño Pilawas, 14°20'00"N, 085°04'00"W, 200 m, 06 March 2008 (♀ and fr.), *I. Coronado and A. Fernández 4408* (HULE, MO); Reserva Biológica de Bosawas, comunidad de Inipuwas, sobre el transecto Limsi, 14°23'00"N, 085°09'00"W, 170 m, 28 June 2008 (fr.), *I. Coronado and A. Fernández 4736-A* (MEXU-image, MO).

Common name and uses: In Honduras *Carpotroche caceresiae* is known as “altis” (*P. R. House 1823, 1891, 2272*), “cacao de monte” (*C. Perry 38*), and in Nicaragua as “sipi kuku parah” (*C. Aker et al. 862*). Label information for *P. R. House 1823*, indicates that oil is extracted from the fruit but without specifying its use.

Carpotroche caceresiae can be diagnosed by the combination of whitish to pale green, 6–8 winged fruits whose wings have entire to weakly sinuate margins, and the depressions between whose wings are populated by numerous small triangular crests (0.2–0.9 cm high), hermaphrodite flowers with the combination of narrow petals, long filaments and entire (not lacerated) stigmas. The leaves with dentate laminae, and lower surface pubescence comprising minute hairs.

With respect to the whitish to pale green fruit with

small crests between the wings *Carpotroche caceresiae* is similar to *C. brasiliensis* (Raddi) Endl., which has dextrorse or sinistrorse wings (vs. vertical in *C. caceresiae*), and *C. longifolia* (Poepp.) Benth., which has dentate, fimbriate or lacerate wings (vs. wings being entire or weakly sinuate in *C. caceresiae*) (Fig. 4C–E, 5A, B).

Material of *Carpotroche caceresiae* from Honduras has been previously attributed to *C. platyptera* (Fig. 5C, 10), by several authors (e.g., Standley 1930, 1931 [see plate XLVII]; Yuncker 1940; Molina Rosito 1975; Nelson 2008), none of whom cited herbarium specimens. In addition, of the specimens from Honduras cited by Sleumer (1980) in his monograph, we were not able to locate *Record* and *Kuylen 69* or *Wilson 298*, while *P. C. Standley 54875, 54885* (F-image) corresponds to material of *Meliosma* sp. (Sabiaceae). The remainder of the collections cited by Sleumer correspond to *C. caceresiae*. We therefore conclude that *C. platyptera* is absent from Honduras.

According to our delimitation of the species in Nicaragua, *C. platyptera* is known only from the south (Río San Juan Department) whilst *C. caceresiae* occurs in the north of the country (Atlántico Norte and Jinotega Departments, Fig. 6).

Of the 11 species accepted by Sleumer (1980), *C. platyptera* is restricted to Central America (Nicaragua, Panama (?), and the Caribbean side of Costa Rica) and unique in having red, pink or orange fruits when fresh (*C. ramosii* is sometimes described as having a similar coloration). The remaining species of *Carpotroche* have fruits that are yellowish, cream or lime-green (see Table 1). Curiously, the red/orange fruits are found only on the Caribbean slope of the Mesoamerican region. Whilst *Carpotroche platyptera* has been attributed to Ecuador (Sleumer 1980; León-Yáñez 1999), most of the material cited (e.g. *Y. Mexia 8436*, MO, U-image, US-image) corresponds to *C. ramosii* (Fig. 1E–G).

Our revision of herbarium material did not recover any clear morphological differences between the flowers of *C. caceresiae* and *C. longifolia* or *C. platyptera*. This is not surprising given the state of preservation of these delicate flowers in herbarium material. For the purposes of recovering such differences we recommend that researchers collect flowering material in spirit and that they take macro images of the flowers.

It should be noted that the flower dimensions given here should be considered as underestimates since most of the examined specimens were in bud, broken or wrinkled to the point that rehydration was problematic.

The key presented below is mainly based on herbarium specimens from Costa Rica. *Carpotroche longifolia* was not included in the key because physical specimens from Panama were not located.

PRELIMINARY KEY TO THE SPECIES OF *CARPOTROCHE* IN MESOAMERICA

- 1a. Lamina lower surface densely pubescent, the indument covering all of the surface and soft to the touch *C. platyptera*
 1b. Lamina lower surface sparsely pubescent, the indument not covering all of the surface and not apparent to the touch 2
 2a. Fruits yellowish, cream or lime-green when fresh, with crests between the wings *C. caceresiae*
 2b. Fruits reddish, pink or orange when fresh, without crests between the wings 3
 3a. Laminae (33.5–) 51–64 × (10.5–) 13–18.5 cm, base long cuneate; twigs bearing leaves (0.5–) 0.8–1.2 cm thick; stipules 0.9–1.7 cm long *C. crassiramea*
 3b. Laminae 15.5–35 × 3.7–11 (–13.5) cm, base cuneate; twigs bearing leaves 0.3–0.6 cm thick; stipules 0.2–0.4 (–0.6) cm long *C. glaucescens*

TABLE 1. Species of *Carpotroche* with green/white fruits. Information from Sleumer 1980, except where otherwise specified.

SPECIES	N° SEPAL ♀ FLOWERS	N° PETAL ♂ FLOWERS	STAMENS	STYLODES	STIGMAS	FRUIT BROAD (cm)	FRUIT N° OF WINGS	FRUIT TUBERCLED BETWEEN WINGS	FRUIT MARGEN WINGS	FRUIT WING COVERING	REGION
<i>C. amazonica</i> Mart. ex Eichler	2 or 3 (rarely 4)	9	50–60	10	Somewhat lacerate distally	5.8	10	Yes	Entire	Covering each other	SA
<i>C. brasiliensis</i> (Raddi) Endl.	3	9 (–12)	50–60	5–7	Subcapitate, cristate- lobulate	(4.4)– 5–8.7%	(8–) 10–14	No	Dextrorse or sinistorse wings or crests	Partly covering each other	SA
<i>C. caceresiae</i> D. Santam.	2	5–6	18–21	4	Subcapitate, not lacerate		6–8	Yes	Entire to slightly wavy	Not covering each other	CA
<i>C. crispidentata</i> Ducke	3	8 or 9	40	ca. 5	Lacerate	3–7#	10–12	No	Irregularly obtusely crisped-dentate	Not covering each other	SA
<i>C. froesiana</i> Sleumer	3	6	Numerous	Not described	Not described	2	Not described	No	Entire to slightly wavy	Partly covering each other	SA
<i>C. grandiflora</i> Spruce ex Eichler	3	9–10	ca. 80	Not described	Not described	ca. 6	(10–) 12 (–14)	No	Entire	Partly covering each other	SA
<i>C. integrifolia</i> Kuhlmann	2	5 or 6	20–25	4	Bipartite and a little lacerate distally	1.8–2.3	6	No	Entire	Not covering each other	SA
<i>C. longifolia</i> Benth.	2 or 3	(5–) 6–7 (–10)	Numerous	5–6	Subcapitate	2.5–4	9–12	Yes	Dentate, fimbriate or lacerate	Not covering each other	CA, SA
<i>C. pacifica</i> (Cuatrec.) Cuatrec.**	(2) 3	7	32	5 (in fruit)	Not described	4	10	No	Dentate	Not covering each other	SA
<i>C. ramosii</i> (Cuatrec.) Cuatrec.**	3	5	20	4	Smooth	2.5	8	No	Entire	Not covering each other	SA
<i>C. surinamensis</i> Uittien	3	6–7	30–40	4 or 5	Lacerate- palmatifid distally	3–4 (–5?)	8–10	Not described	Subentire, revolute	Not covering each other	SA

** from Cuatrecasas 1944; # from Zmarzly 2007; % from Achariaceae in Flora do Brasil 2020. Region CA=Central America; SA=South America.

A list of representative specimens of *Carpotroche crassiramea*, *C. glaucescens*, and *C. platyptera* is presented below.

Carpotroche crassiramea Pittier. Contr. U.S. Natl. Herb. 12: 180. 1909. TYPE. COSTA RICA. [Limón]: In forest around Banana River near Port Limon, [s.d.] May 1903 (fl., fr.), [O. F.] Cook & [C. B.] Doyle 424 (Holotype: US [accession number: 474262; barcode: US00114644], image). Fig. 8.

Additional specimens examined: COSTA RICA. Limón: San Miguel de Sixaola, 09°33'60"N, 082°38'20"W, 40 m, 03 March 1999 (fr.), *E. Alfaro 2078* (CR); Banana River, [s.d.] 1903 (fr.), O. F. Cook & C. B. Doyle s.n. (US-474763, image); Ca. 8 km en línea recta suroeste de Bananito Sur, 09°49'23"N, 083°03'45"W, 75 m, 05 November 2016 (imm. fr.), *B. Hammel and I. Pérez 27195* (CR); Finca Selva Bananito, a lo largo del Río Carbón, 09°49'30"N, 083°03'50"W, 100 m, 13 April 2008 (fr.), *B. Hammel et al. 24707* (CR-2 sheets); Sector Gandoca, entrada al muelle de la laguna Gandoca, 09°35'18"N, 082°32'17"W, 1 m, 08 October 2002 (imm. fr.), *J. González 2247* (CR); Manzanillo, siguiendo el camino del "gobierno," hacia Punta Mona, hasta laguna innominada (de aguas turbias), 09°38'21"N, 082°39'03"W, 0–70 m, 30 January 2003 (fr.), *J. González et al. 2814* (CR); Puerto Viejo, Punta Uva, Finca Tabacón, 09°37'30"N, 082°41'40"W, 50–100 m, 5 June 1996 (fr.), *R. González et al. 184* (CR); Fila Matama, Cerro Muchilla, Falda NW, Río Bananito, Selva Bananito Lodge, 09°49'30"N, 082°03'50"W, 100 m, 25 January. 2001 (fr.), *J. F. Morales*

7737 (CR); Parque Nacional Tortuguero, 2 km al Sur de Tortuguero, 10°31'N, 083°30'W, 4 m, 13 October 1998 (fr.), *R. Robles 2110* (CR); Cerro Muchilla, fila Matama, entrando por el pueblo El Progreso, 09°47'50"N, 083°05'90"W, 850 m, 09 April 1989 (fr.). *R. Robles and A. Chacón 2734* (CR); río Blanco, Las Brisas de Veragua, propiedad de Veragua Rain Forest, trayecto entre el restaurante y el serpentario, 09°55'28"N, 083°11'28"W, 387 m, 01 March 2011 (fr.), *J. Sánchez et al. 2218* (CR); Valle de La Estrella, propiedad de Selva Bananito Lodge, 09°49'84"N, 082°04'23"W, 133 m, 12 April 2011 (fr.), *J. Sánchez et al. 2302* (CR); Valle La Estrella, Fila Matama, ca. 11 km SW del Pueblo de Aguas Zarcas, alrededores del campamento El Hotel, 09°49'04"N, 083°09'31"W, 800–900 m, 01 November 2007 (fr.), *A. Rodríguez et al. 11617* (CR); Fila Matama, cerca de 11 km SW del pueblo de Aguas Zarcas, camino que lleva al rancho El Hotel, 09°49'26"N, 083°09'42"W, 700–800, 19 October 2007 (fr.), *D. Santamaría 6499, 6507* (CR); on trail to Point 2, forest close to edge of field adjoining Bananito Lodge, 09°49'07"N, 083°04'04"W, 130 m, 25 March 2010 (fr.), *D. Solano et al. 6175* (CR); Point 6, forest close to edge of field adjoining Bananito Lodge, 09°49'01"N, 083°04'06"W, 100 m, 24 March 2010 (fr.), *N. Zamora et al. 4864* (CR).

Carpotroche glaucescens Pittier. Contr. U.S. Natl. Herb. 12: 178. 1909. TYPE. COSTA RICA. [Limón]: Grape Point, coast of Talamanca, [s.d.] September 1900, *H. Pittier 14019* [as 14089 in the original description] (Holotype: US [accession number: 577934; barcode US00114648, image]). Fig. 9.



FIGURE 8. *Carpotroche crassiramea* Pittier. **A**, herbarium specimen; **B**, branch with leaves; **C**, Floral bud and open flower in lateral view; **D**, flower; **E**, fruit. Images by Museo Nacional de Costa Rica (A; *D. Santamaría 6499*, CR); Alexandre K. Monro (B–E; *N. Zamora et al. 4864*).

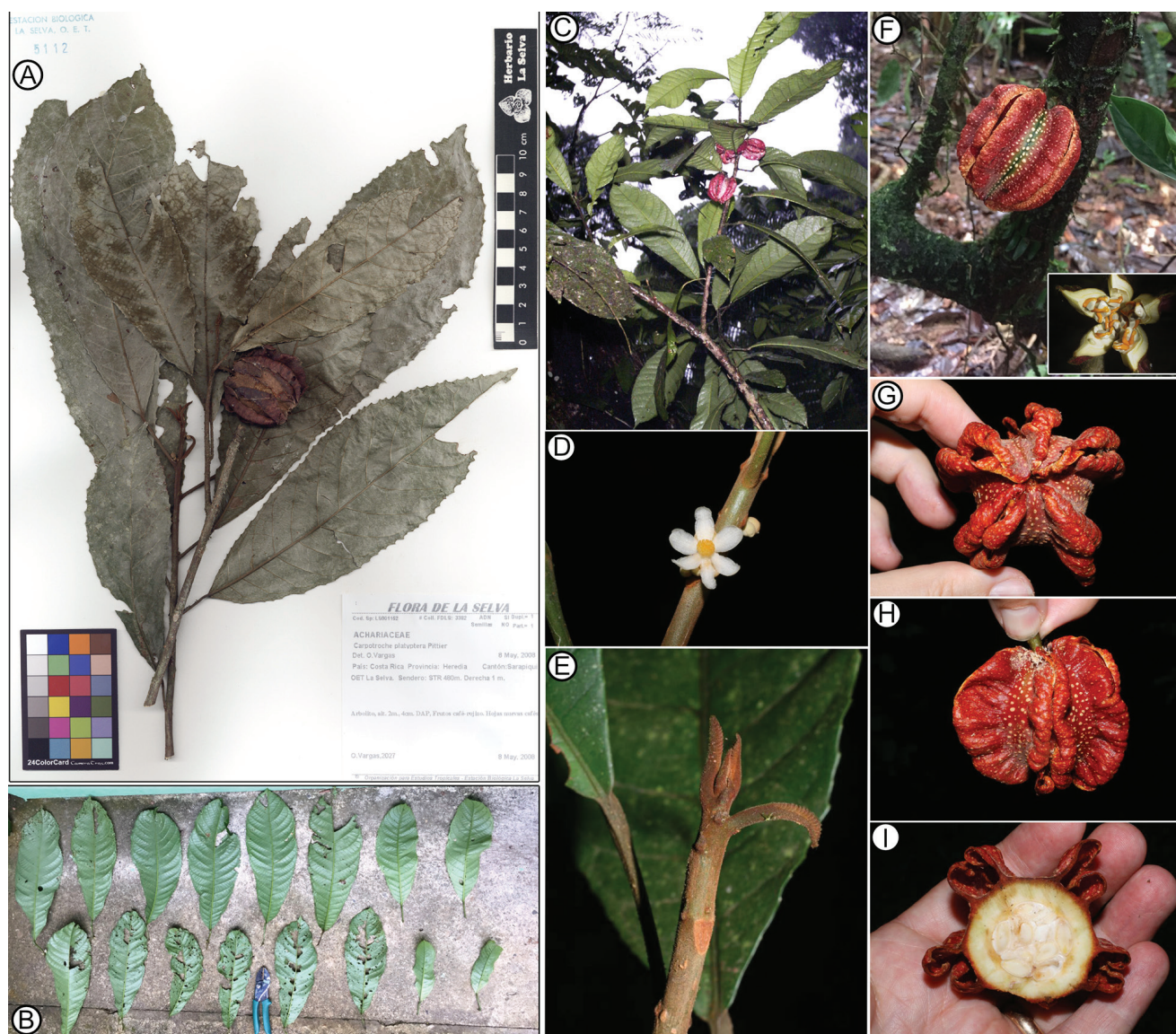


FIGURE 9. *Carpotroche glaucescens* Pittier. **A**, herbarium specimen; **B**, leaf variations; **C**, branch with fruits; **D**, flower; **E**, branch apex; **F**, fruit in the trunk and seeds (insert); **G**, fruit, front view; **H**, fruit, lateral view; **I**, fruit, cut. Images by Flórlula Digital de La Estación Biológica La Selva (**A**; *O. Vargas* 2027, LSCR); **D**. Santamaría-Aguilar (**B**, **F**); Orlando Vargas (**C** and **F** insert); Robbin Moran (**E** and **G**–**I**). Photos **B**–**I** taken at La Selva Biological Station).

Additional specimens examined: COSTA RICA. Heredia: Parque Nacional Braulio Carrillo, estación Magsasay, Sarapiquí, 10°24'18"N, 084°03'30"W, 200 m, 05 July 1990 (fl. bud), *D. Acevedo 124* (CR); Parque Nacional Braulio Carrillo, sector Magsasay, del cruce del río Peje 900 m por el transecto altitudinal, cruce a La Selva, 10°24'09"N, 084°02'37"W, 200–208 m, 07 May 2009 (fl. bud), *L. Acosta and J. Blanco 11175* (CR); Parque Nacional Braulio Carrillo, Estación Biológica Magsasay, 10°24'03"N, 084°03'03"W, 200 m, 23 June 1990 (fr.), *E. Alcázar 105* (CR.); original wet forest and cocoa plantation on the property of Dr. L. Holdridge, about 2 km upstream on the Rio Puerto Viejo, 10°25'N, 083°59'W, 100 m, 05–06 January 1967 (fr.), *W. Burger and G. Mata 4166* (CR); *ibid*, 05–06 January 1967 (fl. bud), *W. Burger and G. Mata 4251* (CR); Magsasay,

Finca de Bernardo Gómez, 700 m, 21 January 1983 (fr.), *I. A. Chacón 195* (CR); Parque Nacional Braulio Carrillo, estación Magsasay, detrás de la estación, 10°14'05"N, 084°03'10"W, 150 m, 29 September 1990 (fr.), *A. Fernández 85* (CR-2 sheets); río Peje, estación Magsasay, orillas del sendero a la poza de los Padres, 10°24'18"N, 084°03'30"W, 200 m, 26 September 1992 (fr.), *A. Fernández 390* (CR); Parque Nacional Braulio Carrillo, estación El Ceibo, sendero a la toma de agua, 10°20'00"N, 084°04'00"W, 450–550 m, 15 March 2003 (fl. bud), *J. González 3206* (CR); OET La Selva, sendero STR de 5000 a 6200 m, 24 August 2004 (fl. bud), *J. González and D. Solano 6867* (LSCR); OET La Selva, sendero oriental, hasta la intersección con el sendero Holdridge y Sábalo Esquina, 10 September 2004 (fr.), *J. González and D. Solano 6922* (LSCR-2 sheets);

OET La Selva, sendero SOC de 0–1450 m, 08 July 2008 (fl. bud), *J. González* 7684 (LSCR); La Virgen, Estación Biológica La Tirimbina, sendero Ajillo, 06 June 2008 (fl. bud), *J. González et al.* 9872 (LSCR); La Virgen, Estación Biológica La Tirimbina, sendero Botarrama, 24 June 2008 (fr.), *J. González* 9887 (LSCR); *ibid.*, 19 November 2008 (fl. bud), *J. González* 10478 (LSCR); *ibid.*, 11 March 2009 (fr.), *J. González* 10640 (LSCR); Finca La Selva, the OTS Field Station, south boundary, along Q. [Quebrada] El Salto, 100 m, 02 March 1980 (fr.), *B. Hammel* 7947 (LSCR, NY); Finca La Selva, along the east loop trail, 10°26'N, 084°01'W, [0–100 m], 12 February 1974 (fl. bud), *G. S. Hartshorn* 1367 (CR, LSCR); La Selva, camino Lindero Sur, 10°26'00"N, 084°02'00"W, 0–100 m, 01 October 2003 (fl. bud), *R. Kriebel et al.* 3990 (CR); La Selva Research Field Station of OTS, SRI trail between 300 and 500, 10°26'00"N, 084°02'00"W, 100 m, 14 May 2002 (fr.), *L. Landrum* 10230 (CR); Istarú Farm, La Tirimbina, 220 m, 17 September 1971 (fr.), *R. W. Lent* 2141 (CR, NY); camino de Puerto Viejo a río Frío, 10°15'39"N, 083°53'25"W, 100 m, 02 September 1993 (fr.), *V. Ramírez et al.* 86 (CR); Bijagual, camino a la

estación Magsasay, 10°24'00"N, 084°05'20"W, 200 m, 14 January 1994 (fr.), *V. Ramírez et al.* 214 (CR-2 sheets); OET La Selva, sendero CEN 100, 01 July 2004 (fr.), *D. Solano* 1156 (LSCR); Rara Avis, ca. 15 km al suroeste de Horquetas, alrededores del Hotel y Quebradita “Charral,” 10°17'N, 084°02'W, 400 m, 20 September 1989 (fr.), *O. Vargas* 147 (CR); OET La Selva, sendero STR 480, 08 May 2008 (fr.), *O. Vargas* 2027 (LSCR); Finca La Selva, the OTS field stations, sendero Suroeste at 1050, 100 m, 17 June 1995 (fl. bud), *M. K. Whitson* 117 (CR); Finca La Selva, the OTS field stations, El Peje trail at 600 m, 100 m, 17 Jun. 1995 (fr.), *R. L. Wilbur and T. Mowbray* 64682 (CR). Limón: Pococí. R. N. F. S. Barra del Colorado, Sardinas, 10°38'38"N, 084°44'10"W, 15–20 m, 12 December 1992 (fl. bud), *F. Araya* 174 (CR-2 sheets); R. N. F. S. Barra del Colorado sector Cor[c]orí, 10°35'40"N, 084°45'00"W, 100 m, 08 October 1990 (fr.), *E. Rojas* 198 (CR); Parque Nacional Tortuguero, estación Agua Fría, sendero Agua Fría hasta entrada Sendero Aguacate, 10°26'40"N, 084°34'40"W, 20 m, 01 December 1990 (fr.), *J. Solano* 278 (CR-2 sheets); Puerto Viejo along the road to El Muelle, 10°28'N, 083°58'W, 100 m, 08 January 1967 (fl.,

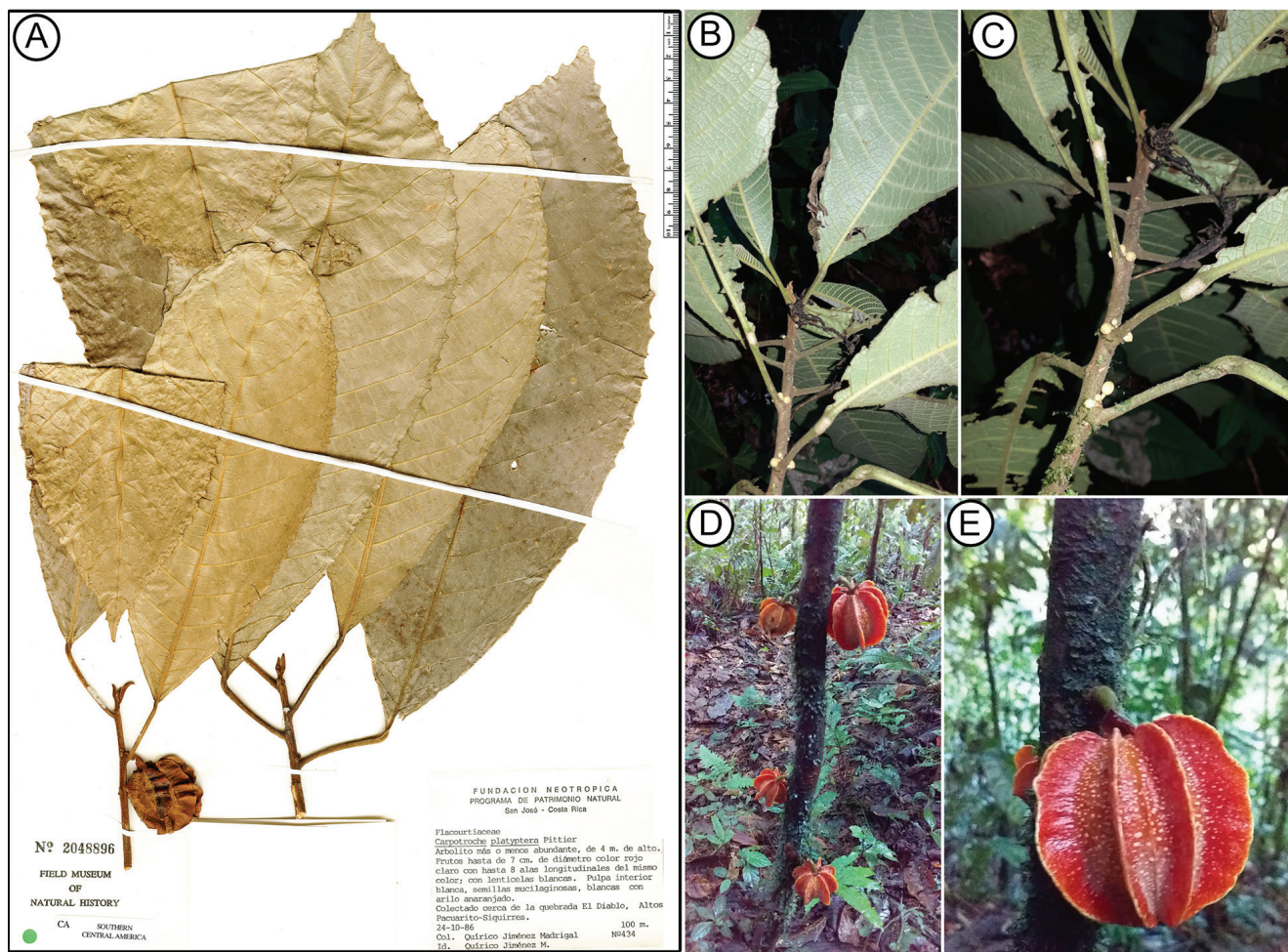


FIGURE 10. *Carpotroche platyptera* Pittier. **A**, Herbarium specimen collected in the vicinity of the type locality; **B**, Leaf base, venations; **C**, Branch with flowers buds; **D–E**, Fruits. Images by Field Museum (A; *Q. Jiménez* 434, F); B–E by Isidro Chacón, without voucher specimen, but taken in La Alegría, Alto la Botella de Siquirres, place where this species has been collected previously (e.g. *J. González et al.* 8074, LSCR).

fr.), *W. Burger and G. Mata 4319* (CR); Fila Matama, San Juan de Chirripocito de Pococí, 09°53'30"N, 084°11'30"W, 400 m, 12 March 1995 (fr.), *A. Rodríguez 628* (CR).

Carpotroche platyptera Pittier. Contr. U.S. Natl. Herb. 12: 178. 1909. TYPE. COSTA RICA. [Limón]: [Matina] Río Hondo, plains of Santa Clara, 15 February 1903 (fr.), *H. Pittier 16634* (holotype: US [accession number: 578981; barcode US00114651], image!; Isotypes: K! [barcode: K000471382], P [barcode: P04693053], image!). Fig. 10.

Additional specimens examined: NICARAGUA. Río San Juan: Santa Crucita de la Gloria, 5 km al NE de Sábalo, 11°03'N, 084°25'W, 70 m, 26 February 1984 (fr.), *P. P. Moreno 23374* (MO, P-2 sheets, image); La Gloria, 3.5 km al NE del poblado de Boca de Sábalo, 11°03'N, 084°26'W, 70 m, 20 March 1985 (fr.), *P. P. Moreno 25455* (MO, P-image). COSTA RICA. Alajuela: Río Peñas Blancas canyon, Nene Castro farm, 4 km NW of La Tigra, 10°22'00"N, 084°37'00"W, 200 m, 08 September 1994 (fl. bud), *W. Haber 11860* (CR); Guatuso, asentamiento campesino La Garroba, 10°45'N, 084°52'W, 80–100 m, 09 November 1987 (fr.), *G. Herrera 1179* (CR); Boca Tapada, finca Daniel Murillo, parcela # 9, 10°42'02"N, 084°13'08"W, 200–300 m, 06 July 2005 (st.), *D. Santamaría et al. 2305* (CR); San Carlos, Boca Tapada, Laguna de Lagarto lodge, 10°38'47"N, 084°02'33"W, 50 m, 05 December 2004 (fr.), *D. Solano 1503* (CR). Cartago: 24 km NE of Turrialba on hwy to Limón, then E at Tres Equis on jeep road 1.5 km, 09°58'N, 083°34'W, 450–525 m, 10 May 1983 (fr.), *R. Liesner et al. 15350* (CR, MBM-image).

Limón: [Bonilla], La Colombiana Farm of the United Fruit Co., [10°09'00"N, 083°34'48"W], 70 m, 06–07 March 1924 (fr.), *P. C. Standley 36751* (US-image); *ibid.*, 06–07 March 1924 (fl. bud), *P. C. Standley 36851* (US-image); *ibid.*, 06–07 March 1924 (fr. probably in the envelope), *P. C. Standley 36860* (US-image); *ibid.*, 06–07 March 1924 (fl. bud), *P. C. Standley 36953* (US-image); finca Montecristo, on the Río Reventazón below Cairo, [10°07'N, 83°32'W], 25 m, 18–19 February 1926 (fl. bud), *P. C. Standley and J. Valerio 48471* (US-image); *ibid.*, 18–19 February 1926 (fl. bud), *P. C. Standley and J. Valerio 48547* (US-image); *ibid.*, 18–19 February 1926 (fl. bud), *P. C. Standley and J. Valerio 48558* (US-image); *ibid.*, 18–19 February 1926 (fl. bud), *P. C. Standley and J. Valerio 48585* (US-image); *ibid.*, 18–19 February 1926 (fl. bud., fr.), *P. C. Standley and J. Valerio 48588* (US-image); *ibid.*, 19 February 1926 (fl. bud), *P. C. Standley and J. Valerio 48788* (US-image); [Matina], Finca La Lola, Madre de Dios, [10°06'N, 83°23'W], 50–75 m, 25 March 1949 (fr.), *L. Holdridge 2526* (CR); P. N. [Parque Nacional] Barbilla, sendero Topoyiyo, 10°59'25"N, 083°26'30"W, 300 m, 05 May 1999 (fr.), *E. Mora 320* (CR, NY); Siquirres, cerca de la quebrada el Diablo, Altos de Pacuarito, [10°06'N, 083°28'W], 100 m, 24 October 1986 (fr.), *Q. Jiménez 434* (CR, F-image); La Alegría, Alto la Botella, 800–1000 m, 11 August 2006 (fls. bud., imm. fr.), *J. González et al. 8074* (LSCR); Siquirres, en las colinas montañosas, 17 October 1973 (fr.), *L. J. Poveda 725* (CR); Finca de don J. Berrocal, 60–70 m, 04 October 1986 (fr.), *N. Zamora et al. 1305* (CR-2 sheets).

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