Flora of Panama. Part VI. Family 91. Burseraceae

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FLORA OF PANAMA

BY ROBERT E. WOODSON, JR. AND ROBERT W. SCHERY
AND COLLABORATORS

Part VI

FAMILY 91. BURSERACEAE[1]

DUNCAN M. PORTER[2]

Trees or shrubs, resin ducts present in the inner bark. *Leaves* alternate, usually odd-pinnate, deciduous or persistent; stipules usually absent. *Inflorescences* axillary to rarely terminal cymose panicles or racemes; plants mostly dioecious. *Flowers* small, regular, hypogynous, 3–5-merous, usually functionally unisexual; sepals 3–5, connate at least basally, imbricate or valvate, persistent; petals 3–5, free or rarely connate into a tube, imbricate or valvate; stamens 6–10, in 1–2 whorls, usually sterile in carpellate flowers, the filaments usually free, inserted below or rarely on the disc, the anthers 2-loculed, versatile, introrse, longitudinally dehiscent; disc intrastaminal or rarely extrastaminal, nectariferous; gynoecium 2–5-carpelled, syncarpous, the ovary 2–5-lobed and -loculed, usually rudimentary in staminate flowers, the ovules 2 per locule, anatropous, epitropous, placentation axile, the style 1, usually short, the stigma 2–5-lobed. *Fruits* more or less drupaceous, the pericarp coriaceous to fleshy, ultimately dehiscent by 2–5 valves; pyrenes 1–5, usually 1-seeded; endosperm absent, the embryo usually straight, the cotyledons contortuplicate or flat, usually lobed, the radicle superior.

A family of about 20 genera and 600 species, reaching its greatest development in tropical America, Malaysia, and northwestern Africa. Four genera are known from Panama. Also to be expected from Darién is the genus *Dacryodes* Vahl, the American species of which have been revised by Cuatrecasas (Trop. Woods 106: 46–65. 1957). The evergreen trees of this genus have unisexual 3-merous flowers with 3 connate sepals, 3 free petals, 6 stamens with connivent anthers, and a 2–3-loculed ovary; the fruit is drupaceous, with a single large pyrene, it is "oblong-ovoid or ellipsoid, with a glabrous, carnose, corrugate pericarp when dry, with a rather thin corneous or cartilaginous endocarp, apical stigma and digitate and folded cotyledons" (Cuatrecasas, op. cit., p. 47).

Bark, leaves, and fruits of all members of the family contain fragrant resins that lead many collectors to comment upon the turpentine-like odors of their specimens.

Useful references:

Brizicky, G. K. The genera of *Simaroubaceae* and *Burseraceae* in the Southeastern United States. Jour. Arnold Arbor. 43: 173–186. 1962.

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Cuatrecasas, J. Prima flora colombiana. I. *Burseraceae.* Webbia 12: 375–441. 1957.

Swart, J. J. A monograph of the genus *Protium* and some allied genera. Rec. Trav. Bot. Néerl. 39: 211–446. 1942.

a. Petals free.
  b. Ovary 2–3-lobed and -loculed, the stigma 2–3-lobed; pyrenes 1 (rarely 2) per fruit on the same plant.....1. *Bursera*
  bb. Ovary 4–5-lobed and -loculed, the stigma 4–5-lobed; pyrenes 1–2(–5) per fruit on the same plant.....2. *Protium*
aa. Petals connate below to form a tube.
  c. Sepals and petals 4–5.....3. *Tetragastris*
  cc. Sepals and petals 3.....4. *Trattinnickia*

1. BURSERA

Bursera Jacq. *ex* L., Sp. Pl. ed. 2. 471. 1762, *nom. cons.*

Terebinthus P. Br., Civ. Nat. Hist. Jamaica 345. 1756, non *Terebinthus* P. Mill., Gard. Dict. Abr. ed. 4. 1754.
Simaruba Boehmer *in* Ludwig, Def. Gen. Pl. ed. 3. 513. 1760.
Elaphrium Jacq., Enum. Syst. Pl. Carib. 3. 1760.

Trees or shrubs; bark smooth or rough, the older bark peeling off in thin papery sheets or thick plate-like scales. *Leaves* odd-pinnate, bipinnate, or 1- to many-foliolate, usually crowded at the ends of the branches, completely deciduous during the dry season; leaflets opposite, membranaceous to coriaceous, petiolulate to sessile, the margins entire to toothed. *Inflorescences* axillary raceme-like panicles, appearing just before or simultaneously with to rarely after the new leaves; plants dioecious or polygamodioecious. *Flowers* small, 3–5-merous, usually functionally unisexual; sepals 3–5, connate at least basally, imbricate; petals 3–5, whitish to yellow, longer than the sepals, spreading and recurved, induplicate-valvate; stamens 6–10, the filaments subulate, free, inserted at the base of the disc, the anthers oblong, dorsifixed, smaller and abortive in carpellate flowers; disc annular, 6–10-lobed; gynoecium 2–3-carpelled, the ovary 2–3-lobed and -loculed, ovoid, sessile, small and abortive in staminate flowers, the ovules collateral, pendulous, 2 per locule, the style short, the stigma capitate, 2–3-lobed. *Fruits* drupaceous, subglobular to ellipsoid or obovoid, 2–3-angled, resinous, the exocarp and mesocarp coriaceous, dehiscing at maturity by 2–3 valves; pyrenes usually 1, usually 1-seeded; endosperm absent, the embryo straight or curved, the cotyledons foliaceous, contortuplicate, phanerocotyler.

A tropical and subtropical New World genus of perhaps 100 species, two occuring in Panama. The entire genus is in need of a careful revision like that done for the species of southwestern Mexico by McVaugh and Rzedowski (Kew Bull. 18: 317–382. 1965).

a. Leaflet margins crenate, the rachis winged; flowers 4-merous; fruits dehiscing by 2 valves .....1. *B. tomentosa*
aa. Leaflet margins entire, the rachis not winged; flowers 3- or 5-merous; fruits dehiscing by 3 valves .....2. *B. simaruba*

1. **Bursera tomentosa** (Jacq.) Tr. & Planch., Ann. Sci. Nat. Bot. Sér. 5. 14: 304. 1872. — FIG. 1.

Elaphrium tomentosum Jacq., Enum. Syst. Pl. Carib. 19. 1760.
Terebinthus tomentosa (Jacq.) W. F. Wight *in* Rose, Contr. U. S. Natl. Herb. 10: 122. 1906.
Bursera panamensis Pittier, Jour. Washington Acad. Sci. 11: 229. 1921.

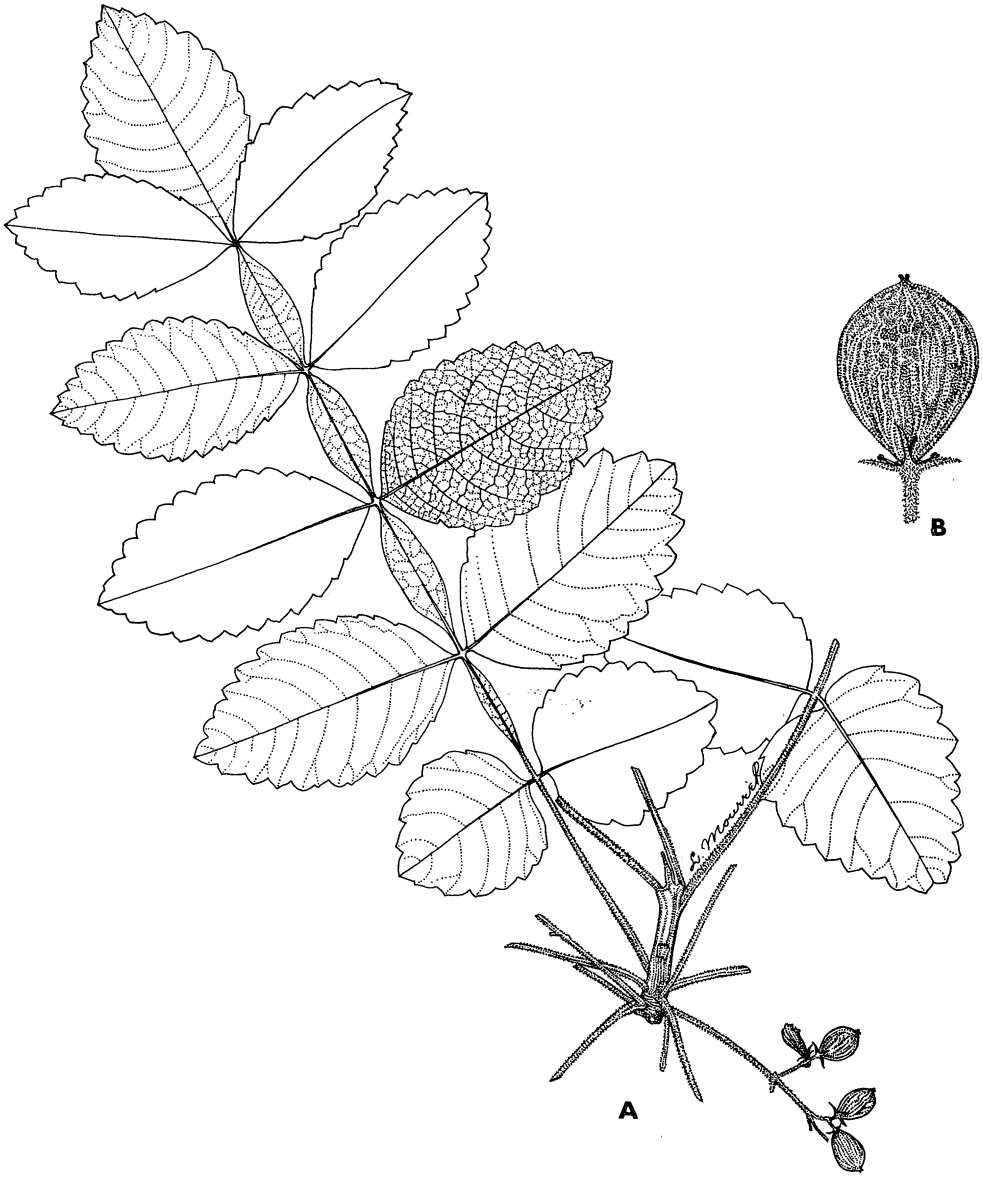

FIGURE 1. *Bursera tomentosa* (Jacq.) *Tr. & Planch.*—*A.* Habit (× 7/10).—B. Fruit (× 2½). [After *Dwyer 1114* (MO).]

Small *trees,* 5–10 m high; bark on the branches red, glabrate; branchlets tomentose, yellowish. *Leaves* odd-pinnate, grayish- or yellowish-tomentose, becoming less so with age, 5–20 cm long; petioles not winged, 10–44 mm long; leaflets (5–)7–11, elliptic to ovate elliptic or lanceolate-elliptic, slightly inequilateral, the laterals rounded to acute apically and obtuse basally, the terminals acute apically and basally, coriaceous, the margins crenate, tomentose and lighter beneath, less pubescent above with shorter trichomes, 27–62 mm long and 14–25 mm wide, the middle pairs usually largest, sessile or with petiolules to 1 mm long; rachis winged, the wing elliptic to oblanceolate, to 9 mm wide. *Inflorescences* tomentose, the staminate 1 cm long, the carpellate 2–6.5 cm long in fruit. *Flowers* 4-merous, with tomentose pedicels 3–6 mm long; staminate flowers with the sepals 4, connate basally, ovate, tomentose, ca. 1 mm long, the petals 4, ovate, pubescent, 1.5 mm long and less than 1 mm wide, thickened slightly and incurved apically, the stamens 8, the filaments less than 1 mm long, those opposite the sepals longer, the disc 8-lobed; carpellate flowers with the sepals 4, acute, 2–3 mm long, persistent in fruit, the stamens often persistent in fruit, the stigma 2-lobed, persistent in fruit. *Fruits* obovoid, glabrous, green, maturing copper-red and drying brown, 7–8 mm long and 5–7 mm in diameter, dehiscing by 2 valves; pyrenes 1, 1-seeded, bony, whitish, ovoid, convex, 6–8.5 mm long and 5–8 mm wide; seed coat black.

Following his description of *Bursera panamensis,* Pittier acknowledged its close relationship to *B. tomentosa.* The holotype specimen of the former falls well within the range of variation exhibited by the later in Panama.

This species occurs in Costa Rica, Panama, Columbia, Venezuela, and the Caribbean islands of Aruba, Bonaire, and Curaçao. In Panama known to flower in May, and to fruit in June through October, and December.

COCLE: Aguadulce, along outskirts of tidal belt, *Pittier 4493* (US, holotype of *Bursera panamensis*). HERRERA: Ocú, edge of 60 year-old forest, *Ebinger 1064* (MO, US). LOS SANTOS: Las Tablas, *Dwyer 1114* (MO). Pocrí, near Las Tablas, *Dwyer 114* (MO). PANAMA: Vicinity of Bejuco, *Allen 1806* (MO); typical dry deciduous scrub, common, *Allen 4515* (MO). Along road from Interamerican Highway to Coronado Beach, thorn forests and secondary thickets, *Duke 11810* (MO). Vicinity of Las Lajas Bridge, Panama National Highway, *Bartlett & Lasser 16644* (MO). Nueva Gorgona, near beach, *Duke 4503* (MO). VERAGUAS: Vicinity of Río Santa María ca. 5 mi. N of Santiago, *Blum & Tyson 617* (MO).

Bursera tomentosa occurs in the deciduous seasonal forests of Pacific Panama, the driest area on the isthmus. "Sometimes used for living fence posts" (fide *Allen 4515*). According to the label on *Blum & Tyson 617,* the fruit has a "lemon-like odor."

2. **Bursera simaruba** (L.) Sarg., Gard. & Forest 3: 260. 1890.

Pistacia simaruba L., Sp. Pl. 1026. 1753.
Bursera gummifera L., Sp. Pl. ed. 2. 471. 1762.
Terebinthus simaruba (L.) W. F. Wight *in* Rose, Contr. U. S. Natl. Herb. 10: 122. 1906.
Elaphrium simaruba (L.) Rose, N. Amer. Fl. 25: 246. 1911.

Trees, 5–20 m high; bark coppery-red, shiny, thin, peeling off in thin papery sheets to expose a smooth bright-green layer; branchlets glabrous to rarely yellow-

ish-woolly, becoming reddish-brown, covered with yellowish lenticels and conspicuously marked by large elevated cordate leaf scars. *Leaves* odd-pinnate, 21–35 cm long and 12–23.5 cm wide; petioles puberulent basally and sparingly pubescent above, or glabrous to rarely yellowish-woolly, 7–11.5 cm long; leaflets 5–7(–9), long-acuminate, inequilateral basally, the laterals broadly ovate to ovate-oblong, the terminals obovate, membranaceous to coriaceous, the margins entire, conspicuously lanate when young to nearly glabrate in age, becoming sparingly pubescent above, at least the veins pubescent beneath, slightly shiny above, paler beneath, the blades 4.5–14.5 cm long and 2.5–8 cm wide; petiolules pubescent to glabrous, 5–31 mm long; rachis not winged. *Inflorescences* usually glabrous, reddish; staminate 17–28 cm long, longer than the young leaves; carpellate 4–10.5 cm long, ca. as long as the young leaves. *Flowers* 3- or 5-merous, with glabrous pedicels 2–4 mm long in flower and 5–16 mm long in fruit; staminate 5-merous, the calyx shallowly 5-lobed, the lobes less than 1 mm long, the petals 5, ovate-elliptic, acute and incurved apically, 2–2.5 mm long and 1 mm wide, the stamens 10, ca. as long as the petals, the filaments 1.5 mm long, the disc 5-lobed; carpellate 3-merous, the calyx lobes 3, the petals 3, ovate, acute and incurved apically, 2 mm long and ca. 1 mm wide, the stamens 6, ca. half as long as the petals, the ovary 3-loculed, ovoid, ca. 2 mm high, the stigma 3-lobed. *Fruits* subglobular, pointed at both ends, slightly 3-angled, green to bright pink, maturing reddish-brown and drying brownish, 8–13 mm long and 7–9 mm in diameter, dehiscing by 3 obovate valves; pyrenes 1(–2), 1-seeded, 3-angled, bony, lenticular-ovoid, pinkish to whitish, attached to the pedicel by a persistent whitish column ca. 2 mm long.

Widespread throughout the Caribbean region, occurring from coastal northeastern Mexico through Central America, and southern Florida through the West Indies, to Panama, Colombia, and Venezuela. In Panama flowering from mid-March to mid-June, and collected in fruit in all months but September.

Bursera simaruba is both widespread and variable. Panamanian collections tend to have leaves and leaflets that are larger than those seen from elsewhere, and there is some variation within the isthmus in terms of leaflet size, shape, and pubescence. However, the combination of a thin, papery, coppery-red, peeling bark, and the complete loss of leaves during the dry season, make this tree immediately recognizable in the field. Perhaps there is more than one taxon represented by what has been called *B. simaruba,* as pointed out by Williams and Cuatrecasas (Trop. Woods 110: 32. 1959), but this cannot be determined until a thorough review is made of the genus.

CANAL ZONE: Barro Colorado Island, shore N of Fuertes House, *Woodworth & Vestal 741* (A); Fuertes Inlet, *Shattuck 1023* (F, MO); shoreline of Miller Peninsula S of Orchid Isle, *Croat 6723* (MO); Peña Blanca Point, *Shattuck 498* (F, MO), shoreline, large cove, *Croat 8372* (MO); S of island (Barro Colorado Island?), *P. White 114* (F, MO). Farfan Beach area, *Tyson 1804* (MO). Fort Amador, on causeway and islands, *Tyson 2023* (MO). Near beach at Fort Kobbe, *Duke 4219* (MO). Seedlings, across street from Gorgas Hospital, *Duke & Bristan 8302* (MO). Madden Dam, second growth, *Ebinger 833* (MO); cut-over area across highway from Small Boat Landing, *Lewis et al. 5297* (MO). Vicinity of Miraflores Lake, moist shaded habitat, *G. White 159* (GH, MO). Sosa Hill, Balboa, brushy slope, occasional, *Standley 26483* (A, US). CHIRIQUI: Progreso, *Cooper & Slater 313* (US). Río San Cristóbal, 2 mi. W of David, alt. 150 ft, *Tyson 920* (MO). COCLE: Penonomé

and vicinity, alt. 50–1000 ft, *Williams 439* (US). DARIEN: Forests around Pinogana, *Pittier 6566* (US). Headwaters of Río Chico, heavy forest, alt. 500–700 ft, *Allen 4644* (MO). Río Pucro, below village of Pucro, *Duke 13117* (MO). HERRERA: Vicinity of Ocú, alt. 100 m, *Allen 4064* (MO). PANAMA: Cermeño, *Dwyer & Robyns 111* (MO). Farfan Beach Road, *Kirkbride & Elias 67* (MO). Isla Espiritu Santo, common, *Duke 10432* (MO). Isla San José, East Harbor, rocky bluffs, *Erlanson 158* (GH, US); Main Beach, rocky coastal bluff, *Erlanson 107* (GH, US); rocky cliffs near sea, *Johnston 63* (GH). Isla Taboga, moist thicket, *Standley 27077* (US); moist wooded slope, common, *Standley 27928* (US); alt. ca. 0–186 m, *Woodson et al. 1503* (A, F, MO). 2 mi. N of La Chorrera, secondary forest, *Lewis et al. 5190* (MO). Near Playa Río Mar, thorn forest, coastal scrub, and *Curatella* savanna, alt. 10–100 ft, *Duke 11781* (US). Río Mar, *Tyson et al. 2306* (US). Roadside savanna between Río Pacora and Chepo, *Dwyer et al. 5114* (MO). Near Río Tapía, Juan Díaz region, *Maxon & Harvey 6638* (US). Near big swamp E of Río Tocúman, wet forest, *Standley 26583* (US). Sabana de Juan Corso, near Chepo, alt. 60–80 m, *Pittier 4670* (GH, US). VERAGUAS: Vicinity of Santa Fé-Río Santa María, alt. 1000 ft, *Allen 4423* (MO).

In Panama *Bursera simaruba* occurs in areas where the vegetation is deciduous seasonal forest, monsoon forest, and evergreen seasonal forest. It appears to be a species of advanced secondary growth.

Seemann (The Botany of the Voyage of *H. M. S. Herald,* p. 118) reported that, "This tree is of middle size; it is used for making fences; the wood is easy to cut, and the sticks, when put into the ground, soon produce young shoots. The gum that exudes from the stem is applied to wounds, and considered to have very beneficial effects." Comments on the labels of many recent collections attest that *Bursera simaruba* still has its uses, both medicinally and as living fence posts.

As is to be expected with a plant both common and economically important, a number of common names have been recorded for *Bursera simaruba.* Those used in Panama are *almácigo* (fide *Cooper & Slater 313* and *Standley 27928*), *carate* (fide *Standley 27928*), *gumbo-limbo* (fide *Woodworth & Vestal 741*), *hue-chi-chi* (fide *Allen 4644*), and *palo mulatto* (fide *Maxon & Harvey 6638*).

2. PROTIUM

Protium Burm. f., Fl. Ind. 88. 1768, *nom. cons.*

Tingulong Rumph., Auct. 54. 1755.
Icica Aubl., Hist. Pl. Gui. Fr. 1: 337. 1775.
Icicopsis Engl. *in* Mart., Fl. Bras. 12(2): 107. 1891.

Trees or shrubs. Leaves alternate, odd-pinnate or rarely 1-foliolate, petiolate; leaflets (1–)3–9(–13), usually distinctly acuminate, the margin usually entire, petiolulate; stipules absent. *Inflorescenses* axillary or rarely subterminal panicles or racemes. *Flowers* 4–5-merous, sessile or pedicellate, functionally unisexual; calyx 4–5-lobed, imbricate, persistent in fruit; petals 4–5, free, usually somewhat fleshy, induplicate-valvate, deciduous; stamens 8–10, slightly reduced and abortive in carpellate flowers, the filaments subulate to setose, free, inserted at the base of the disc, the anthers more or less oblong, dorsifixed to basifixed; disc 8–10-lobed, annular or cupuliform, thick, fleshy, pubescent to glabrous; gynoecium, 4–5-carpelled, the ovary 4–5-lobed and -loculed, ovoid or globose, pubescent to glabrous, abortive in staminate flowers, the ovules 2 per locule, subapical, collateral, pendulous, the style short, the stigma capitate, 4–5-lobed, usually persistent in fruit. Fruit drupaceous, globose to ovoid, ellipsoid, or turbinate, often

somewhat oblique, mesocarp fleshy and resinous, usually dehiscent by 2–5 valves; pyrenes 1–5, smooth, bony, 1-seeded; embryo straight, the cotyledons simple and plano-convex.

A tropical genus of perhaps 100 species, mainly American, but also with species in Madagascar, the Mascarenes, and Asia from India through the Malayan Archipelago. Seven taxa occur in Panama. Most species are South American, but in Panama only the two subspecies of *Protium tenuifolium* (Engl.) Engl. have South American affinities, the other five being Central American.

Protium is a taxonomically difficult genus. Many species have been based on scanty material, and a modern revision is badly needed. Sterile collections are almost impossible to identify to species without fertile material for comparison.

a. Leaves and inflorescences glabrous ..... 1. *P. panamense*
aa. Leaves (at least petioles, rachises, and petiolules) and inflorescences variously pubescent.
  b. Flowers 4-merous, distinctly pedicellate; fruits pedicellate, stipitate.
    c. Pedicels, calices, and petals yellowish-woolly ..... 2. *P. pittieri*
    cc. Pedicels, calices, and petals appressed-pubescent to sparsely puberulent.
      d. Petioles, rachises, and petiolules densely brownish-hirtellous..... 3. *P. costaricense*
      dd. Petioles, rachises, and petiolules minutely puberulent.
        e. Leaflets broadly elliptic to oblong or ovate, abruptly acuminate, acute basally ..... 4. *P. glabrum*
        ee. Leaflets narrowly elliptic, obtuse or obtusely subacuminate, obtuse basally ..... 5. *P. inconforme*
  bb. Flowers 5-merous, subsessile or sessile; fruits sessile, not stipitate.
    f. Inflorescences and calices minutely puberulent... 6. *P. tenuifolium* ssp. *mcleodii*
    ff. Inflorescences and calices ferrugineous-tomentose ..... 7. *P. tenuifolium* ssp. *sessiliflorum*

1. **Protium panamense** (Rose) I. M. Johnston, Contr. Gray Herb. 70: 72. 1924. — FIG. 2.

Icica panamensis Rose, N. Amer. Fl. 25: 260. 1911.

Trees or shrubs, 3–40 m high; branchlets striate, gray-barked, dotted with pale-brown lenticels, youngest parts minutely appressed-puberulent, soon glabrate. *Leaves* odd-pinnate, glabrous, the petioles, rachis, and petiolules often glaucous, 23–60 cm long; petioles striate, canaliculate, swollen apically and basally, 6–12.5 cm long; leaflets 3–7(–9), ovate-lanceolate to oblong, elliptic, or ovate, usually abrupty acuminate, rounded basally, coriaceous, the margins entire and repandous, the laterals inequilateral, 10.5–36.5 cm long and 4–12.5 cm wide, the terminals usually largest, to 38 cm long and 15 cm wide; petiolules striate, the laterals 11–32 mm long, the terminals to 85 mm long. *Inflorescences* compact axillary (occasionally cauliferous?) panicles, or rarely small racemes, branched from the base, glabrous, the carpellate to 7.5 cm long (to 10 cm long in fruit), the staminate to 10.5 cm long. *Flowers* yellow 4(–5)-merous; pedicels absent to 3.5 mm long in staminate flowers, 1–2 mm long in carpellate flowers; calyx cupuliform, 1.5 mm high, glabrous, 4(–5)-lobed, the lobes obtuse, acute apically, spreading; petals 4(–5), triangular, acute, more or less spreading, inflexed-apiculate, the margins papillose, 3 mm long, 1–1.5 mm wide; stamens 8(–10), 2 mm long; disc 8(–10)-lobed; ovary conical, 4(–5)-lobed, glabrous,

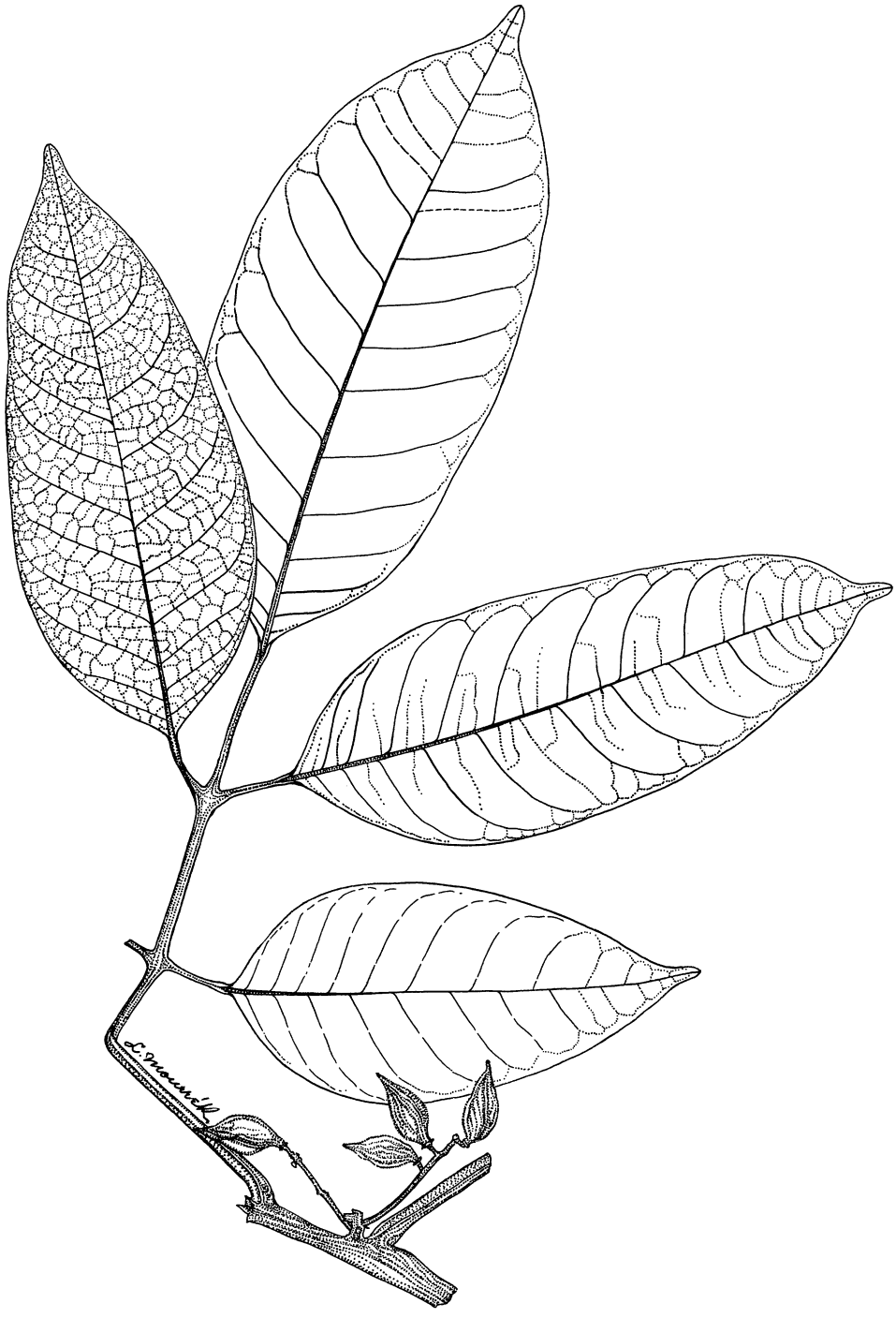

FIGURE 2. *Protium panamense* (Rose) I. M. Johnston, habit (× ½). [After *Tyson & Blum 3755* (MO).]

ca. 1 mm high in staminate flowers, 2 mm high and tapering into the style in carpellate flowers, the stigma 4(–5)-lobed, persistent in fruit. *Fruits* ellipsoid to ovoid, more or less angled when dry, apiculate, stipitate, glabrous, green to yellow, becoming reddish at maturity, the mesocarp thick, white, 17–26 mm long and 9–21 mm in diameter, dehiscing by 2–4 valves, the valves red within; pyrenes 1(–4), white.

Endemic to Panama. Known to flower in January, February, April, July, August, September, and October, but collected in fruit in every month.

BOCAS DEL TORO: Almirante region, Cricamola, *Cooper 517* (F, US); Daytonia Farm, *Cooper 433* (F, GH, US). Vicinity of Chiriquí Lagoon, Darkland, *von Wedel 2625* (GH, MO, US); Fish Creek Hills, *von Wedel 2407* (GH, MO, US); Old Bank Island, *von Wedel 2106, 2115* (both GH, MO, US). Duwebdulup Peak, N of Río Terebe across from Quebrada Huron, alt. 300–900 ft, *Kirkbride & Duke 563* (MO). Vicinity of Río Toro Amarillo, Finca Vieja, alt. ca. 200 m, *Solis Rojas 434* (MO). CANAL ZONE: Agua Clara Reservoir, *Stevens 583* (US). Barro Colorado Island, *Bailey & Bailey 103, 319* (both F), *Brown 34, 38* (both F), *Dwyer 1435* (F, MO), *Kenoyer 677* (US), *Knight 12* (F), *Zetek 3467* (F); shores, *Bangham 405* (A, F, US), *424* (A, F); NE shore, *Salvoza 858* (A); NE to N shore, *Salvoza 884* (A); W side, *Wilson 125* (F, MO); shoreline N of dock, *Croat 7124* (MO); shoreline S of Colorado Point, *Croat 7866* (MO); shore of cove N of Drayton House, *Woodworth & Vestal 559* (A, F, MO); Fairchild Point, *Croat 4832* (MO); bohio at shore of cove S of French Lock Site, *Woodworth & Vestal 462* (A, F, MO); W side of Gross Point Peninsula, *Croat 5087* (MO); forest along shore E of Lab, *Killip 40015* (US); shore 2 mi. E of Lab, *Woodworth & Vestal 490* (A, F, MO); near #8 Light House Clearing, *Croat 6384* (MO); E edge of Orchid Island near French Cut and Gross Point, *Croat 8389* (MO); shoreline of large cove S of Orchid Island near Miller Trail, *Croat 6600* (MO); Salud Point, *Croat 4235* (MO); shore W of Salud Point, *Woodworth & Vestal 425* (A, F, MO); shoreline of E side of large cove E of Slothia Island, *Croat 6067* (MO); shoreline of large cove SW of Slothia Island, *Croat 7350* (MO); E shore of cove S of N tip of Slothia Island, E of dump cove, *Oppenheimer 66-8-11-1337* (MO); Snyder-Molino Trail, *Ebinger 9* (MO, US); Snyder-Molino Trail 1, *Shattuck 1172* (F, MO, US); Snyder-Molino Trail 250, *Croat 4409* (MO). Vicinity of Hill C-6, Camp Pina, Fort Sherman, *Duke 4397* (MO). Road from Fort San Lorenzo to Fort Sherman, *Tyson & Blum 3755* (MO). Frijoles, *Stevens 1269* (US). Gatun Railroad Station, *Hayes 1* (A, F, GH, US; probably isotypes of *Icica panamensis*), *Hayes 462* (US, holotype of *I. panamensis*). Forest along Pavon Road, *Johnston 1540* (A). Sheltered shaded seacliff, mouth of Tortuguilla Creek, *Johnston 1520* (A). COCLE: Boca del Toabré, confluence of Río Toabré & Río Coclé del Norte, advanced secondary forest, *Lewis et al. 5482* (MO). COLON: Camp Betija, Donoso District, alt. 60–150 m, *Holdridge 6256* (MO). Vicinity of Camp Pina, alt. 0–50 m, *Allen 3429* (MO). In forests, Loma de La Gloria, near Fató (Nombre de Dios), alt. 10–104 m, *Pittier 4082* (F, GH, US). SAN BLAS: Isla Pino near Mulatuppo, alt. to 200 ft, *Elias 1717* (MO).

Protium panamense is the most wide-spread species of the genus in Panama, although known only from the Caribbean side of the Continental Divide, and is to be expected in both Costa Rica and Colombia. It occurs in evergreen seasonal forests and monsoon forests. Like *P. glabrum,* it has been reported to have "stilt roots similar to those of *Cecropia*" (fide *Johnston 1540*). According to Dr. Thomas B. Croat (personal communication), "At maturity one valve usually falls exposing the fleshy-white mesocarp, often against the red interior of the other valve." No common names have been recorded by collectors.

2. **Protium pittieri** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica pittieri Rose, N. Amer. Fl. 25. 260. 1911.

Trees or shrubs, to 8 m high; branchlets striate, yellowish-woolly when young, becoming almost glabrate. *Leaves* odd-pinnate, 35–48 cm long; petioles striate,

canaliculate above, yellowish-woolly when young, becoming minutely puberulent, 7.5–17.5 cm long; leaflets 3–7, obovate, ovate, or lanceolate to elliptic, abruptly short-acuminate, the laterals inequilateral basally, subcoriaceous, the margins undulate, yellowish-woolly, becoming glabrate, the midribs becoming minutely puberulent above and beneath, the laterals 16–22 cm long and 7–9.5 cm wide, the terminals 16–23 cm long and 8–13 cm wide; petiolules canaliculate, thickened apically, yellowish-woolly when young, becoming minutely puberulent, the laterals 12–18 mm long, the terminals 38–62 mm long. *Inflorescences* axillary panicles, branched from the base, yellowish-woolly, becoming appressed-pubescent, 1–7 cm long in bud, to 9.5 cm long in fruit. *Flowers* yellow, 4-merous; pedicels yellowish-woolly, ca. 1 mm long; calyx yellowish-wooly, 4-lobed, the lobes triangular, acute; petals 4, yellowish-woolly. *Fruits* oblong, more or less acute apically, stipitate, sparsely appressed-pubescent, brown, with abundant yellowish lenticels, the mesocarp thick, white, 3–4 cm long and 1.5–3 cm in diameter, dehiscing by 2–4 valves; pyrenes 1–2, brownish.

Costa Rica and Panama. In Panama known to flower in November and to fruit in April.

BOCAS DEL TORO: Río Teribe, between Quebrada Huron and Quebrada Schlunjik, *Kirkbride & Duke 462* (MO). Vicinity of Chiriquí Lagoon, Water Valley, *von Wedel 1566* (F, GH, MO).

Protium pittieri occurs in areas of evergreen seasonal forest. The fruits are edible (fide *Kirkbride & Duke 462*).

3. **Protium costaricense** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica costaricensis Rose, N. Amer. Fl. 25: 259. 1911.
Icica confusa Rose, op. cit. 25: 260. 1911.
Protium confusum (Rose) Pittier, Contr. U. S. Natl. Herb. 20: 479. 1922.
Protium salvozae Standley, Jour. Arnold Arbor, 11: 122. 1930.

Trees, 4–8 m high; branchlets densely brownish-hirtellous and minutely puberulent, marked with light lenticels. *Leaves* odd-pinnate, 13–44 cm long, 10.5–24 cm wide; petioles canaliculate, 2.5–6.5 cm long, they and rachises densely brownish-hirtellous and minutely puberulent; leaflets (3–)5–7(–9), elliptic, oblong, ovate, or obovate, slightly inequilateral, abruptly acuminate, cuneate basally, subcoriaceous, margins entire, brownish-hirtellous and minutely puberulent, especially on the veins, becoming glabrate between the veins, the laterals 6–14 cm long and 2.5–6 cm wide, the terminals 8.5–11.5 cm long and 3.5–5.5 cm wide, the lowermost pair smallest; petiolules slightly swollen apically, densely brownish-hirtellous and minutely puberulent, the laterals 5–10 mm long, the terminals 18–26 mm long. *Inflorescences* axillary panicles, few-branched from the base, densely brownish-hirtellous and minutely puberulent, becoming glabrate, 1–5 cm long. *Flowers* yellow, 4-merous; pedicels sparsely puberulent, 1.5–2 mm long, calyx cupuliform, 1 mm high, 4-lobed, the lobes broadly triangular, acuminate, a little shorter than the tube, sparsely puberulent; petals 4 oblong-triangular, the upper half spreading, sparsely puberulent on both surfaces, the margins papillose, inflexed apiculate apically, 3 mm long and 1.5 mm wide; stamens 8, 2 mm high in carpellate flowers, the filaments subulate, dilated

basally; disc 8-lobed, annular, glabrous, less than 1 mm high, surrounding the base of the ovary; ovary ovoid, pubescent, tapering into the style, 1.5 mm high in carpellate flowers, the style persistent in fruit, the stigma 4-lobed. *Fruits* obliquely ovoid, acute, stipitate, puberulent to almost glabrate, the exocarp red, spotted with lighter lenticels, 13–16 mm long and 11–12 mm in diameter; pyrenes 1, white.

Costa Rica and Panama. In Panama known to flower in February and to fruit in May and September.

CANAL ZONE: Barro Colorado Island, wet forest, *Standley 41081* (US); near Cabin 2, *Salvoza 948* (F); clearing at Drayton House, *Croat 5769, 8262* (both MO); shore of cove W of Drayton House, *Woodworth & Vestal 605* (A, F, MO); Drayton House to Armour Cabin, *Bangham 513* (F holotype of *P. salvozae;* A, US, isotypes); Wheeler Trail, 1600, *Croat 6295* (MO).

According to the label on *Croat 8262,* the plant has "no strong odor," and the bark is "like strong sandpaper." It occurs in monsoon forests.

4. **Protium glabrum** (Rose) Engl., Nat. Pfl. ed. 2. 19a: 414. 1931.

Icica glabra Rose, N. Amer. Fl. 25: 259. 1911.
Protium ternatum Pittier, Contr. U. S. Natl. Herb. 20: 478. 1922.
Protium copal var. *glabrum* (Rose) Swart, Rec. Trav. Bot. Néerl. 39: 332. 1942.
Protium copal var. *ternatum* (Pittier) Swart, op. cit. 39: 333. 1942.

Trees, 6–12 m high. *Leaves* odd-pinnate, becoming more or less glabrate, to 30 cm long; petioles canaliculate, minutely puberulent, 2–8.5 cm long; leaflets 3–5(–9), broadly elliptic to oblong or ovate, slightly inequilateral, abruptly acuminate, acute basally, subcoriaceous, minutely puberulent, becoming glabrate, 6.5–19 cm long and 2–8 cm wide; petiolules canaliculate, thickened apically and basally, minutely puberulent, the laterals 8–13 mm long, the terminals 2–5 cm long. *Inflorescences* axillary panicles, slender, branched from the base, usually few-flowered, sparingly appressed-pubescent, 1–13.5 cm long. *Flowers* yellow, 4-merous; pedicels sparingly appressed-pubescent, 2–2.5 mm long; calyx shallowly 4-lobed, the lobes broad and rounded, spreading, sparingly appressed-pubescent, ca. 1 mm high; petals 4, broadly ovate, spreading apically, sparingly appressed-pubescent, pubescent adaxially, the margins papillose, 3 mm long and 1.5 mm wide; stamens 8, the filaments subulate, 1.5 mm long; disc 8-lobed, sulcate, thick, glabrous, covering ca. half the ovary in carpellate flowers and as high as the ovary in staminate flowers, forming a prominent glabrous collar at the base of the fruit; ovary ovoid, appressed-pubescent in carpellate flowers, glabrous in staminate flowers, the stigma 4-lobed. *Fruits* ovoid, apiculate, stipitate, minutely pubescent, especially apically and basally, reddish, the mesocarp pink or white, 11–25 m long and 10–17 mm in diameter; pyrenes (1–)2–3, green.

This inaptly-named species was described by Rose as having glabrous branches, leaflets, and ovaries. However, examination of the holotype specimen [*Tonduz 6682,* Costa Rica (US)] shows this not to be the case.

Costa Rica and Panama. In Panama known to flower in July and August, and to fruit in May, July, and August.

CANAL ZONE: 12 mi. S of Colón, *Tyson et al. 4475* (GH, MO, US). Vicinity of Río Providencia, in forest understory, *Blum & Tyson 2327* (MO). Hills SW of Gatún, in forest, alt. 600 ft, *Johnston 1586* (A, MO). COLON: Achiote, *Tyson et al. 4540* (MO). Along Río Fató above Nombre de Díos, in forests or thickets, alt. 10–100 m. *Pittier 3949* (US), *4190* (US, holotype of *P. ternatum;* GH, US, isotypes), *4191* (F, US). PANAMA: Cerro Jefe, forest edge and road bank, alt. ca. 2900 ft, *Dwyer & Gauger 7339* (MO).

Protium glabrum is found on the Caribbean side of the Continental Divide in areas of monsoon forest and seasonal evergreen forest. In fruits containing two pyrenes, invariably the opposite carpels are fertile, the two between them being sterile.

The label on *Johnston 1586* states that the plant had "*Cecropia*-like stilt-buttresses." Butressing is not uncommon in the Burseraceae, but few New World species have been reported to form them.

5. **Protium inconforme** Pittier, Contr. U. S. Natl. Herb. 20: 478. 1922.

Protium copal var. *inconforme* (Pittier) Swart, Rec. Trav. Bot. Néerl. 39: 333. 1942.

Trees, to 6 m high. *Leaves* odd-pinnate, 8–22 cm long; petioles canaliculate, minutely puberulent, 11–19 mm long; leaflets 3–7, some often missing, narrowly elliptic, slightly inequilateral, obtuse or obtusely subacuminate, obtuse basally, the midvein minutely puberulent above to glabrate, 6–14.5 cm long and 1.5–4 cm wide; petiolules canaliculate, somewhat swollen apically, minutely puberulent, the laterals 2–6 mm long, the terminals 8–24 mm long. *Inflorescences* axillary racemes, branched from the base, few-flowered, minutely puberulent, 6–20 mm long. *Flowers* 4-merous; pedicels appressed-puberulent; calyx appressed-puberulent, ca. 1 mm high, 4-lobed, the lobes broad, short, obtuse; petals 4, spreading apically, appressed-puberulent, pubescent adaxially, inflexed-apiculate, the margins papillose, 2–2.5 mm long and 1–1.5 mm wide; stamens ca. 1 mm high in carpellate flowers; disc glabrous, surrounding the ovary only basally; ovary ovoid, appressed-pubescent, ca. 1 mm high, the style persistent in fruit, the stigma 4-lobed. *Fruits* oblong or ellipsoid to ovoid, apiculate, stipulate, green flushed dull purple, pubescent when young, becoming glabrate except apically, 15–18 mm long and 6–13 mm in diameter; pyrenes 1–2.

Endemic to Panama. Known to flower in March and April, and to fruit in December, February, and March.

CHIRIQUI: Around Caldera, alt. 200–300 m, *Pittier 3350* (US, holotype; F, GH, isotypes). 12.4 mi. N of David, edge of steep river bank, *Lewis et al. 707* (MO). LOS SANTOS: Guanico, forest of espavé, caoba, and cedro espino, alt. 117 ft, *Stern et al. 1840* (MO, US). Ridge W of Río Pedregal, *Holdridge 6237* (MO).

The sterile specimen *Holdridge 6201* (MO) from "LOS SANTOS: Area east of Cambutal on lower hills" is probably this species, but it is impossible to tell from vegetative material alone.

This species is known from southwestern Panama in areas of monsoon forest or deciduous seasonal forest. It is called *chutra* (fide *Holdridge 6237*). This is also the name ascribed to it by Pittier, following his type description.

6. **Protium tenuifolium** ssp. **mcleodii** (I. M. Johnston) D. M. Porter, Ann. Missouri Bot. Gard. 56: 475. 1969[1970].

Protium mcleodii I. M. Johnston, Sargentia 8: 164. 1949.

Trees, 6–16 m high; branchlets somewhat glaucous, minutely puberulent, becoming glabrate. *Leaves* odd-pinnate, 17.5–38.5 cm long and 14.5–28 cm wide; petioles canaliculate, minutely puberulent, soon glabrate, 4–11 cm long; leaflets 7–11, oblong, abruptly acuminate, obtuse and inequilateral basally, membranaceous to subcoriaceous, often minutely papillose, the margins entire, 5–15 cm long and 2–5 cm wide, the lowermost pair smallest and reflexed; petiolules swollen apically and basally, minutely puberulent, soon glabrate, the laterals 4–11 mm long, the terminals to 24 mm long. *Inflorescences* axillary panicles, minutely puberulent; staminate with the branches widely spreading, 6.5–10 cm long and 3.5–7.5 cm wide; carpellate with the branches few, divaricate, 4.5–9.5 cm long. *Flowers* yellowish, 5-merous, subsessile to sessile; staminate with the calyx 5-lobed, less than 1 mm long, the petals 5, 1.5 mm long and ca. 0.5 mm wide, the stamens 10, 1 mm long, the disc 10-lobed, tomentulose; carpellate with the calyx cupuliform, minutely puberulent, 5-lobed, the lobes triangular, less than 1 mm long, subequal to the tube, the petals 5, thick, not reflexed, glabrous, slightly ridged abaxially, inflexed-apiculate, the margins papillose, 2.5 mm long and 1 mm wide, the stamens 10, the disc 10-lobed, tomentulose, the ovary ovoid, tomentulose, immersed in the disc basally, ca. 1 mm high, the stigma 5-lobed, usually persistent in fruit. *Fruits* obliquely ovoid to turbinate, minutely puberulent, becoming glabarate, 13–16 mm long and 8–19 mm in diameter; pyrenes 1(–5).

Endemic to Panama. Known to flower in March, April, May, and November, and to fruit in March, April, May, and July.

DARIEN: Forest near Piriaque, peak 800–1000 ft. alt., *Duke 8061* (MO). PANAMA: San José Island, in forest near thickets, area W of East Loop, *Johnston 586* (GH); vicinity of Goat Farm, near Río Mata Puerco, *Erlanson 186* (GH, US); forest back of Naval Station, *Johnston 420* (GH, US), *562* (GH, MO); edge of thicket, Naval Station Road, *Johnston 557* (GH, holotype; MO, US, isotypes); valley of Río Mata Puerco, *Erlanson 67* (GH); near South Beach, *Erlanson 45* (US); understory tree in *Tetragastris* forest, between South Road & Playa Grande, *Johnston 654* (GH, US). Trapiche Island, *Miller 1880, 1891, 1904* (all US), *Allen 2632* (F, GH).

Protium tenuifolium is a widespread species of northern South America. The two Panamanian subspecies are the northernmost representatives of this taxonomically difficult group.

This subspecies occurs in monsoon forests. Unlike most Panamanian Burseraceae, both flowers and fruits often are found on the same inflorescence. Known as *Conejo* (fide *Miller 1880*).

7. **Protium tenuifolium** ssp. **sessiliflorum** (Rose) D. M. Porter, Ann. Missouri Bot. Gard. 56: 475. 1969[1970].—FIG. 3.

Icica sessiliflora Rose, N. Amer. Fl. 25: 259. 1911.
Protium sessiliflorum (Rose) Standley, Jour. Washington Acad. Sci. 15: 459. 1925.
Protium neglectum var. *panamense* Swart, Rec. Trav. Bot. Néerl. 39: 205. 1942.
Protium neglectum var. *sessiliflorum* (Rose) Swart, op. cit. 39: 385. 1942.

Trees, 5–18 m high; branchlets brown, glabrous, dotted with paler lenticels. *Leaves* odd-pinnate, 31–48 cm long; petioles canaliculate, sparsely puberulent, soon glabrate, 7.5–13 cm long; leaflets 5–9(–13), oblong to oblanceolate, obovate, or ovate, inequilateral, abruptly acuminate, acute to obtuse basally, coriaceous, glabrous, usually minutely papillose, the margins undulate, 10–27 cm long and 5–12 cm wide, the basal pair usually reflexed; petiolules thickened apically and sometimes basally, sparsely puberulent, the laterals 6–30 mm long, the terminals 20–67 mm long. *Inflorescences* axillary panicles, the branches spreading, ferrugineous-tomentulose; staminate 11–24.5 cm long and to 16 cm in diameter; carpellate stout, branched from the base, 6–16 cm long and to 6.5 cm in diameter. *Flowers* 5-merous, sessile; staminate with the calyx 5-lobed, 1 mm high, ferrugineous-pubescent, the petals 5, lanceolate, glabrous, somewhat keeled abaxially, inflexed-apiculate, the margins papillose, 2.5–3 mm long and ca. 1 mm wide, the stamens 10, the filaments subulate, 1 mm long, the disc 5-lobed, ferrugineous-tomentose; carpellate with the disc ferrugineous-tomentose, the ovary 5-lobed, the stigma 5-lobed, persistent on the fruit. *Fruits* ovoid, somewhat oblique, fleshy, 2–5-lobed, sessile, green, maturing red, tomentulose when young, becoming glabrate except apically, dotted with minute ferrugineous papillae, the mesocarp white, 12–16 mm high and 8–20 mm in diameter, dehiscing by 2–5 valves; pyrenes 1(–5).

Costa Rica and Panama. In Panama known to flower from January through May and in September, and to fruit in February and May through September.

CANAL ZONE: Barro Colorado Island, *Bailey & Bailey 294* (F, holotype of *P. neglectum* var. *panamense*), *Dwyer 1470*, *Tyson 4204* (both MO); wet forest, *Standley 40984* (US); NE to N shore, *Salvoza 888* (A); W side on shore, *Wilson 134* (MO); large cove N of dock, *Croat 6099* (MO); along shore E of dock, *Ebinger 217* (MO, US); shoreline S of Colorado Point, *Croat 8754* (MO); shoreline between small cove N of dock and Fairchild Point, *Croat 6233* (MO); Gatun Lake to point where one turns from Canal, *Bangham 427* (A, F); frequent near Laboratory, etc., *Kenoyer 422* (US); shoreline from tip of Pearson Trail peninsula SW to third large cove, *Croat 5404* (MO); shoreline, Peña Blanca Bay, *Croat 8309* (MO); second cove E of Slothia Island, *Croat 5151* (MO); Wheeler Trail, *Starry 125* (MO), *139* (F). Roadside woods, George Green Memorial, Madden Forest, *Dwyer & Elias 7523* (MO). Road K-9, along Río Cocolí, *Stern et al. 10* (GH, MO, US). CHIRIQUI: Progreso, *Cooper & Slater 259*, frequent in upper part of understory, *169* (both F, US). DARIEN: Piriaque, camp at river, *Tyson et al. 4743* (MO); forest 1–4 mi. N of Pucro, *Duke 13022* (MO); Río Tuqueza below Quebrada Venado, *Bristan 1082* (MO); cuipo forests near Santa Fé, *Duke 12895* (MO). PANAMA: Rocky slopes along Río Chagres above Alhajuela, alt. 30–100 m, *Pittier 3522* (US). Woods along Panamerican Highway ca. halfway between El Llano and Río Mamoní, *Duke 5628* (MO.).

This wide-ranging subspecies occurs in areas of monsoon forest and seasonal evergreen forest. Common names reported are *anime* (fide *Standley 40984*), *chutras* (fide *Cooper & Slater 169*), and *comida del mono* (fide *Cooper & Slater 259*).

3. TETRAGASTRIS

Tetragastris Gaertn., Fruct. Sem. Pl. 2: 130. 1790.

Hedwigia Swartz, Prodr. Veg. Ind. Occ. 4. 1788, non *Hedwigia* Beauv., Mag. Encycl. 5: 304. 1804, *nom. cons.*

Trees or shrubs. *Leaves* alternate, odd-pinnate, membranaceous to coriaceous; leaflets 5–11, acuminate apically, the laterals inequilateral basally, the margins

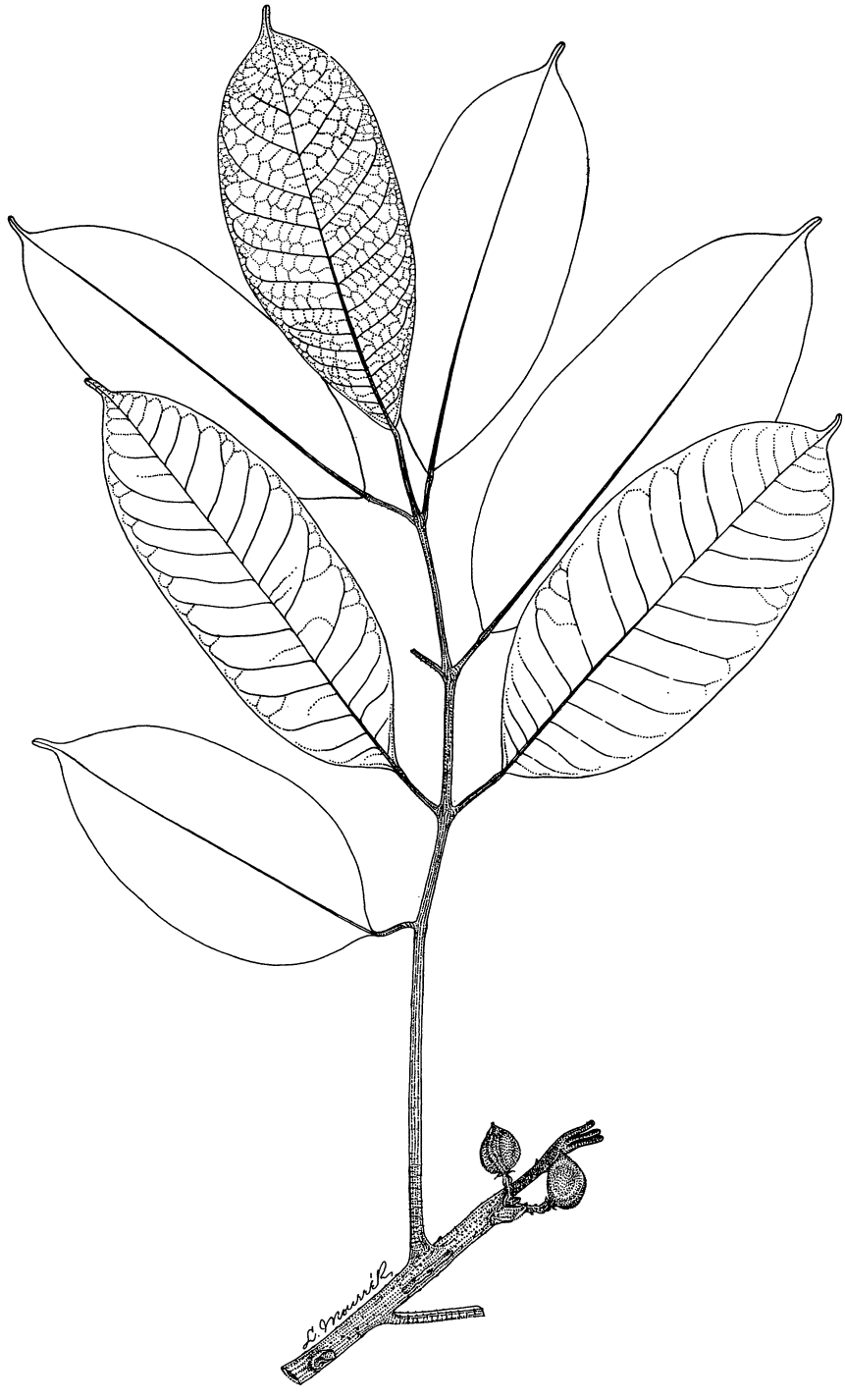

FIGURE 3. *Protium tenuifolium* ssp. *sessiliflorum* (Rose) D. M. Porter, habit (× 3/8). [After *Tyson 4204* (MO).]

entire. *Inflorescences* axillary to subterminal or terminal panicles, shorter than the leaves; plants dioecious or polygamous. *Flowers* small, 4–5-merous, calyx synsepalous, cupular, 4–5-lobed, lobes short, equal, imbricate, and persistent in fruit; corolla sympetalous, tubular, fleshy, 4–5-lobed, lobes alternating with the calyx-lobes, equal, induplicate-valvate, inflexed-apiculate; stamens 8–10, the filaments free or rarely adnate to the petals, inserted at the base of the disc, the anthers introrse, dehiscing longitudinally; disc thick, fleshy, glabrous, 8–10-lobed; gynoecium 4–5-carpelled, the ovary 4–5-lobed and -loculed, partly immersed in the disc, the ovules apical, pendulous, 2 per locule, the style short, the stigma 4–5-lobed. *Fruits* drupaceous, valvate, 2–5-lobed, 1–5-loculed, the exocarp coriaceous, the mesocarp thick and resinous, septicidally dehiscent; pyrene 1–5, smooth, woody, 1-seeded, separated by a distinct layer of mesocarp; endosperm absent, the cotyledons simple, plano-convex.

A Neotropical genus of about a dozen species occuring from Brazil northward through the West Indies to Hispaniola and through Central America to British Honduras. Two species are known from Panama.

a. Flowers 5-merous; leaves sparingly pubescent ..... 1. *T. panamensis*
aa. Flowers 4-merous; petioles and the midveins of the leaflets densely yellowish-tomentose ..... 2. *T. tomentosa*

1. **Tetragastris panamensis** (Engl.) O. Kuntze, Rev. Gen. Pl. 1: 107. 1891. —FIG. 4A–C.

Hedwigia panamensis Engl., Bot. Jahrb. Syst. 1: 42. 1881.
Tetragastris stevensonii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 4: 216. 1929.
Tetragastris panamensis var. *hirtella* Swart, Rec. Trav. Bot. Néerl. 39: 207. 1942.

Trees or rarely shrubs, 3–35 m high; crown widely-spreading; branches grayish, the branchlets densely yellowish-puberulent when young, becoming glabrate and reddish and dotted with elliptical reddish lenticels when older. *Leaves* 15–37 cm long; petioles striate, with scattered minute trichomes, canaliculate above, broadened basally, 4–14 cm long; leaflets 7–9(–11), coriaceous, sparingly pubescent, 5–21 cm long and 17–72 mm wide, the terminals oblong to oblanceolate or elliptic, broadly obtuse to long-acuminate apically, usually larger, the laterals oblong-lanceolate, long-acuminate, inequilateral basally, the lowermost pair smallest and often reflexed; petiolules sparingly pubescent, canaliculate above, swollen apically and/or basally, the laterals 2–12 mm long, the terminals 12–45 mm long. *Inflorescences* axillary, loosely-branched, slender to spreading, yellowish-puberulent, 3–15 cm long; buds yellow, sometimes tinged with red. *Flowers* whitish to greenish-yellow or yellow, 5-merous; pedicels yellowish-puberulent, ca. 1 mm long; calyx broadly cupular, shallowly lobed, yellowish-puberulent, 2–2.5 mm wide and 1–1.5 mm high, the lobes 5, broadly rounded, spreading a little; corolla yellowish, densely yellowish-puberulent without, glabrous within, 3–5 mm long, the lobes 5, thick, acute, 1–2 mm long; stamens 10, 1 mm long, ca. ½ as long as the corolla tube, covering the ovary in carpellate flowers, the filaments short, inserted at the base of the disc between the lobes, the anthers sagittate, 3–5 times as long as the filaments, smaller and abortive in carpellate flowers; disc annular, 10-lobed, as high as the filaments; ovary

ovoid, 5-lobed, 5-loculed, 1.5 mm in diameter, sparingly pubescent, and reaching to above the stamens in carpellate flowers, pyramidal, glabrous, and abortive in staminate flowers, surrounded basally by the disc, the style pyramidal, ca. 1

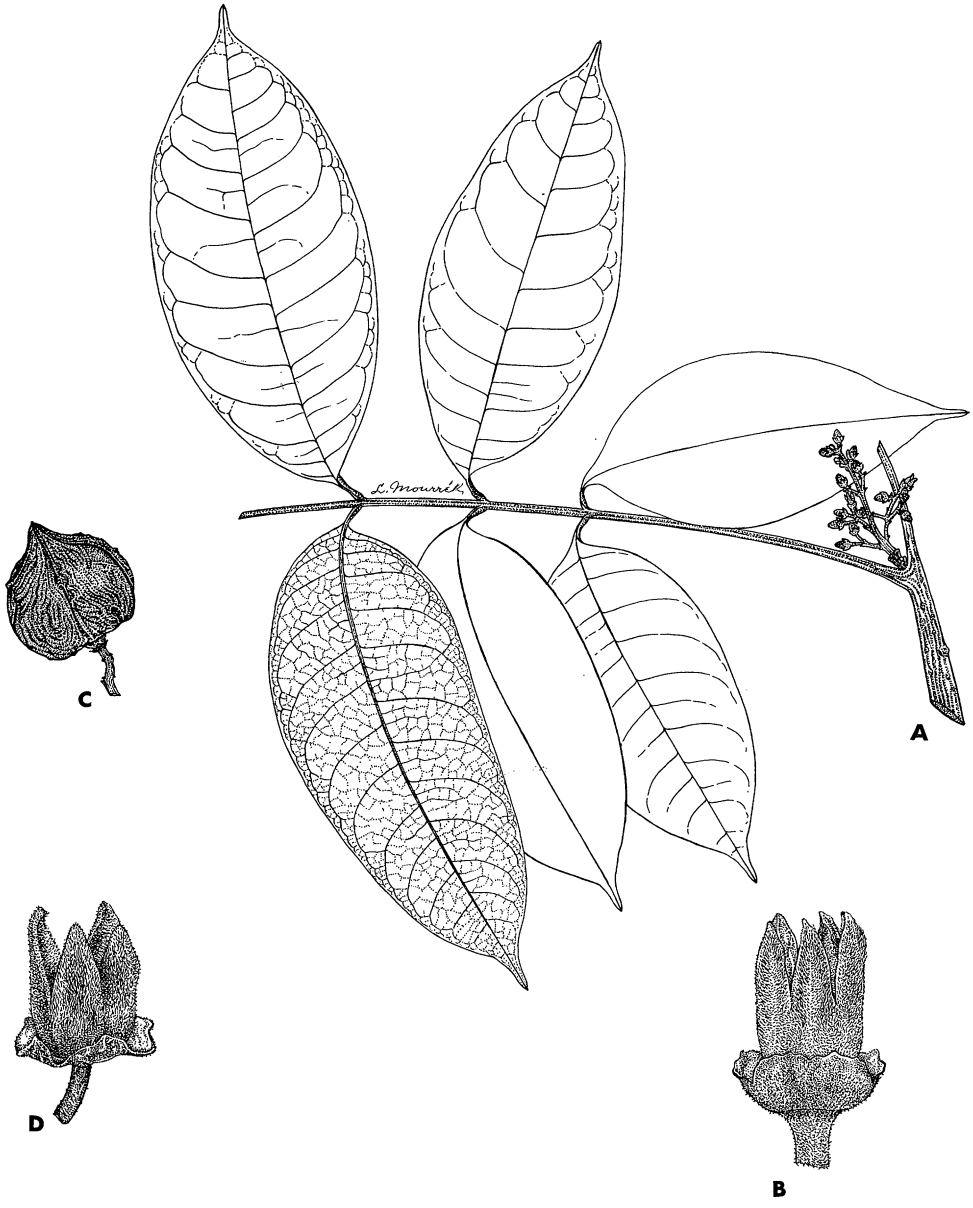

FIGURE 4. *Tetragastris*.—A–C. *T. panamensis* (Engl.) O. Kuntze.—*A*. Habit (× ⅔). —B. Flower (× 6½).—C. Fruit (×2⅓). [A, after *Stern et al. 520* (MO); B, after *Dwyer 1669* (MO); C, after *Holdridge 6250* (MO).]—D. *T. tomentosa* D. M. Porter, flower (× 6½). [D, after *von Wedel 2398* (MO).]

mm high, persistent on the fruit, the stigma 5-lobed, spherical. *Fruits* fleshy when immature, becoming broadly more or less turbinate capsules, 2–5-lobed, 1–5-loculed, 1.5–2.5 cm high and 1.5–3 cm in diameter, broadest above the base and sloping toward the obtuse apex, attached to the pedicel at the middle of the centrally depressed broader end, usually slightly ridged between the lobes, dehiscent by 2–5-valves, the interior surfaces of the valves red, the exocarp green, becoming purplish, red, or brown, mesocarp reddish, white at dehiscence, firm, gelatinous, 1–2 mm thick, sparingly hirtellous to usually glabrate; pyrenes 1–5, smooth, white, 12–13 mm high.

Tetragastris panamensis var. *hirtella* was erected by Swart on the basis of the presence of hirtellous ovaries and fruits. However, the examination of a large series of specimens of *T. panamensis*, from both Central and South America, shows that this trait does not warrant taxonomic recognition. All ovaries examined were pubescent in carpellate flowers and glabrous in staminate flowers, while fruits ranged from sparingly hirtellous to usually glabrate.

This species occurs in British Honduras, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, the Guianas, Brazil, and Peru. In Panama it is known to flower in June, July, August, October, and December, and to bear fruit in all months but December.

CANAL ZONE: Barro Colorado Island, *Kenoyer 426A* (US), *Shattuck 631* (MO); Fuertes Cove, *Croat 8122* (MO); shoreline of large cove leading to Fuertes House, *Croat 6823, 6839* (both MO); E shore of cove S of N tip of Slothia Island, *Oppenheimer 66-3-28-1358* (MO); Snyder-Molino Trail 325, *Croat 6739, 8081* (both MO), 50 m N of trail, *Croat 8101* (MO). Coco Solo, dense woods with man-made drainage ditches, *Dwyer & Duke 7874* (MO). Near beach at Fort Kobbe, wooded S slope facing ocean, *Duke 4729* (MO). COCLE: Penonomé and vicinity, alt. 50–1000 ft, *Williams 201* (US). COLON: Donoso district, Camp Betija, alt. 60–150 m, *Holdridge 6250* (MO). DARIEN: Vicinity of Cana, alt. 2500 ft, *Stern et al. 520* (GH, MO, US). Piriaque, camp at river, *Tyson et al. 4747* (MO); forest near Piriaque, peak 800–1000 ft high, *Duke 8060* (MO); Pico Piriaque, *Duke 8150* (MO). Vicinity of Piñas, *Duke 10596* (MO). Forest 1–4 mi. N of Pucro, *Duke 13042* (MO). Puerto Santa Dorothea, *Dwyer 2214* (MO, US). Punta Guayabo Chiquita, steep hills near shore, *Stern & Chambers 164* (A, F, MO, US). Río Pucro, below Pucro, *Duke 13121* (MO). PANAMA: E slope of Cerro Jefe, in *Clusia* forest, alt. 2700 ft, *Tyson 3388* (GH, MO). El Cermeño, *Zetek 4997* (F, MO). Isla Espiritu Santo, *Duke 10447* (MO). Juan Díaz, moist thicket, *Standley 30647* (US). Vicinity of Pacora, alt. 0–20 m, *Allen 3451* (GH, MO, US). Gallery forest along Río Terable, near Panamerican Highway and El Llano, *Duke 5662* (MO). San José Island, *Johnston 658* (GH); thickets bordering Bald Hill, *Erlanson 300* (GH, US); Loop at Little Butch, *Johnston 911* (GH); Loop Road, dominant forest tree in Marino Basin, *Johnston 202* (GH); along stream in M-area, *Johnston 4* (GH, US); road SW of Red Hill, *Johnston 138* (GH, MO, US); Río Marino below Red Hill, along stream, *Johnston 555* (GH, US); valley of Río Marino, Area 7a, *Erlanson 342* (GH, US); N fork of Río Marino, moist dense forest along stream, *Johnston 398* (GH); between South Road and Playa Grande, forming forest, *Johnston 275* (GH, MO). SAN BLAS: Without locality, *Cooper 290* (GH). Chucunaque, 2–10 mi. above Cuna-Darién boundary, *Duke 8571* (MO). Permí, *Cooper 265* (F, US). VERAGUAS: Canazas, bank of Río Canazas, *Tyson 3633* (MO). Isla de Coiba, *Dwyer 1633* (F, GH), *1669, 2320A* (both MO), 2327 (GH). Vicinity of Río Santa Maria, ca. 5 mi. N of Santiago, *Blum 625* (MO). WITHOUT LOCALITY: *Duchassaing*, 1851 (GH).

According to Johnston (Sargentia 8: 165. 1949), *Tetragastris panamensis* is an important forest tree on San José Island, where it may make up more than half of the canopy layer in both small or large tracts of forest. It is widespread in Panama, having been collected mainly on the Pacific side of the Continental

Divide. It occurs in areas of evergreen seasonal forest, monsoon forest, and deciduous seasonal forest.

The fruits of this species usually are described as indehiscent. The fruits are fleshy when immature, but they dehisce by from two to five valves when mature. Johnston (Sargentia 8: 166. 1949) gives a detailed description of the fruits of *Tetragastris panamensis*.

Common names reported for *Tetragastris panamensis* in Panama are *animé* (fide *Stern & Chambers 164*), *cedro macho* (fide *Duke 10596*), *fruta de loro* (fide *Duke 8060*) and *secuadro* (fide *Duke 8150*). A number of collectors have remarked on the aromatic sap of this species, and the label on *Johnston 275* states, "Fruit and herbage with a pleasant rather spicy terpentine odor." According to the label on *Duke 10596*, the fruits (probably the mesocarp only) are edible.

2. **Tetragastris tomentosa** D. M. Porter, Madroño 20: [in press]. — FIG. 4D.

A *tree* ca. 8 m high; branchlets densely yellowish-tomentose. *Leaves* 37 cm long or longer and to 24.5 cm wide; petioles striate, densely yellowish-tomentose, canaliculate above, 84 mm long; leaflets 7(?), membranaceous, elliptic to ovate, abruptly acuminate, slightly inequilateral basally, the main vein densely yellowish-tomentose below, minutely puberulent above, the secondary veins and blade with scattered trichomes on both surfaces, to 18.5 cm long and 9 cm wide, the laterals largest, the lowermost smallest and reflexed; petiolules densely yellowish-tomentose, canaliculate above, swollen apically, the laterals 15–24 mm long, the terminals 48–59 mm long. *Staminate inflorescences* axillary, branched from the base, spreading, densely yellowish-tomentose, to 19 cm long. *Staminate flowers* cream-yellow, 4-merous; pedicels sparsely yellowish-tomentose, 1.5–3 mm long; calyx broadly cupular, sparsely yellowish-tomentose, ca. 1 mm high and 2.5 mm wide, the lobes 4, acute, spreading; corolla yellowish, densely yellowish-tomentose without, pubescent within, ca. 3 mm long, the lobes 4, thick, acute, 1–1.5 mm long and ca. 1 mm wide; stamens 8, ca. as high as the corolla tube, the filaments subulate, inserted at the base of the disc between the lobes, the 4 opposite the sepals adnate basally to the corolla below the clefts, the anthers sagittate, basifixed; disc sulcate, 8-lobed, half as high as the ovary; ovary tomentose, ovoid, ca. 1 mm in diameter, half immersed in the disc, the style columnar. *Fruits* unknown.

Known only from the type collection.

BOCAS DEL TORO: Fish Creek Hills, *von Wedel 2398* (MO, holotype; F, GH, isotypes).

4. TRATTINNICKIA[3]

Trattinnickia Willd., Sp. Pl. ed. 4. 4: 887. 1805.

Trees, bark with resinous ducts. *Leaves* alternate, odd-pinnate, scattered, chartaceous to coriaceous; leaflets 5–19, opposite, acuminate apically, margins

[3]Swart, and most other botanists, have spelled this name *Trattinickia*. However, as Little (Phytologia 18: 410. 1969) has indicated, Willdenow used the spelling *Trattinnickia* in his original publication of the genus. The genus is named for the Austrian botanist Leopold Trattinnick (1764–1849), usually spelled Trattinick in the botanical literature. According to Barnhart (Biographical Notes Upon Botanists. 3: 398. 1965), "Pritzel and Neilreich spell this name Trattinick [as does F. A. Stafleu, Taxonomic Literature. 1967]; but on all his books and papers it appears invariably Trattinnick."

entire to sinuous, the laterals inequilateral basally. *Inflorescences* axillary to subterminal or terminal panicles or thryses; plants dioecious or polygamous to monoecious. *Flowers* small, 3-merous, calyx synsepalous, irregularly 3-lobed, imbricate, the lobes persistent in fruit; corolla sympetalous, fleshy, more or less tubular, 3-lobed, induplicate-valvate, inflexed-apiculate; stamens 6, the filaments short and dilated, free, inserted on the base of the disc in staminate flowers and on the disc margin in carpellate flowers; disc annular, 6-lobed; gynoecium 3-carpelled, the ovary 2–3-lobed and -loculed, fleshy, surrounded basally by the disc, abortive in staminate flowers, the ovules apical, pendulous, 2 per locule. *Fruits* drupaceous, the exocarp membranaceous, the mesocarp thick and resinous; pyrenes (1–)2, 1-seeded, corregated, thick, and woody, nearly connate, separated only by a thin layer of mesocarp; endosperm absent, the cotyledons contortuplicate.

A Neotropical, mainly South American, genus of about ten species occurring from Brazil and Peru northward to Panama and the West Indian island of St. Vincent. Two species occur in Panama. *Trattinnickia panamensis* Standley & Williams, described from Bajo Chorro, Chiriquí, is a member of the genus *Guarea* (Meliaceae). It is probably a synonym of *G. tonduzii* C. DC.

a. Leaflets scabrous, rough to the touch; inflorescences sparsely hispidulous. . . . 1. *T. aspera*
aa. Leaflets glabrous, not rough to the touch; inflorescences puberulent. . . . 2. *T. burserifolia*

1. **Trattinnickia aspera** (Standley) Swart, Rec. Trav. Bot. Néerl. 39: 426. 1942. — FIG. 5.

Protium asperum Standley, Trop. Woods 8: 4. 1926.

Trees, 15–50 m high, bark fragrant. *Leaves* scabrous, to perhaps 1.5 m long; petioles striate, canaliculate above, 8–29 cm long; leaflets 7–11(–19), ovate or ovate-lanceolate to oblong or elliptic, laterals slightly inequilateral, narrowly to broadly acuminate, cuneate to cordate basally, the margins repand to sinuous, chartaceous to coriaceous, scabridulous on both surfaces, sparingly hispidulous below, the veins more so, the lateral veins prominent below, 10–31 cm long and 4–12.5 cm wide, the middle pairs largest; petiolules hispidulous, the laterals 3–7 mm long, the terminals 29–46 mm long. *Inflorescences* axillary panicles, the peduncles and branchlets angled, striate, and sparsely hispidulous, 12–20 cm long in fruit. *Flowers* with the pedicels angled, hispidulous, 4–13 mm long in fruit, the androecium and gynoecium unknown. *Fruits* rhomboid, ridged, glabrous, acute apically, green to greenish-brown, 9–12 mm long and 8–11 mm in diameter; pyrenes 2, separated by a thin line of mesocarp, 1-seeded.

Trattinnickia aspera apparently is endemic to Panama. Known to fruit from November through April; the flowers are unknown, flowering specimens apparently never having been collected. However, the stiff scabrous leaves readily identify this species even when sterile.

BOCAS DEL TORO: Near Almirante, United Fruit Company Fruit Dale Farm, abundant, *Seibert 1589* (MO). CANAL ZONE: Barro Colorado Island, *Kenoyer 674* (US); wet forest, *Standley 40815* (US), *41161* (US, holotype; US, isotype), *Zetek 5088* (F, MO, US); Pearson Trail 500, *Croat 4137* (MO); Snyder-Molino Trail, *Shattuck 769* (F, MO); forest SW of Lab Clearing 100 ft N of Snyder-Molino Trail, *Croat 7674* (MO). PANAMA: Río Indio drainage ca. 9 mi. E of Transisthmian Highway, rain forest, medium slope, clay loam soil, alt. 800 ft, *Barbour 1056* (F, US).

The three areas from which this species is known are all on the Caribbean side of the Continental Divide. It apparently grows in monsoon forest and evergreen seasonal forest.

The collection *Barbour 1056* has been cited as a paratype of *Trattinnickia barbourii* Little (Phytologia 18: 410. 1969), the holotype of which is from Ecuador. However, the Panamanian collection falls under the range of variation exhibited by *T. aspera*. The Ecuadorian collection has not been seen.

Common names reported for *Trattinnickia aspera* are *caraña* (fide *Barbour 1056*) and *caraño* (fide *Standley 40815*). The labels of several collections men-

FIGURE 5. *Trattinnickia aspera* (Standley) Swart.—A. Leaf (× 3/8). B. Infructescence (× 3/8). [A, after *Croat 4137* (MO); B, after *Croat 7674*. (MO).]

tion the fragrant resin of the bark, and that on *Standley 40815* states that the tree "exudes large amounts of fragrant balsam that is gathered for market."

2. **Trattinnickia burserifolia** Mart., Nov. Gen. Sp. Pl. 3: 93. 1829.

Tree, to 30 m high; branchlets dark, puberulent, provided with lanceolate grayish lenticles. *Leaves* 18.5–28 mm long; petioles minutely puberulent, thickened basally, 3.5–7.5 cm long; leaflets 5–11, oblong to elliptic, the laterals inequilateral, abruptly acuminate, narrowly cuneate basally, the margins entire, coriaceous, glabrous, smooth and lustrous above, duller beneath, 7–12 cm long and 3–4 cm wide, the lowermost pair smallest; petiolules striate, minutely puberulent, the laterals 3–6 mm long, the terminals to 12 mm long. *Inflorescences* axillary or subterminal thryses, branched from the base, puberulent, the branches spreading, 7–13 cm long in fruit. *Flowers* with the pedicels puberulent, 2–3 mm long in fruit; "3-merous, 3–4 mm long and 2–2.5 mm in diam. Calyx cupuliform, nearly half as long as the flower; its lobes triangular, obtuse, as long as the tube. Corolla tubular, outside papillose, inside glabrous but near the apex provided with some hairs, carnose, red; its lobes ovate-triangular, acute, about as long as the tube. Stamens in the masc. fl. as long as the tube of the corolla, in the fem. fl. shorter; filaments very short, much dilated; anthers elliptic, apiculate. Disc annular, 6-lobed, glabrous, 0.25 mm high. Pistil glabrous, in the masc. fl. forming with the disc a hardly 1 mm high cone, in the fem. fl. 2 mm high; ovary conical ovoid, 1.5 mm high; stigma 2-lobed, sessile." *Fruits* globose, glabrous, the exocarp brown, thin, slightly wrinkled, 6–7 mm in diameter.

This species is known from Panama, Colombia, Venezuela, the Guianas, Brazil, and the West Indian island of St. Vincent. The single collection known from Panama is in fruit (September), and the floral description above is taken from Swart (Rec. Trav. Bot. Néerl. 39: 432. 1942).

COCLE: Region N of El Valle de Antón, alt. 1000 m, 30 m high, *Allen 3725* (F, GH, MO).

The fruits on this collection have been damaged by insects, but leaf characters definitely place it as *Trattinnickia burserifolia.*

INDEX OF LATIN NAMES

Numbers in **bold face** type refer to descriptions; numbers in roman type refer to synonyms; numbers with dagger (†) refer to names incidentally mentioned.