

In Panama, known principally from tropical moist forest in the Canal Zone (both slopes), all along the Atlantic slope, and in Darién; known also from premontane wet forest in Colón and Darién.

See Fig. 380.

Doliocarpus multiflorus Standl., J. Wash. Acad. Sci. 15:285. 1925

Liana; all but the youngest stems with thin, flaky bark. Petioles 1–2.5 cm long, canaliculate; blades obovate to elliptic, abruptly acuminate, mostly acute at base, 9–25 cm long, 3.5–10 cm wide, glabrous above, at first appressed-pubescent on veins below, the axils often tufted, glabrate in age. Cincinni axillary or borne on leafless stems, fasciculate, the axes pubescent; flowers few, pedicellate, 7–9 mm broad; sepals 5, ± rounded and concave, glabrous to slightly pubescent on both surfaces; petals 3 or 4, white, 3–5 mm long, soon falling; stamens many, persistent, ca 5 mm long; ovary 1, glabrous to slightly pubescent; style 1–2 mm long; stigma peltate. Fruits globose, ca 1 cm diam, red or purplish-red, often with sparse, ± appressed trichomes, splitting regularly into 2 valves; seeds 2. *Croat 9507, 13488.*

Apparently uncommon in flower; seen both along the shore and in the vicinity of the Laboratory Clearing where sterile plants are frequent in the canopy. Seasonal behavior poorly known. Flowers from January to March (sometimes to April). The fruits probably mature mostly in April and May.

Sometimes confused with specimens of *D. major*, but may be distinguished by lacking punctate leaves and having glabrous fruits. This species was reported by Standley as *D. multiflorus* Standl., but that name was considered synonymous with *D. guianensis* (Aubl.) Gilg. by Hunter in the *Flora of Panama* (1965). Kubitzki (1971) considered *D. multiflorus* and *D. guianensis* as distinct species, however, with *D. guianensis* restricted to Venezuela and the Guianas. *D. guianensis* is distinguished by having a pubescent ovary.

Belize to Panama; Cuba. In Panama, known only from tropical moist forest in the Canal Zone (Atlantic slope) and Colón, though very likely to be found on the Pacific slope in Darién.

Doliocarpus olivaceus Sprague & L. O. Wms. ex Standl., Contr. U.S. Natl. Herb. 27:265. 1928

Liana; stems and leaves glabrate. Petioles 1–3 cm long, often narrowly winged, slightly enlarged at base; blades oblong-elliptic to oblong-obovate, acuminate, acute to obtuse at base, 8–22 cm long, 4–9 cm wide, subentire to obscurely dentate. Fascicles small, axillary, usually on defoliated stems; pedicels 4–10 mm long; sepals 3 or 4 (sometimes to 6), irregular, mostly rounded or ovate, concave, glabrous outside, appressed-pubescent inside; petals 2 or 3 (sometimes to 5), obovate, 10–15 mm long, 6–10 mm wide, pale yellow, soon falling; stamens 35–60, to 7 mm long, deciduous; anthers ca 1 mm long; ovary subglobose, densely pubescent with stiff straight tri-

chomes; style glabrous, to 7 mm long. Fruits globose, 1.5–2 cm diam, red at maturity, densely puberulent and with sparser hispid trichomes, dehiscent into 2 valves at maturity, the valves fleshy, flattening out, splitting irregularly at about the middle and spreading widely; seeds 2, mostly enveloped by a fleshy white aril. *Croat 6820, 14873.*

Occasional in the forest and at the edge of the lake; common in the canopy at least in the vicinity of the Laboratory Clearing. More abundant in the old forest than any other *Doliocarpus*. Flowers chiefly in May and June. The fruits mature from August to December, especially in September and October.

The manner of dehiscence of the fruit is probably unique among *Doliocarpus* in Panama. The fruits are larger than those of any other species of the genus in Panama.

Known only from Panama, from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

See Figs. 381 and 382.

SAURAUIA Willd.

Saurauia laevigata Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 18:267. 1862

S. zetekiana Standl.

Tree, 5–30 m tall; stems with prominent leaf scars; younger parts and axes of inflorescences sparsely to densely stellate-pubescent. Petioles 1–3 (9) cm long; blades ± elliptic to obovate, acute to abruptly acuminate, obtuse at base, 6–22 cm long, 2–10 cm wide, glabrous but with sparse, scalelike, stellate trichomes often on veins, the margins serrate to serrulate, the midrib usually arched, the lateral margins held somewhat erect. Inflorescences thyriform, from upper axils, to 20 cm long; pedicels 1–4 (6) mm long; flowers white, sweetly aromatic, usually 4-parted, rarely 3- or 5-parted; sepals ± rounded, ciliate; petals ± oblong, ca 5 mm long, rounded to emarginate at apex, spreading at anthesis, connate at base; stamens 20–30, to 4 mm long, weakly fused to base of petals and borne among villous tufts; anthers yellow, to 1.7 mm long, the thecae divergent, dehiscent chiefly at apex; ovary ± obovoid, the locules equaling the petals, ca 1.3 mm long; styles usually 4, ca 1 mm long. Berries globose, ca 1 cm diam, usually (3)4(5)-sulcate, glabrous, white and fleshy at maturity; seeds many, ca 1 mm long, markedly reticulate to alveolate. *Bangham 578, Salvoza 998.*

Apparently rare if still present on the island; not seen in recent years. Uncommon in adjacent areas of the Canal Zone. Flowers in July and August (elsewhere in Panama rarely as early as May or as late as September). The fruits mature by September or October.

Southern Mexico to Colombia. In Panama, mainly in upland areas but, according to Hunter in the *Flora of Panama* (1965), one of the few species capable of spreading across lowland barriers. In Panama, known from

tropical moist forest in the Canal Zone, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Coclé.

TETRACERA L.

Tetracera hydrophila Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 17:20. 1862

T. ovalifolia sensu auct. non DC.

Androdioecious liana; trichomes of younger parts dense and stellate, interspersed with sparse and simple ones, the leaves and stems usually glabrate in age. Petioles 1.5–3.5 cm long, winged mostly in apical half; blades ± ovate to elliptic, rounded to abruptly short-acuminate at apex, rounded to obtuse at base, 4–17 cm long, 4–9 cm wide (to 28 cm long and 13 cm wide on juvenile leaves), chiefly stellate-pubescent except on veins, pustular, entire or becoming serrulate toward apex; lateral veins in fewer than 15 pairs. Flowers unisexual, 1–1.5 cm wide, pedicellate; sepals 5, obovate, to 5 mm long (longer in fruit), glabrous or slightly pubescent inside; petals 4 or 5, white, obovate, 7–9 mm long; stamens very numerous, 5 mm long, somewhat reduced and nonfunctional in pistillate flowers; carpels 2–5, pyriform; styles 1 per carpel, 1–2 mm long, held above stamens in pistillate flowers, reduced in staminate flowers; stigma simple. Follicles 2–5, glabrous, tawny, 6–8 mm long (excluding style), dehiscing along inner side; seeds 1–4, ± reniform, ca 4 mm long, shiny, black, enveloped by a lacerate red aril. *Croat 6575*.

Uncommon; collected only along the shore and along Lutz Creek. Seasonal behavior uncertain. On BCI no flowers have been collected. All collections in central Panama, however, indicate that the species may flower twice a year, once in the dry season, with the fruits maturing from July to October, and once in the late rainy season (October and November), with the fruits maturing in the middle of the dry season.

Although Standley reported this taxon as *T. sessiliflora* Tr. and Planch., a synonym of *T. portobellensis*, his description leaves no doubt that he was referring to *T. hydrophila*. *T. hydrophila* was mistakenly reported by Hunter in the *Flora of Panama* (1965) as *T. ovalifolia* DC., a synonym of *T. costata* subsp. *rotundifolia* (J. E. Smith) Kub., known only from the Guianas.

Belize to Panama, Colombia, and Ecuador. In Panama,

probably occurring in all lowland areas; known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá (San José Island) and from premontane wet forest in Bocas del Toro.

Tetracera portobellensis Beurl., Kongl. Vetensk. Acad. Handl. 113. 1854

T. sessiliflora Tr. & Planch.

Androdioecious liana or scandent shrub; young stems, petioles, and axes of inflorescences with moderate to dense stellate pubescence interspersed with simple trichomes. Petioles 3–10 mm long, winged full length; blades elliptic to obovate, rounded to abruptly acuminate (rarely short-acuminate), acute to obtuse and decurrent on petiole at base, 5–18 cm long, 3–8 cm wide, the pubescence minute, pustular, stellate on both surfaces, the simple trichomes mostly restricted to veins; lateral veins in 15–25 pairs. Panicles spikelike; flowers unisexual, usually sessile, 4–5 mm broad, closely congested; sepals 5; petals (2)3(4), pale yellow to greenish-white, rounded at apex, soon falling, the margin folded inward; stamens numerous, to ca 5 mm long, reduced in pistillate flowers; pistils reduced in staminate flowers; style usually directed to one side; stigma ± spatulate-truncate. Follicle 1, glabrous, shiny, dark brown, 5–7 mm long (excluding prominent beak), dehiscing on one side from style downward to expose seed; seeds 1–4, shiny, black, 3–4 mm long, enveloped at least in part by a deeply lacerate red aril (this becoming pale yellow on drying). *Croat 9375, 13997*.

Frequent along the shore and in the forest. Flowering may be induced throughout much of the year, but the chief flowering period is the early dry season (December to March, especially January and February). Flowering appears to be induced by drought. Severing a vine in the proper stage of bud will soon cause the flowers to open. The fruits mature mostly from March to May (sometimes from February).

This species was mistakenly reported by Standley (1933) as *T. oblongata* DC. Although Standley reported *T. sessiliflora* Tr. & Planch., a synonym of *T. portobellensis*, his description leaves no doubt that he was referring to *T. hydrophila* Tr. & Planch.

Mexico to Colombia. In Panama, growing primarily in the wet lowland areas of the Atlantic slope; known from tropical moist forest in the Canal Zone (Atlantic slope)

KEY TO THE SPECIES OF TETRACERA

- Blades with usually more than 15 pairs of major lateral veins; follicle 1; petioles usually less than 1 cm long; flowers sessile or nearly so, in very dense glomerules *T. portobellensis* Beurl.
- Blades with usually fewer than 15 pairs of major lateral veins; follicles 2–5; petioles usually longer than 1 cm; flowers usually pedicellate, the glomerules not very densely congested:
- Blades usually rounded to truncate at base, the upper surface usually moderately smooth; petioles winged mostly only to about middle; sepals sparsely pubescent or glabrous inside *T. hydrophila* Tr. & Planch.
- Blades usually obtuse to attenuate at base, the upper surface coarsely asperous; petioles winged usually to base; sepals densely pubescent inside *T. volubilis* L.

and Bocas del Toro, from tropical dry forest in Darién (Garachiné), and from premontane wet forest in Colón. See Fig. 383.

Tetracera volubilis L., Sp. Pl. 533. 1753

Chumico, Pasmó de sol

Androdioecious liana; bark on older stems thin and flaky; most parts with both stellate and simple trichomes. Petioles 5–20 mm long, winged to base; blades obovate to ± elliptic, rounded and abruptly acuminate to obtuse at apex, obtuse to attenuate at base, decurrent on petiole, 6–20 cm long, 3–9.5 cm wide, entire to serrate, the simple trichomes sparse except on veins of lower leaf surface, the pubescence of upper surface often deciduous except for pustular bases; lateral veins in 10–15 (20) pairs. Flowers unisexual, 5–10 mm wide, pedicellate, rarely subsessile; sepals 5, densely pubescent inside; petals 3–5, obovate, to 5 mm long, white; stamens very numerous, about equaling petals, reduced in pistillate flowers; carpels 4 or 5, pyriform, usually pubescent with stiff white trichomes near apex, reduced in staminate flowers; styles 1 per carpel, ca 1.5 mm long. Follicles 4 or 5, glabrous to apically barbed, brown at maturity, 6–8 mm long, dehiscent along inner side; aril red (pale yellow on drying), at first enclosing seed; seeds 1–4, shiny, 3–4 mm long. *Croat 6569, 6802.*

Frequent along the shore and within the forest, sometimes at the top of the canopy. Flowers usually from August to November, especially in September and October, rarely as early as June. The fruits mature chiefly from January to March.

Mexico to Colombia, Venezuela, Amazonian Brazil, and Peru; Cuba and Jamaica. In Panama, known principally from tropical moist forest in the Canal Zone, Panamá, and Darién, but also from tropical dry forest in Coclé and from premontane moist forest in Panamá.

89. OCHNACEAE

Glabrous trees or shrubs. Leaves alternate, petiolate, sometimes clustered at apex of stems; blades simple, undulate or serrate; venation pinnate; stipules present. Panicles racemose, terminal; flowers bisexual, actinomorphic (or zygomorphic by disposition of sexual parts in *Cespedezia*), solitary or fasciculate; sepals 5, shortly united at base; petals 5, free, yellow; stamens 10 or many; anthers 2-celled, basifixed, dehiscent by oblique terminal pores; pistil 1; ovary superior, borne on conspicuous toral disk or gynophore, deeply lobed (5-locular and

5-carpellate with axile placentation in *Ouratea*, 1-locular and 5-carpellate with intrusive parietal placentation in *Cespedezia*); style 1; stigma undifferentiated or 5-lobed. Fruits septically dehiscent capsules with many winged seeds (*Cespedezia*) or 5 monocarpic drupelets of 1 seed on the swollen torus; seeds with or without endosperm.

The two BCI species have little in common superficially but are individually unique and not confused with any other species.

Flowers are well suited for insect pollination. Those of *Cespedezia* are probably pollinated by large bees.

Drupes of *Ouratea lucens* are well suited for ornithochory, though they may be dispersed in part by animals other than birds. Seeds of *Cespedezia macrophylla* are wind dispersed.

About 25–40 genera with 400–600 species; subtropics and tropics.

CESPEDEZIA Goudot

Cespedezia macrophylla Seem., Bot. Voy. Herald 97. 1853

Membrillo, Membrillo macho, John Crow wood

Tree, 5–20 (25) m tall, to 50 (70) dbh, often buttressed, with aerial roots. Leaves clustered at apex of branches; stipules densely imbricate, to 7 cm long, ca 1 cm wide, becoming weathered and subligneous; petioles to 1 cm long; blades linear-obovate, usually obtuse at apex, cuneate at base, 20–100 cm long, 15–25 cm wide, glabrous, coriaceous, the margins uneven; lateral veins prominent. Panicles terminal, large, exceeding uppermost leaves; flowers 5-parted, somewhat zygomorphic; sepals ca 5 mm long, thick, divergent at anthesis; petals yellow, obovate, concave, 2–3 cm long; stamens ca 80; filaments ca 1 cm long; anthers linear, ca 1 cm long, clustered opposite pistil; pistil stipitate, held to one side of flower, the stipe ca 6 mm long; ovary ca 1 cm long and 5 mm wide; style minute. Capsules narrowly ellipsoid, to 4 (6.5) cm long and 1 cm diam, splitting longitudinally into 5 narrow segments; seeds many, small, with 2 long, narrow, lateral wings, the seminiferous area ca 2 mm long and 1 mm wide, the wings to 1 cm long, ca 1 mm wide at seed, tapering to a narrow point. *Croat 8163.*

Occasional, on the shore. Flowers principally in the late rainy season to the middle of the dry season (August to March). The fruits probably mature principally in the dry season.

The flowering plant is impressive for its huge yellow panicles.

Nicaragua to Colombia. In Panama, characteristic of

KEY TO THE SPECIES OF OCHNACEAE

- Plants large trees; leaves to 1 m long, clustered at apex of branches; panicles to 1 m long; fruits capsular, with many small winged seeds *Cespedezia macrophylla* Seem.
 Plants shrubs or small trees; leaves less than 25 cm long, not clustered; panicles racemose, less than 20 cm long; fruits with 5 sessile drupelets attached to a red receptacle
 *Ouratea lucens* (H.B.K.) Engler



Fig. 383. *Tetracera portobellensis*



Fig. 385.
Souroubea sympetala

Fig. 384. *Marcgravia nepenthoides*



tropical wet forest (Tosi, 1971); known also from tropical moist forest all along the Atlantic slope and from the Canal Zone, Panamá, and Darién, from tropical dry forest in Coclé (Penonomé), and from premontane wet forest in Coclé (El Valle).

OURATEA Aubl.

Ouratea lucens (H.B.K.) Engler in Mart., Fl. Brasil. 12(2):350. 1896

O. nitida (Sw.) Engler; *O. wrightii* (Van Tiegh.) Riley

Wild pigeon plum

Glabrous shrub or small tree, to 8 m tall. Stipules lanceolate, 4–6 mm long; petioles 5–12 mm long; blades variable, lanceolate to oblong-elliptic to rarely obovate, acuminate, nearly rounded to cuneate at base, 5–22 cm long, 2–7.5 cm wide, the margins serrate to serrulate; veins not raised except midrib below. Inflorescences racemose, terminal or upper-axillary, 2–14 cm long, bracteate especially at base, the bracts lanceolate, to 5 mm long; pedicels 5–10 mm long, articulate at base; flowers 5-parted in bud; sepals 5–7(9) mm long, ovate; petals obovate, to 9 mm long, soon falling; stamens 10, connivent; anthers subsessile, subulate, to 5 mm long; style ca 6 mm long, subsistent. Fruits of 5 elliptic drupelets, black at maturity, to 10 mm long, sessile on a receptacle, the receptacle prominent, ± rounded or club-shaped, red; seeds 1 per drupelet. *Croat 8727*.

Frequent in the forest. Flowers from the late rainy season to the middle of the dry season (October to March). The fruits mature primarily in the dry season (December to April), though the receptacle may well persist until July.

Mexico to Panama. In Panama, ecologically variable; Bocas del Toro, Los Santos, Panamá, and Darién, from premontane wet forest in Chiriquí, Panamá, and Darién, from tropical wet forest in Darién, and from premontane rain forest in Panamá and Darién.

90. MARCGRAVIACEAE

Hemiepiphytic lianas. Leaves alternate, petiolate; blades simple, entire, glabrous, coriaceous, with inconspicuous hypophyllous glands; venation pinnate; stipules lacking. Racemes or umbels terminal, bracteate, with prominent nectaries; flowers bisexual, actinomorphic, often fragrant; sepals 4 or 5, free; corolla 5-lobed; stamens 5 (*Souroubea*) or many (*Marcgravia*); anthers 2-celled, dehiscing longitudinally; ovary superior, 5-locular (*Souroubea*) or about

10-locular (*Marcgravia*); ovules numerous; stigma sessile, 5-radiate. Fruits leathery, fleshy capsules; seeds many, with little or no endosperm.

Marcgraviaceae are recognized by being liana-like epiphytes with prominent nectaries subtending the flowers.

Marcgravia nepenthoides is probably pollinated by bats (Vogel, 1958). At least some species of *Marcgravia* are also pollinated by hummingbirds (Proctor & Yeo, 1973). The pollination system of *Souroubea sympetala* is unknown, but because of the red coloration of the inflorescence, I suspect hummingbirds.

Four or five genera and 100–125 species; New World tropics.

MARCGRAVIA L.

Marcgravia nepenthoides Seem., J. Bot. 8:245. 1870

Glabrous hemiepiphytic shrub or liana; trunk usually less than 6 cm diam, usually ascending a single tree, the ultimate branches slender, long-pendent, the smaller branches somewhat angulate. Petioles less than 1 cm long; blades obovate-oblong to elliptic-oblong, acuminate, rounded at base, 10–23(35) cm long, 4–7(9) cm wide, with a row of minute glands along margins below. Inflorescences terminal, umbelliform, pendent; pedicels spreading, to 3.5 cm long (to 4.5 cm in fruit), turned downward just before the apex; flowers 25–30, radially disposed from a ± globose rachis; bracteoles and sepals ± suborbicular; sepals 4, persistent in fruit, to 4 mm long and 6.5 mm wide, the inner 2 smaller; petals connate into a deciduous cap 8–10 mm long; stamens 25–30, pendent; filaments linear, flattened, 3–8 mm long; anthers ca 2 mm long; ovary subglobose, ca 3 mm diam, ca 10-locular; style short; nectaries 5 or 6, dark violet-purple, dipper-shaped, 6–9 cm long, the cup to 3.5 cm long and to 2.8 cm wide, somewhat constricted at apex, the stalk to 5.5 cm long. Capsules depressed-globose, apiculate, to 1.2 cm diam, brown; exocarp thin; mesocarp fleshy, red; seeds numerous, ca 1 mm long. *Croat 7033*.

Occasional, in the forest; juvenile plants ascending trees are more common. Flowers and fruits most abundantly in the dry season, although some flowers are seen as early as September. Plants are generally not found in the crown of a tree but rather on the trunk below the crown.

On the Atlantic slope from Belize to Panama. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro.

See Fig. 384.

KEY TO THE SPECIES OF MARCGRAVIACEAE

- Inflorescences umbelliform, with 25–30 radially disposed flowers subtended by 5 or 6 dipper-shaped nectaries; capsules less than 1.5 cm diam *Marcgravia nepenthoides* Seem.
 Inflorescences racemose, the continuation of an unbranched stem; capsules more than 2 cm diam
 *Souroubea sympetala* Gilg.

SOUROUBEA Aubl.

Souroubea sympetala Gilg., Bot. Jahrb. Syst. 25 Beibl. 60:32. 1898

S. guianensis Aubl.

Hemiepiphytic, vinelike shrub, usually fastened to other vegetation with numerous, long, aerial roots; stems with papery-brown outer bark, often rooting at nodes. Petioles to 12 mm long; blades mostly obovate, rounded to obtuse at apex, acute at base, 8–14 (16) cm long, 3.5–6 (8) cm wide, thick, with 1 or 2 rows of minute glands within 1 cm of margins below. Inflorescences terminal, mostly 15–25 cm long, the continuation of an unbranched stem; pedicels 1–4 cm long, reduced near apex, densely and minutely ferruginous-pubescent; sepals 5, rounded, 2–3 mm long, very thick, imbricate, persisting; corolla greenish-yellow, to 14 mm wide, divided to basal third, broadly spreading or reflexed, rounded at apex, the lobes 5; stamens 5, alternate; anthers held above rim, 2–3 mm long, reddish; filaments about as long as thick; stigma sessile, 5-lobed, becoming soft and appearing to be receptive only after corolla has fallen, the lobes rupturing irregularly in radial pattern from center, becoming sticky; nectaries subtending flowers club-shaped, markedly auriculate, straddling pedicel, the auricles red, flattened, to ca 18 mm long. Capsules depressed-globose, 2–3 cm broad, the 5 thick valves deciduous at maturity, exposing a bright red-orange, fleshy mesocarp; seeds many, reddish-brown, sausage-shaped, 4–5 mm long, partly exposed from mesocarp. *Croat 7272, 7950.*

Occasional, on the shore and within the forest where the branches may be found in the top of the crown. Flowers from November to July, mostly from December to March. Fruit maturity time is uncertain.

In some cases the flowers never open; the apical part of the tube is removed as a calyptra before the lobes unfold.

Scattered from Belize to Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Panamá and from tropical wet forest in Colón. See Fig. 385.

91. THEACEAE

Glabrous shrubs or trees. Leaves alternate, spirally disposed, petiolate; blades simple, \pm entire; venation pinnate, obscure; stipules lacking. Flowers bisexual, actinomorphic, solitary in axils, subtended by 2 sepaloid bracteoles; sepals 5, free, unequal, imbricate; petals 5, briefly connate at base, whitish; stamens many, free, in 2 series; anthers 2-celled, dehiscing longitudinally; ovary superior, 2-locular, probably 4–6-carpellate; placentation axile; ovules 4 or 5 per cell, anatropous; style 1; stigma punctiform. Fruits irregularly dehiscent capsules; seeds few, with scanty endosperm.

Members of the family are distinguished by the several whorls of numerous stamens adnate to the petals, the unequal sepals, and the irregularly dehiscent fruit with bright red seeds.

Flowers have numerous exerted stamens and an exerted style. Their pollination system is unknown.

The bright red seeds are probably dispersed by birds.

Thirty genera and 500 species; principally in the Old World tropics, but with many in the New World tropics and some in temperate areas.

TERNSTROEMIA Mutis ex L.f.

Ternstroemia tepezapote Schlechter & Cham., Linnaea 6:420. 1831

T. seemannii Tr. & Planch.

Manglillo, Manzanilla de sabana

Glabrous shrub or tree, 2–15 (20) m tall, to 30 cm dbh; bark reddish-brown, thin. Leaves alternate, clustered at apex of branches, thick; petioles less than 1 cm long; blades oblong-elliptic to oblanceolate, bluntly acuminate, obtuse to rounded at base, 5–12 cm long, 2.5–5 cm wide; veins except midrib indistinct. Flowers 5-parted, solitary in axils, pleasantly aromatic (anise-like), on pedicels 2–5 cm long; calyx subtended by 2 sepaloid bracteoles to 4 mm long; sepals unequal, \pm broadly ovate, ca 1 cm long, white to greenish-white; petals white, yellow at apex, \pm equaling length of sepals, connate at base; stamens many, included; filaments united and adnate to corolla at base; anthers with a prolonged connective at apex; ovary conical, 2-celled; ovules 4 or 5 per cell; style slender, pointed. Fruits broadly ovoid, 1–2 cm wide, cream-colored at maturity, often with tinges of red, the outer wall thick, bursting irregularly at maturity; seeds few, \pm ovoid-cylindrical, to ca 10 mm long and 5 mm wide at base, with a thin, bright-red, pulpy covering. *Croat 14963.*

Rare; collected along the shore of Orchid Island, along the northern shore of BCI, and in the forest on Zetek Trail. Flowers in the late dry season, in March and April; sometimes flowering a second time from late September to November. The fruits mature from July to September.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Coclé, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Panamá and Darién.

See Fig. 386.

92. GUTTIFERAE
(CLUSIACEAE)

Terrestrial or hemiepiphytic trees or shrubs, usually glabrous, with milky or colored sap. Leaves opposite, petiolate; blades simple, entire, usually coriaceous; venation pinnate, the lateral veins parallel; stipules lacking. Panicles, racemes, or umbellate cymes (*Symphonia*), terminal or axillary, bracteate; flowers mostly unisexual (dioecious or polygamodioecious), sometimes bisexual (*Symphonia*, *Marila*, *Vismia*, *Tovomitopsis nicaraguensis*), mostly fragrant, actinomorphic; sepals 2–5, free or basally connate, mostly subequal; petals 4–6 and free or lacking;

KEY TO THE TAXA OF GUTTIFERAE

- Leaves rounded or emarginate at apex, usually obovate (except *Calophyllum*):
- Lateral veins sharply ascending at ca 45° angle or less to midrib; trees epiphytic; flowers pink to greenish:
 - Flowers and fruits 5–9-parted; petals white to pinkish, more than 2 cm long; fruits more than 2.5 cm broad *Clusia odorata* Seem.
 - Flowers and fruits 4-parted; petals green, less than 1 cm long; fruits less than 1.5 cm broad *Havetiopsis flexilis* Planch. & Tr.
 - Lateral veins nearly perpendicular to midrib, branching at 60° angle or more; trees not epiphytic; flowers yellow or white:
 - Leaves usually more than twice as long as broad, lacking crossveins between major lateral veins; pedicels less than 1 cm long; inflorescences usually more than 3 cm long; flowers yellow, less than 1 cm long; seed 1; trees common in the forest *Calophyllum longifolium* Willd.
 - Leaves usually less than twice as long as broad, with prominent crossveins between major lateral veins; pedicels more than 1 cm long; inflorescences less than 3 cm long; flowers white; seeds 2–4; trees cultivated in the Laboratory Clearing *Mammea americana* L.
- Leaves acute to acuminate at apex:
- Plants bearing dense, brown, stellate trichomes especially on the lower leaf surfaces and axes of inflorescences, the leaf blades pellucid- or opaque-punctate; petals densely woolly inside *Vismia*
 - Plants glabrous, punctate or not; petals not woolly-pubescent inside:
 - Flowers solitary or fasciculate:
 - Bisexual flowers solitary or paired; style sessile, the conspicuous, broad, 5–7-lobed stigma persisting in fruit; tree cultivated in the Laboratory Clearing *Garcinia mangostana* L.
 - Flowers fasciculate; style not sessile or at least not 5–7-lobed and persisting in fruit:
 - Flowers red, more than 1 cm diam at anthesis; inflorescences terminal; leaves less than 8 cm long; tree usually more than 20 m tall *Symphonia globulifera* L.f.
 - Flowers white, less than 1 cm diam at anthesis; inflorescences axillary; at least some leaves more than 8 cm long; tree usually less than 10 m tall *Rheedia*
 - Flowers paniculate or racemose:
 - Flowers in pendent racemes; fruits linear capsules, with many minute comose seeds; secondary lateral veins closely parallel, perpendicular to primary lateral veins and connecting them *Marila laxiflora* Rusby
 - Flowers in panicles; fruits globular or obovate, the seeds not as above; secondary lateral veins not at all parallel, not perpendicular to or connecting primary lateral veins:
 - Flower buds globular and less than 5 mm diam; fruits globular, the 5 styles reduced to black dots at the apex *Tovomitopsis nicaraguensis* Planch. & Tr.
 - Flower buds oblong or globular and more than 5 mm diam; fruits obovate, the styles long, conspicuous, persistent *Tovomita*

stamens many (4 in *Havetiopsis*), sometimes fascicled, sometimes inserted on the disk or reduced to staminodia; anthers 2-celled, introrse, dehiscent longitudinally; ovary superior, 1- to many-locular, 3- to many-carpellate; placentation axile; ovules 1 to many per locule, anatropous; styles as many as the carpels, united or free; stigmas as many as carpels, often sessile. Fruits usually fleshy capsules, sometimes drupaceous or baccate, with several valves; seeds sometimes arillate, lacking endosperm.

Guttiferae are most easily recognized by the usually thick leaves frequently with closely parallel veins, the colored sap (usually yellow, orange, or red), and the frequently unisexual flowers.

Flowers are relatively primitive and open. *Symphonia globulifera* is pollinated by hummingbirds. In Costa Rica, *Clusia* flowers are visited by *Eulaema* (D. Janzen, pers. comm.). See additional comments under *Clusia* and *Symphonia*.

The fruits of several native species, including *Sym-*

phonia globulifera, *Calophyllum longifolium*, and both species of *Rheedia*, are chiefly mammal dispersed. Fruits of *Rheedia acuminata* and *R. edulis* are taken by white-faced monkeys (Oppenheimer, 1968; Hladik & Hladik, 1969), which generally swallow the seeds. *Rheedia edulis* fruits are also taken by the bat *Artibeus jamaicensis* Leach in Mexico (Yazquez-Yanes et al., 1975). Species that have capsules with small arillate seeds or colorful fruit interiors, such as *Tovomitopsis* and species of *Tovomita* and *Clusia*, are probably chiefly bird dispersed. However, howler monkeys are reported to eat the fruits of *Clusia odorata* (Carpenter, 1934). *Vismia*, with indehiscent, baccate, many-seeded fruits, is probably also chiefly bird dispersed. *Marila* has wind-dispersed seeds. Fruits of *Calophyllum* are hydrochorous (Ridley, 1930) and are also taken by bats (Bonaccorso, 1975; Yazquez-Yanes et al., 1975).

About 40–45 genera and 1,000 species; mostly in the subtropics and tropics.



Fig. 386.
Ternstroemia tepezapote



Fig. 387. *Clusia odorata*,
roots encircling supporting tree

CALOPHYLLUM L.**Calophyllum longifolium** Willd., Ges. Naturf.

Freunde Berl. Mag. 5:80. 1811

María, Calaba

Polygamous tree, to 35 m high; trunk ca 1 m dbh, buttressed; outer bark with short fissures, thick, irregular on the inner edge; inner bark reddish with white mottling, forming sap droplets; sap yellow, viscid, with the odor of fresh pumpkin; wood white, soft, lightweight; plant glabrous except for dense, minute, ferruginous trichomes on young stems and inflorescences. Petioles 2–4 cm long, stout; blades oblong, rounded to emarginate at apex, mostly obtuse at base, 11–20 cm long, 4.5–9.5 cm wide (to 30 cm long and 8.5 cm wide on juveniles), coriaceous; lateral veins very fine and parallel, secondary lateral veins lacking. Racemes short, to 4.5 cm long; inflorescence branches, petals, and sepals densely ferruginous-tomentose; pedicels less than 5 mm long; buds globose; sepals 4, ± orbicular to broadly elliptic, concave, ca 6–8 mm long, yellow, markedly unequal in width on a single flower, the outermost wider, about half as wide as long; petals lacking; stamens 10–12; filaments ca 2 mm long; anthers ca 1.8 mm long; ovary ovoid, ca 4.5 mm long; style ca 2 mm long; stigma capitate, much broader than the style. Fruits round, green, ca 3 cm diam; exocarp thin, green; mesocarp ± corky, thick; endocarp thin, shell-like, containing a single large seed. *Croat 8532, Foster 1480.*

Frequent in the forest, especially in the younger forest. Flowers throughout the rainy season, principally in late rainy season (October to November, rarely as late as January). The fruits mature principally in the late dry and early rainy seasons (March to July). J. Oppenheimer (pers. comm.) reports that white-faced monkeys eat the fruits from May to August.

Panama, Colombia, Surinam, Brazil, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet forest in Colón and Darién.

CLUSIA L.**Clusia odorata** Seem., Bot. Voy. Herald 89. 1853

Copey, Cope, Matapalo, Tar gum tree

Diocious, hemiepiphytic tree, to 10 m tall; trunk to 15 cm dbh; branches spiraled, stiff and spreading, densely rooting at the nodes, the roots often extending back to the host tree and enveloping it for support; stems glabrous with prominent leaf scars; sap pale yellow to bright orange (in time), not copious. Petioles to 2 cm long; blades obovate, rounded at apex (sometimes acute to acuminate on juvenile leaves), acute to obtuse at base, 5–15 cm long, 3–10 cm wide, very thick, dark green and glossy above, dull below, coriaceous; veins indistinct, drying with many fine veins. Panicles stout, bracteate, divaricately branched, terminal; buds depressed-globose; pedicels stout, to 1 cm long; flowers thick, 5-parted, spreading at anthesis, to 4.5 cm diam, white to pink, the lobes often marked with maroon or magenta at base

or apex; sepals 2, concave, unequal, persisting in fruit; petals 4–10, broadly oblong, 2–2.5 cm long; androecium of staminate flowers cushion-shaped, ca 1 cm wide and 5 mm high with numerous anthers; pollen white, granular, compressed in round or oval pouches ca 1 mm diam, embedded just beneath the sticky surface of the disk; pistillate flowers similar to staminate but the gynoecium divided into (4)9(15) segments, the petals falling soon after anthesis, the sepals closing. Capsules subglobose, 2.5–3 cm long, dehiscent into 5–9 parts at maturity; valves thick, ± spreading to expose the colorful mass of seeds; seeds numerous, reddish, curved-oblong, ca 5 mm long, embedded in a deeply divided, bright-orange aril. *Croat 14957.*

Frequent epiphyte in the forest or on exposed shorelines; epiphytic on rocks or on trees near the edge of the water. Plants are usually supported on tree trunks or large branches but their branches may grow into the top of the canopy. Apparently flowers and fruits sporadically throughout the year.

Where plants occur along the shore, the branches usually root at the nodes with the roots hanging in the water. The pollen sacs of the staminate flowers burst under the slightest pressure, and abundant pollen oozes out (sometimes explosively). Though the pollen is not at all tacky, the surface of the androecium is covered with an abundance of yellowish, tasteless, resinlike substance, which no doubt allows the pollinator to pick up pollen (perhaps on its feet). Several species of small bees, including *Trigona* spp., have been seen visiting the flowers.

Nicaragua to Panama, probably to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Veraguas, Herrera, Panamá, and Darién, from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Campana), and from tropical wet forest in Coclé (La Mesa) and Panamá.

See Fig. 387.

GARCINIA L.**Garcinia mangostana** L., Sp. Pl. 443. 1753

Mangosteen

Small, glabrous, polygamous tree, to 10 m tall; sap yellow. Petioles ca 2 cm long, with a swollen appendage above the articulation at the base; blades oblong-elliptic, acuminate and downturned at apex, obtuse to rounded at base, 15–22 cm long, 6.5–10.5 cm wide, bicolorous, darker above, coriaceous. Bisexual flowers solitary or paired, terminal; staminate flowers in 3–9-flowered, terminal fascicles; pedicels 1.5–2.5 cm long, stout; sepals 4, concave, coriaceous, persistent, often reddish inside; petals 4–6, fleshy, white to reddish, 1–1.7 cm long; bisexual flowers with many stamens ca 5 mm long (much shorter than the pistil); pistil bearing a broad, flat, 4–7-lobed stigma; stigma enlarged and persistent in fruit. Fruits ± depressed-globose, to 5 cm long and 6.5 cm wide, pale green to purplish at maturity; exocarp thick, with copious yellow sap; mesocarp sweet, tasty; seeds 5–7, ellipsoid, to 2.5 cm long. *Croat 4561, 5800.*

Cultivated at the Laboratory Clearing. Flowers in

March and April, with the fruits maturing in May and June.

Native to the Malay region; cultivated in tropical areas, widely so in the Canal Zone.

HAVETIOPSIS Planch. & Tr.

Havetiopsis flexilis Spruce ex Planch. & Tr., Ann. Sci. Nat. Bot., sér. 4, 14:246. 1860

Diocious, hemiepiphytic tree, usually less than 4 m tall, growing in upper levels of canopy or on stumps along the lake shore, glabrous. Petioles 5–15 mm long; blades obovate, rounded or emarginate at apex, acute at base, 6–10 cm long, 4–6 cm wide, coriaceous. Inflorescences divaricately branched, terminal, short, shorter than the subtending leaves; axes flattened or quadrangulate, each branch subtended by a minute bract; pedicels short, the bracts apical, opposite, connate at base; flowers unisexual; buds globular or depressed-globular; sepals 4, concave, round, to ca 5 mm long, the margins \pm scarious, the outermost sepals smaller, united at base; petals 4, round, ca 5 mm long, greenish marked with violet-purple, very thick especially the inner pair; stamens 4, ca 2 mm long; filaments very thick basally, about as long as the anthers, narrowed below the anther; anthers introrse; pollen white, powdery; pistillate flowers similar to staminate ones but with the stamens to 2.3 mm long, nonfunctional, the anthers much shorter than the filaments; sepals and petals persisting in fruit; styles 4, short, persistent in fruit. Capsules subglobular, to 1.2 cm diam, often obscurely 4-sided and weakly 4-lobed at apex, 4-valved, 4-locular, green or tinged with purple at maturity, splitting open to display seeds; seeds many, orange, oblong, ca 3.5 mm long, enveloped in a red-orange matrix. *Croat 14884, 16195.*

Frequent in the forest and along the shore. Flowers in the dry season (February to May), with the fruits maturing mostly in the rainy season (April to October).

Panama to Colombia, Venezuela, Brazil, and Peru. In Panama, known only from tropical moist forest on BCI. This is the first report for the genus in Central America.

See Fig. 388.

MAMMEA L.

Mammea americana L., Sp. Pl. 512. 1753

Mamey de cartagena

Monoecious to polygamous tree, to 20 m tall; trunk to 50 cm dbh; bark \pm smooth; sap pale yellow. Petioles to ca 1 cm long; blades oval to obovate, rounded or emarginate at apex, rounded to obtuse at base, 8–16 cm long, 5–10 cm wide, thick, with pellucid glandular dots; major lateral veins departing midrib at nearly 90°, the cross-veins numerous and about as prominent as lateral veins. Flowers fragrant, axillary, solitary or few, clustered on short stout stalks; pedicels 1–1.5 cm long; buds globose; sepals 2, nearly round, concave, ca 1.5 cm long; petals white, 4–6 (usually 6), obovate, spreading, 2–2.5 cm long; staminate flowers with a cluster of yellow stamens ca 2

cm diam, ca 1 cm long; pistillate flowers with the pistil 2–4-celled; style short, bilobed; stigmas \pm reniform. Fruits \pm globose, apiculate, to ca 12 cm diam, brownish; exocarp thick; mesocarp red to yellow, with white sap; seeds 2–4, oblong, ca two-thirds the length of the fruit, reddish-brown. *Croat 5787.*

Cultivated in the Laboratory Clearing. Flowers in the rainy season, especially the early rainy season. The fruits require most of the year to develop and probably mature during the dry season of the following year.

Native to the West Indies; spread by cultivation to most parts of the New World tropics; known also from the Old World tropics. In Panama, cultivated.

MARILA Sw.

Marila laxiflora Rusby, Mem. Torrey Bot. Club 6:9. 1896

Small tree, to 20 m tall, glabrous except for inconspicuous pubescence on young stems, petioles, and inflorescence branches. Petioles 6–15 mm long; blades oblong-elliptic, acuminate, obtuse to rounded at base, 11–25 cm long, 5–9 cm wide, often with conspicuous pellucid dots in areoles below; midrib and major lateral veins prominently raised below, the major lateral veins connected by numerous parallel, sinuate, tertiary veins mostly at \pm right angles to major laterals, the reticulate veins below anastomosing. Racemes axillary, 15–20 cm long, pendent, sparsely flowered; flowers green, fragrant, mostly bisexual; pedicels stout, ca 8 mm long, \pm perpendicular to rachis; sepals 4 or 5, ovate, 7–9 mm long; petals 4 or 5, \pm oblong or elliptic, about as long as calyx; stamens numerous, yellowish-brown, forming a \pm globular mass; filaments nearly free; stigma 1, \pm sessile, subentire, sticky. Capsules \pm linear, 4–7 cm long, less than 5 mm diam, splitting longitudinally into 2 or 4 segments; seeds many, dark, ellipsoid, ca 0.6 mm long, comose at both ends, the trichomes light brown, 2–3 mm long. *Croat 10806.*

Collected twice near the Laboratory Clearing, not seen otherwise. Flowers from March to August, chiefly in the rainy season (July to August). Mature fruits known from April and November.

The genus is unusual among the Guttiferae of Panama in having wind-dispersed seeds.

Known only from Panama, from wetter regions of tropical moist forest in the Canal Zone, Coclé, Panamá, and Darién, from premontane wet forest in the Canal Zone (Pipeline Road), Colón (Achiote), and Panamá (Cerro Campana), and from premontane rain forest in Panamá (Cerro Jefe).

RHEEDIA L.

Rheedia acuminata (R. & P.) Planch. & Tr., Ann. Sci. Nat. Bot., sér. 4, 14:314. 1860

R. madruno (H.B.K.) Planch. & Tr.

Madroño, Fruta de mono, Machari, Satro, Cero

Glabrous, polygamodioecious tree, to 9 (20) m tall, less than 15 cm dbh; outer bark very thin; inner bark reddish;

KEY TO THE SPECIES OF RHEEDIA

- Pedicels often more than 2.5 cm long; fruits usually ovoid, to 5 cm long, with dense protuberances
 *R. acuminata* (R. & P.) Planch. & Tr.
 Pedicels usually less than 2.5 cm long; fruits globular, less than 3 cm diam, smooth
 *R. edulis* (Seem.) Planch. & Tr.

wood hard; sap yellow, in branches and trunk. Petioles 1–2.5 cm long, somewhat swollen at base with a short appendage on the inner side above the articulation; blades elliptic, acuminate, mostly acute at base, 7.5–22 cm long, 2.5–8 cm wide, the midrib often arched; lateral veins and submarginal collecting vein visible on both surfaces (prominulous above when dry). Fascicles axillary, sessile, often at leafless nodes; pedicels slender, usually 2.5–3.5 cm long (rarely shorter); sepals 2, rounded at apex, \pm united at base, ca 3 mm long; petals 4, nearly orbicular, to 7 mm long, creamy-white, strongly reflexed at anthesis; bisexual flowers with fewer stamens than the staminate flowers; style short; stigma discoid, as broad as or broader than ovary. Fruits ovoid to globular, often weakly flattened, to 5 cm long and 4 cm wide, yellow, densely covered with puberulent, flattened protuberances to 3 mm long; exocarp thick, moderately hard; mesocarp thin, sweet; seeds usually 2, longer than broad. *Croat 8240, 13847.*

Occasional, in the forest. Flowers in the dry season (rarely in the late rainy season). The fruits mature mostly from April to August.

Monkeys are fond of the fruits. Mature fruits are usually all removed in a very short time.

Mexico to Peru. In Panama, known from wetter parts of tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién and from premontane wet and tropical wet forests in Colón, Panamá, and Darién.

Rheedia edulis (Seem.) Planch. & Tr., *Ann. Sci. Nat. Bot.*, sér. 4, 14:310. 1860
 Sastra, Cero, Chaparrón

Glabrous, polygamodioecious tree, to 10 (30) m tall; trunk usually less than 15 cm dbh, with sparse yellow sap; outer bark thin; inner bark reddish; younger parts with white or pale yellowish sap. Petioles 1–2.5 cm long, somewhat swollen at base with a short appendage on the inner side above the articulation; blades narrowly elliptic, acute to weakly acuminate, \pm attenuate at base, 12–20 (25) cm long, 4–7 (10) cm wide, thick; lateral veins and collecting vein scarcely visible, not prominulous above when dry. Fascicles dense, globular, sessile, ca 4 cm wide, usually borne on leafless stems; pedicels 7–20 mm long; flowers small, aromatic, numerous; sepals 2, concave, rounded at apex, \pm united at base; petals 4, ovate to orbicular, rounded at apex, white, 5–7 mm long, strongly reflexed at anthesis; staminate flowers with the stamens free, 16–30 (usually nearer 16), ca 3 mm long, erect to somewhat spreading, borne around a fleshy disk; anthers minute, about as broad as long, the thecae mostly directed upward; pistillode broad, cushion-shaped; bisexual flowers with the stamens 6–12, ca 2 mm long,

alternating with the lobes of a fleshy disk; ovary ovoid, ca 2.7 mm long; style very short; stigma discoid, ca three-fourths as broad as ovary. Fruits subglobular to ovoid, 2–2.8 cm long, to 2.3 cm wide, glabrous, at first green and densely whitish-punctate, becoming pale yellow to orange at maturity; exocarp thin, ca 2 mm thick, leathery; mesocarp thick, fleshy, white, tasty, sticking to seeds; seeds 1 or 2, oblong, to 2 cm long and 1 cm wide, with yellow latex, covered with a thin, brown, \pm fibrous layer. *Croat 13921, 14454.*

Frequent in the forest. Flowers from January to April, especially in February and March (rarely earlier or later elsewhere in Panama). The fruits mature principally from May to July, but some persist much later into the rainy season.

Sterile individuals are difficult to distinguish from *R. acuminata*.

Mexico, Panama, and Peru. In Panama, usually lower than 900 m elevation; known principally from wetter parts of tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, but also from premontane wet and tropical wet forests in Los Santos (Loma Prieta and along the Serranía de Cañazas).

See Fig. 389.

SYMPHONIA L.f.

Symphonia globulifera L.f., *Suppl. Pl. Syst. Veg.* 302. 1781

Barillo, Bogum, Cerillo, Cero, Sambo gum

Glabrous tree, usually to 30 m or more tall; trunk 50–120 cm diam, usually bearing numerous, large, adventitious roots near the base; outer bark thick, brown, slightly fissured; inner bark thick, much lighter, forming sap droplets when cut; sap yellow, copious. Petioles less than 1 cm long, canaliculate; blades narrowly elliptic, acuminate, acute to obtuse at base, 5–8 cm long, 2–3 cm wide; veins numerous, 1–2 mm apart. Inflorescences of large, globular, terminal, umbelliform fascicles to ca 6 cm diam, borne among the leaves; flowers numerous, bisexual, red; pedicels 5–15 mm long (to 25 mm in fruit), drying angulate; sepals 5, imbricate, unequal, suborbicular, coriaceous, usually broader than long, to 5 mm long, 5–8 mm wide; corolla depressed-globose, ca 15 mm wide and 8 mm high; petals strongly concave and imbricate, their apical margins directed inward and contacting the androecium; disk cupular, at the base of the staminal tube; staminal tube to 15 mm long and 4.5 mm wide, markedly infolded at about the middle, incised to ca 5 mm at apex between the anthers, the lobes 5, arcuate-spreading, each bearing 2–4 linear anthers on the outer



Fig. 388. *Havetiopsis flexilis*



Fig. 389. *Rheedea edulis*

Fig. 390. *Symphonia globulifera*



surface well below the apex; anthers to 2.7 mm long; ovary 5-locular; ovules 2–8 per locule; style to ca 6 mm long, frequently persisting in fruit, the lobes 4, stout, spreading, inserted between the lobes of the staminal tube. Fruits \pm round, 2.5–3.5 (4) cm diam; exocarp thin, leathery; mesocarp fibrous, 6–9 mm thick, yellow-green or brown; seeds usually 1 (to 3), 2–2.5 cm long, ellipsoid to subglobose, red, with yellow sap forming in droplets when cut, marked externally by irregular grooves. *Croat 9517*.

Frequent in the older forest. Flowers throughout the year but with a peak from June to August; individual trees may remain in flower for 2 months. The fruits mature in 1 or 2 months, so trees may still be bearing flowers when their first fruits mature.

The flowers are visited frequently by hummingbirds on BCI.

Belize south along the Atlantic slope to Panama and tropical South America; West Indies; tropical Africa; appearing to like water and growing in great abundance in swamp forests. In Panama, a characteristic species of tropical moist and tropical wet forest (Tosi, 1971), growing from sea level to 300 m; known from wetter parts of tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, and Darién, from premontane wet forest in Chiriquí, Coclé, Colón, and Panamá, and from tropical wet forest in Colón, Coclé, and Panamá. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 390.

TOVOMITA Aubl.

Tovomita longifolia (L. C. Rich.) Hochr., Ann.

Conserv. Jard. Bot. Genève 21:66. 1919

Glabrous, dioecious tree, to 12 m tall; trunk to ca 20 cm dbh, the base often with weakly developed stilt-roots; branches slender, often drooping; sap yellow. Petioles 2–2.5 (5) cm long; blades oblong-obovate, acute to bluntly acuminate at apex (rarely rounded), acute at base, (10)12–35 cm long, (4.5)7.5–13 cm wide; lateral veins in 6–12 pairs. Panicles terminal, short-pedunculate, to 10 cm long, the branches divaricate, often \pm flattened; flowers unisexual, many, ca 3 cm broad, arranged in dichasia, the buds globose; sepals 4, the outer pair smaller, strongly concave, reflexed at anthesis; petals 5, elliptic to oblong or obovate, to 13 mm long, white or yellowish; staminate flowers with numerous stamens in a cluster 15 mm wide and ca 5 mm long, free or somewhat connate; filaments fleshy, broader than the tapered anther, the innermost

curved outward; pistillode glabrous, conical, with 5 short styles; pistillate flowers fewer, somewhat smaller; ovary 4- or 5-locular; ovules 1(2) per locule, erect; style very short; stigmas 5, cuneate-obovate; staminodia many, ca 2.5 mm long. Fruits obovoid, ca 4 cm long (including stipe), rounded at apex, with 5 persistent styles to 5 mm long, the stigmas discoid, ca 2.5 mm diam; staminodia persistent. *Croat 14452, Dare 1116*.

Rare, in the forest, known only from the vicinity of the Laboratory Clearing. Throughout its range the species has been collected in flower nearly all year but especially in the late dry or early rainy seasons. On BCI flowers have been seen in late April and in May. Most fruits were mature in the rainy season.

Panama to the Guianas and Brazil. In Panama, known from tropical moist forest on BCI, from tropical wet forest in Colón, from premontane wet or tropical wet forest in Panamá (Rio Tuquesa), and from premontane rain forest in Panamá (Cerro Jefe).

See Fig. 391.

Tovomita stylosa Hemsl., Biol. Centr.-Amer. Bot.

1:88. 1879

Glabrous, dioecious shrub or small tree, to 7 m tall; sap yellow, more abundant in twigs than in trunk. Petioles 1–3 cm long, canaliculate; blades broadly elliptic to obovate, acute to abruptly acuminate and \pm downturned at apex, cuneate to obtuse at base, 3–15 cm long, 2–6.5 cm wide, entire; lateral veins in 3–7 pairs, \pm impressed above. Panicles terminal, bracteate, less than 4 cm long; bracts acute, mostly 1–2.3 mm long; branches flattened; pedicels 4–13 mm long; flowers unisexual, the buds oblong; staminate flowers cylindrical in bud; calyx bilobed, spathaceous, splitting on one side and recurving to expose other parts, ca 1 cm long, greenish; petals 4, \pm equaling calyx, white, free, to 2 mm wide, hooked inward at apex; stamens many, 5–7.5 mm long; filaments white; anthers minute, longitudinally dehiscent; pistillode to 1 mm high, with 4 sessile stigmas; pistillate flowers similar to staminate ones; ovary glabrous; styles 4, only slightly exceeding staminodia, persisting in fruit; staminodia numerous, ca 7 mm long. Fruits \pm obovate, 1.5–2 cm long, 4-lobed (at least when dry), splitting to expose red interior when ripe, 4-carpellate, each carpel with one seed; exocarp usually with scurfy, lenticellate areas; seeds oblong, ca 7 mm long. *Croat 11164, Oppenheimer 1521*.

Occasional, in the forest. Flowering in the rainy season (June to September), rarely earlier during the dry season elsewhere. Some fruits develop to full size by August but most mature in the dry season.

KEY TO THE SPECIES OF TOVOMITA

- Leaves less than 15 cm long; flower buds oblong; stamens fewer than 20; fruits 1.5–2 cm long, 4-carpellate, the surface with scurfy areas; styles 4, slender *T. stylosa* Hemsl.
 Leaves more than 15 cm long; flower buds globular, often more than 1 cm diam; stamens 20 or more; fruits ca 4 cm long, 5-carpellate, the surface smooth; styles 5, stout
 *T. longifolia* (L. C. Rich.) Hochr.



Fig. 392. *Tovomita stylosa*



Fig. 391.
Tovomita longifolia



Fig. 393. *Tovomitopsis nicaraguensis*

Known from Panama and Colombia (Chocó). In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet and tropical wet forests in Colón, Panamá, and Darién.

See Fig. 392.

TOVOMITOPSIS Planch. & Tr.

Tovomitopsis nicaraguensis Oerst. ex Planch. & Tr.,
Ann. Sci. Nat. Bot., sér. 4, 14:266. 1860

Tovomita nicaraguensis (Oerst.) L. O. Wms.; *Chrysochlamys eclipses* L. O. Wms.

Polygamous or dioecious shrub or small tree, 3–11 m tall, to 24 cm dbh, essentially glabrous; sap yellow, not copious. Petioles to 3 cm long; blades elliptic, acuminate, acute at base, mostly 12–22 cm long, 4.5–11 cm wide, moderately thick, drying brown to rusty, especially below; lateral veins in 6–11 pairs. Panicles terminal, to 16 cm long, the branches divaricate, each subtended by a small bract; pedicels stout, ca 5 mm long; flowers bisexual, ca 5 mm long, arranged in dichasia; sepals 5, reddish, broadly rounded, concave, very unequal, the outermost reduced, the inner few with the margin thin, ± erose; petals 5, yellow, ovate, ca 4 mm long, ± concave, thick medially, thin along the margin; staminate flowers not seen (possibly lacking); bisexual flowers with the stamens to ca 20, ca 1.5 mm long, of irregular sizes, longer and shorter ones generally alternating; filaments flattened and fused to at least the middle; pistil ca 2 mm long; stigmas 5, pitlike, subapical. Fruits red, round to obovoid, ca 2 cm long, with 5 black dots at the apex (style bases), dehiscent into 5 parts at maturity to expose seeds; valves thick, 3–4 cm long, tasting bitter even at maturity; seeds 1 per carpel, ± oblong, black, ca 1 cm long, mounted between the wings of the 5-lobed central column, the aril white, not sweet but edible. *Croat 4651, 11479, 12663.*

Common in the old forest. Flowers from July to September. The fruits mature in late dry and early rainy seasons (March to June).

It is uncertain if the species is dioecious or, as is often the case in the Guttiferae, polygamous.

Nicaragua to Panama. In Panama, known from tropical

moist forest in the Canal Zone, Bocas del Toro, and Darién and from premontane wet forest in the Canal Zone (Pipeline Road) and Panamá (Cerro Jefe).

See Fig. 393.

VISMIA Vand.*

Vismia baccifera (L.) Tr. & Planch., Ann. Sci. Nat.
Bot., sér. 4, 18:300. 1862

Achiote tigre, Sangre de perro, Sangrillo, Pinta-mozo

Shrub or small tree, to 5 m tall; older stems with reddish-brown flaky bark; younger stems, petioles, lower blade surfaces, sepals, and axes of inflorescences densely stellate-tomentose with usually brown, sessile trichomes; sap yellow to bright orange, drying red. Petioles 1–2.5 cm long; blades extremely variable, mostly ovate to elliptic, acute to acuminate, obtuse to rounded or truncate at base, 7–17 cm long, 2.5–10 cm wide, green above, yellowish-brown to dark brown below (depending on extent of ferruginous pubescence), reddish-pellucid-punctate. Panicles terminal, mostly to 8 cm long; pedicels ca 5 mm long; flowers bisexual, ca 1 cm long, 5-parted, without conspicuous aroma; sepals thick, 7–9 mm long, acute, valvate, closing to protect ovary after flowering, spreading in fruit, at least some with one or more margins thin and glabrous; petals obovate, round at apex, to ca 1.3 cm long, yellowish to transparent with vertical orange streaks, glabrous outside, densely woolly inside; staminal columns 5, exceeding styles, less than 7 mm long, alternating with short woolly staminodia; anthers many, directed outward against woolly inner surface of petals; pistil ovoid, becoming 5-lobed, glabrous, sometimes punctate; styles 5, diverging outward between staminal columns, persisting in fruit; stigmas capitate; nectar copious, stored chiefly in the calyx. Berries ovoid, ca 1.5 cm long, firm, green and fleshy at maturity, the styles, calyx, and weathered petals persisting; seeds many, cylindrical, straight or curved, 2–2.7 mm long, in several vertical stacks, faintly reticulate. *Croat 6695.*

Abundant in older clearings; common along the edge of the lake. Apparently flowers twice per year. The principal flowering season is during the early dry season,

KEY TO THE SPECIES OF VISMIA

- Leaf blades shallowly cordate at base, with red opaque punctations; petals white with purple specks or streaks, recurved at anthesis *V. macrophylla* Kunth
- Leaf blades acute to rounded at base, with black opaque or reddish pellucid punctations; petals green to pale orange:
- Leaves broadest at the base, usually more than 6 cm wide, sometimes ferruginous-tomentose; sepals generally not reflexed in fruit; flowers bisexual; petals yellowish to transparent with orange streaks *V. baccifera* (L.) Tr. & Planch.
- Leaves broadest near the middle, usually less than 6 cm wide; sepals strongly recurved in fruit; flowers both bisexual and pistillate in the same inflorescence; petals greenish
- *V. billbergiana* Beurl.

*After this treatment went to press, Norman K. B. Robson, British Museum of Natural History, submitted his treatment of *Vismia* for publication in the *Flora of Panama*. Two of the species he recognized from the BCI material I have treated as *V. baccifera*: *V. latiseptala* N. Robson (Panama and Colombia), represented by *Croat 4910, 6110, 6416, 6695, 10736, 11089, and 11286*, and *V. panamensis* Duch. & Walp. (Nicaragua to Panama), represented by *Croat 4614, 4619, 4956, 5523, 5636, and 8664*.

with the first fruits maturing by late April. A second wave of flowering occurs during the early rainy season, mostly in July, with scattered flowering later in the rainy season; the fruits are apparently all mature before the end of the rainy season.

The species is quite variable in terms of both leaf shape and indument. Standley (1933) reported the species under three names, *V. dealbata* H.B.K., *V. ferruginea* H.B.K., and *V. guianensis* (Aubl.) Pers. *V. guianensis* does not occur on BCI. The white- and brown-leaved forms were treated by Ewan (1962) in his treatment of South American *Vismia* as the subsp. *dealbata* (H.B.K.) Ewan and subsp. *ferruginea* (H.B.K.) Ewan, respectively.

Small green halictid bees visit flowers of this species. The bee generally alights atop the corolla, pushes its way into the flower between the petals and staminal clusters, and generally disappears from sight. Leaving the flower, the bee may back out or turn around and come out frontwards.

Mexico to Colombia, Venezuela, the Guianas, and Brazil. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Panamá, from tropical wet forest in Colón and Panamá, and from premontane rain forest in Chiriquí and Panamá.

See Fig. 394.

Vismia billbergiana Beurl., Handl. Svenska Vet. Akad., sér. 4, 2:117. 1856
V. viridiflora Tr. & Planch.

Polygamous shrub or slender tree, to 6 m tall; sap yellow or orange; stems, peduncles, pedicels, exposed parts of calyces, and lower leaf surfaces with an inconspicuous, thin, usually dense layer of stellate trichomes. Petioles 6–13 mm long; blades narrowly ovate-elliptic, acuminate, obtuse to rounded at base, 7–13 cm long, 2.5–5 cm wide, with black opaque punctations especially on lower surface. Panicles terminal or upper-axillary, to 10 cm long; flowers 5-parted, with both bisexual and pistillate flowers on the same inflorescence; bisexual flowers ca 1 cm long; sepals to 7 mm long, glabrate inside, persisting and strongly reflexed in fruit; petals obovate, green and glabrous outside, densely white-woolly inside, ca 1 cm long; stamens numerous, included; staminal columns 5, opposite the petals, densely woolly, alternating with staminodia; ovary ± glabrous, 5-ribbed; styles 5, recurved, protruding outward between staminal columns; stigma capitate; nectar copious around the base of the ovary; staminodia 5, prominent, densely pubescent, less than 2 mm long, sometimes yellow; pistillate flowers with the sepals 5–6 mm long, 1 sepal with a villous line of trichomes inside; petals lacking; staminodia, ovary, and styles as in bisexual flowers. Berries ovoid, 1–1.5 cm long, green. *Croat 5089*.

Uncommon in the forest along trails, occasional at some points along the shoreline. Flowers principally in the dry season, especially in January and February, with most fruits maturing in April and May. Individuals often

flower again in April or May when they have mature fruits, and a few flowers are also seen in September and October.

The species differs from *V. baccifera* and *V. macrophylla* in preferring to grow along the edges of shady areas and not in open areas.

Costa Rica to Colombia. In Panama, known from premontane moist forest in Panamá, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Coclé, and Panamá, from premontane moist forest in the Canal Zone, Veraguas, and Coclé, and from tropical wet forest in Colón, Veraguas, Panamá, and Darién.

See Fig. 395.

Vismia macrophylla Kunth in H.B.K., Nov. Gen. & Sp. 5:184. 1822

V. angusta Miq.; *V. latifolia* sensu Reich. in Mart. non (Aubl.) Choisy

Sangrillo, Pinta-mozo

Tree, 4–12 m tall, usually less than 15 cm dbh; bark usually loose and shaggy; sap copious, orange, drying red; stems, petioles, and axes of inflorescences densely stellate-ferruginous. Petioles 1.5–2.5 cm long; blades narrowly ovate-oblong, acuminate, rounded to subcordate at base, 17–30 cm long, 5.5–9 cm wide, the upper surface glabrous except for midrib, the lower surface, especially the veins, densely stellate-ferruginous and with reddish opaque punctations. Panicles terminal, ca 6 cm long; peduncles to 6 cm long, bearing a pair of leaflike bracts at the apex; major branches usually opposite; pedicels short, less than 2 mm long, thick; flowers bisexual, 5-parted, aromatic, ca 12 mm long; calyx to ca 7 mm long, ovate, broadly acute at apex, densely stellate-ferruginous, thick except for the thin scarious margins on one or both sides of 3 sepals; petals, inner surface of sepals, upper edge of ovary, and styles with conspicuous violet-purple punctations or streaks; petals white with purple spots, oblong, to 13 mm long and 3 mm wide, the apex blunt to acute and recurved from about the middle, densely matted-villous inside; staminal columns 5, flattened and glabrous at base, densely villous above; stamens many, of various lengths, directed outward against the villous surface of petals or becoming exserted; ovary ovoid, glabrous; styles 5, exserted, to 6.5 mm long, united near the base, persistent in fruit; stigma thick, bilobed; staminodia orange-red, ca 2 mm long, glabrous below, villous above, alternating with petals. Berries globose to ovoid, ca 1.5 cm long, green or olive-brown; seeds numerous, cylindrical, straight or curved, reddish-brown, faintly reticulate, ca 3 mm long. *Croat 5322, 6434*.

Occasional, along the shore on the north side of the island. Flowers early in the rainy season, mostly from May to August. The fruits develop to mature size before the end of the rainy season, but some persist through the dry season.

The species is popular with insects in the Canal Zone when it is in flower, and wasps, bees, and butterflies of several species visit it. Small bees of the family Anthophoridae protrude their heads into the flower and are possibly a legitimate pollinator. Wilson (1971) reported



Fig. 394. *Vismia baccifera*

Fig. 395. *Vismia billbergiana*



that fruits are eaten by the bat *Miconycteris hirsuta*. The fruits are probably removed principally by birds.

Belize south to the Guianas, Brazil, Bolivia, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Veraguas and Panamá, and from tropical wet forest in Colón and Veraguas.

93. BIXACEAE

Shrubs or small trees, with red-orange sap. Leaves alternate, petiolate; blades simple, entire; venation pinnate, palmate at the base; stipules present. Panicles terminal; flowers bisexual, actinomorphic; sepals 5, free, imbricate; petals 5, free, imbricate, showy; stamens numerous, free, on a thick receptacle; anthers 2-celled, dehiscing by 2 apical pores; ovary superior, 1-locular, 2-carpellate; placentation parietal; ovules numerous, anatropous; style 1, simple; stigma shortly bilobed. Fruits usually spiny, loculicidal capsules; seeds numerous, with fleshy testa, with endosperm.

Bixa can be recognized by having numerous stamens and a spiny reddish capsule.

One genus; native in tropical America, now widely distributed in the tropics.

BIXA L.

Bixa orellana L., Sp. Pl. 512. 1753

Achote, Achioté, Anatto

Shrub or small tree, 1.5–8 (15) m tall; trunk to 10 (15) cm dbh; branchlets reddish-brown. Stipules narrowly ovate, ca 1 cm long, caducous; petioles slender, 2–10 (14) cm long, slightly enlarged at apex; blades ovate or ovate-lanceolate, acuminate, rounded to truncate or cordate at base, 5–27 cm long, 3–18 cm wide, glabrous or sparsely lepidote above, densely lepidote below, the scales minute, reddish-brown; palmate veins at base 5. Panicles terminal, variable in size, mostly 5–15 cm long; inflorescence branches, pedicels, and calyces densely reddish-brown-lepidote outside; pedicels to 1 cm long, with 5 conspicuous glands below calyx; sepals 5, orbicular, ca 1 cm diam, concave; petals 5, obovate, 2–3 cm long, 1–2 cm wide, white (rarely pinkish); stamens many, 1–1.5 cm long; filaments slender, white, glabrous; anthers yellow, horseshoe-shaped, 1–1.5 mm long; ovary globose to pyriform, densely to sparsely bristly; style 1–1.5 cm long. Capsules variable in size, shape, and indument throughout the species' range, usually \pm globose to ovoid, 1.5–4.5 cm long, brown to red, with sparse to dense, short, flexible spines; seeds many, \pm irregular, red, ca 5 mm long, the testa fleshy. *Croat 7875, 12294.*

Occasional, along the shore. Flowers from September to February (sometimes from August). The fruits mature from January to June, with old dehisced capsules hanging on as late as September.

In Costa Rica bees are the most common visitors and

presumed pollinators, especially *Eulaema* (D. Janzen, pers. comm.), *Xylocopa*, *Trigona*, and *Melipona* (Heithaus, 1973). In Ecuador the flowers are visited by female *Eulaema cingulata*, *E. polychroma*, *E. homichlora*, and *E. meriana* for pollen (Dodson & Frymire, 1961).

The spines on the fruits are not functional in epizoochorous dispersal, but probably prevent the fruits from being eaten prematurely.

A red condiment and cosmetic is obtained from the seeds (Duke, 1968).

Throughout the tropics and subtropics of the world. In Panama, from tropical moist forest in all provinces, from premontane moist forest in Los Santos and Panamá, from premontane wet forest in Panamá (Chimán), and from tropical wet forest in Colón.

94. COCHLOSPERMACEAE

Trees or shrubs. Leaves alternate, petiolate; blades simple, palmately lobed; venation at base palmate; stipules present. Panicles terminal; flowers bisexual, slightly zygomorphic; sepals 4 or 5, free, unequal, imbricate; petals 4 or 5, free, imbricate, showy; stamens numerous, unequal, free; anthers 2-celled, basifixed or dorsifixed, dehiscing by terminal porelike slits; ovary superior, 1-locular, 3–5-carpellate; placentation parietal, often intruding; ovules numerous, anatropous; style 1; stigma simple, minute, dentate. Fruits loculicidal capsules; seeds densely long-lanate, with oily endosperm.

Three genera and 255 species; tropics.

COCHLOSPERMUM Kunth

Cochlospermum vitifolium (Willd.) Spreng., Syst.

Veg. 2:596. 1825

Brazilian rose, Poro-poro

Tree, 3–12 m tall, mostly to 10 cm dbh (sometimes to 70 cm dbh elsewhere); wood very soft; branches few; branchlets densely pubescent, becoming sparsely so in age. Stipules subulate, small, caducous; petioles to 30 cm long; blades usually palmately 5-lobed, cordate at base, mostly 12–25 cm wide, glabrous above, puberulent below, the lobes acute to acuminate, the margins usually crenate. Flowers yellow, pedicellate, the inflorescence branches recurved near apex; sepals 4 or 5, unequal, the 2 outer sepals ovate to oblong-obovate, usually rounded at apex, 12–18 mm long, 7–9 mm wide, the 3 inner sepals mostly obovate to subrotund, rounded at apex, 20–22 mm long, 16–20 mm wide; petals 4 or 5, obovate, 5–6 cm long, often emarginate at apex; stamens yellow, numerous, the outer ones longer, curved inward near apex; anthers slender, somewhat curved; pollen dehiscing from a single apical pore; style longer than stamens, at first \pm erect, later recurved and about equaling height of anthers, the apical part somewhat hooked; stigma simple. Capsules \pm obovoid, 5-valved, to 8 cm long; seeds reniform, 4–5 mm long, bearing many cottonlike fibers. *Croat 7690.*

Probably once common, now rare; known only from

a few places along the shore, especially the north edge of Orchid Island. Flowers throughout the dry season (December to April). The fruits mature in late dry and early rainy seasons (March to July). Leaves fall throughout most of the dry season.

The species can be recognized at once by the large yellow flower with numerous stamens and by the palmately lobed leaf. A large pollinator, such as a bat, bird, or large bee, would be the most effective for this large flower with protruding style. Primary pollinators in Costa Rica are large bees, principally in the families Anthophoridae and Xylocopidae (G. Frankie, pers. comm.). Capsules open broadly, but the wind-dispersed seeds leave only a few at a time, the rest being held by the outer capsule valves, which curve sharply inward and hold the cottony mass of seeds.

Mexico to northern South America. In Panama, a characteristic component of tropical dry forest (Holdridge & Budowski, 1956) and a common invader (Holdridge, 1970); known from tropical moist forest in the Canal Zone, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone, Los Santos, and Coclé, and from tropical wet forest in Panamá (Cerro Campana); cultivated in San Blas (Duke, 1968).

See Fig. 396.

95. VIOLACEAE

Trees or shrubs. Leaves alternate (*Hybanthus*) or opposite (*Rinorea*), petiolate; blades simple, entire to serrate; venation pinnate, frequently palmate at base; stipules present. Flowers bisexual, actinomorphic (*Rinorea*) or zygomorphic (*Hybanthus*), solitary in the axils (*Hybanthus*) or in few-flowered terminal racemes (*Rinorea*); sepals 5, free, imbricate; petals 5, equal (unequal in *Hybanthus*), \pm white; stamens 5, free; anthers 2-celled, with a broadly expanded, scalelike connective, dehiscing longitudinally; ovary superior, 1-locular, 3-carpellate; placentation parietal; ovules 1 or 3 per placenta; style 1; stigma simple. Fruits 3-valved, loculicidally and elastically dehiscent capsules; seeds few, with fleshy endosperm.

Members of the family may be distinguished on BCI by having appendaged stamens and three-sided capsules with a few globose seeds.

Flowers are insect pollinated, those of *Hybanthus* probably by bees.

Seeds are probably bird dispersed. Oppenheimer (1968) reported that, while white-faced monkeys eat im-

mature seeds of *Hybanthus prunifolius*, they do not take mature seeds. Mature capsules of *Hybanthus* become constricted and forcibly expel the seeds (R. Foster, pers. comm.).

Some 22 genera and 900 species; widely distributed.

HYBANTHUS Jacq.

Hybanthus prunifolius (Schult.) Schulze, Notizbl. Bot. Gart. Berlin-Dahlem 12:114. 1934

H. anomalus (H.B.K.) Melch.

Shrub or small tree, 1–6 m tall, sparsely pubescent on lower leaf surfaces and midribs above, densely so on young stems, pedicels, and bracts. Leaves alternate; stipules triangular, to 3 mm long, whitish, subpersistent; petioles to 7 mm long; blades elliptic, acuminate, acute at base, 5–15 cm long, 2.5–6 cm wide, remotely prominently serrate-crenate. Flowers solitary in axils, puberulent; pedicels ca 1.5 cm long, articulate above middle, bracteolate at base; sepals 5, triangular-ovate, acute, ca 9 mm long, persistent; petals 5, white, unequal, the anterior petal 3.5–4 cm long, 1.5–2.5 cm wide, spatulate, with the median lobe green to pale yellow below middle, puberulent inside near base, the remaining petals \pm oblong, the lateral ones ca 1.5 cm long, longer than the posterior ones; stamens 5; anthers ca 3 cm long, the connective appendages brown, much exceeding anthers, weakly fused laterally to form nectariferous appendages at bases of anthers; filaments very short; style ca 5 mm long, curved near apex toward anterior petal, persistent; stigma terminal, held well above staminal appendages. Capsules ellipsoid, 3-sided, acute, 1–2 cm long; seeds ovoid, 4–5 mm long, tan. *Croat 8900*.

Often very abundant in the forest, more common in the old forest; one of the most abundant species on the island. Flowers in sporadic bursts throughout the dry season, rarely in the middle of the rainy season, usually within 2 weeks after a heavy rain following a period of drought (R. Foster, pers. comm.).

Recognized by the persistent whitish stipules and bracteoles. On one occasion many of the trees were stripped of their leaves by a small caterpillar, leaving the understory vegetation very open.

Costa Rica to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Coclé, Panamá, and Darién, from tropical wet forest in Colón and Darién, and from premontane rain forest in Darién. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

KEY TO THE SPECIES OF VIOLACEAE

- Leaves alternate; flowers solitary *Hybanthus prunifolius* (Schult.) Schulze
 Leaves opposite; flowers in short racemes:
 Petals slightly longer than sepals, the sepals 3–4.5 mm long; bracteoles exceeding pedicels; leaf blades usually inequilateral at base and rounded to subcordate
 *Rinorea sylvatica* (Seem.) O. Kuntze
 Petals more than twice as long as sepals, the sepals 1–1.5 mm long; bracteoles shorter than pedicels; leaf blades usually equilateral and obtuse to acute at base . . . *Rinorea squamata* S. F. Blake



Fig. 396. *Cochlospermum vitifolium*

Fig. 397. *Rinorea sylvatica*



RINOREA Aubl.

Rinorea squamata S. F. Blake, Contr. U.S. Natl. Herb. 20:516. 1924
Guayacillo, Molenillo

Shrub or small tree, 2–5 (12) m tall, 5–10 (20) cm dbh, minutely ferruginous-puberulent and sparsely hirsute on young stems, petioles, leaf veins (especially below), inflorescence branches, pedicels, bracteoles, and calyces. Leaves opposite; stipules small, deciduous; petioles 3–8 mm long; blades mostly obovate-elliptic, caudate-acuminate, obtuse to acute and usually \pm equilateral at base, 6–13 cm long, 2.5–5 cm wide, subentire to serrulate. Racemes terminal, to 6 cm long; pedicels to 2.5 mm long; bracteoles broadly ovate, less than 1 mm long; sepals 5, ovate, \pm equal, 1–1.5 mm long; petals 5, \pm equal, oblong, 4–4.5 mm long, white or yellowish, minutely ciliate; stamens 5, 2.5–3 mm long; filaments free, ca 1 mm long, with a dorsal appendage nearly as long as and attached to basal half of filaments; anthers ca 1 mm long, the connective expanded, brownish; style ca 2.5 mm long, glabrous. Capsules ovoid, ca 2 cm long, trilobate, hirsute-hispid; valves thick; seeds few, ca 6 mm long. *Croat 8771.*

Occasional, in the forest. Seasonal behavior uncertain. Flowers at least in October and March. The fruits are known from June and July.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from tropical wet forest in Darién.

Rinorea sylvatica (Seem.) O. Kuntze, Rev. Gen. Pl. 1:42. 1891

Shrub or small tree, mostly 2.5–3.5 m tall; young branches, petioles, and leaf veins below puberulent and hirsute. Leaves opposite; stipules triangular, to 6 mm long, deciduous; petioles 3–8 mm long; blades obovate to elliptic, acuminate, usually inequilateral and rounded to subcordate at base, 9–16 cm long, 4–6.5 cm wide, subentire to crenulate. Racemes terminal, to 4 cm long; bracteoles ovate, 2–3 mm long, longer than pedicels; rachises, pedicels, sepals, and midribs of petals appressed-hirtellous; pedicels to 2 mm long; flowers few, aromatic;

sepals 5, unequal, acuminate, the longest nearly equaling petals; petals 5, cream-colored, to 5 mm long, acute and spreading at apex; stamens 5, to 4 mm long, included; filaments free, to 1 mm long, stout, lacking appendages; anthers sagittate, ca 1.5 mm long, the connective expanded, burnt orange; ovary bearing appressed rufous pubescence; style simple, ca 2.5 cm long, included, pubescent on basal half. Capsules ellipsoid, markedly trilobate, ca 2.5 cm long, splitting widely at maturity; valves puberulent, reticulate; seeds 3 per valve, ca 4.5 mm long, densely puberulent. *Croat 8463, 8481.*

Common at least in some areas of the forest. Flowers and fruits principally from December to May, rarely in the middle of the rainy season. Flower buds are performed at the end of the rainy season, and the flowers open rapidly after a heavy rain following a period of drought (R. Foster, pers. comm.).

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

See Fig. 397.

96. FLACOURTIACEAE

Trees or shrubs, the branchlets sometimes spiny. Leaves alternate, petiolate; blades simple, entire or serrate, often pellucid-punctate; venation pinnate (palmate at base in *Hasseltia*); stipules present or absent. Inflorescences terminal, axillary, or leaf-opposed, cymose, fasciculate or spicate, bracteate; flowers bisexual or unisexual (dioecious), actinomorphic; calyx 4- or 5-lobed, the lobes united at base (3 sepals in *Lindackeria*, 4 in *Hasseltia*); petals 4 or 5 (6–12 in *Lindackeria*), alternate with sepals, or frequently lacking; stamens (6)10 to many, alternating with equal number of staminodia, or staminodia lacking; anthers 2-celled, introrse, dehiscing longitudinally; intrastaminal disk often present; ovary superior, sometimes stalked, 1-locular, 3- or 4-carpellate; placentation parietal; ovules many; style 1, simple or 2–5-branched, or styles 3; stigma simple (sometimes lobed), globular. Fruits berries with few to many seeds or 3-valved capsules with arillate seeds and abundant endosperm.

A morphologically very diverse family. Most species have serrate leaf margins, and many have pellucid dots

KEY TO THE TAXA OF FLACOURTIACEAE

Inflorescences fasciculate and axillary; petals lacking:

Flowers unisexual; leaves lacking pellucid punctations, lacking stipules; plants with branches often bearing spines *Xylosma*

Flowers bisexual; leaves pellucid-punctate (except *Casearia commersoniana*), stipulate; plants unarmed (except *C. aculeata*):

Leaves densely pubescent, especially petioles; mature fruits more than 5 cm diam; flowers precocious, in axils of terminal leaflets only *Zuelania guidonia* (Sw.) Britt. & Millsp.

Leaves not densely pubescent; mature fruits less than 5 cm diam; flowers not precocious (or precocious and axillary all along branches in *C. aculeata*):

Stamens 6–12 (15), alternating with staminodial appendages; capsules usually less than 2 cm diam (to 2.5 cm diam in *C. arguta*); younger parts of plant often pubescent

. *Casearia*

Stamens 10 or more, lacking appendages; capsules usually more than 2 cm diam (1.5–2 cm in *Laetia procera*); younger parts of plant mostly glabrous *Laetia*

Inflorescences not fasciculate, terminal or upper-axillary; petals lacking or not:

Leaf blades entire; petioles more than 5 cm long; petals more numerous than sepals; fruits bearing prickles *Lindackeria laurina* Presl

Leaf blades usually toothed; petioles usually less than 4 cm long; petals lacking or as many as sepals; fruits lacking prickles:

Petals present:

Leaves with 3 palmate veins at base, \pm glabrous, with 2 large glands at base of blade above *Hasseltia floribunda* H.B.K.

Leaves pinnately veined throughout, conspicuously pubescent below, with 1 or 2 stalked glands at apex of petiole below *Banara guianensis* Aubl.

Petals lacking:

Flowers many, less than 2 mm broad, sessile, in congested spikes *Tetrathylacium johansenii* Standl.

Flowers relatively few, more than 8 mm broad, pedicellate, in open inflorescences:

Staminodia alternating with stamens; inflorescences cymose-corymbiform; leaf blades rounded to subcordate at base, equilateral *Casearia corymbosa* H.B.K.

Staminodia lacking; inflorescences dichasial; blades oblique at base, acute to obtuse *Laetia thammia* L.

or glandular teeth. All except *Banara*, *Hasseltia*, *Tetrathylacium*, and *Xylosma* have fleshy capsules with several to many seeds embedded in an orange or red matrix.

Flowers are pollinated by many kinds of small insects (Heithaus, 1973).

Seeds of species with capsular arillate seeds, such as *Casearia*, *Laetia*, *Lindackeria*, and *Zuelania*, are probably dispersed chiefly by birds, as are those with small colorful berries, such as *Hasseltia floribunda* and *Xylosma*. Fruits of *H. floribunda* are also taken by the white-faced monkey (Hladik & Hladik, 1969). Those of *Tetrathylacium johansenii* are bat dispersed (Bonaccorso, 1975).

Some 84–93 genera and about 1,000 species; tropics and subtropics.

BANARA Aubl.

Banara guianensis Aubl., Hist. Pl. Guiane Fr. 1:548, pl. 217. 1775

Shrub or small tree, to 6 m tall; stems with short appressed pubescence when young, glabrate in age. Stipules triangular, minute, persistent; petioles 3–15 mm long, densely appressed-pubescent, with 1 or 2 stalked glands near apex on lower surface; blades oblong-ovate to oblong-elliptic, acuminate, usually rounded to truncate at base, 7–16 cm long, 3–7 cm wide, the pubescence short, appressed, sparse above, the margins serrate, the teeth gland-tipped. Panicles narrow, to 12 cm long, terminal or opposite leaves; inflorescence branches, sepals, and petals densely whitish-tomentose; peduncles to 5 cm long; pedicels ca 5–9 mm long; flowers 4-parted; sepals ovate, 4–6 mm long, persistent in fruit; petals narrowly ovate, greenish-yellow, alternating with sepals, subpersistent in fruit; stamens many; style simple. Berries globose or depressed-globose, ca 8 mm diam, glabrous, green to blackish, with a long stout apiculum at apex; seeds many, tiny. *Foster 1175*.

Rare, in the forest. Flowers from May to July (rarely as early as January elsewhere). The fruits are mature principally from July to September.

The fruits are probably chiefly bird dispersed.

Costa Rica to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Coclé, and Panamá, from tropical dry forest in Coclé, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Colón and Coclé, and from premontane rain forest in Coclé.

CASEARIA Jacq.

The genus is recognized by its conspicuously pellucid-punctate leaves with small stipules and its bisexual, apetalous flowers. The flowers usually grow in bracteate fasciculate inflorescences in leaf axils and have four to six sepals and six to fifteen stamens, which alternate with staminodia.

Casearia aculeata Jacq., Enum. Pl. Carib. 21. 1760

C. guianensis (Aubl.) Urban var. *rafflesioides* Croat

Tree, ca 5 m tall; trunk ca 7 cm dbh, with simple spines near base; branches and branchlets glabrate to densely strigillose or puberulent; branches arching, wide-spreading, often with straight, stout, sharp branch-spines. Stipules deltoid to narrowly triangular, ca 2 mm long; petioles 2–8 mm long; blades ovate to elliptic or obovate or oblanceolate, acuminate to acute or rounded at apex, obtuse to attenuate and decurrent at base, 2.5–11 cm long, 1.3–4 cm wide, glabrous or with sparse, \pm appressed pubescence, weakly or not at all pellucid-punctate, the margins crenate-serrate, the teeth obscure to sharp, glandular and incurled. Fascicles sparse, sessile, axillary; bracteoles connate, sparsely pubescent, whitish to translucent, very thin, the outermost \pm triangular, very short, the inner ones oval, rounded at apex; pedicels 1.5–3 mm long, slender, to 3 mm wide when dried, sparsely villous, articulate at about middle, usually longer than bracteoles; flowers greenish-white, ca 7 mm diam; sepals 4–6, 3–3.5 (5.5) mm long, strigillose outside, blunt to rounded at apex, spreading at anthesis; corolla lacking; stamens 7 or 8 (9), ca 4 mm long, erect at anthesis, fused into a ring at base, alternating with densely villous stami-

KEY TO THE SPECIES OF CASEARIA

Stigmas 3:

Style simple; blades densely pellucid-punctate; calyx 2–3 mm long *C. sylvestris* Sw.
 Style with 3 branches; blades lacking pellucid-punctations; calyx 3–5 mm long

. *C. commersoniana* Camb.

Stigma 1:

Inflorescences cymose-corymbiform; capsules to 1.5 cm long *C. corymbosa* H.B.K.

Inflorescences fasciculate:

Fascicles distinctly short-pedunculate; blades oblong, finely toothed

. *C. arborea* (L. C. Rich.) Urban

Fascicles sessile or nearly so:

Leaf blades coarsely serrate; sepals 5–7 mm long, gradually tapered to a \pm sharp-pointed apex, united at base into a tube 1–1.5 mm long; leaves present at time of flowering, falling at time of fruiting; fruits to 2.5 cm diam; plants rare or no longer present on the island *C. arguta* H.B.K.

Leaf blades entire or shallowly toothed; sepals 3–6 mm long, \pm oblong, usually rounded at apex, not markedly united at base; leaves present or absent at flowering time, present at time of fruiting; fruits less than 1 cm wide; plants occasional to common on BCI:

Leaves elliptic (rarely obovate), mature at time of flowering, drying green on flowering collections, to 9.5 cm long and 4.5 cm wide (usually to 7.5 cm long and 2.5 cm wide); stipules deltoid to narrowly triangular, 1.5–2 mm long; branchlets frequently with stout, sharp branch-spines (branches ending in a sharp spine); pedicels articulate usually at about middle *C. aculeata* Jacq.

Leaves obovate, usually very young or even lacking at time of flowering, drying blackish on flowering collections, the blades of at least the larger leaves more than 9.5 cm long and 4.5 cm wide; stipules narrowly triangular to subulate, 2–5 mm long; branchlets lacking branch-spines; pedicels articulate usually well below middle *C. guianensis* (Aubl.) Urban

nodia, the staminal tube glabrous outside, pubescent inside; filaments \pm glabrous; anthers 1 mm long, introrse, equaling height of style; pollen yellowish, \pm tacky; ovary sparsely villous, narrowly ovate; style short; stigma globular, viscid, short-puberulent. Capsules 3-valved, round to ellipsoid, to ca 1 cm long, pale green to white, often marked with purple; valves maroon inside, marked with prominent white spots; seeds of irregular shapes, ca 4 mm long, enveloped in a pale orange aril. *Croat 11777, 13268, 14057.*

Occasional, in the forest. Flowers in March and April. The fruits mature from April to June.

Distinguished from *C. guianensis* by having elliptic leaves present at the time of flowering and by having sharp branch-spines. Other differences are discussed elsewhere (Croat, 1975b).

H. Sleumer considers *Casearia stjohnii* I. M. Johnston synonymous (pers. comm.); I consider it distinct (Croat, 1975b), though probably more closely related to *C. aculeata* than (as I had originally thought) to *C. guianensis*. *Casearia stjohnii* flowers later than *C. aculeata* (June and July), with the fruits maturing during August and September. It also has thicker, longer inflorescence bracts and much stouter, more densely pubescent pedicels.

Mexico to Colombia, Venezuela, Peru, and Brazil. In Panama, known principally from wetter parts of tropical moist forest in the Canal Zone, Panamá, and Darién.

Casearia arborea (L. C. Rich.) Urban, Symb. Ant. 4:421. 1910

Tree, to 20 m tall and 25 cm dbh; branches puberulent when young. Petioles to 5 mm long; blades oblong-

elliptic, often weakly inequilateral, long-acuminate, acute to rounded at base, 6–15 cm long, 2–6 cm wide, conspicuously pellucid-punctate or pellucid-lineolate, finely crenulate-serrate; veins puberulent. Fascicles dense, stalked; peduncles to 4 mm long; pedicels to 4 mm long, articulated near middle; pedicels and calyces densely short-pubescent; flowers white to greenish; calyx 4–4.5 mm long, the lobes 5, united at base, persistent in fruit; corolla lacking; stamens 10, slightly shorter than calyx lobes; filaments unequal; staminodia shorter than shortest anthers, cupular, villous at apex; ovary pubescent at apex; style short, simple; stigma globular. Capsules subglobose, apiculate, 4–5 mm long, pilose at apex, 3-valved, splitting at maturity; seeds 1–6, pyriform, brown, punctate; aril orange, fimbriate-lacerate. *Croat 11779, 16210.*

Occasional, in the forest. Flowers mostly in June and July (rarely as early as March). The fruits mature from July to September (sometimes to January).

Belize to the Guianas, Brazil, Peru, and Bolivia; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, from premontane wet forest in the Canal Zone and Colón, and from premontane rain forest in Panamá.

Casearia arguta H.B.K., Nov. Gen. & Sp. 5:364. 1823
Pica lingua, Raspa lingua

Shrub or small tree, 2–10(12) m tall; trunk to 12 cm diam; branchlets often densely ferruginous-pubescent, becoming glabrous and lenticellate. Leaves deciduous; petioles usually less than 5 mm long; blades \pm oblong-elliptic, acuminate, \pm acute at base, 9–17 cm long, 2.5–6 cm wide, usually pellucid-punctate, pubescent on veins on

both surfaces (especially below), the margins coarsely serrate with gland-tipped teeth. Fascicles dense, sessile, axillary, ca 2 cm broad; pedicels somewhat shorter than flowers, articulated near base; flowers greenish-white, with a moderately sweet aroma, 4–5 mm long; calyx 5-lobed, united near base, spreading at anthesis; corolla lacking; stamens usually 10, stiffly erect, alternating with very pubescent staminodia, the 5 alternating with calyx lobes somewhat shorter than the others; anthers with apical bristles; style held above anthers in bud; stigma round, minutely bristled, the surface with an abundant sticky fluid; ovary conspicuously pubescent, the pubescence merging with that of staminodia. Capsules \pm globose, to 2.5 cm diam, yellow at maturity, nearly glabrous; seeds numerous, irregular, to 8 mm long, embedded in a sweet, juicy, orange matrix.

Common in the Canal Zone and to be expected on the island, but not seen in recent years. It was reported by Standley for the island, but no collections have been found. Flowers in the late rainy and early dry seasons; according to Allen (1956), it flowers several times at short intervals. The fruits mature in the late dry and early rainy seasons. Plants lose their leaves in the late dry season, while still bearing fruit, and remain leafless for a short time.

The flowers are visited by *Trigona* bees.

Throughout the tropics of the Western Hemisphere. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Veraguas, Panamá, and Darién; known also from tropical dry forest in Herrera and Coclé and from premontane wet forest in Chiriquí and Coclé.

Casearia commersoniana Camb. in St.-Hil., Adr. Juss. & Camb., Fl. Bras. Merid. 2:235. 1830

C. javitensis sensu auct. non H.B.K.

Small tree, usually less than 10 (15) m tall; trunk 10–20 cm dbh; bark smooth; branches \pm glabrous. Petioles to 5 mm long; blades \pm narrowly elliptic, long-acuminate, acute to obtuse at base, 7–25 cm long, 2.5–9 cm wide, glabrous, lacking pellucid punctations, coarsely serrate to crenate or nearly entire. Fascicles axillary, to 2.5 cm diam; pedicels and sepals pubescent; pedicels to 1 cm long, articulated below middle; flowers few to many, white or greenish; sepals 4 or 5, 3–4 (5) mm long; corolla lacking; stamens 9–15, longer than sepals; ovary sparsely to rather densely pubescent; style with 3 short branches; stigmas capitate. Capsules subglobose, ca 1 cm diam, apiculate, green turning red or brown; seeds 1 or 2, subglobose, 4–5 mm long. *Croat 6389, 6561.*

Occasional, on the shore or along trails. Flowers mostly from June to September, with the fruits maturing from August to October.

Southern Mexico to northern South America. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Panamá, and Darién; known also from premontane wet forest in Chiriquí and Panamá and from tropical wet forest in Colón and Panamá.

See Fig. 398.

Casearia corymbosa H.B.K., Nov. Gen. & Sp.

5:366. 1823

Comida de loro, Mamar, Mako, Carano

Deciduous shrub or small tree, 1.5–7.5 m tall. Petioles 3–15 mm long; blades \pm elliptic to oblong-obovate, variable but usually blunt-acuminate at apex, narrowed to an obtuse to subcordate base, 6–16 cm long, 3.5–5.5 cm wide, conspicuously pellucid-punctate and pellucid-lineate, glabrous above, glabrous to puberulent below, minutely serrulate to crenulate-serrate. Corymbx axillary, cymose; pedicels to 6 mm long, articulated below middle; flowers white or greenish; calyx ca 5 mm long, 5-lobed; corolla lacking; stamens 8, ca 3 mm long; filaments villous; anthers introrse; staminodia densely pubescent, one-third to one-half as long as stamens; ovary sparsely pilose; stigma \pm globose, held at level of anthers. Capsules globose to ellipsoid, with usually 3 longitudinal ridges, to 1.5 cm long, glabrous, orange to red at maturity; seeds 1–3, \pm ovoid, to 7 mm long, covered with resinous glands, with an incomplete red aril.

Reported by Standley (1933); the species could not easily be confused by him with any other, but I have not seen any collections from the island. Elsewhere in Panama, flowers commonly in the late dry season and early rainy season (April and May). The fruits are mature in the late rainy and early dry seasons. Leaves fall in the dry season and grow in again at the time of flowering.

The species has been confused with *Casearia nitida* (L.) Jacq. in the *Flora of Panama* (Robyns, 1968) and elsewhere. As indicated by Adams (1972), *Casearia nitida* occurs only in the West Indies and is distinct from *C. corymbosa*.

Mexico to Colombia. In Panama, ecologically variable; most commonly found in tropical moist forest in the Canal Zone, along the Atlantic slope, and in Veraguas, Panamá, and Darién; known also from premontane dry forest in the Canal Zone, from tropical dry forest in Los Santos and Panamá, and from premontane wet forest in Colón (Nombre de Dios).

Casearia guianensis (Aubl.) Urban, Symb. Ant.

3:322. 1902

Palo de la cruz

Shrub or small tree, (1.5) 3–6 (10) m tall; trunk to 12 cm dbh; stems glabrous to puberulent. Leaves deciduous; stipules subulate, 2–5 mm long, densely pubescent, caducous; petioles 2–10 mm long; blades mostly obovate, abruptly acuminate, acute and \pm decurrent at base, 5–18 cm long, 2–8.5 cm wide, glabrous or puberulent on veins especially below, pellucid-punctate and pellucid-lineate, \pm entire to shallowly crenate-serrate, the teeth often sharp. Fascicles dense, in old leaf axils; pedicels and calyx puberulent; pedicels 2.7–4.7 mm long at anthesis, articulated shortly above base, elongating to 8 mm in fruit; flowers white, with a faint sweet aroma, precocious; calyx deeply 4–6-lobed, 4–6 mm long, the lobes spreading; corolla lacking; stamens (7) 8, \pm glabrous, 2.5–3.5 mm long, alternating and uniting with much shorter, densely villous staminodia; ovary villous; stigma globular,



Fig. 398. *Casearia commersoniana*

Fig. 399. *Hasseltia floribunda*



held \pm at level of anthers. Capsules ellipsoid, 8–14 mm long, green often becoming violet-purple at least at apex, splitting into 3 parts; valves red inside; seeds several, irregular, brown, ca 3 mm long, enveloped in an orange aril. *Croat 8391, 8747.*

Common along the shore and at the margins of clearings; occasional in the young forest. Flowers commonly from March to May. The fruits mature from March through June. Leaves fall before flowering, and new leaves begin to develop near the time of flowering in the late dry season.

The species is similar to *Casearia aculeata*. See that species for a discussion.

Costa Rica to Venezuela, the Guianas, and Brazil (Pará). In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Panamá, and Darién.

Casearia sylvestris Sw., Fl. Ind. Occ. 752. 1798

Corta lengua

Shrub or small tree, 2–10 m tall; trunk to 12 cm dbh; branchlets puberulent when young, sometimes on one side only. Stipules minute, caducous; petioles 3–10 mm long, canaliculate; blades \pm oblong-elliptic, long-acuminate and downturned at apex, \pm acute to obtuse at base and sometimes inequilateral, mostly 2–14 cm long, 2.5–5 cm wide, glabrous, conspicuously pellucid-punctate, the margins entire to obscurely toothed, undulate. Flowers greenish-white or purple, 2–3 mm long, in dense axillary clusters; pedicels to 5 mm long, articulate near middle, the basal part persisting; calyx lobes 5, broadly ovate, divided to near base; corolla lacking; stamens 10; filaments united to calyx tube, unequal, the longer ones opposite calyx lobes; anthers broader than long, of 2 lengths, held horizontal, dehiscing downward; staminodia broad, densely pubescent, alternating with and shorter than stamens; ovary \pm glabrous; style at level between long and short anthers; stigmas 3, globular, \pm sessile. Capsules \pm globose, 3–4 mm long, apiculate, pubescent at apex, surrounded by persistent calyx, reddish or purple at maturity, 3-valved; seeds 2–6, ca 2 mm long, with an incomplete red aril. *Croat 4977, 6442.*

Frequent in the forest, especially the young forest, and along the shore. Flowers principally from August to December with sporadic flowering in the dry season. The fruits mature in about 1 month.

Throughout tropical America. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Veraguas, Coclé, Panamá, and Darién; known also from premontane wet forest in Chiriquí and Panamá.

HASSELLTIA Kunth

Hasseltia floribunda H.B.K., Nov. Gen. & Sp. 7:232, pl. 651. 1825

Raspa lengua, Parimontón

Small tree, 4–20 m tall; trunk to 30 cm dbh, often forming stilt-roots when leaning; outer bark smooth, thin; inner bark tan, granular, streaked with harder dark areas; young stems, petioles, and midribs above sparsely pubescent. Petioles 1–4 cm long; blades \pm elliptic, acuminate, obtuse at base and with 2 green glands on upper surface, 7–22 cm long, 4–11 cm wide, coarsely serrate; palmate veins at base 3, with a second pair of lateral veins arising in apical half to two-thirds of blade. Umbels divaricately branched, often broader than long; inflorescence branches, pedicels, and flowers puberulent; flowers 4-parted; sepals acute at apex; petals white, narrowly spatulate, to 2.7 mm long, equaling sepals; both petals and sepals recurved at anthesis; stamens numerous, 3–4 mm long; ovary \pm stalked, nearly glabrous; style to 2 mm long; stigma simple. Berries subglobose, to 8 mm long, red turning dark violet-purple at maturity; seeds 1 or 2, to 5 mm long. *Croat 7273.*

Common in the forest, especially the young forest. Flowers mostly in the dry season, but as late as June. Most fruits mature in the late dry and early rainy seasons. Plants may develop a second inflorescence from the base of the infructescence at about the time the fruits are maturing.

Fruits are eaten by white-faced monkeys in June (Hladik & Hladik, 1969).

Honduras to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién and from tropical wet forest in Colón (Portobelo). Reported from premontane wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Fig. 399.

LAETIA Loeff. ex L.

Laetia procera (Poepp. & Endl.) Eichl. in Mart., Fl. Brasil. 13(1):453. 1871

Casearia belizensis Standl.

Tall tree, probably exceeding 30 m; branches and petioles usually glaucous. Leaves distichous; stipules minute, caducous; petioles 4–15 mm long; blades elliptic-oblong, abruptly short-acuminate, rounded to minutely cordate at base, usually 7–22 cm long, 3.5–5 cm wide, minutely appressed-denticulate, somewhat pellucid-punctate, paler

KEY TO THE SPECIES OF LAETIA

- Leaves usually more than 14 cm long, rounded to subcordate at base; fruits glabrous
 *L. procera* (Poepp. & Endl.) Eichl.
 Leaves less than 12 cm long, acute at base; fruits bearing dense, short, brown, tomentulose
 pubescence *L. thammia* L.

below than above. Umbelliform fascicles of 4–25 (30) flowers, arising from leaf axils or from points ca 5 mm above axils or taking place of leaf along stem, arising on basal two-thirds of branch; pedicels 5–12 mm long; sepals somewhat petaloid, obtuse-reflexing, 2–4 mm long; corolla lacking; stamens 12–20; filaments ca 2 mm long; anthers ca 1 mm long, oblong; style simple, 1–2 mm long, persisting on fruit. Capsules berrylike, 1.5–2 cm thick, glabrous, subglobose; seeds 10–20, pitted, ca 3 mm long. *Knight 1301*.

Apparently rare; restricted to the old forest. Seasonal behavior not certain. Flowers mostly from April to July and fruits in August and September elsewhere.

Belize to Panama and the Guianas to Brazil; West Indies. In Panama, known only from tropical moist forest in the Canal Zone. Reported from premontane wet and tropical wet forests in Costa Rica (Holdridge et al., 1971).

***Lactia thamnina* L., Pl. Jam. Pugil. 31. 1759**

Conejo

Glabrous tree, to 10 m tall; branches lenticellate, terete. Stipules minute, caducous; petioles canaliculate, ca 1 cm long; blades \pm elliptic, acuminate, acute and inequilateral at base, 5–12 cm long, 2–3.5 cm wide, pellucid-punctate and glabrous, crenulate. Flowers white to greenish-white, in axillary dichasia to ca 8 cm long, usually only a few open at a time; bracts minute; pedicels puberulent, 9–13 mm long, articulated near base; sepals 4, caducous, \pm elliptic or boat-shaped, rounded at apex, to 9 mm long; corolla and staminodia lacking; stamens many, to 8 mm long; filaments often puberulent; ovary ovoid; style short; stigma simple. Capsules \pm globose, to 4 cm diam, with dense, short, brown, tomentulose pubescence; exocarp thick; valves 3, thick, red inside when dehiscent; seeds irregular, rounded, to 6 mm long, embedded in an orange mesocarp. *Croat 13977*.

Occasional, in some areas of the old forest and along the margin of the lake on the south side of the island. Flowers mostly from March to May, with the fruits maturing from June to September. Frankie, Baker, and Opler (1974) reported that the species may flower more than once a year. Leaves probably fall during the dry season.

Southern Mexico to northern South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Veraguas (Coiba Island), and Panamá and from tropical wet forest in Colón (Miguel de la Borda).

LINDACKERIA Presl

***Lindackeria laurina* Presl, Rel. Haenk. 2:89, pl.**

65. 1835

Oncoba laurina (Presl) Warb.

Guavo cimarron, Carbonero, Uvre, Chopo cucullo, Amarillo carbonero

Tree, 3–8 (15) m tall, 5–35 cm dbh; wood yellow; stems weakly striate, brown or with a thin gray flaky crust, the

leaf scars 3-sided, raised. Petioles 5–11 cm long, canaliculate, somewhat swollen at apex; blades \pm oblong-elliptic, long-acuminate, obtuse to rounded at base, 10–30 cm long, 5–11 cm wide, glabrous, the midrib raised above. Panicles axillary and terminal, to ca 20 cm long; pedicels to 1.5 cm long; flowers ca 1.2 cm diam, conspicuous and sweetly scented; sepals 3, reflexed at anthesis, caducous; petals 6–12, white, blunt at apex; stamens numerous, unequal, exserted; anthers slightly bifid at apex; style 4–6 mm long; stigma shortly trilobate. Capsules 1–1.5 cm diam, covered with stiff bristles, dehiscent into 3 or 4 parts to expose seed; seed usually solitary, smooth, broadly ovate, ca 7 mm long, flattened on one side, gray-coated, with a shiny, bright red, lateral aril. *Croat 6097, 7753*.

Locally abundant along some areas of the shore, especially on the southern side of the island; frequent in the forest. Flowers principally in the rainy season from May to October, rarely as early as April or as late as December. The fruits mature in the early dry season (January to March). Many leaves fall in late June.

Southern Mexico to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Colón.

TETRATHYLACIUM Poepp. & Endl.

***Tetrathylacium johansenii* Standl., J. Wash. Acad. Sci. 15:479. 1925**

Tree, 5–30 m tall; trunk ca 55 cm dbh; bark thin, brown, with many small vertical fissures; branchlets glabrous to puberulent. Stipules foliaceous, \pm oblong, to 17 mm long; petioles to 7 mm long; blades \pm oblong, acuminate, usually broadest above middle, gradually narrowed to rounded or subcordate base, mostly 12–20 (25) cm long, 3–6 (9) cm wide, glabrous except sometimes on midrib below, with depressions in axils of larger veins below, entire to usually obscurely toothed, the teeth gland-tipped. Inflorescences paniculate-spicate, to 8 cm long; flowers bisexual, white, very numerous, sessile, angulate, congested on secondary rachises to 4.5 cm long; calyx ca 2 mm long, with 4 minute lobes; corolla lacking; stamens 4, at first included with the anthers directed inward, becoming exserted with the anthers turned outward and folding over apex of sepals; anthers as broad as long; style short; stigma simple, held just below and adjacent to anthers. Fruits baccate, globose to obovoid, to 2.5 cm long, glabrous at maturity; seeds numerous, ovoid, to 2 mm long. *Croat 10152*.

Uncommon to rare. The tree usually loses its leaves in the early rainy season and immediately puts on new ones. Flower buds appear with the new leaves, and most flowers are seen from April through June. The fruits mature quickly, mostly from May to August. Mature fruits have been collected in Colón (Santa Rita Ridge) in January.

The fruits are probably dispersed chiefly by mammals.



Fig. 400. *Tetrathylacium johansenii*



Fig. 401. *Xylosma chloranthum*



Fig. 402.
Xylosma oligandrum

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién and from premontane wet forest in Colón (Santa Rita Ridge).

See Fig. 400.

XYLOSMA Forst.f.

Xylosma chloranthum Donn. Sm., Bot. Gaz. (Crawfordsville) 57:415–16. 1914

Dioecious shrub or tree, to 5 m tall, glabrous except for puberulence on young stems; trunk usually with large branched spines; stems prominently lenticellate, unarmed or armed with straight stiff axillary spines to 2.5 cm long (perhaps only on juveniles). Petioles 3–5 mm long; blades narrowly ovate to lanceolate-elliptic, long-acuminate, acute to rounded at base, 8–19 cm long, 2–6 cm wide, obtusely glandular-crenate, shiny on both surfaces, lacking pellucid-punctations; reticulate veins prominulous on both sides. Flowers fasciculate, yellowish, usually growing in leafless axils; pedicels 3–7 mm long, puberulent, articulate in basal third of staminate flowers and near middle of fruiting pedicel; sepals 4 or 5, very broadly ovate to nearly rounded, 1.5–2 mm long, ferruginous-puberulent and glandular near apex, ± ciliate near apex; corolla lacking; stamens 22–29 (35), to 6 mm long, glabrous; disk prominently undulate-lobed; style (3)4(5)-lobed, the lobes short and spreading. Berries ellipsoid, ca 6 mm long; seeds few, ovoid, to 4.5 mm long. *Croat 10087, 11617, Foster 785.*

Infrequent, in the forest. Flowers during the dry season and especially in the early rainy season, usually in May while plants are still devoid of leaves. The fruits develop within a short time, often even before the leaves have been replaced, usually in May and June.

The taxonomy of the genus *Xylosma* is among the most seriously in need of work of all Central American plant genera. The names used here thus will remain doubtful until a complete revision of the group can be made. This taxon has been confused with *X. excelsa* Standl. & L. O. Wms., which differs by being much taller (13–25 m), by being polygamous, and by bearing leaves at flowering time. *X. chloranthum* has also been confused with *X. intermedia* (Seem.) Tr. & Planch., which has polygamous flowers and has been transferred to the genus *Eichlerodendron*.

Belize, Guatemala, Costa Rica, and Panama, probably throughout Central America. In Panama, known from tropical moist forest in the Canal Zone and Panamá and

from premontane wet forest in Colón (Santa Rita Ridge), Chiriquí (near Boquete), and Panamá (Cerro Azul). Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 401.

Xylosma oligandrum Donn. Sm., Bot. Gaz. (Crawfordsville) 23:235. 1897

X. sylvicola Standl.

Dioecious tree, to (2)5(10) m tall, often branching near ground; trunk spineless (elsewhere with branched spines); larger branches sparsely armed with a few simple spines to 1 cm long; stems glabrous. Petioles ca 5 mm long, glabrous to puberulent; blades elliptic, acuminate, acute to obtuse at base, 8–16 cm long, 3.5–7.5 cm wide, glabrous except sometimes puberulent on midrib below, the margins with minute, gland-tipped teeth. Inflorescences very short racemes usually less than 3.3 cm long, often appearing glomerulate; pedicels 5–8 mm long, not articulate, puberulent, subtended by triangular to oblong bracts to 2 mm long; flowers unisexual; calyx deeply 4-lobed, to 1.3 mm long, the lobes ovate, rounded at apex, minutely ciliate, often weakly keeled, glabrous on outside, weakly pubescent inside; corolla lacking; stamens 8–16, to 2.7 mm long, glabrous; anthers as broad as long; disk of staminate flowers 9–12-lobed, the lobes rounded, irregular, the disk of pistillate flowers entire or bipartite; ovary ellipsoid to obovoid, ca 1.5 mm long; style with 2 short flattened branches, each with 2 rounded lobes. Berries ellipsoid to obovoid, 8–12 mm long, to 9 mm wide, becoming orange, then bright red, finally violet-purple at maturity; exocarp thin; mesocarp fleshy; seeds 1–3, ovoid, ca 5 mm long. *Croat 14640, 14642, Knight 1201.*

Occasional in some areas of the older forest; not seen elsewhere on the island. Flowers from March to July, mostly in the early rainy season. Mature fruits have been seen from April to September.

Knight 1201 has both staminate- and pistillate-flowered twigs. If the two branches were taken from the same plant, the species is not always dioecious. Field observations show only the dioecious condition, however. In contrast to *X. chloranthum*, this species flowers and fruits without losing leaves. The plants of this species from Coclé (El Valle) differ in having smaller, sometimes thicker leaves 3–10 cm long and 1.5–4.5 cm wide. Calyx lobes also average slightly larger and are more pubescent on the inner surface. The species corresponds to *Xylosma* species #2 in the *Flora of Panama* (Robyns, 1968).

Mexico (Chiapas) to Panama. In Panama, known from

KEY TO THE SPECIES OF XYLOSMA

- Leaves lanceolate-elliptic, usually more than 2.5 times as long as broad, with conspicuous crenate teeth; branched spines on trunk of mature plant; pedicels articulate; sepals pubescent only at glandular apex; stamens 22 or more *X. chloranthum* Donn. Sm.
 Leaves ± elliptic, usually less than 2.5 times as long as broad, minutely toothed; branched spines lacking; pedicels not articulate; sepals pubescent inside, not glandular at apex; stamens 16 or less *X. oligandrum* Donn. Sm.



Fig. 404. *Zuelania guidonia*



Fig. 403. *Zuelania guidonia*



Fig. 405. *Turnera panamensis*

tropical moist forest on BCI and from premontane wet forest in Coclé (El Valle).

See Fig. 402.

ZUELANIA A. Rich.

Zuelania guidonia (Sw.) Britt. & Millsp., Bahama Fl. 285. 1920

Cagajón, Caranon

Tree, 10–25 m tall, to 50 cm dbh; branches dark, conspicuously covered with light lenticels (and raised leaf bases on older wood). Leaves deciduous, often clustered near apex of branchlets; stipules lanceolate, 3–6 mm long, densely pubescent; petioles 5–20 mm long, densely brown-hirsute; blades ± oblong-elliptic, short-acuminate, rounded to subcordate at base, 6–16 (25) cm long, 2–6 (9) cm wide, densely pubescent below, sparsely so above, pellucid-punctate, obscurely serrulate. Inflorescences of globose fascicles in uppermost axils of leafless branches; flowers precocious, ca 1.5 cm broad, white or yellow, with a faint, rather foul aroma; pedicels and sepals conspicuously pubescent; pedicels to 18 mm long, articulate a few mm above base; sepals 5, 6–7 mm long, ± rounded at apex; corolla lacking; stamens numerous, exerted, ca 4 mm long, interspersed with staminodia about half as long; both stamens and staminodia united into a flat platelike base; anthers introrse; ovary densely short-tomentose; style short; stigma as broad as ovary. Capsules fleshy, depressed-globose, somewhat 3-sided, rounded at apex, subcordate at base, mostly 6–8 cm diam, usually dark brown at maturity, softly pubescent; valves thick, exposing bright orange matrix and seeds; seeds many, obovoid, ca 4 mm long, angular, white. *Croat 4962, 13995.*

Frequent in the forest, especially the young forest. Leaves fall sometime before flowering. Flowers mostly from February to May, before or during the onset of new leaves. Leaves are often not full size before the fruits reach maturity from April to June.

Southern Mexico to Panama; West Indies, Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical dry forest in Coclé (Penonomé). Reported from premontane moist forest in Costa Rica (Holdridge et al., 1971).

See Figs. 403 and 404.

97. TURNERACEAE

Shrub. Leaves alternate, petiolate; blades simple, serrate; venation pinnate; stipules present. Flowers bisexual, actinomorphic, solitary in axils, often on short branchlets, heterostylous (in BCI species); sepals 5, free, imbricate; petals 5, free, clawed, showy; stamens 5, free, attached to hypanthium; anthers 2-celled, dehiscent longitudinally; ovary superior, 1-locular, 3-carpellate; placentation parietal; ovules many, anatropous; styles 3; stigmas penicillate. Fruits 3-valved, loculicidal capsules; seeds many, arillate, with endosperm.

Turnera is distinguished by the leaves with glandular-crenate margins, the heterostylous orange flowers with a hypanthium and fimbriate-tipped stigmas, and the arillate seeds.

Flowers are insect pollinated (Doctors van Leewen, 1938). *Turnera* is pollinated by small bees in Guanacaste, Costa Rica (D. Janzen, pers. comm.).

The arillate seeds are probably ornithochorous.

Seven or 8 genera and about 120 species; American and African subtropics and tropics.

TURNERA L.

Turnera panamensis Urban, Jahrb. Königl. Bot. Gart. Berlin 2:92. 1883

Shrub, to 4 m tall; branches appressed-puberulent. Stipules subulate, to 4 mm long, subpersistent; petioles to 5 mm long, canaliculate above; blades ± elliptic, acuminate, acute and decurrent at base, mostly 10–15 (18) cm long and 3.5–5 (6) cm wide, glabrate above, puberulent below, glandular-crenate; veins prominent; flowers 5-parted, solitary, on short, bracteate, axillary branches, heterostylous; sepals ribbed, long-acuminate, to 1.5 cm long; petals orange, 2–3.5 cm long, blunt at apex, inserted near throat of hypanthium, widely spreading at anthesis, caducous; stamens 5; filaments either to 6 mm or to 12 mm long, their respective styles to 8 mm or to 5 mm long; stigmas numerous. Capsules 3-valved, ovoid, 6–13 mm long, minutely tuberculate, brown at maturity; seeds numerous, fewer than 10 per valve, ± oblong-curved, puberulent, striate, subtended by an aril, the aril collar-shaped, displayed on valves of open capsule. *Croat 7335.*

Frequent in the forest, especially in the old forest, and along the shore. Flowers and fruits sporadically throughout the year. Plants flower in a distinct synchronous wave if a period of drought is followed by a heavy rain (R. Foster, pers. comm.).

Distinguished by the orange flowers and glandular-crenate leaves.

Known only from Panama, from tropical moist forest in the Canal Zone and Panamá.

See Fig. 405.

98. PASSIFLORACEAE

Vines or lianas, climbing by means of simple, axillary tendrils. Leaves alternate; petioles usually bearing prominent, often stalked glands; blades simple, usually 2- or 3-lobed, the margins entire or serrate; venation palmate, palmate at base, or rarely strictly pinnate; stipules present. Flowers bisexual, actinomorphic, rarely apetalous, solitary or paired (rarely in racemes), axillary; peduncles jointed (often mistaken for a pedicel), bearing 3, often setaceous bracts; sepals 5, free, horned below the tip, often showy; petals 5, free, showy (lacking in *P. coriacea*); corona (petaloid structure between petals and stamens) of several series; corona and perianth parts attached to hypanthium; operculum (ring of tissue within corona)

membranous, sometimes plicate; stamens 5, attached to androgynophore (the fused staminate and pistillate parts); anthers 2-celled, versatile, dehiscing longitudinally; ovary superior, at apex of androgynophore, 1-locular, 3-carpellate; placentation parietal; ovules many, anatropous; styles 3 or stigmas sessile; stigmas 3, capitate. Fruits berries; seeds many, with fleshy endosperm, embedded in usually clear, fleshy, sweet mesocarp.

The family is represented on the island only by the genus *Passiflora*. The genus is recognized by being tendriled vines with glandular petioles, by the showy, solitary or paired flowers with a modified corona and an androgynophore (complex structure containing both staminate and pistillate parts), and by the fleshy, many-seeded, usually tasty fruits.

The flowers are very specialized. Most probably follow the behavior of *Passiflora foetida* and *P. vitifolia* as reported by Janzen (1968). After the flower opens, the styles become deflected, which promotes outcrossing. During first visits to the flower the pollinating organism receives only pollen, but later visits bring it in contact with the stigmas. *P. vitifolia*, which is hummingbird pollinated, has strong stigmal deflection 30–180 minutes after opening. Janzen (1968) reported that the flowers open asynchronously between 5:30 and 7:30 A.M. and are repeatedly visited. Possibly all blue- and white-flowered species are bee pollinated (G. Frankie, pers. comm.), though the possibility of self-pollination (Lewis, 1966) cannot be overlooked. *P. foetida* is reported by Janzen to open synchronously in the early morning hours and is visited almost immediately by bees of the genus *Psiloglossa* (Colletidae); stigmal deflections take place within 30 minutes and all visiting activity ends in about 45 minutes. Flowers of *Passiflora* last but a single day and most wither well before the day is over.

Fruits are endozoochorous. Most seeds of the small, thin-walled fruits are probably dispersed chiefly by birds, whereas the larger-fruited species, such as *P. ambigua*, *P. menispermifolia*, *P. nitida*, *P. seemannii*, *P. vitifolia*, and *P. williamsii*, are probably dispersed chiefly by arboreal frugivores. Peccaries and white-tailed deer eat fruits of *P. vitifolia* (N. Smythe, pers. comm.). Many of these species have rinds so thick and leathery that only the larger birds would attempt to peck them open. Once fruits are opened by monkeys and other animals, birds might be instrumental in the dispersal of any seeds left, but the fleshy, sweet, translucent substance covering the seeds of nearly all species of *Passiflora* is very tasty, and opened fruits are seldom found with any seeds remaining. I suspect that animals spit out the seeds after sucking on them for a while because the seeds become very bitter or astringent.

Twelve genera and 600 species; subtropics and tropics.

PASSIFLORA L.

Passiflora ambigua Hemsl., Bot. Mag. 128, pl. 7822. 1902

Coarse vine, essentially glabrous, with simple tendrils in leaf axils. Stipules filiform, inconspicuous, not persistent; petioles 1.5–3 cm long, bearing 2 thick glands 0.5 to 1 cm above base; blades ovate to oblong-elliptic, acuminate, obtuse to subcordate at base, 10–20 cm long, 5–8(9) cm wide, subcoriaceous. Flowers solitary, adjacent to tendrils; peduncles ca 3 cm long (to 7 cm long in fruit), surmounted by 2 involucre bracts, the bracts free, trifid at apex, ca 3 cm long or longer, subfoliaceous; sepals 5, narrowly oblong, 4–6 cm long, maroon, with a slender appendage 2–4 mm long at apex; petals 5, narrowly

KEY TO THE SPECIES OF PASSIFLORA

- Stipules subreniform, 1.5 cm long and 1 cm wide *P. menispermifolia* H.B.K.
 Stipules mostly linear, to 2 mm wide:
 Blades peltate *P. coriacea* Adr. Juss.
 Blades basifixed:
 Blades 2- or 3-lobed at least to middle:
 Blades deeply 3-lobed, cordate at base; flowers and fruits more than 3 cm across:
 Palmate leaf veins 5; flowers deep scarlet, at least 10 cm diam; plants common
 *P. vitifolia* H.B.K.
 Palmate leaf veins 3; flowers white with pink, at most 7 cm diam; plants rare
 *P. williamsii* Killip
 Blades broadly 2-lobed, rounded at base; flowers and fruits less than 3 cm across:
 Blades more than 3 cm long along midvein; flowers paired *P. biflora* Lam.
 Blades less than 2.5 cm long along midvein; flowers generally solitary *P. punctata* L.
 Blades at most shallowly lobed (juvenile leaves of *P. seemannii* lobed):
 Blades shallowly 3-lobed or with the lobes reduced to angles:
 Petioles bearing 2 large auriculate glands near the base; flowers less than 3 cm diam,
 greenish-white *P. auriculata* H.B.K.
 Petioles eglandular; flowers more than 3 cm diam, white *P. foetida* L. var. *isthmia* Killip
 Blades not lobed:
 Blades deeply cordate and palmately veined *P. seemannii* Griseb.
 Blades at most rounded at base, not palmately veined:
 Blades at least serrulate; sepals lacking appendages *P. nitida* H.B.K.
 Blades entire; sepals with slender appendage at apex *P. ambigua* Hemsl.

lanceolate, 3–4 cm long, white outside, purplish inside; stamens 5; filaments ca half as long as corolla, purplish. Fruits ovoid to globose, to 15 cm long, greenish-yellow with whitish spots; exocarp 1–2 cm thick; seeds many, ca 8 mm long, with many small pits. *Croat 11858, Zetek 3480, s.n.*

Apparently rare; collected only once recently. Flowers from December to April. Mature fruits have been collected in the early rainy season, from May to July.

Southern Mexico to Colombia (Chocó). In Panama, known from tropical moist forest in the Canal Zone (around Gatun Lake) and Bocas del Toro, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón and Panamá; no doubt in Darién as well since it has been found in adjacent Colombia.

Passiflora auriculata H.B.K., Nov. Gen. & Sp.

2:131. 1817

Vine, with simple axillary tendrils. Stipules bristle-like, to 1 cm long; petioles 1.5–2.5 cm long, biglandular near base, the glands large, ear-shaped, to ca 3 mm long; blades \pm ovate, shallowly trilobate (generally with the lateral lobes reduced to angles), 7–15 cm long, 4–10 cm wide, glabrous to puberulent, with numerous brownish glands ca 1 mm diam. Flowers paired in leaf axils; peduncles ca 1 cm long in flower (ca 1.5 cm long in fruit), inconspicuously jointed above middle, the bracts inconspicuous; sepals 5, oblong-lanceolate, ca 1 cm long, foliaceous; petals 5, linear, shorter than sepals, whitish; filaments of corona about as long as sepals; stamens 5, united to ca 4 mm at base. Berries globose, 1–2 cm diam, yellow-green, becoming black when mature, scattered-puberulent; seeds many, ca 3.5 mm long, reticulate, dark. *Croat 5617.*

Occasional along the shore and to be expected in clearings. Flowers from October to March (sometimes from August), with the fruits maturing from March to July.

Nicaragua to Brazil and Bolivia. In Panama, known principally from premontane wet forest in Colón, Coclé, Panamá, and Darién; known also from tropical moist forest in the Canal Zone (Atlantic slope) and Bocas del Toro and from tropical wet forest in Panamá and Darién.

Passiflora biflora Lam., Encycl. Méth. Bot. 3:36. 1789

Guate-guate, Camacarlata, Calzoncillo

Vine, woody at base, essentially glabrous; stems striate. Stipules minutely setose, with 4 or 5 pairs of round glands essentially only in the central part, the first pair at the very base; petioles eglandular, to 2 cm long; blades broadly bilobed (occasionally with a small central lobe as well), V-shaped, obtuse to rounded at base, 3–5 (10) cm long in the center, 4–9 cm wide, distinctly lighter below, glabrescent, with a slender apiculum at apex of midvein and each lobe; palmate veins 3. Flowers paired in axils, 3–4 cm diam; peduncles to 2 cm long, jointed at or below the middle, with 3 slender bracts at articulation; hypanthium ca 3 mm deep, depressed at point of attachment to pedicel; sepals 5, lanceolate, 1.5–2 cm long, hooded, creamy white; petals 5, lanceolate, 1–1.5 cm long, creamy white; corona filaments in 2 series, the outer of

oblong filaments ca 7 mm long, yellow, the inner of narrowly linear filaments ca 5 mm long, reddish; operculum closely plicate, 3 mm high; gynophore ca 5 mm long; stamens 5, fused into tube around style; anthers dorsifixed, held below stigma, spreading and dehiscing extrorsely; ovary \pm tomentulose. Berries globose, 1.5–1.8 cm diam, yellow-green and mottled, becoming purple when mature; seeds many, to 3 mm long, reticulate, becoming dark. *Croat 5416, 5707.*

Occasional, along the shore over low vegetation in *Annona-Acrostichum* associations and in clearings. Flowers and fruits throughout the year.

Mexico to Colombia and Venezuela. In Panama, widespread and ecologically variable; known from tropical moist forest in all provinces, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Veraguas, and Panamá, from tropical wet forest in Colón and Darién, and from premontane rain forest in Chiriquí.

Passiflora coriacea Adr. Juss., Ann. Mus. Natl. Hist.

Nat. 6:109. 1805

Vine, sometimes trailing on the ground, \pm glabrous. Stipules narrowly linear, ca 5 mm long, persistent; petioles 1–4 cm long, bearing a pair of ear-shaped glands in apical half; blades peltate (the petiole attached 3–13 mm from base of blade), trilobate, broadly rounded to cordate at base, 3–7 cm long, 6–25 cm wide, the central lobe occasionally suppressed to a mucro, the lateral lobes nearly horizontal, abruptly acuminate; palmate veins 5. Flowers generally paired, axillary but also racemose, the racemes opposite the leaves; peduncles jointed above the middle, the bracts inconspicuous and deciduous; sepals 5, lanceolate, ca 1.5 cm long, greenish-white to cream-colored, apetalous; corona in 2 series, the outer of filaments to 10 mm long, the inner of a few glandular filaments at most 5 mm long; operculum not generally plicate, ca 2 mm high; gynophore ca 10 mm long; ovary glabrous. Berries globose, 1–2 cm diam, the exocarp generally fleshy, glaucous, green and perhaps speckled when immature, maturing dark blue; seeds many, ca 5 mm long, with about a dozen contiguous pits on each side, drying dark. *Croat 5414a, 6732.*

Occasional, on the shore and in the young forest. Flowers throughout the year, principally in the dry season, with most fruits maturing from May to July.

Southern Mexico to the Guianas, Bolivia, and Peru. In Panama, known from tropical moist forest in the central Canal Zone and from premontane wet forest in Coclé and Panamá.

Passiflora foetida L. var. *isthmia* Killip, Publ. Field

Mus. Nat. Hist., Bot. Ser. 19:497. 1938

P. hispida DC.

Vine, often creeping on the ground, yellow-pubescent on all parts, the trichomes ca 2 mm long, sometimes gland-tipped. Stipules about half encircling stem, deeply cleft with linear lobes, bearing glandular trichomes; petioles



Fig. 406. *Passiflora foetida* var. *isthmia*

Fig. 407. *Passiflora nitida*



2–8 cm long, eglandular but with glandular trichomes; blades variable, deltoid in ours, shallowly trilobate (the lobes abruptly acuminate), cordate at base, 5–8 cm long and 5–8 cm wide; palmate veins 5–7. Flowers strongly scented, solitary in leaf axils; peduncles 3–6 cm long, jointed directly beneath the flower, the bracts foliaceous, 2–3.5 cm long, 2- or 3-pinnatifid, the ultimate segments filiform, gland-tipped; sepals 5, \pm lanceolate, ca 2 cm long, white; petals 5, similar to sepals but slightly shorter; filaments of corona in several series, the longer to 1.5 cm long, purple below, the shorter ca 2 mm long; operculum erect, ca 1 mm long, denticulate. Berries inflated, ovoid, yellowish, ca 2.5 cm long, minutely apiculate at apex, subcordate at base, usually obscurely 3-sulcate and with 3 indistinct lines of dehiscence (apparently nonfunctional?); exocarp very thin; seeds numerous, ovoid-flattened, ca 5 mm long and 2.5 mm wide, slightly sculptured, black, shiny, trilobate at base, bearing at apex a slender funicle ca twice length of seed. *Croat 4641, 7400.*

Occasional, in clearings. Flowers and fruits throughout the year. In Costa Rica the species begins to flower in June (beginning of the rainy season) and flowers into the following dry season (Janzen, 1968).

The species is a cosmopolitan weed native throughout the American tropics; the variety *isthmia* extends from Panama along the Pacific coast to Ecuador. In Panama, widespread in weedy areas; known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Panamá and Darién, from tropical dry forest in Panamá, from premontane wet forest in Bocas del Toro and Chiriquí, and from tropical wet forest in Colón and Darién.

See Fig. 406.

***Passiflora menispermifolia* H.B.K., Nov. Gen. & Sp. 2:137. 1817**

Vine; stems densely hispid-hirsute. Stipules conspicuous, subreniform, ca 1.5 cm long and 1 cm wide, cuspidate at one end, usually glandular-denticulate; petioles 1.5–5 (9) cm long, bearing 4–8 glands; blades suborbicular, 8–14 cm long, 8–13 cm wide, angulately trilobate, cordate at base, sometimes glandular-denticulate, definitely lighter and pilose below, densely pilose above, the middle lobes much larger, to 8 cm wide; palmate veins 5–7. Flowers solitary; peduncles 2–3 cm long, jointed directly beneath the flower, the bracts narrowly lanceolate, ca 10 mm long, at most 3 mm wide; sepals 5, lanceolate-oblong, 2–3 cm long, greenish-white, awned at apex, the awn little, off-white; petals 5, oblong, 2.5–3.5 cm long, light violet; filaments of corona in several series, the outermost to 2.5 cm long, glandular; operculum membranous, erect, divided above into numerous filaments ca 5 mm long; stigmas 3, ca 13 mm long. Berries narrowly ovoid, 6 cm long or more, ca 2 cm diam, glabrous; seeds ca 5 mm long, coarsely reticulate (fruit description from *Flora of Panama*, Woodson & Schery, 1958). *Aviles 21b, Woodworth & Vestal 634.*

Not seen on the island in recent years. Seasonal behav-

ior uncertain. Probably flowering and fruiting throughout the year.

Nicaragua to northwestern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, and Panamá and from premontane wet forest in Chiriquí (Boquete).

***Passiflora nitida* H.B.K., Nov. Gen. & Sp. 2:130. 1817**

Coarse vine, glabrous. Stipules linear; petioles 1.5–2 cm long, biglandular above the middle; blades ovate-oblong, acuminate, rounded to subcordate at base, 11–19 cm long, 6–11 cm wide, subcoriaceous, serrulate. Flowers solitary; peduncles 2–3.5 cm long, jointed directly beneath the flower, bracteate, the bracts 2, conspicuous, ovate-elliptic, ca 3.5 cm long and 2.5 cm wide, rounded at apex and base; sepals 5, oblong-elliptic, to 5 cm long, greenish outside, white inside; petals 6, similar, white; filaments of corona about 4 cm long, white with pink and blue; stamens 5, purple; pistil pinkish. Berries obovoid, blunt at apex, red-orange to orange-red or magenta, densely punctate with lighter dots (these often run together), 6–8 cm long, 4.5–6 cm wide, glabrous, the withered flower often persisting; pericarp 1–1.5 cm thick, spongy; seeds obovate, ca 7 mm long, punctate, black. *Shattuck 675, Zetek 3620.*

Occasional, high in the forest canopy. Flowers in Panama from December to May. Mature fruits have been seen throughout the year, mostly from April to September.

The Panamanian collections of this species have generally greater dimensions than those from South America. Also, the petiolar glands are slightly below the apex (about one-third of the way down the petiole), instead of at the apex as on South American species.

Panama to the Guianas, northern Brazil, and Peru. In Panama, known from tropical moist forest on BCI, from premontane wet forest in the Canal Zone, Colón, and Panamá, and from premontane rain forest in Darién (summit of Cerro Pirre).

See Fig. 407.

***Passiflora punctata* L., Sp. Pl. 957. 1753**

P. misera H.B.K.

Slender vine, essentially glabrous; stems striate. Stipules usually persistent, narrowly subulate, ca 2 mm long; leaf blades of 2, \pm oblong lobes directed at nearly 180° angle to each other (rarely with a small central lobe), truncate or subcordate at base, 1–2.5 cm long, 5–13 cm broad, the lobes rounded and mucronulate, the lower surface glaucescent with 3–5 pairs of round glands usually along midribs especially in axils of lateral veins; palmate veins 3. Flowers generally solitary in leaf axils; peduncles 3–9 cm long, obscurely jointed immediately below to 1 cm below the flowers, the bracts inconspicuous, setaceous, ca 1 mm long; calyx tube campanulate, ca 4 mm deep, the lobes 5, lanceolate, ca 1.5 cm long, light yellowish-green; petals 5, oblong, ca 1 cm long, greenish-white; filaments of corona in 2 series, the outer to 10 mm long, mostly

pale purple, the inner ca 5 mm long, purplish, narrower; operculum plicate, ca 3 mm high, incurved, purplish; gynophore slender, to 8 mm long, purple; ovary narrowly ellipsoid, to 4 mm long, purple, capitate. Berries globose, ca 1.5 cm diam, deep blue; seeds ovate, ca 3 mm long, transversely ridged, the ridges rugulose. *Croat 8273, 8278.*

Uncommon, along the shore. Flowers and fruits throughout the year.

The distinction is obscure between this species and *P. misera* H.B.K., which is therefore not recognized here.

The petals, sepals, and outer series of corona filaments reflexed somewhat at anthesis. Anthesis occurs in the early morning, and plants collected at 10:30 A.M. usually have all flowers closed. Nectar is probably enclosed within the operculum, within which many holes are seen.

Panama to Argentina. In Panama, known only from tropical moist forest around Gatun Lake.

Passiflora seemannii Griseb., *Bonplandia* 6:7. 1858

Guate-guate

Stout vine, glabrous; stems to at least 5 mm diam, striate. Stipules somewhat persistent, narrowly linear, 10–15 mm long; petioles 3–10 cm long, biglandular near apex; blades broadly ovate-cordate, rounded and mucronulate to apiculate at apex, 5–10 cm long, 6–11 cm wide, the basal sinus ca 3 cm deep, the lower surface glaucous, eglandular, the margins subentire to serrulate; palmate veins 7–9; juvenile leaves trilobate. Flowers solitary in leaf axils, ca 8 cm diam; peduncles 6–9 cm long (to 10 cm long when in fruit), jointed directly beneath flowers, the bracts 3, fused, 2.5–5 cm long, the lobes broadly ovate, white, purple-tinged; hypanthium ca 2 cm deep; sepals 5, ovate-lanceolate, 3.5–4 cm long, appendaged, greenish-white, sometimes tinged with violet; petals 5, oblong-lanceolate, ca 3.5 cm long, purple, the entire perianth strongly reflexed when open; corona filaments in 2 series, the inner erect, incurved at apex, to 2.5 cm long, banded with purple and white, the outer ca 1 cm long; staminal filaments fused except at apex; anthers shedding pollen after beginning of fruit development; operculum 2 mm high, denticulate; gynophore ca 2 cm long in flower; ovary ovoid; styles 3; stigmas broad, yellow. Berries broadly oblong to ovoid, at least 4–5 cm long and 3.5 cm broad, green, weakly pruinose, densely speckled with light green spots, the exocarp thick, white inside; seeds many, stalked, orbicular-ovate, ca 3 mm long, punctate. *Shattuck 692, Wetmore & Abbe 147.*

Uncommon along the shore. Flowers mostly from October to March, sometimes from August. The fruits mature from January to March.

Native to Panama and Colombia; cultivated elsewhere. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Panamá and Darién; known also from premontane wet forest in Chiriquí and Panamá and from tropical wet forest in Colón and Panamá.

See Fig. 408.

Passiflora vitifolia H.B.K., *Nov. Gen. & Sp.* 2:138. 1817

Guate-guate, Pasionaria, Granadilla, Granadillo de monte

Liana; stems to at least 1.5 cm diam, \pm densely ferruginous-pubescent on all parts. Stipules deciduous, subsetaceous, ca 5 mm long; petioles 2–6 cm long, inconspicuously glandular toward base; blades deeply trilobate, \pm deeply cordate, 7–14 cm long, 9–14 cm wide, the lobes acute to acuminate at apex, the central lobe larger, the upper surface sparsely strigillose except on tomentulose veins, the lower surface softly ferruginous-pubescent, the glands minute, 2 to several, around base of each sinus; palmate veins 5. Flowers solitary in axils, often borne on young leafless branches, 10–15 cm wide when open; peduncles 3–5.5 cm long (to 6.5 cm long in fruit), the bracts 3, free, lanceolate, 2.5–3 cm long, glabrescent, glandular-serrate, generally with a larger (1 mm across) disk-shaped pair of glands toward the base; sepals 5, narrowly lanceolate, 6–8 cm long, 1–2 cm wide, with a long slender appendage at apex; petals 5, linear-lanceolate, 4–6 cm long; both sepals and petals deep scarlet to magenta, reflexed when open; corona filaments in 3 series, the outer longest, to 2 cm long, erect, bright red or bright yellow; anthers 5, green, held perpendicular on gynophore; operculum deflexed, to 1 cm long, fimbriate; gynophore ca 1 cm long, pale red; ovary densely tomentulose. Berries ovoid, 5–8 cm diam, puberulent, greenish-yellow with darker stripes and bands of lighter splotches, very fragrant; seeds \pm flattened, ca 6 mm long and 5 mm wide, reticulate with numerous small punctations, light-colored. *Croat 4766, 8319.*

Frequent in the forest. Flowers from December to May, elsewhere in Panama also from July to November. Fruit maturity time not determined.

Native to lowland forests from Nicaragua to Venezuela and Peru; cultivated in the West Indies and elsewhere. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Colón, Coclé, and Panamá, and from tropical wet forest in Colón, Coclé, Panamá, and Darién.

Passiflora williamsii Killip, *J. Wash. Acad. Sci.*

12:262. 1922

Coarse vine, \pm densely puberulent on all parts. Stipules 6–7 mm long; petioles 4–6 cm long, bearing a pair of prominent glands 1–2 cm from base and sometimes a second pair above them; blades trilobate to about middle, truncate to generally deeply cordate at base, 9–13 cm long and wide, the lobes acuminate, the central lobe stronger and contracted toward the base, the upper surface glabrescent except on strigillose veins, the lower surface minutely crisp-villous, sparsely so in age, distinctly biglandular at base of each sinus, the glands ca 1 mm long, the margins subentire to serrulate; palmate veins at base 3. Flowers solitary in axils, 6–7 cm diam; peduncles to 2 cm long in flower, the bracts 3, united at base, ca 2.5 cm long, tomentulose; sepals 5, oblong, 2.5–3.5 cm long, with a slender appendage at apex; petals 5, oblong-spatulate,



Fig. 408. *Passiflora seemannii*



Fig. 409. *Carica cauliflora*

ca 2 cm long, white inside, spotted with dark pink; corona with the outer filaments shorter, 6–7 mm long, the middle series 2–2.5 cm long; operculum 2 mm long, entire; ovary densely white-tomentose. Berries globose, puberulent, to 5 cm long, green, lacking markings. *Zetek 4352*.

Collected only once on the island and not seen in recent years. Flowers elsewhere in Panama from February to June, and fruits from July.

Known only from Panama, from tropical moist forest in the Canal Zone and Los Santos (Loma Prieta) and from premontane rain forest in Darién.

99. CARICACEAE

Dioecious trees and shrubs with milky sap; trunk branched or not, herbaceous to soft-wooded. Leaves alternate, petiolate, clustered at ends of stems; blades palmately compound (*Jacaratia*) or simple and palmately lobed with palmate veins at base (*Carica*); stipules lacking. Corymbs, cymes, or racemes upper-axillary; flowers actinomorphic, few (pistillate) or many (staminate); calyx small, 5-lobed; corolla tubular and 5-lobed (staminate) or 5-lobed to near base (pistillate), showy; stamens 8 or 10, in 2 series; anthers 2-celled, dehiscent longitudinally; ovary superior, unilocular, 5-carpellate; placentation parietal, often intruding; ovules numerous; stigmas 5, free, linear, simple or branched. Fruits large berries; seeds many, with fleshy endosperm.

These pachycaulous, soft-wooded trees, which may look like overgrown herbs, are not confused with any other plants on the island.

The natural method of pollination is unknown. A number of different birds and insects, including hummingbirds, butterflies, *Trigona* bees, hawkmoths, and noctuid moths, have been seen taking nectar from staminate flowers (Traub et al., 1942; Allan, 1963). In contrast, pistillate flowers have no nectar and are less scented, but they have been observed being visited by moths and mosquitoes (Baker, 1973). Parthenocarpy has also been reported for *Carica* (Badillo, 1971), at least for *C. papaya*.

Although there is no *Carica papaya* growing wild on the island, the tasty fruits of *C. cauliflora* become soft enough to be pecked open by birds and would be attractive to other animals also. The bats *Carollia perspicillata* and *Artibeus jamaicensis* (Phyllostomidae) eat fruits of *C. papaya* in Trinidad (Goodwin & Greenhall, 1961). The cultivated *C. papaya* on BCI attracts opossums and prehensile-tailed porcupines (N. Smythe, pers. comm.).

Four genera and 31 species (Badillo, 1971), mostly of the genus *Carica*; mostly in the neotropics (one genus with two species in Africa).

CARICA L.

Carica cauliflora Jacq., Hort. Schoenbr. 3:33, t. 311. 1798

Unbranched dioecious tree, 3–6 m tall, to 10 cm dbh, mostly glabrous. Leaves in a dense terminal crown; petioles mostly more than 50 cm long, hollow, with slightly milky sap; blades ovate, shallowly 5-lobed when mature, cordate, 30–70 cm long, the lobes acute at apex, often broadly incised; palmate veins at base 5. Staminate inflorescences dichotomously branched, ca 30 cm long; pedicels very short; flowers many, ca 3 cm long; calyx deeply 5-lobed, ca 1.5 mm long, green; corolla light yellow, 5-lobed, the lobes spreading, linear-oblong, 12–20 mm long; anthers 10, nearly sessile, linear-spatulate, to 4 mm long. Pistillate inflorescences contracted, ca 7-flowered, 2.5–5 cm long; calyx lobes ca 2 mm long; corolla 5-lobed to base, ca 2.5 cm long, white or yellowish, the apices reddish; ovary glabrous; style ca 3 mm long; stigmas 5, linear, ca 1 cm long. Fruits maturing well below leaves, sometimes near base of trunk, borne on thick warty protuberances, the fruiting pedicels to 5 cm long and 8 mm diam; berries obovate, ca 8 cm long and 6 cm wide, minutely apiculate, becoming orange; exocarp to 7 mm thick, forming whitish droplets when cut; mesocarp sweet, pithy, white to translucent, with aroma of fresh grapes; seeds many, ovate, 10–12 mm long, the ridges 5 or 6, deep, corky. *Foster 1394*.

Rare; collected once by Aviles and once by Foster near the shore between the ends of Zetek and Armour trails. Flowers in the dry season (February and March). Some fruits have been seen in June and November.

Southern Mexico to Colombia and Venezuela; Trinidad. In Panama, known only from tropical moist forest in the Canal Zone, Veraguas, and Darién.

See Fig. 409.

Carica papaya L., Sp. Pl. 1466. 1753

Papaya

Unbranched tree, mostly to 6 m tall, essentially glabrous, dioecious or rarely polygamous or monoecious. Leaves in a dense terminal crown; petioles to 70 cm long; blades ovate, deeply 5–9-lobed, cordate at base, the lobes broadly pinnatifid when mature, 20–40 cm long, obscurely acuminate; palmate veins at base 7–9. Staminate inflorescences axillary; flowers many, short-pedicellate, ca 2 cm long; sepals 5, ca 1 mm long, green; corolla cream-yellow, the tube slender, the limb 5-lobed, the lobes oblong; stamens in 2 series, ca 2.5 mm long. Pistillate inflorescences of 1–3 flowers on pedicels to 2.5 cm long; calyx

KEY TO THE SPECIES OF CARICACEAE

- Leaves compound; trees more than 20 m tall *Jacaratia spinosa* (Aubl.) A. DC.
 Leaves simple, lobed; trees less than 8 m tall, soft-wooded:
 Leaves shallowly lobed, the palmate veins at base 5 *Carica cauliflora* Jacq.
 Leaves deeply lobed, the palmate veins at base 7–9 *Carica papaya* L.

lobes ca 1 mm long, green; corolla 5-lobed to base, 5–7 cm long, cream-yellow; style to 1 cm long; stigmas 5, usually with 1 or 2 short branches. Fruits maturing within crown of leaves; berries variable. *Croat 5907*.

Cultivated at the Laboratory Clearing. Flowers sporadically year-round.

Sex changes in the flowers are reported under different ecological conditions (Percival, 1965).

Native to the American tropics; now widespread in cultivation. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Panamá (Chimán), and from tropical wet forest in Colón (Portobelo).

JACARATIA C. DC.

Jacaratia spinosa (Aubl.) A. DC., Prodr. 15(1):419. 1864

Diocious tree, 20–40 m tall; trunk 0.8–1 m dbh, armed or unarmed, branched near apex, the branches slender, short, ascending, armed with short, stout, conical spines at least near their ends. Leaves palmately compound; petioles 10–25 cm long; leaflets 5–12, lanceolate, acuminate at apex, narrowly attenuated at base to an obscure petiolule 6–18 cm long, 2–6 cm wide, dark green above, glaucous below. Staminate inflorescences pedunculate, laxly cymose, 7–9 cm long; peduncles 6–12 cm long; bracts minute; pedicels 3–4 mm long; flowers many, tubular; calyx tube 1 mm long; corolla greenish-white, the tube 10–14 mm long, 3–4 mm wide, the lobes ovate-rounded, 7–8 mm long; stamens 8, in 2 unequal series, united in a short tube; filaments pilose; pistillode filiform, to 11 mm long. Pistillate flowers usually solitary, the other flowers not developing; peduncles 8–10 cm long; bracts 11–13 mm long; calyx tube 1–1.5 mm long; corolla divided almost to base, the tube 2 mm long, the lobes fleshy, 2–3.3 cm long, 7 mm wide; ovary narrowly ovoid, subpentagonal, 11–20 mm long; styles lacking; stigmas 5, narrowly linear, 7–8 mm long. Fruits ± ellipsoid, sometimes ovoid, obtuse or sometimes apiculate at apex, obtuse at base, to 12 cm long and 3.5 cm diam, pendent, yellow or orangish; seeds many, ovoid. *Foster 2816*.

Collected once on Balboa Trail. Seasonal behavior uncertain. Some flowers have been seen in March and mature fruits in September.

Nicaragua and the Guianas to northern Argentina, probably from Colombia and Venezuela. In Panama, known only from tropical moist forest on BCI and from tropical wet forest in Colón.

100. BEGONIACEAE

Fleshy, monoecious, annual or perennial, erect or scandent, terrestrial, epiphytic, or semiaquatic herbs. Leaves alternate, petiolate; blades simple, serrate, mostly asymmetrical at base; venation pinnate and usually also palmate at base; stipules present. Cymes terminal or axillary, bracteate; flowers few, unisexual, usually slightly zygomorphic; staminate flowers with 2 or 4 tepals, when 4, the outer pair valvate, the inner pair imbricate; stamens numerous in many whorls, free or basally connate, inserted on the receptacle; anthers 2-celled, basifixed, longitudinally dehiscent; pistillate flowers with 4 or 5 separate, undifferentiated, imbricate, showy tepals; ovary inferior, 3-locular; placentation axile; ovules numerous, anatropous; styles 3, bifid; stigmas spiraled, strongly papillose on all sides. Fruits unequally 3-winged, loculicidal capsules; seeds many, minute, lacking endosperm.

In Panama the family consists of only *Begonia*, which can be recognized by its succulent stems, asymmetrical leaves, unisexual flowers with four unequal tepals, and asymmetrical winged fruits.

Pollination system is unknown.

Though the fruits are winged, they are not themselves dispersed. At maturity the walls of the fruit split open along the bottom on all three sides, allowing the seeds to pass through slowly. Seeds are minute, dispersed at least in part by the fluttering of the fruit in the wind. The wing causes the fruit to flutter, ensuring that most seeds fall out only when there are air currents to carry them away. Seeds are also partly dispersed by rain wash (Ridley, 1930).

Five genera and over 800 species, mostly of *Begonia*; widespread in the subtropics and tropics.

BEGONIA L.

Begonia filipes Benth., Bot. Voy. Sulphur 101. 1845

Ala de angel, Hierba de agua

Weak, monoecious, annual herb, 15–60 cm tall, usually epiphytic; stems juicy, glabrous, reddish, weakly ridged. Petioles to 5 cm long; stipules oblong-ovate, 6–12 mm long, translucent, the apex very slender; blades very asymmetrical, semioval, acuminate, rounded at base, 3–10 cm long, 1–5 cm wide, appressed-pilose above, glabrous below, the margins crenate-dentate, ciliate. Cymes axillary or terminal; flowers white, few; bracts with deeply lacerate margins; staminate tepals 2, ovate, to 3.5 mm long, their margins sealed before anthesis; stamens to 18, on a short column; pistillate tepals 4(5),

KEY TO THE SPECIES OF BEGONIA

Leaves cordate, not strongly asymmetrical; herbs growing in marshy habitats *B. patula* Haw.

Leaves not cordate, strongly asymmetrical; herbs not growing in marshy habitats:

Plants suffrutescent perennials; all tepals more than 5 mm long; largest wing on fruit more than 1.2 cm wide *B. guaduensis* H.B.K.

Plants herbaceous annuals; pistillate tepals less than 5 mm long; wings of fruit less than 1.2 cm wide *B. filipes* Benth.

ca 2 mm long; styles 3, bipartite; stigmas spiraled, receptive before opening of staminate tepals. Capsules glabrous, 3-winged, the wings very unequal, the largest to 1 cm wide; seeds \pm round, minute, very numerous.

Croat 4318.

Occasional, in clearings and in somewhat open areas of the forest, loosely rooted in soil or more commonly epiphytic on mossy tree trunks; possibly locally abundant. Flowers and fruits all year, but flowering begins principally in the late rainy season. Most fruits mature in the early dry season. Leaves sometimes fall when plants have mature fruits.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, Chiriquí (San Félix), Panamá, and Darién.

Begonia guaduensis H.B.K., Nov. Gen. & Sp.

7:178. 1825

B. serratifolia C. DC.

Monoecious, erect or scandent, perennial herb, to 1(2) m long; stems woody at base, glabrous. Stipules oblong-ovate, acuminate, ca 8 mm long; petioles 2–20 mm long; blades strongly asymmetrical, lanceolate to elliptic-lanceolate, somewhat acuminate, inequilateral at base, one side cuneate, the other rounded, 5–9 cm long, 1.5–4 cm wide, membranaceous, glabrous, the margins doubly crenate-serrate, ciliate. Cymes dichotomously branched; flowers pinkish-white; bracts often deciduous, ovate, ca 5 mm long; staminate tepals 4, unequal, the outer 2 ovate, 8–15 mm long, the inner 2 elliptic-lanceolate, about half as long as outer; stamens numerous; pistillate tepals 5, subequal, elliptic, to 10 mm long; styles 3, bipartite; stigmas branched and finally spiraled. Capsules elliptic-oblancheolate, 3-winged, the wings very unequal, the largest triangular, ascending, 1.5 cm wide; seeds very numerous, elliptic, 0.3 mm long. *Croat 7374.*

Rare, in the forest. Flowers as early as September but usually not until December. The fruits develop quickly, some of mature size usually occurring with flowers on the same inflorescence. Plants are often leafless or nearly so when the plant is in full fruit.

Panama to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone,

Chiriquí (San Félix), Los Santos (Tonosí), and Darién and from premontane wet forest in Veraguas (west of Soná).

Begonia patula Haw., J. Wash. Acad. Sci. 40:245. 1950

B. ciliibracteola C. DC.; *B. fischeri* Schrank var. *tovarensis* (Klotzsch) Irmsch.

Erect, monoecious, perennial herb, sometimes aquatic, to 1.2 m tall, fleshy; stems red, sparsely brown-pilose to glabrous. Stipules ovate-oblong, to 1 cm long, caducous; petioles 5–45 mm long; blades weakly asymmetrical, \pm broadly ovate, acute or rounded at apex, cordate at base, 2–9 cm long, about as broad as or broader than long, glabrous above, mostly brown-pilose below, the margins crenate-serrate, ciliate; veins palmate at base. Inflorescences cymes of few flowers; bracts persistent, ovate, 2–4 mm long; staminate tepals 4, the outer 2 orbicular and ca 8 mm long, the inner 2 smaller, narrowly obovate; stamens numerous; pistillate tepals 5, obovate, 3–6 mm long; styles 3, bipartite, stigmas spiraled. Capsules 10–15 mm long, the 3 wings decurrent, very unequal, the largest ascending, often hooked, to 23 mm wide; seeds minute, fusiform. *Bailey & Bailey 644, Kenoyer 460.*

At least at one time a component of the floating masses of vegetation that border the shores, but not seen in recent years. Probably flowers and fruits throughout the year.

Mexico to Colombia, Venezuela, Peru, and Bolivia; Cuba. In Panama, known from marshy areas in tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Coclé (El Valle).

101. CACTACEAE

Epiphytic succulent herbs or shrubs, climbing by roots; stems chlorophyllous, terete to angled or flattened, with watery sap; areoles generally naked. Leaves lacking. Flowers bisexual, actinomorphic, solitary, sessile on the side of the stem; tepals 5 to many, petaloid, weakly differentiated, connate in a hypanthium; stamens twice as many as the tepals or numerous, spirally attached to hypanthium; anthers 2-celled, dehiscing longitudinally; ovary superior, 1-locular, 3- to many-carpellate; placentas

KEY TO THE TAXA OF CACTACEAE

- Stems terete; flowers minute, white; fruits round *Rhipsalis cassytha* Gaertn.
- Stems terete only at base, mostly angulate or prominently flattened:
 - Flowers 7.5–9(11) cm long; filaments white to yellowish
 - *Epiphyllum phyllanthus* (L.) Haw. var. *columbiense* (Weber) Kimn.
 - Flowers 24–29 cm long; filaments white or orange to reddish:
 - Filaments orange; tepals 4–5 cm long; fruits 4.5–7.5 cm long
 - *Epiphyllum phyllanthus* (L.) Haw. var. *rubrocoronatum* Kimn.
 - Filaments white; tepals mostly 2–3 cm long (rarely to 4); fruits 7–9 cm long
 - *Epiphyllum phyllanthus* (L.) Haw. var. *phyllanthus*

Epiphyllum phyllanthus var. *phyllanthus*, which occurs in the Canal Zone, may occur on the island. Some specimens (*Aviles 103b*) appear closest to that variety, but since they are sterile it is impossible to be certain.

few to several, parietal; ovules numerous, anatropous; style 1; stigmas as many as carpels, radiating. Fruits fleshy berries; seeds few to many, the endosperm viscid (*Rhipsalis*) or lacking.

The generally epiphytic, leafless aspect of the plants makes them hard to confuse with any other family.

Although nothing is known of the pollination of *Rhipsalis cassytha*, it can be concluded with little doubt that *Epiphyllum phyllanthus* is pollinated by hawkmoths (Porsch, 1939). Kimmach (1964) reported that flowers of *Epiphyllum* open at night and have a strong fragrance exuded during the night. Both of these features are strongly correlated with hawkmoth or other moth pollination. Moreover, because the nectar source is at the base of the very long, slender floral tube, the hawkmoth is probably the only pollinator capable of reaching it.

The fruits have tiny seeds embedded in a sweet sticky matrix. The larger fleshy fruits of *Epiphyllum* have been observed being pecked open by birds. There is no reason, however, to believe that they are not also dispersed by other arboreal animals. The small sticky seeds, which must germinate on tree branches, are most ideally suited to bird dispersal.

Genera mostly ill defined and of uncertain number, species about 1,800; almost all native in subtropical and tropical America.

EPIPHYLLUM Haw.

***Epiphyllum phyllanthus* (L.) Haw. var. columbiense** (Weber) Kimm., Cact. Succ. J. (Los Angeles) 36:114. 1964

Leafless epiphyte, glabrous; stems green, usually flexible and pendent, 3-sided in basal half, flattened and to 3 cm wide distally, the margins \pm regularly and obtusely serrate-lobed. Flowers borne along margins of ultimate stems, 7.5–9 (11) cm long, the limb 4.5–6 cm wide; perianth tube white, 5.5–9.5 cm long, bracteolate, the bracteoles slender, appressed at base, recurved at apex; tepals many, the outer 1.5–3 cm long, the inner 2–2.5 cm long; stamens many, cream-colored to yellow; filaments ca 7 mm long; anthers ca 1 mm long; style 6.5–8 cm long; stigma lobes ca 5 mm long. Berries green, 4–4.5 cm long, to 2.5 cm wide; seeds numerous, ca 2.5 mm long, the surface with closely spaced pits. *Croat 8256, Shattuck 603.*

Frequent, high in the canopy of the forest. Seasonal behavior not determined.

Costa Rica to Colombia and Ecuador. In Panama, known only from tropical moist forest in the Canal Zone and Chiriquí (Puerto Armuelles).

***Epiphyllum phyllanthus* (L.) Haw. var. rubrocoronatum** Kimm., Cact. Succ. J. (Los Angeles) 36:110. 1964

Leafless epiphyte, glabrous, often occurring in association with ant nests; stems green, usually stiff and pendent, terete at base, becoming 3-sided and mostly less than 2.5 cm broad, at apex 2-edged and to 7 (9) cm wide and less than 5 mm thick, the margins regularly and obtusely

crenate-lobed. Flowers borne along margins of ultimate stems, 24–29 cm long, the limb 9–11 cm wide; perianth tube usually pinkish, 21–26 cm long, slenderly bracteolate; tepals many, slender, 4–5 cm long, the outer pinkish, the inner white and broader than the outer; stamens many, orange; filaments exerted 2–3 cm; anthers ca 3 mm long; style exerted 2.5–4 cm above throat; stigma lobes 9–13, 5–6 mm long, both style and stigma orange. Berries angulate, 4.5–7.5 cm long, to 3 cm wide, magenta, the bracteoles persisting; seeds numerous, ca 3 mm long. *Croat 14059.*

Apparently uncommon, though possibly common since it usually grows high in the canopy at 10–30 m, sometimes on branches in the crotch of a tree but generally on top of the canopy in association with *Aechmea tillandsioides* var. *kienastii* (22. Bromeliaceae). Seasonal behavior uncertain. Some flowers have been seen in the dry season. Some fruits have been seen in the late dry and early rainy seasons.

Panama, Colombia, and Ecuador. In Panama, known only from tropical moist forest in the Canal Zone.

RHIPSALIS Gaertn.

***Rhipsalis cassytha* Gaertn., Fruct. & Sem. Pl.**

1:137. 1788

Mistletoe cactus

Slender, leafless epiphyte, 1–2 (9) m long; stems green, succulent, terete, pendent, sparsely branched, dichotomous or in false whorls, ca 5 mm thick, the areoles very inconspicuous, glabrous to minutely puberulent. Flowers lateral, solitary, sessile, greenish-white; tepals ca 2 mm long, the segments few (sometimes as few as 5), \pm free, usually spreading; stamens shorter than and about twice as numerous as tepals; filaments inserted on margin of hypanthium; style longer than tepals; stigmas 3 or 4. Berries fleshy, depressed-globose, to 9 mm long and 6 mm wide; exocarp thin; seeds several, to 1.3 mm long, about twice as long as broad, usually curved, dark brown, embedded in a sweet, sticky, watery matrix. *Croat 6742.*

Occasional, high in the canopy. Seasonal behavior not determined.

The fruits are probably dispersed by birds. Removing the fruit usually squeezes the seeds from the lower end, an action which probably frequently results in seeds' sticking to the outer edge of a bird's beak. Later, when the bird cleans its beak or feeds on bark insects, the seeds are deposited where they can germinate.

Throughout tropical America; Ceylon, tropical Africa. In Panama, known only from tropical moist forest in the Canal Zone and Bocas del Toro.

102. LYTHRACEAE

Trees, shrubs, or herbs. Leaves opposite, petiolate; blades simple, entire, sometimes punctate; venation pinnate; stipules present, minute. Flowers with a hypanthium, bisexual, actinomorphic (slightly zygomorphic in *Cu-*phaea**), sometimes glandular, solitary and terminal (in

KEY TO THE SPECIES OF LYTHRACEAE

- Flowers large, fleshy, parted 12 or more times, white to yellow; fruits woody capsules more than 4 cm diam with winged seeds; trees usually more than 5 m tall *Lafoensia puniceifolia* DC.
- Flowers small, 3–6-parted, white to magenta or violet; fruits small capsules less than 1 cm diam with wingless seeds; trees or herbs less than 2.5 m tall:
- Plants with small orange punctations on leaves, flowers, and fruits (black when dry), shrubs or small trees more than 1 m tall; petals white *Adenaria floribunda* H.B.K.
- Plants lacking punctations, herbs less than 50 cm tall; petals violet to reddish-violet or violet-purple *Cuphea carthagenensis* (Jacq.) Macbr.

Lafoensia) or in axillary clusters; calyx 4–6- or many-lobed (*Lafoensia*); petals showy, free, of the same number as and alternate with calyx lobes, arising from upper inner surface of hypanthium, crumpled in bud; stamens twice as many as petals, in 2 series, usually unequal; anthers 2-celled, introrse, dorsifixed, dehiscent longitudinally; ovary superior, 1- or 2-locular, 2-carpellate; placentation axile; ovules many, anatropous; style 1; stigma capitate. Fruits capsules, variously dehiscent, sometimes explosively so; seeds many, sometimes winged (*Lafoensia*), lacking endosperm.

A small but diverse family. The BCI species seemingly have little in common and are apparently diverse in both their pollination and diaspore strategies. Their only common features are the hypanthium, the superior ovary, and the crumpled petals. All are distinct species not confused with any other.

The flowers of both *Cuphea* and *Adenaria* are heterostylous and seem suited to insect pollination. *Cuphea*, which is zygomorphic, is probably pollinated by small bees. H. Baker (pers. comm.) reports some *Cuphea* and *Adenaria* to be self-pollinated, however. *Lafoensia puniceifolia* is bat pollinated (Vogel, 1958; Baker, 1973). I have seen petals falling from open flowers in the early morning, which also suggests nocturnal pollination.

The fruits of *Adenaria floribunda*, though several-seeded, are apparently indehiscent. The thin exocarp shatters easily, usually causing the cluster of fruits to break up as well. I suspect the fruits are taken by birds, which scatter some of the seeds and eat others. Diaspores of *Cuphea* are autochorous; those of *Lafoensia* are wind dispersed.

Some 22 genera and 500 species; in all regions, but most numerous in the American tropics.

ADENARIA Kunth

Adenaria floribunda H.B.K., Nov. Gen. & Sp.
6:188. 1824

Fruta de pavo

Shrub, to 2.5 m tall; stems pubescent and glandular, the younger ones often tetragonal and purplish-red. Petioles short, ca 5 mm long; blades lanceolate, acuminate, acute to obtuse at base, mostly 5–13 cm long and 2–5 cm wide, sparsely glandular on both sides (drying as black dots), glabrous to inconspicuously but densely puberulent above, puberulent below, the trichomes larger below and chiefly on veins. Flowers 4- or 5-parted, many, tristylous,

in axillary short-pedunculate clusters; peduncles 1–7 mm long; pedicels 5–7 mm long; hypanthium campanulate, 2–4 mm long; calyx lobes deltoid; petals obovate, white, to ca 2.5 mm long in the short- and long-styled flowers, to 4 mm long in the intermediate-styled flowers; stamens 8 or 10, the short-styled flowers with the stamens 3–4.5 mm long, the style to 1 mm long, the intermediate-styled flowers with stamens 4.5–5.5 mm long, the style to 1.5 mm long, the long-styled flowers with stamens to 3 mm long, the style to 3 mm long; ovary ovoid, short-stipitate; ovary and style pubescent; outside of hypanthium, calyx, petals, ovary, and style with orange glands (drying black). Fruits thin-walled, indehiscent capsules, ovoid or globose, bearing the persistent style, becoming red at apex, ca 4–5 mm long; seeds many, clustered in a globular mass, ca 1 mm long, broadest at apex, tapered to narrow base. *Croat 8325, 14942.*

Occasional, in clearings. Flowers from March to November. The fruits probably mature within 3 or 4 months.

Mexico to Argentina. In Panama, known from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién and from premontane moist forest in the Canal Zone and Panamá.

CUPHEA P. Browne

Cuphea carthagenensis (Jacq.) Macbr., Publ. Field
Columbian Mus., Bot. Ser. 8:124. 1930

Herb, to 50 cm tall, mostly erect; stems brownish, with long, straight, glandular trichomes interspersed with short curved trichomes, subwoody at base in age. Stipules minute; petioles less than 5 mm long; blades lanceolate to elliptic or ovate, acute at apex, acute to attenuate at base, 1–5 cm long, 0.5–2 cm wide, strigose and scabrous below, bearing sparse, long, straight trichomes above, the margins bearing short trichomes. Flowers 6-parted, generally solitary in reduced interpetiolar cymes, the leaves on the inflorescence much reduced near apex; peduncles and pedicels short; hypanthium \pm swollen on one side and weakly gibbous at base, to 7 mm long, prominently ribbed, with long trichomes on ribs, enclosing fruit at maturity; calyx lobes short, deltoid; petals spatulate, violet to reddish-violet or violet-purple, to 3 mm long, borne on upper margin of hypanthium, spreading; stamens (11)12, unequal, attached about midway on hypanthium, included; anthers violet, minute, introrse; ovary thin-walled; style to 1 mm long; stigma broader than style. Fruits capsules, bursting at maturity under

tension of the placenta, the placenta stout, reflexing and flinging seeds from the ovary; seeds 3–7, orbicular to elliptic, somewhat flattened, 1–2.5 mm long, with a narrow margin. *Croat 11991*.

Occasional, in the Lighthouse Clearing. Flowers from April to September.

United States, Central America, and South America. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Herrera, and Panamá, from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from lower montane wet forest and lower montane rain forest in Chiriquí.

LAFOENSIA Vand.

Lafoensia puniceifolia DC., *Mém. Soc. Phys. Genève* 3(2):86, t. 1. 1828

Amarillo, Amarillo fruto, Amarillo de fruto, Amarillo papito, Pino amarillo

Glabrous tree, usually 10–15(27) m tall; trunk to 1 m dbh; outer bark coarse, fissured, brown, thick; inner bark fine, thick, reddish, blending into lemon-yellow wood; sap lacking odor. Leaves deciduous; petioles 4–7 mm long; blades oblong-elliptic, acuminate, obtuse at base, 3–9 cm long, 1–3 cm wide, the acumen often broad at apex, the lower surface with a small pore at apex of midrib. Flowers 12–16-parted, solitary but clustered at apex in leafy pseudoracemes; pedicels 2–3 cm long, stout; bracteoles 2, small, deciduous, at base of flower; hypanthium campanulate, 2–4 cm long, nearly as wide, lobed ca one-third its length, the lobes acuminate; petals yellow or greenish-white, attached ca 5 mm below opening of hypanthium, obovate, 2.5–3 cm long; stamens many, long-exserted; filaments to 9 cm long, becoming reddish, united at base into a fleshy perigynous cup continuous

with the ovary; ovary turbinate, ca 1 cm long; style to 10 cm long. Capsules woody, ellipsoid, 4.5–6.5 cm long, brown, pointed at apex; pericarp 3–5 mm thick; seeds numerous, oblong, 2–4 cm long, winged. *Croat 7948*.

Common along the shore; occasional in the forest. Flowers from September to December. The fruits mature in the dry season (January to April).

This genus was reported by Nevlng in the *Flora of Panama* (1958) to have indehiscent fruits, but the fruits of *L. puniceifolia* are irregularly dehiscent. After the exocarp of the fruit falls free, the mass of winged seeds are exposed and blow away, usually a layer at a time.

Scattered from Mexico to Bolivia. In Panama, reported by Holdridge (1970) from low to middle elevations in moist areas and by Tosi (1971) as a characteristic component of tropical moist forest; known from tropical moist forest on BCI and in Panamá and Darién and from premontane moist forest in Panamá.

See Figs. 410 and 411.

103. LECYTHIDACEAE

Glabrous trees, occasionally buttressed. Leaves alternate, often clustered at ends of branches, petiolate; blades simple, entire or serrate; venation pinnate; stipules lacking. Corymbs or panicles subterminal, axillary or cauliflorous, bracteate; flowers large, bisexual, actinomorphic, occasionally fragrant; calyx generally 6-lobed, the fused portion forming a hypanthium (sometimes obscure in *Gustavia*); petals 4–12, equal or unequal; stamens many, in several series, often arising at the base from an androphore (occasionally only on one side of androphore in *Couratari*); anthers 2-celled, basifixed, dehiscing longitudinally; ovary inferior, 2–6-locular; placentation axile or pendulous; ovules 1 to several per locule, anatropous; style simple; stigma of several radicate slits. Fruits circumscissilely dehiscent capsules or indehiscent and baccate with a leathery exocarp (1-seeded berries in *Grias*,

KEY TO THE SPECIES OF LECYTHIDACEAE

- Leaves less than 18 cm long; capsules woody, ± cylindrical pyxidia to 12 cm long *Couratari panamensis* Standl.
- Leaves to 1 m or more long; fruits not as above, fleshy pyxidia or berries:
 - Flowers small; petals 4(5), to 2 cm long; fruits ellipsoid, the seed 1 *Grias fendleri* Seem.
 - Flowers large; petals 6–12, to 7 cm long; fruits subglobose, the seeds several:
 - Flowers always cauline (borne below the leaves); fruits 7–10 cm wide *Gustavia superba* (H.B.K.) Berg
 - Flowers always or mostly subterminal (borne above the leaves):
 - Leaf blades 73–100 cm long, 10–21 cm wide, with 45–54 pairs of lateral veins; flowers always subterminal; floral bracts 80–105 mm long, 30–35 mm wide; bracteoles 45–65 mm long, 34–48 mm wide; calyx lobes ovate to oblong, 29–55 mm long, 24–55 mm wide; fruits with an orange endocarp *Gustavia grandibracteata* Croat & Mori
 - Leaf blades 30–72 cm long, 4.5–10 cm wide, with 22–31 pairs of lateral veins; flowers mostly subterminal, infrequently cauline; floral bracts 8–12 mm long, 5–7 mm wide; bracteoles 7–11 mm long, 5–8 mm wide; calyx lobes broadly triangular, 4 mm long, 14 mm wide; fruits with a creamy white endocarp *Gustavia fosteri* Mori

Gustavia grandibracteata will probably be found on the island, although it has not been seen yet. It is common around swamps in the Canal Zone.



Fig. 411. *Lafoensia punicifolia*



Fig. 410.
Lafoensia punicifolia

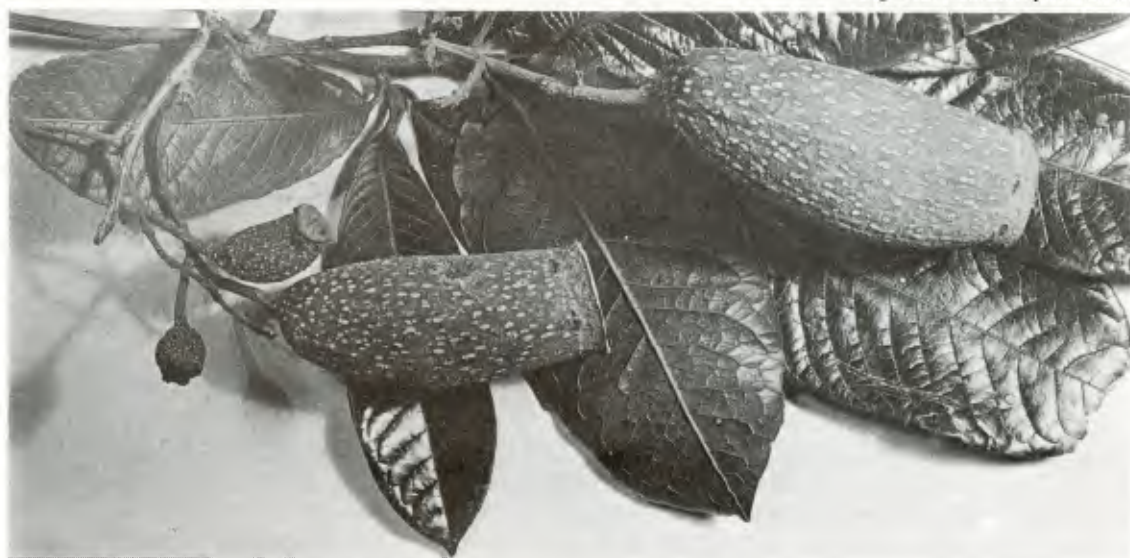


Fig. 412. *Couratari panamensis*

1- to few-seeded pyxidia in *Gustavia*); seeds 1 to several per locule, sometimes winged (*Couratari*), lacking endosperm.

Members of the family are distinguished by their unusual flowers with numerous petals, many stamens (sometimes on one side of the androphore and folded over), and an inferior ovary with a sessile, simple stigma.

The flowers are best suited to bee pollination. (See the discussion under *Gustavia superba*.) They do not last more than 1 day whether they are pollinated or not (Prance, 1976).

The fruits of *Grias* and *Gustavia* are dispersed by arboreal frugivores such as white-faced and howler monkeys (Oppenheimer, 1968; Hladik & Hladik, 1969; Carpenter, 1934), though agoutis, spiny rats, and peccaries are important in transporting seeds (Enders, 1935; N. Smythe, pers. comm.). Generally the orange mesocarp is eaten, leaving the seeds unharmed—perhaps they are toxic, as Mori (1970) showed for those of *Lecythis*. *Couratari panamensis* has wind-dispersed seeds.

Either 24 genera and about 450 species (Adams, 1972) or 15 genera and 325 species (Willis, 1966); mostly in wet tropical regions.

COURATARI Aubl.

Couratari panamensis Standl., Publ. Field Columbian Mus., Bot. Ser. 4:239. 1929

Coco, Coco de mono, Coquito, Congolo, Carapelo

Tree, to 40 m tall, to 75 cm or more dbh; buttresses 1–2 m high; outer bark reddish-brown, hard, moderately coarse, with weak vertical fissures; inner bark pale; wood reddish-brown, hard; stems minutely ferruginous-hirtellous, at least when young, angulate on drying. Petioles 5–15 mm long, glabrate; blades oblong to oblong-elliptic, acute to short-acuminate, obtuse to rounded at base, 5.5–18 cm long, 2–8 (10) cm wide, hirtellous to glabrate on midrib and veins, the margins irregular. Panicles terminal, bearing few to many flowers; flowers with a faint, somewhat unpleasant aroma, precocious or occurring with new leaves, sometimes on a few leafless branches while other branches fully leaved; pedicels 1.5–2.5 cm long; calyx deeply 6-lobed, the lobes imbricate, \pm ovate, obtuse; petals 6, lavender to rose, to ca 2.5 cm long, rounded at apex, often minutely fimbriate, of unequal widths, 2 petals \pm spatulate, usually broader, to 1.3 cm wide, the others narrowly oblong, to 8 mm wide; androphore produced into a prominent hood spirally involute then reversely revolute, the whole structure subglobular, slightly broader than high, to 1.7 cm wide, \pm magenta and white, the basal part of the androphore shaped like a soap dish, whitish inside, magenta on margins; stamens mostly 13–18, arranged around the stigmatic orifice, ca 1 mm long; anthers rounded, flattened, about as long as filament; ovary 3-celled; stylar orifice ca 1.5 mm diam; stigma \pm sessile, minutely 3-radiate. Capsules woody, narrowly cylindrical-campanulate pyxidia, slightly asymmetrical, brown, conspicuously lenticellate, 7–12 cm long, 3–4 cm diam, pendent at maturity; cap and the strong central placenta falling free to allow dispersal of seeds

through orifice; seeds several per locule, prominently winged, thin, ca 7 cm long. *Croat 8061, 16507.*

Rare; only a few individuals known on the island. Flowers from July through August, but an individual may flower only once every two years. Allen (1956) reported flowering in late September on the Osa Peninsula in Costa Rica. The fruits mature in February and March.

Wind is probably important in dislodging the seeds from the dangling, pendent fruits.

Costa Rica and Panama. In Panama, known principally from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and Panamá; known also from premontane wet forest in the Canal Zone (Pipeline Road). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 412.

GRIAS L.

Grias fendleri Seem., Bot. Voy. Herald 126. 1854

Jaguey, Membrillo, Membrillo macho, Sapo

Glabrous tree, to 7 (25) m tall; trunk smooth; wood hard; branches stout, thick. Leaves alternate, clustered at apices of branches, sessile; blades oblanceolate, acuminate at apex, gradually attenuate from above middle to a decurrent subpetiolar base, to 1 m long, 25 (40) cm wide. Umbelliform clusters cauliflorous, on both trunk and branches below leaves, bearing few flowers; flowers sweetly aromatic; hypanthium and calyx ca 8 mm long; calyx often splitting irregularly in age; petals 4 (5), ovate, white, to 17 mm long, to 11 mm wide, sometimes unequal, the innermost reduced or more markedly concave than the others; stamens numerous, the outermost longer, to 9 mm long; filaments fleshy, often turned inward near apex, the thecae 2 per stamen, loosely attached; ovary bright red at apex; stigma sessile, consisting of (3)4 equidistant radial slits, apparently secreting a viscous fluid. Berries ellipsoid, indehiscent, becoming ribbed in age, to 5 cm long (only immature fruits seen); seed 1. *Croat 13961.*

Known from a single area along the shore of Gigante Bay. Flowers asynchronously from February to May. Time of fruit maturity is uncertain.

Costa Rica (Osa Peninsula) and Panama. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and Chiriquí and from tropical wet forest in Colón. Tosi (1971) reported this genus to be characteristic of tropical wet forest in Panama. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 413.

GUSTAVIA L.

Gustavia fosteri Mori, Brittonia 30:340. 1978

Small tree, to 4 m tall; leaf-bearing branches 5–8 mm diam, the internodes 4–21 cm long. Leaves in 1–5 clusters at apices of branches, 9–16 per cluster; petioles 0.5–5 cm long, 3–5 mm thick at blade juncture; blades oblanceolate to narrowly oblanceolate, attenuate to acuminate

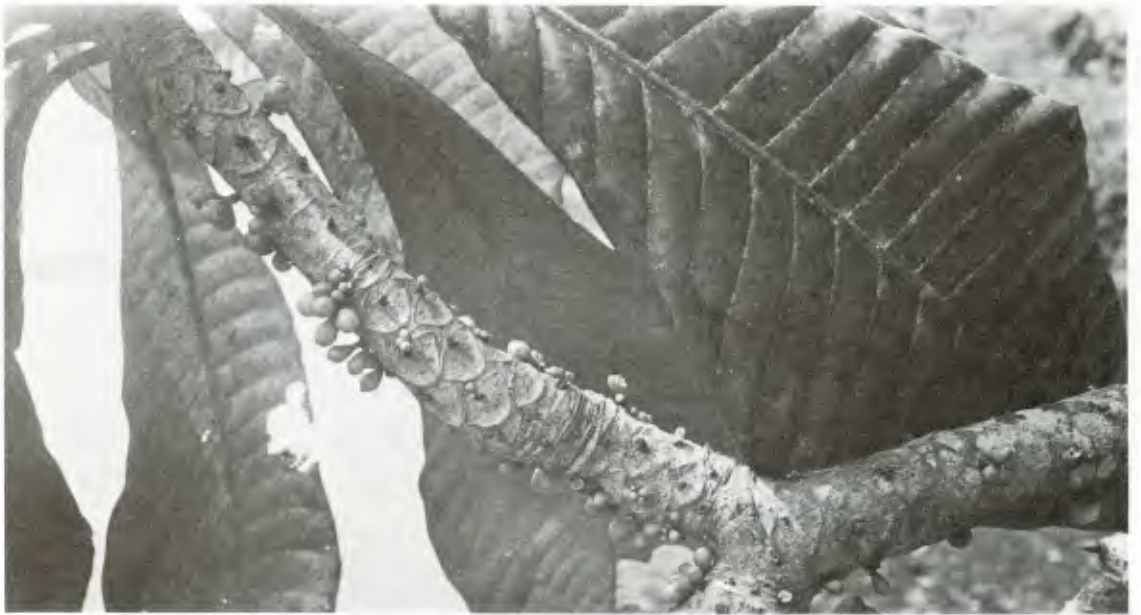


Fig. 413. *Grias fendleri*

Fig. 414. *Gustavia superba*



Fig. 415. *Gustavia superba*



at apex, tapered from middle to an acute base, 30–72 cm long, 4.5–10 cm wide, glabrous, chartaceous, the margins serrate apically, entire basally; lateral veins in 22–31 pairs, the intramarginal vein well developed. Inflorescences subterminal, infrequently cauline, with up to 13 flowers; rachis 5–6.5 cm long, 9–12 mm wide at base; pedicels 6–7.5 cm long; basal bract 1, triangular to narrowly triangular, 8–12 mm long, 5–7 mm wide, the bracteoles 2, ovate to narrowly ovate, cucullate, 7–11 mm long, 5–8 mm wide, inserted slightly above the middle; flowers 10–14 cm diam; calyx lobes 4, broadly triangular, 4 mm long, 14 mm wide; petals 8, narrowly obovate to oblanceolate, 5.5–6.5 cm long, 2–2.5 cm wide, light pink throughout; androphore connate at base, light pink, 11–12 mm high; outermost filaments white at the base, dark pink above, 18–19 mm long; anthers yellow, 2.5–3.5 mm long; ovary puberulent, 5-locular, white-pubescent at apex; ovules 20–30 per locule; style conical, 3 mm long; stigma with 5(6) lobes. Pyxidia globose, truncate at apex, 5 cm long, 5 cm wide, obscurely 4-costate, the calyx lobes persistent, the operculum nearly as wide as the fruit; funiculi white, 5 mm long, 4–5 mm wide; seeds several, cream-colored, irregularly 3-sided in cross section, 3–3.5 cm long, 2.2–2.4 cm diam, surrounded by a creamy white endocarp. *Foster 2790* (holotype, *MO*; isotype, *F*).

Apparently rare; collected once by R. Foster near the junction of Snyder-Molino and Wheeler trails. The species has been observed in flower in June and July, and with mature fruits in September and October.

The closest relative of *G. fosteri* is *G. angustifolia* Benth. of the dry coastal forests of Ecuador. The principal difference between these two species is the glabrous lower leaf surface of *G. fosteri*, in contrast to the pubescent surface of *G. angustifolia*.

The species is easily confused with the much more abundant *G. superba*, but is distinguished by having its leaves grouped in several verticils at the branch ends instead of scattered along the ends of the branches, by its mostly terminal instead of cauline inflorescences, by its calyx of four broadly triangular lobes (the calyx in *G. superba* is entire), and by its petals being light pink throughout instead of white with flushes of pink. Also the fruit has a white instead of orange mesocarp at maturity, and the leaves of *G. fosteri* tend to be smaller than leaves of *G. superba*.

Known only from BCI.

Gustavia superba (H.B.K.) Berg, *Linnaea* 27:444. 1856
Membrillo, Membrillo hembra

Trees, mostly 6–10 (15) m tall; trunks usually less than 20 cm dbh, branching infrequently; wood moderately hard. Leaves alternate, crowded at ends of stout branches; petioles very short or to 11 cm long on juveniles; blades elliptic-oblanceolate, abruptly acuminate, narrowly cuneate and more or less decurrent onto petiole, mostly to 1 m or more long and 25 cm wide, glabrous, coarsely toothed. Corymb short, beneath leaves; pedicels stout, to ca 8 cm long, minutely puberulent; flowers mostly to

12 cm diam; hypanthium turbinate, to 2.5 cm wide; calyx obscure; petals 6–12, unequal, \pm spatulate, oblong, to 7 cm long and 3.5 cm wide, white to cream or spotted with lavender, especially on outside; stamens many, ca 4 cm long, fused one-third their length into a yellowish ring; filaments fleshy, arched inward, often tinged with lavender above, constricted just below anther; stigma short-conical. Pyxidia depressed-globose, 7–10 cm broad, to ca 8 cm long, indehiscent, baccate, with a prominent raised ring at apex, green or pale yellow to orange at maturity with irregular brown lenticels and minute longitudinal ribs, often with a foul odor at maturity; seeds few, fleshy, irregularly shaped, to ca 6 cm long. *Croat 5095, 8812*.

Abundant in the forest, most abundant in the younger forest. Flowers from March to June (sometimes from January). The fruits mature from June to August, sometimes from April and especially in July; they are eaten by white-faced monkeys as early as April (Hladik & Hladik, 1969).

At anthesis the flowers have a sweet aroma, but they become foul-smelling like the fruit in age. Euglossine-like bees have been observed making rapid and repeated visits to the flower. Either the bee enters the staminal tube or it ruffles rapidly through the stamens as if to shake pollen loose. Usually the bee enters the staminal tube and in every case entry was from the lower edge, which is V-shaped, owing to the inflexed stamens. The upper edge of the V-shaped opening through which the bee enters is directly over the stigma. Mori & Kallunki (1976) reported *Gustavia superba* to be self-compatible and observed the species being visited by various bees, including a species of *Melipona* (Apidae), various species of *Trigona* (Apidae), a species of *Xylocopa* (Xylocopidae), and a species of Halictidae. R. Foster (pers. comm.) suggests that bats may be more important in pollination of *Gustavia* and bees may be only incidental pollinators.

The species is easily confused with *G. grandibracteata* Croat & Mori, which is to be expected on the island. The key for this family gives the distinguishing characteristics. Woodson and Schery in the *Flora of Panama* (1958a) reported the range of *G. superba* to be as far south as Ecuador; they were confusing the species with *G. angustifolia* Benth., which occurs there.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé.

See Figs. 414 and 415.

104. RHIZOPHORACEAE

Shrubs or trees. Leaves opposite, petiolate; blades simple, dentate; venation pinnate; stipules present, interpetiolar. Fascicles bracteate, upper-axillary; flowers bisexual, actinomorphic, mostly numerous; calyx campanulate, 4- or 5-lobed, the lobes valvate; petals 4 or 5, free, white;

stamens many, united basally by the filaments, inserted on a disk; anthers 4-celled, introrse, dehiscent longitudinally; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules 2 per locule, pendulous, anatropous; style 1; stigma capitate. Fruits 3-valved, tardily dehiscent, septicial capsules; seeds about 3, arillate, usually with endosperm.

Only two genera occur in Panama. *Rhizophora*, a genus of mangroves, does not occur on BCI. *Cassipourea* is distinguished by its opposite leaves, its interpetiolar stipules, and its spatulate, lacinate petals. It is surely insect pollinated. Fruits are adapted for dispersal by birds.

Sixteen genera and 120 or more species; tropics.

CASSIPOUREA Aubl.

Cassipourea elliptica (Sw.) Poir., Dict. Suppl.
2:131. 1811

C. podantha Standl.

Huesito, Limoncillo, Goat wood

Shrub or tree, to 13 (17) m tall; stems nearly glabrous, ± roughened with lenticels. Stipules interpetiolar, 4–5 mm long, caducous; petioles 3–10 mm long; blades ovate to elliptic, acute to acuminate at apex, cuneate at base, 5–16 cm long, 2–6.5 cm wide, glabrous, often weakly toothed in apical half. Fascicles upper-axillary; flowers 4- or 5-parted, usually numerous; pedicels 2–5 mm long, articulate beneath flower; calyx campanulate, valvate in bud, thick, to 5 mm long, glabrous outside, sericeous inside, exuding a yellowish sap when cut, persistent and reddish in fruit; petals white, spatulate, thin and lacinate, usually pilose, to ca 7 mm long; stamens 15–25, included, ca 7 mm long; filaments slender, often united at base; anthers to ca 1 mm long, 4-celled (owing to a partition in the thecae); ovary depressed-globose; style to 6.5 mm long, persistent in fruit; stigma and apex of ovary sericeous; stigma capitate. Capsules elliptic to obovoid, ca 1 cm long, yellowish at maturity, fleshy, glabrous except for few trichomes at apex, splitting into 3 parts to expose seeds; seeds 2(4), brown, covered with a white, much-folded aril. *Croat 5371, 6132.*

Frequent along the shore on the north side of the island; uncommon in the young forest. Flowers and fruits throughout the year, especially from April to August. Allen (1956) reported the species to be common in mangrove swamps and to flower in May. Frankie, Baker, and Opler (1974) reported the species to be bimodal in its flowering, with some flowers during January and February and some during July and August in Costa Rica; the fruits there mature from July to October.

Allen (1956) reported the tree to be as tall as 30 m. The flowers have abundant pollen and seem well suited to pollination by pollen-collecting insects.

Seeds are shiny and arillate and are probably bird dispersed.

Guatemala to Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in the Canal Zone and Panamá, from tropical wet forest in Colón, Panamá, and Darién, and from premontane rain forest in Darién (Cerro Pirre).

105. COMBRETACEAE

Trees, shrubs, or lianas, sometimes bearing spines. Leaves alternate or opposite, petiolate; blades simple, entire; venation pinnate; stipules lacking. Inflorescences spikes, panicles, or simple or paniculate racemes, axillary, bracteate; flowers bisexual, actinomorphic or slightly zygomorphic; calyx campanulate or cupulate, forming a hypanthium, 4- or 5-lobed; petals 4 or 5 or lacking (*Terminalia*), attached to the calyx; stamens 8–10, free, in 2 series, inserted on the calyx tube; intrastaminal disk present; anthers 2-celled, versatile, dehiscent longitudinally; ovary very small and inconspicuous when immature, inferior, 1-locular, apparently 1-carpellate; placentation apical; ovules usually 2, sometimes 4–6, anatropous, all suspended from a single funiculus; style 1, slender; stigma simple, capitate or undifferentiated. Fruits indehiscent pseudocarps, with 2–5 wings or ridges; seed single, lacking endosperm.

Combretaceae are distinguished by the usually small, white, open flowers congested into spikes or racemes with exerted stamens (double the number of perianth lobes), by having all ovules suspended from the apex by a slender funiculus, and by the usually winged fruits.

The flowers are mostly small, white, open, and bowl- or cup-shaped with stamens and style long and protruding. They are usually very numerous and fit the brush-type pollination syndrome of van der Pijl (1966). Small amounts of easily accessible nectar have usually been observed. I have seen flowers of *Combretum cacoucia* and *C. fruticosum* visited by hummingbirds.

The winged fruits of all species except *Combretum cacoucia* and *C. laxum* var. *epiphyticum* are wind dispersed and generally good fliers. *Combretum cacoucia* and *C. laxum* var. *epiphyticum* have fruits that are very buoyant and no doubt chiefly water dispersed (Croat, 1974b).

Eighteen genera and about 500 species; subtropics and tropics.

KEY TO THE GENERA OF COMBRETACEAE

- Plants lianas; petals present; fruits 4- or 5-winged or -ridged, the wings or ridges all equal *Combretum*

 Plants trees; petals lacking; fruits with 2 prominent wings and 1–3 shallow ridges or vestigial wings
 *Terminalia*

KEY TO THE SPECIES OF COMBRETUM

- Corolla red; upper hypanthium and calyx more than 12 mm long; fruits more than 3 cm long, with 5 ridges *C. cacoucia* Exell
- Corolla white or yellowish; upper hypanthium and calyx less than 10 mm long; fruits less than 3 cm long, with 4 ridges or 4 or 5 wings:
- Stamens more than 1 cm long; plants bearing minute, golden scales on underside of leaves and on hypanthia, calyces, and fruits *C. fruticosum* (Loefl.) Stuntz
- Stamens less than 1 cm long; plants not golden-lepidote:
- Flowers 5-parted; fruits mostly less than 1.5 cm long, with 5 wings *C. decandrum* Jacq.
- Flowers 4-parted; fruits more than 1.5 cm long, with 4 wings or ridges:
- Fruits 4-angled or, if winged, the divisions less than halfway to center of fruit; plants flowering in March and April, with the fruits maturing in August and September; young stems, axes of inflorescences, and petioles densely ferruginous-tomentose; lower leaf surfaces conspicuously puberulent *C. laxum* Jacq. var. *epiphyticum* (Pitt.) Croat
- Fruits 4-winged, divided nearly to center of fruit; plants flowering mostly in October and November, with the fruits maturing from January to March; young stems, axes of inflorescence, and petioles glabrous or puberulent, never densely ferruginous-tomentose; lower leaf surfaces glabrous *C. laxum* Jacq. var. *laxum*

COMBRETUM Loefl.

Combretum cacoucia Exell in Sandw., Bull. Misc. Inform. 1931:469. 1931

Liana; branchlets rufous-pilose. Leaves opposite; petioles 5–10 mm long, articulate above base; blades broadly ovate to oblong-elliptic, mostly acuminate at apex, subcordate at base, 8–20 cm long, 4–8 cm wide, shiny when fresh, at most short-pilose on veins below, chartaceous. Racemes to 35 cm long; flowers bright red, slightly zygomorphic, each subtended by a lanceolate, caducous bract to 15 mm long; pedicels ca 5 mm long; lower hypanthium (ovary) ca 5 mm long, the upper hypanthium campanulate, to 2 cm long; pedicels, hypanthia, and calyx lobes densely ferruginous-tomentose; calyx lobes 5, triangular, to 5 mm long; petals 5, ovate to elliptic, to 1 cm long, mucronate, affixed at apex of hypanthium; stamens 10, attached at 2 different heights on calyx tube, 1.5–2.5 cm long; ovary topped by a strigose disk; style ca 3 cm long, barely exceeding stamens. Fruits narrowly ellipsoid, longitudinally 5-ridged, 5–6 cm long, dry. *Wilson 116*.

Collected once on the island. Probably rare this far south of the Caribbean coast, the plant is much more common in regions near the Caribbean. Flowers in the dry season (January to May). Some mature fruits have been seen in April.

Hummingbirds, no doubt the natural pollinator, have been observed visiting these slender, bright-red, tubular flowers with abundant nectar.

Belize to Brazil. In Panama, principally near the Caribbean coast; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and San Blas, from premontane wet forest in the Canal Zone and Colón, and from tropical wet forest in Colón.

Combretum decandrum Jacq., Enum. Syst. Pl. Ins. Carib. 19. 1760

Liana; trunk to 12 cm diam near ground; outer bark coarse, flaky, thin; inner bark weakly and irregularly

ringed; branches bearing stout, straight or recurved spines to 4.5 cm long (mostly less than 1.5 cm long on upper stems); juvenile stems slender, leafless, chlorophyllous, bearing slender spines becoming somewhat recurved in age. Leaves alternate or subopposite, deciduous; petioles 5–15 mm long, articulate 1–5 mm above base, the lower part accrescent, persistent; blades narrowly ovate to oblong-elliptic, acuminate, rounded or subcordate and often inequilateral at base, 5–15 cm long, 3–7 cm wide, mostly pellucid-punctate, glabrous or pubescent on veins below, the axils usually with tufts of trichomes, the midrib commonly arched. Panicles large, terminal and upper-axillary, becoming axillary by new growth; flowers white, subsessile or short-pedicellate, 5-parted, actinomorphic, usually 6–7 mm wide; calyx and hypanthium together ca 4 mm long, the upper hypanthium and calyx campanulate to cup-shaped, glabrous, the lower hypanthium glabrous or weakly pubescent with erect trichomes; calyx lobes triangular, ca 0.5 mm long; petals 5, obovate-elliptic, 2–3 mm long, pubescent; stamens 10, exserted; filaments ca 4 mm long; disk present; style ca 4 mm long. Fruits ovoid to orbicular, 1–1.4 cm long, acute to rounded and weakly emarginate at apex, acute at base, broadly 5-winged, glabrous, brown at maturity. *Croat 5545, 14818*.

Often seen as juvenile or adult leafless plants on the forest floor, but rarely encountered with leaves except high in the canopy or along the shore, where it is common. Accrescent petiole bases serve the same function as spines, i.e., assisting in climbing by preventing the branches from slipping. Flowers from March to May, rarely later in the rainy season. The fruits mature from April to July.

Fallen fruits of this species may be easily distinguished from those of *C. laxum* and *C. fruticosum* by being smaller and having five wings.

Mexico to Colombia. In Panama, known from tropical moist forest in the Canal Zone and Los Santos and from premontane moist forest in Darién.

See Figs. 416, 417, and fig. on p. 20.



Fig. 416. *Combretum decandrum*

Fig. 417. *Combretum decandrum*



Combretum fruticosum (Loefl.) Stuntz, U.S.D.A.

Bur. Pl. Industr. Invent. Seeds 31:86. 1914

C. farinosum H.B.K.

Chupachupa

Liana; periderm of older stems sometimes peeling off as fibers; leaves, rachises, and calyces bearing somewhat sunken scales (especially lower leaf surfaces). Leaves opposite; petioles 7–10 mm long; blades \pm elliptic, acuminate and mostly falcate at apex, cuneate or rounded at base, 6–12 cm long, 2–6 cm wide, yellowish below owing to golden scales. Panicles terminal or upper-axillary; flowers 4-parted, actinomorphic, pellucid-punctate, yellowish-green or yellow, sessile or subsessile, densely arranged along branches, the branches 1-sided, spikelike, mostly 9–12 cm long; hypanthium (ovary and calyx tube together) ca 1 cm long, the upper part campanulate, golden-scaly; calyx lobes short, acute, exceeding petals; petals minute, yellow; stamens 8, yellowish, 15–20 mm long, subtended by the pilose, funnel-shaped disk; stamens and style folded in bud; anthers shedding some pollen in bud; style unfolding first, equaling or exceeding anthers after anthesis. Fruits more or less orbicular, rounded to emarginate at apex, obtuse to subcordate at base, generally 12–18 mm long, 13–25 mm wide, the wings 4, flexible, to 9 mm wide, reddish-brown to purplish, sparsely covered with dark brown scales. *Croat 7947, Hladik 39.*

Occasional, on the shore and in the canopy of the forest. Flowers principally from November to January. The fruits mature mostly from January to April.

The flowers produce copious nectar and are frequented by hummingbirds, other small birds, and insects. Loose fallen fruits can be distinguished by being four-winged and conspicuously lepidote.

Mexico to Argentina. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from premontane dry forest in Panamá, from tropical dry forest in Herrera, Coclé, and Panamá, from premontane moist forest in the Canal Zone, Los Santos, and Panamá, and from premontane wet forest in Veraguas and Panamá.

See Fig. 418.

Combretum laxum Jacq. var. **laxum**, Enum. Syst.

Pl. Ins. Carib. 19. 1760

Liana. Leaves opposite or subopposite; petioles 2–7 mm long, \pm glabrous; blades lanceolate to oblong-elliptic or ovate-elliptic, acuminate at apex, obtuse to rounded and inconspicuously subcordate at base (the sinus 1–2 mm deep), glabrous, often obscurely punctate, prominently arched along midrib, drying dark. Panicles terminal or upper-axillary; flowers sessile, actinomorphic, white or yellowish, very fragrant, 4-parted; lower hypanthium ovate-oblong, densely dark-strigose in basal two-thirds, sparsely so above, the upper hypanthium cup-shaped, ca 1.5 mm long including lobes, sparsely strigose; calyx lobes broadly triangular; petals rounded, ca 1 mm wide, white, spreading, \pm clawed at base; stamens 8, ca 4 mm long, exserted; style to 4 mm long. Fruits ovoid to sub-orbicular, emarginate at apex, cordate at base, 1.5–2 cm

long, 1.5–1.7 cm wide, yellowish-brown, winged, the wings 4, to 7 mm wide, the body of the fruit to 4 mm wide. *Croat 8405, Foster 1327.*

Frequent in the forest and along the shore, usually high in the canopy. Flowers mostly in October and November, but the flowers sometimes persist until February. The fruits mature from January to March.

Loose fallen fruits can be distinguished by having four wings and by being glabrous or at least not conspicuously lepidote as in *C. fruticosum*.

Mexico to northern Argentina. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

See Fig. 419.

Combretum laxum Jacq. var. **epiphyticum** (Pitt.)

Croat, Phytologia 28:189. 1974

C. epiphyticum Pitt.

Shrub or low sprawling liana, usually to 8 m tall. Leaves opposite; petioles 2–7 mm long, densely ferruginous-tomentose; blades ovate-elliptic to oblong-elliptic to obovate, gradually to abruptly acuminate at apex, rounded at base and inconspicuously subcordate (the sinus 2–4 mm deep), 6–16 cm long, 2.5–7 cm wide, the upper surface sparsely short-pilose throughout, the trichomes somewhat denser on midrib and deciduous in age except along midrib, the lower surface similarly pubescent but the trichomes denser, persisting in age; lateral veins in 10–14 pairs, the secondary lateral veins usually continuous between primary lateral veins. Panicles terminal or upper-axillary; inflorescence branches opposite or in whorls of 3, the lower ones subtended by small leaves, the upper ones by lanceolate, caducous bracts ca 4 mm long; rachises, peduncles, and ovary very densely ferruginous-tomentose; flowers sessile, actinomorphic, closely aggregated, subtended by a subulate, caducous bracteole to 1.5 mm long; lower hypanthium ovoid, ca 1 mm long, the upper hypanthium cup-shaped, 1.2–1.5 mm long including the calyx lobes; calyx lobes 4, triangular; petals 4, broadly obovate, ca 1 mm diam, white, glabrous; stamens 8, ca 4 mm long, glabrous; anthers reddish-brown, broader than long, ca 0.5 mm broad; disk thin, dark brown, adnate to calyx, glabrous; style glabrous, subulate. Fruits ovoid in outline, acute at apex, obtuse at base, 1.7–2.2 cm long, prominently ridged longitudinally, the ridges 4, sharp, winglike, extending less than halfway to center of fruit. *Croat 5090.*

Apparently rare; known only from the shore of Peña Blanca Peninsula. Flowers in March and April. The fruits mature in August and September.

The taxon was considered conspecific with *C. laxum* by Exell in the *Flora of Panama* (1958), but recent studies (Croat, 1974b) show this taxon to differ substantially from *C. laxum*, especially in phenology and fruit morphology (see key).

Known only from Panama, from tropical moist forest in the Canal Zone (Atlantic slope) and from tropical wet forest in Veraguas (Bahía Honda). Apparently always associated with bodies of water.

See Fig. 420.

Fig. 418.
Combretum fruticosum



Fig. 419. *Combretum laxum*
var. *laxum*



Fig. 420. *Combretum laxum* var. *epiphyticum*





Fig. 421. *Terminalia amazonica*

Fig. 422. *Terminalia amazonica*



KEY TO THE SPECIES OF TERMINALIA

- Stamens less than 4 mm long; wings of fruit less than 7 mm wide; leaves mostly subcoriaceous . . .
 *T. amazonica* (J. F. Gmel.) Exell
 Stamens more than 4 mm long; wings of fruit more than 10 mm wide; leaves mostly membranous
 at maturity *T. chiriquensis* Pitt.

TERMINALIA L.

Terminalia amazonica (J. F. Gmel.) Exell in Pulle, Fl. Surinam 3:173. 1935

T. hayesii Pitt.

Amarillo, Amarillo real, Guayabo de montana, Nargusta

Tree, to 35 m tall, often with sucker shoots; trunk buttressed to 2 m high, to 1 m or more diam above buttresses; outer bark brown, soft, with shallow vertical fissures, flaking; inner bark reddish or tan, hard, ringed; branches sympodial; young parts rufous-pubescent. Leaves alternate, clustered at ends of branchlets; petioles rufous-pubescent; blades obovate, obtuse to abruptly acuminate at apex, cuneate at base, 6–9 cm long, 2–3.5 cm wide, mostly subcoriaceous, sparsely pubescent, becoming glabrate except for tufts of trichomes in axils below. Spikes slender, pubescent, axillary, 6–9 cm long; flowers 5-parted, greenish-white; receptacle slender at base, broadened and shallowly cupular above; calyx lobes deltoid; petals lacking; disk densely pilose; stamens 10, exerted, to 3.5 mm long; style usually shorter than stamens; stigma simple. Fruits winged, the wings 2, to 5 mm long and 7 mm wide, green turning brown. *Croat 5606, 7858.*

Common tree in the forest, sometimes in water at the edge of the lake; seedlings have been seen in marshes. Flowers and fruits from February to May (sometimes to July). Trees are leafless for a short time, with the flowers appearing before and during the onset of new leaf growth.

Pennington and Sarukhan (1968) reported this species to be 75 m tall and 3 m dbh in southern Mexico.

Mexico to Guyana, Brazil, and Peru; Trinidad. In Panama, a characteristic component of tropical moist forest (Tosi, 1971); known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Panamá, and from tropical wet forest in Colón.

See Figs. 421 and 422.

Terminalia chiriquensis Pitt., Contr. U.S. Natl. Herb. 18:238. 1917

Guayabo de monte

Tree, to 35 m tall; trunk to 90 cm dbh; buttresses many, to 1.5 m high, occasionally with many protruding knots; outer bark loose, falling away from trunk in large pieces; inner bark at first pale lemon-yellow, soon becoming tan; stems rufous-pubescent when young, soon glabrous and fissured. Leaves alternate; petioles 3–10 mm long; blades ± narrowly elliptic, acuminate, acute and sometimes falcate and inequilateral at base, mostly 5–15 cm long, 3–6 cm wide, mostly membranous, glabrous, minutely

and densely pellucid-punctate, arched along the midrib; reticulate veins prominent. Inflorescences terminal, to 15 cm long; flowers yellowish-green, sessile; upper receptacle cup-shaped, ca 2.5 mm long; calyx lobes triangular, reflexed, ca 1 mm long, pubescent outside, lanate inside; petals lacking; stamens 8, exerted, to 7 mm long. Fruits broadly 2-winged, with a single medial ridge on one side, to 2.5 cm long and 3.8 cm wide, emarginate at apex with the tissue sharply twisted to one side. *Croat 13922.*

Uncommon, in the forest. Flowers mostly in the early dry season, especially in January. The fruits mature quickly and are dispersed mostly by the beginning of the rainy season. Leaves drop in June.

Possibly more than one species exists. R. Foster (pers. comm.) has detected striking differences in fruits from different plants of this species. In one type the seeds are about half as long as broad, with the medial ridge straight. In the other type, the seed is 1.5 times as long as broad, with the medial groove twisted into a weak S from one end to the other. No intermediate forms have been seen and nothing is known of the significance of the differences. According to the label on *Skutch 3990* (Costa Rica), the flowers are protogynous. The typical *T. chiriquensis* has a smooth white trunk.

Allen (1956) reported this species as *T. lucens* Hoffm., but that species was published as *T. lucens* Hoffm. ex Mart. and is from Brazil.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Los Santos.

106. MYRTACEAE

Trees or occasionally shrubs; most parts punctate. Leaves sometimes aromatic, opposite, petiolate; blades simple, entire to undulate; venation pinnate; stipules lacking. Flowers sometimes solitary but mostly in terminal or axillary, cymose spikes or racemes, sometimes panicles, the flowers mostly sweetly aromatic, bisexual, actinomorphic, subtended by a pair of bracteoles; calyx 4- or 5-parted; petals 4 or 5, imbricate, mostly white; stamens many; anthers 2-celled, introrse, dorsifixed, dehiscent longitudinally; ovary inferior, 1-locular, 3-carpellate; placentation parietal; ovules 2 to many per placenta; style and stigma 1. Fruits berries; seeds usually 1, sometimes many (*Calycolpus*, *Psidium*), with little or no endosperm.

Members of the family are easily distinguished by the opposite, glandular-punctate leaves, the usually small flowers with many stamens and caducous petals, and the persistent glandular sepals at the apex of the fruit.

The flowers are of the brush type, with many exerted stamens, an exerted style, and nectar. In Costa Rica

KEY TO THE TAXA OF MYRTACEAE

Ovules numerous; seeds many:

Buds open; calyx lobes distinct and equal after anthesis; berries less than 1.5 cm diam

..... *Calycolpus warscewiczianus* Berg

Buds closed; sepals not reflexed until anthesis, often rupturing from bud irregularly and un-

equally; berries more than 2 cm diam *Psidium*

Ovules few; seeds 1 or 2:

Flowers 5-parted (petals 5, the calyx 2–5-lobed in *Psidium anglohondurense*):

Seed 1; calyx regularly 5-lobed *Myrcia*

Seeds usually 2; calyx irregularly 2–5-lobed *Psidium anglohondurense* (Lund.) McVaugh

Flowers 4-parted:

Flowers large, the calyx more than 1 cm diam, the sepals usually more than 7 mm long, the petals 1–2 cm long *Syzygium jambos* (L.) Alston

Flowers small, the calyx less than 1 cm diam, the sepals less than 7 mm long, the petals usually less than 7 mm long (to 12 mm in *E. uniflora*) *Eugenia*

Eugenia oerstediana attracts the bees *Anlacoscelis* (Anthophoridae) and *Trigona* (Heithaus, 1973).

The fruits are endozoochorous. Those of *Myrcia*, *Calycolpus*, and most species of *Eugenia* are small, colorful, and fleshy, suggesting bird dispersal. Ridley (1930) reported that *Eugenia* is dispersed principally by birds, fruit bats, and monkeys. Several species of *Eugenia* on BCI are eaten by arboreal frugivores, especially *E. coloradensis* and *E. nesiotica*. Bats take the fruits of *E. nesiotica* (Wilson, 1971), *Psidium guajava* (Goodwin & Greenhall, 1961), and *Syzygium jambos*. Oppenheimer (1968) reported that white-faced monkeys usually remove only the pulp of *Eugenia nesiotica* and spit the seed out. *Psidium* species and *Syzygium jambos* are probably taken by larger animals also. *Psidium guajava* is reportedly eaten by spider monkeys (Hladik & Hladik, 1969) and by coatis (Kaufmann, 1962).

About 60 genera and nearly 3,000 species; chiefly in the tropics of the Southern Hemisphere.

CALYCOLPUS Berg

***Calycolpus warscewiczianus* Berg, Linnaea**

27:382. 1856

Guayabillo

Glabrous tree, to 7 m tall. Petioles 2–3 mm long; blades ovate to oblong-elliptic, acuminate, obtuse to rounded at base, mostly 4–9 cm long, 1.5–3 cm wide, pellucid-punctate. Flowers usually solitary (to 3) in axils, sometimes pseudoterminal and in clusters of 5 or fewer,

sweetly aromatic, 5-parted, to 4 cm diam; pedicels 1–5 cm long, with a pair of minute, caducous bracteoles below calyx; calyx lobed almost to base, the lobes oblong, to 1 cm long, with a faint midrib, persisting in fruit; petals obovate-oblong, ca 1.5 cm long, white or white tinged with pink (especially on outside), spreading at anthesis; stamens many; style simple; ovules numerous. Berries subglobose, ca 1 cm long; seeds many, ca 3 mm long, tan. Croat 7682.

Occasional, along the shore. Flowers and fruits principally during the dry season (December to April), but also during the rainy season.

Wilson (1971) reported that the fruits are eaten by the bat *Micronycteris hirsuta*.

Costa Rica and Panama. In Panama, most commonly from tropical moist forest in the Canal Zone, Panamá, and Coclé, but known also from premontane dry forest in Coclé (Penonomé) and from premontane wet forest in Panamá (Cerro Campana).

See Fig. 423.

EUGENIA L.

***Eugenia coloradensis* Standl., Trop. Woods**

52:27. 1937

E. melanosticta Standl.

Guayabito de monte

Tree, to 15 m tall, glabrous except for sparse pubescence on midrib of leaves above and all over young leaves.

Petioles 5–10 mm long; blades mostly oblong-elliptic,

KEY TO THE SPECIES OF EUGENIA

Flowers precocious; fruits 1.5–3 cm wide, smooth; youngest stems, petioles, and midribs and margins of blades sometimes with \pm erect, reddish-brown trichomes, otherwise essentially glabrous; inflorescences fasciculate *E. nesiotica* Standl.

Flowers not precocious; fruits usually less than 1.5 cm wide (sometimes larger in *E. uniflora* but 8-ribbed); pubescence not as above; inflorescences fasciculate or branched:

● Flowers not fasciculate:

Leaves less than 4 cm wide; flowers small, the sepals less than 1.5 mm long, the calyx less than 4 mm broad at anthesis; fruits less than 1 cm long *E. oerstediana* Berg

Leaves mostly more than 4 cm wide; flowers larger, the sepals to 2.5 mm long, the calyx more than 6 mm broad; fruits more than 1 cm long *E. coloradensis* Standl.

- Flowers fasciculate or peduncles very short:

- Pedicels more than 1 cm long in flower; leaves glabrous in age, ovate, less than 6 cm long (more than half as broad); fruits ribbed, sometimes more than 2.5 cm diam; plants rare or absent *E. uniflora* L.
- Pedicels less than 1 cm long in flower; leaves usually pubescent at least below, not broadly ovate; fruits not ribbed, less than 1 cm diam:
 - Leaves appressed-pubescent on both surfaces; fruits ca 8 mm diam at maturity *E. galalonensis* (Griseb.) Krug & Urban
 - Leaves not appressed-pubescent; fruits less than 8 mm diam:
 - Leaf blades less than 6 cm long, usually glabrous above except on midrib *E. principium* McVaugh
 - Leaf blades more than 6 cm long, both surfaces covered with ferruginous soft pubescence *E. venezuelensis* Berg

acute to bluntly acuminate, rounded to obtuse at base, 6–13 (17) cm long, 2.5–6 (7.5) cm wide, pellucid-punctate. Racemes axillary or terminal, of few flowers, to 7 cm long, sometimes gathered into a panicle at apex of branches; pedicels 5–10 mm long; flowers pellucid-punctate, 4-parted; sepals unequal, suborbicular or longer than broad, to 2.5 mm long, persistent and somewhat accrescent in fruit; petals oblong to obovate, 5–7 mm long, white, concave, ciliate; stamens numerous, the innermost much shorter than style, gradually increasing in length outwardly, the outermost as long as style; style ca 5 mm long; stigma simple. Berries ovoid-globose, to 2.5 cm long and 1.5 cm wide, violet-purple to dark violet at maturity; seed 1. *Croat 15001, Foster 1185.*

Infrequent, in the forest and along the shore. Some flowers were seen in bud in June. The fruits have been seen mostly from July to October.

Costa Rica and Panama. In Panama, known only from tropical moist forest in the Canal Zone and Darién.

Eugenia galalonensis (Griseb.) Krug & Urban, Bot. Jahrb. Syst. 19:641. 1895

Tree, to 6 (15) m tall; young stems, petioles, and leaves minutely appressed-pubescent to glabrate in age. Petioles 4–7 (10) mm long; blades \pm elliptic, bluntly to narrowly acuminate, mostly acute at base, 5.5–10 cm long, 3–4.5 cm wide, pellucid-punctate; reticulate veins obscure. Racemes 2 or 3, superposed, axillary, less than 1.5 cm long; pedicels 2–7 mm long; bracts ovate-triangular, less than 1 mm long; bracteoles broadly ovate, connate, forming an involucre to 1.5 mm wide and 0.5 mm high; flowers 4-parted, the buds 2.5–3.5 mm long; hypanthium campanulate, ca 1 mm long, appressed-pubescent; calyx lobes rounded, in unequal pairs; petals greenish-white; stamens ca 50, to 5 mm long; disk pubescent around base of style; style 5–6.5 mm long; ovary bilocular; ovules 8–10 per locule; stigma simple. Fruits globose, 6–8 mm diam, glabrate, green turning yellow then red and finally maroon at maturity; seed 1, globose, 4–5 mm diam, black. *Croat 8280.*

Seen once on the shore near Drayton House, but no flowers have been seen on the island. In Central America flowers from December to May; BCI plants probably flower in December and January. Full-sized fruits have been seen on BCI in February.

The flower description given here is based on the *Flora of Guatemala* (McVaugh, 1963), where the fruits are described as obovoid or short-ellipsoid.

Guatemala to Colombia (Santa Marta). In Panama, known only from tropical moist forest on BCI.

Eugenia nesiotica Standl., Field Mus. Nat. Hist., Bot. Ser. 17:203. 1937
Guayabillo

Tree, 10–15 m tall; bark flaking; young stems, petioles, and midribs and margins of leaves short-rufous-pubescent, glabrate in age. Leaves deciduous; petioles 2–6 mm long; blades ovate to elliptic, bluntly acuminate, obtuse to acute at base, 4–5 cm long, 1–2 cm wide, pellucid-punctate; reticulate veins prominulous. Fascicles axillary; pedicels slender, 1–2 cm long, short-pubescent; flowers precocious, 4-parted; sepals ovate, 2–3 mm long, reflexed at anthesis, puberulent, often persisting in fruit; petals orbicular, 3–5 mm long, white, glabrous or ciliate; stamens many; style to 5 mm long; stigma simple. Berries globose, 1.5–3 cm diam, red at maturity; exocarp thin, punctate; mesocarp thick, fleshy, sweet; seed 1, round, 6–10 mm diam. *Croat 10314, Foster 776.*

Frequent in the forest, especially in the young forest. Flowers in the late dry or early rainy seasons after the leaves fall. The fruits mature mostly in late May and June (sometimes in July). Leaves grow in again after flowering.

The species is distinguished from other species of *Eugenia* on the island by its prominulous reticulate veins. *Starry 109*, cited by Standley (1933) as *Eugenia* sp., is this species.

Wilson (1971) reported that fruits are eaten by the bat *Micronycteris hirsuta*.

Known only from Panama, from tropical moist and premontane moist forests in the Canal Zone.

See Fig. 424.

Eugenia oerstediana Berg, Linnæa 27:285. 1856
Sequarra

Tree, mostly 8–15 m tall, to 20 cm dbh; bark smooth, light brown, soft; youngest stems brown, inconspicuously puberulent. Petioles 3–5 mm long; blades \pm elliptic, long-acuminate, acute or obtuse at base, 4–8 cm long,



Fig. 423. *Calycolpus warscewiczianus*

Fig. 424. *Eugenia nesiotica*



2–3.5 cm wide, glabrous except for puberulent midrib above, pellucid-punctate, the margins slightly undulate. Racemes axillary, of few flowers; inflorescence branches minutely puberulent; pedicels mostly 5–12 mm long; flowers white, 4-parted; sepals and petals glandular-dotted; sepals ovate, 1–1.5 mm long, persisting in fruit, reflexed at anthesis; petals white, broadly ovate, 2–3 mm long; stamens many; style simple. Berries globose to ellipsoid, to 9 mm long, bright red at maturity; seed 1, ± reniform, 4–5 mm long. *Croat 7486, 7761.*

Occasional, in the forest. Flowers in January and February. The fruits probably mature in February and March. At least some plants lose all their leaves in mid-February, with the new leaves growing in again soon.

Mexico, Costa Rica, and Panama. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién.

Eugenia principium McVaugh, Fieldiana, Bot. 29:451. 1963

Shrub or small tree, to 3 m tall; young stems, petioles, midribs, pedicels, and hypanthia bearing dense, short, erect trichomes. Petioles 1–2 mm long; blades ovate or elliptic, bluntly acuminate, mostly obtuse at base, 3.5–6 cm long, 1.5–2.5 cm wide, pellucid-punctate, ± thick, the margins revolute and ciliate. Racemes or umbels abbreviated, nearly glabrous; pedicels slender, to 1 cm long, bearing 2 bracts beneath the hypanthium; flowers 4-parted; sepals ovate, ca 2 mm long, spreading at anthesis, glandular-dotted, persisting in fruit; petals obovate, ca 5 mm long, pellucid-dotted, ciliate; stamens numerous, ca 5 mm long; style simple. Berries globose, 4–5 mm diam, at first green, turning orange and finally black, glandular-dotted; seed 1, globose, ca 4 mm diam. *Croat 5457.*

Rare, seen only on the shore north of the Front #8 Lighthouse Clearing. Seasonal behavior not determined.

Mexico and Panama, probably elsewhere in Central America. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Panamá, and Darién.

Eugenia uniflora L., Sp. Pl. 470. 1753
Surinam cherry

Shrub or small tree, to 10 m tall; stems glabrate in age. Petioles ca 2 mm long; blades ovate, short-acuminate, rounded to subcordate at base, 2–6 cm long, 1.5–3 cm wide, glabrous in age, pellucid-punctate. Flowers 4-parted, solitary or in fascicles, axillary; pedicels slender, to 2 cm long; sepals ovate, to 4 mm long, ciliate; petals white, obovate, to 12 mm long; stamens many; style 1.

Berries depressed-globose, to 3 cm diam, ribbed, red at maturity; seed 1. *Shattuck 71.*

Collected once, possibly from a cultivated plant, since the species is reportedly cultivated and has not been seen in recent years on the island. Seasonal behavior not determined.

Native to tropical America; cultivated throughout the tropics and subtropics. In Panama, known only from this collection.

Eugenia venezuelensis Berg, Linnaea 27:188. 1854
E. organoides Berg; *E. banghamii* Standl.

Shrub or small tree, to 6 m tall; stems densely spreading-pubescent, less so in age. Petioles stout, ca 3 mm long, densely pubescent; blades ± elliptic, acuminate, obtuse to rounded at base, 4–12 cm long, 1.5–4.5 cm wide, pellucid-punctate, the surfaces sparsely pubescent, the midrib densely so, the margins revolute and ciliate. Glomerules dense, axillary, among leaves or at defoliated nodes, less than 1 cm long, densely pubescent; pedicels obsolete or nearly so; flowers 4-parted; sepals ovate, 1–2 mm long, spreading at anthesis, ciliate, with ± inconspicuous glandular dots, persisting in fruit; petals white, obovate, 3–4 mm long, glabrous; anthers many, long-exserted; style long-exserted, more than 1 cm long. Berries globose, 4–7 mm diam, at first green turning red and finally black at maturity, glabrous, glandular-dotted; seed 1, globose, 4–5 mm diam. *Croat 5556, 6131.*

Occasional, along the shore. Flowers mostly from February to August. The fruits develop in about 1 month.

Mexico to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Coclé, Panamá, and Darién, from premontane dry forest in Coclé (near Penonomé), and from premontane wet forest in Panamá (Cerro Azul).

MYRCIA DC. ex Guillem.

Myrcia fosteri Croat, Ann. Missouri Bot. Gard. 61:886. 1974

Slender tree, 3–8 m tall; trunk to ca 7 cm dbh. Petioles 2–6 mm long, bearing sparse to dense, ± appressed pubescence of short brownish trichomes; blades lanceolate to elliptic, abruptly caudate-acuminate, acute or rarely obtuse at base, 3–8 (10) cm long, 1–3 (3.5) cm wide, inconspicuously pubescent all over, more densely so on midrib above and below, glabrous above in age except on midrib, pellucid-punctate, thin, the acumen often as much as one-fourth the length of the blade, the margins entire, ± revolute especially near base; second-

KEY TO THE SPECIES OF MYRCIA

- Largest leaf blades less than 10 cm long and 3.5 cm wide; flower buds 1.5–2 mm long; fruits globose to depressed-globose, less than 5 mm long *M. fosteri* Croat
Largest leaf blades more than 10 cm long and 3.5 cm wide; flower buds 2–3 mm long; fruits ellipsoid to obovoid, to 1 cm long *M. gatunensis* Standl.

ary veins not prominulous below when dry. Racemes or panicles axillary, 1–2.5 cm long; pedicels 1–1.5 mm long; flowers 5-parted; calyx to ca 2.5 mm wide, the lobes short-triangular to rounded; axes of inflorescences, pedicels, and hypanthia bearing dense, erect to more commonly appressed pubescence; petals orbicular, ca 1.7 mm long, pellucid-punctate, white, soon falling; stamens numerous, to 3.5 mm long; ovary and basal half of style short-villous, together to 5.5 mm long; style simple. Berries globose to depressed-globose, to ca 5 mm long, 6–8 mm diam, green turning blue-gray and finally blue-black at maturity; seed 1, \pm globose, ca 4 mm diam, smooth, the seed coat thin, brown. *Croat 15147* (type), *Foster 2371*.

Occasional in the younger forest; locally abundant along Miller Trail 100–300 and at Wheeler Trail 700. Flowers in late June and in July. The fruits mature in September and October.

Known only from Panama, from tropical moist forest on BCI and in Darién (*Tyson et al. 4756*, *Stern et al. 719*).

***Myrcia gatunensis* Standl.**, Publ. Field Columbian

Mus., Bot. Ser. 4:154. 1929

Pimiento

Tree, 3–12 m tall; stems and inflorescences minutely pubescent. Petioles 2–6 mm long, bearing sparse to dense, appressed to erect pubescence; blades lanceolate-oblong or elliptical, gradually acuminate, acute to obtuse or rarely rounded at base, 5–16 cm long, 1.5–5 cm wide, glabrous and \pm shiny above except on midrib, glabrous to inconspicuously puberulent below, usually glabrous in age, pellucid-punctate, usually moderately thick, the acumen usually less than one-sixth the length of the blade, the margins entire, weakly revolute; veins of lower surface \pm prominulous when dried. Panicles axillary or terminal, 1.5–9 cm long; pedicels to ca 2 cm long; flowers 5-parted; receptacle produced into a densely silvery-puberulent, button-shaped structure above calyx; calyx to 4 mm wide, the lobes ca 1.5 mm long, \pm rounded, pellucid-punctate; pedicel and calyx densely pubescent with short silvery trichomes, those of the calyx very dense and mostly appressed; petals orbicular, 1.5–2 mm long, white, pellucid-punctate, soon falling; stamens numerous; style pubescent in basal half. Berries ellipsoid to obovoid, prominently pellucid-punctate, to ca 1 cm long and 8 mm wide, usually considerably longer than broad, green becoming greenish-yellow and finally

blue-black at maturity; seed 1. *Croat 6133*, *Foster 1120*.

Frequent along the shore on the eastern side of the island, apparently preferring forest edges near water. Flowering principally from June to August. Flowering collections believed to be this species were made in Bocas del Toro in February. The fruits mature mostly in August and September, sometimes as early as June.

There is considerable doubt that *M. gatunensis* Standl. is the oldest name for this taxon. Material of what I believe to be the same species has been identified by McVaugh and others as *M. fallax* (L. C. Rich.) DC. and *M. splendens* (Sw.) DC. In calculating the range for *M. gatunensis* I have limited myself to material that I am confident is the same species as the BCI material. The species is probably more wide-ranging, however, and it is certainly not restricted to BCI as is indicated in the *Flora of Panama* (Amshoff, 1958).

Known only from Panama, but probably ranging into Costa Rica and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from tropical wet forest in Colón (Salúd).

PSIDIUM L.

***Psidium anglohondurense* (Lund.) McVaugh,**

Wrightia 2(3):123. 1961

Eugenia schippii Standl.

Glabrous tree, 10–20 m tall, to 40 cm dbh; stems terete, grayish, the nodes somewhat to conspicuously swollen, the branching mostly dichotomous. Petioles 1–5 mm long, \pm terete or flattened on upper surface, sometimes roughened; blades oblong-elliptic, gradually long-acuminate (the acumen sometimes downturned), broadly to narrowly acute to very weakly attenuate at base, 7–16 (20) cm long, 2–5 cm wide, markedly bicolorous, both surfaces dull, the upper surface with sunken midrib, the lower surface and midrib prominently punctate, the margins weakly revolute; lateral veins 2–6 mm apart, obscure, with a collecting vein 2–3 mm from margin, the reticulate veins very obscure; new flush of leaves \pm maroon. Flowers few to several at leafless, swollen nodes; pedicels 2–5 mm long, the bracts solitary or paired, borne apically, \pm round or ovate to \pm acute, pellucid-punctate, ciliate, usually closely appressed to the hypanthium; flower buds globose to obovoid, ca 7 mm long; calyx completely closed in bud, splitting \pm irregularly, 2–5-lobed, the lobes rounded to acute at apex, 3–3.5 mm long, persisting

KEY TO THE SPECIES OF PSIDIUM

- Plants decidedly pubescent on most parts; lateral veins of leaves in 12 pairs or more and prominently raised; plants cultivated at the Laboratory Clearing *P. guajava* L.
 Plants \pm glabrous; lateral veins of leaves in 8 pairs or fewer or not at all raised; plants of the forest:
 Twigs 4-sided; fruits usually more than 3.5 cm diam; seeds many; blades with the lateral veins in 8 pairs or fewer, prominulous *P. friedrichsthalium* (Berg) Niedenzu
 Twigs terete; fruits usually less than 3.5 cm diam; seeds 2; blades with the lateral veins in 12 pairs or more, obscure *P. anglohondurense* (Lund.) McVaugh



Fig. 425. *Psidium
friedrichsthalianum*



Fig. 426. *Syzygium jambos*

in fruit; petals 5, \pm rounded, concave, inconspicuously ciliate, white, ca 5 mm long; stamens numerous; stamens and style \pm equaling petals; style glabrous, narrowly tapered to apex; ovules numerous, flattened and reniform, less than 1 mm diam. Berries globose to depressed-globose, 2–3.5 cm diam, green tinged with red (probably also becoming completely red) when mature; seeds usually 2, horseshoe-shaped, ca 2 cm long and 3 mm wide. *Croat 16213*.

Apparently rare, in the old forest; known from the vicinity of Zetek Trail 300–400, where seedlings are common. Mature fruits have been seen on BCI in July. Both flowers and immature fruits are seen elsewhere in Panama in August. In Belize the flowers are seen in May and mature fruits in August and November. Owing to its unusual C-shaped embryo, which lacks a hard bony testa, it is possible that the species does not even belong in the genus *Psidium* (R. McVaugh, pers. comm.). Panamanian material differs from that of plants from Belize in having shorter pedicels and calyx lobes that are essentially glabrous inside rather than strongly pubescent.

Fruits on *Lao & Holdridge 194* (Salúd, Colón Province) were heavily infested with gall-forming insects, which caused the fruits to be somewhat lobed.

Guatemala, Belize, and Panama. In Panama, known from tropical moist forest on BCI and from tropical wet forest in Colón (Salúd).

Psidium friedrichsthalianum (Berg) Niedenzu in Engler & Prantl, *Nat. Pfl.* 3(7):69. 1893
Guayabo de agua, Wild guavo

Small tree, nearly glabrous, to 9 (12) m tall; bark thin, reddish-brown, peeling in thin strips (similar to *P. guajava*); wood hard, fine-grained; branchlets with 4 thin narrow ribs, appearing square; young stems and petioles sometimes bearing fine, sparse pubescence. Leaves opposite or nearly so; petioles 3–6 mm long; blades oblong or elliptic, acuminate, obtuse to rounded at base, 4–12 cm long, 2.5–5 cm wide; major lateral veins in ca 8 pairs, faint above and prominent below. Cymes axillary, of 1–3 flowers; peduncles 1–2.5 cm long; calyx closed and globose in bud with a short apiculum, 2- or 3-lobed when open, sometimes persisting in fruit, stiff, concave inside, ca 1 cm long; petals 5, orbicular, 1–1.5 cm long, white; stamens numerous; anthers oblong, dorsifixed, dehiscing longitudinally; ovary glabrous; stigma peltate. Berries \pm globose, 3–6 cm diam, green to yellowish at maturity, white inside, with a tart, acidlike taste; seeds many, irregularly obovoid or reniform, 6–8 mm long, tan. *Croat 16584*.

Apparently uncommon as an adult, known only from the forest near Wheeler Trail 1300; seedlings common in some areas of the forest above the escarpment south of the Big Trees on Armour Trail. Probably flowering and fruiting all year.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá.

See Fig. 425.

Psidium guajava L., *Sp. Pl.* 470. 1753

Guava, Guayaha, Guayava peluda

Shrub or small tree, to 5 (10) m tall, to 25 cm dbh; stems glandular-dotted; young stems, petioles, lower leaf surfaces, and midribs above densely short-pubescent. Petioles ca 5 mm long; blades oblong-elliptic, obtuse or apiculate at apex, obtuse to rounded at base, 7–12 cm long, 3.5–6 cm wide, glabrate in age, pellucid-punctate; lateral veins in 12 pairs or more, prominently raised. Flowers solitary in axils, 5-parted; pedicels 1–2 cm long; pedicel and outside of calyx short-pubescent; calyx lobes triangular, to 1 cm long, sericeous inside; petals ovate, white, 1.5–2 cm long, sparsely pubescent outside, glabrous inside; stamens numerous; style simple. Berries globose or pear-shaped, to 6 cm diam, green turning yellow-pink; seeds many. *Croat 5299, 8385*.

Cultivated in the Laboratory Clearing; growing spontaneously on the shore at the end of Peña Blanca Peninsula and on Orchid and Slothia islands. Flowers in the dry season. The fruits mature in the late rainy season and the early dry season.

Immature fruits are eaten by white-faced and spider monkeys (Hladik & Hladik, 1969; Oppenheimer, 1968).

Cultivated throughout the tropics; common in secondary growth. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane dry forest in Coclé (Penonomé), and from premontane wet forest in Coclé (El Valle) and Panamá (Cerro Jefe).

SYZYGIUM Gaertn.

Syzygium jambos (L.) Alston in Trimen, *Handb. Fl. Ceylon*, Suppl. 6:115. 1931

Eugenia jambos L.

Pamarosa, Rose apple

Glabrous trees, to 15 m tall, ca 30 cm dbh. Petioles 5–10 mm long; blades oblong-lanceolate, acuminate, acute to obtuse at base, 12–22 cm long, 3–5 cm wide, pellucid-punctate. Flowers 1–5 at ends of branchlets, 4-parted, glabrous; pedicels ca 1.5 cm long; receptacle 1–1.5 cm long; sepals semicircular, recurved at anthesis, 5–7 mm long, persistent in fruit; petals white, 1–2 cm long, ovate, pellucid-punctate; stamens many; stamens and style long-exserted. Berries subglobose to pear-shaped, 2–3 cm diam, green to pinkish or yellowish at maturity; seeds 2 to several. *Croat 7413*.

Infrequent, along some areas of the shore. The species is apparently naturalized but may be the result of former habitation. Flowers mainly in the dry season (rarely November to as late as May). Fruit maturity time has not been determined.

Native to the East Indies; cultivated and escaped throughout tropical America. In Panama, reported from low and middle elevations in moist and wet areas, often in pastures (Holdridge, 1970); known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Panamá.

See Fig. 426.

107. MELASTOMATACEAE

Shrubs and small trees, sometimes herbs, rarely vines (*Adelobotrys*), rarely hemiepiphytic (*Topobaea*); stems occasionally winged or angled. Leaves opposite, petiolate (sessile in *Mouriri*); blades simple, entire or serrate; principal veins palmate at base, usually pliveined or rarely (in *Mouriri*) only the midrib present; stipules lacking. Flowers bisexual, actinomorphic (the androecium and style may be slightly zygomorphic); perianth 4–7 (8)-parted; calyx lobed, arising from hypanthium, sometimes with a small exterior tooth on the hypanthium at each calyx lobe; petals free, usually clawed, showy; stamens about twice as many as petals, free; anthers 2- or 4-celled, opening by terminal pores, the connective prolonged at base into a prominent appendage; ovary superior or inferior, mostly 3–5-locular, 3–5-carpellate; placentation axile; ovules numerous, anatropous; style 1, simple; stigma \pm capitate. Fruits loculicidal capsules if from a superior ovary, \pm enclosed in the persistent hypanthium, or berries if from an inferior ovary; seeds exalbuminous, usually numerous (1 in *Mouriri*).

Members of the family (except *Mouriri myrtilloides*) can be distinguished by the pliveined leaves and by the usually fleshy fruits with many, small, usually wedge-shaped seeds. The anthers are usually tapered to the apex and have terminal pores.

The flowers are probably pollinated by bees, especially of the genus *Trigona*. I have observed large bees (probably *Eulaema*) drumming pollen from *Topobaea praecox* (see that species description for details). In Costa Rica *Miconia argentea* is primarily visited by *Melipona beechii* (G. Frankie, pers. comm.). *Schwackaea cupheoides* in Costa Rica is visited by the halictid bees *Caenaugochlora* and *Augochlora*.

The fruits are chiefly endozoochorous. Those that are chiefly bird dispersed include *Leandra dichotoma*, *Ossaea quinqueneria*, and *Mouriri myrtilloides*, as well as species of *Conostegia*, *Clidemia*, and *Miconia*. Fruits of *Topobaea praecox* and possibly *Henriettea succosa* are also taken by birds. Fruits of *Bellucia grossularioides*,

though possibly dispersed by mammals or larger birds, become soft at maturity and could be pecked open by smaller birds. Oppenheimer (1968) reported that mature fruits of *Miconia argentea* are eaten by white-faced monkeys. They are also taken by coatis (Kaufmann, 1962). Hladik and Hladik (1969) reported that fruits of *Mouriri myrtilloides* are eaten by white-faced, spider, and howler monkeys nearly all year.

Seeds of several species are wind dispersed, including *Schwackaea cupheoides*, *Tibouchina longifolia*, *Arthrostema alatum*, and *Adelobotrys adscendens*.

About 200–240 genera and 3,000–4,500 species; throughout the tropics, but most abundant in South America.

ACIOTIS D. Don

Aciotis levyana Cogn. in Mart., Fl. Brasil.

14(3):460. 1885

Herb, to 1 m tall, pubescent, the trichomes long, simple, chiefly gland-tipped toward the apex of blade and on petioles and stems; stems square, the corners usually winged and ciliolate. Petioles 1–4 cm long, often winged laterally; blades \pm ovate to oblong-ovate, acuminate, obtuse to subcordate at base, mostly 6–13 cm long, 3.5–6.5 cm wide; veins 5–7. Cymes terminal, divaricately branched, the branches usually square and weakly winged; flowers 4-parted; hypanthium globose, fleshy, \pm inflated, both the hypanthium and calyx lobes hispid; calyx lobes minute, curved outward; petals to 4.3 mm long, soon falling, white or pinkish; stamens 8, erect, mounted on rim of hypanthium, to 3.5 mm long, shorter than sepals at anthesis, then elongating; ovary superior; style slightly longer, straight. Capsules globose, thin-walled, dehiscent irregularly; seeds cochleate (shaped like a snail shell), brown, somewhat foveolate, less than 1 mm long. *Bailey & Bailey 581*.

Collected once on the island and, though abundant elsewhere in Panama, not seen recently on the island. The species could be expected to occur from time to time in

KEY TO THE TAXA OF MELASTOMATACEAE

Fruits loculicidal capsules (not obvious in *Aciotis levyana*); ovary superior, free from the hypanthium; stems usually either winged or more or less angulate (not winged or angulate in *Tibouchina* or *Adelobotrys*):

Stems conspicuously winged:

Stem wings markedly ciliolate with long simple or glandular trichomes; capsules round

. *Aciotis levyana* Cogn.

Stem wings glabrous (stems may be sparsely pubescent with glandular trichomes); capsules campanulate

. *Arthrostema alatum* Tr.

Stems terete or square but lacking conspicuous wings:

Plants climbing vines in the forest; calyx tube widely spreading

. *Adelobotrys adscendens* (Sw.) Tr.

Plants erect herbs in open areas; calyx tube not widely spreading:

Stems glabrous or with pubescence restricted chiefly to angles; trichomes of upper blade surface free to base; flowers solitary, the petals usually pinkish; capsules oblong

. *Schwackaea cupheoides* (Benth.) Durand

Stems pubescent all over; trichomes of upper leaf surface adnate to the epidermis for a part of their length; flowers in cymes, the petals white (rarely pinkish); capsules ovate to rounded

. *Tibouchina longifolia* (Vahl) Baill.

- Fruits berries; ovary wholly or partly inferior; stems terete:
 Leaves with a single vein (the midrib), the blades sessile, to 8.5 cm long; anthers with 2 short longitudinal slits; berries with 1 seed *Mouriri myrtilloides* (Sw.) Poir. subsp. *parvifolia* (Benth.) Morley
- Leaves with 3 to several veins; blades petiolate, usually more than 7 cm long; anthers opening by terminal or subterminal pores; berries with many seeds:
 Flowers each subtended by 2 pairs of decussate bracts on base of hypanthium; petals thin, rose-purple, ca 1.5 cm long; anthers connate in a ring, with 2 pores; plants usually hemiepiphytic *Topobaea praecox* Gleason
- Flowers not individually subtended by decussate bracts; petals white (to pink) or much smaller than 1.5 cm; anthers free, usually with a single pore (2 in *Bellucia*); plants shrubs, trees, or vines, not hemiepiphytic:
 Plants vines; calyx plate-shaped, widely spreading, the teeth minute or obscure; petals ca 1 cm long, rounded at apex; blades thick, rounded to cordate at base *Adelobotrys ascendens* (Sw.) Tr.
- Plants trees or shrubs; calyx not plate-shaped or widely spreading, often conspicuously toothed:
 Inflorescences lateral or axillary (rarely terminal in *Clidemia capitellata*):
 Hypanthium and calyx lobes together more than 1.2 cm long:
 Leaf blades glabrous on veins below (except sometimes along margins of veins); stems glabrous or inconspicuously puberulent; hypanthium more than 2 cm wide *Bellucia grossularioides* (L.) Tr.
- Leaf blades appressed-pubescent on veins below; stems conspicuously appressed-pubescent; hypanthium less than 1 cm wide *Henriettea succosa* (Aubl.) DC.
- Hypanthium and calyx lobes together less than 1 cm long:
 Leaf blades obtuse to rounded or cordate at base, not decurrent on petiole *Clidemia* (in part)
- Leaf blades attenuate at base and decurrent on petiole:
 Inflorescences usually at leafless nodes, 2 cm long or less; major lateral veins \pm evenly spaced in basal fourth of blade *Clidemia septuplinervia* Cogn.
- Inflorescences usually at current leaf nodes, 2–5 cm long; major lateral veins principally from a single point near base of blade *Ossaea quinquenervia* (P. Mill.) Cogn.
- Inflorescences terminal:
 Petals acute or acuminate; panicles long and slender, often reddish; pubescence of inflorescences and stems simple, long, spreading or retrorse; leaves conspicuously pubescent *Leandra dichotoma* (D. Don) Cogn.
- Petals obtuse to rounded (acute in *Conostegia cinnamomea* but its stems not hirsute):
 Calyx calyptrate in bud (i.e., its lobes forming a united cap over petals, not opening in the regular manner but becoming severed from the flower at its base and falling free) *Conostegia*
- Calyx open in bud, the lobes present at anthesis (often small):
 Plants with 3 types of pubescence on younger stems and petioles (stellate-tomentose, glandular-hirsute, and simple-hirsute); petals 8–10 mm long *Clidemia octona* (Bonpl.) L. O. Wms.
- Plants never with 3 types of pubescence at one time; petals less than 5 mm long *Miconia*

the larger clearings. Flowers and fruits throughout the year.

Guatemala to Ecuador. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in Coclé and Panamá, and from tropical wet forest on the Atlantic slope in Veraguas, Colón, and Coclé.

ADELOBOTRYS DC.

Adelobotrys ascendens (Sw.) Tr., J. Bot. 5:210. 1867

Liana or scandent shrub climbing to several meters; stems terete to ribbed, becoming glabrate in age, sometimes with fine roots along their length; younger parts, petioles, and inflorescences densely brown-strigose. Petioles 6–30

mm long; blades ovate to subrotund, acuminate, rounded to cordate at base, 4.5–15 cm long, 3–7 cm wide, thick, entire or denticulate, glabrous or strigose above, strigose below; veins usually 5. Panicles 10–40 cm long, of umbels of 2–6 flowers; pedicels 2–5 mm long; flowers 5-parted; hypanthium ca 5 mm long, higher than ovary; calyx tube widely spreading, persisting and to 6 mm wide in fruit, the teeth minute or obscure; petals obovate, white to pinkish, ca 1 cm long, rounded at apex, spreading; stamens 10, about as long as petals; filaments flattened, sometimes blue; anthers linear, deflexed, 6–10 mm long, the connective elaborate, with a short part directed upward and a longer, dorsal, forked appendage directed basally \pm parallel to the thecae; ovary superior; style shorter than stamens, becoming recurved near apex. Fruiting hypanthia conspicuously ribbed at maturity, to 8 mm long, the

outer wall of fruit and the calyx eventually weathering away, the thin inner wall held in place by the stout ribs, the ribs then attached only at base; seeds very numerous, obcylindrical, ca 1 mm long, wind dispersed. *Foster 2090*.

Rare; collected once in the old forest. Probably flowers and fruits throughout the year.

The fruits are not obviously capsular until maturity. Seeds are slowly dispersed as if by a saltshaker.

Mexico to Peru (Loreto), Bolivia, and Brazil; Jamaica. In Panama, known from tropical moist forest on BCI and in Coclé and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón, Coclé, Panamá, and Darién.

ARTHROSTEMA Pav. ex D. Don

Arthrostemum alatum Tr., Trans. Linn. Soc. London 28:35. 1871

Herb, to 60 cm tall; stems succulent, square, the edges narrowly winged; trichomes sparse, red, gland-tipped, on stems and inflorescences, including hypanthia and petals. Petioles to 3.5 cm long, winged; blades ovate, acute to acuminate, truncate to subcordate at base, 3–7 cm long, 1.5–4.5 cm wide, setose above, glabrous below, serrulate and ciliate; veins 5. Cymes terminal, divaricately branched, usually with a solitary flower between branches; flowers 4-parted, ± sessile; hypanthium campanulate, to 4 mm long; calyx tube obscurely lobed, accrescent in fruit; petals pink to lavender, ca 3 mm long; stamens 8, ± equal; anthers with the connective prolonged somewhat at base; filaments united to calyx tube; ovary superior; style straight, about as long as stamens. Capsules campanulate, ca 1 cm long, 4-valved, loosening at base and acting as a wind ballast; seeds numerous, minute, cochleate, with grooves and minute tubercles on the rounded side. *Croat 6150*.

Uncommon, in the Laboratory Clearing. Flowers from August to October. Mature fruits seen in October.

Southern Mexico to Venezuela. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

BELLUCIA Neck. ex Raf.

Bellucia grossularioides (L.) Tr., Trans. Linn. Soc. London 28:141. 1871

Small tree, to 5 (10) m tall, glabrous except sometimes for puberulence on stems and lower leaf surfaces. Petioles to 6 cm, stout; blades broadly elliptic, obtuse to short-acuminate, obtuse to rounded at base, 15–35 cm long, 10–20 cm wide, entire, pliveined, the major veins 3–5, soon becoming glabrous. Cymes axillary, frequently on leafless branches and on trunk; pedicels 1–2.4 cm long; flowers with an intense, sweet aroma at anthesis, ca 6 cm wide; hypanthium hemispherical; calyx 1.5–2 cm long, hyaline, dehiscing irregularly at anthesis and falling free from the hypanthium; petals 5 or 6 (to 8), oblong, thick, white or pink, to 3 cm long, broader and often very oblique at apex, spreading at anthesis; stamens 10–16,

to 1.8 mm long; filaments about as long as anthers; anthers obovate, turned inward, yellowish, with 2 small terminal pores, both the thecae and connective swollen; ovary inferior; style straight, stout, at first medially positioned, soon pushed to one side of flower; stigma large, to 4 mm wide, capitate, held well above stamens. Berries ± globose, to ca 3 cm diam, pale green at maturity; seeds tan, numerous, ca 0.7 mm long, about twice as long as broad. *Shattuck 1119*.

Collected by O. Shattuck on Gigante Bay and possibly still occurring there, although the species is undoubtedly more abundant elsewhere. Flowers during July and August; mature fruits have been seen in October.

The species has been confused with *B. axinanthera* Tr., which is more abundant and apparently more ecologically variable as well, occurring in Panamanian life zones ranging from premontane moist to premontane rain forests. *B. costaricensis* Cogn., reported by Gleason (1958) in the *Flora of Panama*, is a synonym of *B. axinanthera*. The calyx of *B. axinanthera* differs from that of *B. grossularioides* by being regularly dehiscent, with lobes that are thick, regularly acute, and persistent in fruit. The calyx lobes of *B. grossularioides* are hyaline, and their dehiscence is irregular and often circumscissile.

Southern Mexico to Amazonian Brazil and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién.

CLIDEMIA D. Don

Clidemia is distinguished by having axillary inflorescences and petals rounded at the apex. The ovary is inferior. Most species are conspicuously pubescent.

Clidemia capitellata (Bonpl.) D. Don ex DC., Prodr. 3:159. 1828

C. neglecta D. Don

Shrub, 1–3 m tall; stems, inflorescences, and lower leaf surfaces densely pubescent with both stalked-stellate and simple trichomes, the simple trichomes often glandular-tipped, usually longer than the stellate ones. Petioles 1–5 cm long; blades ovate to ovate-oblong, acuminate, obtuse to rounded at base, 6–15 (20) cm long, 3–7 (9) cm wide, minutely toothed, pubescent above, the trichomes long, simple, set on bulbous projections of surface appearing as depressions on lower surface; veins 5–7. Flowers sessile, 5-parted, clustered and well spaced on a strong central axis and at the ends of short branches; hypanthium and calyx tube together 3–4 mm long; calyx lobes 1–1.5 mm long, the exterior teeth slender, ca 1 mm longer than calyx lobes; petals white, 4.5–5 mm long, spreading at anthesis and later closing; stamens folded in bud, all directed to one side at anthesis, the terminal pore of the anthers held somewhat beneath style; style erect or held to one side; stigma held just above the ± closed petals after stamens shrivel. Berries subglobose, purple, densely pubescent, ca 6 mm diam; seeds minute, numerous. *Croat 11770*.

Though the species is common in the Canal Zone in disturbed areas, it is uncommon on the island and has

KEY TO THE SPECIES OF CLIDEMIA

- Flowers 4-parted, the flowers or at least the fruits often occurring on a leafless stem below leaves:
 Leaf blades usually attenuate at base and decurrent on petiole, not cordate *C. septuplinervia* Cogn.
 Leaf blades cordate or subcordate at base *C. purpureo-violacea* Cogn.
- Flowers 5- to 8-parted:
 Pubescences of simple trichomes only:
 Plants with stems, blades, and inflorescence branches setose, the trichomes to 1 cm long *C. collina* Gleason
 Plants ± hirsute all over, the trichomes ca 1 mm long or less *C. dentata* DC.
- Pubescence (at least on stems) of 3 types: stellate, simple, and simple gland-tipped:
 Trichomes of upper blade surface often on conspicuous projections appearing as depressions from the underside; simple trichomes only slightly or a few times longer than the stellate ones; petals 4–5 mm long *C. capitellata* (Bonpl.) DC.
 Trichomes of upper blade surface distributed evenly, the blades lacking projections; simple trichomes usually many times longer than the stellate ones; petals 8–13 mm long *C. octona* (Bonpl.) L. O. Wms.

been collected only at Gross Point. Flowers and fruits throughout the year.

Recognized by its unusual inflorescences and pustular leaves.

Southern Mexico to Colombia; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién Provinces; known also from premontane moist forest in the Canal Zone, from premontane wet forest in Bocas del Toro, Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Darién and on the Atlantic slope in Veraguas, Colón, and Coclé.

See Fig. 427.

Clidemia collina Gleason, *Phytologia* 3:359. 1950

Slender shrub, to 2 m tall; stems, petioles, major veins of lower blade surfaces, and inflorescences conspicuously setose, the trichomes of stems mostly to 1 cm long, often deciduous in age. Petioles 1–3 cm long, the basal part densely setose and usually encrusted with ant detritus, the apical part with swollen domatia inhabited by small brown ants; blades ± elliptic, gradually acuminate, narrowly rounded at base, 15–32 cm long, 5.5–11.5 cm wide, very sparsely setose above, more densely so on major veins below, conspicuously ciliate, pliveined, the veins 7. Flowers 5-parted, in densely setose, branched, axillary clusters; pedicels pink; hypanthium and calyx tube campanulate, ca 3 mm long, the upper part with setae 6–10 mm long; calyx lobes blunt, 1–2 mm long, the exterior teeth slender, setose, about as long as or longer than sepals; petals white, oblong-obovate, rounded at apex, 4–6 mm long; stamens straight, yellow, to 5.5 mm long; anthers to 3 mm long with a single terminal pore; style only slightly exceeding stamens. Fruiting hypanthia unknown. *Foster 2355*.

Apparently rare on BCI, collected once south of Zetek Trail 800. Seasonal behavior not determined. Flowers at least in April and May, with some fruits maturing in August.

Known only from Panama, from tropical moist forest on BCI and in Bocas del Toro and from premontane wet forest in Coclé (El Valle).

Clidemia dentata D. Don ex DC., *Prodr.* 3:158. 1828

Shrub, 1–4 m tall, densely pubescent with long, stiff, erect or recurved trichomes. Leaves paired, one often smaller than the other; petioles to 1.5 cm long; blades narrowly ovate-elliptic, acuminate, acute to rounded and usually unequal at base, 6–20 cm long, 2.5–8 cm wide, entire or minutely serrate, pliveined, the veins 5–7. Inflorescences short, paniculate or racemose, bearing few flowers; hypanthium and calyx bell-shaped, 3–4 mm long; calyx truncate, the exterior teeth subulate, to 4 mm long; petals 5, white, turning brown on drying, oblong, 5–7 mm long; stamens to 4 mm long; filaments arcuate below anthers; style slightly shorter than petals; stigma simple. Berries subglobose, to 1 cm diam, green turning blue-black at maturity; seeds minute, numerous. *Croat 11940*.

Uncommon, within the forest and at the edges of clearings. Flowers and fruits throughout the year.

Southern Mexico to Bolivia and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Coclé, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Bocas del Toro and Coclé, and from tropical wet forest in Colón, Coclé, and Darién.

See Fig. 428.

Clidemia octona (Bonpl.) L. O. Wms., *Fieldiana, Bot.* 29:558. 1963

Heterotrichum octonum (Bonpl.) DC.

Shrub, (1)2–3(5) m tall; stems, petioles, peduncles, and hypanthia with both stellate and simple trichomes, the simple ones in part very long, in part short and glandular. Leaf pairs sometimes unequal; petioles 2–10 cm long; blades ovate, acuminate, cordate at base, 8–20 cm long, 6–12 cm wide, chiefly with long simple trichomes above and short stellate ones below, denticulate; veins 7. Panicles upper-axillary and subterminal; flowers 7- or 8-parted; hypanthium and calyx lobes together to 5 mm long, the exterior teeth slender, much longer than calyx lobes, ca 1.5 mm long; petals obovate, 8–13 mm long, white, broadly spreading; stamens folded in bud, erect and radially symmetrical at anthesis; anthers ca 6 mm long, gradually tapered to apex with a single termi-



Fig. 427.
Clidemia capitellata



Fig. 428.
Clidemia dentata



Fig. 429.
Clidemia octona

nal pore; style stout, erect in bud, elongating after anthesis, held to one side well above anthers, to ca 1 cm long. Berries purple at maturity, 1–1.5 cm diam, the pubescence of the hypanthium persisting; seeds minute, numerous. *Croat 11848*.

Occasional, at the edge of the forest. Flowers and fruits throughout the year.

Southern Mexico to Peru and Brazil; Cuba, Jamaica. In Panama, known from premontane moist forest in the Canal Zone and Veraguas, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane wet forest in the Canal Zone, Chiriquí, and Panamá, and from tropical wet forest in Panamá and Darién.

See Fig. 429.

Clidemia purpureo-violacea Cogn., Bull. Soc. Roy. Bot. Belgique sér. 2, 30(1):263. 1891

Slender shrub, 1–5 m tall, often arching; stems glabrous in age. Petioles 1–8 cm long, bearing minute, furfuraceous, stellate pubescence; blades broadly ovate, acuminate, rounded to cordate at base, 12–22 cm long, 3–14 cm wide, minutely stellate-pubescent on veins below and above near base, minutely denticulate and ciliate, \pm maroon below; veins 5–7. Inflorescences axillary, small, paniculate, to ca 1.5 cm long, mostly below leaves; branches of inflorescence inconspicuously stellate-pubescent; flowers 4-parted, pale red, ca 4 mm diam; hypanthium \pm globose, 2–3 mm long, minutely pubescent, the trichomes borne on minute papillae, often deciduous; exterior teeth ending in deflexed setae ca 0.5 mm long; calyx lobes 0.5–0.7 mm long, markedly recurved with a submarginal projection forming the crown; petals oblong, rounded at apex, ca 1.5 mm long; stamens erect, ca 3 mm long; style ca 2 mm long, becoming directed to one side. Berries to 5 mm long, \pm globose, at first red-violet, turning purple-black at maturity; seeds minute, numerous. *Croat 14551*.

Rare, known only from deep ravines in the vicinity of Creek #8. Flowers and fruits from April to December. Most fruits mature during the rainy season.

Costa Rica to Colombia. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién; known also from premontane wet forest in Panamá and from tropical wet forest in Darién.

Clidemia septuplinervia Cogn. in Mart., Fl. Brasil. 14(4):506. 1888

Shrub, 1.5–3(7) m tall; stems, petioles, lower leaf surfaces, axes of inflorescences, and hypanthia bearing very minute, reddish-brown, granular puberulence. Leaf pairs sometimes unequal; petioles to 6 cm long; blades ovate to elliptic, acuminate, attenuate (rarely rounded) and sometimes inequilateral at base, decurrent onto petiole, 11–24 cm long, 5–12 cm wide, glabrous above, sparsely ciliate, subentire, pliveined, the veins 5–7. Cymes axillary, minute, ca 1 cm long, usually occurring on leafless stems; hypanthium ovoid or oblong, to 3 mm long; calyx lobes 4, rounded, ca 1 mm long, reddish, the exterior teeth slender, 3–4 times as long as sepals with a few long bristles; petals 4, pink or white. Berries globose, 3–5 mm diam, green then red turning blue at maturity, minutely puberulent; seeds minute, numerous. *Foster 1096*.

Collected once west of Armour Trail 100–200. Flowers and fruits throughout the year.

Belize to Colombia, Peru, and Brazil; Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién, from tropical wet forest in Veraguas (Atlantic slope), Colón, Panamá, and Darién, and from premontane rain forest in Darién.

CONOSTEGIA D. Don

Conostegia is distinguished by having terminal inflorescences, petals obtuse or rounded at apex (acute in *C. cinnamomea*), and flower buds with a calyprate calyx (i.e., the entire calyx deciduous as a unit leaving an irregular scar). The ovary is inferior.

Conostegia bracteata Tr., J. Bot. 5:209. 1867

Shrub, to 3.5 m tall, conspicuously hirsute except on petals and inner flower parts, the trichomes long, simple, sometimes slightly branching, especially on main veins and below inflorescences. Petioles to 2 cm long; blades narrowly elliptic to oblanceolate, acuminate, acute to obtuse at base, 9.5–20 cm long, 4–8 cm wide, obscurely serrulate; veins 3. Panicles to ca 10 cm long; flowers in small glomerules subtended by oblong-ovate bracts to 8 mm long; hypanthium 2.5–3 mm long at anthesis; petals (5)6(7), obovate, rounded to truncate at apex,

KEY TO THE SPECIES OF CONOSTEGIA

Leaf blades glabrous above or nearly so at least at maturity; trichomes of lower surface sessile, stellate (minute in *C. cinnamomea*):

Lower leaf surface completely concealed by a fine close mat of brownish stellate trichomes *C. xalapensis* (Bonpl.) DC.

Lower leaf surface not concealed by trichomes, sparsely pubescent at maturity (often superficially glabrous) *C. cinnamomea* (Beurl.) Wurdack

Leaf blades conspicuously pubescent above, the trichomes chiefly or entirely simple:

Trichomes of lower blade surface all simple (rarely a few on principal veins branched but not stellate) *C. bracteata* Tr.

Trichomes of lower blade surface often both simple and stellate, the stellate trichomes mostly stalked *C. speciosa* Naud.



Fig. 430. *Conostegia bracteata*



Fig. 431.
Conostegia cinnamomea



Fig. 432. *Henriettea succosa*

white, 7–8 mm long; bracts and petals burnt-orange when dry; stamens 12–18, 5–6 mm long; filaments geniculate below anthers; anthers with terminal pores all directed toward style in vicinity of stigma; style straight. Berries round, hirsute, black and shiny, 8–12 mm wide; seeds minute, numerous. *Croat 11079*.

Occasional, in the forest. Flowers from March to July (rarely later). The fruits mature from August to November.

Nicaragua to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, from premontane wet forest in Coclé and Panamá, from tropical wet forest in Panamá and Darién, and from premontane rain forest in Darién.

See Fig. 430.

Conostegia cinnamomea (Beurl.) Wurdack, *Phytologia* 38:287. 1978

C. micromeris Standl.

Shrub, usually 1.5–3.5 m tall; younger parts furfuraceous with stellate trichomes, soon glabrate. Petioles 2–5 (10) mm long; blades broadest at about middle, gradually tapered to both ends, acuminate, mostly 6–22 cm long, 2.5–8.5 cm wide, bicolorous, glabrate above, sparsely stellate-pubescent below especially on veins, pliveined, the margins entire or minutely wavy (sinuate), the veins 5–7. Terminal compound dichasia 3–6 cm long, divaricately branched, the branches opposite, each subtended by a pair of narrow bracts; flowers sessile or short-pedunculate, minutely furfuraceous, the buds 3–4.7 cm long, distinctly apiculate, short-pedicellate; hypanthium 2–3 mm long at anthesis; petals (4) 5, white to pink, 4–4.7 mm long, acute at apex, recurved, soon falling; stamens (8) 10, erect at anthesis; filaments flattened, slightly longer than the anthers, markedly curved; anthers with terminal pores; style ca 5 mm long. Berries depressed-globose, to 6 mm diam, green turning light blue then deep purple at maturity; seeds minute, numerous. *Croat 6250*.

Frequent in the forest. Flowers and fruits throughout the year, principally from July to September.

Recognized by its small, inconspicuous inflorescences with beaked buds. The flowers fall off soon, and the plant seldom appears to be conspicuously in flower.

Nicaragua to western Colombia. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién; known also from premontane wet forest in Coclé and from tropical wet and premontane rain forests in Darién.

See Fig. 431.

Conostegia speciosa Naud., *Ann. Sci. Nat. Bot.*, sér. 3, 16:109. 1851

Shrub, seldom more than 2 m tall, very densely pubescent on all external surfaces, the trichomes of stems and inflorescences stalked-stellate. Petioles 1–4 cm long; blades ± ovate, acuminate, obtuse to rounded at base, 10–27 cm long, 5.5–13 cm wide, rugulose and mostly simple-pubescent above, with both stalked-stellate and simple

trichomes below, minutely serrate, pliveined, the veins 5–7, raised below. Panicles congested, ± maroon, terminal; flowers ca 1.5 cm diam, opening few at a time, often on same inflorescence with fruits, the buds violet, ovoid; petals 6 or 7, white to pink, ± rounded; stamens 12 or 14, directed to one side, geniculate below anther; anthers all with apices clustered around stigma; style short and thick, strongly bent to one side near apex; stigma green. Berries densely pubescent, dark purple, ca 1.5 cm diam; seeds minute, numerous. *Croat 6340*.

Common in clearings; occasional along the margin of the lake. Flowers and fruits throughout the year.

Foster 1134 and *1211*, collected along the shore on Peña Blanca Point, represent an extreme variation of *C. speciosa* or possibly a distinct variety of it. It has been suggested by C. Schnell (pers. comm.) that they are hybrids between *C. speciosa* Naud. and *C. subcrustulata* (Beurl.) Tr. In general appearance they look like *C. speciosa*, but they have only sessile stellate trichomes on the lower leaf surface as in *C. subcrustulata*.

Costa Rica to northern South America; Jamaica. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Coclé, and from tropical wet forest in Colón and Coclé.

Conostegia xalapensis (Bonpl.) D. Don ex DC., *Prodr.* 3:175. 1828

Canallito

Shrub or small tree, to 10 m tall (often only 3–4 m on BCI); all parts except interior parts of flowers and upper blade surfaces densely pubescent, the trichomes ± sessile, brown, stellate. Petioles 1–2.5 cm long; blades ± lanceolate, acuminate, obtuse to cuneate at base, 5–25 cm long, 1.7–8 cm wide, glabrate above in age, usually serrate, pliveined, the veins 3–5. Inflorescences terminal, paniculate; flower buds pyriform; petals 5, glabrous, white (drying yellow), obovate, ca 5 mm long; stamens 10; filaments bent sharply below anthers; anthers with terminal pores, all directed to one side of the flower (as is the stigma), the connective thickened on upper side; style bent to one side, thickened at apex; stigma papillate. Berries densely stellate-pubescent, green to purple at maturity, to 8 mm diam; seeds minute, numerous. *Croat 12281*.

Uncommon, collected only along the shore on the north side of the island. Flowers and fruits throughout the year.

Southern Mexico to northern South America; Cuba. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Veraguas (Atlantic slope), Colón, Panamá, and Darién, and from premontane rain, lower montane moist, and lower montane wet forests in Chiriquí.

HENRIETTEA DC.**Henriettea succosa** (Aubl.) DC., Prodr. 3:178. 1828

Tree, to 10 m tall; young stems and petioles densely strigose. Petioles 1–2 cm long, stout; blades elliptic to obovate, short-acuminate, obtuse at base, 11–22 cm long, 6–10 cm wide, ciliate, pliveined, the upper surface scabrous especially on veins, the lower surface strigose especially on veins, the trichomes densely matted, stout, acropetal, densely branched near base, the veins 3–5. Flowers 5-parted, few, short-pedicellate, in small axillary clusters on usually leafless stems; hypanthium and calyx together 1.2–1.5 cm long at anthesis, densely and coarsely strigose; calyx prolonged, the lobes acute, the exterior teeth minute or concealed; petals obovate, clawed, white or pinkish, with a conspicuous medial vein, pubescent near apex and outside along vein, to 1.2 cm long, the margins thin, often minutely lacerate; stamens and style erect at one side, the style then curving to one side, the stamens to the other; stamens 10, purple, ca 1.5 cm long; anthers ca 8 mm long, subulate, slightly S-shaped, \pm equaling length of filaments, with a terminal pore, the connective lobed at base; ovary inferior; style enlarged at apex. Berries remaining enclosed in the green hypanthium, \pm globose, to 1 cm diam, turning purple; seeds minute, numerous. *Croat 6592*.

Rare, collected recently only along the shore of Gross Peninsula. Apparently flowers throughout the rainy season, rarely in the late dry season. Fruit maturity time undetermined.

Central America to the Guianas and eastern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Colón and Panamá, and from tropical wet and premontane rain forests in Panamá.

See Fig. 432.

LEANDRA Raddi**Leandra dichotoma** (D. Don) Cogn. in Mart., Fl.

Brasil. 14(4):200. 1886

Shrub, 1–3 m tall, densely hirsute except on petals and inner flower parts, the trichomes on lower leaf surfaces of various lengths, those of stems and axes of inflorescences retrorse at least at base. Petioles 2–9 cm long; blades ovate to ovate-elliptic, long-acuminate, obtuse to rounded at base, 11–25 cm long, 5.5–15 cm wide, ciliate and denticulate; veins 5–7. Panicles slender, usually terminal, reddish, usually 10–20 cm long; flowers small, usually 5-parted; hypanthium often with gland-tipped trichomes, together with calyx ca 3 mm long, the lobes minute, the exterior teeth subulate, longer than lobes; petals acute, 2.5–3 mm long, white to pinkish; stamens usually twice the number of petals; ovary inferior; style longer than stamens, erect or \pm curved to one side. Berries round, to 6 mm diam, purple, hirsute; seeds minute, numerous. *Croat 12507*.

Common, especially along streams. Apparently flowers and fruits throughout the year.

Belize and Guatemala to Panama and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Veraguas and Darién on the Pacific slope, from premontane wet forest in Colón, Coclé, and Panamá, from tropical wet forest in Colón, Coclé, Panamá, and Darién, and from premontane rain forest in Bocas del Toro and Panamá.

See Fig. 433.

MICONIA R. & P.

Miconia is distinguished mostly by the terminal inflorescences, the petals rounded at the apex, and the open calyx buds. It has an inferior ovary. The fleshy fruits have numerous minute seeds.

Miconia affinis DC., Prodr. 3:187. 1828

M. microcarpa DC.; *M. beurlingii* Tr.

Shrub or small tree, usually 3–7 m tall; younger parts of stems and petioles, panicles, and hypanthia stellate-tomentose. Petioles 1–2 cm long; blades \pm oblong-elliptic, acuminate, acute to obtuse at base, 9–28 cm long, 3.5–12 cm wide, glabrate to sparsely appressed-stellate on both surfaces (at least on veins below), the midrib sometimes arched; veins from the base 3–5. Panicles terminal, to 15 cm long, almost as broad; hypanthium 1.5–2.5 mm long; calyx lobes 5, rounded to triangular, the exterior teeth often nearly as long, slender; petals 5, white, to 2.7 mm long, spreading; stamens 10; style straight, erect, at first much shorter than stamens, elongating to ca 6 mm and \pm equaling pores of stamens; stamens \pm erect; filaments curved, geniculate below anthers. Axes of fruiting inflorescences reddish; berries depressed-globose, green becoming whitish, turning blue and finally purple-black at maturity, 3 mm long, 6 mm wide; seeds numerous, minute. *Croat 11443*.

Occasional, in the forest. Flowers mostly in the dry season (January to June), with the fruits maturing mainly from June to October. Plants may flower more than once per year.

The species has been confused with *M. hyperprasina* Naud., which is known only from southern Mexico and Guatemala.

Elsewhere in Panama, *Trigona* bees have been seen collecting pollen from this species.

Mexico to Panama, Colombia, and the Amazon basin in Peru, Brazil, Venezuela, and French Guiana; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Colón, Coclé, and Panamá, and from premontane rain forest in Panamá and Darién.

Miconia argentea (Sw.) DC., Prodr. 3:182. 1828

Cainillo, Cainillo de cerro, Dos caras, Friega platos, Gorgojo, Gorgojillo, Mancha-mancha, Oreja de mula, Palo negro, Papelillo

Tree, to 15 (20) m tall, canescent except on upper leaf surfaces, the trichomes dense, fine, stellate; trunk to 50 cm dbh, with coarse shaggy bark in age; younger stems flattened, the edges twisted at the nodes. Leaves de-

KEY TO THE SPECIES OF MICONIA

Lower blade surface *conspicuously* pubescent:

Trichomes simple (sometimes bristled, branched, or rarely stellate in *M. shattuckii*):

Upper leaf surface very sparsely pubescent with simple trichomes, the lower surface with both simple and bristled trichomes (rarely stellate) *M. shattuckii* Standl.

Both leaf surfaces rather conspicuously pubescent, the trichomes simple, not branched or barbed along their length:

Blades to 6 cm wide; pubescence on upper stems, inflorescence, and petioles of purplish trichomes to 10 mm long *M. lacera* (Bonpl.) Naud.

Blades more than 6 cm wide; pubescence densely strigose, the trichomes less than 5 mm long *M. nervosa* (Smith) Tr.

Trichomes stellate:

Leaves sessile; trichomes of lower leaf surface not contiguous *M. impetiolearis* (Sw.) DC. var. *impetiolearis*

Leaves petiolate:

Blades very sparsely pubescent, with simple trichomes above and sessile stellate trichomes below, denser on veins *M. rufostellulata* Pitt.

Blades \pm glabrous above, the lower surface with stellate trichomes contiguous throughout:

Hypanthium much longer than broad, together with the calyx to 5 mm long; calyx flared, broader than hypanthium at anthesis; petals more than 5 mm long, densely stellate-pubescent outside; fruits more than 8 mm diam at maturity, densely stellate-pubescent; leaf blades usually 2 times longer than broad *M. serrulata* (DC.) Naud.

Hypanthium not much longer than broad, together with the calyx ca 2 mm long; calyx not flared, not obviously broader than hypanthium at anthesis; petals to 3 mm long, glabrous; mature fruits usually less than 6 mm diam (rarely to 8 mm in *M. argentea*), not densely stellate-pubescent; leaf blades usually ca 1.5 times longer than broad:

Blades whitish below, the veins scarcely if at all darker than the surface; branchlet pubescence pale, stellate, the trichomes \pm strictly sessile; trees often large, the trunks frequently more than 15 cm dbh, the bark then usually shaggy *M. argentea* (Sw.) DC.

Blades tan to brown below, the veins considerably darker than the surface; branchlet pubescence dark brown, the trichomes at least in part \pm stalked and not strictly stellate; trees small, the trunks usually less than 10 cm dbh, the bark deeply fissured but not shaggy *M. elata* (Sw.) DC.

Lower blade surface glabrous or essentially so (at least at maturity):

Plants wholly glabrous (*M. lateriflora* sometimes with minute, appressed, simple trichomes):

Blade margins often obscurely crenate, sparsely ciliate; hypanthium oblong, its lobes to 2 mm long *M. lateriflora* Cogn.

Blade margins entire, not ciliate; hypanthium narrowly bell-shaped or round, its lobes very short or obsolete:

Blades broadest below the middle, often rounded or obtuse at base, drying dark, usually less than 4.5 cm wide; anthers linear, not tapering to apex *M. borealis* Gleason

Blades broadest at middle, usually acute to obtuse at base, drying green, bicolorous, mostly more than 4.5 cm wide; anthers subulate, tapering to apex *M. hondurensis* Donn. Sm.

Plants with younger parts usually densely stellate-pubescent, some trichomes persisting on smaller stems in age:

Upper blade surface sparsely pubescent with simple trichomes, the lower surface often maroon; plants slender arching shrubs *M. rufostellulata* Pitt.

Upper blade surface glabrous or very sparsely and inconspicuously pubescent with stellate trichomes:

Blades ending abruptly on petiole, the lateral veins departing midrib at or near base:

Blades \pm ovate or lanceolate, rounded to slightly subcordate at base, broadest well below the middle, usually less than 4.5 cm wide; flowering hypanthium less than 1.5 mm long; fruits to 3 mm diam *M. borealis* Gleason

Blades elliptic to oblong-elliptic, acute to obtuse at base, broadest at about the middle, usually more than 4.5 cm wide; flowering hypanthium 2–3 mm long; fruits to 6 mm diam *M. affinis* DC.

Blades \pm decurrent on petiole, the lateral veins usually departing midrib somewhat above the base:

Blades usually undulate-denticulate, drying green, abruptly narrowed at the base, the decurrent portion broad, often irregular and undulate, ending abruptly very near base of petiole *M. prasina* (Sw.) DC.

Blades usually entire or nearly so, drying blackened, gradually narrowed at the base, the decurrent portion narrow, gradually diminishing, almost imperceptibly, well above base of petiole *M. lonchophylla* Naud.



Fig. 433. *Leandra dichotoma*

Fig. 434. *Miconia argentea*



cusate; petioles 2–6 cm long; blades broadly elliptic, abruptly short-acuminate to acute at apex, rounded at base, 8–30 cm long, 6–18 cm wide, entire or denticulate, veins from base 5; (juveniles with the leaf blades \pm ovate, to 38 cm long and 27 cm wide, the upper surface bearing sparse simple trichomes, the margins more denticulate, ciliate). Panicles terminal, to 25 cm long, widely branched; flowers many, sessile, 5-parted; hypanthium and calyx together ca 2 mm long, the calyx with obscure lobes; petals inequilateral, white, 2–3 mm long; stamens 10, erect at anthesis, of 2 sizes, the longer series somewhat longer than style, the shorter series slightly shorter than style, the connective of larger set prolonged at base into 2 small lateral lobes; anthers with a terminal pore as broad as anther; style to 4 mm long; stigma capitate. Berries globose, 4–8 mm diam, blue-purple at maturity, stellate-pubescent; seeds numerous, minute. *Croat 13104*.

Common in the forest, especially the younger forest; seedlings common. Flowers principally in the dry season (December to May), with the fruits maturing from January to June. J. Oppenheimer (pers. comm.) says fruits are eaten from March to May by white-faced monkeys. Trees are leafless during the dry season.

E. Morton (pers. comm.) reports that elsewhere in the Canal Zone fruits are eaten while still green by a variety of birds.

Southern Mexico to Panama. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from premontane dry forest in Los Santos, from tropical dry forest in Coclé, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 434.

Miconia borealis Gleason, Bull. Torrey Bot. Club 55:118. 1928

Shrub or small tree, to 5 m tall; younger stems finely stellate-pubescent, glabrous and often reddish in age. Petioles 5–15 mm long; blades narrowly ovate to lanceolate-oblong, long-acuminate, rounded to slightly cordate at base, 6–12 (15) cm long, 2.5–4.5 cm wide, entire, sparsely stellate-pubescent becoming glabrate, drying dark; veins 3 (rarely 5). Panicles terminal and upper-axillary, to 10 cm long; flowers 5-parted; hypanthium 1–1.5 mm long, obscurely lobed, \pm glabrous, lacking exterior teeth; petals white, recurved, ca 2 mm long; stamens folded in bud, held erect and exceeding style at anthesis, the style then lengthening to equal height of anthers (held in close proximity); filaments flat, recurving over edge of flower and withdrawing anthers from vicinity of style; anthers white, the apical pore as wide as anther. Inflorescences purplish in fruit; berries blue-black, ca 3 mm diam; seeds numerous, minute, white, translucent. *Foster 1345*.

Probably common on the island at one time, now rare, persisting only on the shore. The plant is abundant in the Canal Zone along Gaillard Highway between Gamboa and the Pacific coast. Flowers June to February, with the fruits maturing from August to May.

The style may not be receptive until the pollen has been removed from the anthers.

Southern Mexico to Panama; Cuba. In Panama, known from tropical moist forest in all provinces, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón, Chiriquí, Veraguas, Coclé, and Panamá, and from tropical wet forest in Colón, Coclé, Panamá, and Darién.

Miconia elata (Sw.) DC., Prodr. 3:182. 1828

Tree, 3.5–11 (13) m tall; trunk usually 6–15 cm dbh; bark with moderately close, deep vertical fissures, but not flaking; young stems, axes of inflorescences, petioles, and underside of veins densely rufous-pubescent, the trichomes pinnately branched, often somewhat stalked. Petioles to 9 cm long; blades broadly elliptic, obtuse to abruptly short-acuminate, obtuse to rounded at base, 9–35 cm long, 6–18 cm wide, denticulate, the surface below canescent and completely covered with trichomes, these sessile, stellate, in part with a brown center; veins 5, dark. Panicles large, terminal, 18–22 cm long, branched many times, the branches \pm flattened or angulate; flowers \pm sessile; hypanthium and calyx together 1.5–2 mm long, campanulate, the teeth obscure or lacking; petals 5, white, obovate, to 1.5 mm long. Berries round to depressed-globose, to 6 mm diam, white to lavender-blue, probably becoming purple-black at full maturity; seeds numerous, minute. *Croat 5693, 15070*.

Known only from shoreline north of the dock and south of Fairchild Point, but undoubtedly more abundant. Seasonal behavior uncertain. Flowers at least in January, February, and May. Mature fruits have been seen in April, May, and October.

Easily confused with *M. argentea*, which is similar in most respects except pubescence, trunk bark, and stature.

Mexico to Panama and Venezuela; West Indies. In Panama, known only from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in the Canal Zone.

Miconia hondurensis Donn. Sm., Bot. Gaz. (Crawfordsville) 40:3. 1905

Tree, to 12 m tall; glabrous except on youngest parts; trunk to 17 cm dbh; bark soft, vertically fissured, flaky. Petioles 1–4 cm long; blades elliptic, acuminate, acute to obtuse at base, mostly 9–20 cm long, 4.5–8 cm wide, moderately bicolorous, pliveined, the veins 3, the lateral veins departing midrib very near base. Panicles terminal, mostly less than 15 cm long; pedicels short, often minutely pubescent together with basal part of hypanthium; flowers 8–10 mm long; hypanthium and calyx together 3–4 mm long; calyx flared, weakly 5-lobed; petals 5, white, oblong, to ca 5 mm long, spreading at anthesis; stamens 10 (often slightly unequal), the longest \pm equaling petals; filaments geniculate; anthers tapered to apex, directed to one side, the connective lobed at base; style ca 12 mm long, broadly curved at anthesis; stigma curved in same direction as anthers. Fruiting inflorescences

violet-purple; berries round, 7–8 mm diam, black, glabrate; seeds lunate, ca 2.7 mm long. *Croat 13800, 14467.*

Uncommon, in the forest. Flowers in the middle of the dry season (February and March), with the fruits maturing in April and May.

Belize to Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in the Canal Zone.

***Miconia impetiolearis* (Sw.) D. Don ex DC. var.**

impetiolearis, Prodr. 3:183. 1828

Oreja de mula, Dos caras

Shrub or tree, ca 3 (5) m tall, bearing conspicuous, ferruginous-stellate pubescence except on older stems, upper leaf surfaces, petals, and inner flower parts. Leaves sessile; blades obovate-elliptic to oblong-elliptic, gradually to abruptly acuminate, cordate at base, 12–45 cm long, 7–15 cm wide, soon glabrous above, entire or denticulate, pliveined, the surface visible between the trichomes below, the veins 3–5. Panicles sessile, to 27 cm long, almost as wide as long; flowers white; hypanthium truncate, 2.5–3 mm long; petals 5, white, reflexed, rounded at apex; stamens 10, somewhat spreading, in 2 series, the longer series with anthers held just above stigma; anthers curved, the connective expanded and toothed at base of anther; style straight, erect, ca 6 mm long. Berries globose, to 9 mm diam, sparsely stellate-puberulent, green then bright red becoming black at maturity; seeds numerous, minute. *Croat 8052.*

Occasional in some areas of the forest, especially near the Tower Clearing and near the end of Barbour Trail; rare or absent elsewhere. Few observations have been made of the variety *impetiolearis*, but BCI individuals flower in the middle of the dry season (February and March), with the fruits maturing in the late dry season to early rainy season (April and May).

The species is represented on the island by the typical variety. The variety *panduriformis*, well represented elsewhere in the Canal Zone, flowers synchronously at least twice a year. The first synchronous flowering, possibly the largest, occurs in late February or March. Later flowerings may involve other individuals or the same inflorescence, making it possible for a single inflorescence to have both mature fruits and a new batch of flowers.

Southern Mexico to Panama; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién; known also from premontane moist forest in the Canal Zone.

***Miconia lacera* (Bonpl.) Naud., Ann. Sci. Nat. Bot., sér. 3, 16:152. 1851**

Shrub, to 2 (4) m tall; stems, petioles, and axes of inflorescences with many violet-purple to red-violet trichomes mostly 5–10 mm long. Petioles 1–3.5 cm long; blades \pm ovate-lanceolate to narrowly elliptic, acuminate, obtuse to rounded or slightly subcordate at base, 5–15 cm long, 2–6.5 cm wide, more or less pilose on both sides especially on veins, entire to serrulate and ciliate; veins from base 3–5. Panicles very congested in flower, branched

or unbranched, to 4 cm long, the trichomes at first whitish becoming colored in fruit; flowers ca 6 mm wide, secund, in a staggered row; hypanthium usually glabrous; calyx spreading, its lobes deeply lacerate and markedly ciliate, the exterior teeth equaling calyx lobes; petals 5, white to pinkish, 3–4 mm long, often emarginate at apex; stamens and style folded in bud; stamens red-violet, \pm directed to one side; anthers 1.7 mm long, their terminal pores held in close proximity to style; style directed like the stamens. Berries subglobose, 6–7 mm diam, black, shiny; seeds numerous, minute, brown. *Croat 6126.*

Occasional in clearings and infrequent within the forest. Elsewhere in the Canal Zone it is frequent in open areas. Plants flower more than once per year and may bear both flowers and fruits on different branches. Flowers from March to August. The fruits mature principally from June to October but are seen all year.

The plant apparently does not produce nectar and is probably visited by small pollen feeders. The anthers do not forcibly expel the pollen, but the grains come out readily if the stamens are pulled back and then released.

Mexico to Peru; West Indies, Trinidad. In Panama, widespread and ecologically variable; known from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Herrera, Coclé, Panamá, and Darién, from premontane wet forest in the Canal Zone, Colón, Coclé, and Panamá, from tropical wet forest in Veraguas (Atlantic slope), Colón, Coclé, Panamá, and Darién, and from premontane rain forest in Panamá.

See Fig. 435.

***Miconia lateriflora* Cogn., Bol. Mus. Paraense Hist.**

Nat. 5:255. 1909

Ossaea disparilis Standl.; *O. disparilis* Standl. var. *adenophora* Standl.

Shrub, to 3 m tall, \pm glabrous. Petioles 1–3 (5) cm long; blades \pm elliptic, narrowly long-acuminate, attenuate to obtuse at base, 7–20 (25) cm long, 3–9 (12) cm wide, entire to crenulate and ciliate, the cilia continuous with the lateral veins; veins 3. Panicles terminal, loose and open, sparsely branched, the branches often red in fruit; flowers few, usually 4-parted, sessile, in terminal glomerules; inflorescence branches often sparsely stellate-pubescent; hypanthium tubular, 3.5–4 mm long, often sparsely stellate-pubescent, sometimes also glandular-pilose; calyx nearly obsolete, the external teeth narrowly triangular, 1.5–2 mm long; petals white, obovate (sometimes obcordate), 1.6–1.8 mm long; stamens to ca 5.3 mm long; anthers subulate, 3–3.5 mm long, the connective minutely bilobed at base; style erect, as long as stamens. Fruiting hypanthia ovoid, ca 2 cm long, strongly 8-ribbed, blue; seeds numerous, minute. *Croat 10822.*

Apparently rare on the island, seen on Shannon Trail in a steep ravine and at Pearson Trail 400. Flowers principally in June and July, with the fruits maturing probably in September and October.

Belize to northern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Colón



Fig. 435. *Miconia lacera*

Fig. 436. *Miconia nervosa*



Fig. 437.
Miconia prasina



and Panamá, and from tropical wet forest in Bocas del Toro, Panamá, and Darién.

Miconia lonchophylla Naud., Ann. Sci. Nat. Bot., sér. 3, 16:176. 1851

Shrub or small tree, to 6 m tall; young stems, petioles, and axes of inflorescences moderately to densely pubescent with small, sessile, stellate trichomes. Petioles 6–25 mm long; blades narrowly elliptic, acuminate, attenuate and decurrent on petiole at base, 9–29 cm long, 3–8 cm wide, pliveined, drying blackened, sparsely stellate-pubescent below, usually soon becoming glabrate above, the veins sometimes pubescent, the margins entire or rarely sinuate to denticulate, the midrib often arched; major veins 3, usually arising well above base, with a weak submarginal vein. Panicles terminal, to ca 15 cm long; hypanthium and calyx ca 2 mm long, sparsely stellate-pubescent, the calyx teeth thin, obtuse to rounded, the external teeth thick, minute; petals 3, oblong, 1.8–2.7 mm long, often markedly oblique at apex, white; stamens 10; anthers 1.5–2 mm long, oblong-linear, the connective shortly prolonged at base, the two terminal pores about as broad as thecae; style about as long as stamens; stigma at first cupuliform, becoming capitate. Fruiting inflorescences with red axes; berries depressed-globose, 5–6 mm diam, at first red, becoming black at maturity; seeds numerous, minute. *Croat 14609, 15052.*

Adult plants rare, seen only on Orchid Island and on the eastern side of Gross Peninsula; juveniles slightly more common. Known from few observations. Flowers at least from the late dry to early rainy seasons (April to May), with the fruits maturing shortly afterwards (May to July).

Costa Rica to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Darién and from premontane wet forest in Panamá. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

Miconia nervosa (Smith) Tr., Trans. Linn. Soc. London 28:111. 1871

Shrub, 2–3 m tall, densely soft-pubescent, the trichomes on petals and inner flower parts simple, \pm stiff, those on stems, petioles, and axes of inflorescences appressed-ascending. Leaf pairs often unequal; petioles 5–20 mm long; blades elliptic, acuminate at apex, acute to attenuate at base, 7–28 cm long, 3.5–12 cm wide, pliveined, ciliate, sparsely pubescent on upper surface, softly pubescent to subsericeous on lower surface, the pubescence much denser on veins especially above, the veins 5–7; juveniles with the blades purplish below. Panicles narrow, branched or unbranched, 5–15 cm long, usually less than 3 cm wide, the main axis reddish; flowers 5-parted, sessile; hypanthium 2.5–4 mm long, appressed-pubescent; petals strongly reflexed at anthesis, white, rounded at apex; stamens isomorphic; anthers tapered toward apex, the connective inconspicuously prolonged at base; ovary pubescent; style ca 6 mm long; stigma truncate. Berries depressed-globose, to 12 mm wide, pale orange-red becoming gray-blue to purple at maturity, fleshy, densely

pubescent; seeds brown, \pm sticky, narrowly wedge-shaped, ca 0.7 mm long. *Croat 12872.*

Occasional in the older forest; uncommon elsewhere. Flowers and fruits throughout the year.

Southern Mexico to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, from tropical wet forest in Veraguas (Atlantic slope), Colón, and Darién, and from premontane rain forest in Darién.

See Fig. 436.

Miconia prasina (Sw.) DC., Prodr. 3:188. 1828

Shrub or tree, usually 2–8 m tall; stems, petioles, axes of inflorescences, and hypanthia bearing \pm dense, ferruginous, stellate pubescence (especially stems and petioles). Petioles very short; blades elliptic to narrowly elliptic, acuminate (the acumen often somewhat twisted), acute at base and decurrent onto petiole, 12–26 cm long, 4.5–14 cm wide, entire or more commonly undulate-denticulate, glabrate or sparsely stellate-pubescent above (at least in age), pubescent with sparse, sessile, stellate trichomes below at least on veins, pliveined, the veins 3, sometimes reddish. Panicles terminal, 8–23 cm long; hypanthium 2–3 mm long, reddish; calyx lobes 5, obtuse to rounded or obscure, the submarginal teeth small and inconspicuous or lacking; petals 5, obovate, to 3 mm long, white, densely papillate-puberulent in distal three-fourths, strongly recurved at anthesis; stamens 10, at first erect; filaments curved, geniculate below anther; anthers to 3 mm long, tapered to apex, the terminal pore held in vicinity of style, later recurved over sides of hypanthium; style erect, straight, to ca 5.7 mm long. Berries depressed-globose, ca 6–9 mm diam, to 5 mm long when fully mature, lavender-blue, becoming purple at maturity, sparsely pubescent; seeds numerous, minute. *Croat 8555.*

Collected once on Gross Peninsula. Populations usually flower twice during the dry season, once near the onset of the dry season and again in about the middle of the dry season. At the second flowering the plants may also bear fruits from the earlier flowering period. The second flowering is the heavier, with most fruits maturing in the early rainy season, chiefly in July and August.

Southern Mexico to Bolivia and Paraguay; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone (Ancón), from premontane wet forest in Colón and Chiriquí, from tropical wet forest in Colón, Coclé, Panamá, and Darién, and from premontane rain forest in Panamá.

See Fig. 437.

Miconia rufostellulata Pitt., J. Wash. Acad. Sci. 13:390. 1923

Shrub, to 2 m tall, often vinelike; stems, petioles, inflorescences, and underside of veins sparsely to densely, minutely stellate-pubescent; stems glabrous in age. Petioles 4–12 mm long; blades lanceolate, acuminate, rounded to subcordate at base, 4–14 cm long, 1.5–3.5 cm wide, setose above, maroon below, entire to denticulate, ciliate,

the cilia terminating the small veins; veins 3, from base or pliveined from very near base. Panicles or racemes small, terminal; bracts subulate; flowers 4-parted; hypanthium cup-shaped, 1.5–2 mm long; calyx to 2.2 mm long, the lobes triangular, persisting in fruit, the exterior teeth subulate and divergent at apex, often longer than sepals; petals oblong-obovate, white, to 2.5 mm long; stamens dimorphic; anthers 2–2.5 mm long, the connective of the larger pair dilated; stigma capitate. Berries globose, 4–5 mm diam, 10-ribbed, sparsely stellate-pubescent; mature fruits not seen. *Croat 15106*.

Rare, along Barbour and Chapman trails. In Darién, flowers in March and fruits in June and July.

Characterized by the reddish lower leaf surface. Description of the flower parts is based on the type.

Known only from the type collection from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in the Canal Zone (Pipeline Road).

Miconia serrulata (DC.) Naud., *Ann. Sci. Nat. Bot.*, sér. 3, 16:118. 1851

Shrub or tree, 3–10 m tall; stems, axes of inflorescences, petioles, and veins of lower leaf surfaces bearing dense, brown, stellate pubescence, the trichomes of stems, inflorescences, and petioles dark brown. Petioles 3–9 cm long; blades ± elliptic, acuminate, narrowly rounded or subcordate at base, 15–33 cm long, 5–14 (21) cm wide, glabrous above, densely matted with stellate trichomes below, denticulate; veins 5–7, from base. Panicles large, terminal, 10–15 cm long, congested toward ends of branches; flowering hypanthium oblong, much longer than broad, the hypanthium and calyx together ca 5 mm long, very densely stellate-canescens; calyx tube 1–2.5 mm long, markedly flared, the lobes obtuse to rounded, the exterior teeth lacking; petals 5, white, obovate, 5–9 mm long, rounded to irregular at apex, densely stellate-pubescent outside, glabrous inside, often densely ciliate with simple trichomes; stamens 10, isomorphic; anthers purplish, slightly curved, tapered toward apex, ca 4.5 (5.8) mm long, the connective pubescent with glandular trichomes, prolonged into 2 short lobes at base; style to 9 mm long, thickened at apex. Berries ca 1 cm diam at maturity, densely stellate-pubescent; seeds numerous, minute. *Croat 12504*.

Collected near Zetek Trail 500 and 1015. Flowering in the late dry season (and probably early rainy season). The fruits develop chiefly in the late rainy season (August to November).

Mexico to Peru, Bolivia, and southeast Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from tropical wet forest in Colón and Darién, and from premontane rain forest in Darién. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

Miconia shattuckii Standl., *Contr. Arnold Arbor.* 5:119, pl. 16. 1933

Shrub or small tree, usually 3–3.5 m tall; branches, petioles, and inflorescences densely to sparsely tomentose, the trichomes with a single irregular axis and numerous,

short, sharp branches. Petioles stout, 1–5 cm long; blades broadly ovate-elliptic, acuminate, rounded to shallowly cordate at base, 20–35 cm long, 12–20 cm wide, dark green and glabrous to sparsely villous above, more densely pubescent below, with both straight and branched trichomes, the branched ones usually restricted to veins, entire or the margins entire or somewhat irregular; veins 5–7, from base (1 weak and submarginal), impressed. Inflorescences terminal, reddish, paniculate, to 12 cm long; pedicels 1.7–2.3 mm long, minutely bracteate; flowers white; hypanthium and calyx pinkish, pubescent with both simple and stellate trichomes, together 2.3–3 mm long; sepals 5, acute, the external teeth minute, often green; petals 5, oblong-obovate, 4.2–5.2 mm long, to 2.4 mm wide, rounded at apex; stamens slightly shorter than corolla; filament geniculate below anther; anthers linear-attenuate, to 2 mm long, each with 1 apical pore; style ca 4 mm long. Berries depressed-globose, 7–10 mm diam, pink when young, becoming violet then black at maturity; seeds numerous, minute. *Croat 12190, 14552*.

Rare; known from a single locality on a creek bank on Shannon Trail. The type was collected earlier on Snyder-Molino Trail. Flowers and fruits in the rainy season. Apparently flowers twice per year, at the beginning of the rainy season and toward the middle of the rainy season. The fruits mature in about 1 month.

Colombia (Antioquia) and Panama. In Panama, known from tropical moist forest on BCI and from lower montane rain forest in Darién.

MOURIRI Aubl.

Mouriri myrtilloides (Sw.) Poir. subsp. ***parvifolia*** (Benth.) Morley, *Brittonia* 23:422. 1971

M. parvifolia Benth.

Guayabillo, Arracheche, Solacra, Cicrito, Kenna

Shrub, usually 2–4 (15) m tall, essentially glabrous, divaricately branched; younger stems ribbed, the ribs 4, thin, sharp, deciduous on older wood. Leaves sessile; blades lanceolate or ovate-lanceolate, acute to acuminate, rounded to subcordate and inequilateral at base, 3–8.5 cm long, 2–3 cm wide, pellucid-punctate, the margins undulate; vein 1 (the midrib). Fascicles axillary, bearing few flowers; pedicels with opposite-decussate bracteoles; flowers 5-parted; hypanthium and calyx together 5–6 mm long, campanulate, the lobes narrowly triangular, to 3 mm long, persisting in fruit; petals white, acuminate, 4–6 mm long, soon falling; stamens 10, exserted, shorter than style; anthers ca 2 mm long, with 2 subterminal, short, porelike slits, the connective darker, thickened toward base, bearing a dorsal gland prolonged at base; ovary inferior; style elongating to more than twice the length of the flower. Berries round, 7–13 mm diam, with persistent hypanthia, green turning deep purple at maturity, indehiscent or splitting open irregularly at maturity, ephemerally sweet; exocarp thin; mesocarp purplish, 2–3 mm thick; seed 1, subglobose, to 7 mm broad, with minute longitudinal ridges. *Croat 11790*.

Common in the forest. Flowers sporadically throughout the year, mostly in August and September but also

in the middle of the dry season. The fruits probably develop in about a month.

Leaves are similar to *Eugenia nesiotica* (106. Myrta-ceae), a tree that flowers before putting on new leaves. Though Melastomataceae are said to lack stipules, this species usually bears interpetiolar structures that are at least stipule-like.

Mexico to Colombia, Ecuador, Peru, Bolivia, and western Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Los Santos, Panamá, and Darién, from tropical dry forest in Coclé, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Coclé.

OSSAEA DC.

Ossaea quinquenervia (P. Mill.) Cogn. in A. DC.,
Monogr. Phan. 7:1064. 1891

O. diversifolia (Bonpl.) Cogn.

Fruta de pava

Shrub, to 1(1.5) m tall; young stems, petioles, and inflorescences bearing dense, minute, brown, stellate pubescence. Petioles 1–3(5) cm long; blades ovate to broadly elliptic, acute to short-acuminate, abruptly attenuate and decurrent nearly to base of petiole, 6–22 cm long, 3.5–11.5 cm wide, glabrate to sparsely pilose above, densely stellate on veins below, denticulate and ciliate with reddish pilose trichomes, plicveined, the veins 5. Cymes loosely branched, paniculate, axillary, 2–5 cm long; flowers 5-parted; hypanthium pink, subglobose to campanulate, glandular-puberulent, sometimes sparsely setose (especially elsewhere); hypanthium and calyx tube together ca 1 mm long; calyx tube prominent, the lobes less than 1 mm long and widely spreading, the lobes and exterior teeth subulate; petals narrowly triangular to ovate, minute, ca 1.2 mm long, white, rounded to acute at apex, with a subapical tooth on outside, spreading at anthesis; stamens 10, erect, to 3.3 mm long, the connective extending somewhat beyond filament; anthers with apical pores; ovary inferior; style erect, to 5.7 mm long. Berries red, turning purple-black, subglobose, to ca 4 mm diam; seeds minute, numerous. *Croat 11429*.

Locally common at the edges of clearings; less frequent in the forest. Flowers and fruits throughout the year.

Costa Rica to northern South América. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Los Santos, Panamá, and Darién on the Pacific slope; known also from premontane moist forest in Panamá (Panamá City), from premontane wet forest in Panamá, and from tropical wet forest in Colón, Panamá, and Darién.

SCHWACKAEA Cogn.

Schwackaea cupheoides (Benth.) Cogn. ex Durand,
Index Gen. Phan. 132. 1888

Branched herb, 7–75 cm tall; stems square, reddish, glabrous to pubescent on nodes and along angles. Petioles very short, to 8 mm long; blades ovate to narrowly elliptic,

acute to acuminate, acute at base, 1–6 cm long, 0.3–2 cm wide, entire, sparsely pubescent, the trichomes above longer and sparser than below; veins 3. Flowers 4-parted, sessile, solitary in leaf axils; hypanthium ca 4 mm long at anthesis (excluding teeth), strigose, the lobes slender, ca 2 mm long, strigose, ciliate; petals pink (rarely white), ca 5 mm long; stamens 8, dimorphic, the outer 4 lavender, their connective longer than the anther, at right angles to filament, the inner 4 stamens yellow, with the anthers much reduced; ovary superior; style \pm equaling height of anthers. Capsules oblong, ca 1 cm long, ribbed, the ribs 8, corky, tuberculate, setose; seeds cochleate, minute, numerous. *Croat 12279*.

Occasional, in clearings and on exposed lakeshore banks. Flowers principally from August to January. The fruits probably mature from September to February.

Capsules probably split open from the apex. The minute globular seeds pass slowly through the passages formed between the long cilia of the persistent sepals, probably only while the wind is blowing.

Southern Mexico to Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

See Fig. 438.

TIBOUCHINA Aubl.

Tibouchina longifolia (Vahl) Baill., *Adansonia*
12:74. 1877

Herb, to 1.5 m tall, becoming woody in age, appressed-pilose. Petioles 5–15 mm long; blades narrowly lanceolate, acute to acuminate, acute to obtuse at base, 4–11 cm long, 1–3.5 cm wide, entire, the trichomes above adnate to the leaf for part of their length; veins 5–7. Cymes terminating stems and branches; flowers 5-parted, often many; hypanthium and calyx densely setose, the lobes slender, 3–4 mm long; petals white (rarely pinkish), obovate, 6–8 mm long, ciliate; stamens 10, folded at anthesis, later unfolding to 5 mm long; anthers yellow, ca 3 mm long, tapered to apex, with a single terminal pore (eventually equaling or exceeding stigma), curved, lobulate at base; ovary superior; style erect; stigma simple. Capsules subglobose, ca 3 mm long; seeds many, cochleate, tuberculate. *Croat 4611*.

Usually locally abundant in clearings. Flowers and fruits throughout the year.

The capsules are somewhat nodding at maturity and are irregularly dehiscent by slender cracks near the apex. The minute seeds pass through when the capsules are shaken in the wind.

Southern Mexico to western Brazil and Bolivia; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Los Santos, Herrera, Panamá, and Darién; known also from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Coclé (Atlantic slope) and Panamá, and from lower montane rain forest in Chiriquí.

TOPOBAEA Aubl.

Topobaea praecox Gleason, *Phytologia* 3:355. 1950

Hemiepiphytic shrub, to 4 m tall, often perched in crotches of trees, not commonly found in top of crown, the trunk to the ground slender, 5–6 cm diam, not twining; stems terete, glabrous; branches arching, pendent, to 4 m long, the youngest stellate-furfuraceous, the internodes short on flowering branches. Leaves immature at flowering time, clustered; petioles 1–5 cm long, stellate-pubescent; blades ovate to oval, acuminate, obtuse to subcordate at base, 3–16 cm long, 1.5–11 cm wide, glabrous above, weakly stellate-pubescent below especially on veins, entire, pliveined or basally veined, the veins 5, the midrib arched. Fascicles axillary, of usually 3 or 4 (to 5) flowers, usually on leafless nodes; pedicels less than 1 cm long; bracts in 2 pairs, at base of each flower, decussate, distinct to the base, broadly rounded, emarginate and recurved at apex, 7–8 mm long, glabrous to sparsely and minutely stellate-pubescent; flowers ca 3 cm wide, 6-parted; hypanthium and calyx to 1 cm long; calyx lobes rounded to obtuse, curved inward in fruit, ± glabrous, tinged with red; petals magenta, obovate, sometimes oblique, 1.5(2.2) cm long, thick at base; stamens 12, to 2.3 cm long; filaments flexed below anthers; anthers to 1.2 cm long, coherent laterally except at apex, horizontal and directed to one side of flower with the style, with 2 subapical pores; ovary inferior; style to 1.6 cm long, held just in front of anthers; stigma simple. Fruiting hypanthia and calyces to ca 1.2 cm long, bowl-shaped; berries contained within persistent sepals; seeds sticky, numerous, dark brown, oblong, to 1.3 mm long, embedded within a fleshy white matrix. *Croat 14953*.

Occasional in the forest high in trees, rarely lower on the lakeshore; probably always somewhat epiphytic. Flowers from March to June, with the fruits probably maturing from June to September. Leaves fall off during the late dry season and are replaced in the early rainy season.

A large bee, possibly *Eulaema mexicana*, was observed drumming pollen out of flowers in an upside-down position. The process takes less than 10 seconds per flower.

Allen (unpublished manuscript) said that a related species, *T. regeliana* Cogn., is at first a strangler, eventually developing a trunk of its own.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién and from premontane wet and tropical wet forests in Coclé, Panamá, and Darién.

108. ONAGRACEAE

Aquatic herbs or erect or prostrate terrestrial herbs; stems sometimes winged. Leaves alternate, sessile or petiolate; blades simple, entire; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, solitary, axillary, bracteolate; calyx 4–6-lobed, forming a hypanthium, the lobes valvate; petals the same number as calyx lobes, clawed, yellow or occasionally white with a yellow spot, free, soon falling; stamens twice the number of calyx lobes, in 2 series; anthers 2-celled, dehiscing longitudinally; ovary inferior, generally 4-locular, 4-carpellate; placentation axile; ovules anatropous, many on each placenta; style simple; stigma capitate. Fruits loculicidally dehiscent capsules; seeds many, lacking endosperm, the raphe (scar of the ovular stalk) often diagnostic.

The family is represented on BCI only by *Ludwigia*.

Distinguished by the usually four-parted flowers, with nearly rounded, clawed, yellow petals and an inferior, multiovulate ovary terminated by a hypanthium and persistent sepals.

Flowers of some species are pollinated at least in part by stingless bees, halictid bees, and other small bees. Pollen grains of the Onagraceae are held together by viscid elastic threads. Bees specialized on this family have pollen baskets made up of long unbranched bristles (Proctor & Yeo, 1973). Some species are self-pollinated (*Ludwigia decurrens*) or mostly self-pollinated (*L. octovalvis*) (P. Raven, pers. comm.).

Plants grow principally in aquatic situations, and the minute, usually buoyant seeds are probably dispersed partly by wind and partly by water.

Some 21 genera and about 650 species; primarily in temperate and subtropical regions.

LUDWIGIA L.

Ludwigia decurrens Walt., *Fl. Carol.* 89. 1788

Jussiaea decurrens (Walt.) DC.

Erect, ± glabrous herb, usually to 1 m tall, branched; stems usually 4-winged. Blades subsessile, lanceolate to linear, attenuate to apex, ± acute at base, mostly 5–12 cm long, 1–3.5 cm wide, prominent lateral veins in 11–16 pairs, conspicuously loop-connected. Flowers solitary in upper axils, 4-parted; sepals lanceolate-ovate, 7–10 mm long; petals yellow, 8–12 mm long; stamens 8, 2–3 mm long; style ca 2 mm long; stigma globose, ca 2 mm thick. Capsules clavate-obpyramidal, (8) 12–20 mm long, 4-angled or 4-winged, the corners dark-ribbed, weather-

KEY TO THE SPECIES OF LUDWIGIA

- Leaves obovate to suborbicular, the petioles conspicuous, one-fourth to fully as long as blade;
plants floating or prostrate on soil, rare *L. helminthorrhiza* (Mart.) Hara
- Leaves lanceolate to linear, the petioles lacking or short, much less than one-fourth as long as
blade; plants often aquatic, but always erect:
Flowers 4-parted; seeds multiseriate in each locule of the capsule, not enclosed in a corky persistent
endocarp:
Capsules club-shaped, conspicuously broadened toward apex, 8–20 mm long; plants rare or
no longer present on the island *L. decurrens* Walt.
- Capsules ± cylindrical, 2–5 cm long; plants common *L. octovalvis* (Jacq.) Raven

Flowers 5- or 6-parted; seeds uniseriate or biseriata in each locule, each seed surrounded by its corky persistent endocarp:

Plants conspicuously pubescent; capsules \pm cylindrical, 2–4.5 cm long; seeds in 1 series in each locule, free within a horseshoe-shaped endocarp; plants common

. *L. leptocarpa* (Nutt.) Hara

Plants glabrous or essentially so (the stems and fruits drying viscid); capsules \pm oblong, less than 1 cm long; seeds in 2 series in each locule, entirely enclosed within endocarp; plants possibly no longer present

. *L. torulosa* (Arn.) Hara

ing into fibers; seeds subcylindrical, less than 1 mm long, free, multiseriate in each locule, the raphe ca one-fifth the width of the body. *Bailey & Bailey 384*.

Possibly no longer occurring on the island; last collected by the Baileys along the shore. Probably flowers and fruits throughout the year.

Southern United States to northern Argentina. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro and from tropical dry forest in Coclé.

Ludwigia helminthorrhiza (Mart.) Hara, J. Jap. Bot. 28:292. 1953

Jussiaea natans H. & B.

Aquatic herb, floating on water or prostrate on mud, \pm glabrous; stem conspicuously rooting at nodes, seldom branching. Petioles 1–3 cm long; blades obovate to sub-orbicular, blunt at apex, abruptly narrowed to petiole, 2–7 cm long, 1.5–4.5 cm wide; lateral veins conspicuous, with a loop-connecting vein. Flowers solitary in axils, usually 5-parted; sepals lanceolate-ovate, ca 5 mm long; petals white with basal yellow spot, oblong-obovate, 8–14 mm long, shortly clawed; stamens 10, unequal, 3–5 mm long; anthers 1–2 mm long; style white, 4–7 mm long; stigma green, slightly lobed, ca 1.5 mm wide. Capsules subcylindrical, 2–3 cm long, ca 3 mm thick; endocarp hard, shining, ca 1.5 mm long; seeds contained in and adnate to the endocarp, uniseriate in each locule. *Shattuck 1132*.

Apparently once common at the edge of the lake and no doubt still occurring in marshy areas on the southern and western edges of the island. Apparently flowers and fruits throughout the year.

Southern Mexico to Peru and Paraguay. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

Ludwigia leptocarpa (Nutt.) Hara, J. Jap. Bot. 28:292. 1953

Jussiaea leptocarpa Nutt.

Herb usually about 1 m tall or shrub to 2.5 m, rooting at lower nodes when in water; stems angulate-winged from below petiole, sparsely white-pilose and puberulent. Blades sessile or on petioles to 10 mm long, lanceolate, usually acute or acuminate at apex, gradually tapered to base, 4–8 (14) cm long, 0.7–2.8 cm wide, usually puberulent on both surfaces, often with longer trichomes on veins. Flowers solitary in axils, 5- or 6-parted; pedicels to ca 2 cm long; sepals lanceolate, acuminate, 5–8 mm

long; petals yellow, obovate, rounded at apex, usually 8–10 mm long (rarely smaller); stamens 10 or 12, in 2 series, the shorter series opposite petals, the longer ones alternate, about as high as stigma; anthers extrorse; style stout, 2–4 mm long; stigma capitate (becoming fleshy); nectaries in U-shaped depressions around base of outer filaments, protected by a close series of arching trichomes from either side; nectar copious. Capsules subcylindrical, striate, 2.5–4.5 cm long, to 3 mm thick, long-pubescent; seeds uniseriate in each locule, ca 1 mm long, surrounded by the horseshoe-shaped corky endocarp. *Croat 11299, 13972*.

Frequent in swampy or moist areas on the shore; often a component of floating masses of vegetation. Flowers and fruits from January to July.

Throughout the tropics and subtropics of the New World. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from tropical dry forest in Coclé, and from premontane wet forest in Chiriquí.

See Fig. 439.

Ludwigia octovalvis (Jacq.) Raven, Kew Bull. 15:476. 1962

Jussiaea suffruticosa L.

Aquatic herb, usually to 1.5 m tall; stems usually branched and weakly or rather densely pubescent. Leaves variable, sessile or short-petiolate, lanceolate or oblong to linear, acute to acuminate at apex, acute to attenuate at base, the larger leaves 6–15 cm long, 0.5–3.5 cm wide. Flowers solitary in axils, 4-parted; sepals ovate or lanceolate, 3–15 mm long; petals obovate, yellow, rounded or emarginate at apex, to 1.5 cm long; stamens 8, in 2 series, the outer 4 opposite petals, the inner 4 around style, longer than style in bud; anthers extrorse; style 1.5–3.5 mm long; stigma \pm globular, held just above anthers at anthesis. Capsules \pm cylindrical, 2–5 cm long, striate with 8 darker ribs, weathering at maturity, splitting apart longitudinally; seeds multiseriate in each locule, free, minute, with the raphe enlarged and as large as body of seed, the seeds dispersed by wind and water. *Croat 6863, 15245*.

Common along the shore, usually in standing water, occasionally as an epiphyte on floating debris. Flowers and fruits principally in the rainy season.

This species as treated here includes both *Jussiaea suffruticosa* L. var. *octofila* (DC.) Munz and var. *ligustri-folia* (H.B.K.) Griseb. as treated by Munz in the *Flora of Panama* (1959).

Throughout the tropics of the world. In Panama, ecologically variable; known from tropical moist forest



Fig. 439. *Ludwigia leptocarpa*

Fig. 438. *Schwackaea cupheoides*



Fig. 440.
Ludwigia octovalvis

in all areas, from tropical dry forest in Coclé, from pre-montane wet forest in Chiriquí, from tropical wet forest in Colón, Coclé, and Darién, and from lower montane wet forest in Chiriquí.

See Fig. 440.

Ludwigia torulosa (Arn.) Hara, J. Jap. Bot. 28:294. 1953

Erect glabrous herb; stems reddish-brown and viscid (at least on drying). Petioles less than 1 cm long; blades narrowly lanceolate, long and gradually tapered to apex, acute at base, 8–13 cm long, 0.5–1.7 cm wide. Flowers solitary in axils, usually 5-parted. Fruits ± oblong, constricted in the middle, ± viscid (at least on drying), less than 1 cm long; seeds many, biseriate in each locule, surrounded by endocarp. *Shattuck 1161*.

Collected once by Shattuck in August 1934 at Zetek House. This collection was not considered by either Standley or Munz in the *Flora of Panama*. Seasonality not known.

Belize, Panama, the Guianas, Brazil, and Bolivia; Cuba, Santo Domingo. In Panama, known only from BCI.

Members of the family are confused with only the Umbelliferae (110) and are most easily recognized by being arborescent and by having panicles with the flowers arranged in small umbels. Except for *Didymopanax* (with a usually laterally compressed fruit), fruits are also characteristic, being more or less globose with a prominent ring around the persisting styles.

The flowers are very open, with dorsifixed versatile anthers that turn inside out, making the pollen easily accessible. Nectar, if present, is also accessible. Flowers are probably pollinated by a wide range of small insects. Hladik (1970) reported that they are visited primarily by bees of the genera *Trigona* and *Melipona*.

The fruits are probably dispersed chiefly by birds, but may be taken by white-faced monkeys (Enders, 1935; Hladik & Hladik, 1969) and perhaps other animals. Fruits of *Didymopanax morototoni* are taken by a variety of birds including guans, manakins, toucans, honeycreepers, pigeons, and woodpeckers (Chapman, 1938). Fruits of *Dendropanax arboreus* are taken by the bat *Artibeus jamaicensis* Leach in Mexico (Yaquez-Yanes et al., 1975).

About 65 genera and about 800 species; mostly in the tropics.

109. ARALIACEAE

DENDROPANAX Dec. & Planch.

Dendropanax arboreus (L.) Dec. & Planch., Rev. Hort.

sér. 4, 3:107. 1854

Gilbertia arborea (L.) Marchal

Vaquero

Tree, 10–20(25) m tall, 25–40(70) cm dbh, glabrous; bark with prominent lenticels, not deeply fissured; wood soft; ultimate branches whorled from apex of stout stems; stems brittle. Leaves simple, alternate; petioles 1–8 cm long; blades variable, mostly elliptic, also ovate-elliptic and obovate-elliptic, obtuse to acuminate and downturned at apex, attenuate to rounded at base, 5.5–15 cm long, 2–8 cm wide, usually entire, rarely with remote apiculate teeth. Racemes terminal, 6–12 cm long, of 3–20 pedunculate umbels, frequently with many umbels along rachis below terminal whorl of umbels; primary peduncle

Terrestrial or epiphytic shrubs or trees. Leaves alternate, petiolate (the petioles often variable in length), simple to pinnately or palmately compound; blades entire, serrate, or lobed, sometimes with T-shaped or branched trichomes; venation pinnate; stipules present, sometimes ligulate. Panicles terminal, compound, the ultimate divisions heads or umbels; flowers bisexual or polygamous (*Oreopanax*), greenish; calyx inconspicuous, with about 5 teeth; petals 5, valvate, arising from the epigynous disk; stamens 5–10, free, alternate with the petals; anthers 2-celled, dorsifixed, dehiscing longitudinally; ovary inferior, 2–10-locular; placentation axile; ovules solitary in each locule, pendulous, anatropous; styles 2–10, free or connate; stigmas terminal or on inner surfaces. Fruits berries; seeds as many as carpels, with copious endosperm.

KEY TO THE SPECIES OF ARALIACEAE

Leaves compound:

- Leaves pinnately 3–9-foliolate; blades sharply serrate; plants cultivated in the Laboratory Clearing *Polyscias guilfoylei* (Bull) Bailey
- Leaves palmately 7–12 foliolate; blades entire; plants frequent in clearings and along the shore *Didymopanax morototoni* (Aubl.) Dec. & Planch.

Leaves simple:

- Flowers sessile or nearly so in dense heads, the heads staminate or bisexual; inflorescence branches usually stellate-pubescent *Oreopanax capitatus* (Jacq.) Dec. & Planch.
- Flowers pedicellate in umbels, bisexual; inflorescence branches glabrous:
 - Leaves usually ± elliptic, infrequently toothed; calyx truncate to weakly lobed; petals more than 2 mm long; fruit ca 10 mm diam; seeds rugose, notched at apex *Dendropanax arboreus* (L.) Dec. & Planch.
 - Leaves usually ± oblong, usually with remote, minute teeth; calyx with 5 deltoid teeth; petals usually less than 1.5 mm long; fruits ca 6 mm diam; seeds appearing smooth, grooved along rounded outer margin *Dendropanax stenodontus* (Standl.) A. C. Smith

and rachis 1.5–6 cm long, bracteate at nodes, the floriferous peduncles 1–5 cm long, often bracteate, the bracts free, ovate, ca 1 cm long; pedicels 3–9 mm long; flowers (3)10–30(50) per umbel, greenish-white, ca 6 mm diam, 5–7-parted; calyx \pm bowl-shaped, truncate and undulate to remotely 5-lobed; petals 5, valvate, (1.3)2–2.5 mm long, acute and cucullate at apex, spreading at anthesis, later reflexed; stamens 5(7), alternate with and longer than petals, to 4 mm long, erect at anthesis, later spreading; anthers ca 1 mm long; styles 5(7), connate at base, the connate part flat or slightly conical, free and held tightly together at apex, later spreading, persistent in fruit, ca 0.5 mm long. Berries globose, ca 1 cm diam, smooth, drying deeply sulcate between seeds with \pm sharp ridges, black-purple at maturity, with a ringlike scar around persistent styles; seeds 5(7), \pm semicircular, flattened, with a sharp margin, ca 7 mm long, tan, notched at apex on inner margin, minutely muricate. *Croat 11751, 17047.*

Frequent in the forest. Flowers from June to December, principally in July and August. The fruits mature in about 1 month. Individuals may bear mature fruits as well as flowers on separate inflorescences. Leaves are lost and quickly replaced in the dry season.

Mexico to Colombia, Venezuela, Ecuador, Peru, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Los Santos, and Darién Provinces, from premontane wet forest in the Canal Zone, Chiriquí, Coclé, Panamá, and Darién, and from lower montane wet forest in Chiriquí. Reported from premontane moist, tropical wet, and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Figs. 441 and 442.

Dendropanax stenodontus (Standl.) A. C. Smith,
Trop. Woods 66:3. 1941

Shrub or small tree, 1–2.5(4) m tall, glabrous; stems striate when dry. Leaves simple, alternate; petioles 1–8 cm long; blades variable, frequently oblong, also elliptic, narrowly elliptic, oval, oblong-ovate or oblong-obovate, usually abruptly long-acuminate at apex, attenuate to rounded at base, 6–25 cm long, 2–10 cm wide, usually with sparse, minute, apiculate teeth. Racemes terminal, 2–8 cm long, of 3–15 pedunculate umbels, usually with few umbels on rachis below terminal whorl of umbels; primary peduncle and rachis 4–7 cm long, bracteate at nodes, the floriferous peduncles 1–5 cm long, bracteate near middle, the bracts free, ovate, ca 0.5 mm long; pedicels 2–9 mm long; flowers 4–35 per umbel, greenish-white to greenish-purple, ca 4.7 mm diam at anthesis, usually drying black to purple; calyx \pm bowl-shaped, lobed, 1–1.8 mm long (mostly less than 1.5 mm), acute and cucullate at apex, spreading at anthesis, later reflexed, the lobes 5, deltoid to apiculate; petals narrowly ovate, 3–3.5 mm long; stamens 5, alternate with and as long as or slightly longer than petals, erect to spreading; anthers ca 0.7 mm long, the thecae directed upward at anthesis; styles 5–9, connate, ca 1 mm long, conical at base, free at apex and held tightly together at anthesis, later spreading,

persistent in fruit. Berries globose, smooth, ca 6 mm long, drying slightly sulcate between seeds; seeds 5, shaped like orange segments, ca 4.3 mm long, tan, deeply grooved on one side along rounded outer margin. *Croat 5409, 11427.*

Occasional, in somewhat disturbed areas at the edges of clearings or on shore; one individual known in the older forest. Flowers from April to August, mostly in July and August, rarely earlier or later. The fruits mature from May to September, mostly in July and August. Individuals may flower two or more times per season and can be found with both flowering and fruiting inflorescences.

Mexico (Chiapas) to Panama. In Panama, known principally from tropical moist forest on the Atlantic slope of the Canal Zone, in adjacent parts of Colón, and in San Blas; known also from premontane wet forest in Colón (near María Chiquita).

See Fig. 443.

DIDYMOPANAX Dec. & Planch.

Didymopanax morototoni (Aubl.) Dec. & Planch.,
Rev. Hort. sér. 4, 3:109. 1854
Mangabe, Gargarán, Pavo, Pava

Tree, to 25(30) m tall; trunk to 40(70) cm dbh; outer bark planar, thin, \pm mottled, marked with vertical rows of minute lenticels, these rubbing off easily; inner bark moderately thick, coarse, mottled tan and white; sap with sweet, strong odor; leaves and inflorescences clustered at apex. Leaves alternate, palmately compound; petioles to 1 m long with a basal ligule ca 1 cm long; petiolules 3–14 cm long; leaflets 7–12, oblong or oblong-oblancoate, acuminate, obtuse to rounded or subcordate at base, 8–45 cm long, 3–19 cm wide, entire, glabrous above, densely and softly ferruginous-pubescent below with T-shaped trichomes; juvenile leaves much thinner, the lower surface with numerous, small, appressed, T-shaped trichomes, the upper surface with long simple trichomes much like those on the conspicuously ciliolate margins. Panicles compound, terminal, 15–50 cm long, with racemose umbels, the pubescence appressed, grayish, the branches subtended by small bracts; flowers bisexual, 5-parted, 7–15 per umbel; calyx cupuliform, 1–1.5 mm long; petals oblong, 1.5–2.5 mm long, glabrous inside; stamens 1.5–2.5 mm long; styles 2, free, ca 1 mm long, erect, spreading in fruit. Berries transversely oblong, flattened, cordate at both ends, ca 5 mm long and 8–10 mm wide; seeds 2. *Croat 4394, 6853; 14584* (juvenile leaves).

Frequent in clearings and along the shore. Flowers from July to December, but mostly in the late rainy season. Allen (1956) reported that the flowers are present from November to February on the Osa Peninsula in Costa Rica. The fruits are common from January to May.

The species is frequently visited by small birds during the fruiting period.

Mexico to Brazil and Argentina; West Indies. In Panama, characteristic of tropical dry and tropical moist forests (Holdridge & Budowski, 1956; Tosi, 1971); known also from premontane moist and premontane wet forests in Panamá and from tropical wet forest in Colón.



Fig. 441. *Dendropanax arboreus*



Fig. 442. *Dendropanax arboreus*



Fig. 443.
Dendropanax stenodontus

OREOPANAX Dec. & Planch.

Oreopanax capitatus (Jacq.) Dec. & Planch., Rev.
Hort. sér. 4, 3:108. 1854

Polygamous shrub or tree, to 15 m, sometimes hemiepiphytic and growing near top of canopy, glabrous except for inflorescences. Leaves simple, whorled near apex of branches; petioles 5–25 cm long, terete; blades ovate, elliptic or obovate, 10–30 (35) cm long, 4–16 (25) cm wide, acute to long-acuminate at apex, acute to rounded at base, the larger ones conspicuously undulate. Panicles terminal, 15–20 (30) cm long, the heads dense, racemose, staminate or bisexual, the inflorescence branches with branched trichomes; bracts at branching nodes small; staminate heads 10–25-flowered, the flowers with 1 or 2 styles; bisexual heads 5–12-flowered, the flowers with 5–10 styles, the styles to ca 1 mm long; stamens to 3 mm long; both types of heads with calyx ca 1 mm long; petals 5, white, oblong, 2–2.5 mm long. Berries subglobose, to 8 mm diam; seeds few. *Croat 11861.*

Frequent in the forest. Seasonality uncertain. Flowers and fruits in the early dry season (January and February), but mostly during the early to the middle of the rainy season (June to October), especially in July and August.

Though generally found to be a small to medium-sized tree growing in the normal manner, at least one plant was seen growing as a hemiepiphyte on another tree at ca 30 m.

Mexico to South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Chiriquí and Coclé, and from lower montane wet and lower montane rain forests in Chiriquí.

POLYSCIAS Forst. & Forst.f.

Polyscias guilfoylei (Bull) Bailey, *Rhodora* 18:153. 1916
Nothopanax guilfoylei (Bull) Merr.
Wild coffee, Coffee tree

Glabrous shrub, 5–7 m tall but usually pruned; stems with elongate lenticels. Leaves imparipinnate; petiole, rachis, and petiolules often purplish and marked with light green streaks; leaflets 3–9, variable, orbicular to ovate-elliptic, obtuse to short-acuminate at apex, acute to rounded at base, attenuate to petiole, mostly 5–12 cm long, 3–7 cm wide, sharply serrate, the margins sometimes white. Panicles large, open, the umbels long-

pedunculate; flowers small, 4- or 5-parted, pedicellate; ovary 5–8-locular. Fruits not seen. *Croat 14549.*

Cultivated in the Laboratory Clearing and usually pruned. Seasonal behavior not determined.

The variety *laciniata* Bailey, with deeply incised margins, is cultivated at Summit Garden (Canal Zone).

Native to Polynesia; cultivated in the American tropics. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro.

110. UMBELLIFERAE
(APIACEAE)

Glabrous perennial herbs (*Spananthe* annual), aquatic (*Hydrocotyle*) or terrestrial, sometimes strong-scented (*Eryngium*). Leaves opposite, alternate, or basal, petiolate; blades simple, usually serrate, spiny, sometimes tripartite in *Eryngium*, peltate in *Hydrocotyle*; venation generally palmate (obscure in *Eryngium*); stipules lacking (*Spananthe* with bristly cilia). Umbels or heads terminal and axillary; flowers bisexual, actinomorphic; calyx 5-lobed (lacking in *Hydrocotyle*); petals 5, free, white; stamens 5, free, alternating with the petals, inserted on an epigynous disk; ovary inferior, 2-locular, 2-carpellate; placentation axile; ovules 1 per locule, anatropous, pendulous; styles 2, basally swollen and forming a depressed stylopodium (lacking in *Eryngium*); stigmatic tips swollen, ± globular. Fruits schizocarps of 2 mericarps; seeds 1 per mericarp, with abundant endosperm.

Umbelliferae are characterized by the usually sheathing petioles, the usually umbellate inflorescences, the bicarpellate, bilocular, inferior ovary, and the schizocarpic fruit.

The flowers of most species are self-compatible, but protandrous, and are pollinated by insects, especially Diptera and unspecialized Hymenoptera (Bell, 1971). Self-pollination is believed to be effected by thrips, which are found in great abundance on the inflorescences.

The fruits do not have any apparent means of dispersal. *Hydrocotyle umbellata* must rely on water currents or perhaps water fowl to disperse its seeds because of its consistent aquatic habitat around the margin of the lake. Leaves of *Eryngium foetidum* are used as a condiment in Panama, and the species has no doubt been dispersed by man.

About 275 genera and 3,000 species; primarily in the North Temperate regions.

KEY TO THE SPECIES OF UMBELLIFERAE

- Plants aquatic; leaves orbicular, peltate *Hydrocotyle umbellata* L.
- Plants not aquatic; leaves not orbicular, not peltate:
 - Plants with basal rosette of linear-oblancoelate leaves; flowers sessile, in densely bracteate heads *Eryngium foetidum* L.
 - Plants lacking basal leaves; flowers pedicellate, in long pedunculate umbels *Spananthe paniculata* Jacq.

ERYNGIUM L.

Eryngium foetidum L., Sp. Pl. 232. 1753

Culantro, Culantro coyote, Fitweed, Spiritweed

Glabrous herb from a stout taproot, to 60 cm tall. Leaves dimorphic; blades of basal rosette linear-oblongate, rounded at apex, cuneate at base, 10–16 cm long, 2.5–4 cm wide, serrate; upper blades opposite, sessile, oblanceolate, often tripartite, apiculate at apex, acute to obtuse at base, 2–3 cm long, 0.5–1.5 cm wide, spinulose-serrate. Flower heads dense, bracteate, cylindrical, ca 1 cm long, subtended by 5 or 6 leaflike bracts greatly exceeding the heads; flowers 5-parted, white, minute, sessile, congested, subtended by a bracteole; bracteoles narrow, exceeding the fruit; sepals widely separated, ovate, mucronate at apex, \pm equaling petals; petals ca 0.5 mm long, refolded inward; stamens nearly twice as long as styles, shed with corolla after anthesis; styles 2, ca 1 mm long, somewhat spreading, exerted earlier than stamens. Fruits \pm globose, ca 2 mm long, conspicuously muricate. *Croat 8672*.

Common in the Laboratory Clearing. Flowers and fruits throughout the year, but the flowers are initiated principally in the dry season.

The plant has a foul aroma in all parts. Crushed leaves are savored by the natives as a condiment in foods.

Throughout the tropics of the New World; introduced into tropical Africa. In Panama, growing in clearings and weedy areas; known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Panamá and Darién, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí, Coclé, and Panamá.

HYDROCOTYLE L.

Hydrocotyle umbellata L., Sp. Pl. 234. 1753

Glabrous herb, usually aquatic, creeping, densely rooting at nodes. Leaves single at each node; petioles 5–20 (40) cm long, fleshy; blades peltate, orbicular, 2–7.5 cm diam, crenate or crenately lobed. Umbels simple, axillary; peduncles long, erect, \pm equaling leaves; flowers 5-parted, several to many on rays 2–25 mm long; sepals lacking; petals 5, white, ca 1 mm long, spreading at anthesis, becoming recurved; stamens spreading, less than half as long as or equaling petals; styles 2, spreading, or directed toward one another; stigmas \pm globular. Fruits ellipsoid, 2-carpellate (rarely 3-carpellate), 1–2 mm long, 2–3 mm broad. *Croat 13233*.

Uncommon, restricted to swampy areas on the south side of the island at the lake's edge; a component of the floating marshes. Flowering and fruiting year-round.

Throughout warmer regions of the New World; tropical southern Africa. In Panama, known from aquatic situations in tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, and Panamá, from tropical dry forest in Coclé, and from premontane wet forest in Chiriquí and Coclé.

SPANANTHE Jacq.

Spananthe paniculata Jacq., Coll. 3:247. 1789

Herb, 20–150 cm tall; stems hollow. Leaves opposite; stipules minute, bristly-ciliate; petioles 1–8 cm long, bearing a tuft of fine trichomes at apex; blades deltoid-ovate or ovate, acuminate, truncate to cordate at base, 2.5–9 (14) cm long, 2–6 (14) cm wide, dentate-crenate, sparsely setose-pubescent on veins, paler below. Umbels simple, axillary; peduncles 1–14 cm long, finely pubescent especially near apex; pedicels slender, 7–10 mm long; flowers 5-parted, minute, white; calyx ca 1 mm long, with apiculate teeth; petals obovate, ca 2 mm long; stamens to 1.5 mm long; anthers ca 0.4 mm long, 0.5 mm wide; styles 2, to 1 mm long; stigma simple. Fruits ovoid, 2–4 mm long, ca 2 mm wide. *Aviles 18*.

Collected once on the island; probably no longer occurring there. Seasonal behavior not determined. Flowers and fruits most abundantly in the rainy season.

Throughout warmer regions of the New World. In Panama, known only from tropical moist forest in the Canal Zone.

111. THEOPHRASTACEAE

Small trees. Leaves alternate, \pm sessile; blades simple, entire; venation pinnate; stipules lacking. Racemes terminal, bearing several flowers; flowers aromatic, bisexual, actinomorphic; sepals 5, free; corolla tubular, 5-lobed, the lobes imbricate, alternating with 5 petaloid stamindia; stamens 5, epipetalous, opposite the corolla lobes; filaments united at the base and adnate to the corolla tube; anthers 2-celled, extrorse, longitudinally dehiscent; ovary superior, 1-locular, 5-carpellate; placentation free-central; ovules many, anatropous; style 1; stigma subsessile, capitate. Fruits irregularly dehiscent capsules; seeds few, immersed in pulp, with fleshy endosperm.

The family is represented on BCI only by *Jacquinia macrocarpa*, which can be distinguished by its sharply apiculate leaf blades and its coriaceous, bright-orange flowers. In Costa Rica hummingbirds visit the flowers on rare occasions (D. Janzen, pers. comm.). Fruits are probably animal dispersed.

Some 32 genera and about 1,000 species; subtropics and tropics.

JACQUINIA L.

Jacquinia macrocarpa Cav., Icon. Pl. 5:55, t. 483. 1799*J. aurantiaca* Ait.

Small tree. Leaves very stiff, elliptic to obovate, acute to rounded at apex with a sharp apiculum, acute at base, 6–10 cm long, 2–3.5 cm wide, \pm sessile, glabrous except on upper midrib. Racemes corymbiform; flowers pleasantly and strongly aromatic; sepals coriaceous, persisting in fruit, the lobes rounded, imbricate, the margins thin; corolla bright orange, coriaceous, the lobes 5, blunt,

alternating with 5 petaloid staminodia; stamens 5, ex-
trorse, held closely together around the style (the pollen
may be shed in bud), after several days folding back
against tube to expose the much shorter stigma; ovary
unilocular; ovules many, on a stalked basal placenta;
stigma capitate, covered with a viscid liquid. Fruits
oblong-elliptic, apiculate, to 7 cm long, yellowish; exo-
carp thick, woody; seeds several, dark brown, hard, shiny.
Croat 12885.

Cultivated at the Laboratory Clearing. Flowers sporadically throughout the year, mostly in the dry season and the early rainy season. The species is not deciduous on BCI (R. Foster, pers. comm.). In Costa Rica, plants lose their leaves within 8 weeks of the first rains and are usually completely leafless by the first week of July, remaining leafless through the rest of the rainy season until late November or December. Flower buds are present within 1 month after new leaf production, and nearly all flowers are open within 2 months. The fruits begin to mature in the middle of the rainy season.

The species has been called *J. aurantiaca* Ait. in Panama; it is not known for certain that *J. aurantiaca* is synonymous with *J. macrocarpa*.

Mexico south to Panama and possibly as far as Ecuador. In Panama, restricted to the Pacific coast at low elevations, frequently found growing with *Hippomane mancinella* (75. Euphorbiaceae; not on BCI); known from premontane dry forest in Los Santos and Herrera, from tropical dry forest in Coclé and Panamá, and from tropical moist forest in the Canal Zone.

112. MYRSINACEAE

Shrubs or sometimes trees; most parts pellucid- or opaque-punctate. Leaves alternate, petiolate; blades simple, entire or sometimes serrulate, sometimes with stellate pubescence; venation pinnate; stipules lacking. Inflorescences terminal or sometimes axillary, ± paniculate, sometimes bracteate; flowers bisexual or sometimes unisexual (*Stylogyne* dioecious), actinomorphic; calyx deeply (4)5-lobed; corolla (4)5-lobed to near base; stamens of the same number as and opposite corolla lobes,

epipetalous, distinct; anthers 2-celled, dorsifixed, introrse, dehiscent longitudinally or by apical pores; ovary superior, 1-locular, (4)5-carpellate; placentation axile; ovules 3 to many; style short; stigma simple. Fruits drupes with fleshy exocarp and stony endocarp; seed with copious endosperm.

Members of the family can be recognized usually by the alternate leaves, by the characteristic pellucid or opaque dots on the leaves and most floral and fruit parts, and by the globose, one-seeded fruits.

Pollination systems are unknown.

The fruits are probably eaten by birds (Ridley, 1930).

Some 32 genera and about 1,000 species; subtropics and tropics.

ARDISIA Sw.

Ardisia bartlettii Lund., Contr. Univ. Michigan Herb. 7:37. 1942

Slender shrub or small tree, to 4 m tall, glabrous. Petioles mostly 5–10 mm long; blades elliptic, weakly or markedly acuminate, acute to attenuate and decurrent at base, mostly 6–15 cm long, 2.5–4.5 cm wide, entire or inconspicuously toothed, densely pellucid-lineolate, the midrib somewhat raised on both surfaces, the lateral veins obscure (at least when fresh). Racemes terminal, corymbose or subumbellate, lavender to red-violet throughout, short, mostly less than 5 cm long; pedicels slender, 4–13 mm long; flowers 5-parted, to 14 mm wide, pellucid-punctate; calyx lobes 5, densely punctate, ca 2 mm long, becoming green, persisting in fruit; corolla ca 7 mm long in bud, ca 12 mm wide when open, the lobes 5, ovate, spreading to recurved, free to near base; stamens 4–5 mm long; filaments short, stout, united with corolla at base; anthers yellow, pointed, 3–4 mm long, dehiscent by apical pores; style simple, slender, slightly exceeding stamens, shorter than petals, at first erect, becoming bent to one side. Drupes subglobose, fleshy, at first ± maroon, becoming purple-black at maturity, 6–8 mm diam; seed globose, ca 5 mm diam. *Croat 11271.*

Frequent in the forest. Flowers from May to September (sometimes from March), with the fruits maturing

KEY TO THE SPECIES OF MYRSINACEAE

- Inflorescences axillary; flowers unisexual; corolla white *Stylogyne standleyi* Lund.
- Inflorescences usually terminal; flowers bisexual; corolla reddish (white in *Ardisia fendleri*):
 - Leaf blades bearing wide bands of minute brownish trichomes on underside along midrib; inflorescence branches, pedicels, and calyces finely reddish-tomentose *Parathesis microcalyx* Donn. Sm.
 - Leaf blades lacking bands of brownish trichomes; inflorescences glabrous or lepidote:
 - Leaf blades often more than 20 cm long, the margins pectinate-dentate with subulate teeth *Ardisia pellucida* Oerst.
 - Leaf blades less than 20 cm long, entire:
 - Inflorescences 10–20 cm long; flowers white; leaf blades more than 4.5 cm wide *Ardisia fendleri* Lund.
 - Inflorescences ca 5 cm long; flowers purplish; leaf blades less than 4.5 cm wide *Ardisia bartlettii* Lund.



Fig. 444. *Ardisia fendleri*

Fig. 445. *Parathesis microcalyx*



from June to October (sometimes to December).

Known only from Panama, from tropical moist forest in the Canal Zone, San Blas, and Darién.

Ardisia fendleri Lund., *Wrightia* 4:45. 1968

Shrub or small tree 2–8 m tall, ± glabrous. Petioles 5–10 mm long, marginate; blades elliptic or oblong-elliptic, acute to shortly acuminate, obtuse at base, 10–20 cm long, 4.5–9.5 cm wide, sparsely appressed-furfuraceous below when young, glabrous in age, with dense, opaque, orange punctations. Inflorescences terminal and axillary, 5–15 cm long, paniculate, the ultimate flower clusters subcorymbose; inflorescence branches and pedicels red; pedicels slender, 3–7 mm long; flowers 5-parted; sepals ovate, 1–1.5 mm long, punctate, persistent in fruit; corolla 3–6 mm long, white, lobed nearly to base, the lobes ± elliptic, 2–3 mm wide, lineate-punctate; stamens ca 4 mm long; anthers ca twice as long as filaments, dehiscent by apical pores; style simple, ca 5 mm long. Drupes globose, 6–7 mm diam, fleshy, green turning red then purple and finally black at maturity; seed globose, hard. *Croat 5560*.

Uncommon. Probably flowers and fruits throughout the year.

Known only from Panama, from tropical moist forest on the Atlantic slope of the Canal Zone and from premontane wet forest in Colón and Coclé.

See Fig. 444.

Ardisia pellucida Oerst., *Vidensk. Meddel.* 1861:130, t. 2. 1861

A. myriodonta Standl.

Shrub, usually less than 60 cm tall (to much taller elsewhere); stems, petioles, lower leaf surfaces, and exposed parts of inflorescences sparsely granular-puberulent. Petioles 1–1.5 (2.5) cm long; blades ± elliptic to oblanceolate, acuminate, cuneate at base, 18–32 cm long, 6–10.5 cm wide, decurrent on petiole as marginal ribs, glabrous and shiny above, dull and often purplish below (with minute red-orange punctations when held to light), pectinate-dentate, the teeth subulate. Panicles small, terminal, violet, usually less than 4 (to 20) cm long, about as broad as long; pedicels 4–11 mm long, slender; calyx deeply lobed, 2–3 mm long, persistent, the lobes 4 or 5, ovate, acuminate, recurved, with orange pellucid punctations near apex; corolla 4–6 mm long, 4- or 5-lobed to near base, the lobes glandular-punctate near apex, violet-purple outside, light violet inside; stamens 4 or 5, 1.8–2 (4) mm long, somewhat exserted; filaments fused to corolla at base; anthers yellow, equaling filaments, dehiscent laterally, beginning at apex; style simple, slender, 2–4 (5) mm long. Drupes depressed-globose, ca 6 mm diam, purple-black at maturity; seed depressed-globose, 4–5 mm diam, brown. *Croat 11156, 14473*.

Occasional, in the old forest above the escarpment. Flowers from March to June (sometimes to August). The fruits mature from May to September.

Lundell (1971) reported that the plant may reach a height of 7 m.

Mexico to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Darién.

PARATHESIS Hook.

Parathesis microcalyx Donn. Sm., *Bot. Gaz.* (Crawfordsville) 48:295. 1909

Shrub, 1–2 m tall; older stems with a smooth, light-brown, corky periderm, the younger stems, lower surface of petioles, underside of midribs, and all exposed parts of inflorescences densely covered with brown, scalelike, stellate trichomes. Petioles 1–2.5 cm long, the upper surface glabrous and concave; blades elliptic to oblanceolate, acuminate, attenuate and decurrent at base, 6–14 cm long, 2.5–4.5 cm wide, densely pellucid-punctate, glabrous except for a narrow band of sparse stellate trichomes on either side of midrib below, thin, entire, the margins somewhat undulate. Panicles congested, terminal, subcorymbiform, 3–7 cm long; pedicels 2–4 mm long; flowers 5-parted, to 5 mm broad; inflorescence branches, pedicels, and calyces finely reddish-tomentose; calyx ca 1.3 mm long, lobed about midway, the lobes triangular, black-punctate, persisting in fruit; corolla magenta, pellucid-lineate, lobed to near base, the lobes slender, papillate-puberulent inside, ca 4 mm long, recurved at anthesis; stamens ca 2 mm long; filaments flattened, broadened somewhat and fused to corolla at base; anthers yellow, equaling filaments in length, dehiscent by longitudinal slits; ovary ovoid, furfuraceous at apex; style simple, slender, to 8 mm long. Drupes white to greenish, ± globose, 4–6 mm diam, smooth, shiny, sparsely stellate-pubescent (densely in juveniles); seed white, shiny, of same shape as fruit, a bit smaller. *Croat 9576, 12416*.

Abundant locally in the swampy area north of Zetek 300; unknown elsewhere on the island. Flowers from April to August, with the fruits maturing from July to September.

Nicaragua to Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién and from tropical wet forest in Darién.

See Fig. 445.

STYLOGYNE A. DC.

Stylogyne standleyi Lund., *Wrightia* 3:110. 1964

Glabrous, dioecious shrub or small tree, usually to ca 3(7) m tall. Petioles ca 1 cm long or less; blades oblong-elliptic to lanceolate-oblong, gradually acuminate (the acumen often twisted), obtuse and decurrent on petiole at base, 12–30 cm long, 6–11 cm wide, minutely pellucid-punctate, thick. Panicles axillary, to 7.5 cm long, sessile or subsessile, pale, glabrous; pedicels 2–4 mm long; flowers 5-parted, white; staminate flowers ca 5.5 mm long; sepals 5, ovate, ca 1.4 mm long, 5-lobed to near base, asymmetrical; stamens to 6 mm long, exserted; filaments to 5 mm long; anthers ca 1.3 mm long, dehiscent

by introrse slits; ovary abortive; style more than 1 mm long. Pistillate flowers with the sepals 5, thick, ovate, densely orange-punctate, 1-1.4 mm long, imbricate, closing to protect young ovary after corolla falls; corolla ca 4.5 cm long, 5-lobed to near base, revolute, asymmetrical, orange-punctate; stamens ca 3 mm long, included; filaments slender, \pm equaling anthers; anthers ca 1.3 mm long; ovary ovoid, glabrous; style 1.5-3 mm long, simple. Fruiting inflorescences with peduncles and pedicels red; drupes subglobose, 7-9 mm diam, violet to blue-violet or black at maturity; exocarp thin; mesocarp fleshy, sweet; seed globose, ca 5 mm diam. *Croat 4878, Foster 1457.*

Occasional to locally common in the forest. Flowers in the early dry season (December to February). The fruits mature from January to September, primarily from March to June.

Costa Rica to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane moist forest in the Canal Zone and Panamá.

113. SAPOTACEAE

Trees with white sap. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules lacking; T-shaped trichomes frequently present. Flower clusters or fascicles in axils or at leafless nodes; flowers bisexual or unisexual (*Pouteria stipitata* dioecious), actinomorphic; sepals 4-6 (8-12 in *Pouteria sapota* and *P. fossicola*), free

or basally connate; corolla \pm tubular, 4- or 5-lobed; stamens 4-6, inserted just below the corolla lobes, in *Pouteria* alternating with an equal number of staminodia, the staminodia alternate with the corolla lobes; anthers 2-celled, basifixed, dehiscent longitudinally; ovary superior, 4- or 5-locular and 4- or 5-carpellate; placentation variously axile; ovules 1 per locule, anatropous; style simple, obscurely 4- or 5-lobed. Fruits berries; seeds 1 or several (*Pouteria stipitata*), lacking endosperm (*Pouteria*) or with copious oily endosperm (*Chrysophyllum*, *Cynodendron*).

With the Lauraceae (58), one of the most difficult tropical families, probably with many undescribed species. Sapotaceae can most easily be distinguished by the milky sap and by the small gamopetalous flowers with the stamens borne at the apex of the short tube and usually alternating with staminodia (*Pouteria*).

The flowers are best suited to insect pollination.

The fruits are eaten by animals, principally arboreal mammals, or by birds, as in the case of the smaller-fruited species or those with moderately thin exocarps such as *Cynodendron panamense*. *Chrysophyllum* and *Cynodendron* are eaten by most frugivorous mammals (Carpenter, 1934; Hladik & Hladik, 1969; Goodwin & Greenhall, 1961; N. Smythe, pers. comm.). *Pouteria fossicola* has large fruits that have been found intact long distances from the tree, presumably rolling after falling to the ground.

About 35-75 poorly defined genera and about 800 species; tropics and subtropics.

KEY TO THE SPECIES OF SAPOTACEAE

- Secondary lateral veins \pm paralleling primary laterals; staminodia lacking:
- Blades coppery-brown-sericeous on lower surface; corolla lobes equaling or slightly exceeding the tube; stigma 7-12-lobed; fruits usually 5-10 cm diam at maturity *Chrysophyllum cainito* L.
 - Blades glabrate or with relatively few whitish trichomes on lower surface; corolla lobes less than half as long as tube; stigma 5-lobed; fruits usually less than 3 cm diam *Cynodendron panamense* (Pitt.) Aubreville
- Secondary laterals not paralleling primary laterals (often perpendicular to them); staminodia present (appearing to be lobes of corolla, the corolla thus appearing to have large and small lobes alternately disposed):
- Leaves mostly more than 16 cm long, usually more than 6 cm wide; sepals 8-12 or more; fruits more than 7 cm long at maturity:
 - Primary lateral veins in 20-50 pairs; sepals often emarginate or more deeply lobed at apex; fruits ellipsoid, ovoid, or subglobose, brown, mealy-roughened on outer surface *Pouteria sapota* (Jacq.) H. E. Moore & Stearn
 - Primary lateral veins in 15-25 pairs; sepals entire or scarcely emarginate; fruits obovoid, yellowish-green, the surface smooth and shiny (drying with wrinkles) or lenticellate *Pouteria fossicola* Cronq.
 - Leaves less than 16 cm long, less than 6 cm wide; sepals 4-6; fruits less than 4 cm long at maturity:
 - Leaf blades usually broadest well beyond middle; corolla 4-lobed, usually less than one-third of way to base, the lobes alternating with staminodia; staminodia similar to corolla lobes but very different from stamens; fruits more than 2.5 cm broad at maturity, yellowish *Pouteria stipitata* Cronq.
 - Leaf blades broadest near middle; corolla usually 6-lobed almost to base of tube; staminodia very different from corolla lobes, similar to stamens; fruits less than 2 cm broad at maturity, purplish *Pouteria unilocularis* (Donn. Sm.) Baehni

CHRYSOPHYLLUM L.**Chrysophyllum cainito** L., Sp. Pl. 192. 1753

Caimito, Star apple

Tree, to 20(25) m tall, ca 70 cm dbh; bark with white latex; wood pinkish, hard, heavy; branchlets and petioles densely brown-sericeous. Petioles 9–16 mm long; blades elliptic, acute or more often abruptly acuminate at apex, obtuse at base, 6.5–12 cm long, 3.5–6 cm wide, glabrous above except on midrib, densely brown-sericeous below, the midrib sunken above; major veins in 15–30 pairs, scarcely more prominent than the secondary lateral veins, forming an obscure collecting vein near margin. Fascicles axillary; pedicels ca 1 cm long; flowers cream-colored, numerous; sepals 5, ca 1.5 mm long; pedicels and outside of sepals densely brown-sericeous; corolla mostly 5-lobed about halfway, ca 4 mm long, sericeous outside; stamens equaling, opposite, and attached to corolla lobes, included; style to 0.5 mm long; stigma with 7–12 marginal lobes. Berries purple, subglobose, 5–10 cm diam; seeds several, oblique-obovate, flattened, to 2.5 cm long, the testa hard, lustrous. *Croat 4630, Foster 1221.*

Rare in the old forest; known also from the Laboratory Clearing and from the shore of Bat Cove. Flowers from July to September. The fruits mature during the dry season of the following year.

Probably native to the West Indies; commonly cultivated and naturalized in the lowland tropics from Mexico to northern South America; introduced into western Africa. In Panama, introduced throughout tropical moist forest and known from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí, Veraguas, Coclé, and Panamá.

CYNODENDRON Baehni**Cynodendron panamense** (Pitt.) Aubreville, Mem.

New York Bot. Gard. 23:215. 1972

Chrysophyllum panamense Pitt.

Cafecillo, Camito

Tree, to 20(25) m tall, to ca 40 cm dbh; outer bark moderately thin, fissured, soft; inner bark reddish, coarsely fibrous; sap white, usually not copious. Petioles 8–25 mm long; blades \pm elliptic, acuminate, acute to obtuse at base, 10–25(33) cm long, 5.5–11(14) cm wide, glabrous above, glabrate to obscurely appressed-pubescent below with short T-shaped trichomes; lateral veins in 10–20 pairs, forming a loose collecting vein near the margin. Fascicles axillary; pedicels to 7 mm long; flowers 5-parted, ca 6 mm long, several to numerous; calyx ca 2 mm long, deeply lobed, the lobes ovate to suborbicular, imbricate; pedicels, calyx, and corolla pubescent with appressed T-shaped trichomes; corolla urceolate, to 5.5 mm long, the lobes short, deltoid to broadly ovate, \pm spreading; stamens equaling and opposite the lobes, attached at base of lobes, ca 0.5 mm long; filaments fused to corolla except at deltoid apex; anthers deltoid-sagittate; pollen scant;

ovary sericeous; style 1–1.5 mm long; stigma 5-lobed. Fruits obovate-spheroid to ovoid, usually depressed at apex and also around pedicel, ca 2 cm diam, purplish-brown; exocarp thin, with some milky sap; mesocarp whitish, fleshy, sweet, tasty; seeds oblique-obovate, flattened, 1–2.5 cm long, brown, the hilum lateral, extending nearly the length of seed. *Croat 7825.*

Frequent in the forest. The species flowers twice per year. The principal flowering period is from June to October, especially in July and August, with the fruits maturing in the late dry season, March and April. A secondary and much smaller flowering period is from January to April, mostly in March and April, with the fruits maturing in the rainy season.

Costa Rica and Panama. In Panama, apparently more common on the Atlantic slope; known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, but also from tropical wet forest in Colón (Salúd). Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

POUTERIA Aubl.**Pouteria fossicola** Cronq., Lloydia 9:289. 1946*Grias megacarpa* Dwyer

Tree, to 12 m tall, usually less than 12 cm dbh; bark thin, brown, flaky; sap milky; branchlets glabrous, with prominent leaf scars. Leaves clustered at apex of branchlets; petioles 1.5–4.5 cm long; blades obovate, usually acuminate, tapered to an obtuse or rounded base, 12–30 cm long, 6–13 cm wide, finely white-strigillose on major veins below and sometimes sparsely so on lower or upper surfaces, drying thin; major veins in 15–25 pairs, the secondary lateral veins mostly perpendicular to the primary lateral veins. Flowers densely clustered on stems below leaves; pedicels ca 5 mm long; sepals ca 8, sericeous except on margins, increasing in size centripetally, to 6 mm long; other flower parts unknown. Fruits obovoid, to 10 cm long and 7.5 cm wide, fleshy and yellow-green, the surface smooth and shiny with a few irregular lentils; seed 1, obovoid, to 6.5 cm long, fleshy, the seed-coat firm, yellowish. *Croat 16636.*

Rare, known from the young forest north-northwest of the Tower Clearing; some fruits have been seen in the old forest south of Armour Trail 700 and on Orchid Island. Flowering season unknown. Mature fruits have been seen in May and July.

Known only from Panama, from tropical moist forest on BCI and from tropical wet forest in Colón (Salúd).

Pouteria sapota (Jacq.) H. E. Moore & Stearn, Taxon 16:383. 1967*Calocarpum mammosum* (L.) Pierre; *P. mammosum* (L.) Cronq.

Mamey, Mamey de tierra

Tree, to 30(40) m tall, to 60 cm dbh; wood buff to reddish, hard and heavy; sap milky; branchlets brown-tomentose. Leaves alternate, clustered near ends of

branches; petioles 1–4.5 cm long; blades oblanceolate to narrowly obovate, usually shortly acuminate, narrowly acute at base, 10–40 cm long, 4–14 cm wide, glabrous above, pubescent below, becoming glabrate in age, the trichomes sparse to dense, brownish, appressed or shortly stalked, T-shaped; primary lateral veins in 20–50 pairs, the secondary laterals perpendicular to and connecting the primary laterals, more prominent than the closely spaced reticulate veins. Flowers subsessile, clustered at leafless nodes; sepals 8–12, spirally imbricate, \pm orbicular, often emarginate or more deeply bilobed at apex, 2–6 mm long (the innermost longest), densely sericeous with T-shaped trichomes except on the thin, glabrous margin; corolla \pm cylindrical, 6–10 mm long, 4- or 5-lobed to about the middle or less; stamens attached at top of tube; filaments 2–3.5 mm long; staminodia linear-lanceolate, 2–3 mm long; ovary densely ascending-sericeous, 5-locular; style 3.5–7 mm long, pubescent to about the middle; stigma 5-lobed. Fruits fleshy, ellipsoid, ovoid, or subglobose, sandpapery outside, 8–20 cm long, brown; mesocarp usually reddish, often milky; seed 1, ellipsoid, 5–6 cm or more long, brown and shiny, with a broad dull scar extending the length of seed. *Knight 1513*.

Collected once on the island. Elsewhere flowers from May to August, with the large fruits maturing almost a year later.

Mexico to northern South America; possibly native only in Mexico and along the Atlantic slope of Central America. In Panama, known from tropical moist forest on BCI and in San Blas, Chiriquí, Herrera, Coclé, and Panamá and from tropical dry forest in Panamá (Taboga Island).

Pouteria stipitata Cronq., *Lloydia* 9:265. 1946

Dioecious(?) tree, to 25 (35) m tall, to 25 cm dbh; outer bark thin, brown, fissured vertically, often flaking off to expose areas of inner bark; inner bark white to tan, lighter than the wood; wood tan, hard; sap milky, sometimes with a strong, foul, pungent odor; stems appressed-pubescent to glabrate in age. Petioles appressed-pubescent, 1–2.5 cm long; blades oblanceolate to oblong-elliptic, acuminate, obtuse to cuneate at base, 9–16 cm long, 2–4.5 (5.5) cm wide, glabrous in age except for appressed trichomes at base of midrib below; major lateral veins usually 5–7 on each side, the secondary veins irregularly anastomosing (only faintly prominulous when dried). Flower clusters dense, often at leafless nodes; pedicels 2–5 mm long; flowers greenish-white; pedicels and calyces densely pubescent, the trichomes short, appressed, T-shaped, less conspicuous on calyx; sepals 4(5), ovate to obovate, ca 2.7 mm long, thin, rounded at apex, ciliate, the inner pair thinner, its margins \pm scarious; corolla tubular, 2.5–4 mm long, lobed, the lobes 4, large, alternating with 4 smaller staminodial lobes, all lobes ciliate; stamens 4, mounted on basal third of corolla tube, alternating with corolla lobes, sometimes directed inward and perpendicular to the corolla, the apices forming a cross; filaments ca twice as long as anthers, narrowed below anthers;

anthers narrowly deltoid, to 1.7 mm long, opposite corolla lobes and shorter than rim; ovary 4-locular, ovoid, very densely hirsute, the trichomes white, ascending, ca twice as long as ovary; style simple, ca twice as long as ovary; stigma simple, held at about the level of apex of corolla tube. Fruits obovoid, ellipsoid or obliquely ellipsoid, to 3.5 cm long and 3 cm diam, yellow, densely velutinous and with longer, stalked, T-shaped trichomes when juvenile, yellow and often glabrate at maturity; seeds 1–4, ellipsoid, ca 1.5 cm long. *Croat 6116, 10293*.

Frequent throughout the forest. Flowers in May and June, with the fruits maturing in August and September.

The species is probably dioecious, since many trees that flowered set no fruit while others set abundant fruit.

Costa Rica and Panama. In Panama, known from tropical moist forest on BCI and in Panamá (San José Island). Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

Pouteria unilocularis (Donn. Sm.) Baehni, *Candollea* 9:273. 1942

Tree, to 25 m tall, mostly 20–50 cm dbh; outer bark thin, brown, fissured and often flaky (at least near base), fine-grained; inner bark tan to light brown, moderately thick, fine-grained; wood white; sap milky, with a foul, pungent odor. Petioles 5–10 mm long, canaliculate; blades oblong-elliptic, narrowly acuminate, acute to attenuate at base, 6–15 cm long, 2.5–5.5 cm wide, \pm glabrous, stiff, usually folded along arched midrib, the reticulate venation prominulous. Flower clusters dense, of usually 15–25 flowers, often at leafless nodes; pedicels 4–5 mm long; flowers greenish-white, ca 2 mm long; sepals 4–6, thick, ovate to rounded, blunt at apex, 1.5–2 mm long; pedicels and sepals \pm equally ferruginous-pubescent with minute T-shaped appressed trichomes, the sepals \pm patulose-pubescent inside; corolla usually 6-lobed, ca 4.5 mm wide, 1.7–2 mm long, lobed nearly to the thickened base, the lobes equal, rounded at apex, ciliate (otherwise glabrous); stamens 5 or 6, shorter than and borne opposite the corolla lobes; filaments fused to corolla tube most of their length; anthers narrowly ovate, less than 1 mm long, pubescent; staminodia 5 or 6, broadly ovate, nearly sessile, borne at about the level of the anthers and alternating with the petals, pubescent at least marginally with trichomes like cilia of corolla lobes; ovary depressed-globose, densely woolly at base, glabrous apically; style to 1.3 mm long, narrowly conical, \pm equaling length of style; stigma simple. Fruits ellipsoid, usually weakly oblique, 2.5–2.8 cm long, 1.5–1.9 cm diam, violet-purple or green heavily tinged with violet-purple at maturity; exocarp yellowish-green inside, hard, to 4 mm thick, with slight milky sap at periphery; seed 1, ellipsoid, ca 1.8 cm long, somewhat compressed, brown, surrounded by a thin, very tasty, sweet, gray mesocarp (the taste soon disappearing), the hilum extending nearly the full length of seed, more than 3 mm wide. *Croat 14874, 17052*.

Occasional, in the forest. Flowers in the early rainy season (June). The fruits mature in August and September.

I suspect that flowers of the species are unisexual, since the flowers investigated showed no sign of pollen.

Known from Guatemala, Belize, Costa Rica, and Panama; no doubt also occurring in intervening areas. In Panama, known from BCI and from tropical wet forest in Panamá (El Llano-Cartí Road).

See Fig. 446.

114. EBENACEAE

Trees. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules lacking. Racemes short, axillary; flowers unisexual (dioecious), actinomorphic; calyx campanulate, 6-lobed, persistent and accrescent in fruit; corolla deeply lobed, the lobes 6, imbricate, white; stamens many; anthers 2-celled, introrse, dehiscing longitudinally; ovary superior, with several locules and carpels; placentation axile; ovules 2 per locule, anatropous; styles several, simple. Fruits berries; seeds many, with copious hard endosperm.

The family is represented in Panama only by *Diospyros*, which is distinguished by its unisexual, 6-parted flowers. Staminate flowers have numerous stamens with prolonged connectives. Flowers of *Diospyros* are probably insect pollinated. Fleshy fruits are no doubt animal dispersed.

Two genera and about 450 species; subtropics and tropics of Western and Eastern hemispheres.

DIOSPYROS L.

Diospyros artanthifolia Mart., Fl. Brasil. 7:7. 1856

Slender dioecious tree, ca 4–15 m tall, to ca 20 cm dbh, unbranched for much of its length; smaller branches long and drooping; most parts moderately to densely hirsute (especially dense on young parts), the upper blade surfaces, petals, and inner flower parts glabrous. Petioles 5 mm long; blades lanceolate to oblong-lanceolate, narrowly acuminate, obtuse to rounded at base, 6–14 cm long, 2.5–4 cm wide (larger in South America), glabrous above except on midrib. Staminate flowers in short axil-

lary cymes, usually only one flower opening at a time; pubescence of branches, pedicels, and calyces crisp-villous; buds narrowly ovate; calyx campanulate, to 3.7 mm long, appressed-pubescent inside except near base, the lobes 6, irregular, triangular, extending one-third to one-half the way to base; corolla white, ca 1 cm long, lobed to near base, the lobes 6, somewhat imbricate, thick, 4 mm wide, with a longitudinal line of sparse pubescence somewhat off-center outside, this diminishing at about middle, the apex asymmetrical and recurved at anthesis; stamens ca 35–40, to 2.7 mm long; filaments less than 11 mm long, narrowed at apex, pubescent along inner side, the trichomes stiff, straight, translucent, extending entire length of connective; anthers apiculate at apex, the connective prolonged one-third to one-half the length of the thecae. Pistillate flowers in ca 5-flowered axillary cymes, subsessile or with pedicels to 5 mm long; corolla and calyx like staminate flowers; staminodia ca 6; ovary ovoid-conical, ca 4 mm wide and long; styles 4 or 5, ca 4 mm long, divergent, united only at base; locules 8 or 10; ovules 1 per locule. Berries subglobose, 8-celled, hispidulous, to 4 cm diam; seeds 8 or 10 or fewer by abortion, ca 20 mm long and 9 mm wide, ca 6 mm thick, black, the endosperm smooth; fruiting calyx scarcely accrescent. (Description of pistillate flowers and fruits taken from White, 1978.)

Rare, in the old forest. Seen in flower in May.

The flowers are open and unspecialized, but because of the rarity of the species and its dioecious condition, it might be expected to have some specialized pollinators.

The fruits are probably mammal dispersed.

Panama to Brazil. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in the Canal Zone, and from tropical wet forest in Colón.

115. LOGANIACEAE

Scandent shrubs, lianas, suffrutices, or annual herbs; stems often tendriled or spiny. Leaves opposite, petiolate; blades simple, entire (sometimes undulate); venation

KEY TO THE SPECIES OF LOGANIACEAE

Leaves pinnately veined:

Spikes usually solitary (rarely 2); calyx lobes glabrous, \pm equal; capsules smooth, the persistent base usually rounded on the ends *Spigelia humboldtiana* Cham. & Schlechter

Spikes often 2–5; calyx lobes and keel scabrid on margins, often unequal; capsules muciculate externally, the persistent base pointed on the ends *Spigelia antheimia* L.

Leaves pliveined:

Inflorescences axillary; leaf axils of major lateral veins below tufted with rufous trichomes; fruits yellow, ca 4 cm diam *Strychnos darriensis* Seem.

Inflorescences terminal; leaf axils not tufted or the trichomes not rufous:

Corolla tube not exceeding calyx; leaf axils tufted with short, white trichomes; larger stems armed with stout spines *Strychnos brachistantha* Standl.

Corolla tube much longer than calyx; leaf axils not tufted:

Plants with stems, leaf surfaces, inflorescence branches, and corolla conspicuously rufous-hirsute; fruits gray-green to bluish-green, 4–7 cm diam *Strychnos toxifera* Benth.

Plants not rufous-hirsute, the leaf pubescence principally on veins below, the corolla glabrous outside; fruits green becoming orange, 6–9 cm diam . . . *Strychnos panamensis* Seem.

pinnate (*Strychnos* pliveined); stipules interpetiolar (sometimes reduced to an interpetiolar line in *Strychnos*). Inflorescences various, in bracteolate, modified dichasia; flowers bisexual, actinomorphic; calyx 4- or 5-lobed; corolla \pm funnellform, 4- or 5-lobed; stamens as many as and alternate with corolla lobes, epipetalous; anthers 2-celled, introrse, dehiscing longitudinally; ovary superior, 2-locular, 2-carpellate; placentation axile; ovules many, amphitropous or anatropous; style 1; stigma \pm capitate. Fruits explosive, septicidal capsules (*Spigelia*) or hard-shelled berries; seeds many, with fleshy or bony endosperm.

Members of the family can be distinguished by a combination of opposite leaves with interpetiolar stipules or stipular lines and a superior, bilocular ovary.

The flowers are tubular and often very slender (especially *Strychnos*) and are probably pollinated by butterflies or moths. Some *Spigelia* are self-pollinated (H. Baker, pers. comm.).

Seeds of *Spigelia* are mechanically dispersed by means of explosively dehiscent capsules. The seeds of *Strychnos* are endozoochorous. They are embedded in a fleshy sweet matrix and are probably taken by arboreal frugivores large enough to break open the thick, usually hardened exocarp. Spider monkeys are very fond of *Strychnos* on BCI. Agoutis eat the partly eaten fruit dropped by the monkeys (N. Smythe, pers. comm.).

About 30 genera and 800 species; subtropics and tropics.

SPIGELIA L.

Spigelia anthelmia L., Sp. Pl. 149. 1753

S. multispica Steud.

Worm grass

Annual herb, small or to more than 1 m tall, nearly glabrous, simple or branched few times, leafless or nearly so except on ultimate segments. Leaves opposite-decussate and petiolate on stems, appearing whorled and usually sessile or nearly so at apex; stipules broadly deltoid, interpetiolar, ca 5 mm long; blades variable but mostly lanceolate-oblong, acute to acuminate, acute at base, 3–18 cm long, 1–6.5 cm wide, scabridulous above and on veins below. Spikes (1)2–5, terminal, simple or infrequently branched, 3–18 cm long; pedicels obsolete or to 1 mm long; flowers closely aggregated near apex, in all stages and eventually continuous with fruits on basal part of spike; sepals 5, linear-lanceolate, ca 3 mm long, thickened at base, keeled, the margins and keel scabrid; corolla narrowly funnellform, 6–15 mm long, white with a red-violet medial line below each lobe, strongly pleated, the lobes 5, acute, spreading; stamens 5, included; filaments fused to tube in basal half, markedly thickened near point of attachment, the free part arched inward; anthers yellow; style slightly exerted above throat, the apical half swollen, pubescent near apex. Capsules explosive, ca 4 mm long and 6 mm wide, 2-carpellate, sulcate medially, bilobed, compressed at right angles to septum, conspicuously muricate except at base, the persistent base pointed at either end; seeds brown, irregular, to 2

mm long, conspicuously tuberculate, mostly 4–6 per carpel. *Croat 7145*.

Uncommon in weedy areas of the Laboratory Clearing and much less frequent on forest trails; once locally abundant in the vicinity of the old orchidarium north of Kodak House. Flowers throughout the year, principally in the rainy season. The fruits mature quickly.

This species contains the toxic, volatile alkaloid spigeline (Blohm, 1962). When the capsule bursts open, the capsule walls become vertically compressed, and the wall and the seeds are usually thrown a distance of more than 1 meter.

Throughout American tropics; tropical Africa; Indonesia. In Panama, known principally from tropical moist forest all along the Atlantic slope and from Los Santos to Darién on the Pacific slope; known also from tropical dry forest in Los Santos and Panamá, from premontane moist forest in the Canal Zone, and from tropical wet forest in Colón, Panamá, and Darién.

Spigelia humboldtiana Cham. & Schlechter, Linnaea 1:200. 1826

Herb or suffrutex, usually less than 50 cm tall; stems often purplish, with 2 pubescent ribs beneath each stipule. Leaves opposite-decussate, those at apex crowded or whorled, connected by an interpetiolar line or sheath; stipules weblike between petioles, rounded or truncate at apex; petioles obsolete or to 1.5 cm long; blades \pm lanceolate-ovate, acute to acuminate, obtuse to rounded and decurrent on petiole at base, 3–8 (10) cm long, 2–3.5 (4.5) cm wide, glabrous or with short stiff trichomes especially above. Flowers in 1 or 2 usually simple spikes; calyx to 4 mm long, glabrous, the lobes 5, slender, \pm equal; corolla white, 1.5–2 cm long, slender, funnellform, abruptly flared above, the lobes 5, \pm ovate, acute, often marginally tinged with purple; stamens 5, included, the free parts beyond flare of corolla tube curved inward; anthers held tightly against style, introrse; style densely pubescent at and above level of anthers, the short trichomes removing pollen from thecae as style elongates; nectar rather sparse, stored at base of tube around ovary. Capsules 4–6 mm broad, smooth externally, the persistent base rounded at both ends; seeds brownish, ovoid, to ca 1.5 mm long, densely muricate. *Croat 15572*.

Frequent along trails or tree-fall areas of the forest and in clearings in shady areas. Flowers throughout the year, principally in the rainy season (May to September). The fruits develop quickly.

Mexico to Argentina. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Coclé, and Darién, from premontane wet forest in Chiriquí, and from premontane rain forest in Darién.

STRYCHNOS L.

Strychnos brachistantha Standl., Field Mus. Nat. Hist., Bot. Ser. 12:412. 1936

Scandent shrub, often to 30 m long; larger stems armed with stout spines (straight on juveniles, recurved on



Fig. 446.
Pouteria unilocularis



Fig. 448.
Strychnos toxifera

Fig. 447. *Strychnos panamensis*



adults); smaller stems sometimes square; branchlets puberulent with minute trichomes, glabrous in age; tendrils forked, the arms coiled like watchsprings. Petioles ca 3 mm long, puberulent with minute trichomes; blades lanceolate to narrowly elliptic, very long-acuminate, obtuse to rounded at base, 2.5–14 cm long, 1–4 cm wide, glabrous except for puberulent midrib below and tufted axils (with short white trichomes) of central pair of veins, entire, minutely and conspicuously undulate on margins, pliveined, the veins 3(5), the secondary lateral veins \pm conspicuous in apical two-thirds of blade. Paniculate cymes terminal, usually hemispheric and bearing many flowers; calyx lobes (4)5, lanceolate to narrowly ovate, acute to acuminate, 1–2 mm long; corolla ca 2 cm long, (4)5-lobed almost to base, the tube ca 0.6 mm long, the lobes oblong, obtuse, densely villous inside, ca twice as long as tube; anthers 5, ca 0.6 mm long, glabrous. Fruits globose, 6–7 cm diam, orange-yellow at maturity; exocarp ca 6 mm thick, smooth; seeds 5–11, obliquely pyramidal, 12–17 mm long, the mesocarp yellowish, tasty. *Croat 14475*.

Apparently rare in the forest; collected once on Drayton Trail. Seasonal behavior uncertain. Flowers in June and July. Old fruits have been seen in September.

Mexico south along the Atlantic slope of Belize, Guatemala, and Nicaragua to Panama. In Panama, known only from tropical moist forest in the Canal Zone.

Strychnos darienensis Seem., Bot. Voy. Herald
166. 1854

Liana; stems divaricately branched, minutely puberulent to glabrate in age; tendrils stout, curled. Petioles and midribs sparsely pubescent; petioles mostly 2–7 mm long; blades usually narrowly elliptic or lanceolate, acuminate, rounded to acute at base, 6–17 cm long, 3–6 cm wide, \pm thick, with brown trichomes on lower surface in axils of central vein pair, pliveined, the veins 3 or 5. Thyrses short, axillary, to 3 cm long; flowers 4(5)-parted; inflorescence branches and calyx lobes to 2 mm long; corolla yellowish, bearded inside tube, 2–3 mm long; filaments attached to corolla tube; style long-exserted, to 7 mm long, glabrous. Fruits globose or ovoid, ca 4 cm diam, yellow at maturity; seeds few, irregularly oblong, to 2 cm long and 1.5 cm wide. *Croat 15079, Foster 1465*.

Rare, in the forest. On BCI some flowers have been seen in December.

Nicaragua and Costa Rica south to the Guianas, Brazil, Ecuador, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Darién and from tropical dry forest in Panamá (Taboga Island).

Strychnos panamensis Seem., Bot. Voy. Herald
166. 1854

Canjura, Fruta de murciélago

Liana or climbing shrub; tendrils short-coiled, pubescent, becoming woody; stems sparsely long-pubescent to glabrous in age. Petioles 1–5(15) mm long, sparsely pubescent especially when young; blades lanceolate to elliptic,

usually acuminate, acute to rounded (rarely cordate) at base, 4.5–12 cm long, 1.5–4(5) cm wide, sometimes sparsely pubescent at base of midrib below, pliveined, the veins 3(5). Cymes pedunculate, terminal; pedicels obsolete or to 3.5 mm long; flowers (4)5-parted; sepals \pm lanceolate, to 4 mm long, ciliate; corolla salverform, 8–24 mm long, the tube greenish-white, very minutely papillate outside, with a broad band of moniliform trichomes on apical third inside, the lobes white, slender, to 4.7 mm long, recurved at anthesis, densely papillate inside; stamens exserted to 3 mm above the rim; anthers ca 8 mm long, attached subbasally; style exserted about twice as far as stamens, expanded somewhat and flat at apex. Fruits globose, 1 to several on a stout woody stalk, at first blue-green, turning orange and usually 6–9 cm diam at maturity; seeds many, 2–3 cm long, irregular, embedded in a fleshy, sweet, orange pulp. *Croat 10229, 12595*.

Common along the shore; apparently less abundant in the forest. Usually flowering from April to August, chiefly from May to July, rarely late in the rainy season or in the early dry season. Full-sized fruits are seen by the late rainy season. They turn orange in the dry season and are removed usually before flowering begins again. Plants usually put on new leaves shortly before flowering.

Pacific slope of tropical Mexico to northeastern Venezuela and northern Colombia. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Coclé, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), and from premontane rain forest in Panamá (summit of Cerro Jefe).

See Fig. 447.

Strychnos toxifera Schomb. ex Benth., J. Bot. (Hooker)
3:240. 1841
Urari

Liana with long reddish trichomes on most parts; oldest stems glabrous; stems divaricately branched; tendrils coiled. Petioles to 6 mm long; blades ovate to elliptic, acuminate, rounded to subcordate at base, 6–20 cm long, 3–8 cm wide, pliveined, the veins 3(5). Cymes terminal, densely reddish-pilose; pedicels less than 5 mm long; flowers 5-parted; sepals lanceolate-linear, to 7 mm long; corolla white or yellow, salverform, the tube to 1.5 cm long, the lobes ca 2 mm long, densely bearded inside; anthers barely exposed at apex of corolla, ca 1 cm long; filaments attached to corolla tube; ovary subglobose, ca 1 mm diam; style exserted ca 2 mm; stigma capitate. Fruits globose, 4–7 cm diam, gray-green turning bluish-green; seeds usually 10–15, ca 2.5 cm diam. *Croat 6766, 7278*.

Occasional, in the forest. Flowers in the early dry season. The fruits mature in the rainy season.

This species is the source of toxiferin, one of the most potent curare alkaloids (Blohm, 1962).

Costa Rica to Ecuador and Amazonian Brazil. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién.

See Fig. 448.

KEY TO THE TAXA OF GENTIANACEAE

- Plants saprophytic, lacking chlorophyll *Voyria*
- Plants not saprophytic; leaves green:
 - Herbs small, less than 1 m tall; leaves usually less than 4 cm wide; flowers reddish, 4-parted, less than 2 cm long; capsules less than 1 cm long *Schultesia lisianthoides* (Griseb.) Hemsl.
 - Herbs large, coarse, more than 1 m tall; leaves usually more than 5 cm wide; flowers green, 5-parted, 2–3 cm long; capsules usually more than 1 cm long *Chelonanthus alatus* (Aubl.) Pulle

116. GENTIANACEAE

Perennial or annual, erect, glabrous herbs (saprophytic and achlorophyllous in *Voyria*). Leaves opposite (sometimes crowded to base), sessile or short-petiolate (scale-like in *Voyria*); blades simple, entire; venation subpinnate (sometimes a few principal veins diverging from near base); stipules lacking. Flowers terminal or axillary, bisexual, mostly actinomorphic (somewhat zygomorphic in *Chelonanthus*), solitary or in simple or compound dichasia; calyx 4- or 5-lobed or 4- or 5-parted; corolla funnellform, 4- or 5-lobed, showy; stamens the same number as and alternate with corolla lobes, epipetalous; anthers borne on filaments or sessile (*Voyria*), 2-celled, introrse, dorsifixed, dehiscent longitudinally; ovary superior, 1-locular (or 2-locular by intrusion of the placentae), 2-carpellate; placentation parietal; ovules numerous, anatropous; style simple; stigma capitate or bilobed. Fruits septicidal, 2-valved capsules; seeds numerous (sometimes winged in *Voyria*), with copious endosperm.

Members of the family on BCI have little in common superficially but are all very distinctive.

Chelonanthus is probably pollinated by moderately large bees. Other pollination systems are not known.

Chelonanthus seeds are minute and are probably wind dispersed. *Voyria* also has minute seeds, but grows on the forest floor where wind dispersal is less likely. Possibly seeds are carried away by insects, birds, or isopods or are transported by water. Water currents on the forest floor capable of transporting such tiny seeds are not uncommon in the rainy season when the fruits mature.

About 70–80 genera and 900–1,000 species; worldwide.

CHELONANTHUS Gilg.

Chelonanthus alatus (Aubl.) Pulle, Enum. Pl. Surinam 376. 1906

Arbol de mal casada

Herb, to 1–1.5(5) m; stems square, glabrous, the corners with thin ribs. Leaves opposite, sessile; blades broadly ovate, acute to short-acuminate at apex, attenuate at base, 4–18 cm long, 3–10 cm wide, thin. Inflorescences terminal, simple or compound dichasia, appearing racemose; flowers pedicellate, usually borne on one side of branches, subtended by ovate bracts 2–3 mm long; calyx ca 6 mm long, coriaceous, the lobes 5, blunt, imbricate, keeled; corolla campanulate, pale green, ± fleshy, weakly 2-lipped, 2–3 cm long, the lobes 5, short, acute but

reflexed so as to appear truncate; stamens 5, held tightly against the lower lip; filaments with a marked bend about midway, thick and flattened at base, fused to basal part of corolla tube; anthers shedding pollen before anthesis, sometimes adhering to each other and to style before anthesis; style broadly bilobed, scarcely exceeding stamens, appressed to anthers. Capsules ± oblong, brown at maturity, 1–1.5 cm long, the valves thick, held between calyx and strong persistent style base; seeds very numerous, minute, somewhat sticky, square or rectangular.

Croat 7258.

Occasional in clearings, especially the Rear #8 Light-house Clearing; infrequent along the shore. Flowers principally in the rainy season, with the fruits maturing during the dry season.

The flowers are probably pollinated by medium-sized bees.

Capsule valves are hygroscopic, arching in dry conditions and allowing wind to pass through to carry away the tiny seeds and straightening again under wet conditions to close the gap.

Mexico to Brazil. In Panama, known principally from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá; known also from tropical moist forest in the Canal Zone and Darién, from tropical wet forest in Darién, and from premontane rain forest in Chiriquí.

See Fig. 449.

SCHULTESIA Mart.

Schultesia lisianthoides (Griseb.) Benth. & Hook. ex Hemsl., Biol. Centr.-Amer. Bot. 2:348. 1882
Sulfatillo

Erect herb, 7–90 cm tall, ± glabrous, unbranched or with few, strongly ascending branches mostly from near apex. Leaves opposite, sessile; blades mostly ovate, acute to short-acuminate at apex, attenuate to amplexicaul at base, 1.5–8(10) cm long, 0.5–4(4.5) cm wide, thin. Inflorescences terminal or upper-axillary, simple or compound dichasia, bearing few flowers; pedicels 1–10 mm long, subtended by bracts, the bracts paired, narrowly ovate, persistent, to 1.5(2) cm long; flowers 4-parted, lavender, 1–1.7 cm long; calyx lobed to near base, ca 6 mm long, the lobes ± lanceolate, strongly keeled; calyx and corolla withering but persisting at apex of fruit; corolla funnellform, shallowly 4-lobed, 1–1.7 cm long; stamens 4–5 mm long; style simple, 2–3 mm long. Capsules fusiform, 6–9 mm long, 2–3 mm diam; valves 2,

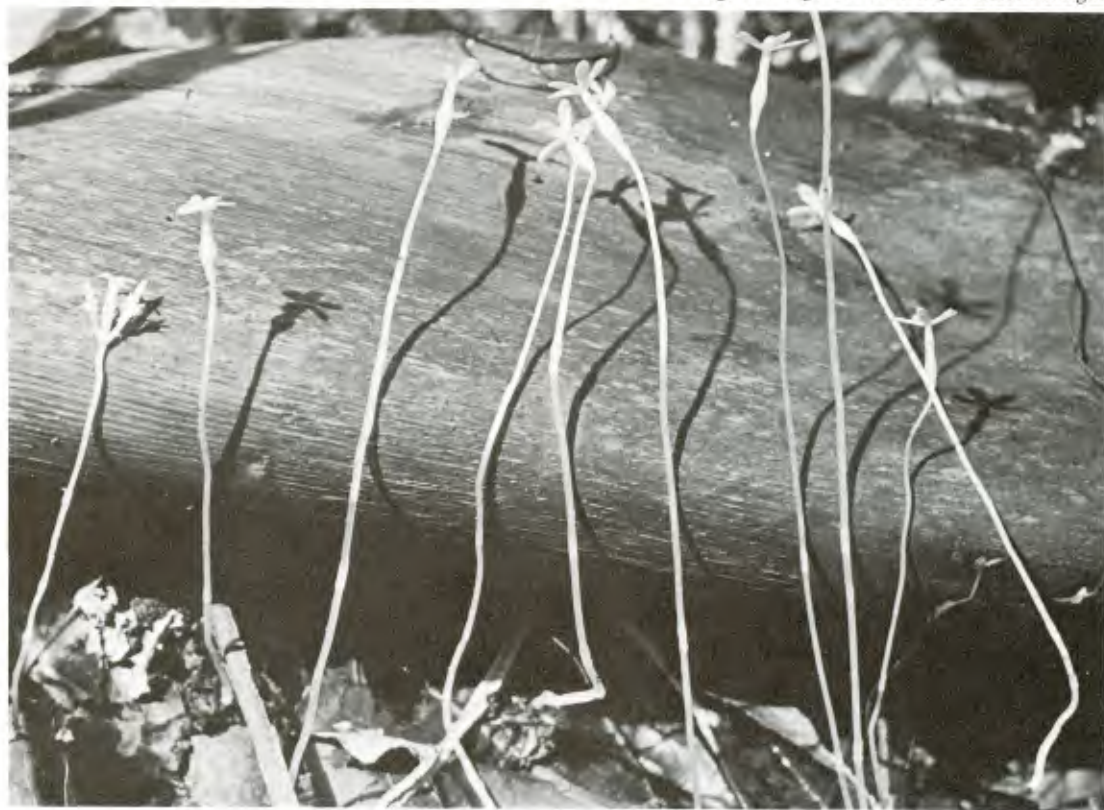


Fig. 449. *Chelonanthus alatus*



Fig. 451. *Nymphoides indica*

Fig. 450. *Voyria alba* at left, *V. tenella* at right



thick, held together at apex by withered corolla; seeds minute, irregularly rounded. *Croat 7783*.

Rare, in clearings along the shore. Flowers and fruits throughout the dry season (December to April).

Seeds are probably wind dispersed in the manner of *Chelonanthus alatus*.

Southern Mexico to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Colón, Veraguas, Los Santos, Herrera, Panamá, and Darién, from tropical dry forest in Los Santos and Coclé, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí and Panamá.

VOYRIA Aubl.

Voyria alba (Standl.) L. O. Wms., *Fieldiana*, Bot. 31:413. 1968

Leiphaimos albus Standl.

Saprophytic herb, white, glabrous, 6–13 (20) cm tall, usually unbranched; stems to 1 mm thick; scales opposite, united, to 4 mm long, borne at the nodes. Flowers 5-parted, ca 1 cm long, in terminal dichasia of few flowers; calyx lobed about midway, ca 3.5 mm long, the lobes very slender; corolla narrowly tubular, the lobes narrowly triangular, to ca 3 mm long, spreading; stamens 5, extrorse, included; filaments connate to tube most of their length; anthers ca 2 mm long, united laterally in a ring surrounding style, the connective narrowed into slender appendages at the base; pollen white, moderately tacky; ovary elongate, slightly broader toward base, 5–6 mm long, gradually narrowed to the style; stigma discoid, ca 0.7 mm broad, much broader than style, slightly exerted from throat at anthesis. Capsules 6–8 mm long; seeds very numerous and minute. *Croat 11180*.

Rare, though sometimes locally abundant in moist areas of the forest, often in rich leaf litter. Flowers and fruits throughout the rainy season. Plants disappear in the dry season.

Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, and Panamá and from premontane wet forest in Colón.

See Fig. 450.

Voyria tenella Hook., *Bot. Misc.* 1:47, pl. 25, f. B. 1829

Leiphaimos simplex (Griseb.) Standl.

Saprophytic herb, to 20 cm tall, unbranched, white except for corolla lobes and base of tube, crosier-shaped when young; stems ca 1 mm thick; scales few, ovate, to 5 mm

long. Flowers pendent, erect at anthesis, solitary, terminal, 5-parted, to 1.7 cm long; calyx hyaline, 2.5–4 mm long; corolla tubular, to 2 cm long, the lobes spreading, to 5 mm long and 1.8 mm wide, violet to blue-violet, rounded at apex, the tube swollen and pale orange in vicinity of ovary, the apical part of throat with ascending short pubescence, with an orange ring at apex just below corolla lobes; anthers 5, \pm sessile, ca 1 mm long, extrorse, blunt at base, connate into a ring, the connective thin, broader toward apex; ovary short-stipitate, narrowly oblong-ellipsoid, to 6.7 mm long (including stipe), narrowed to short style, glandular at base on either side, the glands 2, stalked, to 4.7 mm long, somewhat sunken into ovary; style and stigma together ca 2.7 mm long; stigma discoid and dome-shaped, held just above stamens and ca 1.7 mm below throat of tube. Capsules ellipsoid; seeds very numerous, winged, to 1 mm long. *Croat 6662*.

Infrequent to locally common in the forest, usually in rich, moist areas. Flowers and fruits throughout the rainy season. Plants disappear in the dry season.

Costa Rica to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién and from premontane wet forest in Colón and Panamá.

See Fig. 450.

Voyria truncata (Standl.) Standl. & Steyererm., *Publ. Field Mus. Nat. Hist., Bot. Ser.* 23:78. 1944

Saprophytic herb, to 15 (20) cm tall, \pm glabrous, unbranched or branched few times; stems enclosed by overlapping cauline scales at base; scales dull red, opposite, connate more than half their length, 3–5 mm long. Flowers solitary, 5-parted, 3–5.5 cm long; calyx ca 5 mm long, campanulate; corolla pale yellow to lavender, the narrow tube 3–4 cm long, the lobes spreading, ovate, 7–15 mm long; stamens included, 1–3 mm long; gynoecium to 3.6 cm long; ovary sessile, oblong, truncate apically, to 8–9 mm long, glabrous, eglandular; style filiform, to 2.7 mm long; stigma capitate-peltate, the margins sinuate. Capsules to 1.5 cm long, ca 5 mm diam; seeds wingless, numerous. *Croat 4296a*.

Rare, in rich, dark, moist forest. Seasonal behavior not determined. The few specimens, collected throughout much of the year, indicate that the species may not have a seasonal flowering behavior.

Guatemala, Nicaragua, and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and San Blas and from premontane wet forest in Coclé (near El Valle) and Panamá (near Cerro Campana).

KEY TO THE SPECIES OF VOYRIA

Flowers few to many; flowers and plants white *V. alba* (Standl.) L. O. Wms.

Flowers solitary; flowers or cauline scales usually colored:

Cauline scales many, crowded and overlapping at base of plant, enclosing stem; corolla usually

more than 3 cm long *V. truncata* (Standl.) Standl. & Steyererm.

Cauline scales few, inconspicuous; corolla usually less than 2 cm long *V. tenella* Hook.

117. MENYANTHACEAE

Aquatic herbs. Leaves solitary, alternate, petiolate; blades simple, entire to repand; venation palmate at base; stipules lacking. Umbels terminal; flowers bisexual, actinomorphic; calyx 5-parted; corolla deeply 5-lobed, showy, the lobes induplicate-valvate, alternating with sepals; stamens 5, epipetalous; anthers 2-celled, versatile, dehiscent longitudinally; ovary superior, 1-locular, 2-carpellate; placentation parietal; ovules many, anatropous; style simple; stigma 2-lipped. Fruits capsules, indehiscent or irregularly dehiscent; seeds many, with copious endosperm.

The flowers of *Nymphoides indica* are probably pollinated by small, diurnal bees or flies during the few hours they are open. The *Nymphoides indica* complex is polymorphic in the spectral qualities of its flowers under ultraviolet light. The yellow-flowered races of the West Indies have more contrasting patterns (ultraviolet light is absorbed by the center and reflected by the outer edges) than does the white-flowered race, which occurs in Panama (Ornduff & Mosquin, 1969). After flowering, the pedicels become deflexed and the fruits mature under water (R. Ornduff, pers. comm.).

After capsules ripen and dehisce, seeds surface and are water dispersed. They ultimately sink to the bottom and germinate. Some of the floating seeds are possibly eaten by aquatic birds and thus find their way to the bottom sooner than others.

Five genera and 40 species of swamp or aquatic plants; worldwide.

NYMPHOIDES Seguiet

Nymphoides indica (L.) O. Kuntze, Rev. Gen. Pl. 2:429, 1891

N. humboldtianum (H.B.K.) O. Kuntze

Glabrous, succulent, aquatic herb from submerged rhizomes; stems petiole-like, fleshy, to 1.5 m long. Leaves solitary at apices of stems; blades \pm orbicular, obtuse to rounded at apex, cordate at base, mostly 6–18 cm diam, usually violet-purple to purple on underside, thick. Fascicles dense, umbelliform, borne at nodes; pedicels to 7 cm long, fleshy; calyx lobes 5, lanceolate, acute and cupped inward at apex, ca 6 mm long; both pedicels and sepals glandular-punctate; corolla white, 1–1.8 cm long, 5-lobed for two-thirds its length, the lobes acute, spreading at anthesis, densely pilose inside, the trichomes antrorsely barbed; stamens 5, erect, 5–7 mm long; filaments fused to tube, alternating with tufts of trichomes near summit of tube; ovary narrowly conical, glabrous; style slender; stigma lobes flattened, the margins thickened and undulate. Capsules ellipsoid, 4–6 mm long, tardily dehiscent, eventually rupturing irregularly; seeds 10–18, orbicular, ca 1 mm diam. *Croat 8215*.

Occasional, in quiet lagoons at the edge of the lake, principally on the south side of the island. Probably flowers sporadically through the year.

The small seeds are probably dispersed by water currents.

Throughout the tropics of the world. In Panama, known principally from tropical moist forest in the Canal Zone and Panamá, but also from premontane wet forest in Coclé (El Valle) and from tropical wet forest in Colón (Miguel de la Borda).

See Fig. 451.

118. APOCYNACEAE

Trees, shrubs, lianas, vines, or herbs; sap milky. Leaves alternate, opposite, or whorled, simple; blades entire; venation pinnate; stipules sometimes present, minute; glands frequently in the leaf axils. Flowers bisexual, actinomorphic, 2 to many, in dichasial cymes, thyrses, corymbs or racemes; sepals 5, equal or unequal, sometimes with squamellae inside at base, basally connate, imbricate; corolla tubular, 5-lobed, showy, contorted in bud; stamens 5, attached part of their length to the corolla and alternate with lobes; anthers 2-celled, introrse, dehiscent longitudinally, free or adnate to stigma; gynoeceum usually of 2 distinct, unilocellate, unilocular ovaries, the placentation parietal; less frequently (*Lacmellea*, *Allamanda*) the gynoeceum consisting of a syncarpous, 2-carpellate, 2-locular ovary, the placentation axile; style 1 per pistil (fused together on apocarpous species, later breaking apart with development of the fruit); stigma 1, usually massive and complex, usually pentagonal above, umbrella-shaped below. Fruits usually apocarpous, 2 follicles with many winged seeds, or rarely drupelike berries with few seeds (*Thevetia*, *Lacmellea*) or capsules (*Allamanda*).

Members of the family are very diverse in habit, but can be distinguished by a combination of milky sap and showy flowers contorted in bud. The flowers are somewhat twisted after opening also. All of the vines and the genus *Malouetia* may also be distinguished by their connivent anthers, which are glued to the stigma. Sterile vines are confused with Asclepiadaceae (119).

The flowers are mostly specialized with ample, well-protected nectar. The nearly closed throat of most species indicates they must be pollinated by long-tongued bees or possibly butterflies or hawkmoths. Others are perhaps pollinated by moths (see the discussion of *Odontadenia puncticulosa*). The flowers of *O. macrantha* and of *Stemmadenia grandiflora*, because of the larger, more open corolla, probably have different kinds of pollinators. Bees of the genus *Eulaema* were seen pollinating flowers of *Prestonia* in Ecuador (Dodson & Frymire, 1961) and of *Stemmadenia* in Costa Rica (D. Janzen, pers. comm.). R. Dressler (pers. comm.) reports that *Thevetia ahouai* and *Prestonia* are pollinated by euglossine bees. *Thevetia* is also visited by hummingbirds (H. Baker, pers. comm.). In Veracruz, Mexico, *Tabernaemontana* is pollinated by butterflies (D. Janzen, pers. comm.).

Most seeds are wind dispersed; those of *Lacmellea*

KEY TO THE TAXA OF APOCYNACEAE

- Leaves alternate, ternate, or quaternate (i.e., more than 2 at a node):
 - Leaves quaternate; flowers large, yellow; fruits less than 8 cm long, spiny *Allamanda cathartica* L.
 - Leaves alternate; flowers minute and greenish or flowers whitish with corolla tube less than 4 cm long; fruits not spiny:
 - Flowers whitish, more than 2 cm long; fruits red leathery drupes with 2-4 seeds *Thevetia ahouai* (L.) A. DC.
 - Flowers minute and yellowish to greenish-yellow; fruits large woody follicles with disk-shaped, winged seeds:
 - Leaves with major lateral veins 15-20, easily visible, 4-9 mm apart; calyx 4-5 mm long; corolla ca 10 mm diam; fruits usually less than 10 cm long; seeds to ca 7 cm diam *Aspidosperma megalocarpon* Müll. Arg.
 - Leaves with major veins 30-40, moderately obscure, 2-6 mm apart; calyx 2-3 mm long; corolla ca 6 mm diam; fruits usually more than 11 cm long; seeds 9-10 cm diam *Aspidosperma cruenta* Woods.
- Leaves opposite:
 - Plants trees, herbs, or shrubs; fruits not long and slender (fusiform in *Malouetia guatemalensis*):
 - Plants small herbs growing in open areas, rare; follicles slender, terete, less than 3 cm long *Catharanthus roseus* (L.) G. Don
 - Plants trees or shrubs:
 - Corolla tube less than 5 mm long, the lobes slender, narrowly tapered to sharp apex; follicles fusiform, 10-15 cm long, more than 5 times longer than broad *Malouetia guatemalensis* (Müll. Arg.) Standl.
 - Corolla tube more than 6 mm long, the lobes broad or blunt at apex; fruits less than 8 cm long, less than 2 times longer than broad:
 - Calyx lobes unequal (the larger more than 1 cm long) or corolla tube less than 1 cm long at maturity; fruits ± reniform follicles, with many seeds, the seeds embedded in an orange matrix:
 - Flowers pale orange, more than 4.5 cm wide; sepals unequal, the larger more than 1 cm long; fruits smooth outside, acuminate or pointed at apex *Stemmadenia grandiflora* (Jacq.) Miers
 - Flowers white, less than 2.5 cm wide; sepals equal, less than 3 mm long; fruits scurfy on outside, rounded at apex *Tabernaemontana arborea* Rose
 - Calyx lobes ± equal and less than 1 cm long and corolla tube more than 1 cm long at maturity; fruits drupaceous, with few seeds (less than 5):
 - Corolla double (i.e., ± 10-lobed); fruits apparently not set; plants cultivated shrubs in the Laboratory Clearing *Ervatamia coronaria* (Jacq.) Stapf
 - Corolla single, 5-lobed; fruits yellow-orange, ± ellipsoid, with a persistent style; plants tall forest trees *Lacmellea panamensis* (Woods.) Markg.
 - Plants lianas or herbaceous vines; fruits slender follicles more than 5 cm long (oblong-ellipsoid in *Odontadenia macrantha*):
 - Flowers less than 1 cm long; leaves frequently with pitlike axillary domatia below *Forsteronia*
 - Flowers more than 1 cm long; leaves lacking pitlike axillary domatia below:
 - Leaves with glands at or just below base of midrib or scattered along midrib on upper surface:
 - Flowers greenish-white or greenish-yellow; inflorescences compound; calyx lobes more than 2 mm long; corolla tube less than 2.5 cm long; leaves ± obtuse to rounded at base, the glands at base of midrib only *Mesechites trifida* (Jacq.) Müll. Arg.
 - Flowers yellow with reddish throat; inflorescences simple racemes; calyx lobes less than 2 mm long; corolla tube more than 2.5 cm long; leaves hastate or cordate at base, the glands sparse, along midrib *Mandevilla*
 - Leaves lacking glands:
 - Inflorescences usually of 2(3) flowers; flowers white, with yellow throat; calyx lobes lacking squamellae inside *Rhabdadenia biflora* (Jacq.) Müll. Arg.
 - Inflorescences of several to many flowers; flowers greenish, yellow, or orange (*Prestonia portobellensis* with white corolla lobes marked with orchid lines); calyx lobes bearing squamellae inside:
 - Corolla more than 5 cm long; fruits either oblong-ellipsoid and more than 3 cm wide or fruits cylindrical-fusiform and plants not densely rufescent *Odontadenia*
 - Corolla less than 4 cm long; fruits long and slender (fusiform in *P. ipomiiifolia*, the plants densely rufescent) *Prestonia*

and *Thevetia* are probably mammal dispersed, and those of *Stemmadenia* and *Tabernaemontana* are probably dispersed by both birds and mammals. White-faced monkeys remove the pulpy mesocarp of *Thevetia ahouai* and *Stemmadenia grandiflora*, then spit out the seeds (Oppenheimer, 1968). *Lacmellea panamensis* is eaten by howler monkeys and tamarins (Carpenter, 1934; Enders, 1935). In tropical dry forest in Costa Rica, the fruits of *Stemmadenia donnell-smithii* (Rose) Woods. are taken by several bird species (McDiarmid, Ricklefs & Foster, 1977). Larger birds could easily feed on fruits of *Lacmellea* and *Thevetia* as well.

About 180–300 genera and about 1,300–2,000 species; all regions.

ALLAMANDA L.

Allamanda cathartica L., Mant. Pl. Altera 214. 1771

Liana or arching shrub, to 9 m tall; younger stems sparsely pubescent, becoming glabrous in age. Leaves quaternate, sometimes opposite or alternate apically, subsessile or borne on petioles to 5 mm long; blades obovate to oblanceolate, shortly and abruptly acuminate, obtuse to acute and decurrent on petiole at base, 8–16 cm long, 3–6 cm wide, glabrous or sparsely pubescent below especially on veins, with a submarginal collecting vein. Flowers few, in subterminal cymes; pedicels 2–7 mm long; bracteoles minute; calyx lobes 5, irregular, ± oblong-linear, acute, to 14 mm long; corolla yellow, 8–12 cm wide, the tube to 3.5 cm long, the throat broadened and as long as tube, the lobes 2.5–3.5 cm long, ± rounded, imbricate; stamens situated just above tube; filaments fused to tube, retrorsely barbellate near apex; anthers sharply triangular, free but with their apices held tightly together, the ring of anthers covered above by long, straight trichomes pointing inward from wall of corolla; ovary at first smooth, becoming spiny; style slender, its apex broadly expanded, plungerlike, situated inside the ring of anthers; stigmas 2, short. Capsules ± ellipsoid to obovoid, spiny, 5–8 cm long excluding spines, green at maturity, the spines 5–20 mm long; seeds numerous, disk-shaped, 2–2.5 cm diam, concentrically winged. *Croat 6573*.

Uncommon, on the shore. Plants may be found in flower throughout the year.

Distinguished by its large yellow flowers, quaternate leaves, and spiny capsules. All parts of the plant are reportedly poisonous (Blohm, 1962).

The ovary is surrounded by an active nectary. The broad cylindrical part of the style is also covered with a thick substance, which may attract the pollinator. In the plant's native habitat, the pollinator is unknown, but the organism would need a tongue 3.5–4 cm long to reach the nectar at the base of the constricted tube. Presumably the pollinator's head is thrust into the upper flared part of the corolla. Fruits are occasionally produced in central Panama, so some pollinator must be effective.

The winged seeds are no doubt to some extent wind dispersed, but they are not very good fliers.

Native to northeastern South America, but widely cultivated and escaped in the tropics of the Western and Eastern hemispheres. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién; known also from premontane wet forest in Chiriquí.

ASPIDOSPERMA Mart. & Zucc.

Aspidosperma cruenta Woods., Amer. J. Bot. 22:684. 1935

Alcarreto

Tree, to 35 m tall; trunk to 1 m dbh; outer bark coarse, lenticellate, thin; inner bark thick, granular, light brown, the sap yellow to red, more copious in branches than in trunk, sometimes whitish in juveniles, faintly aromatic; stems densely pubescent when young, glabrous in age, ± ribbed. Leaves alternate; petioles 2–4 cm long, glabrate; blades oblong-elliptic, acute at apex, acute to obtuse at base, 7–12 (26) cm long, 2.5–4.5 (7) cm wide, shiny above, dull and inconspicuously pubescent and sometimes pruinose below, the margins revolute. Thyrses terminal or upper-axillary, corymbose; pedicels 1–2 mm long; calyx 5-lobed, the lobes ca 2 mm long, densely pubescent; corolla tubular-salverform, greenish-yellow, glabrous except on tube inside, the tube 5-ribbed, ca 4 mm long, the lobes lanceolate, ca 1.5 mm long; stamens 5, attached near middle of tube; anthers free, to 1 mm long; filaments about as long as anthers; ovary compressed; stigma 1, capitate. Follicles paired, woody, flattened, shaped like the head of a golf club, to 16 cm long and 10 cm wide, bearing a thick rib medially, brown-tomentose; seeds numerous, flat, 8–10 cm diam, with a thin concentric wing. *Croat 8159*.

Uncommon, found on Pearson Peninsula and at Fairchild Trail 500. Flowers from May to July. The fruits are shed mostly in March and April. Individuals do not appear to flower during the year in which fruits are shed — perhaps they flower only in alternate years (R. Foster, pers. comm.).

Seedlings have both red and yellow sap, the red in the center of the stem. The species has been confused with *A. megalocarpon* Müll. Arg., but bears little resemblance to that species (Gomez Pampa, 1966).

Mexico to Colombia, Venezuela, and the Guianas. In Panama, a typical component of tropical moist forest (Tosi, 1971), known in the Canal Zone and Panamá; known also from premontane wet forest in Colón (Santa Rita Ridge) and from tropical wet forest in Colón.

Aspidosperma megalocarpon Müll. Arg., Linnaea 30:400. 1860

Pelmax, Bayalté, Huichichi, Volador, Ballester

Tree, 20–40 m tall, the trunk conspicuously fluted or involute, to 20–80 cm diam; outer bark gray, relatively smooth, becoming weakly fissured in age; inner bark pale yellow, granular, the sap white, copious; stems and petioles, especially stems, densely mealy-granular-pubescent when young, soon glabrous; stems soon conspicuously

lenticellate. Leaves alternate; petioles 6–15 mm long, weakly canaliculate; blades oblong-elliptic to narrowly elliptic, gradually acuminate at apex, acute to cuneate at base, (3.7)6–14 cm long, 2.2–7.5 cm wide, green above, pale and weakly glaucous below (drying grayish), glabrous or inconspicuously pubescent along midrib, the margins weakly recurved. Panicles axillary, 2–3 cm long, pubescent; pedicels 2–3 mm long; flowers fragrant, ca 1 cm diam; calyx grayish-green, tubular, 4–5 mm long, the lobes rounded, 1–1.5 mm long, pubescent on outside; corolla pale yellow, lobed to about the middle, the tube slender, pubescent inside, the lobes oblong-elliptic, asymmetrical; stamens 5, inserted at throat of tube; ovary ca 1 mm long, glabrous; styles 2, glabrous, united, ca 1.5 mm long; stigma simple. Fruits brown, paired, reniform to suborbicular, flattened, 5.5–12 cm long, densely and obscurely lenticellate, densely mealy-pubescent, becoming glabrous in age; seeds several, tan, orbicular, papery thin, to 7 cm diam, the funicle slender, attached near center of seed, to ca 2.5 cm long. *Garwood & Foster 443*.

Rare in the old forest; collected recently on AMNH Trail. Apparently flowers in the rainy season in Panama—it has been seen in bud in March. Fruiting occurs in the following dry season, in February and March. In Mexico the species is reported to flower from April to September and to fruit from August to February (Pennington & Sarukhan, 1968).

Aspidosperma megalocarpon was confused by Standley (1928) with *A. cruenta*, which is more common on BCI.

Mexico to Colombia (Chocó). In Panama, known from low elevations in tropical moist forest in the Canal Zone, San Blas (Puerto Obaldía), Chiriquí (Burica Peninsula), and Darién.

CATHARANTHUS G. Don

Catharanthus roseus (L.) G. Don, Gen. Hist. Dichl. Pl. 4:95. 1837(1838)

Lochnera rosea (L.) Reichb.

Herb, to 60 cm tall, usually woody at base, sparsely pubescent on leaves and young stems; sap milky. Leaves opposite; petioles 3–10 mm long, with axillary glands; blades obovate to spatulate, mucronulate, acute to attenuate at base, mostly 3.5–6 cm long, 0.7–3 cm wide, slightly succulent. Flowers 1–4, clustered near apex, on pedicels 1–3 mm long; calyx lobes 5, linear-lanceolate,

3–7 mm long, sparsely pubescent; corolla salverform, white to pinkish, the tube 2–2.5 cm long, pubescent inside at throat, the lobes 5, ± obovate, apiculate, 1.5–2.5 cm long; stamens included, attached near apex of tube; anthers free, ca 2 mm long; style 1; stigma 1, massive, pentagonal-umbraculiform. Follicles paired, slender, terete, 1.5–2.5 cm long, longitudinally ridged, with stiff, short trichomes; seeds not seen. *Croat 9389, Ebinger 204*.

Rare, in clearings. Flowers and fruits throughout the year.

Native to Madagascar, but cultivated and escaped throughout the tropics. In Panama, known from tropical moist forest in the Canal Zone and Herrera.

ERVATAMIA Stapf

Ervatamia coronaria (Jacq.) Stapf, Fl. Trop. Africa 4(1):127. 1904

Glabrous ornamental shrub, to 1.5 m tall; sap milky. Leaves opposite; stipules small, glandular, axillary; petioles short; blades elliptic, acuminate, acute to attenuate and decurrent on petiole at base, to 16 cm long and 6 cm wide, glossy. Cymes terminal or axillary; pedicels 1.3–2.5 cm long; flowers ca 4 cm wide, few; calyx lobes ovate, 2–4 mm long; corolla white, double, the tube to 2.5 cm long and greenish, the lobes rounded at apex; stamens in 2 series, the outer attached to the corolla, with anthers free, the inner forming a tube, with anthers reduced and sterile; style 1; stigmas 2. Fruits not seen. *Croat 4629*.

Cultivated in the Laboratory Clearing. Some flowers have been seen at various times throughout the year.

The plant apparently never sets fruit on BCI.

Native to India, but cultivated and escaped throughout the tropics. In Panama, cultivated in tropical moist forest in the Canal Zone and Panamá.

FORSTERONIA G. Meyer

Forsteronia myriantha Donn. Sm., Bot. Gaz. (Crawfordsville) 27:435. 1899

Liana; stems minutely puberulent to papillate when young, becoming glabrate and conspicuously lenticellate. Leaves opposite; stipules inconspicuous; petioles slender, 1–6 mm long, canaliculate, puberulent; blades narrowly elliptic to oval, acute to acuminate at apex, broadly acute to obtuse or rounded at base, 4–12 cm long, 2–5.4 cm

KEY TO THE SPECIES OF FORSTERONIA

- Leaf blades usually conspicuously pubescent on lower surface, at least along midrib, usually lacking axillary pitlike domatia (or domatia inconspicuous); reticulate venation of lower surface obscure or not closely spaced (veins more than 1 mm apart) *F. myriantha* Donn. Sm.
- Leaf blades usually glabrous on lower surface, with conspicuous pitlike axillary domatia; reticulate venation very closely spaced and easily visible (veins less than 1 mm apart):
- Leaf blades to 9 cm long and 3.5 cm wide; midrib lacking glands near base
- *F. peninsularis* Woods.
- Leaf blades usually more than 10 cm long and 3.5 cm wide; midrib with 2 triangular raised glands near base *F. viridescens* S. F. Blake

wide, the upper surface glabrous but with a usually puberulent midrib, the midrib bearing 2 acute glands near petiole, the lower surface glabrous, the midrib and major lateral veins villous and puberulent, the vein axils sometimes with inconspicuous pitlike domatia; reticulate veins not raised but easily visible. Inflorescences terminal, \pm hemispherical; pedicels to 1 mm long; bracteoles narrowly acute, to 3 mm long; bracteoles, rachises, and calyces densely puberulent-papillate to puberulent; flowers white, to 5.5 mm wide; calyx lobes ovate, broadly acute to obtuse, ca 1 mm long, the squamellae inside minute, many; corolla lobed to about the middle, to ca 4 mm long, glabrous to very minutely papillate on outside, villosulous inside on tube, the lobes oblong-ovate, spreading at anthesis; stamens to ca 3 mm long, adhering to style; anthers ca 1.5 mm long, glabrous, exerted at anthesis; ovary ovoid, apocarpous, minutely papillate-puberulent, ca 3 mm long; stigma 1. Fruits unknown. *Foster 4107.*

Apparently rare, in the forest. Reportedly flowers only in February in Panama; flowers elsewhere in April and May.

Guatemala to Panama. In Panama, known only from tropical moist forest in the Canal Zone.

Forsteronia peninsularis Woods., Ann. Missouri Bot. Gard. 22:215. 1935

Liana, \pm glabrous; stems slender, usually less than 1 cm diam; outer bark thin, brown; sap thick, grayish-white. Leaves opposite; stipules inconspicuous; petioles 4–5 mm long, canaliculate; blades narrowly elliptic, acuminate and downturned at apex, acute at base, 2.5–8.5 cm long, 1–3.3 cm wide, glabrous or nearly so, often with pitlike axillary domatia below, the margins revolute; major lateral veins 4–6, obscure. Inflorescences terminal, \pm flat-topped, dichasial cymes, bearing several to many flowers, the branches minutely puberulent, each subtended by an acute bract to 1.3 mm long; pedicels ca 1.5 mm long; flowers 5-parted, ca 7 mm long (excluding pedicel); calyx 2.3 mm long, thickest at base, the lobes acute, thickened medially, imbricate, inconspicuously ciliolate, bearing minute squamellae at base inside, these shorter than nectaries; corolla pale yellow, to 8 mm wide, minutely and inconspicuously puberulent except at base, the tube 2 mm long, as broad as long, with a densely villous ring at apex inside, the lobes spreading, to ca 3.7 mm long, acute at apex, ciliolate; stamens ca 4.7 mm long, exerted at anthesis; filaments fused to tube near base, weakly connate at least below anthers; anthers connate, ca 2.3 mm long, sagittate at base; ovary pubescent; stigma 1, \pm conical, held tightly inside anthers, sticky; nectaries ovate, \pm orange, ca 0.5 mm long, pubescent near apical margin, the nectar stored in corolla tube. Follicles paired, to 15 cm long, 3–4 mm diam, terete, glabrous; seeds oblong-linear, concave on one side, ca 7 mm long, pubescent, with a tuft of trichomes at apex. *Croat 14000, Foster 950.*

Apparently uncommon, in the forest. Flowers from the middle of the dry season to the early rainy season.

Individuals flower for at least a month, with some fruits of nearly mature size on flowering plants. Mature fruiting season unknown.

Belize, Guatemala, Honduras, and Panama, probably ranging all along the Atlantic slope of Central America. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Colón (Santa Rita Ridge) and Los Santos.

Forsteronia viridescens S. F. Blake, Contr. Gray Herb. 52:80. 1917

Liana; stems \pm reddish-brown, minutely lenticellate, ferruginous-pubescent when young; sap milky. Leaves opposite; stipules inconspicuous; petioles less than 5 mm long; blades \pm oblong-elliptic, acute to bluntly short-acuminate, obtuse to acute at base, 7–15.5 cm long, 3–6.5 cm wide, moderately thick, \pm glabrous, with glands at base of midrib above, often with large or small pitlike domatia in or near axils below. Thyrses axillary or terminal, 4–8 cm long, \pm ferruginous-pubescent on all exposed parts; pedicels very short or to 1.5 mm long; bracteoles triangular, to 1.5 mm long; calyx lobes triangular, 1–2.3 mm long, bearing 2 squamellae inside; corolla subcampanulate, cream or white, the tube ca 1 mm long, the lobes ca 2 mm long; stamens ca 1.5 mm long, half-exserted; filaments free; anthers connate, ca 1 mm long; ovary papillate; stigma fusiform, acute, sticky and held tightly inside anthers. Follicles commonly solitary (the result of 1 aborting), slender, mostly 25–50 cm long, to 7 mm wide, bearing dense, short, ferruginous-tomentose pubescence; seeds slender, 1–1.8 cm long, with a tuft of brownish trichomes 2–4.5 cm long at apex. *Foster 950, Weaver & Foster 1614.*

Apparently rare, in the forest. Flowers from March to May in Panama, with the fruits developing to maturity in September and October. The species may flower twice per year, since it flowers chiefly during September in Belize.

Belize, Guatemala, and Panama, probably ranging along the Atlantic slope of Central America. In Panama, known only from tropical moist forest on BCI and in Panamá (San José Island), from premontane wet forest in the Canal Zone (Pipeline Road) and Panamá (Cerro Campana), and from tropical wet forest in Colón.

LACMELLEA Karst.

Lacmellea panamensis (Woods.) Markg., Notizbl. Bot. Gart. Berlin-Dahlem 15:622. 1941

L. edulis sensu auct. non Karst.

Tree, to 20 m tall, \pm glabrous, sometimes armed with short stout spines; outer bark coarse, thin, hard; inner bark thick, tan; sap milky, abundant in trunk, branches, and fruits. Leaves opposite; petioles to 1 cm long; blades oblong-elliptic, acute to long-acuminate, obtuse and decurrent on petiole at base, 5–13 cm long, 2–4 cm wide. Flowers congested in axillary cymes; pedicels 2–4 mm long; calyx lobes \pm rounded, 1–1.5 mm long, ciliate;

corolla narrowly tubular, white, drying burnt-orange, the tube to 3 cm long, puberulent inside, somewhat inflated just above base and at insertion of anthers near apex of tube, the limb to 1.5 cm diam, the lobes spreading, rounded to acute; anthers free, ca 4 mm long; style shorter than anthers at anthesis; stigma 1, cylindrical, papillose. Fruits broadly ellipsoid to obovoid, 2–3 cm long, yellow-orange, with a short persistent style to 3 mm long; exocarp \pm leathery; mesocarp fleshy, sweet and tasty, with copious milky sap; seeds 1–4, usually 2, ellipsoid, usually flattened on one side, ca 1.5 cm long. *Croat 5373*.

Occasional in the forest, most abundant on the slope toward the tower; not seen in higher levels of the old forest. Flowers from March to August, mostly from April to June. The fruits mature from February to June, mostly from March to May of the following year. Juvenile fruits are common in the late rainy season. Leaves of this species are a favorite of sloths and as much as one-fifth of the foliage is sometimes cropped (E. Montgomery, pers. comm.).

Belize, Costa Rica, and Panama, probably ranging along the Atlantic slope of Central America. In Panama, a characteristic species in tropical wet forest (Tosi, 1971); known also from tropical moist forest in the Canal Zone and Darién.

MALOUETIA A. DC.

Malouetia guatemalensis (Müll. Arg.) Standl., J. Wash. Acad. Sci. 15:459. 1925

Mostly glabrous tree, to 15 m tall; sap milky. Leaves opposite; petioles ca 1 cm long; blades elliptic to somewhat ovate, acuminate, obtuse and decurrent on petiole and sometimes inequilateral at base, 8–22 cm long, 2.5–10 cm wide. Inflorescences axillary or occasionally terminal, usually branched, the clusters dense, umbelliform, the branches short, stout, woody; peduncles short, with short bracts; pedicels 3–5 mm long; flowers 5-parted; calyx 3–4 mm long, the lobes acute, stout, glabrate or puberulent; corolla white, ca 12 mm long in bud, minutely puberulent outside and on lobes inside, lobed to slightly beyond middle, the lobes slender, spreading at anthesis, the limb to 2 cm wide, the tube constricted just above sepals, 4–5 mm long; stamens included; anthers ca 1.8 mm long, connate, glued to stigma; ovary rounded above, minutely puberulent; style ca 1.5 mm long, club-shaped; stigma 1, \pm cupulate; nectary conspicuous, deeply lobed, more than half as high as ovary, the lobes usually 5. Follicles paired, fusiform, to 15 cm long and 2.3 cm wide, glabrous; seeds compressed, ca 2 cm long. *Croat 5667, 13486*.

Occasional, at least along the margin of the lake. Flowers mostly from late January to the middle of April (elsewhere on the Atlantic slope of Panama, some flowers are also reported from September to November). Fruits in the late dry and early rainy seasons (April to October). The plant loses its leaves just before flowering and may begin flowering before new leaves are of full size; it is probably not leafless for a long period, putting on new leaves at once.

Throughout Central America. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, San Blas, and Darién and from premontane wet and tropical wet forests in Colón.

See Fig. 452.

MANDEVILLA Lindl.

Mandevilla subsagittata (R. & P.) Woods., Ann. Missouri Bot. Gard. 19:69. 1932

Vine; stems sparsely pubescent. Leaves opposite; petioles 2–7 mm long, sparsely pubescent; blades elliptic to oblong-elliptic, acute to acuminate, narrowly cordate at base, 3–8 cm long, 1–3.5 cm wide, glabrous or pubescent especially along veins and margins, sparsely glandular along midrib. Racemes axillary, 3–6(9) cm long; pedicels 3–5 mm long; bracts linear-lanceolate, 1–5 mm long, scarious; calyx lobes 5, narrowly triangular, 1–1.5 mm long, with a single squamella inside; corolla salverform, yellow with a red throat, the tube 2.5–3 cm long, curved and somewhat gibbous, the lobes 5, spreading, to ca 1.5 cm long; stamens included, attached near throat; anthers ca 1.5 mm long, connate, glued to stigma; nectaries 5, sometimes fewer and united, ca half as high as ovary; stigma 1, pentagonal-umbraculiform. Follicles paired, slender, 8–12 cm long, usually swollen at \pm equal intervals; seeds oblong, ca 5 mm long, densely pubescent with a tuft of brownish trichomes ca 1 cm long at apex, the seminiferous area held within swollen areas of follicle. *Brown 191, White 132*.

Apparently rare; collected only twice on the island. Seasonal behavior uncertain.

Mexico to northern South America. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Chiriquí.

Mandevilla villosa (Miers) Woods., Ann. Missouri Bot. Gard. 19:70. 1932

Vine or slender liana; stems sparsely to densely pubescent. Leaves opposite; petioles pubescent, 1–2 cm long; blades elliptic to obovate, acute to acuminate, truncate

KEY TO THE SPECIES OF MANDEVILLA

- Bracts of inflorescences slender, scarious, 1–5 mm long; calyx lobes ca 1 mm long *M. subsagittata* (R. & P.) Woods.
 Bracts of inflorescences foliaceous, 10–30 mm long; calyx lobes 1.5–3.3 mm long *M. villosa* (Miers) Woods.

Fig. 452.
Malouetia guatemalensis



Fig. 453. *Mandevilla villosa*



Fig. 454. *Mesechites trifida*



to subcordate at base, 3.5–8 cm long, 1.5–4 cm wide, glabrous or sparsely pubescent above, glabrous to densely pubescent below, sparsely glandular along midrib. Cymes short, axillary; pedicels short, each subtended by a bract, the bracts lanceolate-caudate, foliaceous, ciliolate, 1–3 cm long; flowers 5-parted; calyx 1.5–3.3 mm long, turbinate, constricted below the short, triangular lobes; corolla pale yellow, to 3 cm long, the lobes spreading, to 2.3 cm long and 1 cm wide, reddish at base and rim of tube; stamens united to tube; anthers connate in a ring just below rim of corolla, 4 mm long, the free part of filament and the upper half of tube densely pubescent with stiff, white trichomes; style glabrous; stigma 1, pentagonal-umbraculiform, contained inside anthers; nectaries growing together, nearly as high as ovary. Follicles slender, ± moniliform, terete, ca 10–15 cm long, sparsely pubescent; seeds awl-shaped, ca 8 mm long. *Croat 10243, 11614.*

Occasional in clearings, especially the Lighthouse Clearing. Apparently flowers throughout much of the year, but most specimens have been collected in the rainy season, from May to December. Flowering plants may be found with mature fruits from the previous flowering, indicating that individual plants probably flower more than once per year.

Southern Mexico to Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Coclé.

See Fig. 453.

MESECHITES Müll. Arg.

Mesechites trifida (Jacq.) Müll. Arg. in Mart., Fl. Brasil. 6(1):151. 1860

Liana, usually ± herbaceous, mostly glabrous; sap milky; stem with a prominent interpetiolar ridge. Leaves opposite; petioles 5–15 mm long (to 25 mm), usually with 2 pairs of subconical glands at apex, the lower pair sometimes fused into 1 large gland; blades elliptic to oblong-elliptic or ovate, acute to short-acuminate or mucronate at apex, obtuse to rounded at base, 6–11 cm long, 2–4(5.5) cm wide. Racemes short, branched or unbranched, cymose; pedicels to ca 1 cm long; flowers 5-parted, few open at any time; calyx lobes ca 3 mm long, blunt; corolla tube 1.5–2.5 cm long, constricted about midway, green apically, greenish basally, the limb spreading, ca 2.5 cm wide, the lobes green at base, white on margins and at apex; stamens included, 4.7 mm long; filaments fused to

tube, densely pubescent near apex; anthers ca 4 mm long, connate and glued to stigma, the connective pilose; ovary sparsely and minutely muricate; style 1; stigma 1, fusiform-umbraculiform; nectaries separate or growing together; nectar copious. Follicles paired, slender, 15–40 cm long, terete, less than 5 mm diam; seeds many, linear, ca 1 cm long, densely pubescent, with a tuft of trichomes ca 2.5 cm long at apex. *Croat 6698, 7243.*

Occasional along the margins of the forest, no doubt occurring in the canopy as well. Flowers throughout the year, principally in the late rainy to early dry seasons. Fruit maturity time uncertain.

Southern Mexico to northern South America. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, and Panamá; known also from tropical dry forest in Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé and Panamá.

See Fig. 454.

ODONTADENIA Benth.

Odontadenia macrantha (R. & S.) Markg., Fl. Surinam 4(1):461. 1937

O. grandiflora Miq.; *O. hoffmannseggiana* (Steud.) Woods.

Liana, ± glabrous; sap milky, copious in stems; stems hollow, with an interpetiolar ridge. Leaves opposite, sometimes alternate near apex; petioles 1–2 cm long, sometimes purplish; blades ± elliptic, usually acuminate, obtuse to acute at base, 7–23(36) cm long, 4–10(17) cm wide, somewhat folded along midrib, the midrib ± arched, impressed above with a distinct central rib in the groove. Thyrses axillary or terminal, irregularly branched, glabrous; peduncle 4–9 cm long; pedicels 1–2(3) cm long; bracts minute; flowers ca 7 mm long; calyx lobes ovate, to 6 mm long, each with 1 or 2 squamellae inside; corolla funnellform, ca 6 cm long, orange-yellow, the lobes ca 3 cm long, spreading, tinged with red-orange inside near throat, the tube orange, bulbous, 5-lobed, ca 1 cm long, markedly constricted above stamens, the throat ca 3 cm long; stamens near base of tube; filaments and connective of the anthers densely short-pubescent; anthers sagittate, connate, glued to stigma; style 1; stigma 1, fusiform. Follicles paired, obovoid when young, becoming oblong-ellipsoid at maturity, to 22 cm long and 6 cm wide, rounded at base, narrowly rounded and weakly oblique at apex, glabrous, green tinged with brown; seeds many, the seminiferous portion

KEY TO THE SPECIES OF ODONTADENIA

- Corolla yellow-orange; fruits more than 3 cm wide, glabrous; leaves not bicolorous, the midrib canaliculate above, with a raised center ridge, conspicuous reticulate veins lacking *O. macrantha* (R. & S.) Markg.
- Corolla greenish; fruits less than 2 cm wide, densely pubescent; leaves bicolorous, the midrib canaliculate above but lacking a raised center ridge, the reticulate veins conspicuous *O. punctulosa* (L. C. Rich.) Pulle



Fig. 455. *Odontadenia macrantha*



Fig. 456. *Odontadenia macrantha*

Fig. 457.
Odontadenia macrantha



terete, brown, ca 4 cm long, narrowed to a slender stalk and bearing a plume of silky white trichomes ca 7 cm long at apex. *Croat 8315, 16597.*

Common in the forest and along the lakeshore. Flowers throughout the dry season and in the early rainy season, with the fruits maturing during the dry season of the following year.

These widely dispersed, buoyant seeds are commonly found throughout the forest during the dry season. The trichomes of the plume are spreading to erect, with the seed usually suspended vertically. In *O. puncticulosa*, the trichomes of the plume are spread in all directions, but chiefly arched downward and below the seed. As a result, the alignment of the seed during flight is far less dependable than in *O. macrantha*.

Costa Rica south through tropical South America; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá, from premontane dry forest in Herrera, and from premontane wet forest in Panamá.

See Figs. 455, 456, and 457.

Odontadenia puncticulosa (L. C. Rich.) Pulle, Enum. Pl. Surinam 383. 1906

Liana; sap milky, copious; stems glabrous, hollow and lenticellate in age, with a prominent interpetiolar ridge. Leaves opposite, glabrous; stipules 2, broadly ovate, softly puberulent, 2–3 mm long; petioles 1–2 cm long, stout; blades ± elliptic to ovate, shortly and bluntly acuminate, obtuse to subcordate at base on larger leaves, 12–24 cm long, 6–12.5 cm wide, bicolorous, the midrib above pale green, impressed, lacking a central rib; reticulate veins prominulous and very closely spaced below. Thyrses axillary or terminal; axes of inflorescences, pedicels, and calyces densely puberulent; pedicels to 3 cm long; flowers 5-parted; calyx lobes narrowly ovate, 4–9 mm long, each with several squamellae inside; corolla tubular, 5–6.5 cm long, the tube pale green, minutely puberulent, constricted ca 1 cm above base, the lobes white, spreading at anthesis, ca 1 cm long but with one side extended laterally 2–2.5 cm; stamens included, attached at base of corolla throat, ca 2 cm long; filaments and anthers pubescent; anthers 5–6 mm long, connate, glued to the fusiform stigma; stigma 1; nectaries growing together, covering ovary. Follicles paired, widely divergent, cylindrical, 11–16 cm long, 1.5–2 cm diam, densely pubescent with short erect trichomes; pericarp with a thin leathery outer layer and a thicker woody layer; seeds

many, the seminiferous portion cylindrical to angulate or flattened, 13–20 mm long, obscurely striate, brown, narrowed only a few millimeters at apex; plume at apex light brown, to 6 cm long. *Croat 8633, Knight 6988.*

Occasional, in the forest, probably less common than *O. macrantha*. Individuals flower intermittently throughout the dry season. Some fruits have been seen dispersing seeds in August.

Because flowers are a pale greenish color, with a very long corolla tube, and fall profusely in the early morning, I suspect that the plant is pollinated by hawkmoths.

Costa Rica, Panama, the Guianas, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón.

See Figs. 458, 459, and 460.

PRESTONIA R. Br.

Prestonia acutifolia (Benth.) K. Schum. in Engler & Prantl, Nat. Pfl. 4(2):188. 1895

Vine or slender liana; stems with a prominent interpetiolar ridge, the younger stems sparsely puberulent, the older stems lenticellate. Leaves opposite; petioles 0.3–1 cm long, sometimes bearing triangular glands; blades elliptic, acute to acuminate, acute to obtuse at base, 5–10 cm long, 1.5–3.5 cm wide, glabrous above, glabrous to weakly short-pubescent below. Racemes simple, axillary, most parts inconspicuously short-puberulent; pedicels 3–8 mm long; bracteoles minute; flowers 5-parted; calyx lobes triangular, 1.5–2.3 mm long, with a single lacerate squamella inside; corolla salverform, greenish-yellow, with 5 epistaminal appendages deeply included and minute, the tube ca 1.5 cm long, the lobes obliquely obovate, 5–6 mm long; stamens barely exerted; anthers ca 4 mm long, glabrous, connate and glued to stigma; stigma 1; nectaries joined at base, about as high as ovary. Follicles not seen, no doubt paired, terete, and slender as in other *Prestonia*. *Croat 4401, Woodworth & Vestal 498(F).*

Collected recently, only at the Lighthouse Clearing. Seasonal behavior uncertain. Elsewhere in Panama, flowers from November to March.

Panama to South America. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in the Canal Zone, and from premontane rain forest in Darién (Cerro Pirre).

KEY TO THE SPECIES OF PRESTONIA

- Leaves less than 3.5 cm wide; calyx lobes less than 3 mm long *P. acutifolia* (Benth.) K. Schum.
- Leaves mostly more than 5 cm wide; calyx lobes more than 10 mm long:
 - Plants conspicuously brown-pilose on most parts, rare *P. ipamiifolia* A. DC.
 - Plants essentially glabrous or puberulent:
 - Corolla lobes yellow or yellow-green; nectaries thick and fleshy, shorter than ovary; stems often conspicuously covered with large corky lenticels *P. obovata* Standl.
 - Corolla lobes white with orchid markings; nectaries thin, ± translucent, longer than ovary; stems lacking conspicuous, corky lenticels *P. portobellensis* (Beurl.) Woods.



Fig. 458. *Odontadenia puncticulosa*



Fig. 460.
Odontadenia puncticulosa



Fig. 459. *Odontadenia puncticulosa*

Prestonia ipomiifolia A. DC., Prodr. 8:429. 1844

Liana, conspicuously brown-pilose on most parts; younger stems herbaceous. Leaves opposite; petioles 0.5–7 cm long (usually less than 2 cm long), sometimes with conspicuous glands at base; blades elliptic to ovate, acuminate, rounded to subcordate at base, 10–20 (30) cm long, 4–8 (14) cm wide. Racemes congested at leaf nodes; peduncles ca 1.5–2.5 (5) cm long; floral rachis 2.5–3.5 cm long; bracts lanceolate, 1–1.5 cm long; pedicels 3–13 mm long; flowers 5-parted, dense; calyx lobed nearly to base, the lobes lanceolate, 8–15 mm long, glabrate inside, with a single triangular squamella ca 2 mm long inside each lobe; corolla yellow, salverform, to 3 cm long, lobed about one-third its length; stamens slightly exerted from throat, the epistaminal appendages prominent, about as long as orifice; anthers 5–6 mm long, glabrous, connate and glued to stigma; stigma 1; nectaries growing together, higher than ovary. Follicles paired, widely diverging, fusiform, ca 10 cm long, to 2 cm diam, densely rufous-pubescent. *Croat 12411, Shattuck 706.*

Rare, in the forest and along the shore. Flowers in the rainy season (May to November), with the fruits maturing in the dry season (December to February).

Panama, Colombia, and the Guianas. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone (Ancón), and from premontane wet forest in Coclé and Panamá.

Prestonia obovata Standl., J. Wash. Acad. Sci. 15:459. 1925

Liana, essentially glabrous; sap milky; younger stems often with corky lenticels; older stems becoming totally covered with corky tubercles. Leaves opposite; petioles 1–3 cm long, swollen, with several sharp glands in axils; blades mostly obovate, acute to rounded and cuspidate at apex, rounded to obtuse at base, 14–28 cm long, 9–18.5 cm wide, coriaceous, glabrous to minutely puberulent; elsewhere venation sometimes prominent below, with a submarginal collecting vein. Corymbs axillary, long-pedunculate; peduncles and pedicels densely puberulent to glabrous; pedicels to 4 cm long; flowers 5-parted; calyx lobes triangular, 10–15 (20) mm long, pubescent at least near base, with a single squamella inside each lobe; corolla salverform, yellow, 2.5–3.5 cm long, puberulent outside, with 5 white epistaminal appendages held above the prominently raised rim, the rim white to pink, the tube ca 2 cm long, pubescent near anthers; stamens included (just below rim); anthers ca 4 mm long, connate and glued to stigma; stigma 1; nectaries thick and fleshy, shorter than ovary. Follicles paired, 25–35 cm long, often covered with corky tubercles like those of stem; seeds ca 2 mm long, with tufted trichomes at apex, the trichomes 3.5–4 cm long. *Aviles 38.*

Rare, in the forest. Flowers during the dry season and in the early rainy season (January to September, especially in July). The fruits mature in the late rainy to early dry seasons (October to January), especially in the dry season.

Known only from Panama, from tropical moist forest in the Canal Zone, Chiriquí, and Darién, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Panamá and Darién.

Prestonia portobellensis (Beurl.) Woods., Ann. Missouri Bot. Gard. 18:553. 1931

Liana; stems with a prominent interpetiolar ridge, at first coarsely pubescent, minutely lenticellate; sap milky. Leaves opposite, glabrous; petioles ca 1 cm long, glandular in axils; blades elliptic to oblong-elliptic or obovate, very abruptly acuminate and falcate at apex, obtuse to rounded at base, 9–20 (30) cm long, 2.5–10 (15) cm wide. Corymbs axillary, pedunculate; peduncles mostly 1–6 cm long; pedicels 1–2.5 cm long, usually puberulent; flowers 5-parted; calyx lobes 10–15 mm long, ovate to narrowly triangular, each bearing a deltoid squamella inside at base; corolla salverform, constricted just below lobes, the tube greenish, to 18 mm long, pubescent inside at level of stamen attachment, bearing 5 slender appendages above stamens, the tube with a raised yellow rim, the lobes obliquely obovate, white with orchid lines near margin, to 14 mm long, spreading at anthesis; stamens half-exserted; anthers 4–5 mm long, connate and glued to stigma; nectaries thick at base, growing together, the margins thin, toothed, higher than ovary. Follicles paired, often united at apex, 20–40 cm long and 6 mm wide, glabrous; seeds to 14 mm long, ± fusiform, flattened, glabrous but bearing an apical tuft of trichomes 2–3 cm long. *Croat 13497.*

Common along margins of the forest, possibly occurring in the canopy as well. May be found in flower during most of the year, principally in the dry season and early rainy season. The fruits probably mature mostly in the dry season.

Southern Mexico to Panama. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Herrera, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón, Coclé, and Panamá.

See Fig. 461.

RHABDADENIA Müll. Arg.

Rhabdadenia biflora (Jacq.) Müll. Arg. in Mart., Fl. Brasil. 6(1):175. 1860

Mangrove vine, Clavelito

Glabrous liana; sap milky. Leaves opposite; petioles 1–1.5 cm long; blades oblong to oblong-elliptic, acuminate to mucronate, obtuse to acute and decurrent on petiole at base, 4–10 cm long, 1–5 cm wide. Dichasia axillary or subterminal, usually of 1–3 flowers; peduncles 2–8 cm long; pedicels mostly to 1.5 cm long; flowers 5-parted; calyx to 1 cm long, lacking squamellae; corolla white, 5.5–7 cm long, the tube 1.5–2 cm long, retrorsely bearded at point of staminal attachment and below, the



Fig. 461. *Prestonia portobellensis*



Fig. 462. *Stemmadenia grandiflora*,
dehiscent fruit
with exposed seeds



Fig. 463.
Stemmadenia grandiflora

throat conical, pale yellow basally, 2–3 cm long, the lobes somewhat spreading; stamens included, attached at apex of tube proper; anthers ca 4 mm long, connate and glued to stigma, densely bearded apically; nectaries separate or slightly connate. Follicles slender, 10–14 cm long; seeds acicular, 2–3 cm long, with a tuft of long trichomes at apex. *Croat 6574, 8296.*

Occasional, in marshes on the south side of the island. The flowers are seen more or less throughout the year.

Southern Florida through Central America to northern South America; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Panamá, and Darién; known also from premontane moist forest in Panamá and from tropical wet forest in Colón.

STEMMADENIA Benth.

Stemmadenia grandiflora (Jacq.) Miers, Apoc. S. Amer. 75. 1878

Huevo de gato, Lechugo, Venenillo

Glabrous shrub or tree, to 7 m tall; sap milky, copious in all parts; stems grayish-brown, with a prominent interpetiolar ridge. Leaves opposite, the pairs sometimes unequal; petioles 3–10 mm long, (leaving a conspicuous scar); blades mostly oblanceolate, abruptly acuminate (sometimes falcate), acute to obtuse at base, 3–11 (16) cm long, 1.5–4 (6) cm wide, bicolorous. Cymes of few flowers; peduncles short; pedicels to 1 cm long, with a single small bracteole attached ca midway on pedicel; flowers 5-parted; calyx lobes 1.5–3 cm long, irregular, 2 narrow and flat, 3 folded with 1 or more margins reflected; corolla pale orange, the tube 2.5–3.5 cm long, the lobes spreading, ca 5 cm wide, to 2.5–3.5 cm long, much contorted; stamens included, attached about 2 cm above base of tube, held in a tight circle by thick pubescent ribs of corolla wall; anthers ca 4 mm long, free; style equaling stamens; stigmas 2, minute. Follicles reniform, usually paired, ca 5 cm long, smooth on the outside, the apex acuminate, the very thick valves splitting open along upper side to expose fleshy orange mesocarp; seeds many, oblong to rounded, 5–10 mm long, papillate and deeply grooved. *Croat 4223, 11979.*

Frequent in the younger forest, especially along the shore. Flowers and fruits throughout the year.

Seeds are individually borne on flaps of the mesocarp (or the funiculus is much expanded). The flaps probably flip the seeds out of the fruit to some extent.

Mexico to northern South America. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane dry forest in Los Santos, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Coclé, and from tropical wet forest in Colón, Panamá, and Darién.

See Figs. 462 and 463.

TABERNAEMONTANA L.

Tabernaemontana arborea Rose in Donn. Sm., Bot. Gaz. (Crawfordsville) 18:206. 1893
Wild orange

Tree, to 20 m tall and 55 cm dbh, weakly buttressed, sometimes involuted, usually glabrous; bark with small vertical rows of lenticels; wood hard, heavy; sap milky, copious. Leaves opposite; petioles 2–11 mm long, with a prominent interpetiolar ridge (leaving a prominent scar), glandular in axils; blades mostly elliptic to obovate, short-acuminate, obtuse to acute at base, 5–18 cm long, 2.5–6 cm wide, dotted with brown glands below. Corymbs terminal; pedicels to 1 cm long; bracteoles 1.5–2 mm long; flowers fragrant, many, 5-parted; calyx lobes ovate, 1.5–3 mm long, each with several slender squamellae inside at base; corolla white, the limb ca 2 cm wide, the tube to 9 mm long, swollen in basal half, pubescent inside above the point of staminal attachment; stamens included, attached just above base of tube; anthers ca 3.2 mm long, free; style and stigma 1, 5-lobed, ca 2 mm long; nectaries lacking. Follicles 2, reniform, to 7.3 cm long and 5 cm wide; exocarp roughened, splitting at maturity to expose orange matrix and brown seeds; seeds oblong, many, to 13 mm long, longitudinally striate. *Croat 5242, 5419.*

Common in and mostly restricted to the older forest. Flowers mainly from March to June. Flowering time and intensity may vary from year to year. R. Foster (pers. comm.) reports that in one year trees flowered synchronously and heavily over a few weeks, but that in the next year there was intermittent flowering over several months. Time of fruit maturity is uncertain, possibly during the dry season (January to March). The fruits are eaten by white-faced monkeys in June (J. Oppenheimer, pers. comm.).

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet and premontane rain forests in Darién (Cerro Pirre).

See Fig. 464.

THEVETIA L.

Thevetia ahouai (L.) A. DC., Prodr. 8:345. 1844

T. nitida (H.B.K.) A. DC.

Huevo de tigre, Huevo de gato, Cojon de gato, Lavaperro

Shrub or small tree, usually to 6 m or less tall, ± glabrous; sap milky, copious. Leaves alternate; petioles very short or to ca 1 cm long, glandular in axils; blades usually oblanceolate, acute to acuminate, tapered to an acute base, 14–25 (30) cm long, 5–7 (8) cm wide, bicolorous, drying blackened. Cymes mostly terminal, irregular; pedicels to 3 cm long; flowers 5-parted; calyx lobes ovate, 5–7 mm long, spreading, with numerous slender squamellae inside at base; corolla cream, pale yellow or white, the tube



Fig. 464. *Tabernaemontana arborea*

Fig. 465. *Thevetia ahouai*



119. ASCLEPIADACEAE

2.5–4 cm long, densely pubescent near stamens, closed near apex by 5 triangular appendages held opposite and just above stamens, the lobes spreading, twisted, to 2.5 cm long, rounded at apex; stamens included, attached near apex of tube; anthers ca 1.8 mm long, free; style with an expanded apex, the lower margin revolute; stigmas 2, thick. Fruits bright red, fleshy, broader than long, ca 3 cm long, 5 cm wide, and 3.5 cm thick; seeds 2–4, \pm ovoid, rounded on one side, depressed on the other with a markedly raised margin. *Croat 5032, 8359.*

Frequent in the forest, especially the younger forest. The flowers and mature fruits have been seen throughout the year.

Southern Mexico to northern South America. In Panama, known from tropical moist forest in all regions, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in the Canal Zone, Panamá, and Darién, and from tropical wet forest in Colón.

See Fig. 465.

Lianas, vines, or erect herbs with milky sap. Leaves opposite or ternate, simple; blades entire; venation pinnate; stipules lacking. Racemes or umbels terminal or axillary; flowers bisexual, actinomorphic, few to many; sepals 5, basally connate, usually imbricate; corolla 5-lobed, the lobes valvate, showy (in *Asclepias* a colorful corollar corona is present and associated with hornlike appendages); stigma and stamens united into a 5-lobed gynandrium; stamens 5; anthers 2-celled; pollen agglutinated and borne in specialized saclike pollinia, these connected to a uniting gland and to each other by translator arms, the pollinia each separately set into slits in the gynostegium; pistil 1; ovaries 2, superior or nearly so, unilocular; placentation ventral or parietal; ovules anatropous and pendulous; each ovary bearing a style but sharing a single, common, 5-lobed, often much-enlarged stigma. Fruits double follicles (commonly 1 aborted), dehiscent adaxially; seeds silky-comose, with little endosperm.

Members of the family are most easily confused with

KEY TO THE SPECIES OF ASCLEPIADACEAE

- Plants erect herbs, to 1 m or more tall *Asclepias curassavica* L.
 Plants vines, herbaceous or somewhat woody:
 Stems glabrous or nearly so:
 Corolla lobes glabrous (except for cilia on margin); petioles to 1.5 cm long
 *Marsdenia crassipes* Hemsl.
 Corolla lobes conspicuously pubescent on at least part of one or both surfaces:
 Leaf blades ovate to suborbicular, cordate at base, 3.5–12 cm wide; flowers to 6 mm diam
 *Cynanchum cubense* (A. Rich.) Woods.
 Leaf blades linear to oblong, usually not cordate at base, less than 3 cm wide; flowers more
 than 10 mm diam:
 Petioles less than 8 mm long; stems lacking interpetiolar ridges and glands
 *Sarcostemma clausum* (Jacq.) R. & S.
 Petioles more than 10 mm long on mature leaves; stems with prominent interpetiolar
 ridge and glands *Blepharodon mucronatum* (Schlecht.) Dec.
 Stems conspicuously pubescent:
 Vegetative parts with only 1 type of trichome, the trichomes whitish (sometimes deciduous):
 Leaf blades cordate at base; flowers with petals ca 1.5 cm long *Gonolobus allenii* Woods.
 Leaf blades obtuse to rounded at base, not cordate; flowers minute, less than 5 mm diam
 *Cynanchum recurvum* (Rusby) Spellm.
 Vegetative parts with both long, multicellular, usually brownish trichomes and shorter, glandular
 or puberulent pubescence:
 Petals light yellow to whitish or greenish-white, not reticulate-veined, with the margins
 strongly crisped; sepals \pm equaling petals; gynandrium with large, inflated, dorsal
 appendages on anthers *Fischeria funebris* (Donn. Sm.) S. F. Blake
 Petals green-bronze to orange, often reticulate-veined, with the margins not crisped; sepals
 much shorter than petals; gynandrium lacking dorsal appendages on anthers:
 Corolla suburceolate, the tube somewhat constricted toward apex, often more than 10
 mm long; leaves usually more than 12 cm long *Matalea trianae* (Trin.) Spellm.
 Corolla rotate, the tube usually not constricted toward apex, usually 5 mm long or less;
 leaves usually less than 12 cm long:
 Corolla usually reflexed; petals less than 6 mm long (usually 3–4 mm); blades usually
 broadest below middle, the basal sinus usually narrow and 10 mm or more deep
 *Matalea pinquifolia* (Standl.) Woods.
 Corolla spreading; petals more than 6 mm long (usually 12–14 mm); blades often
 broadest above middle, the sinus usually open and less than 5 mm deep
 *Matalea viridiflora* (G. Meyer) Woods.

members of the Apocynaceae (118), which share the same habit and have milky sap. In a few genera, such as *Pres-tonia* in the Apocynaceae, the resemblance of the Asclepiadaceae is very close. Distinguishing characters of the Asclepiadaceae are the pollen in pollinia and the corona derived from the filaments of the stamens. When a corona is present in the Apocynaceae, it is derived from the corolla.

Flowers are insect pollinated, probably by small bees. *Asclepias* is pollinated by butterflies (Heithaus, 1973). I have also seen *Sarcostemma clausum* visited by butterflies. Insects visit the flower in such a way that the sticky gland bearing the pollinia attaches itself to the insect's legs and is carried away to be placed on the stigma of the next plant.

Seeds are exclusively wind dispersed and are remarkably well adapted to remaining airborne with slight amounts of wind.

Some 130–250 genera and about 2,000 species; predominantly in the tropics.

ASCLEPIAS L. (Milkweed)

Asclepias curassavica L., Sp. Pl. 215. 1753

Niño muerto, Pasorín, Yuquillo, Mata

Erect herb, sometimes more than 1 m tall; stems \pm glabrous below, pubescent above; sap milky. Leaves opposite or ternate; petioles 1–2 cm long; blades mostly lanceolate, gradually tapered to both ends, 5–18 cm long, 1–3.2(4) cm wide, glabrous or weakly pubescent. Umbels several, terminal; pedicels crisp-pubescent, 1–2 cm long; calyx green, hidden by reflexed petals, 5-lobed, 2–3 mm long; corolla usually orange-red, 6–8 mm long; corona segments (hoods) bright yellow, broadly ovate, 4–5 mm long, shorter than narrow inner horns of corona; nectar accumulating at base of corona or filling corona almost to brim. Follicles held erect, fusiform, 8–10 cm long and 1–1.5 cm wide, glabrous; seeds brown, ovate, flat, 5–6 mm long, topped by comose tuft ca 2.5 cm long. *Croat 6374*.

Occasional, in clearings. Flowers and fruits throughout the year. Individual plants flower more than once a year.

Plants contain the toxic glucoside asclepidadin (Blohm, 1962). Flowers are probably self-compatible (D. Spellman, pers. comm.).

Southern Florida and Mexico to Argentina; West Indies. A cosmopolitan weed in the tropics, introduced to the Old World as an ornamental. In Panama, known from most areas of tropical moist forest, from tropical dry forest in Herrera, from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from premon-tane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Coclé (Atlantic slope).

BLEPHARODON Dec.

Blepharodon mucronatum (Schlecht.) Dec. in DC., Prodr. 8:603. 1844

Slender vine with copious milky sap, glabrous except on corolla and sometimes upper midrib of leaf; stems

with nodes somewhat enlarged, with prominent inter-petiolar ridge bearing several (usually 3 or 4) glands. Leaves opposite; petioles 1–1.5 cm long; blades \pm oblong to elliptic, acuminate and downturned at apex, rounded or obtuse at base, 3–7.5 cm long, 1–2.5(3) cm wide, bicolorous. Cymes axillary, pedunculate, umbellate, shorter than leaves; peduncles usually shorter than pedicels; pedicels 1–2.5 cm long, slender; flowers 1–1.4 cm wide, 5-parted; calyx lobes oblong-ovate, ca 1.5 mm long, obtuse, glabrous, pale-margined; corolla greenish-white, spreading, deeply lobed, the lobes lanceolate-oblong to triangular, 5–6 mm long, obtuse, densely short-villous inside especially along margin, glabrous outside; gynostegium ca 3 mm long, the corona with 5 semivesicular sacs affixed to staminal tube; anthers terminating in an inflexed membrane; pollinia pendulous, ovoid. Follicles glabrous, fusiform, 7–9 cm long, ca 2 cm wide at widest part, rounded at base, broadest below middle, gradually tapered to narrow, blunt tip; seeds ca 5 mm long, narrowly spatulate, one side prominently papillate, the apical tuft of trichomes ca 4 cm long. *Croat 6375, 13159*.

Seen in Rear #8 Lighthouse Clearing. Flowers from August to October. The fruits mature in the early dry season (December to March).

Very similar to *Sarcostemma clausum*, but almost totally glabrous, with interpetiolar ridges and glands, and with fruits rounded at the base and tapered at the apex.

Mexico to South America. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón, Coclé, and Panamá.

See Figs. 466 and 467.

CYNANCHUM L.

Cynanchum cubense (A. Rich.) Woods., Ann. Missouri Bot. Gard. 28:213. 1941

Large herbaceous vine, climbing to ca 8 m in forest; cut parts with abundant milky sap, this drying chalklike; stems glabrous. Leaves opposite; petioles 4.5–8(12) cm long; blades ovate to suborbicular, acuminate and downturned at apex, cordate at base, 7–15 cm long, 3.5–12 cm wide (juvenile blades to 30 cm long, 20 cm wide), glabrous, with a series of platelike glands at base above, the sides of the blade held somewhat upward. Inflorescences axillary, racemose, becoming panicles of racemes, to 35 cm long, the branches puberulent; pedicels ca 5 mm long; flowers greenish, 5-parted; calyx lobes glabrous, 1.5–3 mm long; petals \pm oblong, ca 3 mm long, flexed at anthesis, the apical half with crisp white trichomes on upper surface; corona shallowly 5-lobed, the lobes ca 6 mm long; gynostegium broadened and ca 2.7 mm wide at apex; pollinia pendulous. Follicles ovate-oblong, terete, acuminate, smooth, 15–21 cm long, 7–10 cm diam; seeds bearing a coma of silky trichomes. *Croat 11175*.

Rare, in the forest. Flowers in July and August. Fruit maturation time unknown.

Cuba, Panama, Colombia, and perhaps southern Mexico. In Panama, known from tropical moist forest in the Canal Zone, Coclé, and Panamá.



Fig. 466. *Blepharodon mucronatum*

Fig. 467. *Blepharodon mucronatum*



Fig. 468.
Mataloa viridiflora

Cynanchum recurvum (Rusby) Spellm., *Phytologia* 25:438. 1973

Slender liana; stems less than 1 cm wide; copious milky sap in all parts; stems, petioles, and leaf blades above weakly strigose. Leaves opposite; petioles 5–9 mm long; blades oblong-elliptic or oblong-ovate, acute to obtuse and often apiculate at apex, obtuse to rounded at base, 2.5–5.8 cm long, 1.5–2.7 cm wide, weakly bicolorous, with a pair of glands at base, weakly strigose above, the pubescence below sparse, appressed, short; reticulation indistinct, most major lateral veins faint. Inflorescences axillary panicles of umbels, to 15 cm long; pedicels 2–4 mm long; flowers 5-parted, rotate-campanulate, yellow-green, 3–4 mm diam, in well-spaced fascicles of usually 5–10 flowers; sepals ovate, rounded or obtuse at apex, 1–1.3 mm long, with a single, small, slender squamella alternating with each sepal; corolla to 9 mm long, lobed to middle or beyond, densely short-pubescent inside except just below corona, the lobes spreading; corona less than 1 mm high, lobed below pollinia, the lobes short, opposite corolla lobes; gynostegium short, about as long as corolla tube. Follicles unknown, but probably \pm fusiform, long-acuminate at apex, 4–5 cm long. *Croat 15000*.

Rare; collected once above the escarpment north of Zetek Trail 200. The plant has been collected in flower only in June.

Costa Rica and Panama to Brazil (mostly Brazil). In Panama, known only from tropical moist forest on BCI.

FISCHERIA DC.

Fischeria funebris (Donn. Sm.) S. F. Blake, *J. Wash. Acad. Sci.* 14:293. 1924

F. martiana var. *funebris* Donn. Sm.

Suffrutescent vine; sap milky; stems and leaves sparsely to densely spreading-hirsute and sparsely puberulent, the hirsute trichomes septate. Leaves opposite; petioles 1–3.5 (7) cm long; blades ovate-elliptic to elliptic, abruptly short-acuminate at apex, cordate at base, 7–15 (22) cm long, 3.5–7 (15) cm wide, the trichomes often more dense and longer on veins especially below. Umbels axillary; peduncles, pedicels, and calyces sparsely to densely hirsute; peduncles 2.5–10 (22) cm long; pedicels 1–3.5 cm long; flowers white, sometimes tinged with pink, the buds \pm globular; calyx lobes 5, lanceolate-linear, long-attenuate, 7–15 mm long; corolla lobes 5, \pm ovate, 5.5–8 mm long, undulate and densely ciliate, densely hirtellous; corona \pm entire, 1.5–2 mm long; the column smooth, 1.5–2 mm high; gynostegium 2.5–3 mm high; stamens with the inflated portions suborbicular in surface outline, the staminal membranes usually triangular and covering most of the stigma head; ovaries usually sparsely pubescent. Follicles \pm fusiform, broader near base, ca 17 cm long and 5 cm diam, blunt at apex; periderm thick; seeds plumed at apex with long white trichomes. *Bailey & Bailey 286, Shattuck 816, Foster s.n.*

Collected recently by R. Foster. Seasonal behavior not determined. Flowers at least from March to June.

Southern Costa Rica to Colombia. In Panama, known

from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién and from premontane wet forest in Coclé (El Valle).

GONOLOBUS Michx.

Gonolobus allenii Woods., *Ann. Missouri Bot. Gard.* 27:333, f. 1. 1940

Vine; stems and leaves sparsely pilose. Leaves opposite; petioles slender, 2–4 cm long; blades ovate-oblong, acuminate, deeply cordate at base, 5–10 cm long, 2–4 cm wide, with 2 or 3 minute, fingerlike glands at base of midrib. Flowers 2–4 in axillary, pedunculate clusters, 5-parted, 2–3 cm diam; peduncles 1–2 cm long; pedicels 2–3 cm long; calyx lobes linear-lanceolate, ca 7 (10) cm long, sparsely pilose outside; corolla greenish, lobed to below middle, the lobes ovate-lanceolate, 1–2 cm long; outer corona fleshy, the margin bearded. Follicles unknown. *Wetmore & Abbe 202*.

Collected once on BCI, but not seen in recent years. This specimen had flowers in January.

Known only from Panama. The type is from premontane wet forest in Coclé (El Valle); the species is known also from tropical moist forest on BCI and from tropical wet forest in Panamá.

MARSDENIA R. Br.

Marsdenia crassipes Hemsl., *Biol. Centr.-Amer. Bot.* 2:337. 1882

Slender glabrous liana; stems terete. Leaves opposite; petioles 1–1.5 cm long; blades ovate to oblong-elliptic, abruptly short-acuminate, usually rounded at base, 8–15 cm long, 5–7 cm wide. Inflorescences axillary, subumbellate, bearing few flowers; peduncles 1–2 mm long; pedicels ca 1 mm long; flowers 5-parted, greenish-yellow; calyx lobes \pm ovate, ca 2 mm long, ciliate; corolla lobes ovate-oblong, ca 2 mm long, spreading, ciliate, with a narrow, whitish margin; corona segments ca 2.5 mm long. Follicles narrowly ellipsoid, ca 13 cm long and 3.5 cm wide; exocarp thick; seeds many, with tuft of long white trichomes at apex. *Shattuck 341(?)*, *Garwood 103*.

Rare. Seasonal behavior undetermined. Flowers at least in June, July, and October, with the fruits maturing in June and August.

Shattuck 341 is a sterile collection probably referable to this species.

Known only from Panama, from tropical moist forest in the Canal Zone (central region), San Blas, and Panamá.

MATALEA Aubl.

Matalea pinquifolia (Standl.) Woods., *Ann. Missouri Bot. Gard.* 28:235. 1941

Vincetoxicum pinquifolium Standl.

Herbaceous or suffrutescent vine; stems densely puberulent and hirsute, the hirsute trichomes fewer, straight, jointed, to ca 3 mm long, often falling away in age. Leaves

opposite, glabrous or with short puberulence; petioles 2–6 cm long; blades ovate-cordate, acuminate, 6–10 cm long, 3–7 cm wide. Inflorescences brown-puberulent, axillary, subumbellate; pedicels to 3 cm long, longer than peduncles; calyx lobes 5, sharp, puberulent outside, glabrous inside, to 3 mm long; corolla lobes 5, reflexed, somewhat orange, reticulate-veined, puberulent outside, long-pilose inside along one margin and apex, 4–6 mm long; corona slightly shorter than gynostegium; gynostegium purple. Follicles \pm lanceolate, long-tapered at apex, \pm rounded at base, 10–13 cm long, 2–4.5 cm wide; pilose and long-tuberculate-muricate; seeds many, brown, flat, with long white trichomes tufted at apex. *Shattuck 612.*

Rare. Flowers mostly from October to December, but also in June. Mature fruits have been seen only in April.

Costa Rica to Colombia, Ecuador, Venezuela, the Guianas, and eastern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in Panamá, and from lower montane wet forest in Chiriquí.

Matalea trianae (Dec. ex Trin.) Spellm., Ann. Missouri Bot. Gard. 62:140. 1975

Suffruticose vine; stems, petioles, midribs of leaf blades, peduncles, and pedicels both densely puberulent and brown-hispid, the hispid trichomes multicellular, to 1.5 mm long. Leaves opposite; petioles 1–3(7) cm long; blades broadly ovate to suborbicular, acute to obtuse and long-cuspidate at apex, subcordate at base, (9)12–18 cm long, (4.2)5–14 cm wide, chartaceous, densely hirsute on both surfaces; major lateral veins in ca 6 pairs. Inflorescences umbelliform, bearing few to several flowers; peduncles 1–2 cm long; pedicels 7–12 mm long; flowers 2–3 cm long, somewhat fetid; calyx green, lobed to the base, the lobes lanceolate to ovate-lanceolate, acute at apex, 10–12 mm long, 5–8 mm wide, puberulent on outside, glabrous inside, ciliate; corolla pale yellowish-green becoming brownish-green, salverform, to ca 4 cm diam, the tube 9–12 mm long, glabrous, constricted at the throat inside, the lobes ovate to suborbicular, 9–12 mm long, reticulate-veined, sparsely hispidulous on outside near apex, hispidulous-papillate on inside; corona of 5 distinct fleshy segments, the apices nearly truncate and equaling corolla tube or slightly exserted; gynostegium ca 6 mm long. Follicles attenuate-ovoid, ca 11 cm long, 3 cm diam, conspicuously 7-winged the entire length of fruit (based on Colombian specimen). *Steiner 81.*

Apparently rare; growing at the edge of the Laboratory Clearing, apparently a recent introduction to the island. Flowers principally in the rainy season, from June to December, especially from July to September. Mature fruits are known only from the dry season, from January to March.

Northern Costa Rica along the Pacific slope into western Colombia and into the Atlantic lowlands of Venezuela. In Panama, ecologically variable; known from tropical dry forest in Coclé and Panamá, from premontane moist forest in Panamá, and from drier parts of tropical moist forest in the Canal Zone and Panamá.

Matalea viridiflora (G. Meyer) Woods., Ann. Missouri Bot. Gard. 28:235. 1941

Vine; sap milky; vegetative parts, especially stems, with strigose to hirsute, multicellular, usually brownish trichomes and also with shorter glandular trichomes. Leaves opposite; petioles 1–4 cm long; blades ovate to oblong-ovate, acuminate, narrowly cordate to subcordate at base, 2.5–11 cm long, 1–5 cm wide, bicolorous, sparsely pubescent on both surfaces, the sinus generally open and shallow, mostly less than 5 mm deep. Cymes axillary, umbelliform; peduncles less than 2 cm long; pedicels mostly 1–2 cm long; flowers 5-parted, few, 2–2.5 cm wide; calyx deeply lobed, the lobes linear-lanceolate, ciliate, 4–5 mm long; corolla spreading, yellowish-green, 12–14 mm long, deeply lobed, glabrous on outside, puberulent inside especially near base, with black reticulate veins, bearing a mammillate process near gynandrium opposite sinus of lobes, the lobes lanceolate-ovate, acute; gynostegium rounded to obtusely 5-angulate, short. Follicles narrowly ovoid, ca 2 cm diam, abruptly tapered toward apex, narrowly 5-ridged, glabrous; seeds narrowly ovate, flattened, ca 5 mm long, brown, minutely papillate and \pm viscid, with a sculptured depression on one side. *Croat 6102, 12882, Shattuck 727.*

Rare, in the Laboratory Clearing. Flowers mostly from August to December. Mature fruits have been seen in the middle of January and in February.

Costa Rica to Colombia, Ecuador, Venezuela, the Guianas, and eastern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí and Panamá.

See Fig. 468.

SARCOSTEMMA R. Br.

Sarcostemma clausum (Jacq.) R. & S., Syst. Veg.

6:114. 1820

Funestrum clausum (Jacq.) Schlechter; *F. seibertii* Woods.

Chiefly herbaceous vine, branched many times, glabrous or sparsely pubescent with loose white trichomes easily wiped off; all cut parts with copious milky sap. Leaves opposite; petioles 5–7(9) mm long; blades linear to elliptic-oblong, acuminate, rounded or weakly cordate at base, 3–7 cm long, 0.5–1.5(3) cm wide. Inflorescences of stalked, axillary umbels, mostly bearing to 30 flowers; peduncles 6–9 cm long; pedicels 12–20 mm long; flowers 5-parted, white, 1–2 cm long (ca 2 cm wide when open); calyx lobes 5, short, ca 3 mm long, sharp-pointed; petals white or pinkish outside, 6–7 mm long, imbricate, ciliate, densely puberulent inside; hoods 5, white, encircling broad gynostegium; pollinia cylindrical, pale yellow, ca 1.2 mm long; style weakly bifurcate, slightly exceeding hoods; nectaries cuplike at base of and alternating with hoods, the nectar may fill the space between hoods (over the pollinia) by capillary action. Follicles 5–9 cm long, ca 1.2 cm thick; seeds numerous, flat, brown, less than 6 mm long, bearing a terminal tuft of fine trichomes 2–3 cm long. *Croat 11928.*

Occasional, on the shore, particularly on the south side of the island; often represented in *Annona-Acrostichum* formations. Flowers throughout the year. The fruits are rarely seen.

Throughout American tropics and subtropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Coclé, and Panamá and from premontane wet forest in Coclé.

See fig. on p. 14.

120. CONVULVACEAE

Terrestrial (sometimes temporarily growing in water), herbaceous vines or lianas (*Maripa*). Leaves alternate, petiolate; blades simple, entire or pinnately parted (*Ipomoea quamoclit* with the lobes filiform); venation pinnate or palmate; stipules lacking. Flowers bisexual, actinomorphic, solitary or in axillary, bracteate umbels or dichasia of few to many flowers; sepals 5, free, often unequal, imbricate, persistent in fruit; corolla funnelliform or salverform, entire or 5-lobed, showy, pleated vertically; stamens 5, attached to base of corolla and alternate with lobes, unequal; anthers 2-celled, introrse or extrorse, dorsifixed, dehiscent longitudinally; nectariferous intrastaminal disk often present; ovary superior, 2- or 3-locular, 2-4-carpellate; placentation axile; ovules 1 or 2 per locule, anatropous; style 1; stigma subglobose or lobed, the lobes 2, hemispherical, minutely ridged, papillose-puberulent; nectary a fleshy ring around the ovary. Fruits loculicidal capsules or indehiscent; seeds usually 4, with hard, cartilaginous endosperm.

Convolvulaceae are recognized by being vines without tendrils and with large, showy, funnelliform flowers with a capitate to globular stigma and stamens of usually unequal lengths. Fruits are more or less globular, have several seeds, and are contained within the persistent calyces.

Most species are bee pollinated. Most of the *Ipomoea* are visited by matinal bees. *Melitoma euglossoides* (Anthophoridae) is oligolectic to *Ipomoea*. In the Guanacaste

area of Costa Rica *Aniseia martinicensis* was observed being visited principally by halictid bees (*Dialictus* and *Augochlora*) and by *Ancyloscelis armata*. The same genus also is visited by *Melitoma euglossoides* (Schlising, 1972). *Merremia*, which does not flower until late morning, as well as *Aniseia*, *Iseia*, and *Maripa*, are probably also bee pollinated. Some species of South American *Maripa* are visited by *Trigona* spp.

Ipomoea quamoclit has a slender tubular red flower. According to R. Cruden (pers. comm.), plants produce abundant nectar between 6:00 and 9:00 A.M., during which time they are visited by hummingbirds. Since the plants are self-fertile, the birds may merely cause self-pollination and only occasional outcrossing. The flowers are visited later in the day by a variety of butterflies. Most plants in cultivation are self-compatible and may set seed without apparent pollination. (I am indebted to D. Austin for much of this information.)

Few species have obvious means of dispersal. *Maripa panamensis* is endozoochorous, probably mostly by monkeys (Oppenheimer, 1968) and parrots. *Aniseia martinicensis*, which grows around the margin of the lake, is probably water dispersed. *Iseia* may also be in part water dispersed (D. Austin, pers. comm.), but it often grows away from bodies of water. According to Austin (pers. comm.) a number of species are probably dependent on man to a great extent for their dispersal, including *Merremia umbellata* and *Ipomoea quamoclit*. Seeds of both of these species are lightweight and might also be wind dispersed.

About 50-55 genera with 1,500-1,650 species; generally distributed.

ANISEIA Choisy

Aniseia martinicensis (Jacq.) Choisy, Mém. Soc. Phys. Genève 8:66. 1839

Herbaceous vine; stems sparsely pubescent with fine appressed trichomes, directed toward base of plant. Petioles 1-2.5 cm long; blades oblong-elliptic, acute and

KEY TO THE TAXA OF CONVULVACEAE

Leaves cordate at base:

Flowers yellow *Merremia umbellata* (L.) Hallier f.

Flowers not yellow, reddish-blue or white:

Flowers solitary on long thickened pedicels; fruits transversely dehiscent capsules

..... *Operculina codonantha* (Benth.) Hallier f.

Flowers 5 or more in cymes; fruits longitudinally dehiscent or indehiscent *Ipomoea*

Leaves not cordate at base:

Leaves pinnately parted into linear lobes; flowers red *Ipomoea quamoclit* L.

Leaves entire:

Flowers lavender; fruits with a prominent beak; flowers often more than 5 per inflorescence

..... *Maripa panamensis* Hemsl.

Flowers white; fruits lacking beak; flowers 1-4 per inflorescence:

Sepals subequal; corolla 3-4 cm long; leaves rounded or emarginate at apex; fruits indehiscent, less than 1.5 cm diam

..... *Iseia luxurians* (Moric.) O'Don.

Sepals with 3 enlarged, winglike; corolla 2-3 cm long; leaves acute to obtuse and apiculate

at apex; fruits dehiscent, ca 2 cm long

..... *Aniseia martinicensis* (Jacq.) Choisy



Fig. 469. *Aniseia martinicensis*

Fig. 470. *Aniseia martinicensis*



apiculate at apex, acute at base, 5–10 cm long, 1.8–3.5 cm wide, glabrous above, appressed-pubescent below. Flowers axillary, mostly solitary or in dichasia of few flowers; calyx ca 1.5 cm long, with the inner 3 sepals winglike, broadly ovate, the outer 2 shorter, sharply pointed; corolla campanulate, pleated, 2–3 cm long, ca 2.5 cm wide when open, white, the triangular areas exposed in bud densely pubescent, the margin with 5 short apiculae; stamens equaling style, little more than half the length of the corolla; filaments pubescent in basal half and united with tube most of their length; pollen shed when stigma apparently receptive; ovary subglobose, ca 5 mm long; style ca 9 mm long. Capsules ovoid, ca 2 cm long, 4-valved; valves scarcely exceeding the persistent sepals, brown outside, silvery and shiny inside; seeds 4, ca 6 mm long, round in outline, \pm wedge-shaped in cross section, brown, bearing short stellate trichomes, at least one margin fringed with a row of brown scales. *Croat 8308*.

Occasional, in marshy areas along the shore, particularly in protected areas. Flowers and fruits throughout the year. Mature fruits may develop while the plant is still flowering.

Seeds float. Their fringe of scales possibly aids in their establishment in a place suitable for germination. Because the dark seeds stand out against the silvery inner valve surfaces, they may be distributed by birds also, though it seems no part is edible unless the exocarp is crushed.

Schlisling (1972) said the style is shorter than the stamens.

Southern Florida and Mexico to Colombia, Venezuela, and Peru; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, and Panamá and from tropical dry forest in Herrera.

See Figs. 469 and 470.

IPOMOEA L.

Ipomoea batatas (L.) Poir. in Lam., *Encycl. Méth.*

Bot. 6:14. 1804

I. triloba sensu auct. non L.

Camote, Sweet potato

Vine; stems and petioles usually very sparsely long-pubescent. Petioles 3–12 cm long, square; blades ovate,

long-acuminate at apex, deeply cordate and palmately veined at base, 2.5–12 (20) cm long, 2.5–10 (18) cm wide, entire, dentate or deeply lobed, glabrous except the veins very sparsely pubescent. Cymes axillary, bearing several flowers (7–15); peduncles 4–9 cm long; pedicels bracteate, 1–6 mm long; sepals 5, oblong, 8–10 mm long, medially ribbed, narrowly long-acuminate, sometimes with long trichomes on outside, usually ciliolate; corolla to ca 3.5 cm long (longer elsewhere), the tube violet outside, red-violet inside, darker near base, glabrous except for white-tipped, glandular trichomes near base inside (also on base of filaments), the limb white, broadly spreading at anthesis (as all *Ipomoea* species); stamens 5, of unequal lengths, 1.3–2.5 cm long; ovary densely hispid; style ca 2 mm long; stigmas obscurely bilobed. Capsules ovoid, ca 5 mm long, splitting into 3 valves, glabrous or hispid on all but basal third; seeds 4, globose, ca 3 mm long, dark brown, glabrous. *Croat 4563, 7250*.

Occasional, in the Laboratory Clearing. Flowers and fruits from October to July, especially in the dry season.

The species is variable and elsewhere may have lobed leaves.

Probably native to Mexico; now cultivated throughout the tropics. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién, from premontane moist forest in Colón, Chiriquí, and Panamá, and from premontane wet forest in Chiriquí, Coclé, and Panamá.

Ipomoea phillomega (Vell.) House, *Ann. New York Acad. Sci.* 18:246. 1908

Suffruticose liana. Petioles 2–9 cm long; blades broadly ovate-cordate, acuminate, 7–20 cm long, 5–20 cm wide, glabrate to moderately pubescent especially on veins below, maroon beneath when young. Flowers in long-pedunculate, dense, axillary clusters; peduncles to 21 cm long, stout; pedicels to 3 cm long, slender; sepals unequal, suborbicular to broadly ovate, 15–18 mm long, rounded at apex or emarginate, ciliate, the outermost 2 larger, enveloping the inner 3; corolla funnellform, red-violet, 4.5–5.5 (8) cm long, glabrous, the tube with sides parallel, 1.1–1.5 cm wide, contracted at base below stamens, abruptly spreading at apex, the limb thin, to ca 4 cm wide, rolling inward upon slightest desiccation; stamens to 1.2 cm long, borne on thick, knoblike, short-

KEY TO THE SPECIES OF IPOMOEA

Blades pinnately divided into linear lobes; corolla bright red, less than 5 mm wide *I. quamoclit* L.

Blades not pinnately divided into linear lobes; corolla not bright red, mostly funnellform:

Sepals acuminate at apex:

Sepals ciliate; corolla usually ca 3.5 cm long; stems bearing sparse, long, deciduous trichomes *I. batatas* (L.) Poir.

Sepals glabrous or very sparsely ciliate; corolla usually 4.5–5.5 cm long; stems glabrous *I. tiliacea* (Willd.) Choisy

Sepals rounded at apex:

Sepals glabrous, scarious on margins with a submarginal apiculum; leaves glabrous below, the cordate lobes often sagittate *I. squamosa* Choisy

Sepals ciliate, not scarious; leaves pubescent below, the cordate lobes rounded *I. phillomega* (Vell.) House



Fig. 471. *Ipomoea phillomega*

Fig. 472.
Ipomoea squamosa

glandular projections, these alternating with similar but smaller projections in a ring immediately below stamens; filaments unequal, red-violet; anthers oblong, basifixed and versatile, 5–7 mm long; style ca 2 cm long, weakly bifid at apex. Capsules globose, partially enclosed in persistent sepals, 1–1.5 cm diam; seeds 4, 3-sided, bearing long dense trichomes at base, with an “eye” at apex on inside. *Croat 16687*.

Occasional, in the forest. Flowers from July to September on BCI. The fruits may mature by late August and be present on the same inflorescence as flowers. Plants may flower continuously for at least 2 months. Austin (1975) reported that the species flowers from June through February elsewhere and perhaps flowers year-round.

Guatemala to Guyana and Peru; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién and from premontane wet and tropical wet forests in Veraguas (Atlantic slope), Colón, and Panamá.

See Fig. 471.

***Ipomoea quamoclit* L., Sp. Pl. 159. 1753**

Cundeamor

Slender, glabrous vine. Petioles to 5 cm long; blades pinnately divided, to 9 cm long and 6 cm wide, the lobes linear, ca 0.5 mm wide. Flowers solitary or clustered 2–5 per cyme on long axillary peduncles to 9 cm long; sepals 5, unequal, 4–8 mm long, 3-ribbed, with mucronate tips; corolla red, 2.5–3 cm long, the tube less than 4 mm wide, the lobes 5, acute; stamens 5, unequal, the longest nearly equaling lobes; filaments pubescent in basal third, fused to tube near base; style equaling longest stamen, coiled and much longer than stamens in bud; stigma globular. Capsules ovoid, 6–8 mm diam; seeds 4, black, with patches of short trichomes. *Croat 4153*.

A rare weedy plant occurring in clearings. Flowers to some extent throughout the year, but especially in the rainy season and early dry season.

Native to tropical America, now widespread in the tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, and Panamá and from premontane moist forest in the Canal Zone and Panamá.

***Ipomoea squamosa* Choisy in DC., Prodr. 9:376. 1845**

I. morelli Duch. & Walp.; *I. vestalii* Standl.

Batatilla

Herbaceous vine, glabrate except for short pubescence on petioles and veins on upper surfaces of young leaves. Petioles to 5 cm long; blades ovate-cordate, gradually acuminate, cordate at base, 5–13 cm long, 2.5–7 cm wide, the lobes ± sagittate. Flowers in axillary, corymbiform clusters; peduncles to 9 cm long, stout; pedicels less than 1 cm long; sepals glabrous, suborbicular, rounded at apex, the 2 outer ones 3–5 mm long, the 3 inner ones 5–10 mm long, the margin scarious, forming a submarginal apiculum; corolla funnelform, 5–8.5 cm long, lavender outside; dark red-violet inside; stamens of irregular lengths, 2–3 cm long at anthesis; filaments fused to lower 1 cm of tube and glandular-villous near base of free part;

anthers introrse, to 4.5 mm long, shedding pollen in bud; style ca 2 cm long, held above anthers in bud but well below anthers at anthesis; stigma white, bilobed; nectary ringlike; nectar copious. Fruits not seen. *Croat 7463*.

Infrequent, in clearings. Flowers in the dry season (December to March).

Mexico to Peru. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane moist forest in Panamá.

See Fig. 472.

***Ipomoea tiliacea* (Willd.) Choisy in DC., Prodr.**

9:375. 1845

Vine, glabrous except sometimes with long trichomes along midribs of blades. Petioles 3–9 cm long; blades ovate-cordate, acuminate, 6–11 (15) cm long, 5–8 cm wide. Flowers in cymose, axillary, pedunculate clusters; peduncles stout, to 6 cm long; pedicels 0.5–1.5 cm long; sepals 5, ovate, ca 1 cm long, acuminate, glabrous (or 1 pubescent), 1 sepal often curling around ovary after flower falls; corolla 4.5–5.5 (6) cm long, lavender to whitish outside, red-violet on tube inside, the rim broadly flaring, the lobes 5, minute, apiculate; stamens 5, all of different lengths, 1.5–2.5 cm long; filaments pubescent, fused to tube near base; anthers opening in bud; style slightly exceeding stamens; stigma lobed, the lobes 2, hemispherical. Capsules ± globose, 6–10 mm diam, splitting into 4 valves; exocarp thin; seeds 4, dark brown, glabrous. *Croat 6869, 7002*.

Apparently uncommon; collected at Burrunga Point at the edge of the clearing. Flowers from July to February. The fruits probably mature in 1 or 2 months. Old capsules may hang on for a long time.

When the level of the lake is high, the stems may be standing in water.

Tropics of Western and Eastern hemispheres. In Panama, restricted to the Atlantic slope; known from tropical moist forest all along the Atlantic slope and from tropical wet forest in Veraguas, Coclé, and Colón.

ISEIA O'Don.

***Iseia luxurians* (Moric.) O'Don., Bol. Soc. Argent.**

Bot. 5:77. 1953

Liana, growing over the canopy, the younger parts herbaceous; stems inconspicuously appressed-pubescent to glabrate. Petioles 1–2.5 cm long; blades ± oblong to ovate, rounded to emarginate and apiculate at apex, rounded to subcordate at base, mostly 4–12 cm long, 2.5–9 cm wide, glabrate or inconspicuously appressed-pubescent on lower surface (especially on younger leaves), the older leaves undulate. Cymes axillary; flowers numerous, 1–4 on each branch, 4–5 cm long at anthesis, densely appressed-puberulent; sepals 5, elliptic, 7–12 mm long, densely to inconspicuously pubescent, rounded and minutely toothed at apex; corolla white, funnelform, 3–4 cm long, broadened above calyx and deeply pleated most of its length, glabrous inside, the outer exposed ribs with long, brown trichomes; stamens 5, unequal, 10–14 mm long; filaments fused in basal half, the fused

KEY TO THE TAXA OF BORAGINACEAE

- Plants coarse herbs; flowers blue *Heliotropium indicum* L.
 Plants trees, shrubs, or lianas; flowers white:
 Plants trees (rarely shrubs, in *C. spinescens*); styles once or twice divided, the stigmas 2 or 4
 *Cordia*
 Plants shrubs or lianas; styles simple *Tournefortia*

121. BORAGINACEAE

Trees or climbing shrubs, lianas, vines, or erect herbs. Leaves alternate or rarely subopposite, petiolate; blades simple, entire or serrate; venation pinnate; stipules lacking. Cymes terminal or axillary, scorpioid, spicate or open, bearing several to many flowers, sometimes arranged in panicles; flowers bisexual (or functionally unisexual), actinomorphic; sepals 5, free or weakly connate, imbricate, or calyx merely 5-lobed or toothed; corolla tubular, 5-lobed or toothed; stamens 5, epipetalous, alternate with corolla lobes, sometimes connate apically; filaments partly fused to tube; anthers 2-celled, introrse, basifixed or basally dorsifixed, dehiscent longitudinally; ovary superior, 2-locular but becoming falsely 4-locular, 2-carpellate; placentation axile; ovules 2 per carpel, anatropous; style 1, simple, with the stigma peltate or conical (*Heliotropium*, *Tournefortia*) or the style twice bifid with the stigma capitate or clavate (*Cordia*). Fruits drupes (*Cordia*) or fleshy and separating at maturity into 2–4 nutlets; seeds generally lacking endosperm.

Members of the family are most easily recognized by their usually conspicuous, helicoid, cymose inflorescences. Some exhibit dimorphic heterostyly (Faegri & van der Pijl, 1966). All Boraginaceae have small, white, tubular or narrowly campanulate corollas, many of which must be pollinated by long-tongued bees or by butterflies. The calyces generally allow good protection of the nectaries. A small beetle was seen in the flower of *Cordia spinescens*. I have seen flowering plants of *Cordia panamensis* visited by butterflies, wasps, and several beetles, including curculionids.

While *Cordia alliodora* has wind-dispersed seeds, those

of *Heliotropium indicum*, *Cordia spinescens*, and all species of *Tournefortia* are probably chiefly bird dispersed. *Cordia bicolor*, *C. lasiocalyx*, and *C. panamensis* are dispersed by both mammals and birds. *Cordia bicolor* and *C. lasiocalyx* are reportedly swallowed by white-faced monkeys without being bitten into: the seed coat gives off a strongly astringent substance when broken; and defecated seeds germinate (Oppenheimer, 1968). *Cordia bicolor* is eaten by the bat *Artibeus jamaicensis* in Trinidad (Goodwin & Greenhall, 1961).

Some 100 genera and about 2,000 species; of cosmopolitan distribution.

CORDIA L.

Cordia alliodora (R. & P.) Cham., *Linnaea* 8:121. 1833
 Laurel, Laurel blanco, Laurel negro, Capa

Tree, to 25 m tall and 40 (90) cm dbh; buttresses weak; bark smooth to coarse, thin, usually coarsely lenticellate, sometimes deeply fissured; inner bark and wood white instantly after slashing, turning tan within seconds and brown within a few minutes; sap with sweet aroma; younger stems and branches, leaves, calyces, pedicels, and axes of inflorescences sparsely to densely stellate-pubescent; nodes of stems often swollen and inhabited by ants. Leaves alternate; petioles to 3.5 cm long; blades ± elliptic, acuminate, usually obtuse at base, usually 7–18 cm long, 3–8 cm wide. Cymes irregular, loosely spreading, terminal, the primary branches to ca 20 cm long; flowers bisexual, short-pedicellate, ca 12 mm wide, with a sweet, moderately strong aroma; calyx tubular, ca 5 mm long, 10-ribbed, with 5 small teeth; corolla tube

KEY TO THE SPECIES OF CORDIA

- Peduncles partly united to petioles; inflorescences spicate; corolla lobes very short; fruits red at maturity; plants usually less than 3 m tall *C. spinescens* L.
 Peduncles not united to petioles; inflorescences open, paniculate cymes; corolla conspicuously lobed; fruits not red; plants usually more than 4 m tall:
 Stellate trichomes conspicuous on most parts; stem nodes swollen; fruits minute, cylindrical, not drupaceous, slender, dispersed within dried flower *C. alliodora* (R. & P.) Cham.
 Stellate trichomes lacking; stem nodes not swollen; fruits drupaceous, ovoid to subglobose, conspicuous, not dispersed within dried flower:
 Leaves glabrous on upper surface *C. lasiocalyx* Pitt.
 Leaves conspicuously pubescent on both surfaces:
 Lower blade surface obscured by dense appressed trichomes; fruits densely appressed-pubescent, green to yellow at maturity *C. bicolor* DC.
 Lower blade surface bearing erect trichomes, not at all obscured; fruits ± glabrous, white at maturity *C. panamensis* Riley



Fig. 473. *Cordia alliodora*



Fig. 474.
Cordia lasiocalyx

mostly enclosed by calyx, the lobes 5, \pm spreading at anthesis; stamens 5, slightly shorter than lobes; filaments fused to tube, the free part curved inward and pubescent so as to block entrance to nectary; style exerted from tube but held well below anthers, its branches 4, directed laterally and forming an H-shaped structure above mouth of tube; nectar stored within base of corolla tube. Fruits 1-seeded nuts, cylindrical, ca 6 mm long, persisting within corolla, the corolla soon turning brown and also persisting. *Croat 8104.*

Common in most parts of the forest, particularly abundant in the younger forest. Flowers throughout the dry season, chiefly in February and March. The fruits develop quickly and are dispersed mostly in April and May. Plants begin to lose their leaves at the beginning of the rainy season (May) after most fruits have fallen, remain leafless for 1 or 2 months, and produce new leaves by August or September.

The species is unusual in that it loses its leaves during the early part of the rainy season when most species are actively vegetating. This phenomenon has as yet been unexplained. Despite this apparent handicap, the species is nevertheless a successful competitor. The fruits are dispersed when the dried, buoyant flower is released and blown away.

Throughout the American tropics. In Panama, a common invader (Holdridge, 1970) and characteristic of premontane moist, tropical moist, and premontane wet forests (Tosi, 1971); known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and from Los Santos to Darién on the Pacific slope and from tropical wet forest in Colón (west of the Canal Zone).

See Fig. 473.

***Cordia bicolor* DC., Prodr. 9:485. 1845**

Tree, usually 8–14 (20) m tall; younger parts appressed-pubescent. Leaves alternate; petioles usually 4–8 mm long; blades elliptic to ovate, acuminate to acute at apex, obtuse to rounded at base, 10–18 cm long, 5–8 cm wide, \pm entire, darker and moderately appressed-pubescent above, paler below with slender appressed trichomes on veins, the trichomes obscuring the surface. Panicles open, with flowers in small cymes; flowers bisexual; calyx tubular-campanulate, ca 4 mm long, with 5 small, \pm unequal teeth, persistent in fruit; corolla white, salverform, 4.5–6 cm long, 5-lobed ca one-third its length; stamens 5, exerted; filaments ca 3 mm long; anthers ca 1.5 mm long; ovary ovoid; style lobed, the lobes 4, exerted, clavate. Drupes ovoid, ca 1 cm long, attached at base, dull green turning yellow, with dense, short, appressed trichomes; seeds ovoid, ca 8 mm long. *Croat 5630.*

Frequent in the forest. Flowers from February to May, especially in February and March, with the fruits maturing from May to July. Different branches of the tree may not flower synchronously.

Sporadic in Central America and northeastern South America; southernmost Lesser Antilles. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Panamá (Altos de Río Pacora, ca 800 m elevation).

***Cordia lasiocalyx* Pitt., Contr. U.S. Natl. Herb. 18:251. 1917**

Shrub or small tree, to 4 m tall, glabrous except for sparse, short trichomes on lower leaf surfaces, often divaricately branched with a leaf between the branches. Leaves alternate; petioles 4–8 (10) mm long; blades oblong-elliptic to obovate, abruptly caudate-acuminate, acute to obtuse and decurrent at base, 6–14 cm long, 2.5–5.5 cm wide, entire. Panicles axillary or terminal, open, to ca 6 cm long; flowers nearly sessile, perfect; calyx cupulate, 2.5–3 mm long, the lobes 3, deltoid, ca 2 mm long; corolla funnellform, 8–10 mm long, white, 5-lobed ca half its length; stamens 5, exerted; filaments 3–3.5 mm long; anthers ca 1.4 mm long; ovary ovoid; style slender; stigmas 4, clavate. Drupes irregularly ovoid, ca 5 mm long and 9–15 mm wide, white, attached at its side; exocarp thin; mesocarp thin, gelatinous, sticky, sweet; seed ca 1 cm long. *Croat 8572.*

Frequent in the forest; juvenile plants more common than adults. Flowers mostly from February to April, especially in March, with the fruits maturing from late April to June.

Known only from Panama, from tropical moist forest in the Canal Zone and Darién and from tropical dry forest in Darién (Garachiné).

See Fig. 474.

***Cordia panamensis* Riley, Bull. Misc. Inform. 1927:135. 1927**

Shrub or slender tree, to 7 (15) m tall, functionally dioecious (see discussion below), strigose nearly throughout and hirsute on stems and axes of inflorescences. Leaves alternate or subopposite, dimorphic; petioles 5–15 mm long; larger blades ovate to ovate-elliptic, acute at apex, \pm rounded at base, 16–30 cm long, 7–15 cm wide, \pm entire, asperous, the midrib arched; smaller blades subopposite to the larger ones and usually less than half their length, ovate-orbicular. Inflorescences large, usually terminal, the cymes paniculate; flowers white, sessile, functionally unisexual; calyx 3.3–4 mm long, 5-dentate, pubescent; corolla ca 4 mm long; staminate flowers with corolla campanulate, lobed more than one-third its length, the lobes 5, recurved; stamens 5, 4–5 mm long, exerted ca 2.3 mm above rim; filaments united to basal two-thirds of tube, pubescent above point of attachment; ovary and style together to 3 mm long; ovary depressed-globose, orange; style narrowly conical, included, branched, each branch bifid near apex; nectar abundant; pistillate flowers with corolla salverform; stamens reduced, included, less than 2 mm long; ovary ovoid-oblong; style well developed, exerted, branched, each branch bifid near apex, the lobes clavate and recurved. Drupes subglobose to ovate, ca 1 cm diam, white at maturity; seeds tan, subglobose, ca 6 mm long. *Croat 10390, 11967.*

Occasional, in the forest. Flowers in early rainy season (May to July). The fruits mature rarely as early as June, mostly in September and October, rarely as late as November.

According to Nowicke in the *Flora of Panama* (1969) and Bawa and Opler (1975), the species is functionally

dioecious. However, a tree on the slopes of Cerro Campana (*Croat 14667*), apparently staminate, was probably the same tree from which fruit was collected a year earlier.

El Salvador to Panama and probably northern South America; reported as a doubtful species from the Valley of the Magdalena River by Jimenez S. (1970). In Panama, wide-ranging; known from all tropical moist forest areas except in Bocas del Toro; known also from tropical dry forest in Los Santos (Las Tablas) and from tropical wet forest in Colón (west of the Canal Zone).

***Cordia spinescens* L., Mant. Pl. Altera 206. 1771**

C. ferruginea (Lam.) R. & S.

Arching shrub or small tree, to 5 m tall. Leaves alternate; petioles 1–2.5 cm long; blades ovate to elliptic, acute to acuminate, rounded to obtuse at base, 8–16 cm long, 4–9 cm wide, usually irregularly dentate, sparsely strigose above, lighter and softly pubescent below. Inflorescences branched or unbranched, axillary; peduncle partly united to petiole; flowers sessile, in spikes; calyx cupular, ca 2–3 mm long, its lobes 5, curving inward to protect ovary after flower falls, enlarging and becoming red in fruit; corolla white, 3–4 mm long, glabrous outside, with gland-tipped trichomes inside, the lobes 5, short, toothed; stamens 5, slightly exerted at anthesis; filaments fused to tube near base, the tube with gland-tipped trichomes below point of fusion with stamens; anthers shedding at least some pollen in bud; style shorter than corolla at anthesis, branched twice; stigmas 4, folded and held just above anthers in bud, apparently receptive. Drupes ovoid, 4–5 mm long, bright red; seed with prominent reticulations, covered with a thin, fleshy mericarp. *Croat 12811*.

Occasional along the shoreline, abundant in Rear #8 Lighthouse Clearing. Flowers and fruits throughout the year, but most flowering occurs in the middle of the rainy season to the early dry season (August to February). Mature fruits are most abundant in the dry season. Since the plant may flower over a long period of time, the same plant may bear flowers and mature fruits.

The plant is probably pollinated by pollen feeders, such as the small beetle seen visiting some open flowers. The fruits are often transformed into galls by insects.

Mexico to Bolivia. In Panama, ecologically widespread; known principally from all regions of tropical moist forest except in the Azuero Peninsula and from tropical wet forest on the Atlantic slope in Colón, Coclé, and Veraguas, but also from a variety of life zones at higher elevations on the Pacific slope, including premontane wet forest in Chiriquí and Coclé and premontane rain, lower montane wet, and lower montane rain forests in Chiriquí.

HELIOTROPIUM L.

***Heliotropium indicum* L., Sp. Pl. 130. 1753**

Flor de Alacran

Coarse herb, to 1.5 m tall; stems conspicuously pubescent with short and longer trichomes. Petioles 1–8 cm long, often ± winged; blades ± ovate, acute at apex, obtuse to rounded and long-attenuate at base, 4–14 cm long, 2–7 cm wide, sparsely pubescent on both sides, the margins irregularly sinuate. Spikes narrow, usually terminal, to 28 cm long; flowers sessile; sepals 5, subulate, 1.5–2 mm long; corolla salverform, blue, the tube 3–4 mm long, the lobes 5, ca 1 mm long; stamens ± sessile; anthers less than 1 mm long; ovary weakly 4-lobed; style stout, simple; stigma conical. Fruits ± ovoid, separating into 4 nutlets at maturity, the nutlets 2–3 mm long, angulate; seeds 1 or 2 per nutlet. *Starry 249*.

Apparently no longer present on the island, though probably common when the island was more weedy; to be expected in the larger clearings and possibly also on exposed areas along the shore. Elsewhere in Panama, flowers and fruits from February to July. The fruits develop quickly. An inflorescence usually contains flowers at the apex and mature fruits at the base.

Widely distributed in the American tropics and Panama. In Panama, ecologically diverse; known from most areas of tropical moist forest as well as from tropical dry forest in Panamá (Taboga Island) and Los Santos (Pocri) and from tropical wet forest on the Atlantic slope.

TOURNEFORTIA L.

***Tournefortia angustiflora* R. & P., Fl. Peruv. 2:25, pl. 151. 1799**

Scandent shrub, to 3 m tall; most parts sparsely pubescent. Petioles very short or to 4 cm long; blades ovate-elliptic to lanceolate-elliptic, acute to acuminate, obtuse to rounded at base, 7–23 cm long, 2.5–10 cm wide, ± entire. Inflorescences of terminal, scorpioid cymes, the branches spikelike, to 8 cm long; flowers sessile or short-pedicellate, 5-parted; sepals slightly connate at base, ovate, 1–1.5 mm long; corolla white to yellow, the tube 10–12 mm long, the lobes ca 2 mm long; stamens ± sessile, borne midway on corolla tube; filaments fused in lower half; anthers ca 2 mm long; ovary ovoid; stigma sessile. Fruits globose, 4–5 mm diam, white, separating into 2–4 nutlets at maturity; nutlets brown, ca 2.5 mm long. *Croat 9100*.

Infrequent, at the edges of clearings; seen at the Laboratory Clearing. Flowers from October to May, chiefly

KEY TO THE SPECIES OF TOURNEFORTIA

Stems conspicuously pubescent with spreading trichomes, the trichomes 3 mm long or more:

- Trichomes on stem 4–6 mm long; sepals 5–7(9) mm long, the trichomes of 2 sizes *T. cuspidata* H.B.K.
- Trichomes on stem to 4 mm long; sepals 2–4 mm long, the trichomes uniform, short *T. hirsutissima* L.

Stems not conspicuously pubescent with spreading trichomes, the trichomes if present usually less than 1 mm long:

Corolla tube more than 10 mm long, nearly glabrous *T. angustiflora* R. & P.

Corolla tube less than 7 mm long, conspicuously pubescent:

Stems and leaves glabrous; corolla lobes more than 1.5 mm long; plants frequent along the shore *T. bicolor* Sw.

Stems and leaves conspicuously pubescent; corolla lobes less than 1 mm long; plants possibly no longer present on the island *T. maculata* Jacq.

from December to April. The fruits mature within about a month and are usually present on the flowering plants after about January, the last being seen about August.

Honduras to Peru. In Panama, ecologically diverse; known from all areas of tropical moist forest except in Chiriquí, from premontane wet forest in Coclé (El Valle), from tropical wet forest in Coclé (Boca de Toabré), and from premontane rain forest in Coclé (Cerro Pilón).

See Fig. 475.

Tournefortia bicolor Sw., Prodr. Veg. Ind. Occ. 40. 1788

Liana or arching shrub. Petioles 0.5–2 cm long; blades elliptic to oblong-elliptic, acute and falcate at apex, obtuse at base, 6–14 cm long, 3–7.5 cm wide, \pm glabrous, entire, often drying blackish. Cymes dense, scorpioid; flowers 5-parted, sessile; sepals slightly connate at base, subulate, 1.5–2 mm long, glabrous; corolla white, the tube ca 5 mm long, the lobes 1.5–2 mm long; stamens nearly sessile, attached ca one-third of the length of corolla tube; anthers ca 1.5 mm long; ovary ovoid; stigma 1, sessile, conical. Fruits globose, 5–6 mm diam, white at maturity, containing 4 nutlets; nutlets brown, ca 4 mm long. *Croat 9560*.

Frequent along the shore. Flowers from December to July, very rarely in the middle of the rainy season, mostly during February and March. The fruits mature within a month and are most common in March and April.

Throughout American tropics. In Panama, known from most areas of tropical moist forest, as well as from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Los Santos (Punta Mala), from premontane wet forest in Chiriquí (Boquete) and Coclé (El Valle), from tropical wet forest in Colón (Miguel de la Borda), and from premontane rain forest in Colón (Santa Rita Ridge) and Panamá (Cerro Jefe).

See Fig. 476.

Tournefortia cuspidata H.B.K., Nov. Gen. & Sp. 3:83. ed. fol. 1818

T. obscura DC.

Vinelike shrub, sometimes growing into canopy at 10 m or more; stems, petioles, and inflorescences densely pubescent, the long trichomes erect, brown, hirsute, 4–6 mm long, the short ones gray, puberulent, less than 0.2 mm long. Leaves short-petiolate; blades usually \pm ovate, acuminate, often falcate and downturned at apex, obtuse to rounded at base, 10–19 cm long, 5–8 cm wide, pubescent on both surfaces especially on veins beneath. Cymes dense, mostly terminal, helicoid; flowers 5-parted, sessile;

sepals narrowly pointed, usually 5–7 mm long; corolla tubular, to 1 cm long, the tube greenish, bearing long appressed trichomes, tapered to flaring rim, the limb white, ca 5 mm wide; stamens fused to tube just above somewhat bulbous base; anthers shedding pollen in bud; ovary ovoid, glabrous; style simple, very short, somewhat globular, held well below anthers; lateral rim of stigma with a \pm sticky secretion. Fruits ovoid to obovoid, 3–4 mm long, fleshy, held within persistent sepals, separating into 4 nutlets at maturity; nutlets irregularly ellipsoid, brown, ca 2.5 mm long. *Croat 13114*.

Occasional on the shore, generally climbing to less than 5 m; uncommon in younger areas of the forest, climbing into the canopy to 10 m or more. Flowers in Panama in all months of the year, but predominantly from January to July. The fruits develop quickly and may be found on flowering inflorescences, mostly maturing in the late dry and early rainy seasons.

Central America and northern South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién and from tropical wet forest in Colón (Miguel de la Borda).

See Fig. 477.

Tournefortia hirsutissima L., Sp. Pl. 140. 1753

Vine or liana, pubescent, the trichomes stiff, 1–4 mm long. Petioles 0.5–1.8 cm long; blades ovate to elliptic, acute to acuminate, rounded to broadly acute at base, 6–17 cm long, 3–8 cm wide, thin. Cymes axillary or terminal, scorpioid; flowers 5-parted, sessile, aromatic; sepals to 3.5 mm long, valvate, narrowly pointed; corolla tubular, white, sericeous outside, glabrous inside, the tube to 9 mm long, the limb to 7 mm broad, the lobes acute to obtuse and apiculate, pleated along middle; stamens dark, sessile, mounted nearly midway on tube; ovary ovoid; stigma conical, sessile, ca three-fourths as broad as ovary. Fruits \pm globose, to 7 mm long, white, fleshy, weakly pubescent, containing 4 nutlets ca 2.5 mm long. *Croat 6246, 11718*.

Common, at least along the shore; probably climbing into lower parts of the canopy. Flowers from April to October, especially in June and July. The fruits develop quickly and are usually present on the flowering inflorescences.

The flowers are visited by butterflies (*Heliconius*) and small bees.

Florida and throughout Mexico and Central America to Panama, Venezuela, Peru, and Bolivia. In Panama, known principally from tropical moist forest in the Canal



Fig. 475. *Tournefortia angustiflora*



Fig. 476. *Tournefortia bicolor*



Fig. 477.
Tournefortia cuspidata

Zone, Bocas del Toro, Panamá, and Darién; known also from premontane wet forest in Chiriquí (Boquete and Río Chiriquí Viejo).

Tournefortia maculata Jacq., Enum. Syst. Pl. Ins.

Carib. 14. 1760

T. peruviana Poir.

Liana or climbing shrub, to 5 m tall; young parts pubescent. Petioles 1–2 cm long; blades ovate to elliptic, acute to acuminate, obtuse at base, 5–14 cm long, 2.5–5 cm wide, glabrous to moderately pubescent, often drying dark. Cymes arranged in irregular panicles, the branches to ca 5 cm long; pedicels very short or to 2 mm in fruit; sepals 5, free, \pm ovate, 1.5–2 mm long, sparsely pubescent; corolla white to yellow, the tube to 6 mm long, the lobes 5, subulate, less than 1 mm long; stamens 5, sessile, attached midway on tube; anthers ca 1 mm long, connate apically; ovary ovoid; style simple, 2–3 mm long; stigma conical. Fruits distinctly lobed, 4–5 mm diam, orange to yellow and separating into 4 nutlets at maturity; nutlets ca 3.5 mm long. *Bailey & Bailey 237 (F)*.

Collected only once on the island and not seen in recent years. Elsewhere in Panama, flowers principally from April to July, with the fruits developing quickly and appearing most abundantly in July.

Mexico to Peru and Brazil; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas (Coiba Island and Santiago), and Panamá, from premontane dry forest in Panamá (Taboga Island), and from premontane wet and lower

montane wet forests in Darién (Cerro Pirre). It appears likely that the species will be found to occur in tropical wet forest as well.

122. VERBENACEAE

Trees, shrubs, lianas, or herbs; stems and twigs sometimes quadrangular. Leaves opposite, petiolate; blades simple, entire or serrate, sometimes lobed (*Clerodendrum*), sometimes glandular beneath; venation pinnate; stipules lacking. Panicles, racemes, spikes, cymes, or heads terminal or axillary; flowers bisexual, actinomorphic or zygomorphic; calyx 4- or 5-lobed; corolla tubular, 4- or 5-lobed, often showy; stamens 4(5), didynamous or equal; anthers 2-celled, dehiscing longitudinally; ovary superior, 2–4-carpellate, the locules as many as carpels or twice as many (by false septation); placentation axile; ovules 1 per apparent locule, anatropous; style 1; stigma simple or bilobed. Fruits of nutlets or dupes of several pyrenes; seeds lacking endosperm.

Verbenaceae are easily confused with the Labiatae (123), but are distinguished by the undivided ovary, the terminal style, and inflorescences that are not verticillate.

Flowers are probably all insect pollinated (Chapman, 1970). *Lantana camara* is visited by several species of butterfly, as species of *Aegiphila* probably are (Chapman, 1970). *Stachytarpheta* in Costa Rica is heavily visited by skippers (Hesperiidae) and by *Eulaema*, *Euglossa*, and large anthophorid bees (Heithaus, 1973).

Lantana camara is chiefly bird dispersed (Leck, 1972).

KEY TO THE SPECIES OF VERBENACEAE

- Leaves compound (opposite and each trifoliolate) *Vitex cooperi* Standl.
 Leaves simple:
 Leaves toothed or lobed:
 Leaves broadly cordate at base, semiorbicular with 3–7 short-acuminate lobes; inflorescences large terminal panicles *Clerodendrum paniculatum* L.
 Leaves not cordate, ovate, finely serrate; inflorescences not paniculiform:
 Flowers in small, long-pedunculate heads; plants common weeds *Lantana camara* L.
 Flowers scattered along long slender spikes; plants rare, probably no longer on the island *Stachytarpheta jamaicensis* (L.) Vahl
 Leaves entire:
 Flowers with calyx and corolla violet; calyx lobes exceeding corolla; inflorescences racemes; leaves stiff, asperous below *Petrea aspera* Turcz.
 Flowers white, yellow, or greenish; calyx shorter than corolla; inflorescence not racemose; leaves not stiff and asperous:
 Trichomes of plants (stems, inflorescence branches, and calyces) dense, appressed, white, ca 1 mm long; inflorescences capituliform; fruits in virtually contiguous clusters at maturity *Aegiphila cephalophora* Standl.
 Trichomes lacking or less than 1 mm long; inflorescences \pm open panicles; fruits not contiguous at maturity:
 Calyx lobed to one-third its length, in fruit splitting to the base; inflorescence branches and young stems terete to slightly angulate; fruits pointed at apex; leaves usually less than 2.5 times as long as broad, usually more than 7 cm wide, often softly villos below *Aegiphila elata* Sw.
 Calyx entire to minutely lobed, in fruit \pm entire; inflorescence branches and young stems usually 4-sulcate; fruits truncate to depressed at apex; leaves usually more than 2.5 times as long as broad, less than 7 cm broad, strigillose, puberulent below *Aegiphila panamensis* Moldenke

Most species of *Aegiphila* are probably bird dispersed and probably also dispersed to some extent by other animals. *Petrea aspera* and possibly also *Stachytarpheta* are wind dispersed.

About 100 genera and some 2,600 species; primarily in the subtropics and tropics in the Southern Hemisphere.

AEGIPHILA Jacq.

Flowers of *Aegiphila* were reported by Moldenke (1934) as being either male-predominant or female-predominant. I am considering these to be merely short-styled and long-styled forms, respectively.

Aegiphila cephalophora Standl., Publ. Field

Columbian Mus., Bot. Ser. 4:156. 1929

Liana, becoming arborescent, to 10 m long; trunk 6–8 cm diam near ground; stems, petioles, and inflorescence branches bearing dense, long, appressed pubescence. Petioles 0.5–1.1 cm long; blades elliptic to ovate-elliptic, acuminate, obtuse to rounded at base, 10–16 cm long, 5–6.5 cm wide, sparsely appressed-pubescent above but more densely so on midrib, the trichomes below dense, acropetal, appressed only on midrib. Cymes terminal or axillary, in dense capitate heads; inflorescence branches and calyces with dense long trichomes; flowers sessile or subsessile; calyx ca 3.5 mm long, enlarging to ca 5 mm in fruit, lobed in apical third, glabrous inside, the lobes 4, obtuse to rounded, persisting in fruit; corolla white, lobed, 6–12 mm long, the tube 4–7 mm long, the lobes 4, ovate, spreading; stamens 4, in long-styled forms to 1 mm long, in short-styled forms to 10 mm long; filaments fused to basal two-thirds of tube; anthers oblong, ca 0.8 mm long; style with the stigma bifid, in long-styled forms the style and stigma each to 8 mm long, in short-styled forms the style and stigma each ca 1.5 mm long. Fruits globose to ellipsoid, to 9 mm diam, in dense, ± globose clusters, green becoming orange at maturity, the surface granular; seeds (2)3 or 4, irregular, to 5 mm long. *Croat 12543, 16511.*

Common; normally growing high in the canopy, but occasionally flowering near the ground in tree-fall areas. Flowers from late June to September (sometimes to December). The fruits mature from September to December.

Apparently endemic to the Canal Zone in tropical moist forest.

Aegiphila elata Sw., Prodr. Veg. Ind. Occ. 31. 1788

Bejuco de peine mico, Guairo santo, Guaro

Liana, becoming shrubby, to 6 m high; stems, petioles, inflorescence branches, and calyces moderately short-pubescent. Petioles 1–2 cm long; blades elliptic to ovate-elliptic, acuminate, obtuse to rounded and often somewhat inequilateral at base, 10–20 cm long, 5–10 cm wide, short-villous below especially on veins, puberulent on veins above, with glandular punctations near midrib especially near base. Panicles axillary or terminal, often thyrsoid; pedicels to 5 mm long; calyx bell-shaped, ca

4 mm long, lobed ca one-third its length, in fruit glabrate, persistent, enlarging to ca 12 mm long, the lobes 4 (5), sometimes irregular, ovate, with a short acumen; corolla greenish to cream-colored, 8–9 mm long, the lobes 4 (5), ovate, acute to blunt at apex, glabrous outside, puberulent inside on tube and on basal part of filaments; stamens 4, long-exserted, 10–12 mm long; anthers oblong, ca 1.3 mm long; pollen white, tacky; style ca 2.5 mm long, slender; stigma bifid, ca 2 mm long. Fruits ± globose, to 1 cm diam, mostly enclosed by the weathering calyx, bright orange at maturity, glabrous; seeds 2–4, to 6 mm long. *Croat 14639, Foster 1240.*

Infrequent, in the forest. Some flowers have been seen in May and old fruits in September.

A few plants showed the calyx to be merely split and essentially bilobed, with one of the lobes bearing two minute teeth.

Mexico to Colombia, Venezuela, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet forest in Colón (Santa Rita Ridge).

Aegiphila panamensis Moldenke, Trop. Woods

25:14. 1931

Shrub or tree, to 15 m tall, to 15 cm dbh; young stems and inflorescence branches usually 4-sulcate; stems, leaves, and exposed parts of inflorescences glabrate to densely pubescent, the trichomes very short, stiff, erect or appressed. Petioles to 1.2 cm long; blades elliptic to narrowly ovate-elliptic, acuminate, acute to obtuse at base, 8–19 cm long, 3–7 cm wide. Panicles axillary and terminal, to 13 cm long, the cymes open; flowers numerous; calyx and pedicel like an inverted cone; pedicels ca 4 mm long; calyx ± entire, ca 2 mm long, enlarging to ca 4 mm; corolla cream, white, or yellowish, puberulent outside, 7–9 mm long, tubular below, soon falling, the lobes 4, ca 3 mm long, globular in bud; stamens 4, in long-styled flowers to 1.5 mm long, in short-styled flowers to 10 mm long; filaments coiled in bud, pubescent near point of fusion with tube; long-styled forms with the style long-exserted, to 10 mm long, the stigma bifid, ca 3.5 mm long, the short-styled forms with the style inserted, the style and stigma each to ca 2 mm long. Fruits drupaceous, ± oblong, truncate and ± depressed at apex, to 12 mm long and 9 mm wide, encircled at base by the accrescent calyx, green turning orange at maturity; seeds 4, white, only slightly shorter than the fruit. *Croat 4094, 6749, 6780.*

Occasional, as a shrub in clearings and open areas or as a tree in the younger forest. Flowers from July to December (sometimes from April). The fruits mature from October to January.

This species is similar to *A. martinicensis* Jacq.

Southern Mexico, Costa Rica, and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Coclé.

See Fig. 478.



Fig. 478. *Aegiphila panamensis*



Fig. 479.
Petrea aspera

CLERODENDRUM L.**Clerodendrum paniculatum** L., Mant. Pl. 90. 1767

Scarlet glorybower, Danger flower, Red pagoda flower

Herb or shrub, to 3 m tall; stems angulate, glabrous except for rings of long trichomes at leaf nodes. Petioles to 30 cm long; blades broadly ovate to suborbicular, acuminate and lobed, cordate and palmiveined at base, 9–25 cm long, 12–30 cm wide, with conspicuous glands 3–8 mm apart on margins, the lobes 5 (sometimes 3 or 7), shallow, acuninate, the lower surface punctate, with many small, whitish, peltate scales. Inflorescences terminal panicles ca 15 cm high and ca 20 cm wide, with reduced leaves at branching nodes; inflorescence branches rose-red, minutely puberulent; pedicels to 12 mm long; flowers 5-parted; calyx campanulate, ca 13 mm long, the tube orange, the lobes obtuse, ca 3 mm long, glandular before bud opens, red; corolla red-orange, the tube slender, 1.5–2 cm long, the lobes paler, spreading, ca 6 mm long; stamens 4, orange-red, exerted to ca 3.5 cm above throat, curved; style exerted ca two-thirds as far as stamens, minutely bilobed at apex, violet-purple. Drupes small, green, ± enclosed in persistent calyx. *Croat 7000.*

Cultivated in the Laboratory Clearing. Flowers principally in the rainy season. No fruits have been seen on BCI.

Native to Asia; cultivated in Europe and in the American tropics and subtropics. In Panama, known only from tropical moist forest in the Canal Zone.

LANTANA L.**Lantana camara** L., Sp. Pl. 627. 1753

Pasarín, Bandera español, Camara, Cinco negritos, Chichiquelite

Herb, usually less than 1.5 m tall, sometimes woody, hirtellous on most parts, sparsely so on upper leaf surfaces. Petioles 4–20 mm long; blades ovate, acute to acuminate, rounded to obtuse at base, then abruptly attenuate to half the length of petioles, 4–11 cm long, 2–5 cm wide, minutely crenate-serrate, scabrous or scaberulous above. Flower heads 1.5–2 cm diam; peduncles to 8 cm long; flowers sessile, bracteate, puberulent outside, the outermost of each head orange-red to burnt-orange, the innermost orange, the bracts acute, ca 3 mm long; calyx ca 2.5 mm long, obscurely 4-lobed, ciliate; corolla tubular, ca 10 mm long, 4-lobed, the tube somewhat expanded and bent above the middle, the limb ca 4 mm wide; stamens 4, fused to tube at 2 levels about midway down tube, the free part of filaments short; anthers often shedding pollen in bud, their thecae distinct; style held somewhat below the lowest pair of anthers; stigma attached laterally, becoming fleshy after anthers have lost their pollen, sometimes secreting a nectarlike substance visited by tiny insects; nectary small, but the nectar often filling base of corolla tube. Drupes round, several to many in a tight cluster, grayish-blue, to 5 mm diam; exocarp thin; mesocarp sweet, tasty; seeds obovate, to 4 mm long. *Croat 6004.*

Abundant in weedier areas of clearings. Flowers and fruits sporadically throughout the year.

Hummingbirds (*Damophila julie* and *Amazilia tzacatl*) visit the flowers for nectar (Leck, 1972).

The fruits are taken by a variety of birds, including manakins, flycatchers, honeycreepers, and tanagers (Leck, 1972).

Pantropical. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Herrera, and Darién, from premontane moist forest in Veraguas and Los Santos, and from premontane wet forest in Coclé.

PETREA L.**Petrea aspera** Turcz., Bull. Soc. Imp. Naturalistes

Moscou 36(3):211. 1863

Viuda, Flor de mayo, Flor de la cruz

Liana, growing into canopy, appearing to be an arching shrub when juvenile; young parts sparsely short-pubescent, glabrate in age; stems sometimes 4-angled. Petioles to 1.5 cm long; blades elliptic, often broadly so, rounded to acuminate at apex, acute to rounded at base, 7–21 cm long, 3.5–11 cm wide, usually stiff, asperous below. Racemes long, ± pendent, upper-axillary, to ca 30 cm long; pedicels ca 11 cm long; flowers 5-parted; calyx light violet, the tube membranous, ridged, ca 6 mm long, the lobes 5, thin, membranous, narrowly obovate, 2–2.5 cm long, a crownlike projection occurring at summit of tube and at base of lobes, ca 3 mm high, acutely 5-lobed to near base, often drying brown, persisting and acting as dispersal mechanism for fruit; corolla violet, salverform, ca 1.5 cm long, lobed to middle, somewhat zygomorphic, puberulent on both surfaces, the tube villous inside near apex, 1 lobe with a white spot near its base; stamens 4, fused to basal two-thirds of tube; filaments villous, ca 2 mm long; anthers held closely together on one side of the tube at its rim; pollen somewhat sticky, adhering to anthers after being shed; style bent slightly at apex in the direction of the white-spotted corolla lobe; stigma held just below anthers. Fruits of 1 or 2 tiny nutlets completely enclosed by the persistent calyx; nutlets ovoid, ca 1.5 mm long, glabrous. *Croat 9432.*

Abundant in the canopy and at the edge of the forest over the lake; one plant grows as an epiphyte from a large ant nest (*Croat 9432*). Flowering and fruiting throughout the year, often in synchronous waves throughout the forest.

Petrea volubilis L. was reported by Moldenke (1973) in the *Flora of Panama* for BCI based on *Aviles 14* and *Shattuck 412*. These specimens do not differ from the typical *P. aspera*, however, and I believe that only a single species of *Petrea* occurs on the island.

Widespread in tropical America from northern Mexico to southern Brazil; Cuba, West Indies; widely cultivated. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Panamá, and Darién.

See Fig. 479.

STACHYTARPHETA Vahl

Stachytarpheta jamaicensis (L.) Vahl, Enum. Pl. 1:206. 1804

Berbena, Blue porterweed, Gervao, Jamaica, Verbena, Vervain, Rinchao, Verbena azul, Brazilian tea, Cola de millo

Herb, to ca 1 m tall, sparingly pubescent to glabrate, sometimes slightly woody basally. Petioles absent or to 1 cm long; blades oblong to oval, obtuse to acute at apex, cuneate at base, decurrent onto petiole, to ca 11 cm long and to ca 4.5 cm wide, scaberulous above, glabrous below but with sparse jointed trichomes on primary veins, the margins serrate and ciliate-scabrous. Spikes terminal, to 20 (50) cm long, terete, 3–4 (5) mm wide; flowers at first erect, later embedded in the thickened rachis; bracts subtending pits in which flowers are immersed, acute, to 5 mm long and ca 1–1.5 mm wide, the margins scarious; calyx tubular, ca 5 mm long, shallowly 4-toothed on the side facing away from stem, notched to 1 mm on side next to stem; corolla salverform, shades of blue, violet, and purple, ca 10 mm long, the tube slightly curved, the limb ca 8 mm wide; perfect stamens 2, inserted above middle of corolla tube, included; filaments very short; thecae divergent; staminodia 2, posterior, minute; style ca 6 mm long, filiform; stigma terminal, persistent on fruit after corolla falls. Fruits oblong-linear, emerging from rachis pits at maturity, dry, splitting into cocci, the cocci 2, long, hard, narrow; seeds 1 per coccus, linear. *Woodworth & Vestal 739.*

Rare. Flowering and fruiting throughout the year.

Alabama and Mexico to Ecuador and Brazil; West Indies; introduced into parts of tropical Africa, Asia, Australia, and Oceania. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Bocas del Toro and Colón.

VITEX L.

Vitex cooperi Standl., Trop. Woods 16:26, 29, 32, nomen nudum 1928; Publ. Field Columbian Mus., Bot. Ser. 4:256. 1929

Tree, to 26 m tall; trunk buttressed and fluted, to 75 cm dbh; outer bark thin, light-colored; branchlets acutely

tetragonal to terete or compressed, densely puberulent when young. Leaves trifoliolate, opposite; petioles 1.3–9.5 cm long, finely appressed-puberulent; petiolules 1–8 mm long, the central one longest, flattened, margined; leaflets unequal with the lateral pair smaller and narrower, the central leaflet rounded and acuminate at apex, acute to acuminate at base, 4–22 cm long, 2.5–10.5 cm wide, entire, shiny and glabrous above, finely puberulent on veins beneath when young, becoming glabrate in age. Inflorescences axillary, solitary, 3.5–14 cm long, 4–6 cm wide, dichotomously branched, finely puberulent throughout, bearing many flowers; peduncles conspicuously flattened, 4.5–7.5 cm long; pedicels 1–3 mm long; bracts ca 1.5 cm long and 4 mm wide; flowers not seen, reportedly blue and lavender. Fruits not seen.

Rare, known only from the vicinity of the Laboratory Clearing; collected sterile once by R. Foster. Elsewhere in Panama, flowers during June and July, with the fruits maturing during July and August.

Guatemala to Panama; sea level to 600 m. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in Chiriquí (Progreso); reportedly fairly common on the Atlantic watershed around Gatun Lake (*Fisher 1*), and no doubt more widespread and common than collections indicate.

123. LABIATAE
(LAMIACEAE)

Annual or perennial herbs, erect or vinelike, pubescent, usually aromatic; stems usually quadrangular. Leaves opposite, sessile or petiolate; blades simple, serrate; venation pinnate; stipules lacking. Cymes bracteate, capituliform or verticillate, contracted, axillary or terminal; flowers bisexual, zygomorphic; calyx tubular or campanulate, 5-lobed; corolla bilabiate, 5-lobed; stamens 2, or 4 and didynamous, epipetalous, often forcefully ejected from flower; anthers 2-celled, the thecae often divergent, introrse, dehiscent longitudinally; ovary superior, 4-lobed, 2-locular, 2-carpellate; placentation basal; ovules 4, anatropous; style 1, arising from depression between lobes; stigma bilobed. Fruits of 4 nutlets (in *Salvia* usually only 1 maturing); seeds 1 per nutlet, with little or no endosperm.

KEY TO THE SPECIES OF LABIATAE

Inflorescences capituliform; flowers white; stamens 4:

 Calyx tubular, more than 5 mm long; nutlets ca 1 mm long *Hyptis capitata* Jacq.

 Calyx campanulate, less than 4 mm long; nutlets less than 1 mm long *Hyptis brevipes* Poit.

Inflorescences verticillate; flowers blue, lavender, or violet; stamens 2 or 4:

 Herbs small, cultivated, once planted at the laboratory, probably no longer present on the island; leaves often variegated *Coleus blumei* Benth.

 Herbs small or large, not cultivated:

 Flowers pedicellate; stamens 2; fruiting calyx with short blunt teeth, conspicuously covered with large gland-tipped trichomes *Salvia occidentalis* Sw.

 Flowers sessile; stamens 4; fruiting calyx with long slender teeth, lacking gland-tipped trichomes but with sessile glands *Hyptis mutabilis* (A. Rich.) Briq.

Recognized by the opposite leaves, squarish stems, and pleasant aroma. Members of the family are closely related to the Boraginaceae (121) and Verbenaceae (122), but are generally not confused with either of these families on BCI.

All BCI species have typical gullet flowers, which are scentless and generally bee pollinated (Faegri & van der Pijl, 1966). The flower is two-lipped, the lower lip serving as a landing platform. The genus *Hyptis* probably has the same pollination syndrome as that of *Eriope* studied by Harley (1971) in Brazil, since most *Hyptis* have the same morphology and triggered release of stamens. *Eriope* flowers open early in the day and are visited by tiny bees. The stamens then spring out, the style later elongates past the stamens, and the stamens become deflexed with the lower lip. The flower usually falls before the day is over.

Nutlets are small and usually numerous. *Hyptis* nutlets exude mucilage copiously when wetted (H. Baker, pers. comm.). They are probably in part dispersed by small birds of clearings and in part merely spilled and scattered by passing animals or the wind. The burlike pseudoheads of *Hyptis brevipes* and *H. capitata* are ballasts set loose by passing animals (van der Pijl, 1968). Ridley (1930) suggested that *H. brevipes* might be epizoochorous by means of its long-pubescent sepaloïd points.

About 180–200 genera and 3,200–3,500 species; cosmopolitan but concentrated in the Mediterranean region.

COLEUS Lour.

Coleus blumei Benth., Lab. Gen. et Sp. 56. 1832

Coleus, Pompolluda, Chontadua, Jacob's coat

Sprawling herb, to 70 cm long; younger stems and petioles densely pubescent. Petioles 1–4 cm long; blades ovate, acute at apex, obtuse to truncate at base, 2–15 cm long, 1.5–10 cm wide, sparsely pubescent above and on veins below, resin-dotted below, crenate, sometimes variegated. Inflorescences terminal, branched, 15–30 cm long; flowers in cymes, purplish; pedicels 1–2 mm long; calyx ca 2 mm long, resin-dotted, unevenly lobed and toothed; corolla ca 1 cm long, the tube recurved, the upper lip bilobed, the lower lip entire, enlarged, boat-shaped; stamens 4; style bifid near apex. Nutlets 4, ca 1 mm diam. *Shattuck 158*.

Formerly cultivated at the laboratory; not seen in recent years, but so commonly cultivated in Panama it is included here. Seasonality uncertain. Possibly flowers and fruits year-round.

Native to the East Indies; cultivated in many places. In Panama, known from BCI and Coclé (El Valle), but no doubt cultivated elsewhere.

HYPTIS Jacq.

Hyptis brevipes Poit., Ann. Mus. Natl. Hist. Nat. 7:465. 1806

Herb, to 60 cm tall, pubescent throughout. Petioles obsolete or to 1 cm long; blades lanceolate-elliptic or ovate,

acute at apex, attenuate at base, to 5 cm long and 2 cm wide, irregularly or doubly serrate, resin-dotted. Inflorescences capitulate, ca 1 cm diam; peduncles to 1 cm long; bracts awl-shaped, ciliate, to 6 mm long; flowers sessile, tufted at base; calyx campanulate, to 3.5 mm long, with 5 spinulose teeth ca 2 mm long; corolla bilabiate, 5-lobed, ca 3 mm long, white; stamens 4, weakly exerted; style bifid at apex. Nutlets 4, oblong-ovoid, ca 0.6 mm long. *Shattuck 479*.

Collected once by O. Shattuck on Wheeler Trail; possibly no longer occurring on the island. Seasonal behavior uncertain. Elsewhere flowers and fruits to some extent all year, but possibly with most flowering from November to January.

Native to Brazil, but now a weed throughout tropical America, Asia, and Polynesia. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Colón.

Hyptis capitata Jacq., Coll. 1:102. 1787

Suspiro de monte

Herb, to 2 m tall, sparsely to moderately pubescent throughout. Petioles slender, 5–20 mm long; blades ovate to rhombic, acute at apex, attenuate at base, 5–12 cm long, 2–6 cm wide, irregularly serrate. Flower heads at first hemispheroid, later globular; flowers numerous, many open at a time in each head; calyx scabrid, hispid at base outside, with a pubescent line inside above nutlets, the lobes 5, slender, at first equaling tube, the tube much longer in fruit; corolla white, ca 4 mm long, slightly exceeding calyx, bilabiate, the middle lobe of upper lip hooded, loosely enclosing the style and 2 longest stamens, folding backward following anthesis; anthers red, closed at anthesis; filaments curling over the edge of upper lip in time; stigma held midway between long and short pairs of stamens, its 2 lobes open at anthesis. Nutlets usually 4, ovoid, ca 1 mm long, smooth. *Croat 4406, 8683*.

Common in clearings. Flowers mostly in the early dry season, with the fruits maturing late in the dry season.

This species differs considerably from *H. mutabilis* in its pollination behavior. Those individuals of *H. mutabilis* observed shed the pollen in the bud, and the stamens were thrown forward violently after being opened forcibly (while the stigma was still unopened). In *H. capitata* only two stamens are held within the upper lip and then only very loosely. Their flowers are probably not forced open and the stamens, when released, do not spring forward violently. Both protandrous and protogynous forms were observed in a single population of *H. capitata*, though the anthers in some plants were shed in bud, with the style remaining unopened until most of the pollen was shed.

Mexico to Colombia, Venezuela, Ecuador, and Peru; Asia and Polynesia. In Panama, widespread; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, Panamá, and Darién, from premontane moist forest in Los Santos and Panamá, and from premontane wet forest in Chiriquí, Coclé, and Panamá.

Hyptis mutabilis (A. Rich.) Briq., Bull. Herb. Boissier 4:788. 1896

Herb, 2–3 (3.5) m tall, aromatic, moderately pubescent on most parts. Petioles obsolete or to 2 cm long; blades ovate or rhombic, acute to acuminate, cuneate to truncate at base, 3–6 cm long, 1.5–3.5 cm wide, serrate or doubly serrate. Panicles verticillate, the verticils each with 3–10 flowers; flowers sessile, emerging 1 at a time in each verticil; calyx toothed, the teeth 5, slender, alternating with erect trichomes in flower (once the flower has fallen the trichomes bend inward to close opening), enlarging and enclosing nutlets in fruit; corolla violet, pubescent, ca 4 mm long, bilabiate, the upper lip bilobed, with a white spot below rim, the lower lip trilobate, the center lobe hooded and marginally fringed, enclosing style and stamens; stamens 4, as long as lobes, fused to tube below lower lip, pubescent distally; anthers withering in age; style at first equaling stamens, later elongating; stigma bilobed, closed when first released, later opening. Nutlets usually 3 or 4, ca 2 mm long, contained within the expanded calyx. *Croat 7461*.

Locally abundant in the Lighthouse Clearing, usually a dominant plant at certain times of the year. Flowers very early in the dry season, with the fruits maturing in the late dry season.

Pollination is effected when an insect (presumably a tiny bee) attempts to force its way into the corolla tube. This releases the stamens and style, which are under tension because of being pushed forward by a flap of tissue at the base of the hooded lobe. See the discussion under *Hyptis capitata* for a comparison of the two species.

A common weed throughout tropical and subtropical America; introduced into the Old World tropics. In Panama, growing in disturbed areas in a variety of life zones; known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Los Santos and Herrera, from premontane moist forest in Los Santos, and from premontane wet forest in Chiriquí and Coclé.

SALVIA L.

Salvia occidentalis Sw., Prodr. Veg. Ind. Occ. 14. 1788

Erect or sprawling herb, usually 30–40 cm long, occasionally vinelike and very long, sparsely pubescent throughout. Petioles 5–20 mm long; blades ovate to triangular, acute at apex, obtuse to attenuate or truncate at base, 1.5–6 cm long, 1–3 cm wide, crenate-serrate. Panicles verticillate, the flowers 6–10 in a verticil; calyx tubular, prominently veined, with capitate glandular trichomes persisting in fruit; corolla ca 2.5 mm long, the tube white, the lower lobe weakly trilobate, blue with white stripes; stamens 2, affixed near apex of tube; filaments with hook-shaped appendages on inner side, these acting as levers to force stamens inward when pressed upon by an insect entering the tube; style held slightly above anthers and adjacent to upper lip; stigma bilobed, the lobes flared. Nutlets smooth, 0.5–1.5 mm long, usually only 1 maturing. *Croat 6943*.

An occasional weedy plant of clearings. Flowers in the early dry season, with the fruits maturing in the late dry season.

The fruits are dispersed by means of the sticky trichomes on the persisting calyx.

Throughout the American tropics. In Panama, growing in disturbed areas in a variety of life zones; known from tropical moist forest in the Canal Zone, Herrera, Coclé, and Panamá, from tropical dry forest in Los Santos, Herrera, and Panamá, from premontane moist forest in Los Santos, and from premontane wet forest in Coclé (El Valle).

124. SOLANACEAE

Trees, shrubs, vines, or herbs, terrestrial or hemiepiphytic (*Markea* and *Lycianthes*); stems often prickly; stellate pubescence often present. Leaves alternate or subopposite, petiolate; blades simple, entire or lobed; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic (zygomorphic in *Browallia*), generally solitary or in cymose axillary clusters; calyx 5-lobed; corolla (4)5-lobed; stamens (4)5 or 4 and didynamous (*Browallia*), epipetalous; anthers 2-celled, dehiscing longitudinally or poricidally (*Solanum*); ovary superior, 1- or 2-locular, 2-carpellate; placentation axile; ovules many (few in *Cestrum*); style 1; stigma minutely bilobed. Fruits generally berries with many seeds, rarely septicidally dehiscent capsules (*Browallia*); seeds with fleshy endosperm.

Members of the family are most easily distinguished by their actinomorphic, gamopetalous, usually plicate corollas and berries of many seeds. They are closely related to the Scrophulariaceae (125), which generally have zygomorphic flowers.

All species are probably insect pollinated. *Solanum* and *Cyphomandra* (G. Frankie, pers. comm.), with apical pores, are mostly pollinated by drumming, pollen-collecting bees. I have seen *Solanum subinermis* visited in this way by *Melipona*, and G. Frankie (pers. comm.) has observed xylocopids drumming flowers of *S. tridynamum* Dun. (*S. amazonicum* Ker.) in Mexico. *Cestrum* species have flowers that open late in the afternoon and are mostly moth pollinated. The flowers fall before mid-morning of the following day.

The fruits are endozoochorous, except perhaps in the case of *Browallia americana*. *Capsicum* has been widely dispersed by man. Most species are dispersed at least in part by birds (Ridley, 1930), but probably especially those of *Cestrum*, *Lycianthes*, *Physalis*, and *Witheringia solanacea*, which have fruits so small as to be unattractive to larger animals. Smaller fruits may be dispersed in their entirety by birds. Because species of Solanaceae have fairly thin-walled fruits, birds probably pick open the larger fruits and take the seeds. On the other hand, spiny rats eat fruits of *Physalis* (Hladik & Hladik, 1969), and white-faced monkeys are reported to eat fruits of *Cestrum* (Oppenheimer, 1968). The fleshy part of the *Cestrum* fruit is sweet, but the seed is bitter and is swallowed whole. Bats may be important in the distribution of fruits

KEY TO THE TAXA OF SOLANACEAE

Plants herbs to ca 1 m tall:

Flowers blue, zygomorphic; fruits capsular *Browallia americana* L.

Flowers not blue, actinomorphic; fruits berries:

Flowers pale yellow or white (often with a dark "eye" at base), solitary in leaf axils; fruits globose berries surrounded by the inflated calyx *Physalis*

Flowers greenish or yellow-green, lacking a dark throat, not solitary in leaf axils; fruits not as above:

Leaf blades \pm alike, not deeply lobed; flowers in dense axillary clusters; fruits ca 8 mm diam, orange-red; plants occasional in clearings *Witheringia solanacea* L'Hér.Leaf blades dimorphic, some entire, others deeply lobed; flowers few in pendent axillary racemes; fruits ca 2 cm diam with green stripes when young; plants probably not on island *Cyphomandra allophylla* (Miers) Hemsl.

Plants trees or shrubs more than 1 m tall:

Corolla narrowly tubular, the tube much longer than lobes; fruits obovoid or ellipsoid, less than 9 mm diam, purple or black at maturity; calyx lobes acute *Cestrum*Corolla not narrowly tubular, the tube usually as short as or much shorter than lobes (tube longer than lobes in *Markea* but corolla campanulate):

Corolla lobes divided nearly to base:

Flowers in very long, pendent cymes in age; petals greenish; anthers to 10 mm long, the connective thickened dorsally; fruits 3–5 cm diam *Cyphomandra hartwegii* (Miers) Dun.

Flowers not in long, pendent cymes; petals white or lavender; anthers with the connective not thickened:

Calyx truncate, sometimes with submarginal teeth reduced to bumps; plants unarmed shrubs *Lycianthes*Calyx 5-lobed (with 5 minute, marginal teeth and appearing truncate in *S. subinermis*); plants shrubs, vines, or herbs, often prickly *Solanum*

Corolla lobes not divided to near base:

Calyx distinctly lobed; plants hemiepiphytic; leaves \pm coriaceous, glabrous beneath; fruits ovoid, yellowish, ca 1.5 cm long; plants in forest *Markea ulei* (Damm.) Cuatr.

Calyx truncate; plants not hemiepiphytic; leaves thin, pubescent beneath; fruits globose or elongate, red at maturity; plants common in clearings:

Flowers solitary in axils; anthers bluish, not apiculate; fruits narrowly ovoid, more than 3 cm long; pubescence of leaves \pm restricted to vein axils below *Capsicum annuum* L. var. *annuum*Flowers clustered in axils; anthers not bluish, apiculate; fruits globular, ca 8 mm diam; pubescence of leaves not restricted to vein axils below *Witheringia solanacea* L'Hér.

as well, especially the long-pendent fruits of *Cyphomandra* and the larger arborescent or lianous *Solanum* species such as *S. hayesii* and *S. lancifolium*. *Markea ulei* is taken by bats (Bonaccorso, 1975). Heithaus, Fleming and Opler (1975) reported species of Solanaceae to be taken by several species of bat. A species of *Solanum* is taken by the bat *Artibeus jamaicensis* Leach in Mexico (Yazquez-Yanes et al., 1975).

About 80 genera and over 3,000 species; concentrated in the New World.

BROWALLIA L.***Browallia americana*** L., Sp. Pl. 631. 1753

Chavelita de monte

Herb, usually less than 1 m tall, puberulent to sparsely villous. Leaves alternate, simple; petioles to 2 cm long; blades ovate, acute to acuminate, acute at base, 1.5–7 cm long, 1–4 cm wide, entire. Flowers 5-parted, short-pedicellate, solitary in axils, 1.5–2 cm long; calyx 6–8 (10) mm long, narrowly campanulate, striate, pubescent;

corolla tube greenish, slender, pubescent, the limb lavender to blue, the throat 1–1.5 cm wide, minutely puberulent apically, with a prominent white or green spot near throat (nectar guide); stamens 4, the upper pair situated in throat near apex opposite nectar guide, the connective broadened, violet-purple, pubescent, their anthers dehiscing into cup-shaped cavities on one side of the much-thickened, elaborate style apex, the lower pair of stamens held slightly below the upper pair, their filaments hooked at apex; ovary 1–1.5 mm long, appressed-pubescent at apex; stigma bilobed. Fruits 4-valved, ellipsoid capsules contained within the accrescent calyx; seeds irregularly round, to 1.5 mm long, muricate. *Croat 10258*.

Uncommon; found in shady places at the Laboratory Clearing. Probably flowering and fruiting all year, especially in the dry season.

American tropics. In Panama, ecologically variable; most common at middle and upper elevations, occurring in most life zones in highland Chiriquí and mountainous regions of central Panama; less frequently from tropical dry forest in Panamá (Taboga Island) and from tropical moist forest in the Canal Zone, Panamá, and Darién.

CAPSICUM L.

Capsicum annuum L. var. **annuum**, Sp. Pl.

188–89, 1753

C. frutescens sensu Standl.

Red pepper, Chile, Aji, Aji picante

Shrub, less than 2 m tall. Leaves alternate or subopposite with a large leaf opposed by a smaller one; petioles to 3 cm long, densely pubescent; blades ovate to elliptic, falcate-acuminate, attenuate at base, 6–11(15) cm long, 2.5–5 cm wide, puberulent above and on veins below, tufted in veins axils below, ciliate. Flowers 5-parted, solitary (rarely paired) in axils; pedicels to more than 2 cm long; calyx truncate, ca 3 mm long, nearly glabrous, the teeth 5, blunt, submarginal, accrescent and persisting in fruit; corolla greenish-white, divided one-half to one-third of the way to base, to ca 17 mm diam, reflexed at anthesis, glabrous on outside, papillate-puberulent inside and on margins, the lobes acute; anthers bluish; filaments violet-purple near apex, fused to tube basally; style slightly exceeding anthers. Berries variable, often ovoid, ca 4.5 cm long, bright red at maturity. *Croat 9007*.

Cultivated at the laboratory. Flowering and fruiting all year, apparently with most fruits maturing during the rainy season.

Probably native to tropical America; cultivated throughout the world and throughout Panama.

CESTRUM L.

Cestrum latifolium Lam., Illustr. 2:5, no. 2275. 1793

Shrub or small tree, to 3.5(12) m tall; stems, especially on younger parts, petioles, and leaves, especially on veins below, sparsely to densely pubescent with weak multicellular trichomes. Leaves alternate; petioles 1–2(4) cm long; blades ovate to elliptic, acuminate, acute to obtuse at base, 7–16(25) cm long, 3.5–8.5 cm wide. Racemes or panicles short, congested, axillary, the branches and calyces pubescent; flowers 5-parted, to 3.5 cm long; calyx 1–3 mm long, the lobes acute; corolla narrowly tubular, 13–18(20) mm long, whitish-yellow or greenish, the lobes 5(6), narrowly acute, 2–2.5 mm long, pubescent outside along margins, glabrous inside; stamens 5, included; filaments fused to tube most of their length; anthers about as broad as long, held just below rim; stigma truncate; style held just above anthers. Berries

obovoid, pink to black at maturity, 5–9 mm long; seeds several. *Croat 11996*.

Uncommon, known from Rear #8 Lighthouse Clearing and from the forest near the Laboratory Clearing. Flowers from April to September, but mostly in the early rainy season, from May to July. The fruits mature from July to November, mostly from August to October.

Nicaragua to the Guianas and Brazil; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Panamá, and Darién, from tropical dry forest in Los Santos, from premontane moist forest in the Canal Zone, from premontane wet forest in Panamá, and from tropical wet forest in Chiriquí.

Cestrum megalophyllum Dun. in DC., Prodr.

13(1):638. 1852

C. baenitzii Ling.

Shrub or small tree, to 8(10) m tall; outer bark thin; young stems green, sparsely crisp-pubescent, glabrous in age. Leaves alternate; petioles to 1.3(2.5) cm long, glabrous; blades narrowly elliptic to obovate-elliptic, acuminate, gradually tapered to an acute or rounded base, 12–25(35) cm long, 3.5–8(12) cm wide, \pm glabrous. Racemes short, axillary, fasciculate; peduncles crisp-pubescent, bracteate; flowers 5-parted, usually many, often on leafless stems; calyx cupular, 2–3.5(4) mm long; corolla salverform, ca 1.5 cm long, the tube greenish, constricted just below lobes, the lobes white, spreading at anthesis, 4–5 mm long; stamens included; filaments fused to tube in basal two-thirds, pubescent near their point of fusion, turned inward below anthers; style slightly longer than stamens; stigma capitate, held just above anthers; nectary inconspicuous at base of ovary. Berries ellipsoid, 6–10 mm long, green becoming whitish then light violet and finally dark violet when mature; mesocarp thin, fleshy, white; seeds 1 or 2, minutely papillate. *Croat 14568*.

Occasional, in the forest. Flowering from November to June, mostly in the dry season, from February to April. The fruits mature in the early rainy season, from May to August.

Guatemala to Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, and Darién, from premontane wet forest in Colón and Chiriquí, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

See Fig. 480.

KEY TO THE SPECIES OF CESTRUM

- Mature leaves pubescent beneath *C. latifolium* Lam.
 Mature leaves glabrous beneath:
 Largest leaves more than 15 cm long, gradually tapered to a usually acute base, often broadest above middle *C. megalophyllum* Dun.
 Largest leaves less than 15 cm long, not gradually tapered to base, broadest at or below middle:
 Filaments conspicuously dentate near base; leaf blades usually acute at base *C. nocturnum* L.
 Filaments not dentate at base; leaf blades usually obtuse to rounded at base *C. racemosum* R. & P.

Cestrum nocturnum L., Sp. Pl. 191. 1753

Dama de noche

Shrub or small tree, to 5 m tall. Leaves alternate; petioles ca 1 cm long; blades ovate, acute to acuminate, obtuse to rounded at base, to 11 cm long, to 5.5 cm wide, minutely puberulent when young, glabrous in age. Panicles axillary or terminal, congested; peduncles with scattered leaf-like bracts; pedicels to 4 mm long, with minute bracteoles; flowers 5-parted; calyx campanulate, puberulent, 2 mm long; corolla greenish to yellowish-white, 14–17 mm long, glabrous outside; stamens equal; filaments ca 3 mm long, dentate near point of insertion; stigma slightly exserted. Berries ellipsoid, to 10 mm long, black at maturity; seeds not studied. *Bangham 429*.

Collected once on the shore. Seasonal behavior uncertain. According to our records, flowers mostly in the dry season, but also in August.

Native to the Antilles, but cultivated and escaped in many other places in tropical America. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro and from tropical wet forest in Colón and Chiriquí.

Cestrum racemosum R. & P., Fl. Peruv. 2:29, pl. 154. 1799

C. panamense Standl.; *C. racemosum* R. & P. var. *panamense* (Standl.) Franc.

Yedi

Tree, to 12 m tall. Leaves alternate; petioles ca 1–2 cm long, glabrate; blades lanceolate-elliptic, long-acuminate, mostly obtuse to rounded at base, 7–15 cm long, 2.5–5 cm wide, ± glabrous. Cymes branched, axillary or terminal, 3–9 cm long, the branches crisp-villous; flowers 5-parted; calyx 2.3–3.3 mm long, the lobes acute, ciliate; corolla to 15 mm long, slender, cream or greenish-white, the lobes villous inside; stamens included; filaments fused to tube most of their length; style flat on end, held slightly above anthers; nectaries golden-yellow. Berries obovoid or ellipsoid, ca 6 mm long, black, with thickened pedicels ca 2 mm long; seeds usually 3, wedge-shaped (like orange segments), densely papillate, ca 4 mm long, embedded in a juicy white matrix, very bitter before maturity, sweet at maturity. *Croat 8899*.

Uncommon, known from the edge of the Laboratory Clearing. Flowering from December to May, mostly in the late dry season and the early rainy season (April to May), rarely as late as September. Frequently flowering more than once per season. The fruits mature mostly from February to December.

Belize to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Chiriquí and

Coclé, and from tropical wet forest in Colón and Coclé. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

CYPHOMANDRA Mart. ex Sendt.**Cyphomandra allophylla** (Miers) Hemsl., Biol. Centr.-Amer. Bot. 2:417. 1882

Solanum allophyllum (Miers) Standl.

Hierba de gallinazo, Hierba gallota

Erect herb, to 1 m tall, glabrate. Leaves 2 or 3 subopposite at a node (often with 1 leaf lobed and the other 2 entire), dimorphic; petioles 1.5–5 cm long, narrowly winged; blades broadly ovate, acuminate, rounded at base, entire or 3–5-lobed, the entire blades 5–6 cm long and 3–4 cm wide, the lobed blades 9–11 cm long and 6–10 cm wide. Racemes short, at the dichotomies of stems; peduncles 1–2 cm long; pedicels ca 1 cm long, broadening at apex; flowers 1–6; calyx ca 2 mm long; corolla white or yellowish, 10–12 mm long, lobed about halfway; filaments ca 1 mm long, attached to dorsal surface of a membranous ring inserted near base of corolla tube; anthers lanceolate, ca 6 mm long, with 2 terminal pores; ovary elongate, conical; stigma punctiform. Berries ellipsoid, ca 2 cm long, white at maturity, sometimes striped with green when young; seeds yellow, flattened, ca 1.5 mm long. *Aviles 105, Zetek 5040*.

Collected twice; not seen in recent years, but it could reoccur in clearings. Flowering and fruiting mostly in the rainy season, but probably to some extent throughout the year.

Known only from the Pacific slope of Panama, from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical dry forest in the Canal Zone.

Cyphomandra hartwegii (Miers) Dun. in DC., Prodr. 13(1):401. 1852

C. heterophylla Donn. Sm., nomen nudum; *C. costaricensis* Donn. Sm.; *C. mollicella* Standl.

Monca prieto

Soft-wooded shrub or tree, to 5 m tall; most parts sparsely to densely puberulent. Leaves alternate or subtended by a smaller leaf; petioles mostly 3–6 (10) cm long; blades ovate, acuminate and often downturned at apex, unequally obtuse to cordate at base, 6–25 (30) cm long, 5–13 cm wide, the upper surface sparsely puberulent to glabrate, some of the trichomes usually glandular-tipped; juvenile leaves often deeply lobed, to 45 cm long and 25 cm wide. Cymes upper-axillary, indeterminate, to 50 cm or more long before flowers cease being produced, pendent; flowers 5-parted, closely spaced on peduncle; pedicels to 3 cm long in flower, elongating and

KEY TO THE SPECIES OF CYPHOMANDRA

- Plants herbs to 1 m tall; leaves 2 or 3 per node, subopposite *C. allophylla* (Miers) Hemsl.
 Plants shrubs or trees to 5 m tall; leaves alternate or opposite with 1 leaf of each pair much smaller
 *C. hartwegii* (Miers) Dun.



Fig. 481.
Cyphomandra hartwegii

Fig. 480. *Cestrum megalophyllum*



Fig. 482. *Markea ulei*



Fig. 483. *Markea ulei*

thickening at apex in fruit; calyx ca 5 mm long, the lobes short, acute to obtuse; corolla green, 1.5–3.5 cm long, the lobes long-tapered, free to calyx; filaments thick, short, fused to corolla tube; anthers to 10 mm long, papillate, the connective swollen, purple, the pores terminal; stigma held just above anthers in bud, elongating after anthesis. Berries globose to ellipsoid, 3–5 cm long, green with lighter stripes, yellow at maturity; seeds numerous, disk-shaped, reniform to round, to 6 mm long. *Croat 9016*.

Uncommon, appearing in tree-fall areas of the forest and at the edges of clearings. The plant flowers unceasingly for long periods, with individual plants flowering for as much as a year or more.

Visited by male *Eulaema bombiformis* bees (*vide* label on *Dressler 3070*).

Honduras to Brazil and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane wet forest in Chiriquí and Panamá, from tropical wet forest in Colón, and from premontane rain forest in Colón, Coclé, and Panamá.

See Fig. 481.

LYCIANTHES (Dun.) Hassl.

Lycianthes maxonii Standl., J. Wash. Acad. Sci. 17:14. 1927

L. maxonii Standl. var. *appendiculata* Standl.

Slender shrub, to 1.5 m tall; younger stems and petioles puberulent; nodes somewhat swollen. Leaves alternate; petioles to 5 mm long; blades mostly oblong-obovate, acuminate, cuneate to obtuse at base, 7–15 cm long, 2–5 cm wide, glabrous, entire, minutely undulate; major veins few, arcuate-ascending. Fascicles very short, axillary, usually with only 1–3 (6) flowers or fruits at any time; pedicels 1–2.5 cm long in flower, to ca 3.5 cm long in fruit; flowers 5-parted; calyx truncate, with 5 short, wart-like protuberances below rim; corolla violet, 5–10 mm long, divided to near base, the lobes spreading at anthesis; stamens yellow, shorter than corolla, held together at apex in a ring; filaments united to tube in basal half, very short; anthers 4 mm long, with 2 terminal pores; ovary ovoid, glabrous; style straight, held well above anthers, nearly equaling length of corolla. Berries globose to obovoid, to 1.2 cm long, orange becoming red at maturity; seeds ca 4 mm long, longer than broad. *Croat 6307*.

Frequent, especially in the old forest. Flowers from March to December, mostly from April to September. The fruits develop within about a month, maturing from April to January, mostly from July to October. Plants usually have flowers and fruits simultaneously.

Usually growing about a meter tall, but becoming nearly twice as tall in areas of the older forest.

Nicaragua to Panama. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Panamá, from tropical wet forest in Colón, from lower montane wet forest in Chiriquí, and from premontane rain forest in Panamá (summit of Cerro Jefe).

Lycianthes synanthera (Sendt.) Bitter, Abh. Naturwiss. Vereine Bremen 23(2):499–500. 1919

Shrub or tree, usually hemiepiphytic, ca 2 (10) m tall, ± glabrous except for tufted axils on lower leaf surfaces. Leaves alternate or subopposite with the pairs unequal; petioles 5–30 mm long; blades ± elliptic, acuminate, acute to obtuse at base, 5–20 cm long, 3–8.5 cm wide. Flowers solitary or in fascicles of few flowers; pedicels ca 1.5 mm long; calyx cyathiform, nearly truncate, 2–3 mm long, becoming woody and 5–6 mm long in fruit; corolla 5-lobed to near base, ca 1 cm long, purplish; stamens 5, ± equal; anthers 6–7 mm long, yellow, united into an ellipsoid column ca 3 mm diam; style exerted. Berries globose, ca 7 mm diam, fleshy; seeds discoid and margined, ca 1.5 mm long, foveate, yellow. *Croat 11899*.

Rare, known only from the area east of Wheeler Trail 1600. Flowers from May to September. The fruits mature from June to October.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, and Panamá, from premontane wet forest in Chiriquí, from tropical wet forest in Coclé and Panamá, and from premontane rain forest in Coclé.

MARKEA L. C. Rich.

Markea ulei (Damm.) Cuatr., Feddes Repert. 61:78. 1958

M. panamensis Standl.

Hemiepiphytic shrub, often associated with ant nests; smaller stems fleshy, sometimes arising from a large, swollen, tuberous stem perched in the crotch of a tree, with only a slender root trailing to the ground; stems and leaves glabrous. Leaves alternate or subopposite with the pairs equal or unequal; petioles less than 1 cm long; blades obovate to broadly elliptic, acuminate, acute to rounded at base, 6–20 cm long, 3–8.5 cm wide, coriaceous. Panicles short, axillary, cymose; peduncles stout, to ca 7 cm long; pedicels 10–14 mm long; flowers 5-parted, ca 1.3 cm long; calyx deeply divided, the lobes oblong-ovate, curved inward, to ca 7 mm long, persisting in fruit; corolla campanulate, to 14 mm long, greenish-yellow, densely pubescent outside with very short glandular

KEY TO THE SPECIES OF LYCIANTHES

- Plants hemiepiphytic; corolla more than 1 cm long *L. synanthera* (Sendt.) Bitter
Plants terrestrial; corolla less than 1 cm long *L. maxonii* Standl.

trichomes, some tinged with purple, the lobes broadly rounded, imbricate, 3–4 mm long; stamens included; filaments fused to tube two-thirds their length; anthers yellow, ca 4 mm long, with longitudinal dehiscence from apex, the connective purplish; ovary yellow; style included, nearly equaling lobes, club-shaped at apex. Berries ovoid, glabrous, smooth, yellow becoming white and fleshy at maturity, 1–1.5 cm long; seeds light brown, ca 2.7 mm long, curved, thicker at one end. *Croat 8911*.

Occasional, occurring from within a few feet above the ground to more than 30 m high. Flowers and fruits throughout the year. Flowering may be heaviest during the middle of the dry season. The fruits probably develop in about a month.

Central Panama to Peru. In Panamá, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet and premontane rain forests in Colón.

See Figs. 482 and 483.

PHYSALIS L.

Physalis angulata L., Sp. Pl. 183. 1753

Herb, generally 25–100 cm tall, glabrous or sparsely and inconspicuously pubescent with antrorse appressed trichomes on stems, leaves, pedicels, calyces, and especially major veins of lower leaf surfaces. Leaves alternate; petioles mostly 1–8 cm long; blades \pm ovate to ovate-lanceolate, acute to acuminate, acute to rounded at base, mostly 3–14 cm long, 1.5–10 cm wide, sparsely and irregularly toothed to entire. Flowers 5-parted, solitary in leaf axils; pedicels slender, 6–12 mm long (longer in fruit); flowering calyx 4–7 mm long, divided to near middle, the lobes sharply acute; corolla pale yellow to white, \pm campanulate, 6–12 mm long, not dark-dotted inside; anthers blue, (1)2–2.5 mm long, considerably shorter than filaments; ovary ovoid, ca 1 mm long; style 3 mm long. Fruiting calyces inflated, ovoid, 2–3.5 cm long and ca 2 cm wide, 10-angled or ribbed, greenish, glabrous to inconspicuously pubescent (especially on lobes); berries globose, ca 1 cm diam, yellow; seeds numerous, disk-shaped, ca 1 mm long. *Ebinger 594*.

Rare, occurring in clearings. Flowering and fruiting throughout the year.

The only collection known from the island is a mixed collection by Ebinger (594), which also contains a specimen of *P. pubescens*. The species is similar to *P. pubescens*, but distinguished by being glabrate or sparsely short-pubescent, by its smooth fruit, and by the lack of a dark eye in the corolla.

Manitoba to southern Argentina; much of the Old

World. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), and from tropical wet forest in Colón.

Physalis pubescens L., Sp. Pl. 183. 1753

Herb, less than 1 m tall, generally densely pubescent on stems, leaves, pedicels, and calyces with long multicellular trichomes. Leaves alternate; petioles mostly 1–7 cm long; blades ovate, acute to acuminate, acute to subcordate and often unequal at base, mostly 2.5–9 cm long, 1.5–6 cm wide, entire or lobed to bluntly toothed. Flowers 5-parted, solitary in leaf axils; pedicels slender, mostly 3–6 mm long, to ca 1 cm long in fruit; flowering calyx 4–10 mm long, divided to middle or beyond, the lobes sharply acute; corolla campanulate, pale yellow, to 1 cm long, with a brown to black or purple spot at base inside and pubescence below the spots; anthers blue, 2–3 mm long, about as long as filaments; ovary ovoid, ca 1.5 mm long; style 4 mm long; stigma capitate. Fruiting calyces inflated, ovoid, to 3 cm long and 2 cm wide, sharply 5-angled with 10 ribs, greenish; berries globose, 1–1.8 cm diam, yellow; seeds numerous, disk-shaped, reticulate, ca 1 mm wide. *Shattuck 45*.

Uncommon, occurring in clearings. Flowering and fruiting throughout the year. Individual plants flower over a long period and most have both flowers and fruits present.

The fruits may be dispersed by animals or wind—the inflated calyx enables the wind to carry them for short distances.

Northeastern United States to Chile and Argentina; warmer regions of the Old World. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from tropical dry and premontane moist forests in Coclé, from premontane wet forest in Panamá, and from tropical wet forest in Los Santos.

SOLANUM L.

Solanum antillarum O. E. Schulz in Urban, Symb.

Ant. 6:164–66. 1909–10

S. parcebarbatum Bitter

Hoja hedionda

Small, almost glabrous tree, 1.5–3 m tall. Leaves opposite in unequal pairs or alternate; petioles obscure or to 1.5 cm long; blades elliptic, gradually acuminate, attenuate and decurrent at base, 3.5–15 cm long, 2–7.5 cm wide, the axils of the lower surface with crisp-villous trichomes. Cymes short, axillary; flowers white, 5-parted,

KEY TO THE SPECIES OF PHYSALIS

- Most parts conspicuously pubescent, the trichomes usually crisp, multicellular; fruits sharply 5-angulate; corolla usually with a dark “eye” at base *P. pubescens* L.
 Most parts glabrate or shortly and inconspicuously pubescent, the trichomes not multicellular; fruits not sharply angulate; corolla lacking dark spots *P. angulata* L.

KEY TO THE SPECIES OF SOLANUM

- Plants usually armed with prickles (usually only on trunk in *S. hayesii*); anthers elongate, attenuate at apex:
- Calyx with 5 minute, marginal teeth *S. subinerme* Jacq.
 - Calyx deeply 5-lobed:
 - Leaves subsessile, the petioles less than 7 mm long *S. jamaicense* P. Mill.
 - Leaves petiolate, the petioles usually more than 1 cm long:
 - Calyx armed; plants scandent *S. lanciifolium* Jacq.
 - Calyx usually unarmed; plants erect:
 - Stems unarmed; leaves glabrate above *S. hayesii* Fern.
 - Stems prickly; leaves densely stalked-stellate above *S. ochraceo-ferrugineum* (Dun.) Fern.
- Plants unarmed; anthers elliptic or cylindrical, obtuse at apex (except in *S. hayesii*):
- Leaves glabrous or bearing simple trichomes:
 - Vein axils tufted below *S. antillarum* O. E. Schulz
 - Vein axils not tufted below *S. arboreum* Dun.
 - Leaves bearing stellate or branched trichomes:
 - Most leaf blades more than 8 cm wide, the upper surface nearly glabrous, the lower surface densely and softly stellate-pubescent; plants stout trees usually more than 6 m tall *S. hayesii* Fern.
 - Most leaf blades less than 8 cm wide, the pubescence various but seldom as above; plants shrubs or small trees usually less than 3 m tall (*S. rugosum* rarely to 5 m):
 - Flowers in lateral corymbs of many flowers; leaves obtuse or rounded at base, minutely and densely white-tomentose below *S. argenteum* Poir.
 - Flowers in large terminal cymes; leaves acute to attenuate at base:
 - Leaves mostly narrowly oblong-elliptic and less than 5 cm wide; trichomes on lower blade surface stalked; calyx lobed halfway to base *S. asperum* L. C. Rich.
 - Leaves mostly elliptic or ovate and more than 5 cm wide; trichomes on lower blade surface stalked or sessile; calyx variously lobed:
 - Trichomes on stems and inflorescences mostly long-stalked; calyx lobed much more than halfway to base *S. umbellatum* P. Mill.
 - Trichomes on stems and inflorescences mostly sessile; calyx lobed halfway to base *S. rugosum* Dun.

pedicellate; peduncles, pedicels, and calyces enlarged in fruit; calyx with 5 short thick lobes; corolla white, 8–9 mm broad at anthesis, deeply lobed, the lobes acute with a median rib; stamens nearly sessile, to 2 mm long; anthers yellow, rounded on dorsal side, the 2 terminal pores directed inward; style to twice as long as stamens. Berries globose, ca 1 cm diam, purple to brownish at maturity; seeds disk-shaped, ca 2.5 mm diam. *Aviles 72, D'Arcy 3988, Woodworth & Vestal 555.*

Occasional, occurring at the edge of the forest along the margin of the lake. Flowering and fruiting to some extent all year but mostly in the dry season and early rainy season.

Recognized by its nearly glabrous leaves with tufted axils below.

Mexico to Venezuela; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá, from premontane wet forest in Chiriquí and Coclé, from tropical wet forest in Coclé, and from premontane rain forest in Coclé.

Solanum arboreum H. & B. ex Dun., Sol. Syn.

20. 1816

S. kenoyeri Standl.

Shrub, 1–2.5(8) m tall, unarmed and ± glabrous. Leaves alternate or subopposite in unequal pairs; petioles less than 1 cm long; blades ± elliptic, long-acuminate, cuneate at base, the larger leaves 20–30 cm long, 8–12 cm

wide, the smaller leaves ca 4 cm long and 3 cm wide. Cymes very short, congested, axillary; pedicels to 1 cm long (lenticellate and to 13 mm long in fruit); flowers 5-parted; calyx usually less than half as long as corolla, lobed to middle or beyond, the lobes ovate, acute; corolla white, to 4(8) mm long, lobed to near base, the lobes ovate, acute, ribbed medially; stamens to 3.5 mm long, orange; anthers nearly sessile, to 3 mm long, the terminal pores directed inward; style elongating to ca 7 mm long, at first erect, becoming directed to one side. Berries ± globose, ca 1 cm diam; seeds many, more or less ellipsoid, ca 3 mm long, 2 mm wide, black. *Croat 11151.*

Rare, in the forest. Flowers and fruits throughout the year, but the flowering is heaviest in April and May and again in August. Most fruits mature in June and July and later in October. Flowering plants frequently bear mature fruits.

Mexico to Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Panamá, and Darién.

See Fig. 484.

Solanum argenteum Poir. in Lam., Encycl. Méth.

Bot., Suppl. 3:755. 1814

S. lepidotum Dun.; *S. salviifolium* Standl. non Lam.

Slender shrub, to 2.5(7) m tall; stems (at least when young), inflorescences, and lower leaf surfaces densely pubescent, the trichomes sessile, short-stalked, white,



Fig. 485. *Solanum hayesii*

Fig. 484. *Solanum arboreum*



Fig. 486. *Solanum jamaicense*

stellate. Leaves usually alternate, sometimes subtended by a much smaller subopposite leaf; petioles ca 0.5 (1) cm long; blades narrowly ovate, acuminate, rounded and often subequal at base, 7–14 (20) cm long, 3–7 cm wide, dark green above, white and sparsely stellate-pubescent below (more densely so on midrib). Corymbs upper-axillary, bearing many flowers; flowers 5-parted; calyx weakly lobed, enlarged in fruit, glabrous inside, the lobes obtuse; corolla white, 5–7 cm long, divided ca three-fourths of the way to base, the tube glabrous; style somewhat shorter than lobes, sparsely stellate-pubescent at base; stamens oblong; filaments short; anthers ca 2 mm long, their terminal pores directed inward. Berries globose, 6–8 mm diam, black, glabrate. *Foster 1711.*

Rare, collected north of Zetek Trail 400 in the old forest and once along the shore (*Wetmore & Abbe 200*). Seasonal behavior uncertain. Apparently flowers and fruits twice per year, once in the dry season (January to April) and once in the rainy season (July and August).

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Panamá, from tropical wet forest in Coclé and Panamá, from premon-tane rain forest in Panamá (summit of Cerro Jefe), and from lower montane wet forest in Chiriquí.

Solanum asperum L. C. Rich., *Actes Soc. Hist. Nat. Paris* 1:107. 1792

Shrub or small tree, to 3.5 (7) m tall; pubescence brown, stellate, dense except on upper leaf surfaces. Leaves alternate; petioles less than 1 cm long; blades narrowly oblong-elliptic, acuminate, attenuate at base and decurrent on petiole, 8–21 cm long, 1.5–6 cm wide. Inflorescences pseudoterminal, congested, the branches terminating in cymes of many flowers; flowers 5-parted, 10–15 mm wide, densely stellate-tomentose; calyx lobed to about middle, the lobes acute, enlarging and persisting in fruit; corolla white, lobed more than midway or to near base, ca 8 mm long, \pm glabrous inside; stamens less than 5 mm long; filaments stout, fused at base to corolla; anthers oblong, blunt, with 2 apical pores and longitudinal slits; ovary at first conspicuously pubescent; style stellate-tomentose, emerging from bud well above anthers, ca 5 mm long. Berries globose, ca 1 cm diam, sparsely puberulent; seeds numerous, ovoid, flattened, ca 1.5 mm long. *Croat 12839.*

Uncommon, occurring in disturbed areas. Flowering mostly throughout the rainy season, with the fruits developing rather soon and persisting into the dry season.

Easily confused with *S. umbellatum*, which tends to have slightly wider leaf blades (to 8 cm) and a more deeply lobed calyx (one-half to three-fourths of the way to base).

Belize to Brazil. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in the Canal Zone, Colón, and Panamá, from tropical wet forest in Colón, and from premontane rain forest in Coclé, Panamá, and Darién.

Solanum hayesii Fern., *Proc. Amer. Acad. Arts* 35:560. 1900

Shrub or tree, to 12 m tall; trunk usually armed with prickles; bark smooth; wood soft; stems densely matted with sessile stellate trichomes, usually unarmed except on juveniles. Leaves alternate; petioles 1.5–4.5 (6) cm long; blades ovate, abruptly acuminate, obtuse to rounded and inequilateral at base, 11–29 cm long, 6–17 cm wide, shiny and glabrous to sparsely stellate-pubescent above (especially on younger leaves), very densely pubescent below with stalked stellate trichomes; juvenile plants with the petioles armed, the leaves lobed, to 42 cm long and 30 cm wide. Inflorescences of usually once-branched, indeterminate racemes on stems below upper leaves, to 6 cm long (longer in fruit); flowers 5-parted, white, densely stellate-tomentose, to 2 cm wide; calyx 3–4 mm long, the lobes \pm truncate and mucronate at apex; corolla deeply lobed, ca 1 cm long; stamens yellow; filaments thick, fused to tube; anthers 3–4.5 mm long, with both terminal pores and longitudinal slits; pollen shed while style short; style thick, to 2 mm long, elongating to 7 mm. Berries globose, to 13 mm diam, yellow at maturity; seeds many, \pm ovoid, ca 3 mm long. *Croat 7706.*

Frequent in the forest; rare along the shore. Flowers throughout much of the year; known to flower from September to May, mostly from November to May. The fruits apparently require several months to mature, but mature fruits may be found on trees that are still flowering during the dry season.

Trees in the species bear flowers all of one type, either short-styled or long-styled. The short styles are 2 mm long, held well beneath the anthers. The long styles first equal the height of the anthers, then lengthen to 7 mm, well above the anthers. Pollen is ready to shed at anthesis, and the stigma is apparently receptive at the same time.

Nicaragua to Peru. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in Colón, Coclé, and Panamá, from tropical wet forest in Colón and Coclé, and from premontane rain forest in Panamá.

See Fig. 485.

Solanum jamaicense P. Mill., *Gard. Dict.* ed. 8. 1768
Frigia plata

Shrub, to 2 (3) m tall, densely stellate-pubescent on all exposed parts, the trichomes chiefly stalked; stems and lower midribs armed. Leaves alternate or subopposite in unequal pairs, sessile or nearly so; blades irregular, \pm rhomboid, acute at apex, cuneate to attenuate at base, the larger leaves 12–21 cm long, 7–15 cm wide, often 3–5-lobed, the smaller leaves 4–11 cm long, 2–6 cm wide, usually rhomboid. Racemes short, congested, axillary, subumbellate; pedicels to ca 2 cm long; flowers 5-parted; calyx divided to near base, the lobes narrowly triangular, to 5 mm long, densely pubescent with long stalked trichomes; corolla white, 6–9 (11) mm long, lobed to near

base, the lobes narrowly triangular, \pm glabrous inside; stamens ca 4.7 mm long; filaments less than 1 mm long; anthers elongate, attenuate at apex; style 6–7 mm long; ovary and style sparsely pubescent. Berries globose, ca 6 mm diam, orange to red at maturity; seeds oblong, orange, flattened, 1.5–2 mm long. *Croat 11987*.

Common in Rear #8 Lighthouse Clearing. Flowering from June to October, especially in July. The fruits mature from August to December, a good many of them in October.

Florida to Panama and parts of South America; the Antilles. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Panamá, from tropical wet forest in Colón and Panamá, and from premontane rain forest in Panamá.

See Fig. 486.

***Solanum lanciifolium* Jacq., Coll. 2:286. 1788**

S. scabrum Vahl non P. Mill.; *S. donnell-smithii* Coult.

Araño gato

Vine or liana, often growing into canopy; stems, petioles, and veins of leaves below armed with recurved spines and stellate-tipped bristles. Leaves alternate or subopposite in slightly unequal pairs; petioles to 4 cm long, stellate-pubescent; blades elliptic, acuminate, acute to rounded at base, 9–25 cm long, 4–8 cm wide, entire to pinnately lobed, the pubescence of both surfaces sparse, short-stalked, sessile, stellate; juveniles with the leaves to 13 cm broad. Racemes axillary, to 7 cm long; peduncles, pedicels, and calyces stellate-pubescent; pedicels to ca 12 mm long; flowers 5-parted; calyx 1–2 mm long, spiny, the lobes abruptly pointed, broadly spreading to recurved, bearing both stellate trichomes and larger simple spines, \pm warty in fruit; corolla lobes lanceolate, violet (owing to dense violet trichomes) and densely stellate-tomentose outside, white and \pm glabrous inside, ca 15 mm long and 3 mm wide, spreading, the tips curved up and in; anthers yellow, \pm sessile, to 13 mm long, tapered to apex, with terminal pores; style about half as long as anthers in bud, longer than anthers at anthesis. Berries globose, 1.3–3 cm diam at maturity, sparsely stellate-pubescent to glabrate, orange or red; seeds yellow, flattened, ca 2.5 mm long. *Croat 14914*.

Seedlings common in the forest; adult plants, usually climbing into the lower parts of the canopy, occasional. Flowers and fruits throughout the year, but the flowers are especially abundant in April.

Mexico to Brazil; West Indies. In Panama, widespread and ecologically variable; known from tropical moist forest in all areas, from premontane dry forest in Los Santos, from tropical dry forest in Los Santos, Coclé, and Panamá, from premontane moist forest in Los Santos, from premontane wet forest in Colón and Chiriquí, from tropical wet forest in Colón and Coclé, from premontane rain forest in Coclé, and from lower montane rain forest in Chiriquí.

***Solanum ochraceo-ferrugineum* (Dun.) Fern., Proc. Amer. Acad. Arts 35:560. 1900**

S. isthmicum Bitter

Shrub or small tree, to 3.5 m tall, densely stellate-pubescent; stems armed with sharp recurved prickles. Leaves alternate or subopposite with the pairs unequal; petioles 1–6 cm long; blades broadly ovate, acuminate, obtuse to truncate and often unequal at base, 9–20 cm long, 5–14 cm wide, subentire to shallowly lobed. Racemes branched, axillary; pedicels 1–1.8 cm long; flowers 5-parted, to 3 cm broad; calyx to 1 cm long, lobed to about middle, the lobes acuminate; corolla white, lobed to beyond middle, 3–5 cm diam and spreading at anthesis, stellate outside, glabrous inside; stamens ca 1 cm long; filaments short; anthers yellow with terminal pores; style somewhat longer than anthers. Berries globose to ovoid, 1–1.5 cm long, yellow at maturity; seeds yellow, compressed, ca 2.5 mm long. *Wetmore & Abbe 176, Woodworth & Vestal 625*.

Rare in clearings; probably more abundant when the vegetation was younger. Flowering to some extent throughout the year, but especially at the beginning of the rainy season in May. Plants apparently may flower more than once per year, because mature fruits have been found on flowering plants and the fruits no doubt require less than a year to mature.

Mexico to South America. In Panama, widespread and ecologically variable; known from tropical moist forest in all areas, from premontane dry forest in Coclé, from tropical dry forest in Coclé, from premontane moist forest in Los Santos, from premontane wet forest in Chiriquí, from tropical wet forest in Panamá, and from lower montane rain forest in Chiriquí.

***Solanum rugosum* Dun. in DC., Prodr. 13(1):108. 1852**

Shrub or small tree, to 5 m tall; stems bearing dense, sessile, stellate trichomes. Leaves alternate or subopposite in unequal pairs; petioles 5–30 mm long; blades broadly lanceolate to elliptic, acuminate, acute to attenuate at base, 8–25 cm long, 2.5–7 cm wide, stellate-pubescent above and below. Cymes dense, long-stalked; peduncles to 20 cm long, branched near apex, stellate-pubescent; pedicels 2–9 mm long; flowers 5-parted; calyx 3–5 mm long; corolla white, ca 1.5 cm broad; stamens ca 3 mm long; ovary broadly ovoid, ca 1.5 mm long; style 3 mm long. Berries ca 1 cm wide, glabrate, yellow at maturity; seeds ca 2 mm long. *Aviles 64, Shattuck 475*.

Several collections exist from previous years, but the plant has not been seen recently on the island. Flowering and fruiting all year, with the flowers especially abundant in the first half of the rainy season.

Belize to Peru and Brazil; the Antilles. In Panama, growing most abundantly in higher and wetter areas; known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Colón, Coclé, and Panamá, from tropical wet forest in Colón and Coclé, and from premontane rain forest in Panamá.



Fig. 487. *Solanum umbellatum*



Fig. 488. *Witheringia solanacea*



Fig. 489. *Witheringia solanacea*

Solanum subinerme Jacq., Enum. Syst. Pl. Ins. Carib. 15. 1760

Shrub, to 1.5(4) m tall, densely to moderately stellate-pubescent; stems armed with stout recurved spines. Leaves alternate or subopposite in unequal pairs; petioles to 2.5 cm long; blades broadly elliptic, short-acuminate, obtuse to rounded and unequal at base, 5.5–12.5(15) cm long, 3.5–7.5 cm wide. Racemes upper-axillary, unbranched; pedicels 6–15 mm long; flowers 5-parted; calyx 2.3–3 mm long, with 5 narrow teeth; corolla violet, 1.5–2 cm long, lobed nearly to base, glabrous to sparsely pubescent inside, spreading at anthesis; stamens ca 1–2 cm long; anthers to 1.5 cm long, yellow, attenuate at apex, with terminal pores; filaments very short; ovary and basal part of style stellate-pubescent; style 5–15 mm long, white with a green tip, exceeding anthers and curved to one side. Berries globose, 1–1.5 cm diam, red or orange; seeds many, brown, flattened, 3–3.5 mm long, 2.5–2.8 mm wide, ca 1.5 mm thick, weakly alveolate. *Croat 7479*.

Occasional, in Rear #8 Lighthouse Clearing. Common elsewhere in the Canal Zone. Flowering and fruiting nearly all year, but with fewer flowers during the late dry and early rainy seasons.

Heterostylous forms may exist within the species (short-styled: *Croat 7479*, *Tyson & Blum 2000*; long-styled: *Croat 7149*, *Zetek 5043*).

Mexico to South America; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in the Canal Zone and Panamá, from tropical wet forest in Panamá, and from premontane rain forest in Coclé and Panamá.

Solanum umbellatum P. Mill., Gard. Dict. ed. 8, no. 27. 1768

Shrub, to 7 m tall (usually less than 2.5 m), unarmed, densely stellate-pubescent, the trichomes of stems and inflorescences coarse and long-stalked. Leaves alternate or subopposite in unequal pairs; petioles to 2.5 cm long; blades narrowly elliptic, long-acuminate, cuneate and decurrent on petiole at base, 8–25 cm long, 2–8 cm wide. Inflorescences pseudoterminal, branched many times, the branches terminating in helicoid cymes of many flowers; pedicels 3–6 mm long; flowers 5-parted, 1–1.5 cm wide, densely stellate-tomentose; calyx 2–5 mm long, lobed one-half to three-quarters its length, stipitate-glandular; corolla 1–1.5 cm long, white, lobed to about middle, \pm glabrous inside; stamens ca 4 mm long; anthers cylindrical, obtuse at apex, with terminal pores directed inward; ovary and style \pm glabrous; style to ca 5 mm long. Berries round, ca 1 cm diam, glabrous, yellow at maturity; seeds many, brown, irregularly ellipsoid to obovoid, ca 1.5 mm long, 1.2 mm wide, flattened, ca 0.5 mm thick, the surface alveolate. *Croat 5106*.

Rare, found at the edge of the Laboratory Clearing. Flowering mostly in the first half of the rainy season, with some flowering at the beginning of the dry season as well. The fruits develop quickly and may be found with flowers.

Mexico to Colombia; Greater Antilles. In Panama,

known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí and Panamá, from tropical wet forest in Colón and Coclé, from premontane rain forest in Chiriquí and Panamá, and from lower montane rain forest in Chiriquí.

See Fig. 487.

WITHERINGIA L'Hér.

Witheringia solanacea L'Hér., Sert. Angl. 33, pl. 1. 1788

Capsicum macrophyllum (Dun.) Standl.

Suffrutescent herb or shrub, to 3(4) m tall; stems, petioles, and midribs often purplish when young, nearly glabrous or sparsely pubescent with short, stiff, uncinuate or appressed trichomes. Leaves alternate or subopposite in unequal pairs; petioles mostly 1–5 cm long, flat and marginally ridged above, the ridges extending along stem to next node; blades ovate to elliptic-oblong, acuminate, obtuse to subcordate and sometimes somewhat inequilateral at base, mostly 8–20 cm long, 3.5–11 cm wide, glabrous or sparsely scabrous and moderately shiny above, duller below, the trichomes sparse or restricted to veins. Fascicles dense, axillary; flowers minutely pubescent, greenish-yellow; calyx truncate, sparsely pubescent, to 2 mm long; corolla 4- or 5-lobed, 6–9 mm long, divided about halfway to base, the lobes spreading; stamens 4 or 5, broad, ca 5.3 mm long; filaments adnate to tube basally, densely villous in basal half; anthers acute at apex; ovary ovoid, glabrous, ca 1 mm long; style 4 mm long. Berries depressed-globose, ca 8 mm diam, orange-red; seeds many, ca 1.3 mm long, densely alveolate-ridged. *Croat 12199*.

Occasional, in the Laboratory Clearing; rarely encountered in the forest as a shrub. Flowering and fruiting all year, but especially during the rainy season. Often occurring with both flowers and mature fruits.

Distinguished by the dense axillary clusters of greenish-yellow flowers and bright red fruits.

Mexico to Brazil; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Colón, Coclé, and Panamá, from premontane rain forest in Chiriquí, Panamá, and Darién, and from lower montane wet forest in Chiriquí.

See Figs. 488 and 489.

125. SCROPHULARIACEAE

Annual herbs, sometimes suffruticose, sometimes aquatic and succulent. Leaves opposite, obscurely petiolate; blades simple, entire to serrate, often glandular-punctate; venation pinnate and usually palmate at base, or strictly palmate; stipules lacking. Flowers bisexual, solitary in the

KEY TO THE SPECIES OF SCROPHULARIACEAE

- Corolla rotate, actinomorphic, densely hirsute inside at base, the lobes equal, all spreading, much longer than the tube; plants often 30–60 cm or more tall *Scoparia dulcis* L.
- Corolla tubular, zygomorphic (bilabiate), not densely hirsute inside at base, the lobes unequal, partly erect, partly spreading, shorter than the tube; plants usually reclining, rarely more than 15 cm tall (except *Stemodia verticillata*, which is usually erect):
- Sepals free, markedly unequal:
- Stems densely villous (visible to naked eye); at least one sepal cordate at base *Bacopa salzmannii* (Benth.) Edw.
- Stems glabrous; sepals not cordate at base *Mecardonia procumbens* (P. Mill.) Small
- Sepals fused at base, mostly equal or subequal, not cordate at base:
- Leaf blades conspicuously dark-punctate beneath; corolla more than 12 mm long; plants often erect and more than 30 cm tall *Stemodia verticillata* (P. Mill.) Hassl.
- Leaf blades not punctate beneath; corolla less than 7 mm long; plants usually reclining or at least less than 15 cm tall:
- Flowers sessile; capsules more than 6 mm long, acute at apex and greatly exceeding sepals *Lindernia diffusa* (L.) Wettst.
- Flowers long-pedicellate; capsules rounded or truncate at apex, shorter than or about as long as sepals *Lindernia crustacea* (L.) F. W. Müll.

leaf axils, sometimes in a terminal raceme, zygomorphic or actinomorphic (*Scoparia*); calyx 4- or 5-lobed, the lobes imbricate, \pm equal or very unequal; corolla 4- or 5-lobed, rotate and 4-lobed near the base (*Scoparia*) or bilabiate, the upper lip entire or 2-lobed, the lower lip usually spreading, 3-lobed; stamens 4, free or didynamous and fused to tube much of their length; anthers 2-celled, introrse, dehiscent longitudinally; ovary superior, 2-locular, 2-carpellate; placentation axile; ovules many, anatropous; style 1, apically dilated; stigma usually bilamellate. Fruits 2-valved septical capsules; seeds many, with fleshy endosperm.

Scrophulariaceae are sometimes confused with the Solanaceae (124), Bignoniaceae (126), and Gesneriaceae (127). They are usually distinguished by being small herbs (on BCI) with small, usually zygomorphic, non-plicate corollas, bilocular ovaries, and small bivalved capsules.

Flowers are insect pollinated. BCI species are typically scentless (Percival, 1965) and well adapted for pollination by small bees, except perhaps *Scoparia dulcis*, which is not zygomorphic.

Seeds do not appear to be well adapted to wide dispersal and are probably spilled locally. Most species grow in open, weedy areas. Elsewhere most Scrophulariaceae are dispersed by browsing animals, which eat the seeds along with the vegetation and pass the seeds unharmed (Ridley, 1930).

About 220 genera and 3,000 species; cosmopolitan.

BACOPA Aubl.

Bacopa salzmannii (Benth.) Wettst. ex Edw., Bol.

Commiss. Geogr. Estado São Paulo 13:176, 181. 1897
B. violacea (Pennell) Standl.

Small aquatic or terrestrial herb; stems simple or branched, thick, succulent, densely brownish-villous. Leaves sessile; blades rounded-ovate, rounded or very obtuse at apex, cordate and clasping at base, usually 8–15

mm long, punctate, glabrous above, glabrous to villous on midrib below; veins several, palmate. Flowers solitary in axils; pedicels usually longer than leaves; calyx 5-parted, the lobes imbricate, the posterior lobe larger, cordate, very obtuse, 4–5 mm long, long-ciliate, the lateral lobes linear-lanceolate; corolla bilabiate, blue or white, 8 mm long, the upper lip 2-lobed, the lower lip 3-lobed; stamens 4, didynamous, included, held against upper lip. Capsules \pm globose, bisulcate; seeds small, numerous. *Shattuck s.n.* (July 15, 1934).

Collected once by Shattuck; possibly still occurring along the shore, but probably not persisting at such low elevations. Seasonal behavior uncertain. Specimens have been collected mostly in the dry season and early rainy season with flowers and fruits.

Southern Mexico to Brazil; from sea level to 1,500 m elevation. In Panama, known from tropical moist forest in the Canal Zone and Panamá.

LINDERNIA Allioni

Lindernia crustacea (L.) F. W. Müll., Syst. Census
Austr. 1:97. 1882

Torenia crustacea (L.) Cham. & Schlecht.

Weak, annual herb, creeping to ascending, 5–15 cm high, inconspicuously scaberulous; stems of older plants branched below many times, rooting at lower nodes, sometimes flushed with purple. Petioles to 4 mm long; blades variable in shape, \pm ovate, obtuse to acute at apex, subcordate to rounded at base and decurrent to base of petiole, 12 mm long and 12 mm wide or smaller, crenate to serrate, ciliate; veins pinnate. Flowers solitary in the axils, the terminal flowers often in an inflorescence of 3; pedicels to 12 mm; calyx \pm bilabiate, 5-parted, 3–4 mm long; corolla bilabiate, \pm 5 mm long, violet to white, the lower lip spreading, 3-lobed; stamens 4, in 2 pairs, held next to upper lip; filaments of one stamen pair longer; thecae divergent; staminodia knotty, arising from near the bottom of the free part of the filament; style to

25 mm long, persistent until later stages of fruit; stigmas 2. Capsules ovoid, to 4 mm long, septicidally dehiscent; seeds numerous, tan, ca 0.3 mm long, the surface granular. *Croat 6579*.

A common plant of open areas of the Laboratory Clearing; no doubt in other clearings as well. Flowers and fruits from May to October.

Throughout the tropics and subtropics. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién and from tropical wet forest in Colón.

***Lindernia diffusa* (L.) Wettst. in Engler & Prantl, Nat. Pfl. 4(3b):79. 1891**

Weak, puberulent, annual herb, creeping to ascending, to ca 12 cm high; stems weakly branching on older plants, rooting at nodes, often flushed with purple. Petioles to 3 mm long, much shorter in plants exposed to sun; blades ovate to orbicular, obtuse to acute at apex, obtuse to cuneate at base, to 2 cm long and 1.5 cm wide, crenate to dentate; veins pinnate. Flowers solitary in axils or clustered at ends of stems, sessile to subsessile; calyx 5-parted, regular or bilabiate, the lobes slender, deeply toothed to about middle, keeled at base, scaberulous on keel and usually on margins; corolla ca 6 mm long, falling soon after anthesis, bilabiate, the upper lip straight, entire, the lower lip with 3 recurved lobes, blue-violet or with the 3 lower lobes white and the upper lobe blue-violet, the tube often yellow below the lower lip; stamens 4, in 2 pairs, held next to upper lip; filaments fused to tube basally, the free part arched inward; anthers of a pair fused together forming a cross-shaped pattern, the filaments of the upper pair with a prominent staminodium arising from the base of the free parts; style 2.5 mm long, positioned beneath the upper lip, remaining on fruit until later stages; stigmas 2. Capsules narrowly ovoid, acute at apex, scaberulous, 6–8 mm long, 2-valved; seeds numerous, tan, \pm ovoid, ca 0.6 mm long, the surface granular. *Croat 11845*.

Locally abundant; known only from open areas of the Laboratory Clearing. Flowers and fruits throughout the rainy season.

Throughout the tropics; possibly native to the Old World tropics. In Panama, known from tropical moist forest in the Canal Zone.

MECARDONIA R. & P.

***Mecardonia procumbens* (P. Mill.) Small, Fl. S.E. U.S. 1065, 1338. 1903**

Bacopa procumbens (P. Mill.) Greenm.

Glabrous, ephemeral herb, creeping or ascending, sometimes rooting at the lower nodes; branches mostly from the base, to 15 cm long, slender, flexuous; stems sometimes strongly angled, sometimes glandular, the glands dark brown, multicellular, peltate; roots mostly short and fibrous. Petioles very short or indistinct; blades ovate, obtuse at apex, cuneate at base, mostly 10–15 mm long, 8–10 mm wide, glandular-punctate on lower surface, the margins crenate in distal two-thirds of blade; major

lateral veins usually 2 or 3 per side. Flowers solitary, seldom geminate, at first terminal, soon axillary, ca 8 mm long; pedicels slender, ca 3 mm long in flower, longer in fruit, the bracts basal, 2–4 mm long, linear, mostly entire; sepals free, the outer 3 ovate, 7 mm long and 2–3 mm wide, accrescent in fruit (becoming 9 mm long and 5 mm wide), acute at apex, obtuse or rounded at base, mostly eglandular, the inner 2 linear, slightly shorter than the outer ones; corolla tubular, exserted, yellow with purple lines, 5–8 mm long, bilabiate, the lobes rounded, sometimes irregularly crenulate, the upper lip reflexed, emarginate, the lower lip 3-lobed, scarcely reflexed, the throat bearded below the upper lip with clavate, unicellular trichomes; stamens 4, ca 3.5 mm long, held against one side of the tube beneath upper lip (a rudimentary staminodium sometimes present); filaments glabrous, inserted at unequal heights in the basal half of the tube, free ca 2 mm; thecae 2 per anther, oblong, held apart on expanded connectives, the connectives consisting of a discoid or ellipsoid expansion at the filament apex and one slender arm to each theca; ovary narrowly ovoid, longitudinally sulcate; style 1.5 mm long, slightly curved, apically flattened; stigma a linear crest on the style. Capsules narrowly ovoid, ca 4 mm long, the walls stramineous, dehiscent loculicidally and septicidally from the apex, enclosed in accrescent calyx, the placenta enlarged, linear, persistent on the withered capsule; seeds numerous, ovoid, 0.3 mm long, longitudinally ridged with a reddish-brown reticulum. *White 149*.

The species is apparently rare and has not been collected since 1938, though it could easily be overlooked.

Southern United States through Mexico and Central and South America to the West Indies and Argentina. In Panama, ecologically variable; known primarily from the drier parts of tropical moist forest in the Canal Zone, San Blas, Chiriquí, Los Santos, Herrera, Panamá, and Darién, but also from premontane dry forest and tropical dry forest in Los Santos, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí and Coclé.

SCOPARIA L.

***Scoparia dulcis* L., Sp. Pl. 116. 1753**

Escoba dulce, Escobilla amarga, Sweet broom

Herb, very small or to 1 m tall, branched, essentially glabrous; stems 6-ribbed. Petioles obscure; blades oblanceolate, acute at apex, narrowly tapered to base, to 3.5 cm long and 1.2 cm wide, densely punctate, crenate; major veins usually 2 or 3 on each side. Flowers solitary or clustered in leaf axils, 4-parted, 4–5 mm wide; pedicels slender, 4–6 mm long; sepals ovate, rounded at apex, 3-veined, ciliate, ca 1.3 mm long; corolla deeply lobed, to 2.7 mm long, densely pilose inside at base, the lobes rounded at apex, white or tinged with lavender; stamens 4, exserted, ca 2 mm long; anthers as broad as long, dehiscing upward; ovary ovoid, glabrous; style to 2.7 mm long, simple, longer than ovary. Capsules ovoid, 2-valved; seeds numerous, minute, irregularly ovoid, reticulate. *Croat 4160*.

Occasional in clearings. Probably flowering and fruiting throughout the year, especially from April to December.

Throughout the tropics. In Panama, known principally from tropical moist forest in all provinces; also known from premontane wet forest in Colón and Coclé and from tropical dry forest in Panamá.

STEMODIA L.

Stemodia verticillata (P. Mill.) Hassl., Contr. Fl. Chaco (Trab. Mus. Farmac. Fac. Ciencias Méd. Buenos Aires) 21:110. 1909
S. parviflora Ait.

Herb, suberect to reclining, to 75 cm long; stems slender, densely viscid-villous. Petioles slender, 2–10 mm long; blades broadly ovate, elliptic-ovate or rhombic-ovate, obtuse to acute at apex, rounded to truncate at base and attenuate-decurrent onto petiole, 0.5–3.5 cm long, 0.4–2.5 cm wide, crenate, sparsely villous on both surfaces, markedly dotted with dark glands beneath. Flowers usually solitary in axils; pedicels and calyces sparsely to densely villous; pedicels very slender, mostly 1–3.5 cm long; sepals 5-parted, subequal, 7–9 mm long, linear-subulate; corolla bilabiate, 12–17 mm long, sparsely short-villous outside, white with purplish streaks in throat, the lower lip spreading, 3-lobed; stamens 4, in 2 pairs, included, held against upper lip; thecae disjunct, stipitate; style dilated at apex. Capsules ovoid; valves 4; seeds ca 5 mm long, flattened. *Standley 41004*.

In clearings; collected by Standley but not seen recently, although it is to be expected. Probably flowers and fruits throughout the year, especially in the dry season.

Mexico to Argentina; West Indies. In Panama, known

from tropical dry forest in Panamá, from premontane moist forest in the Canal Zone, and from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, and Darién.

126. BIGNONIACEAE

Trees or more commonly tendriled lianas; stems sometimes angled; axillary buds with the outer scales often pseudostipular and sometimes foliaceous; interpetiolar glands often present on stem. Leaves opposite, bipinnate or palmately compound, petiolate; blades mostly pinnate and 2- or 3-foliolate, the terminal leaflet often replaced by a simple or forked tendril; leaflets entire or serrate, often glandular; venation mostly pinnate; stipules lacking. Racemes, cymes, thyrses, or rarely panicles terminal or axillary, usually bracteolate, of few or many flowers; flowers bisexual, zygomorphic; calyx cupular or campanulate, truncate to 5-lobed; corolla tubular, bilabiate, generally 5-lobed, the lobes imbricate; stamens 4, usually didynamous, attached to the corolla tube; staminodium usually present; anthers 2-celled, the 2 thecae usually widely divergent; ovary 1, superior, 1- or 2-locular; placentation of 4 vertical ridges, parietal in 1-locular ovaries, axile in 2-locular ovaries; ovules numerous, anatropous; hypogynous disk present; style slender; stigma 2-lobed. Fruits 2-valved, septicidal or loculicidal capsules; seeds numerous, winged or rarely the wing almost lacking, without endosperm.

Members of the family are characterized by flowers with a tubular, showy, bilabiate corolla, four stamens, and anthers with two widely divergent thecae, and by capsular fruits with usually prominently winged seeds.

Pollination is mostly by insects, especially bees, though *Martinella obovata* is pollinated by hummingbirds.

KEY TO THE TAXA OF BIGNONIACEAE

Plants trees, lacking tendrils:

Leaves palmately compound, the leaflets 3–7 *Tabebuia*

Leaves pinnately or bipinnately compound:

Leaves pinnately compound; flowers orange; tree cultivated in the Laboratory Clearing

..... *Spathodea campanulata* Beauv.

Leaves bipinnately compound, the leaflets 3–25 per pinna; flowers lavender-blue; trees common in the forest *Jacaranda copaia* (Aubl.) D. Don

Plants tendriled lianas:

• Flowers predominantly white or yellow (sometimes marked with purple in *Amphilophium*; for fruiting specimens, see the following key to fruits):

◆ Young stems square with sharp angles or with 6–8 prominent angles or ribs; tendrils trifid:

Leaves 2- or 3-ternate; young stems square; flowers whitish-yellow; tendrils arising at nodes, not replacing terminal leaflets; capsules linear

..... *Pleiotoma variabilis* (Jacq.) Miers

Leaves with 2 or 3 leaflets; young stems with 6–8 angles or ribs; flowers white; tendrils replacing terminal leaflets; capsules oblong to elliptical:

Corolla 3–4 cm long, sometimes marked with purple; blades whitish below with stellate trichomes in axils; fruits with smooth surface, usually less than 16 cm long; pseudostipules small, caducous

..... *Amphilophium paniculatum* (L.) H.B.K.

Corolla 4–6 cm long, white turning yellowish in age; blades not whitish below, with plate-shaped glands in axils; fruits with spiny surface, more than 16 cm long; pseudostipules 4 per node, linear-oblong, to 9 mm long

..... *Pithecoctenium crucigerum* (L.) A. Gentry

- ◆ Stems terete or inconspicuously angled; tendrils trifid or not:
 - Interpetiolar glandular fields conspicuous; tendrils trifid:
 - Flowers white throughout; pseudostipules vertically 3-seriate, to 7 mm long; fruits oblong, acute to acuminate at both ends, mostly 12–25 cm long, 3–3.5 cm wide; seeds thick, wingless *Pachyptera kerere* (Aubl.) Sandw.
 - Flowers yellow-orange, pale yellow, or white with a yellow throat; pseudostipules not serially arranged in 2 sets of 3 pairs; fruits blunt on one end or less than 2 cm wide:
 - Flowers white or pale yellow; leaflets with cavellike axillary domatia below; pseudostipules 3-lobed; fruits 3–4 cm wide, blunt or subcordate on lower end *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw.
 - Flowers bright yellow-orange; leaflets lacking domatia in lower axils; pseudostipules simple, inconspicuous; fruits less than 2 cm wide, tapered to lower end *Macfadyena unguis-cati* (L.) A. Gentry
 - Interpetiolar glands lacking; tendrils simple or trifid:
 - Flowers yellow; tendrils simple:
 - Calyx fleshy, completely enveloping corolla in bud (looking much like a fruit), more than 2.5 cm long; capsules compressed-ellipsoid, 6–11.5 cm wide, the valves very woody, more than 5 mm thick *Callichlamys latifolia* (L. C. Rich.) K. Schum.
 - Calyx not fleshy, not completely enveloping corolla in bud, less than 1 cm long; capsules oblong or ellipsoid, less than 6 cm wide, the valves usually less than 5 mm thick:
 - Flowers not subtended by bracts; calyx truncate, much broader than corolla tube; pseudostipules foliaceous, obovate; capsules ellipsoid, 3–5 cm wide *Anemopaegma chrysoleucum* (H.B.K.) Sandw.
 - Flowers subtended by conspicuous bracts; calyx with at least minute teeth and usually bilabiate split, not much broader than corolla tube; pseudostipules not foliaceous; capsules oblong, less than 3 cm wide (those of *A. arthropetiolatum* not known) *Adenocalymma*
 - Flowers white or cream; tendrils simple or trifid:
 - Flowers less than 2 cm long; leaflets lacking conspicuous glands; fruits linear, with prominent, raised lateral margins *Tynnanthus croatianus* A. Gentry
 - Flowers more than 4 cm long; leaflets with glands at least at axils below; fruits not as above:
 - Flowers cream, sparingly yellowish-glandular-lepidote on outside; leaflets with conspicuous glands throughout; fruits linear, gradually attenuate to apex *Stizophyllum riparium* (H.B.K.) Sandw.
 - Flowers white or lavender, with prominent nectar guides from lobes to deep within corolla; leaflets with dense clusters of glands in axils; fruits linear, rounded at end, shiny on surface *Cydista aequinoctalis* (L.) Miers
 - Flowers not white or yellow (shades of purple, blue, pink):
 - Corolla usually less than 4.5 cm long; tendrils simple:
 - Calyx broadly flared, not tubular; corolla pubescent on lobes, the tube glabrous; pseudostipules foliaceous, falcate, to 1 cm long, caducous; leaflet midrib and veins densely villous below, the axils tufted *Arrabidaea patellifera* (Schlecht.) Sandw.
 - Calyx tubular or cupular, not flared at apex; corolla densely pubescent throughout; pseudostipules usually inconspicuous; leaflet midrib glabrous or short-pubescent, the axils glabrous or minutely tufted:
 - Flowers precocious; corolla densely stellate-pubescent; mature leaves stellate at least on midrib; fruits oblong, 9–20 cm long, ca 5 cm wide, smooth; seeds ± round with transparent wings *Xylophragma seemannianum* (O. Kuntze) Sandw.
 - Flowers and fruits not as above:
 - Blades densely puberulent below, whitish, the trichomes contiguous; fruits often rough with coarse, irregular, raised lenticels *Arrabidaea candicans* (L. C. Rich.) DC.
 - Blades not densely puberulent below; fruits not as above:
 - Pseudostipules lanceolate, sharp-pointed, 2–7 mm long; blades drying gray or blackish *Paragonia pyramidata* (L. C. Rich.) Bur.
 - Pseudostipules inconspicuous or lacking:
 - Corolla less than 1.8 cm long; veins of leaflet puberulent below, the surface conspicuously lepidote; blades drying green-brown *Arrabidaea florida* DC.
 - Corolla more than 2 cm long; veins of leaflet glabrate below, the surface minutely and sparsely lepidote; blades and fruits drying reddish *Arrabidaea chica* (H. & B.) Verl.
 - Corolla usually more than 4.5 cm long; tendrils simple or branched:
 - ▲ Calyx more than 12 mm long:
 - Flowers dark purple; leaflets cordate to truncate at base, puberulent below on midrib and lateral veins, lacking tufted axils; tendrils trifid, persistent; fruits more than 60 cm long *Martinella obovata* (H.B.K.) Bur. & K. Schum.

- Flowers not dark purple; leaflets obtuse or rounded at base, ± glabrous below, with or without tufted axils; tendrils simple or caducous; fruits less than 50 cm long:
- Calyx spathaceous; corolla frequently more than 7 cm long; leaves glabrous; petioles glabrous; fruits smooth *Phryganocydia corymbosa* (Vent.) K. Schum.
- Calyx ± equally lobed at apex; corolla less than 7 cm long; leaves glabrate with axillary tufts below; petioles short-pubescent; fruits very rough, short-tuberculate *Arrabidaea verrucosa* (Standl.) A. Gentry

▲ Calyx less than 10 mm long:

- Flowers precocious (appearing when leaves are very young):
- Flowers glandular-lepidote; leaves simple or less often 2- or 3-foliolate, lacking trichomes; capsules long, linear; seeds with opaque wings *Cydista heterophylla* Seib.
- Flowers densely stellate-pubescent; leaves 3-foliolate, or 2-foliolate with a terminal tendril, with stellate trichomes at least on veins below; capsules oblong, to 18(25) cm long; seeds thick, opaque, the wings transparent *Xylophragma seemannianum* (O. Kuntze) Sandw.

Flowers not precocious:

- Flowers lepidote throughout, the nectar guides conspicuous, extending from lobes to near base on 3-lobed side; vein axils of leaflets with fields of contiguous glands below; fruits linear, dark, shiny, smooth *Cydista aequinoctalis* (L.) Miers
- Flowers not glandular-lepidote throughout, with or without prominent nectar guides; vein axils of leaflets with none or few glands below; fruits linear and rough or ellipsoid to globose:
- Corolla densely pubescent outside with moniliform trichomes, ± contiguous; tube constricted within at base, the constriction pubescent; apex of petiole with conspicuous plate-shaped glands; fruits linear, bumpy *Paragonia pyramidata* (L. C. Rich.) Bur.
- Corolla sparsely puberulent and lepidote, the tube not constricted, with nectar guides to near base; apex of petiole lacking conspicuous glands; fruits ellipsoid to globose *Clytostoma binatum* (Thunb.) Sandw.

KEY TO THE BIGNONIACEAE
(ON THE BASIS OF FRUIT CHARACTERS)

■ Capsules not linear:

- Valves spiny-tuberculate:
- Capsules ca 5 cm long, nearly as broad *Clytostoma binatum* (Thunb.) Sandw.
- Capsules to 32 cm long and 8 cm broad *Pithecoctenium crucigerum* (L.) A. Gentry

 Valves not spiny-tuberculate:

- Capsules to about twice as long as broad; plants trees or lianas:
- Plants trees; capsules compressed-oblong, rounded to truncate on both ends, sessile, drying dark brown to black; seeds flat, small-bodied with a thin, orbicular wing; wing hyaline-membranaceous with radial, brownish striations, clearly demarcated from seed body *Jacaranda copaia* (Aubl.) D. Don
- Plants lianas; capsules elliptic, compressed, acute at apex, stipitate ca 1 cm at base, drying yellow-brown; seeds woody, somewhat flattened; wing essentially absent *Anemopaegma chrysoleucum* (H.B.K.) Sandw.

 Capsules more than 2.5 times as long as broad; plants lianas:

- Capsules oblong:
- Capsules 2–2.6 cm thick; seeds (including wing) more than 3 times wider than long, the wing not clearly demarcated from seed body *Ceratophytum tetragonolobum* (Jacq.) Sprague & Sandw.
- Capsules less than 1.5 cm thick; seeds (including wing) ± orbicular or less than 3 times wider than long, the wing absent or clearly demarcated from seed body:
- Valves with a prominent medial ridge; seeds lacking a wing *Pachyptera kerere* (Aubl.) Sandw.
- Valves lacking a medial ridge; seeds with transparent wing *Xylophragma seemannianum* (O. Kuntze) Sandw.

 Capsules oblong-elliptic:

- Capsules more than 20 cm long and more than 6 cm wide *Callichlamys latifolia* (L. C. Rich.) K. Schum.
- Capsules less than 16 cm long and less than 5 cm wide:
- Capsules blunt on both ends, the surface usually roughened and densely lepidote, the valves with a medial groove or ridge *Amphilophium paniculatum* (L.) H.B.K.
- Capsules pointed at apex, stipitate at base, the surface ± smooth, not densely lepidote, the valves lacking a medial groove or ridge *Anemopaegma chrysoleucum* (H.B.K.) Sandw.

- Capsules linear, less than 3 cm wide and many times longer than broad:
 - Capsules \pm terete in cross section; plants trees or lianas:
 - Capsules bumpy with coarse lenticels or tuberculate:
 - Plants trees; capsules with irregular tubercles; seeds with transparent wings *Tabebuia guayacan* (Seem.) Hemsl.
 - Plants lianas:
 - Capsules less than 1.5 cm wide, the ends usually acute, the surface densely and minutely muricate, the bumps discrete and visible to the naked eye; seeds less than 1.5 cm long and less than 4.5 cm wide *Paragonia pyramidata* (L. C. Rich.) Bur.
 - Capsules more than 2.5 cm wide at maturity, the ends both rounded, the surface irregular and densely covered with lenticels but not densely and minutely muricate; seeds more than 1.7 cm long and more than 5.1 cm wide *Adenocalymma apurense* (H.B.K.) Sandw.
 - Capsules lacking bumps or tubercles:
 - Capsules densely pubescent, the trichomes golden-brown, deciduous in patches *Tabebuia ochracea* (Cham.) Standl. var. *neochrysantha* A. Gentry
 - Capsules lacking trichomes *Tabebuia rosea* (Bertol.) DC.
 - Capsules flattened in cross section; plants lianas:
 - Valves with midvein distinctly raised; seeds with hyaline wings sharply demarcated from body *Arrabidaea*
 - Valves with midvein not raised (except *Macfadyena* slightly raised) or indistinct; seeds with opaque wings not sharply demarcated from body (except *Tynnanthus*):
 - Valves conspicuously warty or with sharp tubercles:
 - Valves with the surface like coarse sandpaper, the bumps as broad as long; valves less than 1.4 cm wide; seeds less than 1.5 cm long . . . *Paragonia pyramidata* (L. C. Rich.) Bur.
 - Valves with the surface coarsely tuberculate, the bumps conical and several times longer than broad; valves more than 1.3 cm wide (to 2.5 cm); seeds more than 1.5 cm long *Arrabidaea verrucosa* (Standl.) A. Gentry
 - Valves not conspicuously bumpy or tuberculate, mostly smooth or only irregularly bumpy:
 - Valves each with 2 raised longitudinal ridges (ca halfway between middle and margin) or the valves with lateral margins raised and the corners sharply angled:
 - Fruits with raised lateral margins and square corners, without submarginal ridges, less than 1.2 cm wide; seeds 1.7–2.9 cm wide, with the wings sharply demarcated from body *Tynnanthus croatianus* A. Gentry
 - Fruits lacking raised lateral margins and square corners, with 2 submarginal longitudinal ridges, usually more than 1.5 cm wide; seeds mostly 2.6–5.3 cm wide, with the wings not sharply demarcated from body *Cydista heterophylla* Seib.
 - Valves lacking longitudinal or marginal ridges and square corners:
 - Valves puberulent to very short-villous, at least along margins, thin:
 - Fruits less than 8 mm wide, not much flattened; valves densely villous throughout, the trichomes short, crisped, not straight . . . *Stizophyllum riparium* (H.B.K.) Sandw.
 - Fruits more than 1 cm wide, flattened; valves puberulent near margins, the trichomes straight, erect *Martinella obovata* (H.B.K.) Bur. & K. Schum.
 - Valves lacking trichomes:
 - Fruits obtuse to rounded at apex:
 - Seeds with the wings gradually more transparent toward margin; valves tending to be black, merely bending up on the sides, not curling lengthwise *Cydista aequinoctalis* (L.) Miers
 - Seeds with the wings evenly opaque with a distinct hyaline margin; valves more gray, curling lengthwise after falling *Phryganocydia corymbosa* (Vent.) K. Schum.
 - Fruits acute to acuminate at apex:
 - Fruits less than 30 cm long and more than 2 cm wide; valves thick, irregularly warty; seeds with the wings opaque nearly throughout *Pleonotoma variabilis* (Jacq.) Miers
 - Fruits more than 50 cm long and less than 2 cm wide; valves thin, \pm smooth; seeds with the wings hyaline at tip *Macfadyena unguis-cati* (L.) A. Gentry

Spathodea campanulata is pollinated by perching birds in the Old World, where it is native (probably by Icteridae in the New World). Species pollinated mostly by euglossine bees include *Anemopaegma chrysoleucum*, *Arrabidaea verrucosa*, *Callichlamys latifolia*, *Cydista aequinoctalis*, *Pachyptera kerere*, *Phryganocydia corym-*

bosa, and *Stizophyllum riparium*. Species pollinated mostly by euglossine or anthophorid bees include *Arrabidaea candicans*, *A. patellifera*, and *Xylophragma seemanianum*. Species pollinated mostly by anthophorid bees include *Tabebuia guayacan*, *T. rosea*, and possibly *Macfadyena unguis-cati*. *Tynnanthus croatianus* and *Arrabi-*

daca florida, both with small flowers, are pollinated by skippers (Hesperiidae) and small bees. *Ceratophytum tetragonolobum*, *Paragonia pyramidata*, and *Pithecotenium crucigerum* are probably pollinated in part by *Xylocopa* bees and perhaps in part by anthophorid bees. The flowers of *Amphilophium paniculatum* remain closed until forced open by large bees.

The seeds of most species are wind dispersed. *Anemopaegma chrysoleucum*, *Clytostoma binatum*, and *Pachyptera kerere* have water-dispersed seeds. *Macfadyena unguis-cati* and *Adenocalymma arthropetiolatum* are probably at least partly water dispersed.

Gentry (1974) described five types of phenological classes for the Bignoniaceae. Type 1, associated with bat pollination, is not found on BCI. Type 2, "steady state" pattern, in which a few flowers are produced per day over a long time period, is represented by *Stizophyllum riparium*. Type 3, "cornucopia" pattern, with large numbers of flowers over several weeks, is the most common type among species on BCI. Type 4, "big bang" pattern, represents those species that flower profusely for a short time, such as *Tabebuia guayacan*. Type 5, "multiple bang" pattern, is similar to Type 4, but represents species that flower profusely several times per year; it is best represented on BCI by *Phryganocydia corymbosa*. [Data on pollination, dispersal, and phenology are derived partially from Gentry (1972; 1974).]

About 120 genera and 650–800 species; mostly in tropical America, but also in the tropics and subtropics of the Old World.

ADENOCALYMMA Mart. ex Meisn.

***Adenocalymma apurense* (H.B.K.) Sandw., Lilloa**
3:461. 1938

A. inundatum Mart. ex DC.

Liana; trunk to 10 cm diam, often 4-sulcate; bark smooth, gray; stems with 4 phloem arms in cross section; twigs subterete, glabrous to slightly lepidote, usually drying black with whitish lenticels, the nodes lacking glandular fields; tendrils simple; pseudostipules small, pointed, ovate. Leaves 2- or 3-foliolate; petioles 3.2–6.5 cm long; petiolules 0.9–4 cm long; leaflets ovate to elliptic-ovate, acuminate, rounded to subcordate at base, 4.5–17 cm long, 2.5–8 cm wide, weakly lepidote on both surfaces, drying dark gray or olive, the margins wavy, with a narrow, conspicuous, cartilaginous border. Racemes axillary or terminal; flowers each subtended by a deciduous bract ca 1 cm long; rachises, pedicels, and calyces puberulent;

calyx cupular, 5–8 mm long, bilabiate split for 1–2 mm, usually with plate-shaped glands; corolla bright yellow, tubular-funnelform, 3–7 cm long, puberulent outside, glandular-lepidote inside on lobes; stamens included, the longest pair ca 1.8 cm long; anthers slightly divaricate, 2–3 mm long; staminodium 4–5 mm long; pistil 2.4–2.5 cm long; ovary cylindrical, 3–3.5 cm long, lepidote. Capsules oblong, 10–27 cm long, 2.5–3 cm wide, 1.4–2.2 cm thick, rounded at both ends, not compressed; valves woody and somewhat thickened, gray, with numerous, raised, tannish lenticels, the midrib obscure; seeds 1.7–2.1 cm long, 5.1–7.6 cm wide, the body thick, the wings thin, brown. *Foster 1116 (DUKE)*.

Apparently rare; collected once on Peña Blanca Point along the shore. Flowers elsewhere mostly during the late dry and early rainy seasons (April to August); collected in flower also in February.

The fruits are possibly water dispersed, since plants are usually found along streams or lakes (Gentry, 1972).

Mexico to the Guianas. Gentry (1973b) reported the species to be characteristic of tropical dry forest and edaphically dry regions of tropical moist forest, but none of the specimens he cited are from tropical dry forest according to the Holdridge Life-Zone map of Panama. In Panama, apparently preferring drier regions along streams; known from tropical moist forest in the Canal Zone, Chiriquí, Los Santos, Panamá, and Darién and from premontane moist forest in Darién (Punta Patiño).

***Adenocalymma arthropetiolatum* A. Gentry, Ann.**
Missouri Bot. Gard. 60:789. 1973

Liana; trunk to 3 cm diam; bark smooth, greenish; stems with 4 phloem arms in cross section; twigs subterete to tetragonal, ± glabrous, drying tan to greenish, the nodes lacking glandular fields; tendrils simple; pseudostipules small, 4-scaled, usually narrow. Leaves 2- or 3-foliolate; petioles 1–6.5 cm long, puberulent; petiolules 0.5–4 cm long; leaflets narrowly ovate, acute to acuminate, rounded to shortly subcordate at base, 5–17 cm long, 2–7.5 cm wide, glabrous to puberulent along main veins; reticulate veins prominulous. Racemes terminal or axillary; flowers with a faint musky odor (*vide* Gentry), each subtended by a deciduous bract; rachises, pedicels, and calyces puberulent; calyx cupular, 5–15 mm long, 5-toothed but ± bilabiate, usually with submarginal, sunken glands; corolla bright yellow, 4–8 cm long, puberulent outside and on lobes inside, the tube slender, the apical part campanulate, the 2 upper lobes erect, extending horizontally in front of the tube, the other 3 variously reflexed; sta-

KEY TO THE SPECIES OF ADENOCALYMMA

- Leaflets ovate, drying dark gray or olive, with a whitish, cartilaginous margin, usually lepidote; twigs usually drying dark with pale lenticels; corolla tubular-funnelform; anthers with the thecae only slightly divergent, the connective apiculate *A. apurense* (H.B.K.) Sandw.
Leaflets narrowly ovate, drying green, lacking a whitish margin, usually not lepidote; twigs drying tan; corolla tubular-campanulate; anthers with the thecae very divergent, the connective not extended *A. arthropetiolatum* A. Gentry

mens slightly exerted, the pairs nearly equal, the longer 3.5–3.9 cm long; staminodium 12–21 mm long; pistil 5–6 cm long; ovary narrowly cylindrical, 4–5 mm long, 1.5–2 mm wide, puberulent. Capsules unknown (those of the genus oblong-linear, thick, flattened, woody). *Standley 40912 (US)*.

Apparently rare; collected once. Flowers during the late rainy season in October and November.

Known only from Panama, along rivers in tropical moist forest and premontane wet forest in the Canal Zone and Panamá.

AMPHILOPHIUM Kunth

Amphilophium paniculatum (L.) H.B.K., Nov. Gen. & Sp. 3:116. 1819

Liana; branchlets, petioles, and rachises angled, hexagonal, lepidote, pubescent with stellate and simple trichomes; stems with conspicuous interpetiolar ridges; tendrils trifid; pseudostipules sickle-shaped, to 5 mm long, densely lepidote and stellate-pubescent, caducous. Leaves 2- or 3-foliolate; petioles 2.3–7 cm long; petiolules 0.6–4.3 cm long; leaflets broadly ovate to rounded, acuminate, cordate at base, 2.5–16 cm long, 2–10.7 cm wide, sparsely glandular-lepidote on both surfaces, the upper surface glabrous except on veins, the lower surface tomentulose with dense, short, stellate trichomes and with longer, usually branched trichomes dense on veins and very sparse elsewhere (younger leaves puberulent above). Panicles ± racemose, terminal; flowers 5-parted, aromatic, white, usually variously tinged with maroon, turning deep purple, 3–4 cm long; calyx enveloping one-third of corolla, the margin broad, double, ± lobed and undulate; corolla 3–4 cm long, fleshy, bilabiate, with 3 narrow lobes opposing a single broad lobe; stamens included, the longer pair to 1.8 cm long, the shorter pair to 1.5 cm long, the thecae divaricate, ca 2 mm long; staminodium 3–5 mm long, inserted 4–5 mm from base of corolla; ovary densely tomentulose. Capsules oblong-ellipsoid, blunt to subcordate on either end, 9–16 cm long, to 4.5 cm wide; valves broadly ridged along middle, with an obscure medial groove or ridge, densely glandular-puberulent; seeds chiefly to 1.5(2) cm long and (2.7–3)6.5 cm wide, the wings narrower toward the deeply lacerate lateral margins. *Croat 12499, Foster 1918*.

Uncommon in the forest. The flowers are few and long-lived from May to January. The fruits mature in the middle of the dry season.

Recognized by the unusual double calyx and the hexagonal stems with stellate trichomes.

Mexico to Argentina; West Indies. In Panama, widespread and ecologically variable; known from tropical dry forest in the Canal Zone, Los Santos, Herrera, and Panamá, from tropical moist forest all along the Atlantic slope and on the Pacific slope in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, Veraguas, Coclé, and Panamá, from premontane rain forest in Darién, and from lower montane wet forest in Chiriquí.

ANEMOPAEGMA Mart. ex Meisn.

Anemopaegma chrysoleucum (H.B.K.) Sandw., Lilloa 3:459. 1938

A. punctulatum Pitt. & Standl.

Liana; stems glabrous or sparsely puberulent (especially at nodes), ± terete with interpetiolar ridges; tendrils simple, emerging from between leaflets; pseudostipules foliaceous, obovate, 3–13 mm long, to 10 mm wide, 4 per node. Leaves bifoliolate; petioles 0.7–3.4 cm long; petiolules 0.3–2 cm long; petioles and petiolules puberulent especially on upper surface; leaflets elliptic, acute to acuminate, acute at base and ending abruptly, 5–15 cm long, 1.7–7 cm wide, minutely lepidote. Flowers axillary, emerging from between pairs of pseudostipules; pedicels minutely bracteate, to 1.5 cm long; calyx truncate, ca 1 cm long, with sunken plate-shaped glands near apex, fitting loosely around slender base of corolla tube; corolla 5–10 cm long, 3–4 cm wide at apex, pale yellow outside except for white lobes, papillose-puberulent on lobes inside, 2 lobes opposing the other 3, the lower 2 usually recurved, the tube expanded below lobes, glabrous except in basal third below point where filaments are fused to tube; nectar guides bright yellow, alternating with lobes; stamens included, the longer ones 2.3–3.1 cm long, the shorter ones 1.6–2.1 cm long, the thecae divaricate, 3.5–4.5 mm long; staminodium 3–6 mm long; pistil 5.1–5.6 cm long; ovary rounded-cylindric, to 2.5 mm long. Capsules ellipsoid, smooth, 5–15 cm long, 3–5 cm wide, stipitate at base; seeds oblong, to 1.8 cm long and 2.4 cm wide, with broad opaque wings. *Croat 12683*.

Uncommon; collected chiefly on the shoreline of Gigante Bay. Flowers irregularly through the year, especially during the rainy season, with one or two long-lived flowers open at a time. Most seeds are probably released in the dry season.

The species is easily recognized by its yellow flower and foliaceous pseudostipules. When open, the flowers have a very sweet, pleasant aroma. Corolla tubes are often pierced with a hole 3–4 mm diam just above the edge of the calyx by nectar-stealing insects or birds.

The seeds are water dispersed (Gentry, 1973b).

Belize to Venezuela. In Panama, known from swampy areas of tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, Colón, Panamá, and Darién and from tropical wet forest in Colón and Darién.

ARRABIDAEA DC.

Arrabidaea candicans (L. C. Rich.) DC., Prodr. 9:185. 1845

A. pachycalyx Sprague

Liana; outer bark brown, flaky; branches terete with prominent lenticels even on youngest branchlets, the nodes with interpetiolar glandular fields; tendrils simple; pseudostipules lacking. Leaves 2- or 3-foliolate, bicolorous, often drying reddish above; petioles 1.6–6.1 cm long; petiolules 0.8–3.3 cm long; leaflets oblong-ovate to broadly ovate, sharply to bluntly acuminate, cuneate to

KEY TO THE SPECIES OF ARRABIDAEA

- Capsule valves lacking noticeably raised medial rib, the margins sharply angled and raised; calyx drying dark with paler or thinner margin; corolla usually more than 3.6 cm long *A. corallina* (Jacq.) Sandw.
- Capsule valves with somewhat raised medial rib, the margins rounded; calyx not drying paler or thinner along the margin; corolla usually less than 3.5 cm long (except *A. patellifera*):
- Calyx bilabiate; fruits coarsely and regularly verrucose-tuberculate, the tubercles often to 2 mm or more *A. verrucosa* (Standl.) A. Gentry
- Calyx truncate, usually minutely 5-denticulate; fruits essentially smooth or with irregular coarse but short lenticels, not coarsely and regularly tuberculate:
- Corolla pubescent on lobes, the tube glabrous; calyx reflexed away from base of corolla; pseudostipules foliaceous, falcate, to 1 cm long, caducous; leaves simple or 2-foliolate, the leaflets with the midrib and veins densely villous below, the axils tufted *A. patellifera* (Schlecht.) Sandw.
- Corolla densely pubescent throughout; calyx cupular, enclosing base of corolla; pseudostipules usually inconspicuous; leaves with at least some always 3-foliolate, never simple; leaflets with the midrib glabrous or short-pubescent, the axils glabrous or minutely tufted:
- Blades densely whitish-pubescent below, the trichomes contiguous; fruits rough with raised bumps *A. candidans* (L. C. Rich.) DC.
- Blades not whitish-pubescent below; fruits not as above:
- Corolla less than 1.8 cm long; leaflets with the veins puberulent below, the surface conspicuously lepidote; blades drying green-brown *A. florida* DC.
- Corolla more than 2 cm long; leaflets with the veins glabrate below, the surface minutely, sparsely lepidote; blades and fruits drying reddish *A. chica* (H. & B.) Verl.

cordate at base, 4.5–17 cm long, 2.5–11 cm wide, minutely pubescent or glabrous above, densely white-tomentulose below, usually with a few sunken glands in basal axils.

Inflorescences terminal, showy, pyramidal thyrses; buds lavender; flowers magenta, drying rusty brown; calyx cupular, truncate, 4–6 mm long; corolla 2–3.5 cm long, 2–3 cm broad, densely pubescent outside and on lobes inside, sometimes extending onto 2-lobed side of corolla, the tube white inside; stamens inserted 5–6 mm from base of corolla; filaments retrorse-barbate at point of fusion with tube, the longer pair 1.5–1.6 cm long, the shorter pair 1.1–1.4 cm long, the thecae divaricate, 2–2.5 mm long, shedding pollen in bud; staminodium 4–6 mm long; pistil 1.7–1.8 cm long; ovary linear-oblong, 2–2.5 mm long, finely lepidote; style open and apparently receptive in bud; stigmas recurved, held at level of longest stamens. Capsules 13–34 cm long, ca 1.2 cm wide, acuminate at apex, acute at base, somewhat warty and glandular-lepidote, with a weak medial ridge; seeds to 1 cm long and 3 cm wide. *Croat 5228, 11099.*

Common over the canopy of the forest, extending down to near the lake. Flowers abundantly from November to February (one shore plant in July); individuals flower for about 1 month, with many flowers open at a time. The fruits mature mostly from February to April.

Recognized by its small flowers and densely white-tomentose lower leaf surface.

Southern Mexico to Colombia and Amazonian Brazil. In Panama, commonly known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién; sporadically from tropical dry forest in Herrera and Coclé, from premontane moist forest in the Canal Zone, Coclé, and Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Colón.

Arrabidaea chica (H. & B.) Verl., Rev. Hort. 40:154. 1868

Liana; stems terete, lenticellate, usually with interpetiolar glandular fields, puberulent when young with short white trichomes, glabrous in age; tendrils simple; pseudostipules small. Leaves 2- or 3-foliolate; petioles to 7 cm long, sparsely white-puberulent; petiolules 0.3–4.6 mm long; leaflets ovate, oblong-ovate to oval, acuminate, obtuse to rounded and sometimes inequilateral at base, 4–11 cm long, 3–5.5 cm wide, glabrate, sparsely lepidote, sometimes with a few glands near midrib below, usually drying reddish. Thyrses large, terminal or upper-axillary, pyramidal; calyx cupular, truncate, 2–5 mm long, densely tomentose, the teeth 5, minute; corolla red-violet, 2.3–3 cm long, densely tomentose outside and on lobes inside, the tube white inside, glabrous except at point of fusion of stamens just above base; stamens included, the longer pair 11–13 mm long, the shorter pair 9–10 mm long, the thecae divaricate, 1.5–2 mm long; staminodium 3–4 mm long, inserted 3–4 mm from base of corolla tube; pistil to 1.3 cm long; ovary narrowly cylindrical, finely lepidote, to 2.5 mm long. Capsules linear, to 23 cm long, ca 1 cm wide, flat, ± verrucose, often drying reddish; valves with a raised medial vein; seeds transversely oblong, to 1 cm long and 2.5 cm wide, the wings hyaline. *Croat 5038.*

Occasional. Flowers sporadically at the end of the dry season and throughout the rainy season, but mostly in August and September; individuals produce abundant flowers for over a month. The fruits mature principally during the dry season.

Dried herbarium specimens are conspicuously reddish. Sterile live plants are difficult to recognize, but they can

usually be distinguished by a combination of mostly trifoliolate leaves, narrow, dark-green leaflets, and interpetiolar glandular fields (Gentry, 1973b).

Mexico to Brazil. In Panama, known sporadically from wetter parts of tropical moist forest on BCI and in Bocas del Toro, Coclé, Panamá, and Darién and from premontane wet forest in Chiriquí and Veraguas.

Arrabidaea corallina (Jacq.) Sandw., Kew Bull. 1953:460. 1954

Tendrils simple; pseudostipules inconspicuous. Leaves glabrous with tufted axils beneath. Corolla lavender to magenta. Capsules linear, 12–47 cm long, 1.6–2 cm wide, conspicuously glandular-pitted. *Stoutamire 2085* (MICH).

Rare, if still present; known from a single recently discovered collection made in 1956 at the Rear Lighthouse Clearing. Flowers during the dry season, from February to April.

Mexico to Argentina. Most common in tropical dry forest and premontane moist forest, especially in edaphically dry locations.

Arrabidaea florida DC., Prodr. 9:184. 1845

A. panamensis Sprague

Liana; branchlets terete, lepidote, lenticellate; tendrils simple; pseudostipules small. Leaves 2- or 3-foliolate, minutely glandular-lepidote; petioles 0.9–6.2 cm long; petiolules 0.5–2.7 cm long; petioles and petiolules canaliculate, puberulent; leaflets ovate to elliptic, acuminate, acute to rounded at base, 5–14 cm long, 3–8.5 cm wide, granular-puberulent to glabrous and lepidote with a few round glands near midrib below. Thyrses terminal or upper-axillary; branches, pedicels, and calyces grayish-tomentose; calyx cupular, truncate, 3–4 mm long, the teeth 5, short; corolla abruptly campanulate, 1.4–1.8 cm long, lavender or white, pubescent outside and on lobes inside, the tube flaring above calyx; stamens subexserted; filaments lavender, the longer pair 8–10 mm long, the shorter pair 5–7 mm long, the thecae divaricate, 1.5 mm long; staminodium 3–4 mm long; pistil 8–10 mm long; ovary linear-cylindric, to 1.5 mm long, lepidote. Capsules linear, flattened, 17–23 cm long, ca 1 cm wide; valves densely glandular-lepidote, with a medial groove; seeds ca 8 mm long, 3.5 cm wide, the seminiferous area \pm lunate, opaque, the wings transparent, lacerate on lateral margins. *Croat 11798, 12647*.

Occasional, in the forest canopy and at lower levels on the lakeshore. Flowers from late June through October (to November); the flowers are abundant on an individual for about a month, though each flower lasts only one day. The fruits mature mostly in the late dry season.

Sterile plants are easily confused with *Adenocalymma apurense*, but can be distinguished from that species by lacking cartilaginous leaf margins. *Arrabidaea florida* can also be confused with *Tynnanthus croatianus*, but that species is distinguished by having trifid tendrils (Gentry, 1973b).

Belize to Bolivia. In Panama, known from premontane moist and tropical moist forests in the Canal Zone, Panamá, and Darién.

Arrabidaea patellifera (Schlecht.) Sandw., Kew Bull. 22:413. 1968

Petastoma patelliferum (Schlecht.) Miers; *P. breviflorum* Standl.

Liana; trunk light brown; outer bark soft with large corky lenticels; stems terete, lenticellate, with an interpetiolar ridge, glabrate in age; tendrils simple; pseudostipules foliaceous, to 1 cm long, falcate, caducous. Leaves bifoliolate or rarely simple; petioles 1.1–3.5 cm long; petiolules 0.5–2.2 cm long; petioles and petiolules short-pilose; leaflets ovate to obovate, obtuse to caudate-acuminate, obtuse to rounded or subcordate at base, 5–15 cm long, 3–10 cm wide, lepidote on both surfaces, otherwise glabrous above, villous at least on veins below, usually with tufts or cavellike domatia in axils below, entire or rarely dentate on juveniles. Inflorescences large, pyramidal, axillary or terminal panicles; flowers red-violet to violet-purple, whitish-tipped in bud; branches and pedicels lepidote and white-villous; calyx bowl-shaped, 1–4 mm long, 4–8 mm wide, flared, the margin entire, wavy; corolla 2.5–4.7 cm long, the tube glabrous except for gland-tipped trichomes at point of staminal attachment inside, the lobes sparsely pubescent on both sides; stamens included, with the longer ones 1.1–1.3 cm long, the shorter ones 0.8–1 cm long, the thecae divaricate, to 2 mm long; staminodium 3–4 mm long, held on 2-lobed side of corolla opposite nectar guide, this side whitish and spotted inside; pistil 1.5–2.3 cm long; ovary linear, 1.5–2.5 mm long, slightly lepidote. Capsules linear, flattened, 15–39 cm long, 1.1–1.5 cm wide, with medial rib faint or prominent, densely lepidote, often sparsely whitish-lenticellate; seeds ca 1 cm long and 2.5–4 cm wide, the outer margin rounded to truncate, the lateral margin of wings translucent. *Croat 6052, 13161*.

Common along the shore and occasional in the forest. Flowers most abundantly from July to September (sometimes from June to November), rarely in January and February; the flowers are abundant on an individual vine for over a month, but each flower lasts only one day. The fruits mature mainly in the middle of the dry season.

The species can be recognized by its open, bowl-shaped calyces and white-tipped buds. Vegetative characteristics include the dense pubescence on the main veins beneath, the pubescent petioles and petiolules, and the frequency of simple leaves.

Petastoma breviflorum Standl., reported by Standley as a distinct species on the basis of its shorter corolla, appears to be inseparable from this species. Corolla length in the family is variable.

Southern Mexico to Amazonian Brazil. In Panama, known on the Pacific slope, most commonly from premontane moist forest in the Canal Zone and Panamá; known also from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from tropical

dry forest in Herrera, from premontane wet forest in Chiriquí, Panamá, and Darién, and from tropical wet forest in Panamá.

Arrabidaea verrucosa (Standl.) A. Gentry, Selbeyana 2:43. 1977

Scobinaria verrucosa (Standl.) Seib.; *Martinella verrucosa* (Standl.) Standl.

Liana, glabrous except for moderate pubescence sometimes on leaflet veins below and on young stems, petioles, and petiolules; trunk to 10 cm diam; stems terete, lenticellate, with interpetiolar glandular fields; tendrils simple; pseudostipules small or lacking. Leaves bifoliolate; petioles 1.3–5.1 cm long; petiolules 1–4.2 cm long; petioles and petiolules slightly ribbed at apex; leaflets ovate to ovate-lanceolate, acuminate at apex, obtuse to rounded at base, 8–16 (17) cm long, 4–7 (11.8) cm wide, conspicuously lepidote on both surfaces, with tufts of trichomes in axils below and a few, small, round glands scattered throughout. Panicles axillary and terminal, bearing few flowers; calyx tubular-campanulate, 1.5–2.8 cm long, thin, bilabiate or irregularly 3-lobed, often widely expanded above, sometimes spotted with minute protuberances; corolla with lavender lobes and a white tube, 4.5–6.5 (8) cm long, soft-pubescent outside and on lobes inside, glandular-pubescent on base of stamens and on tube at point of staminal attachment; stamens included, the longer ones 1.7–2 cm long, the shorter ones 1.1–1.4 cm long, the thecae divaricate, ca 3 mm long; staminodium 1–3 mm long; pistil 2.5–2.8 cm long; ovary linear-oblong, ± quadrangular, ca 3 mm long, densely lepidote. Capsules linear, flattened, densely sharp-tuberculate, dark-colored, 18–40 (46) cm long, 1.7–2.3 cm wide; seeds ca 1.7 cm long and 4.5 cm wide, the wings with a transparent margin and rounded lateral sides. *Croat 13983, 15564.*

Occasional, in the forest and along the shore. Flowers abundantly from June through August (to November), in extravagant, long-lasting bursts. The fruits mature in March and April. The species may not flower every year.

The species is distinguished by its flattened corolla tube, its large, bilabiate, membranaceous calyx, and its linear verrucose-tuberculate fruits resembling wood rasps.

Gentry treated this species as *Scobinaria japurensis* (DC.) Sandw. in the *Flora of Panama* (1973b), but he has subsequently considered that taxon a distinct Amazonian species.

Fruits make an oil spot on pressing paper when dried.

Belize to Venezuela and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Panamá, and Darién and from tropical wet forest in Colón, Panamá, and Darién.

CALLICHLAMYS Miq.

Callichlamys latifolia (L. C. Rich.) K. Schum. in Engler & Prantl, *Nat. Pfl.* 4(3b):223. 1894

Liana, ± glabrous and minutely glandular-lepidote throughout; branchlets terete, somewhat lenticellate,

striate in age; tendrils simple; pseudostipules inconspicuous. Leaves usually 3-foliolate, sometimes with a tendril replacing terminal leaflet; petioles 2.5–9 (18) cm long; petiolules 1.1–9.5 cm long; leaflets ovate to elliptic, long-acuminate, acute to rounded at base, 9–16 (37) cm long, 4–7 (22) cm wide, with tufts of trichomes in axils below, with a few round glands along midrib below. Racemes short, terminal or axillary; flowers bright yellow, few; calyx globular to oblong-ellipsoid in bud, thick and spongy, to ca 4.5 (6) cm long, 2 (4.2) cm wide, completely enveloping corolla in bud, splitting somewhat irregularly as corolla emerges; corolla 7–9 (11) cm long, glandular-puberulent, the limb broadly spreading, the tube with stalked, glandular trichomes at point of staminal attachment; stamens included, the longer pair 2.5–3.8 cm long, the shorter pair 1.5–2.3 cm long, the thecae divaricate, 2–3 mm long; staminodium 0.6–1.1 mm long; pistil 5.2–5.7 cm long; ovary ovate-cylindric, 3–4 mm long, ± glabrous. Capsules compressed-ellipsoid, to 32 cm long and 6–11.5 cm wide; valves ca 5 mm thick, glabrous; seeds 2–4 cm long, 6–10 (13) cm wide, tan, somewhat narrowed toward the rounded lateral margins. *Croat 6835, 8058.*

Occasional, in the forest canopy and at lower levels at the margin of the lake. Flowers mostly in October and November, but sporadically throughout the year; on an individual vine a few flowers are open for about a week, followed by a brief burst of flowering. The fruits probably mature in the dry season.

The species can be recognized when sterile by the conspicuous tufts of trichomes in the lower vein axils. Also useful in recognition is the smooth gray bark with whitish lenticels and the red-drying major lateral veins (Gentry, 1973b).

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Panamá, and Darién and from tropical wet forest in Colón.

See Fig. 490.

CERATOPHYTUM Pitt.

Ceratophytum tetragonolobum (Jacq.) Sprague & Sandw., *Bull. Misc. Inform.* 1934:222. 1935

C. tobagense (Urban) Sprague & Sandw.

Liana; stems terete, striate, with prominent elongated lenticels and conspicuous interpetiolar glandular fields; tendrils trifid; pseudostipules at first small, ± triangular, acuminate, paired, diverging in age to expose a third pseudostipule to 8 mm long. Leaves 3-foliolate, or 2-foliolate with a terminal tendril; petioles 3–12 cm long; terminal petiolules 2.1–4.6 cm long, the lateral petiolules 0.3–5.7 cm long; leaflets ovate, ovate-elliptic, oblong-ovate, or rarely obovate, usually abruptly acuminate, usually round to subcordate at base, 6–20 cm long, 4–15 cm wide, weakly coriaceous, domatia in axils of lateral veins cavelike, sometimes barbate at mouth. Panicles terminal, subcorymbose; calyx truncate, 10–13 mm long, coriaceous, glandular-lepidote, with fields of sunken glands in distal half; corolla white, becoming yellowish

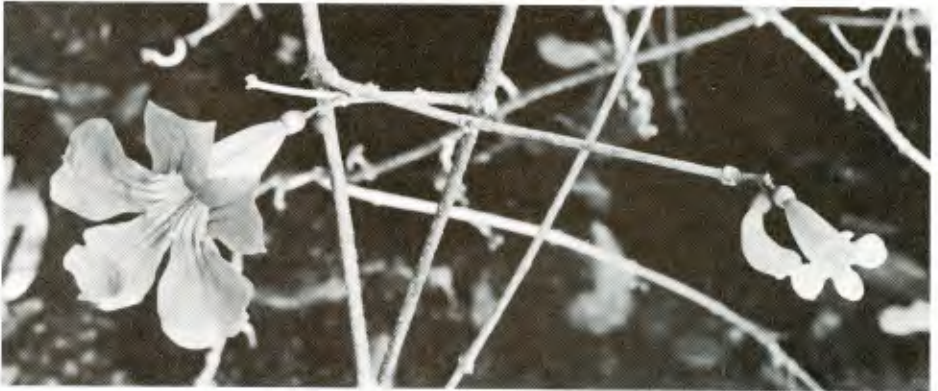


Fig. 490. *Callichlamys latifolia*

Fig. 491. *Cydista aequinoctalis*



Fig. 492. *Cydista heterophylla*



in age, densely pubescent outside and on lobes inside with moniliform trichomes, the tube yellow and glabrous inside, abruptly narrowed just above base, strongly 2-sulcate on 3-lobed side; stamens included, the longer pair 2.2–2.4 cm long, slightly shorter than style, set among a dense ring of trichomes near base; anther thecae divaricate, 4.5–6 mm long; pistil 3.2–3.3 cm long; ovary narrowly cylindrical, 5 mm long, lepidote. Capsules cylindrical, thick, elongated, acute at apex, blunt at base, 25–39 cm long, 3–4 cm wide, 2–2.5 cm thick, tan at maturity, densely covered with minute rounded or ± elongated pits; seeds to 1.5 (1.8) cm long and 4.5 (6.3) cm wide. *Croat 14458*.

Occasional, in the forest canopy; few fertile collections have been made on the island. Flowers at least in April, June, and October; individuals produce a few flowers over a long period. The fruits probably mature in the middle of the dry season.

May be recognized in sterile condition by the woody, trilobate pseudostipules, the prominent interpetiolar glands, the trifid tendrils, and the axillary domatia on the leaflets.

Scattered areas from southern Mexico to Venezuela and Surinam; West Indies. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién.

CLYTOSTOMA Miers ex Bur.

Clytostoma binatum (Thunb.) Sandw., Recueil Trav. Bot. Néerl. 34:235. 1937
C. ocositense (Donn. Sm.) Seib.

Liana, ± glabrous; trunk ± smooth, the nodes weakly swollen; stems terete, often ± 4-sided as a result of longitudinal ridges from below petiole bases; lenticels ± prominent; tendrils simple; pseudostipules clustered, ca 3 mm long (resembling miniature bromeliads). Leaves bifoliolate; petioles 1–2 cm long; petiolules 1–2 cm long, conspicuously articulate at base; leaflets ± elliptic, acuminate at apex, obtuse to rounded at base, 6.5–19 cm long, 2.5–8 cm wide, lepidote above and below, with a few round glands along midrib below especially near base. Flowers sweetly aromatic, terminal, on short leafy or leafless branches, usually 3 or 4 per cluster; pedicels 1.5–2.5 cm long; pedicels and calyces minutely puberulent; calyx campanulate, 4–5 mm long, truncate, with ± submarginal teeth; corolla thistle-colored to pale lavender, 4.5–7.5 (8.5) cm long, tomentulose outside near base and on lobes inside, the tube often white near base outside, white inside, with nectar guides extending down 3-lobed side to near base; stamens included, the longer

pair 1.4–1.9 cm long, the thecae divaricate, 2–3 mm long; pistil to 3 cm long; ovary rounded, short-cylindrical, 2 cm long, 1.5–2 cm wide, 1–1.5 cm thick, densely glandular-pubescent; stigma truncate. Capsules flattened, elliptical to orbicular, ca 5 cm long, the surface echinate; seeds orbicular, ca 2 cm diam with thick, corky wings. *Croat 13963*.

Rare; seen on the north shore of Gigante Bay and on the island north of Burrunga Point. Flowers and fruits throughout the year, with numerous short flowering periods most common in the late rainy season.

The species is recognized in sterile condition by its bromeliad-like pseudostipules (often not present), by its elliptic leaf blades, and by the four darker lines on a subterete to subtetragonal twig (Gentry, 1973b).

The seeds are dispersed by water.

Mexico to Brazil. Gentry (1973b) reported the species to be most common in tropical wet forest, though most of the collections cited were from regions of tropical moist forest, according to the Holdridge Life-Zone map of Panama. In Panama, known from swampy areas of tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién and from tropical wet forest in Colón.

CYDISTA Miers

Cydista aequinoctalis (L.) Miers, Proc. Roy. Hort. Soc. London 3:191. 1863

Liana, mostly glabrous, usually glandular-lepidote; stems terete to strongly tetragonal, striate, usually with interpetiolar ridges; tendrils simple, replacing terminal leaflets; pseudostipules small or lacking. Leaves bifoliolate; petioles and petiolules canaliculate, 1.5–4 cm long; leaflets ovate to elliptic, acuminate, obtuse to rounded and often inequilateral at base, 9–16 cm long, 4–11 cm wide, usually with dense clusters of glands in basal axils below. Inflorescences terminal or axillary racemes or panicles of few flowers; calyx campanulate, 6–10 mm long, the teeth 5, minute; corolla usually 5–8 cm long, weakly bilabiate, pale lavender to white, with yellow throat, glandular-lepidote outside, pubescent inside, the trichomes minute, sessile or short-stalked, brownish, globular, the upper lip less deeply lobed than lower lip; nectar guides lavender, on 3-lobed lower lip of corolla, extending to base of tube; stamens included; filaments broadly arched, the thecae divaricate, 3–4 mm long, the longer pair 1.1–1.7 cm long; pistil 1.6–3.2 cm long; ovary narrowly cylindrical, 2–3 mm long, lepidote. Capsules linear, flattened, 30–56 cm long, 2–2.5 cm wide, glandular-lepidote, shiny as if varnished, lacking an obvious medial

KEY TO THE SPECIES OF CYDISTA

- Flowers precocious; corolla orchid-colored with a white throat; calyx 2- or 3-lobed; capsules with 2 narrow ridges running the length of each valve; leaves often simple *C. heterophylla* Seib.
Flowers not precocious; corolla white or pale lavender with a yellow throat; calyx ± truncate; capsules lacking ridges; leaves bifoliolate *C. aequinoctalis* (L.) Miers

ridge; seeds ca 1.7 cm long and 6 cm broad, the lateral margins smooth, rounded. *Croat 5208, 12645.*

Abundant in the forest canopy and along the shore. Flowers and fruits in numerous short bursts throughout the year.

Sterile material is marked by the \pm tetragonal twigs, glandular fields in the leaf axils of the lower blade surface, and the general lack of pseudostipules (Gentry, 1973b).

Throughout tropical America. In Panama, known from tropical moist forest in all provinces; known also from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 491.

Cydista heterophylla Seib., Publ. Carnegie Inst. Wash. 522:417. 1940

Liana, \pm glabrous and glandular-lepidote; stems terete, lenticellate, striate in age; tendrils simple; pseudostipules small. Leaves usually opposite, sometimes subopposite, rarely alternate, simple or 2- or 3-foliolate, deciduous; petioles 1.5–5 cm long; petiolules 0.5–5.1 cm long; leaflets ovate to ovate-elliptic, acuminate, obtuse to rounded at base, 5–11 (17.5) cm long, 3–8 (11) cm wide, usually with clusters of glands in axils of basal veins below, the veins sometimes sparsely and minutely puberulent; veins at base 3. Flowers in lax axillary racemes on defoliate branches; pedicels 7–15 mm long; calyx usually 2- or 3-lobed, often truncate at base, densely lepidote, 6–8 mm long; corolla funnelform, bilabiate, orchid-colored, 4–7 cm long, glandular-lepidote outside, the lobes softly pubescent on both sides, the tube white, glandular-puberulent on nectar guides; nectar guides darker than lobes, extending from ca midway on lobes to deep in tube on 3-lobed side; stamens included, equaling length of style, the longer pair 1.7–1.8 cm long, the thecae divaricate, 4–5 mm long; staminodium short, sometimes with a reduced anther; pistil 3–3.1 cm long; ovary linear, 4–5 mm long, lepidote. Capsules linear, to 35 cm long and ca 1.5 cm wide, flattened, with 2 narrow, longitudinal ridges; seeds oblong, ca 1 cm long and 2.6–5.3 cm wide, with transparent wings ca 1 cm long. *Croat 8206.*

Rare; collected from the shore. Flowers from April to May (sometimes from February); the flowers appear in a few brief bursts when the plant is leafless. Mature fruits have been reported from adjacent areas of the Canal Zone in June, July, and November.

This species can be recognized when sterile by its tendency to produce simple leaves and by the strongly arcuate pair of basal veins on the blade, each pair with glandular field in its axil (Gentry, 1973b).

Mexico to Colombia. Gentry (1973b) reported this species as most common in tropical dry forest, but perhaps all of the collections cited were made in drier parts of tropical moist forest. In Panama, known from drier parts of tropical moist forest in the Canal Zone, Herrerra, Panamá, and Darién and from premontane moist forest in Panamá.

See Fig. 492.

JACARANDA Ant. Juss.

Jacaranda copaia (Aubl.) D. Don, Edinburgh Philos. J. 9:267. 1823
Palo de bura

Tree, to 45 m tall; trunk 30–50 cm dbh, often buttressed, often wrinkled near base; outer bark fissured, very soft, thin, light brown, flaking; inner bark light tan, with minute reddish-brown sap droplets in time after being slashed; petioles, rachises, and midribs below with granular puberulence. Leaves bipinnate, crowded near apex of branches, to 40 cm long (juvenile branches with the leaves to 1.5 m long); petioles and rachises with medial groove; rachis \pm angulate; pinnae 5–20 per leaf; leaflets 3–25 per pinna, \pm elliptic, inequilateral, 2.5–7 cm long, 1.5–3.5 cm wide, conspicuously punctate on both surfaces, toothed only on juveniles. Flowers precocious, the panicles very large, narrow, borne among leaves near apex of stem, dense but well spaced on rachis; calyx \pm truncate, but often split on one side, 4–7 mm long, densely pubescent with short, branched trichomes, lepidote; corolla lavender-blue, 4–5 cm long, densely pubescent with branched trichomes outside and on lobes inside, the tube constricted 7–8 mm at base, then prominently flaring, somewhat curved, white inside, glabrous except for glandular trichomes near juncture of stamens; stamens included, the longer pair 1.1–1.3 cm long; anthers with one theca very reduced; base of filaments and staminodium with glandular trichomes; staminodium to 3 cm long, tufted at apex; pistil 1.5–1.8 cm long; ovary flattened-cylindrical, 2–2.5 mm long and wide, 1.5 mm thick, glabrous. Capsules shortly and broadly oblong, rounded at both ends, compressed, 8–14 cm long, 5–8 cm broad, glabrous, prominently and minutely lenticellate; seeds suborbicular, to 2.5 cm long and 4 cm wide, the seminiferous area 5–6 mm long, the wings transparent except for veins extending out from center, with a distinct sinus at point of attachment. *Croat 6782, 7888.*

Common to locally abundant in the forest. Flowers from February to May; individuals flower in an extravagant burst that lasts over a month. The fruits mature from July to October, with a few fruits falling as late as April (Foster, 1974). Leaves fall in the early dry season and are replaced after flowering.

Belize to the Guianas, Brazil, and Peru. In Panama, a characteristic tree species of tropical moist forest (Holdridge & Budowski, 1956; Tosi, 1971) and common in secondary areas at low elevations (Holdridge, 1970); known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón and Darién.

See Figs. 493 and 494.

MACFADYENA DC.

Macfadyena unguis-cati (L.) A. Gentry, Brittonia 25:236. 1973

Liana; outer bark thin, gray, forming minute straight longitudinal fissures; stems terete, often with interpetio-



Fig. 493. *Jacaranda copaia*



Fig. 494. *Jacaranda copaia*,
large pilose staminodium and
smaller glabrous style

lar glandular fields (very conspicuous on young stems) with a slight ridge above glands, glabrous or minutely pubescent; tendrils terminal, trifid, hooked (rarely rudimentary); pseudostipules ovate, striate, ca 5 mm long, sub-persistent. Leaves bifoliolate; petioles 1–5 cm long; petiolules 0.5–2.5 cm long; leaflets ovate-elliptic, acuminate at apex, rounded or obtuse to truncate or subcordate at base, 4–14 (16) cm long, 0.7–5 (7) cm wide, glabrous or weakly puberulent on midrib or throughout below, with sunken scurfy scales on both surfaces and with a few, round, sunken glands below on either side of midrib, \pm entire and somewhat undulate. Inflorescences of 1–3 flowers, mostly in simple dichasia, terminal; flowers with a lemonlike aroma; calyx thin, glabrous, 7–8 (18) mm long, the margin truncate or wavy; corolla yellow-orange, often pale yellow on tube, funnel-shaped, 5–9 (10) cm long, the lobes ca 2 cm long, minutely ciliate; nectar guides on 3-lobed lip, faint, minutely glandular, with darker yellow-orange lines extending to base of tube; stamens with the upper pair 2.1–2.4 cm long; filaments shortly glandular-puberulent at point of attachment to tube (ca 5 mm from base); staminodium 0.5–1.5 cm long; pistil 2.8–3.8 cm long; ovary minutely papillate; disk doughnut-shaped, conspicuous; style ca 3 cm long; stigmas 2, broadly spatulate. Capsules linear, flattened, 60–108 cm long, 1–2 cm wide, tapered to acute at apex, blunt at base; valves thin, dark-colored, with a faint medial ridge, otherwise \pm smooth, lepidote; replum thick, woody; seeds 5.5–6 cm wide, ca 1.5 cm long, opaque except for lateral margins, these deeply lacerate. *Croat 10224, 14062, 14645.*

Occasional but locally common in areas of the older forest. Flowers mainly from March to June; individuals flower in a single brief burst. The peak of seed release occurs in the dry season.

The species may be recognized by its trifid tendrils, which are shaped like a cat's claws. It differs from other species of bignoniaceous vines in its habit of growth: juvenile plants are appressed to the trunks and branches they climb; when the plant becomes established, it branches freely, often dangling, and the leaves are larger and free.

Mexico to Argentina; West Indies. Gentry (1973b) reported the species to be most common in tropical dry forest, but few of the collections he cited were from regions of tropical dry forest. In Panama, known principally from premontane moist forest in the Canal Zone and Panamá, also from drier parts of tropical moist forest in the Canal Zone, Panamá, and Darién, and much less commonly from premontane wet forest in Panamá and Darién.

MARTINELLA Baillon

Martinella obovata (H.B.K.) Bur. & K. Schum. in Mart., Fl. Brasil. 8(2):161, pl. 84. 1896

Liana; branches terete, finely striate, with minute gland-tipped trichomes, the nodes with broad interpetiolar ridges; tendrils trifid, the arms hooked; pseudostipules

replaced by small branches or branch scars. Leaves bifoliolate, glabrous except minutely puberulent on veins below; petioles usually at right angles to branchlets, 2–7 cm long; petiolules 4–6 cm long; leaflets \pm ovate, abruptly acuminate to \pm falcate-acuminate, cordate at base, 7–21 cm long, 4–15 cm wide, with round glands scattered along midrib below; major veins often darker than surface (lighter on young leaves). Inflorescences usually axillary flexuous racemes, sweetly aromatic, rarely terminal; pedicels slender, ca 1.5 cm long; calyx to 2 cm long, usually 3-lobed at anthesis, minutely glandular-puberulent or glabrous, with a few impressed glands, the lobes short, abruptly acuminate, 5–9 mm long; corolla bilabiate, 5–7 cm long, the tube curved, white at base, pale violet-purple above, sparsely glandular-lepidote outside above, the lobes dark violet-purple, densely glandular-lepidote; nectar guides on lower 3-lobed side of corolla; tube below point of staminal attachment and base of filaments with short glandular pubescence; stamens probably held against 2-lobed side of corolla, the longer pair 1.5–1.7 cm long; anther thecae divaricate, 2.5–3 mm long; staminodium 1–2 mm long; pistil 3.5–3.7 cm long; ovary linear, 4 mm long, sparsely lepidote or puberulent. Capsules brown, linear, 55–80 (130) cm long, ca 1.9 cm wide, glandular-lepidote, inconspicuously puberulent, especially along margin; seeds 1–1.7 cm long, 4–6 cm wide, the wings thin. *Croat 14658.*

Rare; seen only in the forest near Armour Trail 500. Flowers sporadically throughout the year, especially in the rainy season, in extravagant bursts of flowering that last about a month. The fruits are released from April to September.

The species may be recognized in sterile condition by the trifid tendrils, the long-petiolate, glossy leaves, the prominent, linear, interpetiolar ridges, and the tendency for the petioles and petiolules to bend or twist (Gentry, 1973b).

Belize to Brazil and Bolivia. In Panama, known from wetter parts of tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién, from premontane wet forest in Chiriquí, Colón, and Panamá, and from tropical wet forest in Panamá.

See Fig. 495.

PACHYPTERA DC. ex Meisn.

Pachyptera kerere (Aubl.) Sandw., Recueil Trav.

Bot. Néerl. 34:219. 1937

P. foveolata DC.; *Tanaecium zetekii* Standl.

Liana; stems and petioles \pm striate, the young stems sometimes \pm square, the nodes with glandular fields and an interpetiolar ridge above glands; tendrils trifid; pseudostipules vertically 3-seriate, acute, to 7 mm long. Leaves 2- or 3-foliolate; petioles 0.9–7.1 cm long, with glandular fields at apex; terminal petiolules 1.5–6.1 cm long, the lateral ones 0.5–3.2 cm long; leaflets ovate to elliptic, acuminate, slightly cordate at base, 10–22 cm long, 4–12 cm wide, glabrous or minutely puberulent below especially on veins, sometimes very sparsely glan-



Fig. 495. *Martinella obovata*



Fig. 496. *Pachyptera kerere*

dular throughout. Inflorescences short axillary racemes, densely flowered; calyx 10–16 mm long, often with 2 shallow lobes, one lobe slightly longer and emarginate, short-puberulent, sometimes with conspicuous plate-shaped glands in apical half; corolla 5–10 cm long, white, the tube slender, puberulent outside, glabrous inside except densely glandular-pubescent below point of staminal attachment, bent somewhat about midway, the lobes 5, \pm obovate, glandular-tomentose, with sunken brown glands on lower side near base, the upper 3 lobes erect, the lower 2 recurved; stamens included; filaments fused to corolla tube more than half their length, the longer pair 1.9–2.1 cm long, the shorter pair 1.4–1.6 cm long, the thecae divaricate, 2–4 mm long, densely white-villous; pistil 4.5–4.8 cm long; ovary flattened-cylindrical, 2–3 mm long, minutely papillose; style with 2 broad stigmas held at level of longer set of stamens. Capsules \pm oblong, attenuate at both ends, 10–18 (25) cm long, 2–3.8 cm wide, raised along median with a minute medial rib, minutely puberulent and with scattered, sunken, plate-shaped glands; seeds thick, wingless, opaque, 2.5 cm long and ca 3.5 cm wide, thickened below and tapered to knifelike edge. *Croat 8704, 11085.*

Occasional, usually in areas near the shore where the seeds are water dispersed, but sometimes in areas at considerable distance from the shore. Flowers sporadically throughout the year, mostly from September to April, with a few long-lived flowers at a time. Mature fruits have been seen from April to July.

The species is recognized by its white flower with pubescent anthers, the three-seriate pseudostipules, and the glandular field on the upper surface of the petioles near the apex.

The interpetiolar glandular areas are sometimes eaten away on the stems. Presumably this is done by insects that feed on the glands.

Belize to Amazonian Brazil. In Panama, known from wetter parts of tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Colón, Darién, and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 496.

PARAGONIA Bur.

Paragonia pyramidata (L. C. Rich.) Bur., Vidensk. Meddel. 1893:104. 1894

Liana; trunks to 8–9 cm diam; outer bark corky, roughened, \pm peeling; inner bark light brown, soft; stems terete, with interpetiolar ridges at nodes; tendrils bifid or trifid; pseudostipules lanceolate, sharply pointed, 2–7 mm long. Leaves bifoliolate; petioles 1–4.5 cm long, with large, sunken, plate-shaped glands on upper surface near apex; petiolules 0.7–4.7 cm long; leaflets ovate, obovate, or elliptic, abruptly acuminate and sometimes downturned at apex, mostly obtuse to rounded at base, 8–24 cm long, 3–13 cm wide, often puberulent on veins below, minutely glandular-lepidote, subcoriaceous, usually drying grayish-green. Inflorescences broad terminal

panicles of many flowers; branches puberulent; flowers imperial purple to dark orchid (drying brown); calyx campanulate, truncate or slightly lobed, 5–9 mm long, somewhat warty and gland-dotted; corolla 2–7 cm long, densely velvety outside with moniliform trichomes except at base, glandular and moniliform-pubescent on lobes and throat inside, the tube glabrous inside except at base, constricted near base, fused to filaments; stamens set among short white bristles, the longer pair 1.6–1.9 cm long, the shorter pair 1.2–1.5 cm long; staminodium short; pistil ca 2 cm long; ovary linear, ca 5 mm long, strongly lepidote. Capsules linear, to 50 (61) cm long and 1.5 cm wide, subterete or somewhat flattened with an obscure longitudinal rib, minutely bumpy; seeds 0.8–1.5 cm long, 3.5–4.5 cm wide, rounded and translucent on lateral margins. *Croat 7896, 10161.*

One of the most common bignoniaceous vines on the island. Flowers in extravagant bursts lasting about a month, abundantly in the dry season and erratically throughout the year. Most mature fruits are seen from February to May.

Because of its flower color, it may be confused at a distance with several other species. The high canopy vines can be easily observed along the shore, but, as with other vines of the family, only the fallen flowers are usually seen in the forest.

The species is most easily confused vegetatively with *Ceratophyllum tetragonolobum*, but can be distinguished from that species by having simple or bifid tendrils and by lacking interpetiolar glandular fields (Gentry, 1973b). *C. tetragonolobum* has glandular fields and trifid tendrils.

Mexico to Brazil, Bolivia, and Peru. In Panama, widespread in tropical moist forest; known also from premontane wet forest in the Canal Zone, Coclé, Panamá, and Darién and from tropical wet forest in Colón, Panamá, and Darién.

PHRYGANOCYDIA Mart. ex Bur.

Phryganocydia corymbosa (Vent.) Bur. ex K. Schum. in Engler & Prantl, Nat. Pfl. 4(3b):224, f. 89H. 1894

Liana; trunk usually 5–7 cm diam, conspicuously swollen to ca 9 cm at nodes; outer bark soft, gray-brown; stems terete, striate when dry, with the interpetiolar ridge inconspicuous; tendrils simple, spoon-shaped, with glandular fields at apex; pseudostipules inconspicuous when young, stalked and with spreading forks in age. Leaves bifoliolate; petioles 0.6–3.3 cm long; petiolules 0.5–3 cm long; leaflets ovate to ovate-elliptic, bluntly acuminate, obtuse to rounded at base, 8–14 (22) cm long, 3–10.5 (11) cm wide, thick, essentially glabrous, lepidote, with clusters of glands at base above, drying gray; midrib sometimes conspicuously arched. Panicles short, terminal or upper-axillary, of few flowers; calyx spathaceous, 2.5–4 cm long; corolla tubular-funnelform, 4.5–9 cm long, bilabiate, glabrous except for sparse minute glands especially outside, the lobes 5, lavender, the upper 2 broader than long, united to about middle and often overlapped at margin, the lower 3 free, the tube white-

pubescent only near staminal attachment; nectar guides on lip, dark lavender, fading into tube; stamens included, the longer pair 1.8–2.1 cm long, the shorter pair 1–1.3 cm long, the thecae divaricate, each 3.5–4.5 mm long; staminodium 2–3 mm long. Capsules linear, 35–40 (53) cm long, ca 2.5 cm wide, blunt on both ends, densely lepidote, the medial ridge faint; seeds thin, ca 2 cm long, 4.5–5 (7) cm wide, the seminiferous area 1 cm wide, the margins scarious. *Croat 6089, 8272.*

An abundant canopy vine in all parts of the forest. Flowers throughout the year in short bursts of few flowers, perhaps more abundantly from June to September. The fruits mature throughout the year, each in about 2 months.

Sterile recognition characters include the weakly winged petiolules and the terete, smooth, light-gray twigs (Gentry, 1973b).

Seed release occurs throughout the year (Gentry, 1973b).

Panama to Brazil. In Panama, known principally from tropical moist forest in the Canal Zone, San Blas, Coclé, Panamá, and Darién; known also from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón, Darién, and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 497.

PITHECOCTENIUM Mart. ex Meisn.

Pithecoctenium crucigerum (L.) A. Gentry, *Taxon* 24:123. 1975

P. echinatum (Jacq.) Baillon

Liana; stems 6–8-angled, becoming ribbed in age, glabrous, whitish-lepidote; tendrils trifid or twice-trifid; pseudostipules 4 at each node, linear-oblong, to 9 mm long. Leaves 2- or 3-foliolate; petioles and petiolules 2–6 cm long, puberulent, lepidote; leaflets ovate, abruptly acuminate, round to cordate at base, 7–14 (18) cm long, 6–10 (14.7) cm wide, sparsely puberulent to glabrous and glandular-lepidote above and below, with several round glands in vein axils at base of leaf below, usually ciliate; veins at base 5–7. Racemes terminal, bracteate, to 20 cm long; all exposed parts sparsely to densely tomentose; flowers moderately few, with a musky odor; calyx campanulate, truncate, 1–1.5 cm long, the teeth 5, minute, chiefly submarginal; corolla white, yellowish in age, 4–6 cm long, 5-lobed, bilabiate, the lobes longer than broad, reflexed at maturity, the tube prominently curved above base, with minute, moniliform trichomes especially on lobes and tube outside; stamens held against 3-lobed side of corolla, the longer pair just below throat, 1.7–2.1 cm long, the shorter pair 1.2–1.7 cm long; staminodium less than 1 mm long, inserted near base of corolla tube; pistil 3.3–3.5 mm long; ovary short-cylindrical, 5–6 mm long, swollen at middle, with both simple and multicellular trichomes; style with the 2 lobes about as broad as long. Capsules oblong, heavy, densely spiny, to 32 cm long, 6–8 cm wide; replum thick, bearing elongate perforations along margin; seeds ca 4 cm long and

10 cm wide, the tan, \pm opaque body radiating into a very broad, transparent wing. *Croat 5804, 7022.*

Occasional in the forest; common locally, often covering entire treetops. Flowers mainly in May and June, with the flowers long-lasting. The fruits mature during the following dry season (February to April).

The seeds of this species are the best fliers I know. To watch the seeds make their slow, irregular trip to the ground is always amazing.

Because of its hexagonal twigs it is confused only with *Amphilophium paniculatum*, but may be distinguished by its lack of pubescence, its much-branched tendrils, its bent, white corolla, and its large echinate fruits.

Mexico to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 498.

PLEONOTOMA Miers

Pleonotoma variabilis (Jacq.) Miers, *Proc. Roy. Hort. Soc. London* 3:184. 1863

Liana, glabrous except for pubescence on leaflet midribs and veins below and pilose on axils near base of leaflet below; young stems square; tendrils long, trifid near apex; pseudostipules long, forked. Leaves 3-ternate, or 2-ternate with a tendril or tendril scar; petioles 2.1–6.7 cm long; terminal petiolules 1.2–6.5 cm long; leaflets ovate to elliptic, sometimes falcate, acuminate, obtuse to rounded and sometimes inequilateral at base, 5–15 (16) cm long, 2.5–8.5 (9.5) cm wide, weakly viscid when dried, usually with a few, round, scattered glands. Racemes short, terminal, on short lateral branches; pedicels to 1.5 cm long; calyx campanulate, 6–9 mm long, truncate, minutely toothed; corolla 7–10 cm long, pale yellow throughout or with the lobes white, the tube moderately slender with a few large glands at apex, pubescent inside just below point of staminal attachment, the lobes pubescent and glandular with a few scattered larger glands; stamens included, the longer pair 2.6–2.8 cm long, slightly shorter than style, the shorter pair 1.7–1.9 cm long, the thecae divaricate, to 5 mm long; staminodium 4–5 mm long, inserted ca 2 cm from base of corolla tube. Capsules linear-oblong, acuminate at both ends, to 22 (30) cm long and 2.8 cm wide, glabrous, viscid at least on drying; seeds ca 1.2 cm long and 3.7 (5) cm wide, the lateral margins \pm rounded, the wings \pm opaque. *Croat 7876, 7997a.*

Uncommon, in the forest and along the shore. Flowers in the middle to late dry season. The fruits mature a year later in the dry season.

The only bignoniaceous vine with bicomposite leaves.

Costa Rica to Venezuela; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Panamá, and Darién and from premontane wet forest and tropical wet forest in Panamá and Darién.



Fig. 497. *Phryganocydia corymbosa*



Fig. 498. *Pithecoctenium crucigerum*

SPATHODEA Beauv.***Spathodea campanulata*** Beauv., Fl. Oware 1:47. 1806

African tulip tree

Cultivated tree, 7(25) m tall, pubescent throughout, especially rufous-tomentose on lower leaf surface, inflorescence branches, and calyces; pseudostipules foliaceous, ovate-cordate, 3 cm long, 2 cm wide. Leaves pinnate, 3–19-foliolate, to 50 cm long; petioles 3–7 cm long; petiolules obsolete or to 2 mm long; leaflets \pm elliptic, abruptly acuminate, acute to rounded at base, 7–13 cm long, 4–7 cm wide. Racemes terminal, corymbiform; flowers large, showy; calyx spathaceous, to ca 6 cm long, the lobes curved inward; corolla broadly campanulate, asymmetrical, more deeply cleft on one side, to ca 13 cm long, red-orange, the lobes ovate, the margin yellow and undulate; stamens directed inward toward calyx, often exerted between lowermost lobes like the style; anther thecae divaricate, 8 mm long; ovary narrowly oblong, minutely papillate. Capsules \pm oblong, flattened, smooth, acuminate at apex, obtuse at base, 6–11 (21) cm long, 4–5 (6) cm wide, splitting open on one side; replum perforated, loose at base; seeds ca 2 cm long and 3 cm wide, the wings transparent, the margin smooth. *Croat 5177*.

Cultivated in the Laboratory Clearing. Flowers throughout the year.

The species is easily recognized by its large, red-orange flowers and oblong capsules with winged seeds.

Native to tropical West Africa; cultivated throughout the American tropics.

STIZOPHYLLUM Miers***Stizophyllum riparium*** (H.B.K.) Sandw., Lilloa

3:462. 1938

Adenocalymma flos-ardeae Pitt.; *S. flos-ardeae* (Pitt.) Sandw.

Liana; trunk smooth; outer bark soft; stems terete and striate to squarish and hollow in age, lacking interpetiolar glands; stems, petioles, petiolules, and inflorescence branches with short rufous pubescence; tendrils simple or weakly trifid; pseudostipules small. Leaves 2- or 3-foliolate; petioles 2–11 cm long; terminal petiolules 3.2–7.2 cm long, the lateral petiolules 0.7–4 cm long;

leaflets ovate to obovate, acute to acuminate, usually cordate and sometimes inequilateral at base, 3–20 cm long, 2–12 cm wide, sometimes sparsely hispid above, with short dense pubescence on veins above and below and with pellucid dots and conspicuous round glands throughout, dentate to entire. Racemes short, axillary or terminal; calyx campanulate, 1–1.6 cm long, densely rufous-puberulent, sparsely glandular near apex; corolla 3–5 cm long, cream-colored, papillose-puberulent and sparsely glandular-lepidote outside; stamens included, the longer ones 1.5–1.8 cm long, the shorter ones 1.1–1.2 cm long, the thecae divaricate, 2–2.5 mm long; staminodium 3–5 mm long, inserted ca 1 cm from base of corolla; pistil 2.7–3.1 cm long; ovary linear, tetragonal, to 4 mm long, glandular-lepidote. Capsules elongate-linear, somewhat flattened, elliptical in cross section, 30–60 cm long, 7–8 mm broad, somewhat glandular-lepidote and with dense, short, rufous puberulence; seeds 4–5 mm long, 13–24 cm wide, the wings membranaceous, brown, weakly demarcated. *Croat 10200*.

Seedlings common. One fertile collection was made by J. D. Hood (1040) in 1933. Flowers mostly from April to November, with few, long-lived flowers at a time. Seed release is aseasonal (Gentry, 1972).

The species has been confused with *Stizophyllum perforatum* (Cham.) Miers (now called *S. longisiligum* (Vell.) Burr. ex Baillon), which grows only in Brazil.

The species is recognized by the pellucid dots and conspicuous round glands on the leaf surfaces.

Mexico to Peru and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién, from premontane moist forest in Panamá, and from premontane wet forest and tropical wet forest in Colón, Panamá, and Darién.

TABEBUIA Gomes ex DC.***Tabebuia guayacan*** (Seem.) Hemsl., Biol. Centr.-Amer.

Bot. 2:495. 1882

Guayacán

Tree, 15–40 (50) m tall, to 1.5 (2) m dbh, usually lacking prominent buttresses, glabrous except for minute, simple or stellate trichomes in vein axils of leaflets below and on a few flower parts; outer bark thick, deeply fissured

KEY TO THE SPECIES OF TABEBUIA

- Flowers pink; leaflets and calyces densely whitish-glandular-lepidote, never with trichomes, with plate-shaped glands at least in lower leaflet axils; fruits with a smooth surface *T. rosea* (Bertol.) DC.
- Flowers yellow; leaflets with stellate trichomes below, at least in axils, lacking plate-shaped glands in axils; fruits with a rough surface:
- Leaflets often 7, pubescent only in axils of lateral veins below; calyx pubescent with sparse, thick, stellate trichomes; fruits \pm lepidote, with conspicuous irregular ridges and tubercles *T. guayacan* (Seem.) Hemsl.
- Leaflets rarely 7, pubescent throughout below, at least along veins; calyx woolly-pubescent with shorter stellate and longer barbate or simple trichomes; fruits at least sparsely stellate-pubescent, lacking conspicuous ridges and tubercles *T. ochracea* (Cham.) Standl. var. *neochrysantha* A. Gentry



Fig. 499. *Tabebuia guayacan*



Fig. 500. *Tabebuia rosea*



Fig. 501. *Tabebuia rosea*

vertically, the plates between fissures broken into scales, flaky and shaggy on older trees; wood very hard, heavy; branchlets subtetragonal; pseudostipules and interpetiolar glands lacking. Leaves palmately 5- or 7-foliolate, deciduous; petioles 7–10 (23) cm long; petiolules 2–4.5 cm long; leaflets ovate to elliptic, acuminate, acute to broadly rounded at base, minutely glandular-dotted, entire, the terminal leaflet largest, 9–30 cm long, 3.5–15.5 cm wide. Flowers precocious, the panicles dense, terminal; calyx campanulate, 1–1.5 cm long, usually shallowly 5-lobed, sparsely stellate-pubescent; corolla yellow, 6–11 cm long, almost as wide, glabrous outside, softly pubescent on nectar guides inside, the tube brownish, the lobes 4–4.5 cm long, obovate; stamens held against glabrous side of tube, the longer pair 1.5–2.5 cm long, the shorter 12–17 mm long; filaments arched, each pair of anthers facing each other, the thecae divaricate, 2–3 mm long; pistil 2.4–3.3 cm long; ovary linear, 3–5 mm long, glabrous to lepidote. Capsules cylindrical, terete with conspicuous irregular ridges and tubercles, 30–50 (61) cm long, 1.5–2.5 (2.9) cm diam, glandular-lepidote; seeds 9–11 mm long, 3.5–4 cm wide, the wings hyaline-membranaceous, sharply demarcated from body of seed. *Croat 5388, 7940.*

Frequent in the forest. Flowers almost exclusively in one or two brief bursts during the dry season (January to May), but with occasional asynchronous individuals flowering during the rainy season. The fruits mature mostly near the end of the dry season, but some seeds fall in the early rainy season. Leaves fall during the dry season.

The species can be recognized by having leaves often with seven leaflets and stellate trichomes in the lower vein axils (Gentry, 1973b).

Mexico to Colombia. In Panama, known from tropical moist and tropical wet forests in the Canal Zone, Colón, and Darién, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí.

See Fig. 499.

Tabebuia ochracea* (Cham.) Standl. var. *neochrysantha A. Gentry, *Brittonia* 22:260. 1970

T. heterotricha DC.; *T. chrysantha* (Jacq.) G. Nicholson sensu Sandw. non Jacq.

Tree, to 25 m tall and to 50 cm dbh; outer bark with shallow vertical furrows separating flat-surfaced ridges; wood hard, heavy; branchlets subtetragonal, stellate-pubescent when young, glabrate in age; glands and pseudostipules lacking. Leaves palmately 5-foliolate, deciduous; petioles 6–18 cm long, stellate-pubescent; petiolules 0.2–5.1 cm long; leaflets mostly oblong-obovate, abruptly acuminate, obtuse to truncate (rarely subcordate) at base, membranaceous, lepidote on both surfaces, the pubescence stellate, sparse above and dense below, the margins entire to serrate, the terminal leaflet largest, 5–22 cm long, 1.8–4.4 cm wide. Inflorescences contracted terminal panicles, branches stellate-pubescent; flowers precocious; calyx campanulate, 5-lobed, 8–15 mm long, woolly-pubescent with shorter stellate and longer (to 7 mm) simple trichomes; corolla yellow, tinged reddish in throat, 4–8.3 cm

long, nearly glabrous outside, villous inside, glandular-pubescent at level of stamen insertion, the tube brownish (at least in dried specimens), 3–5.8 cm long; stamens didynamous, the longer ones 1.5–2 cm long, the shorter ones to 1.5 cm long, the thecae divaricate, 1.5–2.5 mm long; staminodium 2–11 mm long; pistil 2–2.7 cm long; ovary linear, to 5 mm long, lepidote to puberulent with simple and stellate trichomes. Capsules cylindrical, terete, tapered at both ends, 13–25 cm long, 1–1.5 cm wide, with golden woolly pubescence of short stellate trichomes and longer, \pm simple trichomes; seeds 4–8 mm long, 1.8–2.9 cm wide, the wings hyaline-membranaceous, distinctly demarcated from body of seed. *Croat 6915.*

Known only as a seedling on BCI, but easily occurring as an adult as well. Elsewhere in Panama flowers from January to April with apparently two brief bursts of flowering. The fruits are mature in the middle to late dry season (Gentry, 1972).

Superficially the species looks much like *T. guayacan*. BCI would be about the limit of the species' range toward the wetter Atlantic slope.

The species *T. ochracea* ranges from Honduras to Brazil; var. *neochrysantha* occupies the northern part of the range, extending as far south as Venezuela. In Panama, the variety is known from drier parts of tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién, from tropical dry forest in Coclé and Herrera, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé.

***Tabebuia rosea* (Bertol.) DC., Prodr. 9:215. 1845**

T. pentaphylla (L.) Hemsl.

Roble, Roble de sabana

Tree, 5–35 m tall, 1 m dbh; outer bark deeply fissured, very thick; inner bark thick, with annular rings; stems, petioles, and leaflets moderately lepidote throughout. Leaves palmately 3–5-foliolate; petioles 5–25 (32) cm long; petiolules 0.2–8 cm long, of varying lengths on one petiole; leaflets broadly elliptic, abruptly acuminate, obtuse to rounded or slightly subcordate at base, 5–22 cm long, 2–11 cm wide, with clusters of round glands in vein axils at base below. Flowers precocious, the panicles terminal, cymose; calyx bilabiate, 1.5–2.5 cm long, densely glandular-lepidote, persisting in fruit; corolla lavender to whitish, 6–11 cm long, glabrous outside, pubescent inside on lobes and especially on nectar guides within tube on 3-lobed side of corolla; stamens with the longer filaments 1.4–2 cm long, the shorter ones 1–1.5 cm long, the thecae divaricate, 2.5–3.5 mm long; staminodium 2–6 mm long, inserted 5–10 mm from base of corolla; pistil 1.9–3.2 cm long; ovary linear, 5–8 mm long, densely lepidote. Capsules cylindrical, elongate, terete or somewhat flattened, 25–35 cm long, ca 1.5 cm wide, densely lepidote and also with a few larger, crateriform glands, lacking projections. *Croat 7771, 8394.*

Frequent throughout the island. Flowers most abundantly in March and April (sometimes in February); individuals produce an extravagant burst of flowers over a long period. The fruits are seen all year; seeds are re-

leased mostly in the early rainy season. Leaves fall possibly twice per year, once in the dry season and again around July.

The species can be recognized when sterile by its leaves, which have five leaflets and are lepidote but otherwise glabrous (Gentry, 1973b).

Mexico to Colombia and Venezuela; West Indies; ranging from near sea level to 1,500 m. In Panama, a characteristic species of tropical dry, premontane moist, and tropical moist forests (Tosi, 1971); known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, Coclé, Panamá, and Darién, and from tropical wet forest in Colón, Veraguas, and Panamá.

See Figs. 500 and 501.

TYNNANTHUS Miers

Tynnanthus croatianus A. Gentry, Ann. Missouri Bot. Gard. 58:93. 1971

Liana; stems terete, glabrous, the young stems moderately lenticellate, the older stems conspicuously roughened; interpetiolar ridges indistinct; tendrils trifid; pseudostipules minute, acute, the apex caducous, leaving a brown scar on base, the base bulbous, less than 2 mm high. Leaves 3-foliolate, or 2-foliolate with a tendril scar, glabrate to inconspicuously pubescent; petioles longer than petiolules, mostly (1.4) 3–7 cm long; terminal petiolule 2.8–3.3 cm long, longer than lateral ones; leaflets ovate-elliptic, abruptly acuminate, obtuse to rounded at base, mostly 5–13 cm long, 2.5–7.5 cm wide, bicolorous, entire; reticulate veins distinct on paler lower surface, the lateral veins in 3–5 pairs. Inflorescences axillary and terminal, paniculate, usually less than 6 cm long, for the most part minutely and densely pubescent; calyx less than 4 mm high, truncate, commonly with 1 obscure tooth, glabrous inside; corolla white, mostly about 1.5 cm long, about as wide, bilabiate, with 2 lobes almost completely fused, glabrous inside, the opposing 3 lobes with nectar guides at base and alternate with them; nectar guides two, yellow; stamens with the longer pair below nectar guides, almost equaling petals; filaments connate near base, the longer ones 1–1.2 cm long, the shorter ones 0.9–1 cm long, the thecae divaricate, ca 1.3 mm long; staminodium ca 5 mm long, inserted 2 mm from base of corolla tube; pistil 16–17 mm long; ovary conical, 1.5–2 mm long, densely pubescent; style pubescent, exceeding anthers; stigmas 2, pointed. Capsules linear, flattened, long-acuminate at apex, to 35 cm long, ca 1 cm wide, 0.5 cm thick, sparsely to densely puberulent (at least when young), the lateral edge with prominently raised margins; seeds 6–7 mm long, to 17 mm wide, the upper edge with rounded corners, the lower edge flat, the corner square. *Croat 11927* (type), *13975*.

Rare, known from the south shore of the island and near the Laboratory Clearing. Flowers mostly in July

and August with extravagant, long-lasting bursts of flowers. The fruits are mature from late November to March.

The species can be recognized in sterile condition by its trifid tendrils, subtetragonal young stems, four-angled pith, and sap with the aroma of cloves (Gentry, 1973b).

Panama and probably Colombia. In Panama, known from tropical moist forest in the Canal Zone, eastern Panamá, and Darién.

XYLOPHRAGMA Sprague

Xylophragma seemannianum (O. Kuntze) Sandw., Kew Bull. 1953:469. 1954

Saldanhaea seemanniana O. Kuntze

Pié de gallo, Pink bell

Liana; stems terete, prominently lenticellate, with interpetiolar glandular fields; most younger parts densely stellate-pubescent; tendrils simple, few, becoming large and woody; pseudostipules inconspicuous or ovate to triangular, to 4 mm long, distichously arranged in dense clusters. Leaves 3-foliolate or with a tendril replacing terminal leaflet, appearing after onset of flowers, deciduous; petioles 7–12 cm long; petiolules 1–7 cm long; leaflets ovate, oblong-ovate, or obovate, abruptly acuminate, obtuse to rounded or subcordate at base, to 13(28) cm long and 7(15) cm wide, stellate-tomentose or glabrate in age except on veins. Panicles dense, in axils of fallen leaves, appearing before new leaves; flowers sweetly aromatic; pedicels, calyces, and corollas (except tube near base) densely pubescent with branched trichomes; calyx narrowly campanulate, 5–7.5(9) mm long, 5-costate, the costae extending beyond margin to form short teeth; corolla lavender-pink, 3.5–5.5(6) cm long, the tube white, glabrous inside; stamens with the longer pair 1.6–2.1 cm long; anther thecae divaricate, 2.3–3.5 mm long; pistil 2.1–2.8 cm long; ovary tapered-cylindrical, ± flattened, 1.5–2.5 mm long, densely lepidote. Capsules oblong, smooth, ± compressed, 9–18(25) cm long, to 5 cm wide; seeds 2–2.5 cm long, to 4.5 cm wide, the body orbicular, tan, cordate at base, to 2 cm wide, the wings transparent. *Croat 13962*, *Foster 705*.

Moderately uncommon. Flowers in the late dry season (March to May), with extravagant, long-lasting bursts of flowers. The fruits mature in the following dry season. Leaves fall during the dry season and are replaced shortly after flowering.

The species can be recognized when sterile by its relatively large leaves with stellate (dendroid) pubescence and by its interpetiolar glandular fields.

Mexico and Belize to Colombia, Venezuela, and the Guianas; Trinidad. In Panama, known only from the Pacific slope (except in the Canal Zone), from drier areas of tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí, Panamá, and Darién.

127. GESNERIACEAE

Epiphytic, hemiepiphytic, or terrestrial shrubs, vines, or perennial herbs, generally succulent; stems usually creeping, loosely rooted. Leaves opposite, petiolate; blades simple, serrate; venation pinnate; stipules lacking. Flowers bisexual, zygomorphic, solitary or in cymose, fasciculate, or racemose inflorescences; peduncles or pedicels bracteate; calyx deeply 5-lobed (may be toothed as well); corolla tubular, bilabiate, 5-lobed, showy; stamens 4, didynamous, epipetalous; anthers connate, 2-celled, dehiscent longitudinally; nectariferous disk ringlike; ovary superior or partly inferior, 1-locular, 2-carpellate; placentation parietal; ovules numerous, anatropous; style 1; stigma 1 and bilobed or scoop-shaped. Fruits loculicidal, 2-valved capsules or berries; seeds many, with abundant endosperm.

Distinguished by being small epiphytic or hemiepiphytic shrubs or vines or soft, juicy-stemmed herbs with opposite, frequently toothed leaves and showy, often somewhat zygomorphic, frequently gibbous flowers with usually four stamens held to one side of the throat.

Columnnea billbergiana, *C. purpurata*, *Kohleria tubiflora*, and probably *Besleria laxiflora* are hummingbird

pollinated. All other species, with the possible exception of *Drymonia serrulata*, for which bat pollination has been suggested (Vogel, 1958), are probably insect pollinated. Euglossine bees are probably responsible for pollination of *Chrysothemis*, *Codonanthe*, *Drymonia*, and *Nautilocalyx*. It is suspected that *Diastema raciferum* may be pollinated by butterflies (H. Wiehler, pers. comm.).

Most species on BCI probably have bird-dispersed seeds, though *Drymonia serrulata* may be in part bat dispersed and *Codonanthe crassifolia* and possibly *Chrysothemis friedrichsthaliana* and *Nautilocalyx panamensis* may be transported by ants. Seeds of *Diastema raciferum* and *Kohleria tubiflora* are dispersed by the wind with a "salt shaker" action.

Some 140 genera and about 1,800 species; mostly in the subtropics and tropics in Asia and Central and South America.

BESLERIA L.

Besleria laxiflora Benth., London J. Bot. 5:361. 1846

Terrestrial shrub or suffrutescent herb; stems densely strigose when young. Leaves elliptic or narrowly oblong,

KEY TO THE SPECIES OF GESNERIACEAE

Flowers white:

Plants terrestrial:

Corolla ca 2 cm long; calyx less than 8 mm long; nectary of 5 individual glands; plants with scaly rhizomes *Diastema raciferum* Benth.

Corolla 4–4.5 cm long; calyx 1.5–2 cm long; nectary of 1 large dorsal gland; plants lacking rhizomes but often with tubers *Nautilocalyx panamensis* (Seem.) Seem.

Plants epiphytic or hemiepiphytic:

Calyx leaflike, the lateral lobes more than 4 cm long; corolla ca 6 cm long, the limb more than 3 cm wide; fruits fleshy, 2-valved, capsular; leaf blades dentate, usually more than 8 cm long *Drymonia serrulata* (Jacq.) Mart.

Calyx small, the lateral lobes less than 1 cm long; corolla less than 4 cm long, the limb less than 2 cm wide; fruits berries; leaf blades entire or serrate, usually less than 6 cm long:

Calyx winged (with long decurrent keels), the lateral lobes at anthesis less than 3 mm long; corolla more than 3 cm long, the limb more than 1.5 cm wide . . . *Codonanthe uleana* Fritsch

Calyx lacking wings or ridges, the lateral lobes at anthesis ca 6 mm long; corolla less than 2.5 cm long, the limb less than 1 cm wide *Codonanthe crassifolia* (Focke) Mort.

Flowers red, yellow, or orange:

Plants usually epiphytic or hemiepiphytic, often high in trees:

Leaves of a pair strongly unequal, the larger one more than 15 cm long; corolla yellow, tubular, 3 cm long, with a subequal limb; fruits rose-orange, ovoid berries; plants rare or possibly no longer on the island *Columnnea purpurata* Hanst.

Leaves of a pair subequal, less than 4 cm long; corolla red-orange, strongly bilabiate, 5–7 cm long; fruits white globose berries; plants occasional *Columnnea billbergiana* Beurl.

Plants terrestrial:

Calyx lobes connate four-fifths of their length, the calyx 5-angled; corolla 8 mm longer than calyx; nectar guides red lines, on 2 lobes; nectary of 1 large dorsal gland; fruits 2-valved capsules *Chrysothemis friedrichsthaliana* (Hanst.) H. E. Moore

Calyx lobes free from one another, the calyx without angles; corolla 15–25 mm longer than calyx; nectar guides lacking; nectary of 5 glands or ring-shaped:

Corolla densely pubescent, 2.5–3 cm long, constricted in throat, the subequal lobes ca 2 mm long; nectary consisting of 5 glands; fruits 2-valved capsules; leaves conspicuously soft-pubescent below *Kohleria tubiflora* (Cav.) Hanst.

Corolla glabrous, ca 2.2 cm long, only slightly constricted in throat, the lobes of the limb ca 3 mm long, flared; nectary ring-shaped; fruits red-orange berries; leaves glabrous or inconspicuously pubescent below *Besleria laxiflora* Benth.

those of a pair equal or unequal, mostly 10–21 cm long, 4–8.5 cm broad, sparsely strigillose on veins beneath. Flowers in umbellate or cymelike clusters; peduncles to 4.5 cm long; pedicels about as long as peduncles; calyx 7.5–14 mm long, orange or red, one-third to one-half as long as corolla, the lobes ovate to ovate-lanceolate, attenuate to a mucro; corolla red or orange, erect, slightly swollen at base, to 2.2 cm long, glabrous on outside, with a glandular throat inside and a ring of pubescence at the staminal insertion; ovary superior, glabrous; stigma shallowly bilobed, the lobes broadened laterally; nectary ring-shaped. Berries globose, 1–12 mm diam, red or orange; seeds many, small, reddish-brown.

Reported by Kenoyer and Standley (1929) from near the laboratory, but the ecology of the Laboratory Clearing has changed so remarkably since that time that it is unlikely that the species still occurs on the island; no collections of it have been seen. Flowers and fruits elsewhere in Panama throughout the year, mostly in the rainy season. Plants often have both flowers and mature fruits.

Mexico to Colombia, Venezuela, the Guianas, and Brazil; from sea level to 1,400 m. In Panama, ecologically variable, but generally growing in weedier habitats than are now common on BCI; known from tropical moist and premontane wet forests in all provinces and apparently from other life zones at higher elevations as well.

CHRYSOTHEMIS Dec.

Chrysothemis friedrichsthaliana (Hanst.) H. E.

Moore, *Baileya* 2:87. 1954

Tussacia friedrichsthaliana Hanst.

Terrestrial or epiphytic herb; stems obscurely 4-sided, succulent, ca 1 cm thick. Petioles short, flattened; leaf blades broadly elliptic, acute to acuminate at apex, cuneate at base and decurrent onto petiole, 8–40 cm long, 4–16 cm wide, irregularly crenate-serrate, short-pilose above, puberulent below especially on midrib and veins, dark green and shiny above, pale below; veins impressed above, raised below. Inflorescences axillary from upper leaves, usually of 3 pedicellate flowers atop a bracteate peduncle; pedicels 1–4 cm long; calyx green or yellow, inflated, mostly to 2 cm long, irregularly 5-lobed, with 5 broad lateral wings; corolla 5-lobed, slightly asymmetrical, 1.9–2.8 cm long, \pm glabrous, yellow or orange at least on the distal part of tube and lobes, the lobes with red lines inside extending somewhat into tube, the tube constricted 3–4 mm above base between the lower 2 lobes; stamens 4, ca 12 mm long; filaments recurved at apex; ovary superior; style mostly glabrous, 5–8 mm long; stigmas bilobed; nectary of 1 large dorsal gland. Capsules 2-valved, fleshy, pubescent, 7–10 mm diam; seeds many, to 0.6 mm long, about twice as long as wide, with a fleshy, enlarged funicle. *Croat 5930, 11708.*

Occasional in the forest and the Laboratory Clearing, often on moist rocks, or rarely on rotting wood. Flowering and fruiting throughout the rainy season (May to December). Individuals flower for a relatively long time,

with some fruits maturing while the plant is still in flower.

Easily recognized by the succulent stems, inflated calyx, and orange flowers with red lines. H. Wiehler (pers. comm.) reports having seen seeds of this species being carried away by ants, with the funicle still attached, both in the field and in the greenhouse. It is not known if this is the sole means of dispersal.

Central America to western Colombia. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Panamá, and Darién; known also from premontane wet forest in Bocas del Toro (Río Guarumo) and from tropical wet forest in Colón (Portobelo).

CODONANTHE (Mart.) Hanst.

Codonanthe crassifolia (Focke) Mort. in Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18:1159. 1938

C. confusa Sandw.

Small epiphytic or hemiepiphytic shrub, usually less than 30 cm long, rooting at nodes, glabrous or with most parts minutely puberulent. Leaves thick; petioles 5–15 mm long; blades variable, ovate to obovate, obtuse to short-acuminate at apex, acute at base, 1.5–6 cm long, 1–2.5 cm wide; lateral veins indistinct. Flowers axillary, 1–4 borne together; pedicels puberulent; calyx puberulent, deeply 5-lobed, ca 5–7 mm long, the lobes slender, the dorsal lobe depressed by corolla, the 4 erect lobes with 3 glands in the sinus, the lateral lobes ca 6 mm long at anthesis; corolla bilabiate, 1.9–2.2 cm long, white, mottled with red inside below the 2-lobed side of lip, minutely puberulent on 3-lobed side, the limb 9–10 mm wide, the lobes rounded, broader than long, the tube gibbous, extending prominently below calyx; stamens 4, included, the longer pair to 2.5 cm long; filaments curved at apex, widened toward base; anthers oblong, to 2 mm long, coherent in pairs or free; staminodium very small; ovary superior, oblong-ovoid, puberulent; style longer than stamens; stigma 1, scoop-shaped, held just above stamens; both stamens and stigmas \pm appressed against the 3-lobed side of corolla; nectary of 1 large dorsal gland. Berries subglobose, 10–12 mm long, 7–9 mm wide, red, \pm glabrous; seeds reddish, slightly curved, ca 2 mm long and 0.7 mm wide, longitudinally striate. *Croat 5916.*

Frequent in the forest, usually rather high in trees. Flowering and fruiting throughout the year, but most abundantly in the rainy season. Fruit development time is probably about 1 month.

Standley considered *Codonanthe calcarata* Hanst. a synonym of this species, but the name was misapplied according to Leeuwenberg (1958).

Like most other members of the genus, *C. crassifolia* is usually associated with ant nests, though many seedlings are found in cracks in tree bark and are not attended by ants. The ant nests frequently also contain *Aechmea tillandsioides* (22. Bromeliaceae).

The fruit is perhaps most logically adapted for bird

dispersal, but ants may carry the seeds away after the fruits have been pecked open by birds. It is possible that fruits occasionally dehisce. In the greenhouse, H. Wiehler (pers. comm.) has shown that, if plants are not watered for a few days while the fruit is still immature and then watered excessively as the fruit ripens prematurely, the fruit will break open from the excess water.

Guatemala to Colombia, Venezuela, the Guianas, and Peru; Trinidad; from sea level to 1,400 m. In Panama, known principally from tropical moist, premontane moist, and tropical wet forests all along the Atlantic slope and from tropical moist forest in Darién; known also from premontane wet forest in Colón (Santa Rita Ridge) and Panamá (Cerro Jefe).

See Fig. 502.

Codonanthe uleana Fritsch, Bot. Jahrb. Syst. 37:492. 1906

Small epiphytic or hemiepiphytic shrub; very much like *Codonanthe crassifolia* but with the leaf blades oblanceolate to obovate, to 9 cm long and 3.5 cm wide; the calyx 5–6 mm long at anthesis, with the underside of each sepal (especially the lowest one) bearing a long decurrent keel, the lateral lobes 1.3–2.5 mm long at anthesis, to 3.5–4 mm long in fruit; the corolla 3.5–3.8 cm long, the limb 1.5–2 cm wide; the anthers with the pores adorned by 2 minute horns. *Wilson 65*.

Not seen recently. Seasonal behavior uncertain, probably much like that of *C. crassifolia*.

Southern Mexico to Brazil (upper Amazon), Peru, and Bolivia. In Panama, known from tropical moist forest in the Canal Zone and Panamá (San José Island) and from premontane wet forest or tropical wet forest in Colón (Santa Rita Ridge).

COLUMNEA L.

Columnea billbergiana Beurl., Kongl. Vetensk. Acad. Handl. 1854:135. 1854

Small epiphytic or hemiepiphytic shrub, usually rather high in trees and pendent; stems brown, branched, 2–4 mm diam, sparsely strigose when young. Leaves of a pair subequal; petioles 2–6 mm long, strigose; blades ovate-lanceolate, acute, broadly cuneate at base, 2–3 cm long, 8–11 mm wide, thick, glabrous above, pale and strigose below; major lateral veins in 3 pairs. Flowers solitary; peduncles 5–10 mm long; pedicels 5–13 mm long, densely pilose, the trichomes long, white or pink, the bracts linear-lanceolate, 3–6 mm long; calyx 8–12 mm long, red, the lobes 5, ovate-lanceolate, acuminate, 5–8 mm long, white-sericeous outside, glabrous inside, denticulate, the teeth 1–4 on each side, glandular; corolla red, 5–7 cm long, slender, swollen and gibbous at base, sparsely hispid outside, 4-lobed, deeply divided on one side, the upper lobe rounded and apiculate at apex, to 1.5 cm long, the lateral lobes connate to upper lobe, the free parts to ca 8 mm long, acute, the lower lobe 1.2–1.8 cm long, somewhat deflexed; stamens 4, exserted; filaments red

except white at base, nearly as long as and held against upper lobe of corolla; ovary superior, glabrous except at apex; style white, glabrous or sparsely glandular-pilose, equaling or slightly longer than stamens; stigma 1, bilobed; nectary of 1 large dorsal gland. Berries white, globose, ca 1.4 cm diam; seeds yellow, embedded in funicular pulp. *Croat 10088*.

Occasional to frequent in the forest. Flowers sparingly all year, but especially in the rainy season. H. Wiehler (pers. comm.) reports a burst of flowering in October for cultivated plants in Panama.

Distinguished by its epiphytic or hemiepiphytic habit and slender zygomorphic flowers. Ridley (1930) discussed the adaptation to ornithochory obvious in the white berry and contrasting red sepals. H. Wiehler (pers. comm.) suspects that *Columnea arguta* Mort., found in areas surrounding BCI, might also be found on the island.

Known only from Panama, from sea level to 1,000 m, most abundantly from premontane wet forest in Coclé and Panamá, but also from tropical wet forest in Colón (Portobelo) and tropical moist forest in the Canal Zone (vicinity of Gatun Lake).

Columnea purpurata Hanst., *Linnaea* 34:386. 1865
Dalbergaria sanguinea (Pers.) Steud.

Shrub, 1.2–1.8 m long, usually hemiepiphytic, rarely terrestrial; stems woody, unbranched, 6–10 mm diam, densely yellowish-hirsute. Leaves clustered at apex of stem, those of a pair strongly unequal; larger ones short-petiolate, on petioles 10–15 mm long, densely hirsute, the blades oblanceolate, long-acuminate, cuneate and inequilateral at base, 13–30 cm long, 4–10 cm wide, serrulate, pilose on both sides, with the major lateral veins in 9–11 pairs; smaller leaf of a pair sessile, ovate, oblique, long-acuminate at apex, obtuse at base, to 3 cm long and 1 cm wide, deeply toothed, hirsute. Flowers fasciculate in upper axils, 5-parted; peduncles very short, bracteate, the bracts scarlet, elliptic or lanceolate, ca 3 cm long, pilose outside, strigose inside, spinulose-toothed, the teeth 4 or 5 per side; calyx ca 3 cm long, scarlet, the lobes lanceolate, 5 mm wide near base, long-acuminate, the pubescence similar to that on bracts; corolla tubular, ca 3 cm long, yellow, the tube ca 4 mm diam at base, expanding to 7 mm diam, contracted toward throat, densely brown-sericeous outside, glabrous inside, the limb narrow, regular, about 6 mm wide, the lobes subequal, erect, 4 mm long and 3 mm wide; stamens 4; filaments glabrous at base, short-pilose above; anthers connate, ca 2 mm long and 2 mm wide; ovary superior, long-pilose; style glabrous; nectary of 1 large dorsal gland. Berries oblong-ovoid, rose-orange; seeds light yellow with enlarged funicles. *Standley 31393*.

Collected once on the island by Standley and possibly no longer occurring there. Probably flowering and fruiting all year.

Southern Mexico to Venezuela, the Guianas, and Bolivia; Trinidad; Hispaniola. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

DIASTEMA Benth.

Diastema raciferum Benth., Bot. Voy. Sulphur
132. 1845

D. exiguum Mort.

Herb, to 17 cm tall, sparsely pilose; rhizomes scaly; basal nodes of stems often with adventitious roots; stems, petioles, and inflorescences often flushed with maroon. Petioles 4–4.5 (7.5) cm long; leaf blades ovate to elliptic, acute, obtuse to subcordate and \pm inequilateral at base, 3.5–10 cm long, 2.5–5.5 cm wide, serrate, with 3 or 4 teeth per cm, sparsely pilose to glabrate above, \pm glaucous and glabrous to pubescent at least on the veins below; veins at margins strongly arching upward. Racemes 1.5–8 cm long, long-bracteate, terminal, but secondary racemes often in leaf axils of more mature plants (at first appearing as mere fascicles of leaves); peduncles 10–35 mm long, the bracts foliaceous, elliptic, ca 5 mm long, entire; pedicels 5–15 (25) mm long; calyx turbinate, 5–8 mm long, acutely 5-lobed to two-thirds its length; corolla white with yellow throat (pink in var. *lilacinum* Mort., perhaps to be found on the island), salverform, weakly bilabiate, ca 2 cm long, substrigose outside, glabrous inside, the lobes 5, rounded, 1–2 mm long; stamens 4, didynamous; filaments slender, free, to ca 10 mm long; anthers free, the thecae orbicular; ovary partially inferior, ovoid, minutely puberulent; style slender, to 8.5 mm long, withering from fruit; stigma 1, deeply bilobed, flat, \pm winglike, ca 1 mm wide; nectary of 5 individual glands, subulate, to 1.3 mm long. Capsules dry, ca 6 mm long, splitting along only 1 side; seeds brown, very small. *Kenoyer 539a*.

Collected once by Kenoyer; an inconspicuous plant of gulleys and ravines, it is probably still growing on the island, though it has not been seen in recent years. The plant dies back during the dry season in areas having a distinct dry season, and the rhizome is protected from desiccation by a layer of scales.

The pollinator is unknown, but H. Wiehler (pers. comm.) indicates that a very similar species in Venezuela is pollinated by the butterfly *Leucothyris makrena makrena* Hew. (Nymphalidae, Ithomiinae).

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Coclé.

DRYMONIA Mart.

Drymonia serrulata (Jacq.) Mart., Prodr. 7:543. 1839

D. spectabilis (H.B.K.) Mart. ex G. Don
Calabash vine

Climbing or creeping vine, hemiepiphytic at least when juvenile, often with many aerial roots; older stems with a paperish red bark; younger parts succulent. Petioles 6–30 mm long; blades asymmetrical, acute to shortly acuminate at apex, oblique at base, 5–17 cm long, 3–9 cm broad, slightly fleshy, dark green and scabrous above, paler below (juvenile leaves often purplish below), gla-

brous to slightly pubescent, the margins dentate. Flowers usually solitary in axils; calyx foliaceous, puberulent, 5–6 cm long, the lobes 5, free, cordate, all but the central one very asymmetrical, persistent in fruit; corolla bilabiate, thick, 5–7 cm long, usually white or cream at least on tube and outer surface, the limb 3.5–4.5 cm wide, the lobes 5, dentate, marked with red or violet-purple inside, the upper lip with nectar guides extending into throat, the lobes smaller, the tube asymmetrical, gibbous at base and below the upper lip, the upper concavity with gland-tipped trichomes; stamens 4; filaments broadened at base, twisting in age to draw anthers to bottom of corolla; anthers ca 8 mm long, held together in pairs in throat of corolla, the apex directed downward, the thecae opening at base of anther; ovary superior; style ca 2.5 cm long, densely glandular-pubescent, held between 2 prominent lobes within the tube basal to the lower lip, elongating after opening of anthers, hollow-tubular at apex; stigma 1, with 2 opposing lobes to 4 mm long; nectary of 1 large dorsal gland. Capsules \pm globose, 10–20 cm long; valves 2, bright orange to red inside, curving back at maturity to expose the cone-shaped cluster of placental and funicular tissue covered with seeds; seeds many, shiny, black, oblong, tapered at ends, twisted, ca 1 mm long. *Croat 6054, 6121*.

Common along the edge of the lake, occurring occasionally in the forest high in the canopy. Flowers from June to January, principally in the early to middle rainy season. The first fruits mature usually by August, and some are no doubt still present well into the dry season.

The pollinator probably hits the apex of the anther as it enters the corolla, turning the anther over and dumping out the pollen.

Seeds are possibly dispersed in part by birds, which might be attracted to the black cluster of seeds sharply contrasted against the red inner valve surfaces. H. Wiehler (pers. comm.) has indicated that the cluster of seeds sometimes smells like cabbage, indicating possible bat dispersal.

Throughout most of tropical America from Mexico to Brazil (Mato Grosso) and Bolivia; Lesser Antilles. In Panama, known principally from tropical moist forest in all regions (except lowland Chiriquí) where forest still exists; known less frequently from premontane wet forest, tropical wet forest, and premontane rain forest in Chiriquí, the Azuero Peninsula, and central Panamá.

See Fig. 503.

KOHLERIA Reg.

Kohleria tubiflora (Cav.) Hanst., Linnaea 34:442.
1865–66

Coarse perennial herb, often more than 1 m tall, \pm villos, the trichomes of varying lengths, longest on stems, petioles, and midribs of lower blade surface; stems often with maroon streaks mottled with smaller, green, elongate spots. Petioles 1–7.5 cm long; blades ovate to oblong, acute, rounded to cordate at base, mostly 4–14 cm long, 2.5–9 cm wide, crenate, bicolorous, often maroon and



Fig. 502. *Codonanthe crassifolia*



Fig. 504. *Kohleria tubiflora*

Fig. 503. *Drymonia serrulata*



soft-pubescent beneath. Flowers axillary, tubular, ca 4.5 cm long, usually 3–5 in each axil, pedicellate; calyx lobes 5, acute, often tipped with maroon, accrescent in fruit; corolla orange-red, 2.5–3 cm long, ca 1 cm wide, constricted near apex, villous outside, glabrous inside except for a few glandular trichomes near apex, the lobes small, rounded, ca 2 mm long, with purple spots on inner surface; stamens 4, ca two-thirds the length of tube; filaments free, curled at apex; anthers nearly as broad as long, at first fused together in a single unit; ovary partly inferior, densely velutinous; style held below constriction of the corolla tube above stamens; stigma bilobed; nectary of 5 distinct glands ca 2.3 mm long, persisting in fruit. Capsules ovoid, ca 1 cm long, reddish, apparently splitting open at maturity by 2 thick valves; seeds reddish, minute, \pm oblong, tapered to both ends, loose at fruit maturity (indicating wind dispersal). *Croat 6355*.

Occasional, in clearings, in open areas of the forest, and on the lakeshore, apparently preferring disturbed banks; may be locally abundant. Flowers principally in the rainy season, especially in the last half of the rainy season. Mature-sized fruits may be seen by October, but the actual time of seed dispersal is not known. Since it appears likely that the seeds may be wind dispersed, they may be shed in the early dry season.

Recognized by the brightly colored, tubular flowers, which are somewhat constricted at the apex, and by the semi-inferior ovary.

Central Costa Rica to Colombia and western Venezuela. In Panama, known most commonly from tropical moist, premontane wet, and tropical wet forests along the Atlantic slope in the vicinity of the Canal Zone and also from tropical moist forest in Darién and from premontane wet forest at higher elevations on the Pacific slope; known infrequently from the Pacific slope of the Canal Zone.

See Fig. 504.

NAUTILICALYX Linden

Nautilocalyx panamensis (Seem.) Seem., Bot. Voy. Herald 250. 1854

Achimenes panamensis (Seem.) Hemsl.; *Episcia panamensis* (Seem.) Mort.

Perennial herb, 10–35 cm tall, lacking rhizomes, often with tubers; stems creeping over soil and weakly rooted; stems and petioles brittle and succulent; all parts except inner surface of corolla moderately to densely villous. Petioles mostly 3–5 cm long, flattened above, often with marginal maroon ribs; blades ovate to oblong, acute or slightly acuminate, acute to rounded at base and \pm oblique, mostly 6–15 cm long, 4–8 cm broad, thin, green and shiny above, dull below, the margins markedly crenate. Flowers axillary, usually in clusters of 3, pedicellate; calyx foliaceous, toothed, irregular, the lobes 5, free, to 2 cm long; corolla white, 4–4.5 cm long, the tube narrow, 7–10 mm wide, with linear grooves inside at base of lower

lobes, the lobes 5–7 mm long, to 10 mm broad; stamens 4, equaling or exceeding style or much shorter; filaments ultimately coiled; ovary superior; style 12–16 mm long; nectary of 1 large dorsal gland. Capsules globose, probably to ca 1 cm diam, sparsely pubescent, the trichomes flattened, crisped. *Croat 11814*.

Occasional in the forest, but locally abundant along trails or open areas. Flowers and fruits throughout the rainy season (July to December).

Distinguished by its terrestrial habit and white flowers. When the flower first opens, the styles are two-thirds as long as the anthers. The filaments are held erect, and the anthers are fused in a 2-2 arrangement. Later, the style elongates and the filaments coil up, pulling the anthers well below the style.

The fruits are similar to those of *Chrysothemis freidrichsthaliana* and are probably dispersed in the same manner.

Apparently restricted to Panama, where it is known from tropical moist forest in the Canal Zone and from premontane wet forest in Panamá (8 km southwest of Cerro Brewster).

128. LENTIBULARIACEAE

Glabrous, aquatic, insectivorous herbs; stems stoloniferous, lacking true roots. Leaves inconspicuous, stolate, or lacking, often replaced by somewhat leaflike, entire or dissected photosynthetic organs which are modified stems; the submerged vegetative parts bearing tubular insect traps. Flowers bisexual, zygomorphic, in bracteolate racemes of few flowers; calyx bilabiate; corolla 5-lobed, bilabiate, the lower lip gibbous; stamens 2, free, epipetalous; anthers 1-celled but constricted, introrse, dehiscing longitudinally; ovary superior, 1-locular, 2-carpellate; placentation free-central; ovules numerous, anatropous; style simple; stigma bilabiate. Fruits 2-valved, loculicidal capsules.

The flowers are very specialized. I have observed visits by skippers and medium-sized bees, but P. Taylor (pers. comm.) believes the flowers to be mostly self-pollinated.

The fruits fall whole and are water dispersed, but the seeds themselves sink (probably a necessary requirement for germination in the soil). Ridley (1930) reported that *Utricularia* is vegetatively dispersed by water currents or by having parts of the plant carried away on the feet of aquatic birds.

Five genera and about 250 species; cosmopolitan.

UTRICULARIA L.

Species of the genus are unusual in that they bear small bladders with trap-door entrances on the submerged parts. Small Crustacea and other small animals are sucked into the bladder by its rapid expansion after coming into contact with a trigger. The decaying animals provide nutrients for the plant (Willis, 1966).

KEY TO THE SPECIES OF UTRICULARIA

- Flowers numerous (rarely fewer than 10), \pm congested in the upper part of scape; spur of corolla lacking stalked glands at apex; pedicels strongly recurved in fruit; seeds circular, with a very narrow, thin, regular wing; stolons flattened, with 2 separated semicircular series of vascular bundles; foliar organs relatively large, repeatedly pinnately divided into very numerous capillary segments *U. foliosa* L.
- Flowers few (rarely more than 5), if more than 2 then relatively distant; spur of corolla with a few stalked glands at apex; pedicels spreading or only slightly reflexed in fruit; seeds with a relatively thick, very irregular wing; stolons terete, with a single central ring of vascular bundles; foliar organs relatively small, sparsely dichotomously divided 1–3 times only, thus with very few ultimate capillary segments *U. obtusa* Sw.

This key to *Utricularia* was provided by Peter Taylor. I have modified it slightly.

***Utricularia foliosa* L., Sp. Pl. 18. 1753**

U. mixta Barnh.

Perennial, submerged, freely suspended, insectivorous, aquatic herb; stolons robust, to several m long, distinctly flattened, to 4 mm wide, with fasciculate branches. Photosynthetic organs pinnate many times, \pm broadly ovate in outline, to 17 cm long, somewhat dimorphic, some with more traps and fewer segments; insect traps borne laterally near base of penultimate segments. Racemes erect, simple, 7–40 cm long; flowers 3–20, congested at anthesis, later spaced on rachis; scape with 1 or 2 scales below lowest flower; bracts subtending flowers broadly ovate to orbicular; pedicels erect, 4–10 mm long, becoming reflexed in fruit and to 16 mm long; calyx lobes 2, subequal, broadly ovate, the lower lobe sometimes toothed; corolla yellow, sometimes with purple veins, bilabiate, the upper lip \pm orbicular, ca twice as long as calyx lobes, the lower lip larger, gibbous, the margin entire or emarginate, the spur conical and ca two-thirds as long as lower lip, its inner surface with stalked glands along central vein; stamens 2; filaments curved; ovary subglobose; ovules few; style short, distinct; stigma bilabiate. Capsules globose, to 8 mm diam, sparsely glandular, indehiscent; seeds 4–12, 2–2.5 mm diam, lenticular, with a narrow wing. *Shattuck* 369.

Collected several times in Gatun Lake, presumably along the shore of the island. This submerged aquatic, easily visible only when in flower, is probably still present. Flowering plants have been seen throughout most of the year, but especially during the early rainy season in July and August. The fruits develop quickly and are often present with flowers and flower buds (P. Taylor, pers. comm.). Vegetative reproduction is probably the prime dispersal tactic, since fruit set is poor (P. Taylor, pers. comm.).

Florida, and Mexico south to Argentina; West Indies, Galápagos Islands; tropical and subtropical Africa. In Panama, known only from the Canal Zone (Gatun Lake).

***Utricularia obtusa* Sw., Prodr. Veg. Ind. Occ. 14. 1788**

Minute, insectivorous, aquatic herb; stolons slender, from base of scape. Photosynthetic organs alternate on stolons, forked 1–3 times, to 2 cm long, the segments

hairlike, glabrous, usually inconspicuous; insect traps stalked, ovoid, ca 1 mm long, replacing a leaf segment at a fork. Racemes erect, simple, to 4 cm long, bearing 1–4 flowers; scapes usually with a scale near middle; bracts subtending flowers ovate; pedicels 8–12 mm long; calyx bilabiate, the lobes subequal; corolla yellow, 6–10 mm long, bilabiate, the upper lip erect, \pm rounded, the margins curled inward, the lower lip descending, prominently inverted and gibbous with the spur conical, its inner surface puberulent, marked with reddish lines; stamens 2, ca 1.5 mm long; filaments prominently curved and broadened toward apex, extending beyond anthers; anthers adjacent to style; ovary ovoid; style thick, short; stigma thin, bilabiate. Capsules globose, 2–4 mm long; seeds lenticular, ca 1 mm long, the wing relatively thick, very irregular. *Croat* 5649.

Abundance unknown because of its tiny nature, but probably restricted to quiet marshes and floating masses of vegetation on the south side of the island. Flowering specimens have been seen in April, May, and September, but flowering behavior is probably less affected by season than by other factors. Some fruits and flowers may be found on the same inflorescence.

This tiny aquatic is not confused with any other species. Reproduction is probably chiefly vegetative, since fruit set is poor (P. Taylor, pers. comm.).

Mexico to Argentina; West Indies; tropical Africa. In Panama, known only from the Canal Zone (Gatun Lake and the backed-up waters of the Rio Chagres above Gamboa).

129. ACANTHACEAE

Trees, shrubs, lianas, vines, or erect or prostrate herbs. Leaves opposite (except *Elytraria*), petiolate, simple; blades entire to serrate; venation pinnate; linear cystoliths often present; stipules lacking. Flowers bisexual, usually zygomorphic (\pm regular in *Trichanthera*), solitary or on axillary or terminal, bracteate scapes or spikes; calyx deeply lobed (reduced in some); corolla tubular, bilabiate, brightly colored; stamens 4 and didynamous or 2, attached to corolla tube; anthers 2-celled, sometimes widely separated by a connective, dehiscing longitudi-

KEY TO THE SPECIES OF ACANTHACEAE

Plants trees, shrubs, or vines, usually more than 1.5 m tall:

Plants vines, herbaceous or woody:

Bracts subtending flowers linear, ca 1 mm wide; flowers solid white; plants usually less than 4 m tall *Justicia graciliflora* (Standl.) D. Gibs.

Bracts subtending flowers \pm ovate or oblong, more than 1 cm wide; flowers white marked with violet-purple; plants usually vines twining high in forest:

Bracts conspicuously pubescent with ascending trichomes; corolla less than 3.5 cm long *Mendoncia gracilis* Turr.

Bracts glabrous or with short, sparse puberulence, not ascending; corolla more than 3.5 cm long *Mendoncia littoralis* Leonard

Plants trees or shrubs:

Flowers reddish:

Inflorescences with many, imbricate, red-orange bracts; blades conspicuously pubescent on both sides; corolla tubular and zygomorphic *Aphelandra sinclairiana* Nees

Inflorescences lacking large red-orange bracts; blades glabrous except for veins below; corolla \pm campanulate *Trichanthera gigantea* (H. & B.) Nees

Flowers white or purple:

Flowers white; shrubs vinelike, in the forest *Justicia graciliflora* (Standl.) D. Gibs.

Flowers purplish; shrubs cultivated in the Laboratory Clearing *Thunbergia erecta* (Benth.) T. Anderson

Plants herbs or suffruticose shrubs usually less than 1 m tall:

Bracts of inflorescence at least in part ovate to obovate, not several times longer than broad:

Flowers and bracts less than 6 mm long; bracts with dense, woolly trichomes; weed in open areas *Nelsonia brunellodes* (Lam.) O. Kuntze

Flowers and bracts usually more than 10 mm long; bracts not densely woolly-pubescent:

Corolla distinctly bilabiate, white with lavender markings medially on inside of lower lip; plants rare, in the forest along trails *Herpetacanthus panamensis* Leonard

Corolla not distinctly bilabiate (sometimes slightly bilabiate), white to lavender throughout:

Corolla less than 1.5 cm long; plants low, often sprawling, growing in clearings *Blechnum brownei* Ant. Juss.

Corolla more than 2 cm long; plants usually erect, often markedly suffruticose, growing along forest trails *Blechnum costaricense* Oerst.

Bracts of inflorescence all slender, several times longer than broad:

Flowers in loose, open, terminal panicles *Justicia pectoralis* Jacq.

Flowers usually closely aggregated in leaf axils or in dense terminal heads or spikes:

Spikes borne on slender scapes 5–20 cm long *Elytraria imbricata* (Vahl) Pers.

Spikes sessile or nearly so:

Inflorescences terminal on stems and branches:

Inflorescences often longer than broad; bracts ca 6 mm long; flowers ca 5 mm long, white with the lower lip violet *Teliostachya alopecuroidea* (Vahl) Nees

Inflorescences as broad as or broader than long; bracts usually more than 15 mm long; flowers ca 4 cm long, lavender to violet *Chaetochlamys panamensis* Lindau*

Inflorescences axillary, at most nodes, at least in upper part of stem:

Flowers few at each node, the corolla more than 2 cm long, lavender or lavender tinged with white; plants in the forest along trails *Ruellia metallica* Leonard

Flowers densely clustered at each node, the corolla 6–8 mm long, white; plants on sandbars and at the edge of the lake *Hygrophila guianensis* Nees

**Chaetochlamys panamensis* is not included in the flora, but since it is a weedy plant likely to occur on the island it is included in the key.

nally; ovary superior, 2-carpellate, 2-locular; placentation axile; ovules 1 to several, anatropous or amphitropous; style 1, slender; stigma cupular to 2- or 3-lipped, sometimes with 1 lip reduced. Fruits usually loculicidal, obpanurate capsules (drupes in *Mendoncia*); seeds usually disk-shaped, lacking endosperm, usually forcibly discharged by jaculators (retinacula, hooklike processes on the placenta).

Recognized by their usually densely bracteated inflo-

rescences with a two-lipped corolla and by the cystoliths in the leaves.

Most Acanthaceae flowers are small and are probably pollinated by small to very small bees. *Aphelandra* is probably hummingbird pollinated, and *Mendoncia* and *Trichanthera gigantea* are possibly bat pollinated. The pollination systems of *Justicia graciliflora* and *Thunbergia erecta*, which have larger flowers, are unknown.

The fruits are typically bivalved, often obpanurate

capsules with disk-shaped seeds that are thrown free from the capsules by springlike arms (jaculators or retinacula). Van der Pijl (1968) reported that the seeds of some species of *Hygrophila* have appressed trichomes that become erect and slimy when wet, apparently increasing buoyancy and aiding in establishment of the seed. Van der Pijl also reported that the capsules of some species of *Ruellia* split after a weak spot becomes wet, but this would effect seed dispersal only when soil moisture might be adequate for germination of the seed. *Elytraria*, *Nelsonia*, and *Mendoncia* lack retinacula. *Mendoncia* fruits are animal dispersed, probably by birds.

Some 250 genera and about 2,500 species; widely distributed in the tropics.

APHELANDRA R. Br.

Aphelandra sinclairiana Nees in Benth., Bot. Voy. Sulphur 146, t. 47. 1846

Shrub, 1.5–3.5(6) m tall; stems densely pubescent with erect trichomes. Leaves thin; petioles and midribs below with pubescence like stem; blades oblanceolate, acuminate, gradually tapered and decurrent onto petiole nearly to base, 10–38 cm long, 3.5–9.5 cm wide, glabrate above except on major veins, densely pubescent below. Inflorescences terminal, densely fine-pubescent, the spikes few to several, densely bracteate, to 13(20) cm long, the bracts \pm obovate, acute or abruptly acuminate, 1–2 cm long, red-orange; sepals 5, acute, subtended by 2 similar bracts; corolla tubular, 6–7 cm long, magenta, bilabiate, the upper lip 4-lobed, the lateral lobes very short, the lower lip entire, reflexed; stamens 4, stiffly erect, somewhat enfolded in and almost equaling upper lip; anthers open at anthesis, held together, with densely pubescent lateral margins; filaments fused to tube near base; style slender, equaling and held between fused stamens; stigma cupular, bilabiate, open at anthesis; nectary not obvious but with the nectar accumulating at base of corolla tube. Capsules 2-valved, puberulent, ca 2.5 cm long; seeds disk-shaped, ca 4 mm long, suspended on a long, recurved retinaculum. *Croat 7760*.

Occasional, in the forest. Flowers usually continuously throughout the dry season (December to April); the flowers appear in succession, usually only a single one at a time from each spike, opening in the morning and usually falling off or wilting before the day is out. The fruits develop quickly, and the lower bracts usually contain mature capsules by the middle of the dry season. Though plants continue to flower in the late dry season (even rarely into the rainy season), the spikes are usually heavy with mature capsules.

No doubt hummingbird pollinated.

Costa Rica and Panama. In Panama, known from tropical wet forest in Bocas del Toro (Quebrada Huron), Colón (Río Buenaventura), Coclé (above El Valle), and Panamá (southwest of Cerro Brewster), but perhaps more abundantly from tropical moist forest on both slopes of the Canal Zone.

BLECHUM P. Browne ex Ant. Juss.

Blechum brownei Ant. Juss., Ann. Mus. Natl. Hist. Nat. 9:270. 1807

B. brownei Ant. Juss. forma *puberulum* Leonard; *B. pyramidatum* (Lam.) Urban

Erect or more commonly sprawling herb, to 70 cm long; stems slender, glabrate to crisp-villous, the pubescence often restricted to lines. Petioles short or to 1.5 cm long; blades ovate to ovate-elliptic, acute to acuminate, rounded to attenuate at base, 1.5–5 cm long, 1–3 cm wide, nearly glabrous to densely pubescent usually with a mixture of short, fine trichomes and larger, coarse, often jointed trichomes, the margins usually markedly ciliate; cystoliths very conspicuous, easily confused with trichomes. Flowers in close, terminal, bracteate clusters, the bracts more densely pubescent than leaves, ovate to lanceolate, 5–20 mm long, long-ciliate; calyx deeply divided, to 3.7 mm long, pubescent, the lobes linear-lanceolate; corolla white or sometimes pale lavender, short-pilose especially on tube, 10–13 mm long, the tube 2.5–3 mm diam, the limb ca 8 mm diam, the short lobes rounded, ciliate; stamens 4, held within tube; filaments fused to one side of tube much of their length, one pair shorter; style held to one side of tube between stamens, one lobe reduced, the other lobe directed into center of throat above anthers. Capsules obovate, 5–6 mm long, densely pubescent, 2-valved, bursting open at maturity to expel several seeds on retinacula; seeds small, dark brown, disk-shaped, ca 1.5 mm diam. *Croat 4604, 6966*.

Abundant in clearings, especially in the Laboratory Clearing. Flowers and fruits principally throughout the dry season (December to May), though flowering also occurs rarely during the rainy season. Plants have often lost many of their leaves by the end of the dry season when the inflorescences contain mostly fruits.

Mexico (east and south) to Guyana, Ecuador, and Peru; West Indies, Galápagos Islands; Oceania. In Panama, an ecologically variable weed; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Herrera, Panamá, and Darién, from premontane dry forest in Los Santos, from tropical dry forest in Coclé and Panamá, and from premontane wet forest in Panamá (Cerro Campana).

See Fig. 505.

Blechum costaricense Oerst., Vidensk. Meddel. 168. 1854

Erect or suberect herb, to 1 m tall, often suffruticose; stems pubescent with crisp, apically recurved trichomes mostly in lines above petioles on either side; internodes swollen, often darkened. Petioles 5–25 mm long, often narrowly winged; blades ovate to ovate-elliptic, lanceolate-elliptic, or lanceolate, acuminate, attenuate to rounded and decurrent onto petiole at base, 4–12 cm long, 1–4.5 cm wide, the upper surface often with stout simple trichomes, the midrib usually appressed-pubescent (at least near base), the lower surface glabrate to moderately pubescent with short fine trichomes, the margins glabrous

to ciliate; veins hispidulous to short-villous; cystoliths very conspicuous, easily confused with trichomes. Inflorescences loosely bracteate, terminal; flowers each subtended by 2 linear bracts ca 1 cm long and 1 ovate bract 1.5–2.5 cm long; all bracts puberulent, conspicuously ciliate; calyx with slender, sharp lobes divided to near base, to ca 5 mm long; corolla \pm salverform, 2–3 cm long, hispidulous outside, glabrous inside, lavender-blue above especially on lobes (rarely white), the lobes ca 5 mm long, rounded, the tube 2.5–3 mm diam, whitish, bent outward from below middle; stamens 4; filaments with the basal one-half to two-thirds fused to tube, affixed to one side of tube somewhat below rim, the inner pair held below outer pair; anthers dehiscing introrsely; pollen somewhat tacky, clinging together in small clusters; style slender, held along staminal side of tube; stigmas densely puberulent, 2-lipped, with one lip very reduced, the other extending across mouth of tube, recurved. Capsules ovoid, 5–8 mm long, somewhat flattened, apically beaked, puberulent; seeds disk-shaped, 2–3 mm diam, brown, the outer margin quickly becoming swollen and sticky upon wetting. *Croat 4365* (typical), *7445* (narrow-leaved form).

Frequent along trails in the forest. Flowers mostly throughout the dry season (December to May), rarely flowering and fruiting during the rainy season. The fruits develop quickly.

The small pollinator probably enters the tube to effect pollination, the style acting as a brush to remove pollen picked up from a previous visit. Pollen is probably deposited on the insect's body when it passes the anthers.

Similar to *B. brownei* in most respects but tending to be more robust and erect, to have much larger flowers and leaves, and not to grow in open areas.

Standley reported this species as *B. panamense* Lindau, which, if considered distinct from *B. costaricense*, does not occur on BCI. Leonard has annotated some BCI collections as *B. dariense* Lindau. Both *B. panamense* and *B. dariense* reportedly have corollas less than 1.7 cm long, whereas most of the plants observed in the forest on BCI have corollas 2.5–3 cm long. Perhaps some hybridization takes place between *B. brownei* and *B. costaricense*, since plants in the forest that grow closest to populations of *B. brownei* frequently have the long trichomes on the upper leaf surface associated with that species. Plants farther away in the forest tend to be nearly glabrous on the upper leaf surface.

Costa Rica and Panama. In Panama, known principally from tropical moist forest on the Atlantic slope in the vicinity of the Canal Zone; known also from tropical moist forest in Chiriquí and Darién and from premontane wet forest in Chiriquí (near Concepción) and Panamá.

ELYTRARIA Michx.

Elytraria imbricata (Vahl) Pers., Synops. Pl. 1:23. 1805

Acaulescent to caulescent suffruticose herb, to ca 60 cm tall; stems \pm glabrous. Leaves alternate to subopposite; blades mostly ovate to oblanceolate, acute to acuminate, gradually narrowed to slender winged petiole, 3–12 cm

long, 1.5–4 cm wide, glabrate to sparsely villous especially on veins, the margins \pm undulate and ciliate; cystoliths apparently lacking. Inflorescences of numerous, upper-axillary or terminal, simple or branched scapes mostly 5–25 cm long (sometimes leafy at apex), closely bracteate, the bracts firm, usually subulate, keeled, with villous margins; spikes 1 to several per scape, to 6 cm long and ca 5 mm wide, the bracts firm, awned-tipped and bearing a pair of thin wings near apex, glabrous outside, densely pubescent inside; bracteoles subulate, ca 3 mm long, the costa ciliate; calyx segments 2, unequal, narrow, the posterior one bidentate; corolla bluish, 5–8 mm long, the tube slender, the limb bilabiate, the lower lip trilobate; stamens 2, barely exerted; anther thecae connate, ca 0.5 mm long; pistillate parts not seen. Capsules narrowly conical, ca 3 mm long and 1 mm diam, glabrous; seeds lacking retinacula. *Croat 6963*.

Rare, on a shady steep slope in the Laboratory Clearing. Flowers in the early dry season. The fruits develop quickly and seeds are dispersed in the dry season as well.

Arizona and Texas through northern and western South America to Ecuador and Brazil (Mato Grosso and Río de Janeiro). In Panama, known from tropical moist forest in the Canal Zone, Colón, Los Santos (Tonosí), and Panamá, from tropical dry forest in Herrera (Pesé), Coclé (Penonomé), and Panamá (Taboga Island), and from premontane wet forest in Chiriquí.

HERPETACANTHUS Nees

Herpetacanthus panamensis Leonard, J. Wash. Acad. Sci. 32:185. 1942

Suffruticose herb, 1 m or more tall, often rooting at basal nodes; stems terete, nodose, brittle, easily breaking at nodes; younger parts with uncinatate trichomes. Petioles 3–5 mm long; blades elliptic, acuminate, attenuate and \pm decurrent at base, 5–14 cm long, 2.5–7.5 cm wide, essentially entire, glabrous and shiny above with minute linear cystoliths, duller on lower surface; veins strigose, the major lateral veins \pm impressed, the reticulate veins conspicuous. Inflorescence bracteate, terminal and axillary, the bracts ovate, acute, pubescent, ciliate; calyx regular, sparsely pubescent, to 5 mm long, deeply lobed, the lobes linear; corolla funnel-shaped, ca 2 cm long, bilabiate, white with lavender markings medially inside on lower lip, glabrous except on lower part of tube inside and on outside of lobes, the tube narrow, the upper lip narrowed to an emarginate tip, the lower lip trilobate; stamens 4, the upper pair with the thecae broadly separated and at different levels on connective; filaments united, the tube ca 1 cm long; anthers 1.2 mm long, longitudinally dehiscent; pistil cylindrical, pubescent, minute; style more than 1 cm long, pubescent; stigmas 2. Fruits capsular, ca 1 cm long, brown; seeds disk-shaped, ca 2 mm diam. *Croat 11900*.

Rare, in open areas of the forest. Seasonal behavior not determined. Collected on BCI in flower in August.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope)



Fig. 505. *Blechnum brownii*



Fig. 506. *Justicia graciliflora*

Fig. 508. *Mendoncia littoralis*



Fig. 507. *Mendoncia gracilis*



and Bocas del Toro and from tropical wet forest in Colón (Santa Rita Ridge).

HYGROPHILA R. Br.

Hygrophila guianensis Nees, London J. Bot. 4:634. 1845

Herb, to 1.2 m tall, sparsely hirtellous to glabrate; stems obtusely quadrangular, branched. Blades lanceolate to lanceolate-linear, acuminate at apex, gradually attenuate at base to an obscure, winged petiole, 5–16 cm long, 0.5–4 cm wide, entire; cystoliths dense but \pm obscure. Flowers sessile, in dense axillary clusters subtended by linear-lanceolate bracts; calyx 5–9 mm long, deeply lobed, the lobes \pm linear; corolla white, bilabiate, 6–8 mm long, puberulent, the tube ca 1 mm diam, the upper lip bidentate, ca 2.5 mm long, the lower lip trilobate; stamens 4, arranged in 2 unequal pairs and fused to tube at base; pistillate parts not seen. Capsules narrowly oblong, acute at apex, 9–12 mm long, ca 1.5 mm wide, glabrous; seeds 16–18, disk-shaped, less than 1 mm wide, brown, the margin discoloured and becoming sticky on wetting. *Croat 6402*.

Frequent on sandbars in lagoons around the edge of the island, especially on the western side. Flowers from November to March, especially from December to February. Since the fruits develop quickly, the same inflorescence may bear both flowers and fruits.

Mexico to central Argentina; West Indies; in marshy areas and along water courses from sea level to 1,500 m. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone and Panamá, from premontane dry forest in Coclé (Antón), and from tropical wet forest in Bocas del Toro (Santa Catalina).

JUSTICIA L.

Justicia graciliflora (Standl.) D. Gibs., Fieldiana, Bot. 34:69. 1972

Beloperone graciliflora Standl.

Vine or clambering shrub, 1–4 m long; stems moderately pubescent when young, glabrate in age. Petioles 5–8 mm long, often pubescent; blades lanceolate to narrowly elliptic, short-acuminate, acute to obtuse and decurrent at base, glabrous with many prominent cystoliths. Panicles terminal, 4–8 cm long, sessile or short-pedunculate, bearing few flowers, the bracts linear, green, 5–7 mm long, ca 1 mm wide; pedicels ca 1 cm long; sepals lanceolate-linear, 2–2.5 cm long, 3–5 mm wide, pale orange, glabrate with linear cystoliths; corolla white, the tube narrow, 3–5 cm long, the limb bilabiate, to 2 cm long, the lower lip deeply, equally trilobate; stamens 2, nearly equaling upper lip; thecae of anthers large, unequal; pistillate parts not seen. Capsules spatulate to oblong, 1.5–2 cm long, rounded and apiculate to acute at apex, obtuse at base, glabrate; seeds subglobose, ca 3.3 mm diam, brown, glabrous. *Croat 7372, Shattuck 602* (type).

Uncommon, in the old forest; collected on Armour, Drayton, and Wheeler trails. Flowers from late November to late January. Mature fruits have been seen in March. On BCI the plant has not been found in the canopy, but it was found growing at about 25 m in a tree in Veraguas Province.

Known only from Panama, from tropical moist forest on BCI and in Darién and from premontane wet forest in Veraguas (west of Santa Fé) and Panamá (Cerro Jefe). See Fig. 506.

Justicia pectoralis Jacq., Enum. Pl. Carib. 11. 1760

Erect herb, to 50(100) cm tall; stems with lines of retrorse pubescence between leaves, often decumbent and rooting at basal nodes. Leaves decussate; petioles 2–12 mm long; blades lanceolate, long-acuminate, acute to obtuse at base, 2–11 cm long, 0.4–2.5 cm wide, \pm glabrous except for upper midrib; cystoliths moderately conspicuous above under magnification. Panicles terminal, dichotomous, to 15 cm long, the branches broadly divergent, densely puberulent, with longer glandular trichomes; bracts ca 2 mm long, 1 mm wide; flowers sessile, sparse; calyx ca 2.5 mm long, the pubescence as on inflorescence branches, the lobes long, sharp, the uppermost shorter; corolla bilabiate, lavender except for white base, the upper lip sparsely pubescent outside, narrow, folded, enclosing style in medial groove, the lower lip trilobate, its middle lobe corrugated with prominently raised, white, lateral veins extending into tube on either side of medial groove; stamens 2, affixed laterally, arching to center; anthers horseshoe-shaped, loosely clasping style; style slender, 7–8 mm long, curved downward at apex. Capsules club-shaped, acute at apex, 6–8 mm long, 1.5 mm broad, puberulent; seeds ca 1.5 mm broad, covered with papillae, the papillae minute, immediately becoming sticky upon wetting. *Croat 10253*.

Occasional, in clearings, especially along the path in the Rear Lighthouse Clearing. Flowers from December to May. The fruits develop quickly and are dispersed in the dry season.

Pollination is effected by a small insect, which crawls into the tube (no doubt with the corrugated, somewhat downturned lower lip acting as a landing platform). In crawling beneath the arched stamens, it spreads pollen on its back. At the same time the style is released from its groove and strikes the pollinator's back.

Wide-ranging and weedy throughout the New World tropics, including the West Indies. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Colón, Chiriquí (David), Panamá, and Darién and from premontane wet forest in Panamá (Chimán).

MENDONCIA Vell. ex Vand.

Mendoncia gracilis Turr., Kew Bull. 1919:418. 1919.

Vine; stems, petioles, and blades pubescent, the trichomes sparse to dense, moderately long, \pm appressed; stems angulate. Petioles canaliculate, ridged above, 1.5–2.5 cm

long; blades ovate to elliptic-ovate, acuminate, rounded to obtuse at base, 5–12 cm long, 2.5–8 cm wide, the pubescence denser on veins; cystoliths not apparent; veins 3 or 4 on each side. Flowers 1–3, in leaf axils; pedicels 1.4–1.8 cm long, densely appressed-pubescent; bracts \pm ovate, keeled, obtuse and minutely cuspidate at apex, truncate at base, 15–17 mm long, 10–13 mm wide, densely pubescent on outer surface with brownish ascending trichomes, glabrous inside; calyx reduced to a minute rim about as high as disk; corolla white, 3–3.5 cm long, bilabiate, glabrous except for stalked, gland-tipped trichomes inside on side of tube below upper lobes, the tube constricted to ca 4 mm wide at middle, expanded at base to ca 5 mm and to ca 7 mm below throat, the lobes to ca 6 mm wide, tinged with violet-purple, especially in throat; stamens 4, in 2, \pm equal pairs; filaments and connective with many sessile glands; style ca 2 cm long, slightly protruding over lower edge of throat; stigmas 2, short, unequal, the larger markedly curved. Fruits similar to those of *M. littoralis*. *Croat 16519*.

Occasional, in the canopy of the forest; probably less abundant than *M. littoralis*. Flowers and fruits principally from December to April.

Panama and Colombia (from the Pacific slope and intermountain valleys in the Departments of Antioquia, Cundinamarca, Valle, and Tolima, usually at 1,000–2,000 m). In Panama, known from tropical moist forest in the Canal Zone and from tropical wet forest in Panamá (Cerro Jefe).

See Fig. 507.

Mendoncia littoralis Leonard, Contr. U.S. Natl. Herb. 31:1. 1951

Herbaceous vine growing into canopy; stems and leaves glabrate to sparsely appressed-pubescent; stems square, the angles ribbed (at least when young). Petioles slender, 2–4 cm long; blades ovate-elliptic, elliptic, or oblong-elliptic, caudate-acuminate, obtuse to rounded at base, 8–16 cm long, 3–7 cm wide, the margins obscurely irregular. Flowers solitary in axils, enclosed in a water-filled pair of bracts before anthesis, emerging from bracts at anthesis, soon falling; pedicels slender, 2.5–3.5 cm long; bracts ovate-elliptic to oblong-elliptic, truncate to weakly bilobed and apiculate at apex, rounded to truncate at base, 2.5–3.3 cm long, ca 2 cm wide, glabrous to sparsely short-puberulent; calyx reduced to a firm annular ring similar to disk (both persistent in fruit); corolla bilabiate, 3.5–5 cm long, glabrous, the tube white, \pm curved, to 4 cm long, constricted to ca 5 mm wide above base, to 10 mm wide at base, the throat oblique, the lobes mottled with violet-purple especially near base, to 1.2 cm long and 1.5 cm wide; stamens 4, in 2 unequal pairs, held against one side of tube below upper edge of throat; filaments \pm flattened, with sessile glands, fused to tube most of their length; anthers 6–10 mm long, the lower pair sometimes longer, the thecae sometimes unequal; style 1.6 cm long, glabrous; stigmas 2, short, unequal. Drupes \pm ovoid, ca 1.5 cm long, purple-black and fleshy at maturity; mesocarp thin; seed 1. *Croat 12413*.

Frequent in the forest, usually in the canopy but often flowering at lower levels, owing to tree falls. Flowers from July to December. The fruits mature from November to March.

Panama and Colombia. In Panama, ecologically variable; known from wetter parts of tropical moist forest in the Canal Zone, San Blas, Chiriquí, Panamá, and Darién, from premontane wet forest in Los Santos, Panamá, and Darién, and from tropical wet forest in San Blas and Chiriquí.

See Fig. 508.

NELSONIA R. Br.

Nelsonia brunellodes (Lam.) O. Kuntze, Rev. Gen. Pl. 2:493. 1891

Prostrate or sprawling herb, densely and softly villous on most parts; stems slender, 15–60 cm long. Petioles 2–20 mm long; blades ovate to ovate-elliptic, acute to obtuse at apex, rounded to attenuate at base, 1.5–7 cm long, 1–3 cm wide. Spikes slender, densely bracteate, terminal and axillary, 1.5–6 cm long and to 6 mm wide; bracts ovate, concave, abruptly acuminate; flowers minute; sepals 4–5 mm long, markedly unequal in width, conspicuously veined, acuminate, villous outside; corolla bilabiate, glabrous, pale violet-purple above middle, the tube white, 4–5 mm long, the limb ca 2 mm broad, the upper lip 2-cleft, the lower lip trilobate, the lobes weakly bilobed; stamens 2, attached near throat; filaments pubescent on free portion; anthers with the thecae moderately separated; style equaling stamens; stigma simple, held beneath anthers. Capsules sessile, ca 4 mm long, narrowly ovate, the valves folding back at maturity; seeds to 10 per capsule, \pm globose, subverrucose, lacking retinaculum. *Croat 8221*.

Occasional, in the Laboratory Clearing in open areas. Flowers from February to April. The fruits develop quickly. Late in the dry season plants are often leafless and have principally mature capsules on their spikes.

Mexico to South America as far south as Brazil (Minas Gerais); West Indies; probably introduced from the Old World, where the species is widely distributed in central Africa and South Asia. In Panama, an ecologically variable weed of open areas; known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién, from premontane dry forest in Los Santos, from premontane wet forest in Panamá, and from tropical wet forest in Coclé (Atlantic slope).

See Fig. 509.

RUELLIA L.

Ruellia metallica Leonard, Publ. Field Mus. Nat. Hist., Bot. Ser. 18:1253. 1938

Suffruticose herb, to ca 50 cm tall; stems weakly quadrangulate, hirtellous or retrorsely strigose on angles, sometimes rooting at basal nodes. Petioles 5–15 mm long; blades elliptic to ovate-elliptic, acuminate at apex, atten-



Fig. 509. *Nelsonia brunellodes*



Fig. 510.
Teliostachya alopecuroidea

uate at base, 6–12 cm long, 2–5 cm wide, \pm glabrous except appressed-strigose on veins below, the margins often minutely irregular; cystoliths conspicuous on both surfaces. Flowers borne in small clusters in uppermost axils; bracts irregular, lanceolate to acicular, shorter than calyx; calyx 6–7 mm long, divided to near base, the lobes narrowly pointed; corolla campanulate, to 2.7 cm long, lavender to lavender tinged with white, weakly puberulent in throat, the tube ca 2 cm long, narrow below middle, ca 1 mm wide, flared to ca 6 mm just below throat, the lobes \pm rounded, spreading; stamens in 2 unequal pairs held well within throat, the uppermost pair ca 1.5 cm long; anthers 1.3 mm long, the connective extending somewhat above thecae; style with 2 unequal stigma lobes. Capsules clavate, acute at apex, ca 1 cm long, weakly puberulent. *Croat 8642*.

Apparently rare, on the forest trails; collected once on Conrad Trail in the old forest. Flowers in the dry season. The fruits develop quickly and the plant usually bears both flowers and fruits.

Nicaragua, Costa Rica, and Panama. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro and from tropical wet forest in Colón, Coclé (Boca de Toabré) and Darién.

TELIOSTACHYA Nees

Teliostachya alopecuroidea (Vahl) Nees in Mart.,

Fl. Brasil. 9:72. 1847

Lepidagathis alopecuroides (Vahl) R. Br. ex Griseb.

Erect or decumbent herb, 15–30(50) cm tall, branched many times, often rooting at basal nodes, moderately pubescent especially on stems and veins of lower leaf surface. Petioles to ca 1 cm long; blades mostly narrowly ovate, acute or obtuse at apex, attenuate at base, 3–9 cm long, 2–3.5 cm wide, \pm entire. Spikes terminal, densely bracteate, 1–5 cm long and 1 cm wide; bracts similar to calyx lobes, lanceolate to oblong, cuspidate-acuminate, ca 6 mm long, ciliolate with conspicuous veins; flowers numerous; calyx lobes very unequal, 4–6 mm long; corolla to ca 5 mm long, bilabiate, white except for violet lower lip, the tube villous inside near apex, the upper lip entire or emarginate, somewhat enclosing stamens, the lower lip trilobate, recurved at anthesis; stamens 4, fused to tube in basal two-thirds; anthers shedding pollen in bud, the thecae distinct, held at 2 levels; style held next to upper lip and somewhat recurved near apex; stigma simple, held between the 2 pairs of anthers. Capsules sessile, ca 4 mm long, glabrous or pubescent near apex; seeds 4, flattened, ca 1 mm wide, pale. *Croat 7967*.

Occasional, along trails; locally abundant. Flowers and fruits mostly from January to April.

Leonard (1951) reported the species to have stamens free at the base. I have found them to be fused to the basal two-thirds of the tube.

Mexico (Yucatán) to Colombia, Venezuela, Brazil, and Peru; Trinidad, West Indies. In Panama, ecologically wide-ranging; known from tropical moist forest in the

Canal Zone and Veraguas, from tropical wet forest in Veraguas, Coclé (both slopes), and Panamá, and from premontane rain forest in Coclé (Cerro Pilón).

See Fig. 510.

THUNBERGIA Retz.

Thunbergia erecta (Benth.) T. Anderson, J. Linn.

Soc., Bot. 7:18. 1864

Shrub, \pm glabrous; stems 4-ribbed, branched many times. Blades ovate, acuminate, acute at base and decurrent onto short, canaliculate petiole, the margins entire to obtusely toothed and somewhat undulate. Flowers solitary on axillary pedicels; corolla 7–8 cm long, violet (purple), the tube white outside, yellow inside; stamens 4, in 2 pairs set in a groove on upper side of tube, to 3 cm long, somewhat irregular, with 2 or 3 recurved lobes; filaments with glandular trichomes; anthers bristled around margins of thecae; style set in groove just above upper pair of stamens; stigma scoop-shaped. Fruits not seen (those of the genus capsular, with the seeds \pm globose and lacking a retinaculum). *Croat 6918*.

Cultivated at the Laboratory Clearing. Flowers sporadically all year, but especially in the rainy season.

Costa Rica and Panama; Jamaica and Puerto Rico. In Panama, known only from tropical moist forest in the Canal Zone.

TRICHANTHERA Kunth

Trichanthera gigantea (H. & B.) Nees in DC., Prodr.

11:218. 1847

Palo de agua, Asedera

Small tree, usually to 10(13) m tall; trunks slender, less than 15 cm dbh, often clustered and stilt-rooted, the leaf scars persisting; stems and branches quadrangular. Petioles to 6 cm long, the pairs often unequal; blades ovate to elliptic, acuminate, mostly obtuse to attenuate at base, mostly 11–20(26) cm long, 4–10(14) cm wide, glabrous except on veins of lower surface; cystoliths short, irregularly oriented, linear, obvious only when dry. Inflorescences terminal, compact, \pm secund panicles 5–15 cm long; branches to ca 6 cm long, densely tomentose, becoming scurfy in age; bracts triangular, ca 3 mm long; flowers \pm regular; calyx 7–10 mm long, deeply lobed, the lobes imbricate, rounded at apex, often tinged with purple; both calyx and corolla densely tomentose outside with both glandular and simple trichomes; corolla 3.5–4 cm long, glabrous and brick red inside, the tube to 3.5 cm long, glabrous near base, the limb 2–3 cm wide; stamens 4, exserted, in 2 pairs, the outermost of each pair slightly shorter, held to one side of tube, to 5 cm long; filaments fused at base in pairs, softly pubescent below with simple and glandular trichomes; anthers ca 6 mm long, introrse, marginally fringed; ovary ovate, sericeous, glabrous and nectariferous at base; style \pm equaling stamens, its upper lobe much reduced; nectaries not obvious. Capsules 1.5–2 cm long, 2-valved, obtuse, silky-

pubescent; seeds 1–4 per capsule, flattened, lenticular, 3–4 mm broad. *Croat 4632*.

Rare, usually occurring along streams. Flowers from January to April, especially in February and March. The fruits mature quickly, the first usually by February, and may be found on the same inflorescence with flowers.

The stamens are a little longer than the style at anthesis. Later they are somewhat bent back and rather distant from the style.

Costa Rica to Colombia, Venezuela, and the Guianas. In Panama, known from tropical moist forest in the Canal Zone, Colón, Los Santos, Coclé, Panamá, and Darién.

130. RUBIACEAE

Trees, shrubs, lianas, vines, or herbs, sometimes epiphytic, occasionally with spines. Leaves opposite or ternate, petiolate; blades simple, entire; stipules interpetiolar, sometimes united, forming a sheath. Flowers bisexual or occasionally unisexual (the plant dioecious), actinomorphic or zygomorphic, the cymes variously modified, terminal or axillary, dichasial, sometimes reduced to racemes or dense clusters, the inflorescences often bracteate; bracts sometimes showy; calyx lobes 4 or 5 (sometimes 2, 6, or 8); corolla 4- or 5(6)-lobed,

KEY TO THE TAXA OF RUBIACEAE

● Plants herbs, vines, or lianas:

Plants vines or lianas:

Flowers both \pm sessile and clustered in leaf axils, white:

Leaves conspicuously scabrous, very asperous above; flowers less than 4 mm long; fruits less than 4.5 mm diam *Diodia sarmentosa* Sw.

Leaves not conspicuously scabrous and asperous above; flowers more than 7 mm long; fruits more than 6 mm diam *Sabicea villosa* R. & S. var. *adpressa* (Wernham) Standl.

Flowers long-pedicellate or not clustered in axils, white, red, or yellow:

Leaves with the trichomes sparse, appressed, slender, ca 0.3 mm long and in inconspicuous axillary tufts below; fruits oblong, 1.5–2 cm long, pubescent, with appressed trichomes *Chomelia psilocarpa* Dwyer & Hayden

Leaves densely white-tomentose or glabrate to glabrous, lacking sparse appressed trichomes, lacking axillary tufts; fruits usually less than 1 cm long:

Plants armed with large recurved spines; flowers yellow, in globular pedunculate clusters; fruits 6–8 (17) mm long *Uncaria tomentosa* (Willd.) DC.

Plants unarmed:

Flowers white or yellowish, in racemes or panicles; calyx lobes very short; fruits white at maturity, much flattened *Chiococca alba* (L.) Hitchc.

Flowers red or pink, solitary or in umbels; calyx lobes long and slender; fruits green to black at maturity, not flattened but sulcate medially *Manettia reclinata* L.

Plants herbs, not scandent (sometimes creeping):

◆ Flowers and fruits sessile or essentially so, clustered in leaf axils, usually many:

Leaves linear or linear-lanceolate, ca 10 times longer than wide; flower clusters 1–2 cm diam *Borreria densiflora* DC.

Leaves otherwise, 2–8 times longer than wide; flower clusters usually less than 1 cm diam:

Leaves all less than 3 cm long, the secondary veins conspicuous *Borreria ocimoides* (Burm.f.) DC.

Leaves mostly more than 3.5 cm long or, if less, with secondary veins not obvious:

Mature capsules 3.5–4.5 mm long; upper leaf surface asperous, with many short scabrous trichomes *Diodia sarmentosa* Sw.

Mature capsules usually less than 3 mm long:

Stems and leaves greatly diminished apically, the distal leaves many times smaller than the leaves lower on the stem; capsules minutely puberulent (the trichomes short and straight), often as broad as or broader than long, often splitting from the bottom; flowers borne in the axils of smaller leaves . . . *Diodia nudata* Standl.

Stems and leaves not greatly diminished apically, the distal leaves at most only a few times shorter than the lower ones; capsules either glabrous or pubescent (the trichomes not short and straight), longer than broad, dehiscing largely from apex:

Capsules glabrous or sparsely pubescent:

Secondary veins on leaves conspicuous below *Borreria laevis* (Lam.) Griseb.

Secondary veins on leaves very inconspicuous below *Spermacoce tenuior* L.

Capsules densely pubescent at least apically:

Leaves 1.5–3 times longer than broad, their trichomes 0.6–1 mm long, often broad-based; calyx lobes more than 0.5 mm long and sharply triangular; plants drying yellow-green; style bifid . . . *Borreria latifolia* (Aubl.) K. Schum.

Leaves 3–4 times longer than broad, scabrid, the trichomes ca 0.2 mm long; calyx lobes less than 0.5 mm long, often blunt or obscure; plants usually drying quite dark *Diodia ocimifolia* (Willd.) Bremekamp

- ◆ Flowers and fruits not as above (not sessile, numerous, and crowded in leaf axils):
 - Leaves slender, less than 5 mm wide; flowers and fruits each less than 4 mm long *Oldenlandia corymbosa* L.
 - Leaves ovate-cordate, more than 2 cm wide; flowers and fruits more than 4 mm long . . . *Geophila*
- Plants trees or shrubs:
 - Ovules 1 per locule:
 - Flowers in dense heads subtended by large, green, red, or violet-purple bracts *Cephaelis*
 - Flowers not in dense heads with large colorful bracts:
 - Corolla less than 1 cm long:
 - Plants trees, usually more than 7 m tall; blades and stems densely pubescent with long, appressed, pale trichomes, the corolla lobes pubescent; fruits ellipsoid-oblong, ca 1 cm long, red to black *Antirrhoea trichantha* (Griseb.) Hemsl.
 - Plants shrubs or small trees, rarely more than 3 m tall (*Psychotria grandis* sometimes larger), variously pubescent; fruits not as above:
 - Plants scandent shrubs, rare; fruits ellipsoid, compressed, white, 4–8 mm diam; seeds 1 or 2; flowers white or yellow, in axillary panicles . . *Chiococca alba* (L.) Hitchc.
 - Plants not as above; fruits ovoid, not at all or only slightly compressed, red, blue, or black (white by rupturing of the exocarp in *P. deflexa*); seeds mostly 2, rarely 5 *Psychotria*
 - Corolla more than 1 cm long:
 - Flowers 4-parted, white; fruits with 1 seed:
 - Leaf blades with pitlike axillary domatia below; fruits white at maturity, ellipsoid, compressed, the seed vertical *Coussarea curvigemmia* Dwyer
 - Leaf blades lacking axillary domatia; fruits blue or black at maturity, globose or depressed-globose, the seed horizontal *Faramea*
 - Flowers 4- or 5-parted, white, red, or yellow; fruits with 2 or more seeds:
 - Flowers white, the tube sericeous; stems often armed with branch-spines; fruits more than 1 cm diam *Guettarda foliacea* Standl.
 - Flowers yellow or red, the tube not sericeous; plants unarmed; fruits less than 1 cm diam:
 - Flowers red or red-orange; corolla more than 3 cm long; leaves subsessile, often subcordate, less than 7 cm wide; plants cultivated shrubs *Ixora coccinea* L.
 - Flowers yellow or orange; corolla less than 2 cm long; leaves petiolate, acute to obtuse at base, more than 7 cm wide; plants not cultivated *Palicourea guianensis* Aubl.
 - Ovules more than 1 per locule:
 - Calyx lobes very unequal, some flowers with 1 lobe greatly expanded and leaflike:
 - Corolla and expanded calyx lobe white; capsules ca 6–10 mm long; seeds winged *Calycophyllum candidissimum* (Vahl) DC.
 - Corolla red, orange, or yellow, the expanded calyx lobe red; capsules usually less than 7 mm long; seeds not winged:
 - Corolla less than 8 mm long; stipules more than 10 mm long; flowers in small pedunculate cymes, densely clustered along a long main axis *Warszewiczia coccinea* (Vahl) Klotzsch
 - Corolla more than 2 cm long; stipules less than 5 mm long; flowers in open panicles *Pogonopus speciosus* (Jacq.) K. Schum.
 - Calyx lobes ± equal:
 - Corolla more than 5 cm long:
 - Corolla funnelform-campanulate, white or yellowish tinged with purple; flowers in dichasial inflorescences; calyx lobes slender, acuminate; fruits compressed-obovoid, the seeds with a thin wing *Coutarea hexandra* (Jacq.) K. Schum.
 - Corolla narrowly tubular, whitish or yellowish, not tinged with purple; inflorescences and calyces various; fruits not as above:
 - Flowers solitary on ends of branches; corolla lobes tapered to slender tip; fruits round, ca 2 cm diam, green with white stripes; calyx with slender teeth, persistent in fruit *Randia formosa* (Jacq.) K. Schum.
 - Flowers clustered on ends of branches; corolla lobes blunt; fruits not as above; calyx lobes short, rounded to acute but not slender:
 - Corolla yellow; fruits globose to ellipsoid, more than 6 cm diam *Tocoyena pittieri* (Standl.) Standl.
 - Corolla white; fruits linear-cylindrical or globose, less than 6 cm diam:
 - Leaves acute to short-acuminate; calyx lobes blunt; style not exerted; anthers exerted; fruits globose, fleshy; seeds probably animal dispersed *Posoqueria latifolia* (Rudge) R. & S.
 - Leaves rounded at apex; calyx lobes acute; style and anthers exerted; fruits linear-cylindrical, capsular; seeds wind dispersed *Cosmibuena skinneri* (Oerst.) Hemsl.

- Corolla less than 5 cm long:
 - Corolla more than 2 cm long (including lobes):
 - Corolla white; fruits globose or ellipsoid, 1.5–3 cm diam, never red:
 - Plants armed with short spines; calyx deeply lobed, the lobes broadly triangular; corolla 5-lobed; fruit often longer than broad, usually prominently lenticellate *Randia armata* (Sw.) DC.
 - Plants unarmed; calyx truncate with minute teeth; corolla 4- or 5-lobed; fruit globose or depressed-globose, smooth, topped by the persistent calyx tube *Alibertia edulis* (A. Rich.) A. Rich.
 - Corolla yellow or red (white at anthesis but soon yellowing in *Genipa*); fruits not as above, either less than 1 cm long or more than 3 cm long or red:
 - Plants moderately large trees, the trunk usually more than 15 cm dbh; corolla sericeous outside, lobed more than halfway; calyx \pm truncate, 7–10 mm wide; fruits more than 5 cm diam; seeds ca 1 cm long *Genipa americana* L.
 - Plants shrubs or small trees, the trunk usually much less than 15 cm dbh; corolla lobed less than halfway; calyx reddish, weakly lobed and less than 4 mm wide, or prominently lobed; fruits less than 2.5 cm diam:
 - Leaves 3 at each node *Hamelia patens* Jacq. var. *glabra* Oerst.
 - Leaves merely paired at each node:
 - Inflorescences terminal, many-flowered, much-branched; stipules 1–2 cm long *Iserfia haenkeana* DC.
 - Inflorescences axillary, short, few-flowered, not much-branched; stipules more than 3.5 cm long *Pentagonia macrophylla* Benth.
 - Corolla less than 2 cm long:
 - Inflorescences corymbose cymes, axillary or sometimes subterminal, with at least 25 minute flowers forming hemispherical clusters on peduncles 3–4 cm long; fruits to 2 mm long and ca 1 mm wide *Chimarrhis parviflora* Standl.
 - Inflorescences and fruits not as above:
 - Inflorescences axillary; flowers 4-parted; corolla greenish-yellow, lobed beyond middle *Hoffmannia woodsonii* Standl.
 - Inflorescences terminal or subterminal; flowers 5-parted:
 - Plants trees; fruits capsular; flowers magenta, in large panicles or white to pale yellow in long slender racemes:
 - Inflorescences paniculate; flowers magenta; leaves not clustered at apex of branches *Macrocnemum glabrescens* (Benth.) Wedd.
 - Inflorescences racemose; flowers white to pale yellow; leaves clustered at apex of branchlets, obovate *Alseis blackiana* Hemsl.
 - Plants shrubs or small trees; fruits fleshy; flowers white, yellow, or red:
 - Flowers orange to red; leaves verticillate, 3, 4, or 5 per node, sometimes opposite *Hamelia patens* Jacq. var. *glabra* Oerst.
 - Flowers yellow or white; leaves not verticillate:
 - Calyx and corolla sericeous; calyx truncate, with minute apiculate teeth; leaves somewhat clustered at ends of branchlets *Amaioua corymbosa* H.B.K.
 - Calyx and corolla not sericeous; calyx regularly lobed; leaves not clustered:
 - Flowers yellow, the corolla more than 1 cm long; fruits red to black; inflorescences about as broad as long *Hamelia axillaris* Sw.
 - Flowers white, the corolla less than 8 mm long; fruits purple; inflorescences long and slender, many times longer than broad *Bertiera guianensis* Aubl.

rarely oblique or bilabiate, showy; stamens equal in number to corolla lobes and alternate with them; anthers 2-celled, introrse, dorsifixed, dehiscent longitudinally; pistil 1; ovary inferior, 2-locular, 2-carpellate; placentation axile or seemingly basal; ovules 1 or more per locule; style 1, slender; stigma simple or 2(5)-lobed. Fruits usually berries or sometimes loculicidal capsules; seeds 2 (or 1 by abortion) to many, sometimes winged, the endosperm usually copious, fleshy, rarely none (*Chomelia* and *Guettarda*).

Recognized by the opposite leaves, interpetiolar stipules, and regular, tubular flowers.

A number of morphological features have evolved in flowers of the family to promote outcrossing. Among these are dimorphic heterostyly (e.g., *Psychotria capitata*, *P. pubescens*, *Cephaelis ipecacuanha*), protogyny (e.g., *Warszewiczia coccinea*, *Alseis blackiana*), and marked protandry (e.g., *Posoqueria latifolia*, *Pogonopus speciosus*). Though basically actinomorphic, flowers of some species have become zygomorphic by modification of the sexual parts, usually by the stamens being clustered on one side of the corolla while the style is held on the opposite side. This zygomorphy is accompanied as well by heterostyly in the case of *Psychotria pubescens*. Probably dimorphic

heterostyly is much more prevalent in *Psychotria* than I have indicated, since it is often not at all apparent from observations of a few individuals and is much more easily observed in the field than from specimens. In *Pogonopus speciosus*, outcrossing is further ensured by a protandry and a marked lateral movement of the stamens after anthesis.

Species with reddish flowers that seem suited for hummingbird pollination include *Hamelia patens*, *Macrocnemum glabrescens* (observed by Chapman, 1931), *Manettia reclinata*, *Ixora coccinea*, *Isertia haenkeana*, *Pogonopus speciosus*, and *Warscewiczia coccinea*. The large red bracts of *W. coccinea* would attract the birds, rather than the flowers themselves. The flowers of *Isertia haenkeana* are yellow, but the calyx and inflorescence branches are reddish. Other species with yellow flowers and bright red bracts, which are possibly also hummingbird pollinated, include *Pentagonia macrophylla* and *Cephaelis tomentosa*. *Cephaelis discolor* with maroon bracts and white flowers may also be hummingbird pollinated, as may be *Hamelia axillaris* with yellow, narrowly funnelform flowers. Hummingbirds have been seen visiting *Psychotria capitata* (pers. obs.) and *Genipa americana* (H. Baker, pers. comm.) and may visit other *Psychotria* species as well.

Butterflies are probably active pollinators of many species but especially *Alseis blackiana*, *Uncaria tomentosa*, *Sabicea villosa*, and possibly *Antirrhoea trichantha*, *Calycophyllum candidissimum*, and many of the suspected moth-pollinated flowers. Butterflies of the genus *Heliconius* (Nymphalidae, Ithomiinae) have been observed visiting the heterostylous flowers of *Psychotria capitata* and species of *Palicourea* (L. Gilbert, pers. comm.). Butterflies may be effective pollinators of many of the other small, white-flowered species such as *Psychotria*, *Borreria*, *Chiococca*, *Bertiera*, *Diodia*, *Geophila*, *Oldenlandia*, and *Spermacoce*. Most of the same species are probably visited by bees as well. In Costa Rica *Heliconius* and pierid butterflies, which frequently visit typical "hummingbird" flowers, visit *Hamelia patens* (Heithaus, 1973).

Flowers with white, mostly slender corollas that generally fall off in the early morning are probably moth pollinated. These include *Faramea occidentalis*, *F. luteovirens*, *Randia armata*, *Guettarda foliacea*, and possibly also *Amaioua corymbosa* and *Alibertia edulis*. Species that seem to be adapted only for hawkmoth pollination include *Posoqueria latifolia*, *Tocoyena pittieri*, *Cosmibuena skinneri*, and *Randia formosa* (see the species description of *Posoqueria latifolia* and Halle, 1967).

Bat pollination is suspected for *Coutarea hexandra* because of floral morphology and time of anthesis.

Despite the fact that few Rubiaceae are definitely adapted to bee pollination, the prevalence of bees as pollinators suggests that many rubiaceous flowers, especially those with shorter tubes, are pollinated by bees. Dressler (1968b) reported that euglossine bees regularly visit flowers of *Sabicea* for nectar. *Genipa americana* in Guanacaste, Costa Rica, is probably bee pollinated (G. Frankie, pers. comm.).

Major dispersal classes in the Rubiaceae are ornitho-

chory and anemochory. Frequently the small black or blue fruits are made more conspicuous by the reddish color of the fruiting inflorescence branches. Species that produce fruits at least partly adapted for dispersal by mammals include *Alibertia edulis*, *Amaioua corymbosa*, *Coussarea curvigemma*, *Faramea* spp., *Genipa americana*, *Guettarda foliacea*, *Pentagonia macrophylla*, *Posoqueria latifolia*, *Randia* spp., and *Tocoyena pittieri*. Most of these are known to be eaten by white-faced monkeys and a few also by spider monkeys and tamarins (Oppenheimer, 1968; Hladik & Hladik, 1969). Oppenheimer (1968) reported that seeds of *Faramea occidentalis*, *Randia armata*, and *Tocoyena pittieri* all germinate after passing through the gut of white-faced monkeys. Fruits of *Coussarea curvigemma* are taken by coatis (Kaufmann, 1962).

Fruits of the genus *Genipa* have been reported to be dispersed by lizards in the West Indies (Ridley, 1930). *G. americana* is dispersed in part by fish (van der Pijl, 1968). I have seen whole fruits floating in the water at the lake margin, so they may be water dispersed in part.

Wind-dispersed species include *Cosmibuena skinneri*, *Alseis blackiana*, *Chimarrhis parviflora*, *Coutarea hexandra*, *Calycophyllum candidissimum*, *Macrocnemum glabrescens*, *Manettia reclinata*, *Uncaria tomentosa*, and *Warscewiczia coccinea*.

The seeds of *Oldenlandia corymbosa* and those of the tribe Spermaceae, including *Borreria*, *Diodia*, and *Spermacoce*, are not clearly adapted for specialized dispersal. Most of these are weedy plants and their seeds are apparently spilled locally. Ridley (1930) reported that seeds of *Borreria*, *Spermacoce*, and *Oldenlandia* are dispersed by rain wash.

Over 450 genera and more than 5,000 species; generally distributed, but most numerous in the tropics.

ALIBERTIA A. Rich. in DC.

Alibertia edulis (A. Rich.) A. Rich. in DC., Prodr. 4:443. 1830

Lagartillo, Madroño, Trompito, Trompo, Wild guava
Glabrous, dioecious shrub or small tree, to 5.5 m tall. Stipules interpetiolar, subpersistent, lanceolate, to 1.5 cm long and 5 mm wide; petioles less than 1 cm long; blades lanceolate-oblong to oblong-elliptic, acuminate, obtuse and decurrent onto petiole at base, 7–20 cm long, 2.5–6 cm wide, with pocketlike domatia in axils below, usually also tufted in axils. Inflorescences very congested, terminal; flowers sessile or subsessile, unisexual, usually few, subtended by one or more pairs of stipules; calyx truncate, 4–6 mm long, with minute, irregular teeth, persisting in fruit; corolla white, 2–3 cm long, densely and inconspicuously tomentose, the tube tomentose outside, sericeous inside except at base, the lobes 4 or 5, lanceolate, narrowly acute, spreading or recurved; stamens 4, sessile, affixed at the middle of the connective; staminate flowers with the anthers to 11 mm long, their apex held near corolla throat, the style elongating to become slightly exerted, the stigmas 2, short and slender, probably not

opening; pistillate flowers with the anthers to 4.7 mm long, deeply included in tube, the style to 1.8 mm long, exserted, the lobes 3–5, spreading and \pm appressed to base of petals. Berries round, 2–3 cm diam, yellowish, becoming black and fleshy; seeds many, flattened, irregular, 4–6 mm long, brown, embedded in a grayish, edible matrix. *Croat 5358, 7390.*

Frequent in the forest. Flowers mostly from April to October but especially in the early rainy season (June and July). The fruits mature from July to December, mostly in August and September. Flowering less frequently at the beginning of the dry season, with the fruits maturing by the end of the dry season.

Mexico (Tabasco) to Panama, Colombia, the Guianas, Amazonian Brazil, and Bolivia; Trinidad and Tobago. In Panama, ecologically variable; known principally from tropical moist forest in the Canal Zone and Bocas del Toro, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién Provinces; known also from tropical dry forest in Coclé, from premontane moist forest in Coclé and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón, Veraguas, and Darién.

See Fig. 511.

ALSEIS Schott

Alseis blackiana Hemsl., *Diag. Pl. Mex.* 30. 1879

Tree, to 15(30) m tall; trunk to 1 m dbh, weakly to strongly involuted vertically in age; outer bark light brown with many vertical fissures, soft and loose; inner bark and wood light in color but turning darker soon after being slashed; young stems, petioles, axes of inflorescences, and pedicels minutely puberulent to strigillose. Leaves clustered at apex of branches; stipules slender, acuminate, 8–12 mm long; petioles 1–2.5 cm long; blades oblanceolate, short-acuminate, acute to obtuse at base, 9–20 cm long, 2.5–7 cm wide, almost glabrous above, sparsely appressed-pubescent and densely puberulent on midrib and main veins below. Racemes slender, upper-axillary, 10–23 cm long and ca 2 cm wide; flowers protogynous, sweetly aromatic; calyx lobes minute, triangular, bluntly acute, thick, usually glabrous; corolla white to pale yellow, 3–3.7 mm long, ca as broad as long, glabrous outside, densely pubescent inside, the lobes 5, bluntly acute, erect or curved inward and holding filaments together; filaments curved outward, ca 9 mm long, fused to tube at very base, densely villous except near apex; anthers ca 1.5 mm long, versatile, held perpendicular to axis of flower; style ca 6 mm long, the branches 2, recurved, protruding from flower before it is fully expanded, soon overtopped by stamens and somewhat obscured among trichomes of filaments; nectary green, longer than calyx, with moderate amounts of nectar. Capsules dense along spike, club-shaped, 10–15 mm long, splitting along one side from apex, the valves persisting after seeds are shed; seeds many, 5–10 mm long, very slender, with a narrow subulate wing on either end. *Croat 5389, 14829.*

Common in all parts of the forest. Flowers in April and May. The fruits are of mature size by June, but do not turn brown and shed seeds until late in the following dry season (R. Foster, pers. comm.).

The species is very similar to and probably not separable from *A. yucatanensis* Standl. in Mexico, *A. shippii* Lund. in Belize, and *A. hondurensis* Standl. in Honduras.

Known only from Panama and Colombia, but probably synonymous with plants ranging from Mexico to northern Colombia. In Panama, known from tropical moist forest in the Canal Zone and Darién.

See Fig. 512.

AMAIOUA Aubl.

Amaioua corymbosa H.B.K., *Nov. Gen. & Sp.* 3:419, pl. 294. 1820
Madroño

Diocious shrub or tree, to 15 m tall; trunk slender or to 20 cm dbh and deeply invaginated; stems sericeous when very young, glabrate in age, with conspicuous leaf scars. Leaves somewhat clustered at apex of branchlets; stipules caducous, to 1 cm long, sericeous, leaving a conspicuous interpetiolar line of trichomes; petioles 6–14 mm long, sericeous to glabrate; blades ovate-elliptic to obovate-elliptic, abruptly short-acuminate, usually obtuse and \pm decurrent onto petiole at base, 7–13(21) cm long, 3.5–8(12) cm wide, glabrous or with sparse long trichomes on major veins below and tufts of trichomes in axils, the margins ciliate and \pm revolute. Flowers fragrant, 5–7-parted, sericeous throughout; staminate flowers in terminal corymbs ca 8 cm long; pistillate flowers similar to but slightly smaller than staminate flowers, in capitulate or corymbose inflorescences; peduncles to 5 cm long; pedicels 2–4 mm long; calyx tubular, 3–4 mm long, with short apiculate teeth; corolla 10–15 mm long, white, the lobes 5, ca 6 mm long, puberulent, spreading at anthesis; anthers subsessile, to 4.3 mm long; style to 9 mm long, included, longer than stamens. Berries ovoid, 1–1.5 cm long, purplish at maturity, in dense axillary clusters, sparsely sericeous; seeds many, irregular, rounded on one side, flattened, 3–5 mm long. *Croat 16214, Foster 1337.*

Occasional, in the forest and along the shore; common on a small promontory midway between the ends of Zetek and Armour trails (R. Foster, pers. comm.). Flowers mostly in July. The fruits apparently mature over a long period and are seen most months of the year; most probably mature during the rainy season and early dry season.

Mexico to Panama, Colombia, Venezuela, the Guianas, Brazil, and Bolivia; Trinidad and West Indies. In Panama, ecologically variable; known principally from the Pacific slope in tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién (probably elsewhere as well); known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, and from tropical wet forest in Colón and Panamá.



Fig. 511. *Alibertia edulis*

Fig. 512. *Alseis blackiana*



Fig. 513. *Borreria densiflora*

ANTIRRHOEA Commers. ex Ant. Juss.

Antirrhoea trichantha (Griseb.) Hemsl., Biol. Centr.-Amer. Bot. 2:42. 1881

Pittoniotis trichantha Griseb.

Tree, to 15 m tall and 25 cm dbh; branchlets puberulent and conspicuously lenticellate; leaf scars prominent. Leaves deciduous, clustered at ends of branches, emerging at time of flowering; stipules long-attenuate, to 1.5 cm long, caducous, appressed-pubescent; petioles 1.2–2.8 cm long; blades ovate to elliptic or obovate, acuminate, acute to obtuse at base, 5–24 cm long, 2–12 cm wide, thin, glabrate above in age except on veins, with long appressed trichomes below; most veins raised below, the smallest ones prominent, parallel, connecting lateral veins. Inflorescences pubescent to glabrate (in fruit) panicles, axillary, densely flowered; flowers 4- or 5-parted, white, with strong sweet aroma, sessile, secund; calyx lobes acute, ca 0.5 mm long; corolla to 5.3 mm long, appressed-pubescent outside, villous inside on lobes, the lobes longer than the tube, reflexed at anthesis; stamens equal in number and about as long as corolla lobes, \pm erect at anthesis; style \pm equaling stamens, divided to ca middle. Drupes oblong, to 1 cm long, bright red and shiny at maturity, sweet and fleshy, becoming brownish when overripe; seed 1, tan, oblong, to 5.3 mm long, \pm flattened, shallowly grooved on each side. *Croat 5214, 11973.*

Rare; known only from the shore on the northern edge of the island. Flowers from March to May, mostly in April. The fruits mature from June to October. Plants apparently lose all their leaves and quickly replace them just before flowering.

Known only from Panama, from drier parts of tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane moist forest in the Canal Zone.

BERTIERA Aubl.

Bertiera guianensis Aubl., Hist. Pl. Guiane Fr. 1:180, pl. 69. 1775

Slender shrub, to 3 m tall; stems glabrate to appressed-pubescent. Leaves glabrous except for pubescence on petioles, veins, and margins, the trichomes sparse, long, \pm appressed; stipules long-acuminate, to 5(10) mm long,

sparsely ciliate, subpersistent, the pairs joined toward base; petioles less than 1 cm long; blades oblong-elliptic, acute to acuminate, obtuse to acute and decurrent at base, 10–19 cm long, 4–8 cm wide. Panicles terminal, to ca 15 cm long, the branches with stiff, long trichomes; flowers secund; calyx lobes acute, less than 1 mm long; corolla tubular, white, 5–8 mm long, shallowly 5-lobed, the lobes narrowly tapered, spreading at anthesis; stamens affixed to tube near apex, slightly exerted above rim; anthers ca 2 mm long, acuminate, narrowly sagittate at base; style to 4.3 mm long, the lobes thick, ca 2 mm long, exerted at anthesis. Berries ellipsoid, to 8 mm long and 3–4 mm wide, fleshy, 10-costate when dry, blue turning purple to purple-black at full maturity, pubescent with long stiff trichomes; seeds several, irregular, usually obtusely 3-angled, ca 1.5 mm diam, densely muricate, tan. *Foster 774.*

Occasional, in the forest; collected by Foster on Wheeler Trail before the junction with Snyder-Molino Trail. Flowers from March to August, especially in June, rarely later in the rainy season. The fruits mature in about 1 month.

Mexico to Panama, Colombia, Venezuela, the Guianas, Brazil, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién and from premontane wet forest in Panamá (Chimán) and Darién.

BORRERIA G. Meyer

Borreria densiflora DC., Prodr. 4:542. 1830

B. spinosa (L.) Schlecht. & Cham.

Erect, glabrous herb, less than 1 m tall; stems \pm square, the corners ribbed, with occasional blunt short protuberances ca 0.3 mm high. Leaves sessile, clustered at nodes; stipules with several prominent bristles, fused to base of leaf; blades linear to linear-lanceolate, acute, gradually tapered to base, the longer ones 4–7 cm long, less than 8 mm wide. Flowers white, in dense globose clusters 1–2 cm diam, terminal or in upper leaf axils, interspersed with slender white bristles; calyx lobes 2, slender, ca 1.3 mm long, persistent, pubescent at base; corolla ca 2 mm long, lobed to near middle, the lobes 4, spreading; stamens with the filaments fused to tube, recurved at apex in bud; anthers held somewhat below the apparently receptive stigma, becoming exerted; style shorter than

KEY TO THE SPECIES OF BORRERIA

- Leaves linear-lanceolate, ca 10 times longer than broad; flower clusters 10–20 mm diam *B. densiflora* DC.

 Leaves 2 or 3 times longer than broad; flower clusters usually less than 7 mm diam:
 Leaves less than 3 cm long *B. ocimoides* (Burm.f.) DC.
 Leaves mostly more than 3 cm long:
 Stems wing-angled; capsules densely pubescent; seeds not grooved
 *B. latifolia* (Aubl.) K. Schum.
 Stems angled but not winged; capsules glabrous or sparsely pubescent; seeds with conspicuous transverse grooves *B. laevis* (Lam.) Griseb.

corolla. Capsules ca 2 mm long and 1 mm wide, pubescent, splitting medially at maturity, the pericarp persistent after seed falls out through the slit opened between calyx lobes; seeds 2, 1 per carpel, oblong, ca 2 mm long and 0.5 mm wide, dark brown. *Croat 12884*.

Occasional, in clearings. Flowers from October to January, mostly in December at the beginning of the dry season. The fruits mature in about 1 month.

Distinguished from other *Borreria* by its habit and the bilobed calyx.

Mexico to Panama, Colombia, and Venezuela; West Indies. In Panama, ecologically variable; known from tropical moist and tropical wet forests at low elevations all along the Atlantic slope and in Chiriquí, Herrera, and Panamá, from tropical dry forest in Panamá (Taboga Island), from tropical wet forest in Veraguas, and from lower montane wet forest in Chiriquí.

See Fig. 513.

Borreria laevis (Lam.) Griseb., Gött. Abh. 7:231. 1857

Herb, erect or \pm sprawling, usually less than 60 cm high; stems angulate, scabrid or glabrous except for minutely pubescent lines below stipules. Stipules united, with several bristles, 2–7 mm long; petioles obscure or to 1 cm long, united with stipules at base; blades ovate to lanceolate, obtuse to acuminate at apex, obtuse and attenuate or cuneate and decurrent at base, essentially glabrous or scabrid on veins above, asperous below, bicolorous, the larger ones 3–9 cm long, 1.5–3 cm wide; veins strongly ascending toward apex. Inflorescences axillary, at most upper nodes; flowers many, usually in various stages of development, interspersed with bristles; calyx 4-lobed, the lobes minute, ciliate, persisting in fruit; corolla white, 2.3–2.7 mm long, 4-parted, divided to about middle, the lobes acute, recurved, sparsely pubescent with moniliform trichomes inside; stamens 4, exerted at anthesis, longer than lobes, equaling or exceeding style; filaments fused to tube; anthers bluish, ca 0.3 mm long, longitudinally dehiscent; style exerted, minutely pubescent; stigma globular. Capsules glabrate to sparsely pubescent, oblong, 1–2 mm long, short-pedicellate, dehiscent irregularly, one cell carrying with it 3 of the 4 calyx lobes; seeds 2, oblong, 1–1.5 mm long, less than 1 mm wide, brown, with prominent transverse grooves opposite the longitudinal sulcus. *Croat 4045, 5984*.

A very abundant weedy plant, found mostly in clearings. Flowers to some extent throughout the year, especially at the beginning of the rainy season (from July to September) and at the beginning of the dry season (January). The fruits mature within a month, sometimes while the plant is still flowering.

Florida and Mexico to Panama, Colombia, Venezuela, the Guianas, Brazil, and Bolivia; West Indies. In Panama, ecologically variable; known principally from tropical moist forest all along the Atlantic slope and in the Canal Zone, Los Santos, Coclé, Panamá, and Darién; known also from premontane moist forest in the Canal Zone, from premontane wet forest in Los Santos and Darién, and from premontane rain forest in Chiriquí.

Borreria latifolia (Aubl.) K. Schum. in Mart., Fl.

Brasil. 6(6):61. 1888

Erect or decumbent, pubescent herb; stems wing-angled, the wings with scabrous trichomes or blunt protuberances. Leaves sessile or subsessile; stipular bristles ciliate; blades ovate-elliptic, lanceolate, or lanceolate-elliptic, acute at apex, cuneate and decurrent at base, 4–6 cm long, 1.5–2.8 cm wide, often yellowish-green when dried, conspicuously strigose on both surfaces, the trichomes, especially above, often broad-based. Flowers sessile, in dense axillary clusters usually less than 7 mm diam; calyx usually acutely 4-lobed, the lobes to 1 mm long, densely crisp-villous; corolla white, 3–4 mm long, 4-lobed, the lobes ca 1 mm long, pinkish at tip, with a few stiff trichomes outside, strongly recurving; stamens shorter than lobes; filaments united to tube; pollen shed in bud, the open stigma generally completely covered with pollen at anthesis; style prominently bifid at apex. Capsules conspicuously crisp-villous, ca 3 mm long, splitting unequally, with 3 of the 4 calyx lobes remaining with one of the 2 segments; seeds 2, elliptic, ca 1.5 mm long and 1 mm wide, brown, minutely papillate. *Croat 6461*.

Occasional, in clearings. Flowers to some extent throughout the year, but most flowers and fruits are seen in the rainy season (September to December). The fruits develop within a month.

Belize to Panama, Colombia, Venezuela, Guyana, and Brazil; Trinidad and Guadeloupe; West Africa. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, Veraguas, and Panamá, and from tropical wet forest in Colón.

Borreria ocimoides (Burm.f.) DC., Prodr. 4:544. 1830

Weak, mostly glabrous herb; stems often branched many times, decumbent, quadrangular, less than 2 mm diam, the 2 opposing sides with narrow marginal ribs, the ribs glabrous or pubescent especially at nodes. Leaves variable, sessile or subsessile; stipules connate, adnate to petiole base, the sheath cup-shaped, minute, with a few slender teeth to 1 mm long; blades ovate to narrowly elliptic or lanceolate, acute to acuminate at apex, acute at base, mostly 1–3 cm long and 4–13 mm wide, scabridulous above, glabrous and paler below, the margins weakly and minutely scabrous. Flowers white, interspersed with white trichomes, in dense axillary clusters less than 1 cm diam; calyx 2-lobed (sometimes 3- or 4-lobed), the lobes slightly exceeding corolla and persistent in fruit; corolla 0.7–1 mm long, 4-lobed to middle or beyond, the lobes acute, pubescent, with long trichomes near middle; stamens alternate with corolla lobes; filaments fused to tube; anthers oval, minute; style shorter than tube; stigma simple or with 2 obscure lobes. Capsules glabrous or puberulent, dehiscent from base or apex into 2 parts; seeds 2, oblong, ca 1 mm long, brown, markedly reticulate. *Croat 8268*.

Occasional, in clearings on rock outcrops or as an epi-

phyte on tree stumps or floating logs on the lakeshore. Flowers and fruits all year, especially at the beginning of the dry season.

Widespread in the tropics. In Panama, known principally from the Pacific slope, from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí, Coclé, and Panamá.

CALYCOPHYLLUM C. DC.

Calycophyllum candidissimum (Vahl) DC., Prodr. 4:367. 1830

Madroño, Alazano, Harino, Lancewood, Lemonwood, Salamo

Tree, 7–17 (25) m tall, to 70 cm dbh; outer bark light, smooth, loose; branches reddish-brown. Stipules ovate, to 1 cm long, caducous; petioles 1–2.5 cm long; blades \pm elliptic or ovate, acuminate, abruptly cuneate at base, mostly 5–13 cm long, 2.5–7 cm wide, glabrous above, sparsely pubescent below; midrib sometimes prominently arched. Flowers in terminal, compound dichasia, sweetly fragrant, each cluster of 3 flowers at first enclosed in a deciduous sheath, the lateral flowers of each cluster on pedicels to 2 mm long, the middle flower sessile, often with one, much-enlarged, conspicuous, white, leaflike calycine lobe (sometimes persisting in fruit), to ca 5 cm long and 3.5 cm wide; corolla white, ca 7 mm long, lobed to half its length, the tube short, densely pubescent at rim, the lobes 4, reflexed; stamens held \pm erect at anthesis, dehiscing inward, later divergent; style much shorter than stamens; stigmas 2, thick, held mostly together at anthesis, later recurved. Capsules oblong-cylindrical, 6–10 mm long, ca 3 mm wide, widest above middle; seeds several, slender, to 5 mm long, with an acuminate wing on either end. *Croat 8661, 12905.*

Rare on the island, but abundant locally in the Canal Zone. Flowers from November to March, especially in the earliest part of the dry season (December). The fruits mature in February and March.

Conspicuous because of the expanded white calyx lobe.

Mexico (Chiapas) to Colombia and Venezuela; Cuba. In Panama, ecologically variable, though found principally on the Pacific slope and characteristic of tropical dry forest (Holdridge & Budowski, 1956) and tropical moist forest (Tosi, 1971); known also from premontane moist forest in Panamá and from premontane wet and premontane rain forests in Coclé.

See Fig. 514.

CEPHAELIS DC.

Cephaelis discolor Polak., *Linnaea* 41:572. 1877

Glabrous shrub, less than 60 cm tall; stems usually unbranched, conspicuously marked with old, cupular leaf scars. Leaves decussate, congested at ends of stems; stipules bilobed nearly to base, the lobes maroon, linear, 6–8 mm long; petioles 1.5–4.5 cm long; blades elliptic to oblanceolate-elliptic, abruptly acuminate at apex, cuneate and decurrent at base, 10–20 cm long, 4–10 cm wide, distinctly bicolorous; major lateral veins in 8–13 pairs, arcuate-ascending, raised on both surfaces, the smaller veins reticulate. Inflorescences globose bracteate masses of many tiny flowers, terminal, maroon, congested between upper leaves; basal bracts rounded, becoming narrowed distally, with fine appendages at base; flowers white, sessile, each surrounded by several oblanceolate, violet-purple bracts 7–10 mm long and to 10 mm wide; calyx lobes 5 (rarely 6), alternate with corolla lobes, narrowly triangular, 1–1.7 mm long, divided more than halfway to base, fused with tube (the free part much shorter than corolla lobes), persisting in fruit; stamens 5 (rarely 6); anthers not seen; style slender; stigmas 2, free, ca 0.7 mm long, curved laterally, surrounded by a low, narrow, furfuraceous disk. Capsules round to \pm oblong, 4–5 mm long, white turning blue; seeds 2, hemispherical, white, only slightly shorter than fruits. *Croat 11870.*

Rare; seen only in the forest in the vicinity of the junction of Wheeler and Drayton trails. Flowers in July and August, probably sometimes earlier and later as well. The fruits mature from August to December, principally from August to October.

Nicaragua, Costa Rica, and Panama. In Panama, known rarely from tropical moist forest in the Canal Zone and Bocas del Toro; known principally at higher elevations from premontane wet and tropical wet forests in Colón, Veraguas, Panamá, and Darién and possibly from premontane rain forest in Darién.

See Fig. 515.

Cephaelis ipecacuanha (Brot.) A. Rich., Bull. Fac.

Med. 4:92. 1818

Raicella

Small shrub, usually less than 50 cm tall, essentially glabrous; internodes moderately long, with ridges on either side of stem below stipules. Leaves sessile or with the petioles to 1.5 cm long; stipules ca 1 cm long, with numerous subulate lobes, subpersistent; blades oblong-obovate or oblong-elliptic, acute to abruptly acuminate

KEY TO THE SPECIES OF CEPHAELIS

- Bracts red, large; plants densely hirsute; shrubs more than 1.5 m tall; flowers yellow *C. tomentosa* (Aubl.) Vahl
 Bracts not red; plants glabrous or sparsely pubescent; shrubs less than 60 cm tall:
 Bracts green; petioles less than 1.5 cm long *C. ipecacuanha* (Brot.) A. Rich.
 Bracts violet-purple; petioles more than 1.5 cm long *C. discolor* Polak.

Fig. 514.
Calycophyllum candidissimum



Fig. 515. *Cephaelis discolor*



Fig. 516.
Cephaelis ipecacuanha

at apex, mostly acute to rounded at base, 8–16 cm long, 3.5–10 cm wide, bicolorous, shiny above, often sparsely pubescent below. Inflorescences capitate, becoming globose in fruit; peduncles 2–3.5 cm long, usually oblique to reflexed; bracts 4, green, the outer ones ovate to broadly rounded and acuminate, 5–13 mm long, the inner ones narrower, \pm oblanceolate and acuminate, enveloping flower; flowers sessile, 5-parted, heterostylous, numerous, ca 1 cm long; calyx \pm truncate or minutely lobed; corolla white, to 1 cm long, glabrous outside, puberulent inside near base of lobes and on most of tube, the lobes recurved; anthers 1.3–1.7 mm long; style lobes 2, short and thick, densely pubescent; short-styled flowers with the style included and the stamens exerted ca 3 mm above rim; long-styled flowers with the style exerted ca 3 mm above rim and the stamens included. Capsules oblong, ca 1 cm long, red becoming blue at maturity; seeds 2, slightly longer than broad, ca 5.3 mm long, flattened on one side, somewhat twisted. *Croat 4104, 15117.*

Common in the forest, especially along trails. Flowers principally from June to August at the beginning of the rainy season, with the fruits developing in about 1 month. Some flowering also occurs at the beginning of the dry season, especially in December.

Distinguished by its small size, its reflexed, bracteate flower heads, and its blue fruits (red when immature).

Central and South America. In Panama, known from tropical moist forest on BCI and in San Blas and Darién and from tropical wet forest in Darién.

See Fig. 516.

Cephaelis tomentosa (Aubl.) Vahl, *Eclog. Amer.*

1:19. 1796

Psychotria poeppigiana Müll. Arg.

Vasika

Densely hirsute shrub, usually less than 2 m tall. Stipules bilobed nearly to base, linear, 1–2 cm long, persistent; petioles short or to 3 cm long; blades \pm elliptic, long-acuminate, obtuse to attenuate at base, 11–24 cm long, 3.5–9 cm wide; major lateral veins arcuate-ascending, often collecting near margin, impressed above, raised below. Inflorescences terminal, capitate, solitary; peduncles 4–9 cm long; flowers 5-parted, surrounded by numerous, narrow, pale bracts and subtended by 2 large bracts, these red, opposite, united at base and mucronate above; calyx minute, lobed midway to base; corolla yellow, rarely tinged with green, ca 12 mm long, the lobes short; filaments fused to corolla tube below middle; anthers 2.5–3.5 mm long, becoming weakly exerted above rim; pollen shed before anthesis; style receptive and held above anthers at anthesis, exerted ca 4 mm above rim; stigma bilobed. Berries bright blue, round to broadly oblong, to 1 cm long; seeds 2, narrow, gradually tapered downward, 7–8 mm long, dark brown, obscurely grooved. *Croat 4362.*

Occasional, in the forest; common elsewhere in the Canal Zone. Flowers and fruits throughout the year, with some flowers and fruits frequently found on the same

inflorescence. The fruits probably mature in 1 or 2 months.

Distinguished by the bright red, opposing bracts, the yellow flowers, and the bright blue fruits.

Mexico to Colombia and the Guianas, south to Amazonian Brazil, Peru, Bolivia, and Argentina; Trinidad. In Panama, ecologically variable, although apparently not occurring in any of the drier areas; known most commonly from wetter parts of tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Los Santos, Panamá, and Darién; known also from premontane wet forest in Colón and Panamá, from tropical wet forest in Colón and Darién, and from premontane rain forest in Coclé and Panamá.

See Fig. 517.

CHIMARRHIS Jacq.

Chimarrhis parviflora Standl., *Trop. Woods*

11:26. 1927

Yema (Ilema) de huevo, Platano, Fiddlewood

Probably a large tree, reported on labels to 18 m tall and 25 cm dbh; stems brownish-puberulent when young, often glabrous in age. Stipules caducous, acuminate, 5–11 (25) mm long, cinereous; petioles 7–20 mm long; blades obovate to elliptic, acute to acuminate at apex, acute to attenuate at base, 7–11 (15) cm long, 1.5–5 (6) cm wide, glabrous above, densely sericeous to inconspicuously appressed-pubescent below especially on major veins, glabrate in age. Cymes corymbose in subterminal or axillary, hemispherical clusters; peduncles (2.5) 3–4 cm long; branches puberulent; flowers protogynous, the style emerging before petals are reflexed; pedicels very short or to 2 mm long; calyx and hypanthium together to 1 mm long, campanulate, \pm glabrous, truncate, with 4 (5) blunt, sparsely ciliate teeth; corolla short-funnelform, ca 3 mm long, the tube nearly obsolete, the 4 lobes oblong, rounded at apex, glabrous but with dense white-villous pubescence inside at point of staminal attachment; stamens 4, exerted, to 5 mm long; anthers narrowly ovoid, to 0.7 mm long; style ca 2.5 mm long, the lobes 2, broader than long. Capsules obovoid, ca 2 mm long and 1 mm wide, shallowly longitudinally sulcate with 6 or 8 weak ribs, splitting medially at maturity and releasing seeds; seeds usually 4, \pm elliptic, ca 1 mm long and 0.5 mm wide, \pm flattened, yellow, covered with wings, the wings many, low, interlocking, scarios, giving the seed a honeycombed appearance. *Croat 11244.*

The single BCI collection, made on Shannon Trail in the middle of July, was in fruit. The branch had fallen from a tree of unknown height. Many of the fruits of this collection had been infected by insects forming brown, fruitlike galls 5 mm long and 4 mm wide. Herbarium material from Panama and Costa Rica shows flowers from April to June, mature fruits in July and August or later.

Costa Rica and Panama. In Panama, known from tropical moist forest on BCI and in Bocas del Toro (the type locality) and from premontane wet forest in Veraguas.



Fig. 517. *Cephaelis tomentosa*



Fig. 518.
Cosmibuena skinneri

Fig. 519.
Coutarea hexandra



CHIOCOCCA P. Browne

Chiococca alba (L.) Hitchc., Annual Rep. Missouri Bot. Gard. 4:94. 1893

Lágrimas de María

Glabrous shrub or slender liana, to 3 m or more long, probably climbing into the canopy, often with pendent, trailing branches. Stipules ovate, long-acuminate, to 4 mm long, entire, persistent; petioles less than 1 cm long; blades ovate to elliptic, acuminate, obtuse to rounded at base, (2)6–10 cm long, (1.3)3–6 cm wide, shiny. Panicles or racemes axillary, to 10 cm long; peduncles to 3 cm long; flowers 5-parted; pedicels 2–3 mm long; calyx ca 1.3 mm long, lobed midway, the lobes deltoid, acute; corolla white, becoming yellowish in age, to 8 mm long, the lobes 2–3 mm long, spreading to reflexed; stamens included, ca 5 mm long; filaments \pm free from corolla, villous at base, and united into a short tube; anthers to 3.7 mm long, longer than filaments; style to 8.5 mm long, exserted, the lobes 2, very short, thick. Berries compressed-ellipsoid, 4–8 mm diam, fleshy, white at maturity; seeds 1 or 2, hemispherical, compressed. *Croat 15266* (Madden Forest).

No collections have been made from the island, but flowers matching this species have been seen in the forest when the species was in flower elsewhere in the Canal Zone. Flowers and fruits to some extent all year, but mostly in August and September. The fruits develop quickly, probably within a month.

Florida and southern Texas through lowland areas of Mexico and Central America to Bolivia and Argentina; West Indies. In Panama, ecologically variable; known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, Herrera, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from premontane rain forest in Panamá.

CHOMELIA Jacq.

Chomelia psilocarpa Dwyer & Hayden, Ann. Missouri Bot. Gard. 54:139. 1967

Arching shrub or liana, widely branched; stems densely appressed-pubescent, becoming glabrate, terete. Stipules lanceolate, 6–10 mm long, entire, caducous; petioles ca 1 cm long, sparsely appressed-pubescent; blades ovate to elliptic, acuminate, obtuse to attenuate and decurrent at base, 6–11 cm long, 3.5–5.5 cm wide, sparsely appressed-pubescent, the trichomes denser on veins below, the axils below inconspicuously tufted, the lower leaf surface of dry specimens finely wrinkled between secondary veins. Cymes axillary, on peduncles to 6 cm long; flowers not seen; sepals 4, oblong, persistent, of 2 lengths, the longer 4–8 mm long, the shorter 2–4 mm long. Berries sessile or short-pedicellate, oblong, 1.5–2 cm long, 7–10 mm wide, sparsely appressed-pubescent; seeds oblong, ca 1 cm long. *Croat 7931, Foster 1117*.

Apparently infrequent, but possibly more abundant than collections and observations indicate; collected as an arching shrub by R. Foster near Wheeler Trail 1100, as a vine by Hayden (143) along the shore south of the dock, and high in the canopy (*Croat 7931*). Mature fruits have been seen from June to August.

Known only from Panama, from tropical moist forest on BCI and in Darién.

COSMIBUENA R. & P.

Cosmibuena skinneri (Oerst.) Hemsl., Biol. Centr.-Amer. Bot. 2:12. 1881

C. paludicola Standl.

Glabrous tree, to 10 m tall and 25 cm dbh (usually less), usually hemiepiphytic. Stipules obovate, 1–2 cm long; petioles 1–2 cm long; blades oval or obovate, rounded at apex, acute and somewhat decurrent at base, 7–18 cm long, 3–9 cm wide, thick, bicolorous, glossy above with 4 or 5 pairs of major lateral veins visible, lighter and dull below with the veins indistinct. Inflorescences terminal; flowers 3–6, clustered at apex of short peduncle; calyx 6–8 mm long, acutely lobed ca one-third its length, the dehiscence circumscissile; corolla white or with the tube somewhat greenish, the tube 5.5–9 cm long, the lobes rounded at apex, 2–4.5 cm long, mostly 1–1.7 cm wide; stamens affixed at apex of tube; filaments fused to corolla tube; anthers ca 1.5 cm long, attached near base, the cells free below; ovary cylindrical, ca 3 cm long; style emerging from tube, with ascending trichomes near apex; stigmas ca 1 cm long. Capsules linear-cylindrical, 8–12 cm long at maturity; seeds numerous, thin, narrowly winged, wind dispersed, 7–13 mm long, less than 1 mm wide, the seminiferous area ca 1 mm long. *Croat 6326, 8519*.

Occasional, in the forest, often hemiepiphytic in trees at 30 m or more; also occurring on rocky shores, especially on the northern edge of Orchid Island and Peña Blanca Peninsula, where the plant is often attached to large boulders. Flowers mostly in August and September (rarely earlier). The fruits mature in the dry season, mostly from February to April.

Possibly also includes South American material going by the name *C. grandiflora* (R. & P.) Rusby and *C. macrocarpa* (Benth.) Klotzsch.

Mexico to Colombia, ranging to Brazil if the additional South American material is included. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién, from premontane wet forest in Colón and Coclé, from tropical wet forest in Colón, and from premontane rain forest in Panamá.

See Fig. 518.

COUSSAREA Aubl.

Coussarea curvigemma Dwyer, Phytologia 38:215. 1978

Small glabrate tree, usually 3–10 m tall; younger stems often puberulent. Leaves very short-petiolate; stipules triangular, 2–3 mm long, caducous; blades elliptic, acumi-

nate, acute to narrowly subcordate at base, 7–17 cm long, 3–9 cm wide, glabrous, the vein axils with pitlike domatia below making bumps above. Inflorescences short congested panicles; branches and flowers minutely puberulent; flowers heterostylous, sweetly aromatic, 4-parted; pedicels 1–2 mm long; calyx ca 1 mm long, with 4 minute teeth, persistent in fruit; corolla tubular, 2–2.5 cm long, slender, white, 4-lobed in apical third; stamens 4, in apical part of tube; anthers pale orange, slender, acuminate at apex, sagittate at base, 5–6 mm long, the lobes extending below free portion of filament; short-styled flowers with the style branched about one-third its length, held between anthers in bud but well below anthers at anthesis (owing to elongation of tube); long-styled flowers with the style 16–18 mm long, lobed ca 1.5 mm, exerted beyond tube opening and beyond anthers ca 3 mm. Drupes ellipsoid and somewhat flattened, to 12 mm long, becoming white, fleshy and sweet at maturity; seed 1(2), ellipsoid, ca 1 cm long. *Croat 5465, 8600.*

Frequent in the forest. Flowers mostly from May to July, sporadically at other times, especially in the early dry season. The fruits develop to mature size by September, but may not ripen until the late rainy or early dry season. J. Oppenheimer (pers. comm.) reports that white-faced monkeys eat the fruits in November and December. According to R. Foster, the species may flower only every other year, alternating with *Faramaea occidentalis*, which replaces it in alternate years as a main source of bird food in the forest.

Flowers are apparently moth pollinated and fall in great numbers in the morning.

The species has been confused with *C. impetiolearis* Donn. Sm., which has subquadrangular branches, the corolla tube to 2 mm wide, elongate anthers to 8 mm long, and fruits to 19 mm long (when dry).

Known only from Panama, from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Colón, and from premontane rain forest in Coclé and Panamá.

COUTAREA Aubl.

Coutarea hexandra (Jacq.) K. Schum. in Mart., Fl. Brasil. 6(6):196. 1889
Niño muerto, Quina

Shrub or tree, to 10 m tall; branches often long and drooping; young stems, petioles, and leaves sparsely pubescent, especially on veins; stems and axes of inflorescences usually lenticellate. Stipules broadly triangular, to 5 mm long, eventually deciduous; petioles to 1 cm long; blades ovate to elliptic, acuminate (sometimes abruptly so), obtuse to rounded at base, 5–13 cm long, 3–7 cm wide, the vein axils often weakly barbate below. Flowers (5)6-parted, with sweet aroma when first open, mostly in 3-flowered clusters, the clusters in terminal or upper-axillary dichasia, subtended by a pair of reduced leaves; peduncles, pedicels, and calyces sparsely pubescent; peduncles to 3 cm long; pedicels 1–1.5 cm long; calyx 7–12 mm long, deeply lobed, the lobes linear; corolla funnelform-campanulate, 7–8.5 cm long, greenish in bud,

white at anthesis or white tinged with violet-purple, sometimes pale lavender outside, pale red-violet inside, glabrous except inside near base, the tube weakly curved, constricted just above base, with faint lavender lines inside below throat, the lobes 2–2.5 cm long, narrowly acute, \pm spreading; stamens 6, equaling length of lobes, exerted above throat at anthesis; filaments densely pubescent toward the base; anthers slender, to 1.8 cm long; style about as long as stamens, the lobes 2, very short, blunt. Capsules 2-carpellate, obovoid, compressed, 3–4.5 cm long and ca 2 cm wide, brown, with many conspicuous lenticels, at first splitting medially from apex, followed by spreading of the 2 valves of each carpel; seeds many, 1.5–2 cm long, elongate, thinly flattened, winged, wind dispersed, the seminiferous area medial, round, ca 4 mm wide. *Croat 4937.*

Occasional; known from along the shore between the Laboratory Clearing and Colorado Point and from the forest near Wheeler Trail 800. Flowers from June to October, mostly in July and August. The fruits are full size by October, but are shed mostly in the dry season, from December to March.

Mexico to the Guianas, Argentina, and Peru; West Indies. In Panama, ecologically variable; known from tropical dry forest in Herrera and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from tropical moist forest in the Canal Zone, Colón, Coclé, Panamá, and Darién, and from premontane wet forest in Chiriquí and Panamá.

See Fig. 519.

DIODIA L.

Diodia denudata Standl., J. Wash. Acad. Sci. 15:105. 1925

Erect perennial herb, usually somewhat scandent, often suffruticose, 1–2 m tall; stems usually glabrous (except at leaf nodes), attenuated toward apex, minutely papillate, square, the corners winged, the wings ending just below stipules on each internode, often free at apex. Stipular bristles united at base, prominent, 3–6 mm long, ciliolate; petioles obscure or to 5 mm long; blades \pm narrowly elliptic, acute at apex, acute to attenuate and often decurrent at base, greatly diminished toward apex of plant, glabrous to scabrid above, especially near margin, minutely scabrid and puberulent on veins below, the larger ones 4.5–10 cm long, 1–3 cm wide; veins arcuate-ascending, often prominently impressed above. Flowers minute, sessile, interspersed with bristles, in axillary clusters less than 1 cm diam; calyx lobes 4, ca 0.5 mm long, persisting in fruit, 3 of the 4 attached to one fruit valve; corolla greenish-white, ca 1.2 mm long, 4-lobed ca halfway, the tube pubescent at rim inside; stamens included; style held at level of stamens; stigmas opening later than stamens. Capsules ca 1 mm long (excluding the persistent calyx), about as broad as long, puberulent, 2-valved, dehiscent basally; seeds 2, ca 1 mm long. *Croat 4373.*

Apparently rare; known only from the forest near the end of Gross Trail. Elsewhere in central Panama seen at the margins of forest. Seasonal behavior uncertain. Flow-

KEY TO THE SPECIES OF DIODIA

- Plants scandent vines, becoming hemiepiphytic; capsules usually more than 4 mm long *D. sarmentosa* Sw.
 Plants erect herbs, terrestrial; capsules less than 3 mm long:
 Stems and leaves greatly reduced near apex of plant, the upper leaves many times smaller than the lower; corolla and mature fruits ca 1 mm long *D. denudata* Standl.
 Stems and leaves not greatly reduced near apex of plant, the upper leaves at least one-third as long as the lower; corolla ca 6 mm long; fruits ca 3 mm long *D. ocimifolia* (Willd.) Bremekamp

ers and fruits at least throughout the dry season and in the early rainy season.

Leaf size and shape are variable. The species was reported in the *Flora of the Canal Zone* (Standley, 1928) as *D. nudata* Standl. This was no doubt a typographical error.

Known only from Panama and Colombia (Chocó). In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Colón (Santa Rita Ridge).

Diodia ocimifolia (Willd.) Bremekamp, Recueil Trav. Bot. Néerl. 31:305. 1934

Hemidiodia ocimifolia (Willd.) K. Schum.

Hierba (yerba) meona

Erect herb, usually less than 1 m tall; stems pubescent or glabrous except for pairs of pubescent lines extending downward from stipules. Leaves sessile or short-petiolate; stipules oblong, pubescent, with ciliate bristles; blades lanceolate, gradually tapered toward both ends, mostly 3.5–9.5 cm long, 0.7–2.5 cm wide, both surfaces \pm scabrous, the trichomes stiff, erect, to ca 0.2 mm long. Flowers sessile, 4-parted, interspersed with long white bristles, in dense axillary clusters less than 1 cm diam; calyx lobes 4, inconspicuous, persisting in fruit; corolla white, sometimes tinged with pink, to 6 mm long, lobed to near middle, glabrous except for throat and base of lobes inside, the lobes spreading; style and stamens subequal, exerted to 2.7 mm above rim; filaments adnate to corolla tube; stigma capitate. Capsules 2-valved, densely pubescent in upper two-thirds, ca 3 mm long; seeds oblong-elliptic, 2.3–2.7 mm long, dark brown, weakly transverse-sulcate. *Croat 12840*.

Common in clearings. Flowers and fruits throughout the year.

This species is in the tribe Spermaceae, a confusing group including *Borreria*, *Diodia*, and *Spermaceae*. All have minute flowers clustered in the leaf axils and two-celled, capsular, longitudinally sulcate fruits. Several genera in this confusing group are difficult to identify because generic lines are drawn largely on the basis of type of fruit dehiscence. It is possible that not all of these genera are valid.

Throughout the American tropics; Malaysia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Herrera, Coclé, and Panamá, from premontane wet forest in Colón, Coclé, and Panamá, and from tropical wet forest in Colón.

Diodia sarmentosa Sw., Prodr. Veg. Ind. Occ. 30. 1788

Vine, sometimes hemiepiphytic; stems to 1 cm diam, woody at base; younger stems green, herbaceous, square, strigose on the surface, more densely pubescent with longer trichomes on ribbed corners; internodes 12–32 mm long. Stipules pubescent, adnate to petioles, with bristles to 6 mm long; petioles 2–4 mm long; blades narrowly elliptic, acuminate, cuneate at base, 3–7 cm long, 1.2–1.8 cm wide, dark green above, asperous and paler below, sparsely pubescent below especially on veins, the margins \pm revolute; lateral veins mostly in 4 pairs, arcuate-ascending and markedly impressed above. Flowers axillary at all upper nodes, usually 6 at each node, white, sessile, soon falling; sepals 5, free, 2.3 mm long, ciliate, \pm unequal, persisting in fruit; corolla ca 3.5 mm long, the lobes 5, ca 2 mm long and 1 mm wide, the tube with a ring of trichomes at middle; stamens exerted ca 1 mm; filaments fused with corolla tube; anthers ca 0.7 mm long; style ca 2.7 mm long; stigma capitate and papillose. Capsules 3–4.5 mm long, to 3 mm diam, reddish-brown at maturity, splitting at apex into 2 halves, both halves remaining closed; seeds oblong-elliptic, 2.5–3 mm long, black or dark brown, minutely reticulate, the inner surface deeply invaginate longitudinally. *Croat 5525*.

Occasional; collected only along the shore, sometimes as a hemiepiphyte on logs in the lake. Apparently flowers and fruits all year. Plants usually bear both flowers and fruits simultaneously.

Similar in many ways to *D. ocimifolia*, but that species is a moderately short herb with smaller fruits and much less scabrous leaves.

Mexico to Panama, Venezuela, the Guianas, eastern Brazil; Greater Antilles; Africa. In Panama, known from tropical moist forest in the Canal Zone and Veraguas and from tropical wet forest in Colón (Miguel de la Borda).

FARAMEA Aubl.

Faramea luteovirens Standl., Contr. U.S. Natl. Herb. 18:138. 1916

Huesito

Glabrous shrub or small tree, to 4 m tall. Stipule body triangular, ending in a stiff cusp, 3–5 mm long, subpersistent; petioles ca 1 cm long; blades elliptic or obovate, abruptly acuminate, obtuse to acute at base, 7–13 cm long, 3–6 cm wide, moderately coriaceous. Flowers 2 or 3, upper-axillary or terminal, aromatic; pedicels thick,

KEY TO THE SPECIES OF FARAMEA

- Flowers 2 or 3 in axils, never in branched inflorescences; pedicels more than 2 cm long *F. luteovirens* Standl.
 Flowers usually numerous, in branched terminal dichasia or umbelliform racemes; pedicels less than 2 cm long *F. occidentalis* (L.) A. Rich.

2–4 cm long; calyx cupular, truncate, ca 3 mm long, persisting in fruit; corolla white, salverform, 2–3 cm long, 4-lobed; ovary 1-celled. Drupes globose or ellipsoid, 1.5–2 cm long, blue or black at maturity; seed 1, deeply excavate on lower side. *Croat 5217, 6725.*

Probably rare; collected twice along the shore of Miller Peninsula. Flowers mostly in the dry season (February to May). The fruits mature mostly from September to November.

Known only from Panama, from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in Colón, San Blas, Chiriquí, and Darién, and from tropical wet forest in Darién.

***Faramea occidentalis* (L.) A. Rich.,** *Mém. Soc. Hist. Nat. Paris* 5:176. 1834

F. zeteki Standl.

Benjamín, Bonewood, Huesillo, Huesito, Palo escrito

Tree, to ca 10 m tall and 20 cm dbh, \pm glabrous; stems usually divaricately branched. Stipules triangular, with a long acicular apex, 1–1.5 cm long, eventually deciduous; petioles 5–15 mm long; blades oblong-elliptic to elliptic, acuminate and downturned at apex, obtuse to acute at base, 13–18 cm long, 4–8(10) cm wide, \pm stiff but not thick. Flowers with strong, sweet aroma, in terminal dichasia or umbelliform racemes to ca 10 cm long; pedicels 4–20 mm long; calyx tubular, truncate, ca 2 mm long at anthesis, persisting in fruit; corolla white, the tube 14–20 mm long, slender, less than 3 mm wide, the lobes 4, narrowly acute, 15–25 mm long, spreading-recurved; stamens 4, attached near apex of tube, included or slightly exerted; anthers to 8 mm long, sharp at apex, blunt at base, attached to filaments near base; style with 2 slender branches more than 4 mm long, at first held below stamens, eventually slightly exerted. Drupes depressed-globose, ca 1 cm diam, bluish-black at maturity; seeds usually 1 by abortion, rounded with a large depression at base. *Croat 6597, 14961.*

Abundant in the forest. Flowers from March to July, mostly in May and June. The fruits mature from April to December, mostly from August to October only every other year.

Flowers are probably moth pollinated; most appear on the ground in late morning. The aroma is intense, much like that of *Quisqualis indica* L. (Combretaceae), a cultivated plant in the Canal Zone, which has flowers opening at dusk.

Scattered from northeastern Mexico to Colombia, Venezuela, Ecuador, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Colón, Veraguas, Los Santos, Panamá, and Darién, from premontane moist forest in Panamá, and from premon-

tane wet forest in Coclé and Darién. Reported from tropical wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

GENIPA L.

***Genipa americana* L.,** *Syst. Nat. ed. 10, 931.* 1759

G. caruto H.B.K.; *G. americana* var. *caruto* (H.B.K.) K. Schum.

Genipap, Guayatil blanco, Guayatil colorado, Jagua, Jagua amarillo, Jagua blanca, Jagua colorado, Jagua negro, Jagua de montaña

Tree, to 20 m tall and to 30(50) cm dbh; outer bark dark, not fissured but with many raised lenticels; stems stout, with prominent scars. Leaves clustered at ends of branches; stipules triangular, to ca 1.5 cm long, entire, deciduous; petioles 5–10 mm long, thick; blades obovate or elliptic, acute or short-acuminate, narrowed to acute or obtuse base, mostly 15–42 cm long, 5–19 cm wide, glabrous above, almost glabrous to densely pubescent below with short erect trichomes. Cymes stout, terminal or subterminal, peduncles short; flowers 5-parted; pedicels ca 1 cm long; calyx truncate or shallowly lobed, 7–10 mm long; corolla yellow or white becoming yellow, thick, sericeous, 2–3 cm long, the limb ca 4 cm wide, the tube 6–10 mm wide, the lobes divided more than halfway, spreading at anthesis, later recurving; stamens exerted; anthers 8–14 mm long, sessile or with a very short filament, attached well below middle of tube, the anther becoming recurved between corolla lobes; style exerted ca 7 mm above rim, the lobes 2, thick, ca 7 mm long, remaining closed until after shedding of pollen. Berries baccate, globose or ellipsoid, 5–7 cm long, becoming fleshy at maturity, the calyx persistent on fruit and forming a thick-rimmed crater ca 1 cm across; seeds numerous, flattened, yellow, ca 1 cm long. *Croat 6163, 12728.*

Frequent in the forest and occasional along the shore. Flowers to some extent throughout the year, but mostly in the rainy season, usually from May to July. The fruits mature in about a year; they are eaten by tamarins in May and June (Hladik & Hladik, 1969). One tree had mature fruits on it for 2 years, during which time it lost its leaves twice. Leaves are usually replaced during the late dry and early rainy seasons.

The sap of the plant, although clear, quickly turns blue. Bawa and Opler (1975) reported this species to be dioecious, but all trees on BCI that flowered also set fruit.

Mexico to Argentina; West Indies. In Panama, ecologically variable, occurring mostly around the Gulf of Panama on the Pacific slope, extending to the Caribbean coast in the region of the canal, and characteristic of

tropical moist forest (Tosi, 1971); known from premontane dry forest in Los Santos, from tropical dry forest in Los Santos, Coclé, and Panamá, from premontane moist forest in the Canal Zone and Los Santos, from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Panamá, and Darién, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Panamá.

See Fig. 520.

GEOPHILA D. Don

Geophila croatii Steyerm., *Phytologia* 35:401. 1977

Low creeping herb, less than 10 cm high; stems long-trailing, rooting at nodes, minutely papillose, the younger ones purplish. Stipules lanceolate to broadly triangular, subacute to acuminate at apex, 3–5 mm long, curved outward, persistent; petioles 3–8 cm long, with marginal rows of thick trichomes on the upper side, the trichomes sometimes directed toward base; blades ovate, acute at apex, cordate at base, 2.5–6 cm long, 2–4.5 cm wide, minutely papillose; veins often purplish. Inflorescences solitary or few, terminal, on short axillary branches from creeping stems; peduncles 3–20 mm long; heads usually bearing 5–7 flowers; flowers sessile or short-pedicellate, 5-parted; pedicels less than 1 mm long before anthesis, 2–3 mm long in fruit; calyx lobes recurved, linear-oblong or narrowly lanceolate, subcaudate, less than 3 mm long before anthesis, to 8–9 mm long in fruit; corolla white, to 5.5 mm long, the lobes slender, sometimes tipped with maroon; stamens included; filaments fused in basal half, the tube with tufts of trichomes at apex; style equaling stamens. Berries ± globose, 3–4 mm diam, red, often more than 3 per cluster; seeds 2, oblong-elliptic, 3.5–6 mm long, flattened on one side, half twisted, faintly 3-ribbed. *Croat* 6647 (type).

Occasional in the forest, but locally abundant along some trails, especially Zetek Trail. Flowering and fruiting throughout the rainy season from June to December, with most flowers seen at the beginning of the rainy season in June and July. The fruits develop in about a month, and some may mature while other plants in the clone are still in flower.

This taxon is most closely related to *G. gracilis* (R. & P.) DC. and has been confused with that species (Williams, 1973). It is distinguished from *G. gracilis* by its glabrous upper leaf surface and longer calyx lobes. It has also been confused with *G. macropoda* (R. & P.) DC., from which it differs by having glabrous, much shorter peduncles, acute to acuminate stipules and leaf apices, glabrous outer surface of floral bracts, glabrous calyx lobes, completely glabrous veins of lower leaf surface,

and abundant cystoliths on the lower surface.

Nicaragua and Panama, probably also in intervening areas. In Panama, known only from BCI.

See Fig. 521.

Geophila repens (L.) I. M. Johnston, *Sargentia* 8:281. 1949

G. herbacea (Jacq.) K. Schum.

Low creeping herb, less than 10 cm high, much like *G. croatii* in habit and vegetative characteristics. Stipules rounded to broadly ovate, ca 2 mm long; petioles 1–5 cm long; blades ovate, rounded to bluntly acute at apex, cordate at base, mostly less than 4.5 cm long. Inflorescences usually solitary; peduncles to 2.5 cm long; flowers solitary or in groups of 2 or 3, sessile; calyx lobes 2–6 mm long, slender, acute to acuminate, persisting in fruit; corolla white, 1.2–1.5 cm long, glabrous or pubescent, the tube 8–10 mm long, the lobes often tinged with lavender, spreading; stamens 5, included, held just below rim of corolla tube; filaments free near apex; style 6–7 mm long, equaling stamens; style branches 2, puberulent. Capsules 1 or 2 per cluster, globose, ca 6 mm diam, red becoming black; seeds 2, ± elliptical, 4–5 mm long, flattened, twisted, faintly ribbed on both sides. *Croat* 10171, 14928.

Common in the forest and locally abundant, usually on trails or in shady, moist places in open areas. Flowers mostly in the rainy season, from May to October, especially in June and July, and sporadically in the dry season. The fruits mature mostly from August to October, but as late as December.

Mexico to Colombia, the Guianas, Peru, and Bolivia; West Indies; Central and West Africa; Polynesia; the Philippines. In Panama, widespread in tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Panamá, and Darién and known from tropical wet forest in Darién and from premontane rain forest in Los Santos.

See Fig. 522.

GUETTARDA L.

Guettarda foliacea Standl., *Contr. U.S. Natl. Herb.* 18:139. 1916

Espino, Guayabo

Tree, usually less than 10 m tall, branched from near ground, often with sucker shoots, the branches often vinelike, armed with stout branch-spines (spines terminating branches) to 5 cm long; stems appressed-pubescent when young, glabrate in age. Stipules lanceolate, to 12 mm long, appressed-pubescent, caducous; petioles 1–2 cm long, pilose above, appressed-pubescent below; blades narrowly elliptic to ovate or obovate-elliptic, acuminate,

KEY TO THE SPECIES OF GEOPHILA

Blades rounded or blunt at apex; flowers 1–3 per cluster; leaves seldom more than 4.5 cm long

. *G. repens* (L.) I. M. Johnston

Blades sharply acute at apex; flowers 4–7 per cluster; leaves often more than 4.5 cm long

. *G. croatii* Steyerm.

Fig. 520.
Genipa americana



Fig. 522. *Geophila repens*



Fig. 521. *Geophila croatii*

Fig. 523.
Guettarda foliacea



obtuse to rounded at base, 6–16 cm long, 2.5–6.5 cm wide, sparsely pubescent (the trichomes denser on veins), sericeous below when young, with tufts of trichomes in lower vein axils below. Inflorescences cymose, axillary, usually spreading, appressed-pubescent, to 7 cm long, bracteate; bracts 5–10 mm long, appressed-pubescent outside, ciliate; peduncles slender, to 3 cm long; flowers sessile; calyx truncate, 2–3 mm long, cupular, appressed-pubescent; corolla narrowly tubular, 2–2.5 cm long, white, shallowly 4-lobed, the lobes spreading, rounded at apex, ca 5 mm long, sericeous outside; anthers 4, sessile, ca 3 mm long, attached just below rim of corolla; pollen golden; style slender, to 2.5 cm long, equaling lobes, exerted above throat at anthesis; stigma globular. Berries globose, 1–3 cm diam, densely short-velutinous, red at maturity, the exocarp thin, the mesocarp sweet and fleshy, 4-loculed; seeds 1 per locule. *Croat 6061, 15160.*

Frequent in the forest. Flowers mostly in late June and early July. The fruits mature mostly by September but often later; they have been observed being eaten during November (J. Oppenheimer, pers. comm.). Sporadic flowering may occur at other times, especially at the beginning of the dry season, with the fruits maturing in the late dry or early rainy seasons.

Animals eat the pericarp and then discard the seed. Elsewhere in the Canal Zone trees have been seen with longer, vinelike branches.

Panama and Colombia. In Panama, known mostly on the Pacific slope, principally from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién, but also from premontane wet forest in Chiriquí.

See Fig. 523.

HAMELIA Jacq.

Hamelia axillaris Sw., Prodr. Veg. Ind. Occ. 46. 1788

Panchus chapa, Guayabo negro

Shrub, usually 1.5–3 (10) m tall; stems puberulent. Stipules 3.3–3.7 mm long, subpersistent, attenuate, the sides folded together; petioles 1.5–4 cm long, puberulent, canaliculate; blades ± elliptic, acuminate, attenuate and decurrent at base, mostly 8–23 cm long, 3.5–7 (9) cm wide, glabrous above, puberulent below at least on veins, with short linear cystoliths visible below upon drying; major lateral veins in 6–9 pairs, arcuate-ascending, the axils often with small tufts of trichomes below, the smaller veins reticulate. Inflorescences terminal, short-branched cymes; flowers yellow or orange; pedicels ca 1 mm long; calyx 4–6 mm long, the lobes 5, ca 1 mm long, somewhat accrescent and persisting in fruit; corolla yellow, cylindrical, to 10 mm long in bud, becoming ±

funneliform, to 13 mm long and ca 5 mm wide, the lobes 5, held mostly erect, 1.3–2 mm long; stamens to 8 mm long; filaments ca 2 mm long, continuous with anthers, the connective extended beyond apex and spatulate; pistil 11–13 mm long; style ± equaling petals; stigma oblong, ca 2.7 mm long. Berries oblong, 5–6 mm long, green turning red then black at maturity, fleshy, 5-celled, each cell with many seeds; seeds less than 1 mm long, brown, densely reticulate. *Croat 6299, 12484.*

Frequent in the forest, especially the older forest. Flowers throughout the rainy season, mostly from June to September. The fruits mature from August to December, mostly from August to October.

Distinguished from other shrubs in the family by the funneliform, yellow flowers and many-seeded berries.

Mexico, Belize, Costa Rica, and Panama to Venezuela, Brazil, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in Panamá and Darién, and from tropical wet forest in Colón and Darién.

Hamelia patens Jacq. var. *glabra* Oerst., Vidensk.

Meddel. 1852:42. 1853

H. nodosa Mart. & Gal.

Red berry, Scarletbush, Uvero

Shrub or small tree, usually less than 6 m tall, nearly glabrous. Leaves verticillate, usually 3 (5) at a node, or opposite; stipules linear-lanceolate, often curved inward, 3 (4) at each node, ca 4 mm long; petioles 1–8 cm long, narrowly winged at least above, often puberulent, sometimes reddish; blades elliptic to oblanceolate, abruptly short-acuminate, obtuse to attenuate and gradually decurrent at base, mostly 9–23 cm long and 4.5–10.5 cm wide, glabrous above, minutely pubescent on veins below, the vein axils barbate, often inconspicuously so. Inflorescences terminal, cymose (the flowers all on upper side of branches), variable in size, to 15 cm long and 20 cm wide; branches often reddish; pedicels 1–5 mm long; calyx lobes short, persisting in fruit; corolla tubular, 15–23 mm long, orange becoming red-orange at anthesis, 5-lobed, prominently ridged below lobes; stamens included; filaments free much of their length; anthers 8–9 mm long, the connective prolonged and acute at apex; pistil 15–24 mm long, equaling corolla tube; stigma 3.5–5 mm long, oblong, swollen. Berries soft, purple or black at maturity, to 13 mm long and 10 mm wide, 5-celled; seeds many, flattened, brown, markedly reticulate. *Croat 4273.*

Occasional, occurring only in clearings, often locally abundant. Flowers and fruits throughout most of the year; the flowering season usually beginning in the late

KEY TO THE SPECIES OF HAMELIA

Leaves verticillate, usually 3, 4 or 5 per node, sometimes opposite; flowers orange to red

..... *H. patens* Jacq. var. *glabra* Oerst.

Leaves not verticillate, 2 per node; flowers yellow *H. axillaris* Sw.

dry and early rainy seasons, with a second flush of flowering activity in the early dry season. The fruits mature in about 1 month.

Leck (1972) reported that four species of birds visit flowers for nectar and nine species take the fruit. Feeding pressures on fruits are so great in the rainy season that even immature fruits are taken. Among the possible pollinators are three hummingbirds, *Thalurania furcata*, *Damophila julie*, and *Amazilia tzacatl*, and one honeycreeper, *Coereba flaveola*. The fruits are taken by a number of birds, including toucans, flycatchers, thrushes, warblers, honeycreepers, and tanagers (Leck, 1972).

Mexico, Nicaragua south to Panama and Venezuela, Amazonian Brazil, Peru, and Bolivia. In Panama, known from tropical moist forest in all provinces and from premontane wet forest in Coclé.

HOFFMANNIA Sw.

Hoffmannia woodsonii Standl., Ann. Missouri Bot. Gard. 28:471. 1941

Weak-stemmed, \pm glabrous shrub, to 1.5(3) m tall, sometimes somewhat decumbent. Stipules minute, ca 1 mm long, raised, triangular, deciduous; petioles 2.5–8 cm long; blades oblanceolate to elliptic, acuminate and weakly falcate (the acumen to 1 cm long), attenuate and decurrent onto petiole at base, 6–18 cm long, 3–8 cm wide. Cymules short-pedunculate, axillary, umbelliform clusters ca 3 cm long, bearing 2–6 flowers; pedicels 5–7 mm long; calyx lobes ca 1 mm long, acute, persistent in fruit; corolla 7–8 mm long, greenish-yellow, the lobes 4, ca 4 mm long, acute, recurved at anthesis; stamens exerted; filaments fused to tube near base; anthers ca 4.3 mm long, introrse, held together in a cluster; style to 8.5 mm long, unbranched, thickened at apex, held well above anthers. Berries ellipsoid, 3–4 mm long, glabrous, delicately ribbed, yellow-green or reddish; seeds many, ca 0.5 mm long. *Croat 13511*.

Known only from the creek north of the laboratory. Flowers from April to August, mostly from May to July. The fruits mature in about a month. Elsewhere in Panama the species may flower in the early dry season.

Costa Rica and Panama; mostly at higher elevations. In Panama, ecologically variable; known from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Los Santos, and Darién, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from premontane rain and lower montane wet forests in Chiriquí.

ISERTIA Schreb.

Isertia haenkeana DC., Prodr. 4:437. 1830
Canelito

Stout shrub, usually 2–3 m tall; stems densely pubescent, usually 4-ribbed. Stipules 1–2 cm long, lobed to base, the lobes separate, oblong-lanceolate, persistent; petioles obscure or to 4 cm long; blades elliptic to obovate, long-

acuminate, gradually tapered to a decurrent base, 10–45 cm long, 3.5–16 cm wide, glabrous above, tomentose and \pm viscid below especially on veins. Panicles stout, terminal, bracteate, reddish-tomentose, 9–22 cm long, the entire inflorescence turning bright orange sometime before fruit maturation; pedicels to ca 2 mm long; calyx cupular, red-orange, minutely 4-lobed, the lobes ca 1.5 mm long; corolla tubular, to 3.5 cm long, yellow, the lobes 4, ca 7 mm long, bearded inside near tip; filaments united to corolla tube, the free part thick, fleshy, flattened; anthers to 3.7 mm long, attached near their apex, the endothecium dark-spotted; style slender, ca 2.5 cm long; stigmas 5, slender, arcuate. Berries 5-carpellate, 6–8 mm long, red becoming black at maturity, each cartilaginous wedge containing many seeds; seeds irregular, reticulate, ca 2 mm diam. *Croat 5076*.

Occasional along the shore and in clearings. Common and showy along roadsides in the Canal Zone. Flowers throughout the rainy season, but mostly in the early rainy season. The fruits mature from the middle of the rainy season until the early dry season.

Mexico to Panama, Colombia, and Venezuela; Cuba. In Panama, ecologically variable; known from tropical moist forest all along the Atlantic slope and on the Pacific slope in the Canal Zone, Veraguas, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Panamá, from tropical wet forest in Bocas del Toro, Colón, Veraguas, Coclé, Panamá, and Darién, and from premontane rain forest in Coclé.

IXORA L.

Ixora coccinea L., Sp. Pl. 110. 1753

Jazmin de coral, Cache de tore

Small shrub, to 2 m tall, glabrous nearly throughout. Leaves sessile or subsessile; stipules to 5 mm long, with cusps as long as the broadly flaring base, subpersistent; blades ovate to oblong-elliptic, apiculate at apex, rounded to shallowly cordate at base, 3.5–7 cm long, 2–3 cm wide (some pairs often markedly reduced), moderately thick. Flowers 4-parted, in terminal, short-pedunculate dichasia; branches reddish; calyx 2–3 mm long, the lobes 4, ca 1 mm long, acute, reddish; corolla red or orange-red, 5–7 cm long, the tube ca 1.5 mm wide, the lobes 4, lanceolate, spreading, to 1.5 cm long; stamens attached to corolla rim; filaments with the free part short; anthers appressed to corolla, 1–2 mm long; style exerted ca 3 mm above rim, the branches short, slender. Berries ca 1 cm long, red becoming dark violet at maturity, the mesocarp pulpy, sweet; seeds 2, ovoid, ca 6 mm long. *Croat 7051*.

Cultivated at the Laboratory Clearing. Apparently flowering throughout the year, but not setting fruit.

Apparently native to Asia; cultivated in Central and South America, the West Indies, and Madagascar. In Panama, known from premontane moist forest in Panamá and from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Coclé, Panamá, and Darién.

MACROCNUM P. Browne**Macrocnemum glabrescens** (Benth.) Wedd., Ann. Sci.

Nat. Bot., sér. 4, 1:76. 1854

Palo cuadrado, Palo blanco, Madroño

Mostly glabrous tree, 8–15 (25) m tall; trunk to 30 (50) cm dbh, all but the smallest involuted in long vertical sections; outer bark reddish-brown, very thin; inner bark tan, thin; sucker shoots often forming near base of trunk. Stipules ovate, to ca 1.8 cm long and 1 cm wide, caducous; petioles obscure or to 3 cm long, glabrate; blades obovate to elliptic, abruptly acuminate, acute to obtuse at base, 7–21 cm long, 2.5–9.5 cm wide, glabrate above, strigose below especially on veins. Panicles terminal or subterminal, to 25 cm long and 20 cm wide; peduncles to 18 cm long, strigose; flowers sessile or subsessile, many, 5-parted; calyx lobes ca 0.5 mm long, blunt; corolla rotate, 1.5 cm long, magenta, the tube at first green, becoming maroon, nearly 1 cm long, densely glandular on basal half inside, pubescent near staminal tufts, glabrous above, the limb ca 1.5 cm broad, each lobe somewhat creased in the middle; filaments fused to corolla tube in basal half, with stiff trichomes directed both upward and downward near junction with tube; anthers opening in bud, held at one side of tube near its rim at 3 levels, the thecae opening broadly toward opposite side of tube; pollen tacky; ovary 2-celled, with many ovules; style held below anthers at anthesis, with the 2 thick stigmas often closed, later elongating, passing between anthers with the stigmas open; nectar copious. Capsules cylindrical, 10–20 mm long, 2–4 mm wide, splitting longitudinally on 2 sides, exposing seeds; seeds minute, membranaceous, winged, ca 3 mm long. *Croat 4806.*

Frequent in the forest, especially in the younger forest, sometimes locally very abundant. Flowers mostly from December to April, especially in January and February, rarely later or earlier (October to June). The fruits mature from February to June, mostly in April and May.

Costa Rica to Colombia (Chocó). In Panama, known most commonly from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién, but also from premontane wet forest in Veraguas and Coclé and from tropical wet forest in Colón and Darién.

MANETTIA L.**Manettia reclinata** L., Mant. Pl. Altera 553. 1771*M. coccinea* (Aubl.) Willd.

Churco-guidave

Vine, to 1 m or more long, glabrate except sometimes sparsely pubescent on leaves. Stipules broadly triangular, minute, caducous; petioles to 1 cm long; blades ovate to elliptic, acuminate, obtuse to acute at base, 2.5–7 cm long, 1.5–3 cm wide. Flowers axillary, solitary or in umbels; peduncles 2–3.5 cm long; pedicels 1–3 cm long; calyx lobes 8, linear-lanceolate, irregular, to 9 mm long, puberulent and ciliate, persisting in fruit; corolla red

(fading to pink), 15–25 mm long at anthesis, puberulent outside especially on tube, the tube with a ring of moniliform trichomes at rim and in basal half above the somewhat expanded base, the lobes (3)4, ovate, to ca 5 mm long, obscurely short-acuminate; stamens 4; filaments adnate to corolla tube; anthers tightly affixed near rim; stigmas 2, thick, oblong, papillate, held well above anthers, receptive while pollen is shed. Capsules 2-valved, 7–10 mm long, to ca 8 mm wide, green to black at maturity, somewhat obovate, with a medial groove, the valves persisting after opening; seeds many, ca 2.7 mm wide, flattened, winged, the margin irregular, the wing thin, broad, round. *Croat 12740.*

Occasional in old clearings or at the edge of the forest along the edge of the lake. Flowers and fruits mostly in the early dry season (especially December), rarely also at other times of the year.

Mexico south to Colombia and Venezuela; Cuba and Jamaica. In Panama, ecologically variable; known from premontane moist forest in the Canal Zone and Panamá, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from premontane wet forest in Chiriquí, Veraguas, and Panamá, from tropical wet forest in Los Santos, Coclé, and Darién, and from premontane rain forest in Chiriquí and Panamá.

OLDENLANDIA L.**Oldenlandia corymbosa** L., Sp. Pl. 119. 1753

Slender herb, often decumbent, ± glabrous except for sparse pubescence on underside of leaves. Leaves ± sessile; stipules minute, persistent, with short flattened trichomes on surface and bristles on upper margin; blades linear-lanceolate or linear, acute at both ends, 1–3 cm long, to 5 mm wide, glaucescent below. Cymes small, axillary, bearing few flowers; peduncles to 12 mm long; flowers 4-parted; pedicels 2–5 mm long; calyx deeply lobed, the lobes 4, narrowly triangular, ca 0.5 mm long, with scabrid margins; corolla white to faintly lavender, to 1.4 mm long, 4-lobed to about middle, the lobes acute to blunt, conspicuously pubescent at base inside; stamens 4, minute, included; anthers introrse, ca 0.3 mm long; style about as long as stigma; stigma held at level of anthers. Capsules 2-carpellate, ca 1.7 mm long and 2.3 mm wide, weakly flattened, with a medial groove, rounded below, ± flat at apex; seeds 1 per carpel, globular, minute (ca 0.5 mm diam), the surface areolate. *Croat 7055.*

Infrequent, in clearings or disturbed areas. Probably flowering and fruiting throughout the year, especially at the beginning of the dry season.

Widespread in the tropics of Western and Eastern hemispheres. In Panama, growing mostly at lower elevations on the Atlantic slope and at higher elevations on the Pacific slope; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién (doubtlessly Colón as well) and from premontane wet forest in Colón and Coclé.

PALICOUREA Aubl.**Palicourea guianensis** Aubl., Hist. Pl. Guiane Fr.

1:173, t. 66. 1775

Shrub or small tree, to about 3.5 m tall; stems quadrangular, stout; stems and leaves glabrous to inconspicuously puberulent on veins. Stipules lobed nearly to base, the lobes obtuse, 5–8 (15) mm long, long-persisting; petioles to 3 cm long; blades ovate to elliptic, acuminate, acute to obtuse and weakly decurrent at base, mostly 12–25 cm long, 6–13 cm wide, chartaceous; major veins raised on both surfaces, the reticulate veins conspicuous. Inflorescences terminal thyriform panicles 12–18 cm long; branchlets minutely puberulent, reddish-orange in flower, becoming red-violet in fruit; peduncles to 10 cm long, quadrangular; pedicels 5–8 mm long; calyx lobes 5, puberulent, spreading at anthesis, to 1 mm long; corolla tubular, ca 1.5 cm long, yellow or orange, weakly inflated near apex, puberulent outside, the lobes 5, minute; stamens included; filaments fused to basal two-thirds of corolla tube, densely pubescent; anthers sagittate, the connective blue above; style bilobed, slightly exerted. Capsules ovoid, 4–8 mm long, purple, apiculate at apex, minutely puberulent; seeds 2, ovate, hemispherical, the inner side flat, the outer side rounded and 3–5-ribbed, roughened. *Croat 11082*.

Frequent at the edges of clearings and along the lake-shore; also in the young forest. Flowers from late April to July, rarely later. The fruits develop in about 1 month, mostly from June to October, but some may be seen throughout the year.

Some collections bearing this name from Darién and Panamá Province (Cerro Jefe) differ from the material described here in having corollas 2–2.5 cm long with the styles not exerted and somewhat shorter than the stamens. They may represent another species or variety of *P. guianensis* or possibly another sexual form. The species is not heterostylous on BCI.

Guatemala to Colombia, Venezuela, the Guianas, Brazil (Pará), and Ecuador; Trinidad and West Indies. In Panamá, known from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Los Santos, Panamá, and Darién, from premontane wet forest in Colón, Panamá, and Darién, and from premontane rain forest in Panamá and Darién.

See Fig. 524.

PENTAGONIA Benth.**Pentagonia macrophylla** Benth., Bot. Voy. Sulphur 105, t. 39. 1845*P. pubescens* Standl.

Hoja de murciélago, Indian ink, Teta de vaca, Tetilla, Wild grape

Shrub, 1.5–5 m tall, often unbranched; stems usually 4-ribbed near apex, sparsely to densely scurfy. Stipules narrowly triangular, 3.5–7 cm long, acuminate; petioles 6–12 cm long, strigose and often scurfy; blades broadly

elliptic to obovate, acute at apex, acute to obtuse at base, 30–65 cm long, 21–37 cm wide, \pm glabrate to short-pilose on both surfaces but especially below. Flowers few, sessile or subsessile, in dense axillary clusters subtended by large reddish bracts; calyx lobes 5, 10–20 mm long, rounded to obtuse, reddish, persisting in fruit; corolla thick, yellow, 3.5–4.5 cm long, 6–10 mm diam, puberulent outside, the lobes 5, ovate, acute, spreading; stamens of irregular lengths, attached to one side of corolla tube, the longest to ca 3 cm long; filaments and tube pubescent at point of fusion of stamens ca 1 cm above base; style ca 2 cm long, the lobes thick, held to one side of tube opposite and below anthers; nectary 5-lobed; nectar copious. Fruits baccate, spherical but \pm tapering into the persistent calyx, to 2.5 cm diam, red to orange-red, 2-carpellate, indehiscent; seeds many, irregularly oblong, ca 4 mm long, brown, somewhat flattened, embedded in a fleshy white matrix. *Croat 6244, 16542*.

Common in the forest, especially the old forest. Flowers from the late dry to the middle of the rainy season, mostly from April to September. The fruits mature from the late rainy season to the dry season of the following year; they are eaten during September and October by white-faced monkeys (Hladik & Hladik, 1969).

Panamá and Colombia (Chocó). In Panamá, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Colón and Coclé, from tropical wet forest in Colón, Coclé, Panamá, and Darién, and from premontane rain forest in Darién.

POGONOPUS Klotzsch**Pogonopus speciosus** (Jacq.) K. Schum. in Mart., Fl. Brasil. 6(6):265. 1889

Chorcha de gallo

Tree, 2–8 m tall and to 20 (30) cm dbh; stems lenticellate, at least the smallest with appressed trichomes. Stipules triangular, to 3 mm high and at least twice as broad, entire, persistent; petioles short or to 3 cm long; blades elliptic to oblanceolate, abruptly acuminate, gradually tapered to base, mostly 8–25 cm long, 3–8 cm wide, sparsely appressed-puberulent on veins below. Inflorescences of cymes forming terminal panicles; flowers 5-parted; pedicels 3–5 mm long; calyx with one lobe greatly enlarged, leaflike, bright red, 3.5–6.5 cm long, often persisting in fruit, the others slender and short; corolla tubular, 2–3 cm long, dark red outside, densely puberulent, the trichomes longer and thicker inside, the tube white inside, the lobes pink; stamens exerted, ca 3.5 cm long, held erect at first, later recurved to one side; filaments fused to tube ca 7 mm at base, the base of the free part surrounded by dense tufts of fine trichomes; anthers purple; style scarcely emerging from flower, with the stigmas closed, later the style erect, nearly as long as stamens, with the stigmas \pm reflexed. Capsules ovoid to obovoid, 5–8 mm long, 4–6 mm wide, with conspicuous whitish lenticels; seeds many, minute, irregularly shaped. *Foster 1411*.



Fig. 524. *Palicourea guianensis*



Fig. 525.
Posoqueria latifolia

Rare, on the shore. Flowers mostly from September to January. The fruits mature in December and January (possibly later).

Mexico to Colombia, Venezuela, and Brazil. In Panama, known from drier parts of tropical moist forest in the Canal Zone, Colón, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from tropical wet forest in Darién.

POSOQUERIA Aubl.

Posoqueria latifolia (Rudge) R. & S., Syst. Veg.

5:227. 1819

Boca vieja, Boca de vieja, Borajo, Fruta de mono, Fruta de murciélago, Huevo de mono, Monkey apple, Mosquitowood, Wild coffee, Borojocito del monte

Glabrous shrub or tree, to 10 m tall; wood red. Stipules acute, 8–12 mm long, caducous; petioles 5–20 mm long; blades elliptic to oblong-elliptic, abruptly short-acuminate, acute to obtuse at base, 7–24 cm long, 3.5–13 cm wide, coriaceous, bicolorous; midrib often arched downward, each side of blade turned somewhat upward along midrib. Corymbs terminal; flowers sweetly aromatic, 5-parted; pedicels obscure or 4–10 mm long; calyx thick and short, ca 5 mm long, the lobes minute and blunt; corolla white, fleshy, the tube 13–16 cm long, glabrous except at rim, the lobes 5, oblong, to 2.5 cm long, blunt, recurved after anthesis; filaments united to corolla tube, exerted above throat after petals recurve; anthers united at anthesis, pushed to one side of tube, bursting apart violently when contacted, 2 pairs remaining united, their filaments reflexing laterally, the fifth filament bending forward across tube, its anther carrying with it almost the entire cobwebby pollen mass; style contained well within tube, ca 9 cm long; stigmas 2, slender, papillate-puberulent, somewhat barbellate at apex. Fruits baccate, 2-locular, round to ovoid, 4–5 cm diam, with a shallow circular crater ca 1 cm diam at apex, mottled green becoming somewhat soft and yellow to orange at maturity; seeds numerous, smooth, irregularly angulate, less than 1.5 cm long, embedded in a sweet orange matrix. *Croat* 6057, 15062.

Occasional to locally common in the forest, especially the younger forest; uncommon along the shore. Probably flowers to some extent all year, but collected from November to June, especially in May and June. Mature fruits are seen from April to December.

The flowers always open in the late afternoon and do not persist through the next day. The anthers are held together until contacted by a flower visitor, presumably

by a hawkmoth at night. When the stamens spring apart, pollen is sprinkled on the visitor. Pollen must be deposited on its tongue as well, because the style never reaches the apex of the corolla tube (Percival, 1965). Visited flowers tend to fall sooner than unvisited ones, the corolla sometimes falling free before the style opens. Halle (1967) reported that the flowers are functionally staminate until after the stamens have been sprung and then are functionally pistillate.

Mexico to Colombia, Venezuela, the Guianas, Peru, and Brazil; Trinidad. In Panama, ecologically variable; known mostly from tropical moist forest all along the Atlantic slope and in the Canal Zone, Veraguas, Los Santos, Panamá, and Darién, but also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón, Veraguas, Panamá, and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 525.

PSYCHOTRIA L.

Psychotria acuminata Benth., Bot. Voy. Sulphur 107. 1845

Shrub, usually less than 2 m tall; stems puberulent or glabrous, the younger stems, petioles, axes of inflorescences, pedicels, and calyces densely but inconspicuously short-puberulent. Stipules bicuspidate nearly to base, persistent, the lobes widely separated, to 3.5 mm long; petioles 5–10 mm long; blades oblong-ovate or elliptic, cuspidate-acuminate, obtuse or rounded and decurrent onto petiole at base, mostly 9–21 cm long and 4–10 cm wide, shiny above and glabrous except for minute puberulence on midrib, dull below; midrib narrow, raised, the lateral veins raised, the reticulate veins conspicuous. Inflorescences terminal, solitary, much shorter than upper leaves; peduncles 1–3 (4.5) cm long, the floriferous part to 4 cm long, 4.5 cm wide; inflorescence branches violet-purple in fruit; flowers short-pedicellate (the pedicel thickening as fruit develops), heterostylous, (3)4- or 5-parted, 4–6 mm long; corolla white, puberulent outside and on lobes inside, the throat yellow, villous at point of staminal attachment; short-styled flowers with the stamens equaling lobes, exerted ca 3 mm above throat, held to one side of tube as in *P. pubescens*, the anthers slender, to 1.2 mm long, the style included, its lobes short; long-styled flowers with the stamens included, \pm equaling tube, the styles ca 7 mm long, exerted 2–3

KEY TO THE SPECIES OF PSYCHOTRIA

Inflorescences axillary:

- Stems and petioles essentially glabrous; peduncles more than 3 cm long *P. uliginosa* Sw.
 Stems and petioles densely pubescent; peduncles less than 3 cm long:
 Mature plants less than 60 cm tall, often unbranched; stipules to ca 4 mm long; fruits blue at maturity *P. emetica* L.f.
 Mature plants more than 1 m tall, usually branched; stipules to ca 15 mm long; fruits red at maturity *P. psychotriifolia* (Seem.) Standl.

Inflorescences terminal:

Leaves and stems pubescent *or* vein axils with pitlike domatia below:Leaves with pitlike domatia in vein axils below *P. horizontalis* Sw.

Leaves lacking pitlike domatia in vein axils:

Leaves densely soft-pubescent below, often more than 20 cm long *P. micrantha* H.B.K.

Leaves not densely pubescent below, at most with sparse, appressed, slender, white trichomes, usually less than 20 cm long:

Stipules persistent, green, bilobed, the lobes widely separated; leaves usually pubescent at least on midrib above:

Bracts conspicuous, exceeding flowers *P. furcata* DC.

Bracts inconspicuous or at least shorter than flowers:

Stipules 10–15 mm long *P. racemosa* (Aubl.) Raeuschel

Stipules less than 9 mm long:

Inflorescences usually less than 4 cm long, pendent; corolla lobes white throughout; mature leaves less than 12 cm long; fruits blue or violet at maturity

..... *P. pittieri* Standl.Inflorescences usually more than 4 cm long, erect and \pm pyramidal; corolla lobes often tinged with violet inside near base; mature leaves more than 12 cm long; fruits purple-black at maturity *P. pubescens* Sw.

Stipules caducous from base, brown, usually 1–2 cm long, bilobed near apex, the lobes held together; leaves glabrous above:

Fruits, including persistent calyx, 10–15 mm long; inflorescences terminal, to ca 10 cm long (not known with certainty for the island but to be expected)

..... *P. calophylla* Standl.

Fruits, including persistent calyx, to 8 mm long; inflorescences terminal or axillary, usually less than 5 cm long:

Flowers clustered in small, dense, bracteate heads; bracts conspicuous, often longer than flowers

..... *P. psychotriifolia* (Seem.) Standl.

Flowers in small open panicles; bracts much shorter than flowers

..... *P. granadensis* Benth

Leaves and stems essentially glabrous (some leaves sparsely puberulent along midrib below), lacking domatia in vein axils:

Stipules deeply bilobed, divided to or almost to base:

Bracts conspicuous, equaling or exceeding flowers:

Bracts purple; leaves 3.5–9 (18) cm long, 1.2–3.6 (7.5) cm wide *P. furcata* DC.Bracts green; leaves 10–16 cm long, 4–6 cm wide *P. brachybotrya* Müll. Arg.

Bracts inconspicuous, shorter than flowers:

Inflorescences much longer than broad; branchlets glabrous; fruits blue then finally white at maturity. *P. deflexa* DC.Inflorescences not longer than broad; branchlets often puberulent; fruits grayish-blue at maturity *P. acuminata* Benth.

Stipules not lobed, or bilobed only halfway:

Flowers in dense clusters subtended by conspicuous bracts *or* bracts longer than flowers:Stipules much shorter than petiole; inflorescences paniculate; floral bracts as broad as long; fruits violet-blue at maturity *P. brachiata* Sw.

Stipules nearly as long as or longer than petiole; inflorescences sessile or paniculate with slender floral bracts; fruits black or red at maturity:

Inflorescences minute (less than 2 cm long), sessile; leaves less than 10 cm long; fruits red at maturity *P. chagrensis* Standl.Inflorescences not minute; leaves usually more than 10 cm long; fruits black at maturity *P. capitata* R. & P.

Flowers not in dense clusters subtended by conspicuous bracts, the bracts not longer than flowers:

Lower midrib of leaves with triangular flaplike protuberances near axils below

..... *P. marginata* Sw.

Lower midrib of leaves lacking protuberances:

Leaf blades on mature stems usually less than 5 cm wide, the petioles less than 1.5 cm long; shrubs ca 1.5–2 m tall *P. carthagenensis* Jacq.

Leaf blades on mature stems more than 5 cm wide or, if less than 5 cm wide, the petioles more than 2 cm long:

Stipules persistent, cuspidate at apex; peduncles more than 8 cm long . . . *P. grandis* Sw.

Stipules caducous, rounded or cleft at apex; peduncles less than 4 cm long:

Leaves 6–14 cm wide; petioles 1.5–6 cm long; reticulate veins not visible

..... *P. limonensis* KrauseLeaves 3.5–7 cm wide; petioles 0.5–4.5 cm long; reticulate veins usually clearly visible *P. granadensis* Benth.

mm. Berries depressed-globose, 5–7 mm diam, usually bilobed, yellow, turning grayish-blue at maturity; seeds 2, hemispherical, ca 3.7 mm diam, smooth (not ribbed as in most species). *Croat 5877, 15077.*

Common in the forest. Flowers mostly from March to July, especially in May and June, and sporadically during the late rainy and dry seasons as well. The fruits mature in 1 or 2 months, mostly from July to October.

Distinguished by the prominently bilobed fruits, cuspidate-acuminate leaves, and persistent, bicuspidate stipules.

Standley (1930b) considered this taxon *P. cuspidata* Bredem. ex R. & S. in his various treatments of the Rubiaceae for Venezuela, Colombia, Bolivia, and Peru. Steyermark (1972) reported that *P. cuspidata* is a species restricted to the coastal cordillera of northern Venezuela.

Mexico (Chiapas) to Colombia, the Guianas, and Brazil (Bahia); Trinidad. In Panama, ecologically variable; known from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane wet forest in the Canal Zone, Colón, Coclé, and Darién, and from tropical wet forest in Colón.

See Fig. 526.

***Psychotria brachiata* Sw., Prodr. Veg. Ind. Occ. 45. 1788**

Shrub or small tree, to 3 (5) m tall, nearly glabrous; branchlets often canaliculate. Stipules ovate, 4–6 mm long, persistent, weakly cleft at apex; petioles 1–3 cm long; blades elliptic to oblong-elliptic or oblanceolate, acuminate, acute to obtuse and decurrent at base, mostly 10–20 cm long, 4.5–8 cm wide, glabrous or sparsely pubescent along midrib below; major lateral veins raised on both surfaces, forming almost right angles with midrib, widely arcuate-ascending, the reticulate veins visible below. Flowers sessile, 5-parted, in closely aggregated clusters in open terminal panicles to 12 (16) cm long and 10 cm wide in fruit; branches sparsely hispidulous, perpendicular to axis; bracts obtuse, equaling or longer than calyx; calyx \pm truncate, to 0.9 mm long, persisting on fruit; corolla campanulate, to 6 mm long, pale yellow to yellow-green, hirtellous outside, glabrous inside, the lobes short, ovate, acute, spreading, bearing a purplish, subapical thickening outside; stamens to 2.7 mm long, included; anthers ca 1 mm long; style to 3.3 mm long, papillate, the branches 2, short, thick, densely papillate-puberulent. Berries closely aggregated, ellipsoid, ca 4 mm long at maturity, violet-blue, sparsely puberulent; seeds 2, hemispherical, ca 4 mm long, the inside face concave, the outside face with 5 ridges. *Croat 12457, 15252a.*

Apparently uncommon in the forest; collected on Shannon and Lathrop trails. Flowers and fruits most of the year, but with most flowers opening from April to August and most fruits maturing in the late rainy season.

Recognized by the yellow flowers, the closely aggregated blue fruits, and the persistent green stipules, which are slightly cleft at the apex. In Panama the species merges almost imperceptibly with the South American

P. caerulea R. & P., which, if taxonomically distinct, has the flowers even more closely congested into conspicuously bracteate heads.

As defined by Steyermark (1972), the species is known from the West Indies (Greater Antilles), Trinidad, and Central America. *P. caerulea* is known from Panama, Colombia, Venezuela, Ecuador, and Peru. In Panama, *P. brachiata* is ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Los Santos, Panamá, and Darién, from premontane wet forest in Veraguas, Panamá, and Darién, and from tropical wet forest in Colón, Coclé (Atlantic slope), and Darién.

***Psychotria brachybotrya* Müll. Arg. in Mart., Fl. Brasil. 6(5):327. 1881**

Shrub, 1–1.8 m tall; stems and leaves glabrate. Stipules persistent, 3–5 mm long, bifid to near base, the lobes distant, acuminate; petioles 1–1.5 cm long; blades \pm elliptic, acute to acuminate, cuneate at base, 10–16 (20) cm long, 4–6 cm wide, drying light green. Racemes short, terminal, usually to 1.5 cm long at anthesis, to 3 cm long in fruit; peduncles lacking or to 1.2 cm long; inflorescence branches, pedicels, and calyces with short, \pm erect, sparse trichomes, the lowermost branches subtended by a distinct, oblong-elliptic bract ca 5 mm long; bracts green, ovate, 2–7 mm long, acute, foliate, persistent, subtending groups of 2–4 (7) flowers, exceeding the flowers; flowers white, sessile, ca 3.5 mm long, the tube ca 2 mm long, the lobes oblong, to ca 1.5 mm long; filaments ca 0.5 mm long, affixed above the middle of the tube; anthers ca 1 mm long; style ca 4 mm long; stigmas 0.2 mm long. Berries \pm globose, 3–4 mm diam, flattened laterally and somewhat grooved, glabrous or sparsely puberulent at least when immature; seeds 2, flat, with a deep groove on the inside surface, rounded and 4- or 5-grooved on the outside surface. *Croat 11132.*

Apparently rare; found in the younger forest south of Fairchild Point and in the forest north of Barbour Trail. Flowers mostly from June to September, principally in July, rarely also in the dry season. The fruits mature from July to October, principally in August.

In Panama, *Psychotria brachybotrya* is most easily confused with *P. involucrata* Sw., a superfluous name for *P. officinalis* (Aubl.) Sw. (Steyermark, 1972). It differs from that species by having distinct bracts beneath the lower inflorescence branches and leaves that usually dry a lighter green. It usually occurs in drier areas than *P. officinalis*, which occurs principally in premontane wet forest and tropical wet forest. *Psychotria brachybotrya* has also been confused with *P. furcata* DC., but is distinguished from that species by its larger, lighter-colored leaves and green, rather than purple, inflorescence bracts.

Panama to Colombia, Venezuela, the Guianas, Brazil, Peru, and Bolivia; Trinidad. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Herrera, Panamá, and Darién, from tropical dry forest in Panamá, and from premontane wet forest in Colón, Panamá, and Darién.



Fig. 526.
Psychotria acuminata



Fig. 527. *Psychotria capitata*

Fig. 528. *Psychotria carthagenensis*



Psychotria capitata R. & P., Fl. Peruv. 2:59. 1799

Shrub, usually to 3(4) m tall; stems glabrous or weakly puberulent. Stipules lanceolate, ca 1.5 cm long, bilobed at apex, deciduous, sometimes purplish; petioles 5–20 mm long; blades elliptic to oblong-elliptic, acuminate, tapered to base and somewhat decurrent, mostly 9–20 cm long, 2.5–7 cm wide, stiff when fresh; lateral veins raised on both surfaces, forming nearly right angles with midrib, sharply ascending near margin, the basal pair often pubescent below. Panicles white at anthesis, long-pedunculate, terminal, solitary, usually longer than broad, to 13 cm long and 7 cm wide (usually smaller), branching at right angles; bracts 5–10 mm long, oblanceolate, often purplish in fruit; flowers white, heterostylous, usually exceeded by bracts, these white at anthesis, becoming green; calyx lobes minute; corolla 4-lobed, ca 1 cm long, the lobes spreading, ovate, acute or rounded, the tube pubescent in upper third inside, the throat yellow; short-styled flowers with the stamens attached at apex of tube, exerted 5–7 mm above throat, the style included, held at apex of throat; long-styled flowers with the stamens included and hidden among long trichomes in throat, the style exerted 5–7 mm above throat. Berries subovate to oblong, 4–6(7) mm long, 3.5–5 mm wide, black; seeds 2, hemispherical, ca 4.7 mm long, 3–4 mm wide, the inside face flat with a slight fissure, the outside face 4- or 5-ridged at maturity. *Croat 12414, 14960.*

Occasional in the forest; common in a few localities, mostly in the old forest; occasional to locally common on Zetek Trail. Flowers and fruits sporadically throughout the year, but mostly in June.

A small black-and-white *Heliconius* butterfly (probably *H. cydno* or possibly *H. sappho*; Nymphalidae, Ithomiinae) visits the flowers at anthesis. The same butterfly visits *Psiguria warszewiczii* (131. Cucurbitaceae). The species is also visited by small hummingbirds.

Belize to Peru and Brazil; Trinidad and Tobago. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién, from premontane wet forest in Colón and Coclé, and from tropical wet forest in Colón, Panamá, and Darién.

See Fig. 527.

Psychotria carthagensis Jacq., Enum. Syst. Pl. Ins. Carib. 16. 1760

Shrub, usually 1.5–2(3) m tall, nearly glabrous; internodes very short. Leaves subsessile or on petioles to 1.5 cm long; stipules ovate-spatulate, 4–6 mm long, abruptly cuspidate, entire, caducous; blades obovate, acute to short-acuminate, attenuate at base, 5–16 cm long, 2.5–5.5 cm wide; veins 6–8 on each side. Panicles solitary, terminal, to 7 cm long; peduncles 2–4 cm long; bracts minute, caducous; flowers sessile; calyx 3–5 mm long, irregularly and usually minutely toothed; corolla white, 3–4 mm long, 5-lobed, the lobes ca 2 mm long; stamens inserted at middle of tube; filaments ca 2 mm long; anthers oblong, ca 1 mm long; style 2–2.5 mm long; stigma bifid, 0.7–1 mm long. Berries oblong to elliptic,

ca 6 mm long and 2.5 mm wide; seeds 2, the inside face flat, the outside face 5- or 6-costate. *Croat 10337.*

Occasional, in the younger forest along Barbour Trail. Seasonal behavior uncertain. Flowers at least throughout the dry season and early in the rainy season, but mostly from April to June. The fruits mature mostly from May to July.

Belize south to Paraguay and southern Brazil; Trinidad and Tobago. In Panama, known from tropical dry forest in Los Santos and Coclé, from premontane moist forest in Veraguas and Los Santos, from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Herrera, Panamá, and Darién, and from premontane wet forest in Coclé.

See Fig. 528.

Psychotria chagrensis Standl., J. Wash. Acad. Sci. 15:105. 1925

Shrub, usually less than 1.2 m tall, glabrous; branchlets slender, mostly \pm erect from upper side of branches. Leaves clustered on ends of small branchlets on upper side of branches; stipules with long slender apex, caducous, 8–15 mm long; petioles obscure or to 8 mm long; blades obovate-elliptic to elliptic, abruptly acuminate, gradually tapered to base and decurrent, 2.5–10 cm long, 1.3–3.5 cm wide, bicolorous; major lateral veins drying with minute wrinkles. Inflorescences less than 2 cm long, terminal, the heads sessile, bearing few flowers, surrounded by scarious, brownish bracts to 1 cm long; flowers heterostylous, 5(6)-parted; calyx thin, enclosed in sheath, irregularly toothed; corolla white, 8–10 mm long, the lobes apiculate inside, recurved at anthesis, the throat densely pubescent above point of staminal attachment; short-styled flowers with the stamens fused to throat near rim, ca 2 mm long, the anthers exerted at anthesis, the style included and ca 2–3 mm long; long-styled flowers with the stamens fused to throat near rim but included, ca 1 mm long, the style ca 10 mm long, exerted ca 5 mm. Berries usually 1–3, narrowly ovate, (5)8–10 mm long, bright red; seeds 2, narrowly ovate, ca 6 mm long, flattened on one side, the other side rounded and with 5 ribs. *Croat 14643.*

Frequent in the forest; collected in the swampy area north of Zetek Trail 300 and on Shannon Trail. Seasonal behavior uncertain. Probably flowers and fruits throughout the year, but most flowers are seen in May and August.

Recognized by the small, obovate-elliptic leaves and minute, sessile flowers in small, brown-bracted heads.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón and Darién.

Psychotria deflexa DC., Prodr. 4:510. 1830

P. patens sensu auct. non Sw.

Garricillo

Glabrous shrub, to 3 m tall; younger stems flattened at nodes. Stipules bilobed nearly to base, the lobes ca 1 cm

long, distant, linear, green, persistent; petioles 2–10 mm long; blades ovate-elliptic, gradually long-acuminate and often somewhat falcate at apex, mostly obtuse to rounded and decurrent at base, 8–18 cm long, 3.5–7 cm wide, entire or minutely crenulate, dark green and glossy above, duller below; midrib narrow, markedly raised, the major lateral veins arcuate-ascending, the reticulate veins conspicuous. Inflorescences pedunculate, terminal, usually 3–10 cm long, narrow, the branches, calyces, and corollas minutely puberulent to glabrous; flowers heterostylous, white, sessile to short-pedicellate; calyx lobes minute, acute; corolla ca 3.3(4) mm long at anthesis, yellow in throat, barbate at point of staminal attachment, the lobes 3–5, recurved; short-styled flowers with the stamens exerted ca 1–2 mm, sometimes unequally so, with 2 ± included, the style included; long-styled flowers with the stamens included, the style exerted ca 1 mm above rim, with 2 slender branches. Berries 2-celled, broader than long, becoming blue (may dry green or black), eventually the exocarp rupturing to expose foamy white mesocarp; seeds 2, globose, 2.5–3 mm diam, the inside face grooved, the outside face subcostate. *Croat 11926, 15575.*

Frequent in the forest, occurring also in clearings. Flowers from May to July. The fruits mature mostly from August to December, especially from August to October.

Distinguished by the slender, terminal inflorescences and persistent, linear, bilobed stipules.

Mexico to Peru and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Herrera, Coclé, Panamá, and Darién, from premontane wet forest in Veraguas, Coclé, and Panamá, and from tropical wet forest in Panamá and Darién.

See Fig. 529.

***Psychotria emetica* L.f., Suppl. Pl. Syst. Veg. 144. 1781**

False ipecac, Rachilla

Shrub, usually less than 60 cm tall; stems strigose, often unbranched. Stipules narrowly lanceolate, ca 4 mm long, strigose, subpersistent; petioles ca 1 cm long, strigose; blades oblong-lanceolate or oblong-obovate, acute to short-acuminate, cuneate to obtuse at base, 8–17 cm long, 2–6.5 cm wide, bicolorous, essentially glabrous above, strigose below especially on veins; major lateral veins often impressed above, arcuate-ascending, forming an obscure collecting vein. Inflorescences axillary, subracemose, bearing few flowers; peduncles to ca 1 cm long; flowers sessile, 4-parted, white, ca 5 mm long, glabrous outside, with very short stiff trichomes inside; corolla lobes acute; stamens 5, attached to corolla tube at about its middle; anthers narrowly oblong, ca 1.5 mm long, pilose. Berries oblong when juvenile, becoming rounded and bright blue, paler and somewhat lavender at maturity, to 1 cm long, the mesocarp foamy; seeds 2, elliptic, ca 5 mm long, brown, flattened on one side, twisted. *Croat 5750.*

Common in the forest. Flowers mostly in the late dry and early rainy seasons, especially in April and May and

again in July and August, with a few flowers seen in June. The fruits mature mostly in the middle rainy season, especially in August and September.

Distinguished by its small size and blue fruits.

Guatemala to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from tropical wet forest in Colón and Panamá.

See Fig. 530.

***Psychotria furcata* DC., Prodr. 4:512. 1830**

P. involuocrata sensu auct.

Shrub, usually 1–1.5(4) m tall; branches slender, terete to flattened, puberulent. Stipules bilobed to base, persistent, the lobes slender, ca 4 mm long; petioles to 5 mm long; blades broadly elliptic to lanceolate-elliptic, acuminate, cuneate and decurrent at base, 3.5–9(18) cm long, 1.2–3.6(7.5) cm wide, glabrous and shiny above (sparsely white-lineolate when dry), sparsely puberulent below especially on veins, membranaceous; lateral veins impressed above, raised below. Inflorescences terminal, solitary, subcapitate, usually 5–20 mm long, contracted, bearing few flowers; bracts maroon, acute, slightly to much longer than corolla; pedicels very thick and maroon in fruit; corolla white, ca 3 mm long; stamens 4 or 5; filaments short, fused part way to tube; anthers linear-oblong, ca 1 mm long; style to 2 mm long; stigma lobes oblong. Berries globose, (3)4–6 mm diam, maroon becoming purple or black at maturity, puberulent; seeds 2, hemispherical, ca 3.3 mm long, the inside face concave, the outside face rounded with 4 or 6 broad ridges. *Croat 6272.*

Frequent in the forest. Flowers in the late dry season and no doubt in the early rainy season. The fruits mature throughout the rainy season and in the early dry season, especially in the middle of the rainy season.

Recognized by the usually small leaves and tiny inflorescences with prominent, violet-purple bracts.

Costa Rica, Panama, and Colombia (Chocó). In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Herrera, Coclé, Panamá, and Darién; known also from premontane wet forest in Colón, Chiriquí, Panamá, and Darién.

***Psychotria granadensis* Benth., Vidensk. Meddel.**

12. 1852

Huesito

Shrub, usually to 2 m tall (shorter along trails probably owing to being cut back), glabrous except for minute puberulence on leaf veins below and on inflorescence branches; stems usually mottled. Stipules 7–15 mm long, bilobed ca one-third the way to base, deciduous, the lobes long-acuminate; petioles 0.5–4.5 cm long; blades oblanceolate to oblong-elliptic, acuminate, attenuate and decurrent at base, 12–18 cm long, 3.5–7 cm wide; midrib and lateral veins often whitish above, the reticulate veins inconspicuous. Inflorescences of usually 3 or 4 panicles,



Fig. 530. *Psychotria emetica*

Fig. 529. *Psychotria deflexa*

Fig. 531. *Psychotria limonensis*



small, terminal, branched, closely compacted, less than 2.5 cm long; flowers sessile, 5-parted; calyx to ca 1 mm long (usually less), the lobes triangular; corolla puberulent outside, glabrous inside except for long trichomes at throat between anthers, the tube campanulate, as long as lobes, the limb to 4 mm diam, the lobes ovate, 1.5–2.7 mm long, spreading to reflexed, acute and swollen at apex, greenish to white; stamens attached at throat and exerted slightly above rim; anthers ca 0.5 mm long, introrse; style 2.5–3 mm long, exerted ca 2 mm; stigmas broader than style, densely papillate-puberulent. Berries ovoid to ellipsoid, ca 4 mm long and wide, becoming red; seeds 2, ca 3 mm long, the inside face flat, with a small longitudinal ridge, the outside face rounded, 4- or 5-ridged. *Croat 7316, 14997.*

Locally common in the old forest above the escarpment, along trails, where it often grows to less than 30 cm tall. This short habit is probably due to clearing of the trails, since elsewhere in the Canal Zone plants reportedly grow much taller. Flowers in June and July. The fruits mature in the late rainy and early dry seasons (October to January).

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone and Veraguas.

***Psychotria grandis* Sw., Prodr. Veg. Ind. Occ. 43. 1788**

Shrub or small tree, to 6 m tall (rarely so tall on BCI); stems glabrous, usually with prominent longitudinal ridges, with prominent leaf scars. Leaves glabrous; stipules broadly ovate, to 12 mm long, 8–13 mm wide, with a cusp 2–3 mm long, cupulate, green, persistent or subsistent; petioles obscure or to 2 cm long; blades mostly oblong-obovate, short-acuminate, gradually tapered to base, 13–28 (50) cm long, 4.5–10 (16.5) cm wide; midrib and major lateral veins raised on both sides, the midrib often whitish. Inflorescences panicles, terminal, to about 30 cm long, often about as wide as long, branched many times; peduncles stout, 8–16 cm long; branches and calyces puberulent; flowers heterostylous; calyx lobes broadly triangular; corolla white, ca 4.5 mm long, lobed more than a third of the way to base, the lobes 5 (6), spreading, glabrous except for dense beard at point of staminal attachment inside; long-styled flowers with the stamens exerted at anthesis, much shorter than style, the style lobes short, nearly as broad as long; short-styled flowers with the stamens exerted ca 2 mm above throat, the style included. Fruiting inflorescences usually overtopped by new growth; berries globose, to 9 mm diam, orange, the pulp fleshy and sweet; seeds 2, hemispherical, 2.5–3 mm long, the inside face planar, ungrooved, the outside face faintly 6-ribbed. *Croat 14872, Duke 8773.*

Occasional as adult plants; seedlings common in some areas beyond the Tower Clearing. Flowers to some extent throughout the year, especially in the early rainy season in June. The fruits probably mature in 4–6 weeks.

Mexico to Colombia and Venezuela; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Panamá, and Darién and from premontane wet forest in Colón, Coclé, Panamá, and Darién.

***Psychotria horizontalis* Sw., Prodr. Veg. Ind. Occ.**

44. 1788

Shrub, 1.5–3 (6) m tall; stems terete or flattened, glabrous. Stipules ovate, to 6 mm long, entire, caducous, often strigose on inside, the trichomes to 1 mm long; petioles 3–11 mm long, slender; blades elliptic to oblanceolate, acuminate, usually ending abruptly and rounded at base, 7–20 cm long, 2.5–7 cm wide, bicolorous, glabrous or sparsely puberulent below, usually with pitlike domatia on bases of secondary veins below, the margins sometimes undulate; veins in 6–11 pairs. Inflorescences terminal, paniculate, pedunculate, usually less than 8 cm long in flower, about as broad as long, somewhat larger in fruit; flowers white, 5-parted, to 7 mm long; calyx lobes to 1 mm long, blunt to lanceolate-linear; corolla lobes acute, strongly recurved at anthesis, the tube bearded inside at point of staminal attachment; anthers in throat held tightly around style; style erect, long-exserted, ca 7 mm long, the lobes 2, enlarged and densely papillate. Berries subglobose, minutely puberulent, red at maturity, 4–5 mm diam; seeds 2, hemispherical, ca 3–5 mm long, the inside face flat, the outside face rounded with 5 broad ribs, the grooves narrow. *Croat 6383.*

Common in the forest. Flowers asynchronously in the late dry and early rainy seasons, from March to August, principally from April to July after the rains begin and only sporadically at other times of the year. The fruits mature principally in August and September, but sometimes as late as December.

Elsewhere the calyx persists, but BCI fruits commonly do not have a persistent calyx. This species and *P. marginata* are the two most abundant species of *Psychotria* on the island.

Mexico to Ecuador; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Coclé, and from tropical wet forest in Darién.

***Psychotria limonensis* Krause, Bot. Jahrb. Syst. 54, Beibl. 119:43. 1916**

Shrub, usually less than 1.5 m tall, glabrate. Leaves opposite-decussate; stipules broad, 5–10 mm long, rounded or sometimes minutely forked at tip, caducous; petioles 1.5–6 cm long; blades broadly elliptic, bluntly acuminate, obtuse to attenuate and decurrent at base, mostly 10–30 cm long and 6–14 cm wide, minutely puberulent on veins, bicolorous; midrib flattened above, the veins forming right angles with midrib, joined by submarginal collecting vein. Inflorescences terminal in flower (sometimes becoming axillary in fruit), 2–8 cm long, somewhat globose, ebracteate; flowers white, congested, to 4 mm long; calyx lobes short, acute; corolla lobed to middle, 5 (6)-parted, with tufts of white trichomes alternating with stamens at apex of tube; stamens equaling corolla lobes; anthers shedding pollen before anthesis; style short; stigma bilobed, the lobes blunt, \pm open in

bud, held somewhat below anthers. Berries subglobose, 6–7 mm wide, bright red at maturity; seeds 2, hemispherical, 3–4 mm long, 3.5–5 mm wide, the inside face planar, the outside face rounded, usually with 5 ridges. *Croat 8717.*

Frequent in the forest. Flowers and fruits to some extent throughout the year, especially in the dry season. Individuals may flower more than once per year and often bear flowers and fruits simultaneously. Most plants are seen in fruit during the early rainy season.

Distinguished by the short height, the large, broadly elliptic leaves, and the short, almost globular inflorescences.

Southern Mexico to northern Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién and from tropical wet forest in Colón.

See Fig. 531.

***Psychotria marginata* Sw., Prodr. Veg. Ind. Occ.**
43. 1788

Shrub, 2–3 (6) m tall, nearly glabrous. Stipules to 11 mm long, entire, caducous; petioles obscure or to 3 cm long, slender, canaliculate above; blades oblong-oblongate to ± elliptic, acuminate, attenuate and decurrent at base, mostly 7–20 cm long and 2.5–6 cm wide, ± bicolorous (drying grayish); major lateral veins impressed above, raised below, the midrib below with flaplike protuberances near axils. Panicles terminal; peduncles 5–8 cm long, often almost as long as floral rachis; flowers white, to 4.7 mm long; pedicels longer than fruit; stamens fused to tube near its pubescent apex, shedding pollen in bud; style held above anthers in bud, exposed by recurved corolla lobes. Berries rounded, 4–8 mm broad, red-orange turning violet-purple at maturity; seeds 2, hemispherical, ca 3.3 mm long, the inside face flat, the outside face rounded, usually with 5 ribs. *Croat 5775.*

Common in the forest; one of the most commonly encountered *Psychotria* on the island. Flowers and fruits throughout the year, mostly in the late rainy and early dry seasons. Individuals usually flower twice per year (R. Foster, pers. comm.). The fruits mature mostly in the early rainy season, from May to July.

The only common *Psychotria* that does not begin flowering after the first rains.

Mexico to Peru and Bolivia; Trinidad, Jamaica, and Cuba. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Veraguas, Los Santos, Panamá, and Darién, from premontane wet forest in Coclé, Panamá, and Darién, and from tropical wet forest in Colón and Darién.

***Psychotria micrantha* H.B.K., Nov. Gen. & Sp.**
3:363, pl. 284. 1819

P. rufescens sensu auct. non H.B.K., non H. & B. ex R. & S.

Shrub, 1.5–5 m tall, softly short-pilose to hirtellous nearly throughout. Stipules ovate, 1–1.5 cm long, bilobed at apex, caducous, one lobe slightly longer than the other; petioles 5–25 mm long; blades oblong-elliptic or obovate,

acuminate, acute to obtuse at base, 12–30 cm long, 5.5–13 cm wide, short-pilose especially on veins below; midrib often ferruginous. Inflorescences terminal or upper-axillary, solitary, to 15 cm long; peduncles 5–8 cm long; flowers 5-parted, clustered at ends of short branches; calyx short, obscurely lobed; corolla white, ca 4 mm long, lobed somewhat past middle, glabrous or puberulent outside, the tube hispid inside at point of staminal attachment, the lobes recurved; stamens included; filaments adnate to basal half of tube; anthers 0.8–1.3 mm long, rigidly attached to filament below middle; style to 3.2 mm long and exserted above throat, the branches short and thick. Berries globose to ellipsoid, 3–4 mm long, pubescent; seeds 2, the inner face flat, the outer face 5-ribbed. *Croat 6235.*

Uncommon, at least as an adult plant in the forest; juvenile plants are more abundant. Flowers mostly from June to August, rarely earlier or later. The fruits mature mostly from August to October.

Nicaragua to southwestern Colombia, Venezuela, Ecuador, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Coclé, and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 532.

***Psychotria pittieri* Standl., Contr. U.S. Natl. Herb.**
18:132. 1916

P. dispersa Standl.

Shrub, usually 1–1.6 m tall; stems and inflorescences moderately pubescent with short, mostly erect, stiff trichomes. Stipules bilobed to base, the lobes linear, 5–7 mm long, subpersistent, green, soon becoming brown; petioles mostly 5–10 mm long; blades mostly elliptic to obovate, acuminate, acute at base, 4–12 cm long, 1.5–4.5 cm wide, glabrate above except on midrib, appressed white-pubescent below especially on veins. Panicles terminal, pendent, 2–10 cm long; flowers subtended by a slender bract to ca 3 mm long; calyx lobes ca 0.5 mm long, acute; corolla white, 4–6 mm long, puberulent outside, the throat pale yellow, the tube minutely pubescent at point of staminal attachment at apex of tube, the lobes strongly recurved; stamens regularly arranged and slightly longer than style, or both style and stamens weakly exserted, or the stamens held in a row on one side of corolla and long-exserted above throat, the style included; style densely papillate-puberulent; stigma bifid, ca 1 mm long, thick. Berries subrotund, 5–6 mm diam, minutely pubescent, fleshy, violet becoming blue at maturity, the pericarp inflated; seeds 2, ± obovate, to 2.7 mm long, brown, the inside face flat, the outside face rounded, obscurely 5-ribbed. *Croat 4107.*

Frequent in the forest. Flowers from March to September, but mostly from May to July. The fruits mature mostly from July to September.

Distinguished by its small size, its pubescence, and its small, pendent inflorescence.

Belize, Costa Rica, and Panama. In Panama, known from tropical moist forest on BCI and in Bocas del Toro and San Blas and from premontane wet forest in Coclé.

Psychotria psychotriifolia (Seem.) Standl., Contr.

U.S. Natl. Herb. 18:133. 1916

Shrub, to 1(2) m tall; young stems, petioles, and parts of inflorescences crisp-pubescent to glabrate. Stipules broad, 7–15 mm long, sharply bilobed at apex, turning brown, caducous; petioles obscure or to 2 cm long; blades oblanceolate, abruptly acuminate, gradually tapered to base and decurrent onto petiole, 9–18 cm long, 3–6 cm wide, glabrous above, puberulent on petiole and major veins below, bicolorous; lateral veins loop-connected near margin. Flower heads dense, short-pedunculate, bracteate, terminal or axillary, the bracts often longer than flowers; flowers sessile, to 4.3 mm long; calyx lobes \pm irregular, to ca 1 mm long, acuminate; corolla lobes spreading, the apex cucullate, lobed on outside, the tube very short; stamens attached at apex of tube, interspersed with and exceeded by dense white trichomes; style shortly exerted, bilobed, papillose-puberulent. Berries ovoid to oblong, ca 7 mm long, red, the mesocarp thick, fleshy, sweet; seeds 2, oblong-elliptic, the inside face flattened, the outside face 5(7)-ribbed. *Croat 12883*.

Rare; collected once along the shore south of Fairchild Point. Flowers mostly in the early rainy season, especially in June, but also in the dry season, especially in early dry season (December). The fruits mature throughout the year, but mostly in the middle of the rainy season.

The species is related to *P. granadensis*, but differs in having the prominently lobed calyx, the short corolla with a very reduced, subrotate tube, the capitate, densely flowered heads, and the minutely puberulent veins of the lower leaf surface.

Costa Rica to Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Veraguas, Panamá, and Darién, from premontane wet forest in Chiriquí and Coclé, and from tropical wet forest in Colón.

See Fig. 533.

Psychotria pubescens Sw., Prodr. Veg. Ind. Occ.

44. 1788

P. hebeclada DC.

Shrub, usually ca 2 m tall; stems and peduncles hispid. Stipules 3–5 mm long, deeply bifid to near base, the lobes linear, subsistent; petioles obscure or to 3 cm long; blades mostly elliptic to oblong-elliptic, acuminate, obtuse to acute and long-decurrent at base, 8–21 cm long, 2–9.5 cm wide, glabrate or minutely asperous above (the trichomes often restricted to veins), hispidulous below especially on veins. Inflorescences terminal, erect, paniculate, rounded or elongated, 3–9 cm long; peduncles to 6 cm long; inflorescences and pedicels purplish; flowers heterostylous; calyx lobes acute, ca 1 mm long; corolla white, 4–7 mm long, 5-lobed, the lobes often tinged with violet near base inside, puberulent outside, villous inside about midway; short-styled flowers with the stamens 5–6.5 mm long, held to one side of tube opposite 2 lobes (less commonly regular), the filaments fused to corolla tube in basal half, the anthers exerted at anthesis (owing

to spreading of corolla lobes), the style at first much shorter than stamens, becoming weakly exerted opposite anthers, its 2 short branches densely papillate; long-styled flowers similar to short-styled ones but with the style exerted 4–5 mm, the anthers included and evenly spaced in tube. Berries \pm flattened-globose, 4–7 mm diam, minutely pubescent, bilobed, purple or black at maturity; seeds 2, oblong-hemispherical, ca 3.3 mm long, the outside face usually with 3(5) ribs, the inside face with a longitudinal groove. *Croat 10846*.

Occasional, most frequently encountered in clearings or open areas. Flowers mostly in the early rainy season, in June and July, rarely earlier or later in the year. The fruits mature from July to December, mostly by September or October.

Mexico to Colombia and Ecuador; West Indies. In Panama, ecologically variable; known from premontane moist forest in the Canal Zone and Panamá, from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Veraguas, Panamá, and Darién, from premontane wet forest in Chiriquí and Coclé, and from tropical wet forest in Colón.

Psychotria racemosa (Aubl.) Raeuschel, Nomen. Bot.

ed. 3. 56. 1797

Shrub, usually less than 2 m tall; stems, lower leaf surfaces, and inflorescence branches usually puberulent. Stipules bilobed nearly to base, the lobes widespreading, 1–1.5 cm long, linear, persisting, turning brown; petioles obscure or to 2 cm long; blades elliptic or oblong-elliptic, acuminate, attenuate and decurrent at base, mostly 8–19 cm long, 3–7.5 cm wide, bicolorous; lateral veins markedly impressed above, raised below, the reticulate veins very conspicuous. Inflorescences short-pedunculate, mostly 2–5 cm long, ca as long as broad, usually terminal; flowers 4–6 mm long, 4- or 5-parted; corolla white or greenish, papillate-puberulent outside and on lobes inside, the throat yellowish, the tube villous above insertion of stamens, the lobes cucullate, spreading, greenish; stamens included, white or purplish, attached just below throat; style and stigma papillate-puberulent; style becoming exerted at anthesis; stigma 5-lobed. Berries somewhat congested, rounded, 5–6 mm diam, green becoming orange and finally purple or black at maturity; seeds 5, ca 2.7 mm long, shaped like segments of an orange, the outside face slightly costate. *Croat 6189a, 15116*.

Frequent in the forest. Flowers from May to July, mostly in June. The fruits mature from August to December, mainly in September.

Distinguished by the closely congested cluster of usually five-celled fruits, whereas all other species have two hemispherical seeds. The mature black fruits disappear quickly.

Costa Rica to Colombia, Venezuela, the Guianas, Brazil, and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in Coclé, Panamá, and



Fig. 532. *Psychotria micrantha*

Fig. 534. *Psychotria racemosa*



Fig. 533. *Psychotria psychotriifolia*



Darién, and possibly from premontane rain forest in Los Santos.

See Fig. 534.

Psychotria uliginosa Sw., Prodr. Veg. Ind. Occ.
43. 1788

Shrub or subshrub, to 2 m tall, \pm glabrous; stems usually simple. Stipules obtuse or truncate, 1.5–3.5 mm long, persistent, connate into a horny sheath; petioles 4–7 cm long; blades obovate to oblong-elliptic, short-acuminate, attenuate at base, 15–30 cm long, 7–11 cm wide; major veins 11–17 on each side. Panicles axillary or subterminal, to 7 (13) cm long; peduncles 2.5–5 (9) cm long; bracts 2–3.5 mm long; flowers sessile or subsessile; calyx cylindrical, ca 1 mm long, \pm truncate; corolla white, ca 4 mm long, the lobes pink, reflexed, horned at tip; stamens 5, attached to corolla near mouth of tube; filaments short; anthers oblong, ca 1 mm long; stigmas 2. Berries oblong, capped by the persistent calyx, 6–7 mm long, red at maturity; seeds 2, hemispherical, the inside face flat, occasionally with a median ridge evident on only 1 seed, the outside face 3-ridged, the middle ridge more prominent. *Starry* 90.

Known only from one collection on Wheeler Trail; possibly no longer present on the island. Flowers in the rainy season (July to December). Mature fruits are present much of the year but mostly in the late rainy and early dry seasons.

Mexico to Colombia, Ecuador, and the Guianas; West Indies. In Panama, known mostly from wetter parts of tropical moist forest or at higher elevations; known also from tropical moist forest on BCI and in Bocas del Toro, San Blas, Veraguas, Los Santos, Coclé, and Darién, from premontane wet forest in Colón, Veraguas, Coclé, Panamá, and Darién, and from premontane rain forest in Panamá.

RANDIA L.

Randia armata (Sw.) DC., Prodr. 4:387. 1830

Jagua macho, Miel quema, Rosetillo

Diocious tree, to 8 (10) m tall, nearly glabrous; branches often with stout spines at ends and sometimes at nodes. Leaves sessile or nearly so; stipules lanceolate to vaguely scoop-shaped, 5–10 mm long, caducous; blades oval or obovate, acuminate, attenuate to cuneate at base, 11–22 cm long, 4–10 cm wide, frequently with tufts of trichomes in vein axils below. Flowers white, in clusters of (1) 2–4 (8) at ends of branches; pedicels slender, 1–2 cm long, sparsely pubescent; calyx 5-lobed, the lobes

spreading and ca 5 mm long; corolla glabrate but with short-villous pubescence in vicinity of anthers, white, the tube greenish, usually 2.5–3 cm long, the limb to ca 3 cm wide, the lobes 5, rounded and oblique at apex; anthers 5, sessile, mounted on rim of tube, ca 5 mm long; style as long as the corolla tube; stigma ca 3 mm long, bilobed, the lobes ca 2 mm wide. Fruits baccate, subglobose to oblong, somewhat longer than broad, 3–4 cm long, 2.5–3 cm wide, densely covered with minute lentils, becoming pale yellow-orange at maturity; seeds numerous, ca 1 cm long and less than 2 mm thick, in 4 separate longitudinal stacks, \pm 3-sided, much flattened. *Croat* 7378, 9131.

Common in the forest. Flowers mostly synchronously between March and June, mostly in April and May; flowering may be completely finished for most individuals in 3 or 4 days. The fruits mature mostly from July to December. Sporadic individuals may flower and fruit at other times of the year. Plants lose their leaves just before flowering, and the flowers usually appear concurrently with new, usually fully formed leaves.

The fruits are eaten by white-faced monkeys (Hladik & Hladik, 1969).

Mexico to Colombia, Venezuela, the Guianas, Brazil, and Bolivia; West Indies. In Panama, known from tropical dry forest in Panamá (Taboga Island), from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Los Santos, Panamá, and Darién, from tropical wet forest in Darién, and from premontane wet forest in Coclé, Panamá, and Darién.

Randia formosa (Jacq.) K. Schum. in Mart., Fl. Brasil.
6(6):342. 1889

Diocious shrub or small tree, unarmed, widely branched; stems glabrous in age, slender. Leaves clustered at ends of small lateral branches; stipules short, broadly triangular, often \pm scoop-shaped, acute, 1.5–3 mm long, brown, persisting below leaf clusters; petioles obscure or to 1 cm long; blades oblanceolate-elliptic, acuminate, attenuate and decurrent at base, mostly 3–11 cm long, 1.5–3 cm wide, sparsely pubescent and dark green above, duller and more densely pubescent below. Flowers single at branch ends, densely sericeous; calyx 13–20 mm long, lobed, persisting in fruit, the lobes 5, linear, 8–10 mm long; corolla tubular, 11–19 cm long, the tube greenish, papillose inside at apex, soon becoming velutinous in upper part, then glabrous, the lobes 5, white, 3–5 cm long, tapered to a slender tip; filaments adnate to tube; anthers 5, ca 5.3 mm long, attached at flared apex of tube; style with ascending trichomes near apex; stigma broadly bilobed, held slightly above anthers. Fruits baccate, \pm

KEY TO THE SPECIES OF RANDIA

- Flowers solitary at ends of branches; corolla 11–19 cm long; fruits \pm spherical, green with whitish bands *R. formosa* (Jacq.) K. Schum.
Flowers usually in clusters of 2–4 at ends of branches; corolla less than 6 cm long; fruits longer than broad, green turning yellow at maturity *R. armata* (Sw.) DC.

Fig. 535.
Randia formosa



Fig. 536. *Tocoyena pittieri*

Fig. 537. *Uncaria tomentosa*



spherical, to 25 mm diam, dark green, with several broad white bands extending from apex to middle or beyond, sparsely covered with appressed trichomes; seeds numerous, flattened laterally, stacked in 4 rows, white. *Croat 11296, 11888.*

Occasional; known from the shore near Colorado Point and in the second growth west of the tower. It occurs at the margins of forest elsewhere in the Canal Zone. Flowers in July and August. The fruits mature in August and September.

Panama to Colombia, Venezuela, Peru, and western Amazonian Brazil; Tobago. In Panama, known from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, Colón, Chiriquí, Panamá, and Darién, and from premontane wet forest in Darién.

See Fig. 535.

SABICEA Aubl.

Sabicea villosa Willd. ex R. & S. var. **adpressa** (Wernham) Standl., Publ. Field Columbian Mus., Bot. Ser. 7:52. 1930

Liana, the younger parts herbaceous; all parts pubescent, the trichomes stiff, \pm appressed, sparse on leaf surfaces but conspicuous on veins below. Stipules broadly ovate, acute, 7–10 mm long, persistent; petioles 5–18 mm long; blades ovate to elliptic, acute to acuminate, obtuse to rounded at base, mostly 6–13 cm long and 2.5–7 cm wide, purplish below when young. Flowers sessile, 5(6)-parted, in short, axillary clusters to 3 cm long; calyx lobes 5–7 mm long, recurved, persisting in fruit; corolla white, 8–10 mm long, the tube glabrous inside except near anthers, the lobes short; anthers 5(6), 1.3–2.3 mm long, opening in bud, fused to tube near base of corolla lobes; style variable, to 5(8) mm long, the branches 5, to 3 mm long, held well below anthers within the narrow corolla tube; nectar copious. Berries globose, ca 10 mm diam, sparsely to densely pubescent, red becoming dark purple; seeds many, tan, minute. *Croat 11725.*

Occasional in older clearings, on trails, and at the margin of the forest along the lake; less commonly climbing to the top of the forest canopy and sometimes rooting in water (*Shattuck 704*). Flowers and fruits to some extent throughout the year, but mostly in the dry season, from December to April, and again from June to August. Most fruits mature in the middle to late rainy season. Flowers and mature fruits are common on the same stem.

The genus is so poorly known that the geographic limits are uncertain. The species is found from Belize and Honduras south to Colombia, Venezuela, and Guyana, and the variety *adpressa* ranges from Costa Rica to Colombia. In Panama, the species consists of two intergrading varieties: the typical variety has spreading trichomes and is found in Bocas del Toro; var. *adpressa*, which is more widespread, is known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane moist forest in the

Canal Zone, and from premontane wet forest in Panamá and Darién. Intermediate forms are found in Bocas del Toro and central Panama on the Atlantic slope.

SPERMACOCE L.

Spermacoce tenuior L., Sp. Pl. 102. 1753

Erect or sprawling herb, glabrous or nearly so, rarely more than 60 cm tall. Leaves short-petiolate; stipules of several slender bristles; blades lanceolate or linear-lanceolate, acuminate, gradually attenuate at base, 3–7 cm long, 5–15 mm wide. Inflorescences 1-sided axillary clusters, bearing many flowers; bracts borne among the sessile flowers, slender but short and inconspicuous; sepals triangular, 0.5–1 mm long (variable throughout the range); corolla white, 1.5–2 mm long, lobed to about middle, conspicuously villous in throat; stamens about as long as tube; pistillate parts not seen. Capsules usually obovoid, ca 3 mm long, glabrous. *Woodworth & Vestal 476.*

Apparently rare; collected only once on the island. Seasonal behavior uncertain. Temperate collections show flowering and fruiting from May to October. A few tropical records show flowering and fruiting mostly in the early rainy season.

The plant is inconspicuous and can be confused with *Diodia ocimifolia*, which can be distinguished by the pubescence on at least the leaves and capsules.

Southwestern Ohio and southern Missouri to Florida, Mexico, Central America, and South America as far south as Argentina and Uruguay; West Indies. In Panama, apparently infrequent; known only from tropical moist forest in the Canal Zone, San Blas, and Panamá, but no doubt growing elsewhere in tropical moist forest.

TOCOYENA Aubl.

Tocoyena pittieri (Standl.) Standl., Contr. Arnold Arbor. 5:151. 1933

Tree, to 15 (25) m tall, \pm glabrous; stems with prominent leaf scars. Leaves clustered at ends of branchlets; stipules triangular, 5–10 mm long; petioles 1–2 cm long; blades obovate, obtuse to acute at apex, cuneate at base, 18–28 cm long, 7–14 cm wide, sparsely pubescent below with pocketlike domatia in most vein axils. Panicles congested, terminal, nearly sessile or on pedicels to 8 mm long; flowers 5-parted; calyx green, obscurely toothed; corolla yellow, becoming yellow-orange, the tube 8–12 cm long, ca 5 mm diam, the lobes obovate, ca 1.5 cm long, rounded at apex, spreading at anthesis, reflexed in age; anthers sessile, attached at base to rim of corolla; stigma exerted, the lobes 2, very thick, becoming reflexed after anthers have fallen. Fruit baccate, globose to ellipsoid, to 11 cm long and 8 (12) cm diam, green, the exocarp to ca 9 mm thick, shiny, yellow inside; seeds many, ovate, ca 19 mm long and 3 mm thick, brown, flattened, irregular, embedded in a fleshy matrix. *Croat 8529, 14877.*

Occasional, in the forest, at least in the vicinity of the Laboratory Clearing. Flowers from March to July, mostly from April to June. The fruits take about a year to mature and are eaten by white-faced and spider monkeys in April and September (Hladik & Hladik, 1969).

Southern Costa Rica to northern Colombia. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

See Fig. 536.

UNCARIA Schreb.

Uncaria tomentosa (Willd.) DC., Prodr. 4:349. 1830

Bejuco de agua

Large armed liana; trunk to 25 cm diam near the ground; outer bark thick, deeply fissured, coarse, dark brown; inner bark somewhat orange; younger stems square, \pm pubescent, armed at nodes with stout, recurved spines to ca 1.5 cm long and ca 1 cm wide at base. Stipules \pm ovate, ca 8 mm long; petioles 1–1.5 cm long; blades ovate to elliptic, bluntly acuminate, rounded to cordate at base, 4–13 cm long, 3–8 cm wide, glabrous above except strigillose on midrib, whitish-strigillose below, the trichomes longer and sparser on veins. Flower heads very dense, globular, pedunculate, axillary or terminal, to 2.5 cm diam, terminating stiff, spinelike peduncles or stiff branches of open panicles ca 10 cm long and 12 cm wide; peduncles 2–4 cm long, flattened, to ca 8 mm wide at base; flowers 5-parted, with sweet aroma, golden-yellow, sessile; calyx cylindrical, ca 2 mm long, truncate, sericeous; corolla tubular, ca 8 mm long, tomentose outside, papillate inside, the lobes to 1.5 mm long, rounded, spreading; stamens fused to rim of corolla tube; anthers exserted, to ca 1.5 mm long; style thickened at apex, unlobed, shorter than anthers in bud, later exserted to ca 3 mm, then often recurving into flower. Capsules ellipsoid, 6–8 (17) mm long, 3–4 mm wide, brown-tomentulose, densely clustered in spherical heads ca 1.5 cm diam, irregularly dehiscent along several lines, only a few of the ovaries in the head developing into fruits; seeds many, elliptic to round, flattened, ca 0.5 mm long, bearing a slender scarious wing ca 1.5 mm long on both ends. *Croat 8288, Montgomery 11.*

Common, growing high in the canopy to 30 m or more. Flowers from January to March, mostly in February. The fruits mature quickly, with the seeds dispersed chiefly in the late dry season, but with at least some seeds persisting into the rainy season, sometimes as late as September.

The fruits form a basketlike structure at maturity, similar to those of *Aristolochia* (44. Aristolochiaceae), which permits the seeds to be slowly carried away in the wind.

Central America, Colombia, Venezuela, and the Guianas; Trinidad. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, Panamá, and Darién.

See Fig. 537.

WARSCIEWICZIA Klotzsch

Warscewiczia coccinea (Vahl) Klotzsch, Monatsb.

Akad. Ber. 497. 1853

Crucero, Guna

Tree, to 15 m tall, nearly glabrous. Leaves sometimes minutely pubescent on petioles and veins; stipules ovate, long-acuminate, to 3 cm long, entire, persistent; petioles to 2.5 cm long, stout; blades oblong-elliptic to elliptic, acuminate, obtuse at base, 15–30 (50) cm long, 6–15 (20) cm wide. Inflorescences terminal and axillary, to 80 cm long, ca 3 cm wide, the cymes short-pedunculate, to 2 cm apart on floral rachis; flowers sessile, 5-parted, protogynous, developing acropetally, densely congested; one flower in each cluster usually bearing a calycine lobe, this red, leaflike, \pm elliptic, long-stipitate, to 12 cm long and 4 cm wide; other calyx lobes to 1 mm long, rounded; corolla funnel-shaped, 6–8 mm long, red-orange, lobed to ca one-third its length, the tube weakly pubescent on the outside and at point of staminal attachment inside, the lobes erect, ovate, blunt; stamens attached somewhat below base of lobes; filaments thick; anthers \pm oblong, ca 1.5 mm long, exserted, attached near base, often held horizontally; pollen arachnoid, tacky, orange; style 4.5–5.5 mm long, the lobes 2, short and thick, exserted from corolla before it is fully expanded (while anthers unopened). Capsules subglobose, 2-valved, ca 5 mm long, persisting; seeds minute, many, probably wind dispersed. *Croat 6032, 7340.*

Rare; seen only along the shore. Flowers from the late dry season to the middle of the rainy season, especially in July and August, sporadically at other times of the year. The fruits mature quickly and are probably mostly dispersed during the late rainy and dry seasons.

The expanded calycine lobe, though turning brown and persisting, apparently serves no direct dispersal function, since the capsule valves persist after the seeds have been shed. It may cause fluttering of the capsule that dislodges the seeds.

Mexico to Colombia, Venezuela, the Guianas, Brazil, and Bolivia; Trinidad; introduced ornamentally to Africa. In Panama, a characteristic tree of tropical moist forest (Holdridge & Budowski, 1956); known from tropical moist forest in the Canal Zone, Colón, Veraguas, Panamá, and Darién, from premontane wet forest in Chiriquí, Veraguas, Coclé, Panamá, and Darién, and from tropical wet forest in Coclé and Darién.

131. CUCURBITACEAE

Herbaceous tendriled vines (sometimes woody at base), the tendrils simple or branched, spiraled, arising from upper side of petiole base; stems often angled or striate. Leaves alternate, petiolate; blades simple, palmately divided, or merely palmately lobed, entire or sharply serrate, often with apiculate teeth; venation palmate; stipules lacking. Flowers 5-parted, unisexual (plants

KEY TO THE TAXA OF CUCURBITACEAE

- Mature leaves divided to the base (each leaflet borne on a distinct petiolule); fruits \pm cylindrical:
 Plants with long sparse trichomes; calyx orange, the lobes acuminate, spreading; corolla yellow
 *Gurania coccinea* Cogn.
 Plants glabrous or nearly so; calyx green, the lobes short, blunt; corolla red or orange *Psiguria*
- Mature leaves not divided to the base (sometimes deeply lobed but not completely to base); fruits cylindrical or not:
 Calyx orange; stems sparsely pilose; flowers densely aggregated, capituliform or umbelliform
 *Gurania* (in part)
- Calyx green; stems not pilose; inflorescences not capituliform or umbelliform:
 Most adult leaves with 5 or more lobes:
 Leaves asperous (at least when dry); anthers straight or slightly curved; fruits ovoid, mottled with light and dark green stripes, indehiscent; flower pedicels lacking leafy bracts
 *Melothria trilobata* Cogn.
 Leaves smooth; anthers conduplicate; fruits turbinate, beaked at apex, orange, fleshy, splitting to expose red seeds; flower pedicels with leafy bract near base
 *Momordica charantia* L.
- Most leaves unlobed or to 3-lobed:
 Leaf blades entire, neither toothed nor lobed; corolla less than 2 mm long; plants forest vines; leaves not asperous above *Sicydium coriaceum* Cogn.
 Leaf blades with the lateral veins ending in sharp or gland-tipped teeth and/or the blades lobed; corolla more than 4 mm long:
 Leaf blades mostly less than 7 cm long, usually not lobed, deeply cordate with a narrow sinus; fruits many-seeded, less than 3 cm long; slender vine *Melothria pendula* L.
 Leaf blades usually more than 8 cm long, lobed or not, not cordate or cordate with a broad sinus; fruits 2–6-seeded or many-seeded and more than 8 cm long:
 Leaf blades mostly obtuse to truncate at base (very slightly cordate in *C. denticulata*); fruits probably always less than 3 cm long *Cayaponia*
 Leaf blades cordate with a broad sinus; fruits globose or gourdlike, more than 7 cm diam:
 Blades \pm entire except for a few glandular teeth; stems glabrous; seeds 6, disk-shaped, more than 4 cm wide *Fevillea cordifolia* L.
 Blades shallowly or deeply 3(7) lobed; stems densely short-villous; seeds numerous, narrowly obovoid, less than 1 cm diam *Posadaea sphaerocarpa* Cogn.

dioecious or monoecious), actinomorphic, axillary, solitary or in cymose (often contracted) panicles; calyx united with the base of corolla into a hypanthium; corolla tubular, campanulate or ovate (*Fevillea*); staminate flowers with the stamens usually partially attached to corolla tube, 2 (*Gurania*, *Psiguria*), or 5 with unilocular anthers longitudinally dehiscent, or 5 variously fused: (a) into 2 pairs and a single stamen (the pairs appearing as simple stamens with 2-locular anthers), (b) into a single column with free or fused anthers variously disposed, or (c) with the anthers fused and the filaments free; pistillode often present; pistillate flowers with the ovary 1, inferior, the carpels basically 5, mostly reduced to 3(4); placentation parietal; ovules usually numerous (solitary in *Sicydium*), anatropous; style 1; style branches or stigmas equaling number of carpels. Fruits pepos (berrylike), usually indehiscent; seeds 1 to many, lacking endosperm.

Members of the family may be recognized by being herbaceous vines with tendrils, by their unisexual, usually tubular to bell-shaped flowers, by their unusually modified staminate flowers, and by their berrylike, many-seeded fruits.

Flowers are often unusually modified, and many no doubt require specialized pollinators. Both *Gurania* and *Psiguria* are pollinated in part by butterflies of the genus

Heliconius, which collect pollen (Ehrlich & Gilbert, 1973). Elsewhere *Gurania* is also pollinated by hummingbirds (L. Gilbert, pers. comm.). Some South American species of *Cayaponia* are bat pollinated (Vogel, 1958).

The fruits of *Melothria*, *Cayaponia*, and *Momordica* are probably dispersed by birds of clearings, those of *Sicydium* by forest birds, and the larger-fruited forest species, *Fevillea*, *Gurania*, and *Psiguria*, by mammals. Squirrels and other rodents may be important in the dispersal of seeds of *Gurania* (L. Gilbert, pers. comm.). *Fevillea cordifolia* is dispersed chiefly along waterways, according to Ridley (1930).

About 100–110 genera and 650–850 species; mainly in the tropics and subtropics.

CAYAPONIA Manso

Cayaponia denticulata Killip ex C. Jeffrey, Kew Bull. 25:206. 1971

Vine, climbing into canopy; stems slender, conspicuously ribbed (at least on drying), densely crisp-villous to puberulent at least in grooves. Petioles 2–2.5 cm long, densely villous, some of the trichomes stouter and uncinat; blades ovate, abruptly acuminate, truncate to weakly

KEY TO THE SPECIES OF CAYAPONIA

- Leaves divided nearly to base into 3 leaflets *C. granatensis* Cogn.
 Leaves entire or lobed, not divided to base:
 Lower blades with densely pubescent veins, lacking winglike margins on drying
 *C. denticulata* C. Jeffrey
 Lower blades with the veins glabrous (except along margins), the blades drying with conspicu-
 ous winglike margins:
 Corolla ca 15 mm long; fruits with 6 seeds *C. glandulosa* (Poepp. & Endl.) Cogn.
 Corolla less than 5 mm long; fruits with 2 or 3 seeds *C. racemosa* (P. Mill.) Cogn.

cordate at base, 8–15 cm long, 5–9 cm wide, chartaceous, the upper surface glabrate except on major veins, the lower surface densely short-villous, the margins entire except for a regular series of free-ending veins forming minute teeth; veins 3 at base, pinnate above, the basal lateral veins extending ca two-thirds the length of blade, all veins prominently raised on underside. Flowers and fruits not seen. *Montgomery* 96.

Collected once in the canopy near the Laboratory Clearing.

The collection was determined by C. Jeffrey. The identification remains dubious until fertile material is collected.

Cayaponia glandulosa (Poepp. & Endl.) Cogn. in A. DC., *Monogr. Phan.* 3:755. 1881
C. poeppigii Cogn.

Monoecious tendriled vine; stems pubescent to glabrate; tendrils 1- or 2-branched below middle. Petioles 2–8 cm long, puberulent; blades cordate to ovate in outline, entire or 3-lobed, 6–19 cm long, 3–18 cm wide, rounded to acute at apex, cordate to cuneate at base, pubescent on both surfaces, the veins usually glabrous except along the margin of the flattened, winglike portion, the upper surface pustulate, the lower surface with sessile glands near the base. Inflorescences axillary, paniculate or racemose, occasionally 1-flowered; rachis to 20 cm long; pedicels 1–5 mm long; calyx campanulate, 5-lobed, ca 1 cm long, pubescent; corolla greenish-white, 5-lobed to below the middle, the lobes ovate-lanceolate to oblong, ca 1.5 cm long, pubescent; staminate flowers with the stamens 3, ca 1 cm long, the filaments filiform, the anthers folded, forming an irregular mass ca 0.7 mm long; pistillate flowers with the ovary ellipsoid, puberulent to glabrate, 4–6 mm long, the styles ca 1.5 cm long, the staminodia minute. Berries ovoid-ellipsoid to subglobose, ca 2 cm long and 1.5 cm diam, black, the surface smooth, glabrous; seeds 6–15, obovate, ca 6 mm long, ca 4 mm wide, compressed, brown and white mottled, the base somewhat truncate. *Kenoyer* 573, *Standley* 41133.

Reported by Standley, but probably no longer occurring on the island—it is less likely to reoccur than is the more common *C. racemosa*. Seasonal behavior not determined.

Panama and Colombia, Venezuela, Ecuador, Peru, and Bolivia. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiri-

quí, and Darién, from tropical wet forest in Colón (Río Guanache), and from either lower montane wet forest or lower montane rain forest in Chiriquí (Las Nubes).

Cayaponia granatensis Cogn. in A. DC., *Monogr. Phan.* 3:794. 1881

Diocious vine; most of the vegetative growth ± herbaceous, but arising from larger woody stems; younger stems and leaves glabrous; tendrils trifid from near base. Petioles 2.5–9 cm long; blades 3-lobed to near base, the lobes oblong to narrowly elliptic, long-acuminate (the acumens sometimes very narrow and to 2.5 cm long), 15–25 cm long, the center lobe 4–9 cm wide, the base truncate to cordate, both surfaces light-punctate, the lower surface also obscurely and minutely papillate; veins at base 3; juvenile leaves entire, ovate-oblong to oblanceolate, becoming 2- or 3-lobed. Staminate flowers in axillary fascicles of few flowers, 3–3.5 cm long, white with green lines; calyx campanulate, glabrous, the tube ca 2 cm long, fused to corolla, the lobes 5, slender, 2–3 mm long; corolla lobes 5, ca 1 cm long, 5–7 mm wide, usually 4- or 5-striate, scabridulous outside, crisp-villous inside and on margins; stamens apparently 3 (actually 5 with 2 pairs of fused stamens); pistillate flowers not studied. Berries globose, ca 1.5 cm diam, reddish (drying orange), glabrous at maturity except near the peduncle, the pericarp weakly coriaceous, ca 1 mm thick or less; seeds few, enveloped in a fleshy matrix, flattened, to 11 mm long, 7 mm wide, 2–3 mm thick. *Foster* 2208, *Croat* 11640.

Occasional, in the old forest, sometimes climbing trunks of trees into the canopy. Flowers at least in March and April and possibly as early as January. The fruits mature in the late dry and early rainy seasons (April and May).

Panama, Colombia, Venezuela, and Peru. In Panama, known from tropical moist forest on BCI and in Darién (Cana), from premontane wet forest in San Blas, and from tropical wet forest in Panamá. It is also known from Cerro Tute in Veraguas (life zone uncertain).

Cayaponia racemosa (P. Mill.) Cogn. in A. DC., *Monogr. Phan.* 3:768. 1881

Monoecious tendriled vine; stems grooved, glabrate to villous; tendrils 2-branched below the middle. Petioles 1.5–6 cm long; blades entire or lobed, cordate to acute at

base and abruptly decurrent onto petiole, 5–15 cm long, 3–15 cm wide, the lobes 3 or 5 (or 7), obtuse to acuminate, the lower surface and midrib of upper surface puberulent to hispid, the upper surface very asperous, with erect to scabrous pustular-based trichomes, the margins with remote gland-tipped teeth; lower midrib with a broad flattened rib along its margin. Flowers unisexual, solitary or few in axils or in axillary racemes, the pistillate flowers slightly smaller than staminate flowers; calyx broadly campanulate, ca 6 mm long, pubescent, the lobes 5, ovate; corolla greenish-white to yellow, 4–5 mm long, densely tomentose on outside, with long slender trichomes inside; stamens apparently 3 (4 fused in 2 pairs); filaments free; anthers coherent, one of them 1-celled; staminodia minute in pistillate flowers; ovary 3-locular (or 1-locular by abortion); stigmas 3, dilated, reflexed. Berries ellipsoid to ovoid, 1.3–2 cm long, 8–10 mm wide, orange to red at maturity, the surface smooth, glabrous; seeds usually 2 or 3, compressed-ellipsoid, ca 8 mm long, orangish-brown, roughened. *Bailey 577.*

A weed of clearings, possibly once common on the island but probably no longer occurring there. Flowers and fruits throughout the rainy season and in the early dry season (July to January). The fruits mature mostly from November to May.

Standley reported the species to be frequent in thickets (1928).

Florida and Mexico to Panama and Colombia and across northern South America to Venezuela, Guyana, Brazil, and Peru; Trinidad, West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Coclé, Panamá, and Darién and from premontane wet forest in Chiriquí (Boquete).

FEVILLEA L.

Fevillea cordifolia L., Sp. Pl. 1013. 1753

Diocious tendriled vine, climbing into canopy; stems glabrous, 5-costate; tendrils branched once near apex. Leaves simple; petioles 2–8 cm long; blades ovate-cordate, acuminate, 4–15 cm long, as broad as long, entire or usually with a few blunt glandular teeth, glabrate to weakly short-pubescent especially on veins above, the veins of lower surface drying flattened, with weblike

axillary pockets; venation palmate. Staminate inflorescences paniculate, terminal or axillary, mostly to 25 cm long; axes, branches, and pedicels densely short-puberulent; each branch bearing a fleshy, ovate to rounded bract at base; pedicels filiform, 2–6 mm long; staminate flowers yellow-green, 5-parted, 7–8 mm diam; calyx ca half as long as corolla, lobed to middle, weakly pubescent and ciliate, the lobes ribbed medially in basal half; corolla lobes broadly obovate, rounded at apex, ca 3–3.5 mm long, glabrous on outer surface, weakly pubescent inside and bearing a narrow flap of tissue medially in basal third of petal; stamens 5, free, extrorse, ca 1 mm long; anthers about as broad as long, equaling or longer than filaments; pistillate flowers similar to staminate, the ovary globose, 3–4 mm diam. Fruits globose or nearly so, smooth (drying with very minute bumps), 7–12 cm diam, bearing a circumferential scar one-fourth to one-third of the way down from apex when juvenile, nearer the apex on mature fruits; seeds 6, in 3 carpels in appressed pairs, lenticular, 5–5.5 cm long, 4–5 cm wide, to ca 1 cm thick but the margin very thin. *Croat 11918.*

Apparently uncommon; seen once in the canopy of the old forest south of Zetek Trail. Flowers from May to August. Mature fruits have been found on the ground during October.

The size of the fruits suggests that they are probably dispersed by larger frugivores, perhaps by monkeys. Some fruits with the thick rind broken open have been found on the ground, so they are possibly dispersed by floor foragers also.

Costa Rica to Ecuador and the Amazon basin; Greater Antilles. In Panama, known only from tropical moist forest in the Canal Zone, Chiriquí (Bartolomé), and Los Santos.

See Fig. 538.

GURANIA Cogn.

Gurania coccinea Cogn., Diagn. Cucurb. Nov. fasc.

1. 42. 1876

Ya te vi

Diocious vine; stems 5–10-sulcate, sparsely white-pilose, tendrils simple. Leaves usually palmately trifoliolate (juvenile leaves sometimes simple and entire or deeply 2- or 3-lobed); petioles 2–6 cm long, sparsely white-

KEY TO THE SPECIES OF GURANIA

Mature leaves divided to the base, each leaflet borne on a distinct petiolule *G. coccinea* Cogn.

Mature leaves not divided to the base (leaves lobed but not to the base):

Staminate flowers long-pedicellate; calyx puberulent or glabrate, lobed less than one-fourth its length, the lobes to 1.2 cm long, much shorter than hypanthium tube; leaves mostly 3-parted; older stems woody, corky; flowers usually borne on older, leafless stems

. *G. megistantha* Donn. Sm.

Staminate flowers nearly sessile; calyx densely villous, lobed more than half its length, the lobes to 4 cm long, equaling or longer than hypanthium tube; many leaves more than 3-parted; older stems herbaceous; flowers not borne on older, leafless stems

. *G. makoyana* (Lem.) Cogn.



Fig. 538. *Fevillea cordifolia*



Fig. 539.
Gurania makoyana



Fig. 540.
Gurania megistantha

pilose; petiolules to 5 mm long; leaflets acuminate, 12–18 cm long, 5–8 cm wide, sparsely pubescent above, more densely so on veins, pilose below especially on veins, the margins irregular, sparsely ciliate, with apiculate teeth; terminal leaflet elliptic to obovate, equilateral, acute at base; lateral leaflets strongly inequilateral, with a broad cordate lobe on outer side. Inflorescences sparsely pilose; flowers 5-parted; calyx orange; corolla yellow; staminate racemes solitary, umbelliform, pendent; peduncles 15–30 cm long; pedicels 4–15 mm long; flowers 10–15 mm long; calyx bulbous at base, lobed one-third to one-half of the way to base, the outer surface pilose, the inner surface papillose-puberulent, the lobes narrowly triangular, 3–5 mm long; corolla lobes densely papillose-puberulent on both surfaces, somewhat longer than calyx; anthers 2, included, sessile, dorsifixed; pistillate flowers solitary or few in axils or on leafless nodes of the flexuous stem, 5–8 cm apart, the stem then usually pendent for 1 m or more; pedicels less than 1 cm long at anthesis (to 2 cm in fruit); calyx to 1.5 cm long, fused to corolla almost throughout; corolla to 2 cm long, densely papillose-puberulent, the lobes 5, narrowly acute, imbricate, 6–9 mm long; style thick, almost as long as corolla lobes. Fruits oblong-elliptic, to 6.5 cm long, somewhat flattened, to 2.3 cm wide and 1.6 cm thick, pale green with lighter spots, becoming faded in age; seeds many, ovoid, \pm flattened, white. *Shattuck 641, Croat 14077.*

Rare, in the older forest, often twining up tree trunks and then hanging pendent from branches. Flowering throughout the dry season (December to April). Mature fruits have been seen during May and June.

The fruits are very bitter before maturity.

Known only from Panama, at elevations to 1,000 m, from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and San Blas (Puerto Obaldía), from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón, Veraguas, and Coclé.

Gurania makoyana (Lem.) Cogn., *Diagn. Cucurb.*

Nov. fasc. 1. 17. 1876

G. seemanniana Cogn.; *G. donnell-smithii* Cogn.

Ya te vi

Diocious vine; stems and leaves sparsely to densely white-villous; tendrils simple. Petioles 4–10 cm long; blades usually deeply (3)5(7)-lobed, 15–30(40) cm long, nearly as wide as long, cordate at base, chartaceous, the lobes acuminate, 4–7 cm wide, with apiculate teeth, the upper surface minutely pustulate; juvenile leaves often entire or shallowly lobed. Inflorescences sparsely to densely pilose; flowers 5-parted; calyx orange; corolla yellow; staminate inflorescences solitary, pendent; peduncles to 15 cm long; staminate flowers sessile, in subglobose clusters; floral rachis 1–2 cm long; calyx ovoid at base, densely villous, the lobes almost filiform, to 4 cm long; corolla fleshy, acute at apex, only slightly exceeding anthers, conspicuously papillose-puberulent, to 15(24) mm long, the tube constricted above anthers; anthers 2, included, dorsifixed, subsessile, narrowly ovate, 5–6 mm

long; pistillate flowers pedicellate, several per axil, on usually leafless nodes at the stem apex; pedicel and ovary together 1.5–2 cm long; pedicels 4–5 cm long in fruit; inner surfaces of calyx and corolla glabrous, otherwise much like staminate flowers. Fruits cylindrical, 4–6 cm long and 2–2.5 cm broad, green at maturity with the old flowers persisting; seeds many, depressed-ellipsoid, 6–9 mm long and 3–5 mm broad, white. *Croat 5674, 9408.*

Occasional, in open areas of the forest and along trails and margins of clearings. Flowering throughout the dry season and in the early rainy season (December to June), perhaps longer. Mature fruits have been seen in the late dry and early rainy seasons.

Guatemala to Panama, perhaps into South America. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón (Santa Rita Ridge), Veraguas, Coclé, and Darién.

See Fig. 539.

Gurania megistantha Donn. Sm., *Bot. Gaz. (Crawfordsville)* 33:251–52. 1902

G. suberosa Standl.

Diocious vine, growing into lower canopy; older stems stout, woody, with a thick, 5–10-sulcate, corky outer bark; younger stems sparsely pilose; tendrils simple. Petioles 3–7(11) cm long, moderately pilose; blades usually deeply trilobate, acuminate, cordate at base, 12–20 cm long, 10–18 cm wide, short, \pm erect-pubescent especially on veins. Flowers unisexual, both sexes in pedunculate, capituliform racemes arising from leafless woody stems, rarely branched from short herbaceous branches, arising from the woody stems; peduncles nearly lacking or to 9 cm long, sparsely strigose; rachis 1–3 cm long; pedicels 1–2.5 cm long, puberulent; calyx orange, tubular, with a bulbous base, 1.5–3.5 cm long, 5-lobed to ca one-fourth its length, the lobes linear, 4–12 mm long, spreading at anthesis; corolla yellow, to 4 cm long, equaling or exceeding calyx at anthesis, fused to calyx tube, the lobes 5, narrowly acute, densely papillose-puberulent outside and on tube inside; staminate flowers with the stamens 2, included, to ca 2 cm long, tapered to apex, the thecae lateral, the connective prolonged and granular-puberulent; pistillate flowers with the stigma bilobed. Fruits similar to those of *G. coccinea* but borne in a tight cluster 4–5 cm long and as much as 2 cm wide. *Croat 5782, 12217.*

Occasional, in the forest. Flowering throughout the year; the flowers are seen more easily than the associated vegetation, which may be high in the canopy. The fruits are rarely seen, but have been recorded in May.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and Panamá, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón, Veraguas, and Coclé.

See Fig. 540.

KEY TO THE SPECIES OF MELOTHRIA

- Leaves not lobed or weakly lobed; plants common in clearings *M. pendula* L.
 Leaves deeply 5-lobed; plants rare or absent from the island *M. trilobata* Cogn.

MELOTHRIA L.

Melothria pendula L., Sp. Pl. 35. 1753

M. guadalupensis (Spreng.) Cogn.

Very slender, small, monoecious vine; stems almost glabrous to weakly pubescent; tendrils simple. Petioles 1–4 cm long; blades cordate-ovate, acute to acuminate, mostly 4–7 (10) cm long and to 7 (10) cm wide, irregularly toothed, sometimes weakly 3–5-lobed, asperous above, the basal sinus open to nearly closed, to 2.5 cm deep. Flowers unisexual, yellow, 5–6 mm long; calyx ca 4 mm long, fused to corolla, the lobes 5, narrow; corolla papillose, the lobes 5, rounded, the limb to 1 cm wide; staminate flowers several, in long-pedunculate racemes, 1–3 cm long; stamens 3; anthers situated in the upper part of corolla tube; filaments fused to corolla in basal half; anthers ca 1.7 mm long, fringed marginally with orange papillae; pistillode globose; pistillate flowers solitary; pedicels to 3 cm long (to 4.5 cm in fruit); calyx and corolla as in staminate flowers; ovary ellipsoid, glabrous, smooth; styles 3, 2–2.7 mm long, connate; stigmas 3, linear. Fruits ovoid, 1.5–2.5 cm long, 1–1.5 cm wide, glabrous, black at maturity, sweet; seeds many, ovoid in outline, flattened, ca 5 mm long, greenish. *Croat 5250, 8277.*

Common in clearings, less so along the shore. Flowering and fruiting throughout the year, especially in the rainy season.

Tropical areas of continental America; Bahamas, West Indies. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, Colón, and San Blas, from tropical dry forest in Panamá (Taboga Island), and from tropical wet forest in Bocas del Toro (Santa Catalina).

Melothria trilobata Cogn. in Mart., Fl. Brasil.

4(6):26. 1878

Wild cucumber, Sandillita

Monoecious vine; stems glabrate to sparsely crisped-pilose; tendrils simple. Petioles 1–5 cm long, sparsely pilose and sometimes also with very short, granular trichomes; blades circular in outline, deeply 5–7-parted, cordate at base, 6–10 cm diam, densely short-pubescent on veins above, sparsely to densely pubescent below, bicolorous, asperous, often minutely white-pustulate, the lobes acute to acuminate and apiculate at apex, the lateral lobes with a basal auricle. Flowers small, 5-parted, similar to those of *M. pendula*; calyx campanulate to sub-cylindrical, ca 3 mm long, the lobes triangular, to 1 mm long; corolla yellow, the lobes ovate-oblong, obtuse, the outer surface villous, the inner surface glabrate; staminate

flowers in axillary, long-pedunculate racemes, the peduncles very slender, the rachis 1–3 cm long, the pedicels very slender, short or to 1 cm long, the stamens 3, free, the filaments short, the anthers oblong, densely ciliate; pistillate flowers solitary, the pedicels ca 1 cm long, the calyx and corolla as in staminate flowers, the ovary ovoid, glabrous, smooth, the styles 3, connate, the stigmas 3, linear, the staminodia 3, minute. Fruits \pm ovoid, 4–5 cm long, almost as long as broad, mottled and striped with light and dark green, dark green at apex, light green at base; seeds whitish, flattened, narrowly ovate, ca 7 mm long and 3 mm wide. *Zetek 4996.*

Collected once on the island; possibly no longer occurring there, but to be expected in clearings and at the edge of the forest. Seasonal behavior not determined.

Mexico to Surinam. In Panama, known most commonly from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién; known also from premontane moist forest in the Canal Zone (Ancón Hill) and from tropical wet forest in Colón (Miguel de la Borda).

MOMORDICA L.

Momordica charantia L., Sp. Pl. 1009. 1753

Balsam pear, Basamino

Slender monoecious vine; stems, petioles, and blades (especially on veins) sparsely short-villous; tendrils simple, leaf-opposing. Petioles mostly 1–2 cm long; blades usually deeply 5–7-lobed, subrounded, 3–6 (12) cm diam, the margins weakly apiculate-toothed, the lobes mostly obtuse and mucronulate at apex, narrow at base, the outer lobes auriculate. Flowers 5-parted, yellow, unisexual, long-pedunculate; staminate flowers ca 1.5 cm diam; calyx pubescent, to 7 mm long, lobed to about middle, the lobes ovate, acute; petals oblong-obovate, rounded at apex, fused to calyx just below lobes, conspicuously veined and pubescent outside and on upper edge inside, the trichomes in part glandular; staminal cluster orange, 4.5–5 mm long; filaments 3, the basal one-third to one-half fused to corolla; anthers to 3 mm, sigmoid-folded, 1 pair borne on each of 2 filaments, a solitary anther borne on the third filament, the mass somewhat agglutinated; pistillate flowers not studied. Fruits turbinate, 5–12 cm long, pointed on both ends, orange, fleshy, echinate, the pericarp 2–3 mm thick, bursting irregularly to expose several seeds; seeds depressed-ellipsoid, roughened on the ends, ca 9 mm long and 5 mm wide, tan, the covering thin, sweet, tasty, bright red. *Croat 6372.*

Infrequent, in clearings. Flowers and fruits throughout the year.

The bright red seeds, displayed against the orange

PSIGURIA Arn. ex Hook.

interior of the fruit, are no doubt dispersed by birds.

In the tropics and subtropics of the Western and Eastern hemispheres. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from premontane dry forest in Los Santos, from premontane wet forest in Panamá, and from tropical wet forest in Chiriquí (San Bartolo Limite).

See Fig. 541.

POSADAEA Cogn.

Posadaea sphaerocarpa Cogn., Bull. Acad. Roy. Sci. Belgique, sér. 3, 20:477. 1890

Monoecious herbaceous vine, sparsely to densely short-villous on most parts; tendrils simple or bifid, thickened toward base. Petioles 3–12 cm long; blades ovate to orbicular, entire to usually weakly or deeply 3-lobed (to 7-lobed), acuminate, cordate at base, usually to 18 cm long and 19 cm broad, membranaceous, the basal sinus about as broad as long, the margins conspicuously and rather remotely toothed; major lateral veins nearly palmate. Flowers white, ebracteolate or minutely bibracteolate; staminate flowers in short, slender, few-flowered racemes; calyx tube campanulate, 8–9 mm long, the lobes ca 3 mm long; corolla yellow, 5-parted, rotate, puberulent outside, the lobes rounded, notched, 8–9 mm long; stamens 3 (1 unilocular, 2 bilocular), attached to corolla tube; anthers dorsifixed, white, 2 mm long, the thecae recurved at apex; pistillate inflorescences 2–5 cm long; calyx lobes 2 mm long; corolla segments ca 1 cm long, 4–5 mm wide; staminodia 5, obtuse, 1.5–2 mm long; ovary elliptic-ovoid, sparsely pubescent; style 3 mm long; stigmas 3, dilated, obcordate, subreflexed, ca 3 mm wide. Fruits globose, gourdlike, 8–10 cm diam, the pulp white, the cortex ± woody, the surface finely warty; peduncles tapered, swollen; seeds numerous, compressed, narrowly obovate, rounded at apex, attenuate at base, 12–14 mm long, 7–8 mm wide, 2–2.5 mm thick. *Shattuck 90.*

Old collections from in or near the Laboratory Clearing are the only record from the island; probably no longer occurring on the island. Seasonality uncertain. Flowers at least in the late rainy and early dry seasons. Mature-sized fruits have been seen in the dry season and may be accompanied by flowers.

Guatemala to Panama, Colombia, the Guianas, Ecuador, and Brazil, doubtless elsewhere; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Panamá (Río Tapia).

Psiguria bignoniacea (Poepp. & Endl.) Wunderlin, Phytologia 38:219. 1978

Anguria pachyphylla Donn. Sm.

Diocious canopy vine, ± glabrous except for sparse pubescence on stems, denser at nodes; stems stout; tendrils simple. Leaves palmately trifoliolate, deeply cordate, thick, coriaceous; petioles 2.5–5 cm long; petiolules 1–2 cm long; terminal leaflet irregularly broadly elliptic, acuminate, acute at base, 12–21 cm long, 8.5–13 cm wide; lateral leaflets asymmetrical, the outer margins irregular, 9–19 cm long, 6–10 cm wide. Flowers red to orange, unisexual; staminate flowers in long-pedunculate spikes; peduncles to 27 cm long; floral rachis 1–2 cm long; calyx tubular, ca 11 mm long, 3–4 mm wide, the lobes 5, short, recurved; corolla orange, extending less than 5 mm beyond calyx, the lobes 5, ± obovate, densely short-pubescent, the tube with a few long trichomes between stamens; anthers 2, sessile, dorsifixed, the connective somewhat produced; pistillate flowers solitary or few in leaf axils, otherwise like staminate flowers. Fruits similar to those of *P. warscewiczii*. *Croat 8082, 16518.*

Rare, known only from the vicinity of Snyder-Molino Trail 200. Flowering season uncertain. Probably flowers to some extent all year. Single plants certainly flower for several months—the plant over Snyder-Molino Trail flowered from at least February to September 1970, but may not have flowered at all during 1971.

Southern Mexico to Peru; at elevations between 170 and 1,000 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, and Darién, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Veraguas and Panamá.

See Fig. 542.

Psiguria warscewiczii (Hook.f.) Wunderlin, Phytologia 38:219. 1978

Anguria warscewiczii Hook.f.

Diocious vine, ± glabrous; stems slender, usually growing over shrubs and trees in the understory; tendrils simple. Leaves palmately trifoliolate, thin; petioles 3–6 cm long; terminal leaflet ± irregularly elliptic, acuminate, cuneate at base, 11–17 cm long, 5–8 cm wide; lateral leaflets asymmetrical bilobed to near middle, the lobes acuminate or rounded, 11–15 cm long, 5.5–10 cm wide. Flowers unisexual, to 2.5 cm long, the limb 1.5–2.5 cm wide; staminate flowers in axillary racemes; peduncles to 27 cm long; pedicels to ca 5 mm long at anthesis;

KEY TO THE SPECIES OF PSIGURIA

- Leaves thick, coriaceous when dry; lateral leaflets often more than 15 cm long, usually only shallowly lobed *P. bignoniacea* (Poepp. & Endl.) Wunderlin
 Leaves very thin, papyraceous when dry; lateral leaflets less than 15 cm long, usually lobed to near middle *P. warscewiczii* (Hook.f.) Wunderlin



Fig. 541. *Momordica charantia*

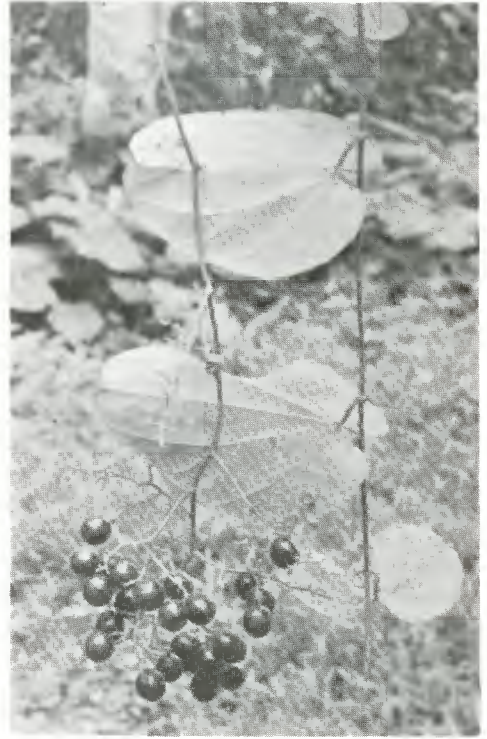


Fig. 544. *Sicydium coriaceum*



Fig. 542. *Psiguria bignoniacea*



Fig. 543. *Psiguria warszewiczii*

calyx tubular, to 2 cm long, slightly bulbous at base, light green, the lobes and warty spots on tube dark green, the lobes 5, short, blunt; petals 5, red-orange, rounded to obovate, 5–10 mm long, densely glandular-tomentose outside and near apex inside, the tube sparsely pubescent inside; anthers 2, sessile, dorsifixed, included, 11–12 mm long, adnate much of their length to corolla tube; pollen grains large, sticky; pistillate flowers solitary or few in axils; styles thick, to 8 mm long, the apex exerted, the 2 lobes bifid, pale orange. Fruits oblong-ellipsoid, 5.5–7 cm long, 1.8–2.5 cm wide, acute at base, beaked at apex, light green with dark green stripes, the flower often persisting; seeds many, stacked in each locule, flattened, irregularly narrow-ovate, light brown, ca 7 mm long.

Croat 4571, 8499.

Frequent in the forest. Flowers and fruits throughout the year, but especially during the rainy season. Plants may have both flowers and mature fruits at the same time.

Trigona bees have been observed visiting the flowers. The species is pollinated by butterflies of the genus *Heliconius* (Nymphalidae, Ithomiinae) (Ehrlich & Gilbert, 1973).

Southern Mexico south at least as far as Colombia, probably more widespread. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from premontane wet forest in Veraguas and Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 543.

SICYDIUM Schlecht.

Sicydium coriaceum Cogn. in A. DC., Monogr. Phan. 3:906. 1881

Slender dioecious vine; stems striate; tendrils branched once. Petioles 1–5 cm long, inconspicuously puberulent and glandular-puberulent, weakly viscid; blades ovate-cordate, acuminate at apex, 5.5–12 cm long, 3.4–9 cm wide, entire, scabridulous to nearly glabrous above except on veins, densely and inconspicuously puberulent and glandular below, both surfaces with small irregular cystoliths visible when dried; palmate veins 5–7, the basal vein with a branch extending into the basal lobes. Panicles terminal or axillary, to 17 cm long; flowers 5-parted, unisexual, to 2 mm wide, greenish; branches and pedicels densely puberulent and glandular-puberulent; calyx crisp-villous, the lobes obtuse, to ca half as long as petals, ca 0.8 mm long, villous on outer surface, ciliate; petals narrowly triangular to ca 1.5 mm long, papillate-puberulent, erose; staminate flowers with the stamens 3, free, borne on a broad flattened disk, the filaments 3–4 times as long as anthers, the anthers straight, 2 with 2 locules, 1 with 1 locule, the pistillode apparently lacking; pistillate flowers with the calyx and corolla as in staminate flowers, the ovary 1-celled, narrowly ovoid, ca 2 mm long, glandular-pubescent, the ovule 1, pendulous, the styles 3. Fruits globose, ca 1 cm diam, indehiscent, fleshy, black; seed 1, globose, ca 7 mm diam, heavily ornamented

with sharp projections of various lengths. *Croat 9572, 12931.*

Rare, growing into trees; seen fertile only once at about 10 m in a tree. Seasonal behavior uncertain. Mature fruits seen in the middle of April. Peruvian collections have been seen with flowers in November and March and fruits in December.

Standley (1933) reported *S. tamnifolium* (H.B.K.) Cogn. and correctly described that plant as having soft pubescence, but the only collections seen are of *S. coriaceum*, which is not soft-pubescent.

Panama to Peru. In Panama, known only from tropical moist forest in the Canal Zone (BCI and near Madden Dam); doubtlessly more widespread.

See Fig. 544.

132. CAMPANULACEAE

Suffrutescent herbs; sap milky. Leaves alternate, petiole, simple, subentire to toothed, estipulate. Flowers solitary in the upper axils, pedicellate; pedicels bracteolate; calyx lobes 5; hypanthium present; corolla tubular, 5-lobed, zygomorphic, bilabiate; stamens 5, epipetalous; filaments connate; anthers 2-celled, connate, dehiscing longitudinally, introrse; ovary 1, inferior, the carpels and locules 2; placentas 2, axile; ovules numerous, anatropous; style 1; stigmas broadly bilobed. Fruits leathery berries.

Only *Centropogon* occurs on BCI. It is easily distinguished by its milky sap, bilabiate reddish flowers with a curved tube, and stamens and anthers fused into a tube.

Some 60–70 genera and 2,000 species; in temperate and tropical areas.

CENTROPOGON Presl

Centropogon cornutus (L.) Druce, Bot. Exch. Club Soc. Brit. Isles 3:416. 1914

Suffrutescent herb, 1–3 m tall, often somewhat scandent; sap milky; stems hollow, glabrous at base, with stiff spreading trichomes above. Petioles 0.5–2 cm long; blades mostly oblong to oblong-elliptic, acute or acuminate at apex, rounded or tapering onto petiole at base, 10–15 (25) cm long, 3–5 cm wide, subentire to denticulate or shallowly crenate-denticulate, glabrous above, glabrous to minutely scaberrulous on veins below. Flowers solitary in upper axils, 6–8 cm long; pedicels erect, puberulent, (3.5)4.5–7(9.5) cm long, the bracteoles paired, ciliate, linear, 4–10(15) mm long, borne at or near base; hypanthium glabrous to bristly-pubescent; calyx lobes 5, ± narrowly lanceolate, 8.5–20 mm long, denticulate, usually wide-spreading at maturity; corolla red or pink (the lobes often white or occasionally the corolla completely white), the tube 3.5–4.5 cm long, curved throughout its length, narrowest at base, gradually widening above, ± glabrous to sparsely short-pubescent outside, glabrous inside, the lobes 5, falcate, triangular, the 2 upper ones 7–9 mm

long, the 3 lower ones slightly shorter with stiff whitish trichomes along margin; filament tube 4.5–6 cm long, white or white and distally pink, sparsely to moderately pilose toward apex, the filaments basally distinct and united to corolla tube; anther tube 7.5–9.5 mm long, densely hirsute, the terminal pubescence of the 2 shorter anthers fused into a triangular, hardened scale about 3 mm long; ovary truncate at apex. Berries depressed-globose, 10–17 mm diam, scarcely inflated, leathery; seeds disk-shaped with rounded edges, ca 0.6–1.8 mm diam, shallowly foveate-reticulate. *Shattuck 424.*

Collected only once on the island, perhaps disappearing as a result of succession, since it is a plant of weedier areas. Specimens have been collected many times in adjoining areas of tropical moist forest in the Canal Zone, but the species is probably more at home in regions of premontane wet forest. Flowers at least from October to February, but also in May and June, possibly all year.

The flowers are well suited to pollination by hummingbirds.

The berries are endozoochorous, possibly taken principally by birds.

Mexico (Oaxaca), Panama, and throughout northern South America, especially in the lowlands, to Bolivia and southern Brazil; Lesser Antilles. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, Panamá, and Darién and from premontane wet forest in Colón (Cerro Santa Rita) and Panamá (Cerro Trinidad).

**133. COMPOSITAE
(ASTERACEAE)**

Erect to decumbent herbs or vines, sometimes small trees or shrubs. Leaves cauline and alternate or opposite, or basal, sessile to petiolate; blades simple or pinnately or palmately lobed, entire or serrate; venation pinnate or occasionally palmate at base; stipules lacking. Heads solitary or in various arrays usually surrounded by spirally arranged bracts (phyllaries); flowers bisexual or unisexual (monoecious or dioecious), subtended by bracts (paleae or chaff); calyx presumably represented by the

chaffy or setaceous pappus (these most fully developed in fruit) or lacking; corolla of disk flowers tubular and generally 5-lobed, sometimes split on one side, central on head when ray flowers present; corolla of ray flowers prominently extended into a ligule, usually peripheral on head when present, showy; stamens 5 (4 in *Rolandra*), attached to the corolla, syngenesious (\pm connate into a ring), rarely free; anthers 2-celled, introrse, dehiscing longitudinally; ovary inferior, unilocular, 2-carpellate; placentation basal; ovule solitary, anatropous; style 1, 2-branched, usually antrorsely barbed, elongating after anthesis, thus pushing pollen from staminal tube; stigmas slender. Fruits achenes; seeds lacking endosperm.

Members of the family are distinguished on BCI by the bracteate heads, often bearing flowers of two kinds: (1) ray flowers around the periphery, these usually showy and often sterile or staminate, rarely lacking; and (2) disk flowers central on the head, not showy, and usually bisexual or pistillate.

The usually small, tubular flowers are probably pollinated principally by butterflies, but they are visited by a number of other types of small insects, such as short-tongued bees (Percival, 1965). (See the discussion of *Mikania micrantha*.) Pollen grains are small and bees specializing on them have pollen baskets that are densely plumose (Proctor & Yeo, 1973). The style, which is usually roughened or antrorsely barbed, usually pushes the sticky and heavily ornamented pollen out of the tube formed by the syngenesious anthers. This displays the pollen near the apex of the tube.

Achenes are chiefly anemochorous and to a lesser extent epizoochorous; a few are endozoochorous. In wind-dispersed achenes the pappus not only acts as a plume to carry the achene in the air, but may also serve to dislodge the achene by its hygroscopic movements. This usually serves to ensure that the achene is presented to the wind during dry, usually windy weather, providing wider dispersal. The pappus provides the same buoyancy in water as it does in air. Ridley (1930) reported that most Compositae seeds float.

In the case of epizoochorous fruits, the pappus is usually modified with prominent recurved awns, which attach themselves to passing animals. Most species of

KEY TO THE TAXA OF COMPOSITAE

- Leaves alternate or all basal:
 - Leaves basal *Chaptalia nutans* (L.) Polak.
 - Leaves borne on stem, not all basal:
 - Ray flowers conspicuous; heads bisexual; flowers white; plants often 3 m tall, the leaves usually deeply lobed, narrowed at base and decurrent onto stem *Verbesina gigantea* Jacq.
 - Ray flowers lacking or inconspicuous; heads discoid:
 - ◆ Individual heads clustered into distinct glomerules or compounded:
 - Leaves white-tomentose below (the trichomes in a dense, appressed, cottony mass), not decreasing markedly in size toward apex of plant; pappus of short scales:
 - Corolla white; outer heads not enveloped in the base of leaflike bracts; phyllaries mostly 2, coriaceous, the outermost with a straight, spinelike tip *Rolandra fruticososa* (L.) O. Kuntze
 - Corolla violet; outer heads enveloped in the base of leaflike bracts, these with a spine-like tip turned outward; phyllaries ca 6, membranaceous, not armed at apex *Spiracantha cornifolia* H.B.K.

Leaves not white-tomentose below, the lowermost largest, markedly decreasing in size toward apex of plant; pappus bristles long and straight or folded:

- Compounded heads globose or hemispheroid, subtended by ovoid bracts; leaves densely soft-pubescent below *Elephantopus mollis* H.B.K.
- Clusters of heads \pm cylindroid or ellipsoid; leaves sparsely pubescent below, the surface punctate *Pseudoelephantopus spicatus* (Aubl.) C. F. Baker

◆ Individual heads free, not clustered into distinct glomerules or compounded:

Plants weak herbs, usually less than 1 m tall; flowers purplish or greenish; phyllaries in 1 long series (plus a shorter set in *Erechtites*), thin and linear; plants often more than 1 cm high; leaves often deeply lobed along their lateral margins:

- Flowers purplish; phyllaries in 1 series; achenes 5-angled; plants abundant *Emilia sonchifolia* (L.) DC.
- Flowers greenish-yellow; phyllaries in 2 series; achenes 10-angled; plants rare or possibly absent *Erechtites hieracifolia* (L.) Raf. var. *cacalioides* (Spreng.) Griseb.

Plants shrubs or herbs, usually more than 1 m tall (except *Conyza apurensis*, *Pluchea odorata*, and *Vernonia cinerea*); flower color various; phyllaries in several series, less than 7 mm long; leaves usually entire to toothed but never deeply lobed along their lateral margins (*Neurolaena lobata* sometimes with a pair of lobes near base):

- Plants usually less than 1.5 m tall; leaf blades obovate or oblanceolate to spatulate:
 - Flowers white to yellow; heads with both disk and ray flowers; leaf blades \pm sparsely pubescent on both surfaces *Conyza*
 - Flowers violet to pink or purple; heads with or without ray flowers:
 - Ray flowers present; leaf blades \pm granular-puberulent . . . *Pluchea odorata* (L.) Cass.
 - Ray flowers absent; leaf blades densely pubescent below with \pm matted trichomes *Vernonia cinerea* (L.) Less.

Plants usually more than 1.5 m tall; leaf blades usually not obovate:

- Flowers yellow; plants large erect herbs, usually 1.5–2.5 m tall; leaf blades markedly serrate, often lobed to near base *Neurolaena lobata* (L.) R. Br.
- Flowers white or pinkish to lavender; plants erect or arching shrubs; leaf blades \pm entire (not markedly serrate or lobed):
 - Leaf blades entire, 3-veined; stems and branches prominently ribbed throughout; plants dioecious *Baccharis trinervis* Pers.
 - Leaf blades pinnately veined, often serrate or denticulate; stems not conspicuously ribbed; plants bisexual *Vernonia*

● Leaves opposite (the uppermost sometimes alternate):

■ Pappus of numerous bristles or plumose bristle-like scales:

Heads with both ray and disk flowers; plants small white-flowered herbs; pappus of plumose bristle-like scales:

- Ray flowers conspicuous; paleae present; pappus of plumose bristles; plants herbaceous *Tridax procumbens* L.
- Ray flowers inconspicuous; paleae lacking; pappus lacking; plants shrubs *Clibadium*

Heads with only disk flowers (including *Clibadium*, with inconspicuous ray flowers):

- Plants vines; phyllaries 4; heads of 4 flowers *Mikania*

Plants erect or arching shrubs or herbs; phyllaries more than 5; heads of many flowers:

- Leaf blades broadest at about the middle:
 - Leaves petiolate, the blades not decurrent onto petiole and not extending onto stem *Koanophyllon wetmorei* (B. L. Robinson) King & H. Robinson
 - Leaves sessile, amplexicaul (the leaf tissue extending onto stem) *Ayapana elata* (Steetz) King & H. Robinson

Leaf blades broadest below the middle:

- Plants small annuals, seldom more than 1 m tall; heads ca 4 mm high (to 6 mm in *F. sinclairii*) *Fleischmannia*

Plants much larger, stout herbs or shrubs; heads usually more than 6 mm high:

Leaves glabrous or sparsely pubescent on lower surface, entire or with a few, widely spaced teeth; plants slender arching shrubs:

- Heads cylindrical, usually less than 4 mm wide; flowers lavender to white; lower blade surface with round, yellow, raised, glandular dots *Chromolaena odorata* (L.) King & H. Robinson

- Heads discoid, usually 6 mm or more wide; flowers usually violet; lower blade with glandular dots lacking or at least not yellow, globular, and raised *Heterocondylus vitalbis* (DC.) King & H. Robinson

Leaves usually densely pubescent on lower surface, regularly and closely dentate or serrate; plants herbaceous:

- Flowers greenish-yellow; blades usually not cordate at base, the margins dentate with mucronate teeth *Schistocarpha oppositifolia* (O. Kuntze) Rydb.
- Flowers greenish-white; blades cordate at base, the margins crenate *Hebeclinium macrophyllum* (L.) DC.

■ Pappus not as above:

Plants ± woody shrubs (sometimes scandent):

Flowers white; pappus lacking *Clibadium surinamense* L.

Flowers yellow or orange; pappus various:

Pappus lacking; fruits globose, ± fleshy at maturity; phyllaries acute at apex; ray flowers present; heads with paleae; plants often scandent *Wulffia baccata* (L.f.) O. Kuntze

Pappus of scarios linear scales; fruits narrowly turbinate, not fleshy; phyllaries blunt to rounded at apex; ray flowers lacking; heads lacking paleae; plants erect

. *Calea prunifolia* H.B.K.

Plants herbaceous, sometimes large:

Leaves pinnately lobed, the lobes several; flowers white; herbs often more than 3 m tall

. *Verbesina gigantea* Jacq.

Leaves not pinnately lobed:

Disk flowers white (sometimes pale yellow):

Plants nearly glabrous; pappus of 2 or 3 bristles or lacking; ray flowers lacking or few

. *Spilanthes alba* L'Hér.

Plants asperous (rough to touch), conspicuously pubescent:

Leaves oblong-lanceolate to linear, less than 2.5 cm wide; heads with minute ray flowers; anthers whitish *Eclipta alba* (L.) Hassk.Leaves mostly ovate, often with hastate lobes, more than 3 cm wide; heads lacking ray flowers; anthers black *Melanthera aspera* (Jacq.) Small

Disk flowers yellow:

Heads chiefly axillary, sessile or short-pedunculate:

Plants usually erect; heads very congested in axils, usually sessile; ray flowers present; achenes of 2 types, ± flattened, with spines around the entire margin or with 2 spines at apex *Synedrella nodiflora* (L.) Gaertn.Plants often decumbent, weak-stemmed; heads loose, often somewhat pedunculate; ray flowers absent; achenes ± turbinate, muricate, several-sided; pappus a small crown *Eleutheranthera ruderalis* (Sw.) Schultz-Bip.

Heads mostly terminal or at least appearing so, the peduncles 1–10 cm long:

Petioles obscure, the blades decurrent along petiole and ± ensheathing stem; plants often decumbent or at least rooting at lower nodes; heads usually to 2.5 cm wide (including ray flowers); inner phyllaries not enveloping achenes

. *Wedelia trilobata* (L.) Hitchc.

Petioles obvious, slender; plants erect, not reclining and rooting at nodes; heads less than 2 cm wide:

Achenes enclosed in subtending phyllaries; pappus lacking; involucre biseriate; blades gradually attenuate at base; plants usually less than 1 m tall

. *Melampodium divaricatum* (L. C. Rich.) DC.Achenes not enclosed in subtending phyllaries; pappus a crownlike cup; involucre not biseriate; blades truncate to abruptly attenuate at base; plants commonly more than 1 m tall *Baltimora recta* L.

this nature occur in weedy situations, which are not so common on BCI. Several species occurring there, however, are probably epizoochorous: *Elephantopus mollis*, *Pseudoelephantopus spicatus*, *Spiracantha cornifolia*, and *Synedrella nodiflora*. *Elephantopus* and *Pseudoelephantopus* have a modified pappus capable of becoming entangled in hair. *Synedrella nodiflora* has the pappus or the entire lateral margin of the achene modified with bumpy projections for epizoochorous dispersal. The diaspore of *Spiracantha cornifolia* is probably a glomerule of several one-flowered heads, which acts like a sandbur rather than individual heads. The inflorescence of *Rolandra fruticosa* breaks up at maturity into small, one-seeded heads. These are dispersed perhaps in part by wind or birds (by endozoochory), but may also be epizoochorous by the action of their awnlike bracts. Similarly, the achenes of *Melanthera aspera* may be dispersed by their

sharp scalelike chaff. *Eclipta alba* lacks a pappus, but the achene itself is viscid and becomes sticky upon wetting (Ridley, 1930). *Wulffia baccata* is endozoochorous and probably bird dispersed.

Approximately 950 genera and 20,000 species; cosmopolitan.

AYAPANA Spach

Ayapana elata (Steetz) King & H. Robinson, *Phytologia* 27:235. 1973

Eupatorium elatum Steetz

Herb, 1–2 m tall, branched many times, sparsely short-pubescent. Leaves mostly opposite, sessile, amplexicaul; blades narrowly lanceolate to oblanceolate, acuminate, narrowed to base and sometimes auricled and clasping

BALTIMORA L.**Baltimora recta** L., Mant. Pl. Altera 228. 1771

Polygamous herb, to 3 m tall, \pm strigose on all parts. Leaves opposite; petioles 8–70 mm long; blades \pm ovate, acuminate, truncate to abruptly attenuate at base, 2.5–15 cm long, 1.5–12 cm wide. Inflorescences terminal racemes or more often large panicles; peduncles 8–33 mm long; heads 7–22 mm diam, 5–8 mm long; phyllaries 3–6, 3.5–6 mm long, ciliate at apex; paleae 3.5–4.2 mm long; ray flowers yellow, 3–8, pistillate, fertile, the ligule 4–6 mm long, the pappus a small crown; disk flowers 16 or more, bisexual, partly fertile, yellow, ca 2.5 mm long, the anthers with the appendage truncate. Achenes 2.4–3.2 mm long, truncate and puberulent at apex; pappus a crownlike cup. *Kenoyer 593*.

Collected once on Orchid Island; not seen in recent years, but very weedy and likely to occur sporadically in clearings and along the shore. Flowers and fruits throughout the year, especially at the beginning of the dry season (December to January).

Mexico to Panama. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Chiriquí, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Herrera and Coclé, from premontane moist forest in the Canal Zone, from premontane wet forest in Veraguas, and from tropical wet forest in Colón.

CALEA L.**Calea prunifolia** H.B.K., Nov. Gen. & Sp. 4:294, t. 406. 1820

Escobilla

Shrub, to 2.5 (5) m tall. Leaves opposite; petioles scabrous, to 1.5 cm long; blades ovate, acute at apex, obtuse to truncate at base and decurrent onto petiole, 4–8 (10) cm long, 2.5–5 (6.8) cm wide, rugose, scabrous especially on veins, asperous on both surfaces. Inflorescences axillary or terminal, corymbiform or umbellate; heads discoid, (3)8–10 mm long; phyllaries in several series, blunt to rounded at apex, often concave submarginally, the margins scarios, the outer series ovate-oblong to rounded, the innermost oblong, glabrous or scattered-hirtellous, 4.8–6.6 mm long; ray flowers lacking; disk corollas yellow, to 6.5 mm long, 5-lobed, the anthers syngenesious, becoming exserted and often directed to one side of flower, the pollen bright yellow, the style exserted, 2-forked, its branches inconspicuously papillate outside. Achenes narrowly turbinate, subterete to angular, black, pubescent, 1.3–3 mm long, with a distinct carpodium 0.5 mm long; pappus shorter than corolla, paleaceous; scales narrow, uniseriate. *Croat 12278*.

Occasional, on the shore of Orchid Island and on the shore near Front #8 Lighthouse. Flowers throughout the rainy season and in the early dry season, from June to February. The fruits may be present until June.

stem at base, 8–25 cm long, 1–5 cm wide, with yellowish, globular, viscid glands on lower surface. Panicles large, terminal, open, corymbose; heads ca 5 mm long, short-pedunculate, bearing many flowers; phyllaries 2–6 mm long, in 2 or 3 series; ray flowers lacking; disk flowers bisexual, white or greenish, the anthers syngenesious, the style shortly exserted. Achenes oblong, ca 1.7 mm long, 4- or 5-angled, sparsely hirtellous on angles; pappus of many, long, whitish bristles. *Croat 9554*.

Occasional along the shore. Flowers and fruits in the dry season (February to April).

Costa Rica, Panama, and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá and from premontane wet forest in Coclé and Panamá.

See Fig. 545.

BACCHARIS L.**Baccharis trinervis** Pers., Synops. Pl. 2:423. 1807

Santa María

Dioecious, slender, arching shrub, to 3 (4) m tall; branches usually scandent; stems closely ribbed, sparsely pubescent. Leaves alternate; petioles short, canaliculate; blades lanceolate-oblong, acuminate, acute to obtuse at base and decurrent onto petiole, 3–10 cm long, 1.5–3.5 cm wide, usually almost glabrous; veins at base 3. Inflorescences terminal or axillary, of compact rounded corymbs at ends of branches; heads 5–7 mm long, discoid, bearing many flowers; phyllaries in several series, ovate to oblong, the apex scarios and ciliate; receptacle convex, conical, 1–2 mm wide, muricate; ray flowers lacking; disk flowers unisexual, greenish-white, with faint fragrance, the paleae 2–4 mm long, deciduous; staminate flowers with the corolla thick, tubular, ca 3.5 mm long, equaling or exceeding pappus, deeply 5-lobed, reflexed at anthesis, the stamens syngenesious, white, becoming slightly exserted, the style stout, the ovary reduced, sterile; pistillate flowers with the corolla very slender, ca two-thirds to three-fourths as long as paleae, the lobes reduced to glandular trichomes, the style slender, bifurcate near apex, almost equaling pappus. Achenes slender, sparsely to densely pubescent; pappus of many whitish bristles. *Croat 7221*.

Frequent at the edges of clearings and along the shore. Flowers and fruits throughout the year.

The flowers are visited by the bees *Trigona cupira* and *T. tataira*.

Southern Mexico south to Argentina (but not east to Venezuela). In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Colón, Veraguas, Los Santos, Herrera, and Darién, from premontane dry forest in Coclé, from tropical dry forest in Los Santos, Herrera, Coclé, and Panamá, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Coclé and Panamá.



Fig. 545. *Ayapana elata*

Fig. 546. *Chromolaena odorata*



Costa Rica to Colombia. In Panama, ecologically variable, but known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién; known also from tropical dry forest in Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in the Canal Zone, Panamá, and Darién, and from tropical wet forest in Colón (Portobelo) and Veraguas.

CHAPTALIA Vent.

Chaptalia nutans (L.) Polak., *Linnaea* 41:582. 1877

Polygamous erect herb, to 80 cm tall; lower leaf blades and the usually solitary scape densely white-arachnoid-pubescent. Leaves 3–6, all basal; petioles clasping; blades \pm lyrate-lobed, much narrowed basally, decurrent onto petiole, 5–10 (34) cm long, 1.5–3 (10) cm wide, the upper surface glabrous. Scape usually nodding at apex, to 60 cm high, bearing a single head 2.5–3 cm long; ray flowers inconspicuous, pistillate, very slender, red-purple, well exceeding the pappus, the styles \pm equaling the pappus; disk flowers bisexual, white, the tube slender, equaling pappus, the anthers syngenesious, not protruding from the tube, the style only slightly emergent from anthers, the stigmas very short. Achenes turbinate, the seminiferous part less than 4 mm long, tapered above into a slender projection; pappus of many bristles, 12–15 mm long, those of the disk flowers longer than those of the ray flowers. *Croat 9205*.

Common in the Laboratory Clearing; seldom seen elsewhere. Flowers and fruits throughout the year.

Southern United States to Argentina; West Indies. In Panama, ecologically variable; known most commonly from tropical moist forest all along the Atlantic slope and in Chiriquí, Los Santos, Herrera, Panamá, and Darién; known also from tropical dry and premontane moist forests in the Canal Zone, from premontane wet forest in Chiriquí, Los Santos, Coclé, and Panamá, and from tropical wet forest in Chiriquí and Panamá.

CHROMOLAENA DC.

Chromolaena odorata (L.) King & H. Robinson,

Phytologia 20:204. 1970

Eupatorium odoratum L.

Christmas bush, Hierba de chiva, Paleca

Slender arching shrub, to 2.5 (3) m tall; branches decussate; stems nearly glabrous to villous, sometimes reddish-brown. Leaves opposite, petiolate; blades \pm rhombic-ovate, acuminate, rounded to cuneate at base, 4–8 (10) cm

long, 2–5.5 cm wide, almost glabrous above, sparsely pubescent below with viscid globular glands (especially conspicuous on dry specimens), the margins coarsely toothed. Inflorescences corymbs, terminating the upper branches, bearing many flowers; heads cylindrical, 7–9 mm long, usually less than 4 mm wide; phyllaries in several series, to 7 mm long and 3.5 mm wide, 3-veined, rounded or acute; ray flowers lacking; disk flowers bisexual, lavender to white, fragrant, the corolla ca 5 mm long, only slightly exceeding the pappus, the lobes papillate-puberulent inside, the filaments fused to basal half of corolla tube, the anthers syngenesious, the style lavender, long-exserted after anthesis, bifurcate much of its length, the distal end papillate. Achenes oblong, 5-ribbed and angular, 4–5 mm long, slightly strigose on ribs; pappus of long white bristles. *Croat 7789*.

Abundant in clearings. Flowers and fruits throughout the dry season, especially from December to February. The fruits may persist until July.

Distinguished by the long-exserted style and long cylindrical heads. The styles perhaps serve the same attracting function as ray flowers, which the flowers lack. Some plants investigated appeared to have no pollen in the anthers even while in bud.

Florida and Texas to Paraguay; West Indies; West Africa; Malaya. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Los Santos, Herrera, Coclé, and Panamá, from premontane moist forest in the Canal Zone, Coclé, and Panamá, from premontane wet forest in Bocas del Toro, Colón, Chiriquí, Veraguas, Coclé, and Panamá, and from tropical wet forest in Colón and Panamá.

See Fig. 546.

CLIBADIUM L.

Clibadium asperum (Aubl.) DC., *Prodr.* 5:506. 1836

Shrub, 1.5–3 m tall; stems densely strigillose. Leaves opposite (or sometimes alternate at branch nodes), asperous; petioles 1.5–7 cm long, strigillose; blades ovate to lanceolate-elliptic, acuminate at apex, attenuate at base, 6–22 (28) cm long, 3–10 cm wide, moderately strigillose on both surfaces, denser on the veins, the margins serrate. Inflorescences corymbose panicles; peduncles 1–2 mm long; heads 4–5 mm long; phyllaries 7–10, ovate to obovate, 3–4 mm long, 2–3 mm wide; paleae lacking; ray flowers 5–9, the corollas 3-lobed, 1.5–2.2 mm long; disk flowers 9–22, the corollas 2.5 mm long, pubescent outside, the anthers 1.3 mm long, villous at least near apex.

KEY TO THE SPECIES OF CLIBADIUM

- Lower surface of leaves with conspicuous reticulate veins, hispid *C. surinamense* L.
 Lower surface of leaves not with conspicuous reticulate veins, glabrate to strigose
 *C. asperum* (Aubl.) DC.

Achenes 1.7–2 mm long, ca 1.5 mm diam, puberulent at apex; pappus lacking. *Croat 12283*.

Apparently rare; collected many years ago by Bailey and found recently on the west side of Orchid Island. Flowers and fruits principally from May to September, occasionally during the rest of the year.

Panama to northern South America. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Chiriquí, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, and from tropical wet forest in Colón and Panamá.

Clibadium surinamense L., Mant. Pl. Altera 294. 1771

Mastranzo de monte

Functionally monoecious shrub, 1–2.5(6) m tall, densely hispidulous to scabrous, the trichomes coarse and erect; stems often mottled with purple. Leaves opposite, asperous; petioles 5–20 mm long; blades ovate-oblong, acute at apex, obtuse to rounded at base, 5–17 cm long, 2.5–8(10) cm wide, scabrous above, ± pilose below, crenate-serrulate; reticulate veins prominently raised. Inflorescences terminal corymbs; heads often secund, sessile, 4–7 mm long; phyllaries 8 or 9, obovate, 3–5 mm long, 2–4.8 mm wide, acute or acuminate, closely imbricate, ciliate; flowers white; ray flowers 3–5, functionally pistillate, lacking stamens, the corolla 3- or 4-lobed, 2–2.7 mm long, the style divided nearly to base, exerted at anthesis while the head appears immature and the disk flowers are still closed; disk flowers 11–14, functionally staminate, the corolla 2.5–3.3 mm long, broadened above, densely pubescent especially on lobes, the anthers syngenesious, the ovary sterile, the style simple, protruding from corolla with anthers. Achenes thick, rounded-obovoid, 2-edged, glabrous except for densely villous apex, black, to 3 mm long; pappus lacking. *Croat 6238, 12584*.

Occasional, on the shore, particularly on the northern edge of the island. Flowers and fruits principally in the rainy season (May to December), but occasionally throughout the rest of the year.

Easily distinguished by the seemingly rayless white heads and by the black phyllaries at maturity.

Stuessy (1975) reported *Croat 12718* as a collection that intergrades with *C. asperum* and suggested that the two taxa may hybridize.

Though the style of the pistillate flower may still be present when staminate flowers open, the pistillate flowers usually have been pollinated and the achene has begun to enlarge. The plants are visited by a variety of insects, including butterflies, small bees, and wasps.

Achenes lack a pappus for dispersal, but the phyllaries

become black at maturity. Birds may remove the entire, few-seeded head.

Costa Rica south to Peru, Bolivia, and Brazil; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Colón, Chiriquí, Veraguas, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Coclé and Herrera, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí, Veraguas, Coclé, and Panamá.

CONYZA Less.

Conyza apurensis Kunth in H.B.K., Nov. Gen. & Sp. 4:73. 1820

Erigeron spathulatum Vahl

Horseweed

Polygamous weak herb, to 1 m tall (smaller in upland areas); most parts sparsely short-pilose, especially at base of stem; stems often branching, weakly ribbed below each leaf. Leaves alternate; petioles slender and narrowly winged on lower leaves, reduced near apex of plant; blades spatulate, rounded at apex, cuneate toward the base, sparingly to densely pilose on both surfaces, strigose on veins below, thin, crenate in apical half, otherwise entire, ciliate, the lower leaves to 12 cm long, and 5 cm wide, becoming gradually smaller toward apex of plant, the upper leaves to 5 cm long and 1 cm wide. Panicles terminal, open, bearing many flowers, with leafy bracts; peduncles slender, 5–25 mm long; heads ± convex, to 4 mm across; phyllaries linear, imbricate, mostly subequal but with a few forming another series, 3–4 mm long, sharply acute or acuminate, sparsely pilose with long weak trichomes, the margins scarious; ray flowers white, pistillate, many, in about 2 series, filiform, ca 2 mm long, inconspicuous, barely exceeding the pappus, the style long-exserted; disk flowers white, bisexual, ca 3 mm long, shallowly 5-lobed, the anthers ca 0.5 mm long, with narrow deltoid appendages at apex, obtuse, the style branches flattened. Achenes compressed, the margins ± thickened by 2 prominent veins, moderately pubescent; pappus of fine strigillose bristles in 1 series, about as long as disk flowers. *Croat 8676*.

Rare; collected at the Laboratory Clearing. Flowers and fruits principally in the early rainy season (April to July).

Large, lowland specimens of *C. apurensis* may be confused with *C. bonariensis*. However, the larger receptacle of *C. apurensis* distinguishes it.

Native to Asia; wide-ranging through tropical America.

KEY TO THE SPECIES OF CONYZA

- Receptacle to 4 mm across; phyllaries 3–4 mm long; leaves crenate in upper half *C. apurensis* Kunth
 Receptacle 2–2.5 mm across; phyllaries 4–6 mm long; leaves entire to sparingly toothed *C. bonariensis* (L.) Cronq.

In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Los Santos, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Darién.

***Conyza bonariensis* (L.) Cronq., Bull. Torrey Bot.**

Club 70:632. 1943

Erigeron bonariensis L.

Tabaquillo

Coarse erect herb, to 1.5 m tall, sparingly branched; most parts sparsely short-pilose; stems striate, green. Leaves alternate, sessile or sometimes with a petiole-like region; blades oblanceolate, rounded to acute, cuneate at base, 6–9 (12) cm long, 1–3 cm wide, largest at base of plant, strigose to glabrate on midrib below, thin, entire to sparingly toothed, ciliate. Panicles terminal, open, bearing many flowers, with leafy bracts; peduncles slender, 5–35 mm long; phyllaries imbricate in ca 2 series, 4–6 mm long, sharply acute or acuminate, sparsely pilose with long weak trichomes, the margins scarious; heads flat or \pm convex, 2–2.5 mm diam; ray flowers pistillate, very numerous, white, capillary, inconspicuous, 3–4.5 mm long; disk flowers bisexual, few, yellow, 2–3 mm long, clearly differentiated about halfway up into a slender, cylindrical limb, shallowly and acutely 5-lobed, the anthers ca 0.8 mm long, narrowly appendaged above, basally auriculate, the style branches broadly flattened, with deltoid appendages. Achenes compressed, ca 1 mm long, pubescent especially toward base, the margins \pm thickened by 2 prominent veins; pappus of fine, strigillose bristles in 1 series, ca 1.5 mm long. *Bailey 363 (BH)*.

Collected once by Bailey near the laboratory. Apparently flowers and fruits principally in the early rainy season (April to September).

Confused with large plants of *C. apurensis*, which have a receptacle to 4 mm diam.

Nearly cosmopolitan in distribution; Cuatrecasas indicated that it may be native to Argentina (1969). In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Los Santos, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí and Panamá, from premontane rain forest in Coclé (Cerro Pilón), from lower montane wet forest in Chiriquí, and from lower montane rain forest in Chiriquí (Cerro Horqueta).

ECLIPTA L.

***Eclipta alba* (L.) Hassk., Pl. Jav. Rar. 528. 1848**

E. prostrata (L.) L.

Polygamous herb, usually more than 75 cm tall but rarely to 1 m, often epiphytic; stems somewhat succulent, usually weak; all parts except flowers appressed-pubescent with stiff white trichomes. Leaves opposite, sessile; blades lanceolate, acute, tapering to base, 5–10 (16) cm long, 1–2.6 cm wide, subtire to serrulate. Heads 1 to several,

axillary, campanulate and ca 5 mm wide in flower, becoming green, cushion-shaped, and to 1 cm wide in fruit; peduncles 1–4.5 cm long, slender; flowers interspersed with paleae, the paleae slender, \pm equaling flowers, bristled near apex; ray flowers pistillate, white, ca 1.5 mm long; disk flowers bisexual, ca 1 mm long, \pm campanulate, 4-lobed, pale yellow to whitish, the stamens syngenesious, the filaments free below, the anthers dark, included, the style branches short, slightly exerted. Achenes 2–4-sided, ca 2.5 mm long, white becoming brown, muricate; pappus reduced to an irregular crown. *Croat 9562*.

Occasional, along the shore, often epiphytic on debris or on tree stumps in the lake. Flowers and fruits throughout the year.

Widespread in the tropics and subtropics. In Panama, known from tropical moist forest all along the Atlantic slope and in the Canal Zone, Chiriquí, Los Santos, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

ELEPHANTOPUS L.

***Elephantopus mollis* H.B.K., Nov. Gen. & Sp. 4:26. 1820**

Bushy perennial herb, mostly 30–150 cm tall; branches few. Leaves alternate, chiefly cauline but near base of stem; petioles obscure, ciliate, clasping at base; blades oblong to obovate or oblanceolate, \pm acute at apex, gradually tapered to decurrent base, to 25 cm long and 8 cm wide at base, resin-dotted, sparsely appressed-pubescent above, densely soft-puberulent below, crenate. Inflorescence a solitary, terminal, corymbose panicle, branched many times; glomerules ca 1 cm long, 1–2 cm wide, with ca 40 heads, compounded at the ends of branches and subtended by ovate bracts; heads discoid, slender, ca 1 cm long, 4-flowered; phyllaries 8, in 2 series; ray flowers lacking; disk flowers bisexual, the corolla 4–5 mm long, white, 5-lobed, the anthers syngenesious, the style weakly barbed outside, emerging from the tube with anthers but elongating beyond them, the short styles recurving. Achenes narrowly turbinate, 2–3 mm long, 10-ribbed, resin-dotted and strigillose; pappus of 5 barbed bristles. *Croat 13155*.

Uncommon, in clearings. Flowers and fruits principally throughout the dry season (January to April).

Throughout the tropics and subtropics of the world. In Panama, very ecologically variable; known from most life zones and all provinces.

ELEUTHERANTHERA Poit. ex Bosc.

***Eleutheranthera ruderalis* (Sw.) Schultz-Bip., Bot. Zeitung (Berlin) 24:165. 1866**

Small herb, to 50 cm tall, frequently creeping; stems 4–6-angulate, short-pilose with white trichomes. Leaves

opposite; petioles to 1 cm long; blades ovate, acute at apex, abruptly attenuate at base, 2–4(6) cm long, 1–2.5(3.5) cm wide, covered with minute, viscid, globular glands, serrate. Inflorescences terminal aggregates of 2–5 heads; heads discoid, ca 1 cm wide, usually solitary or few in axils, short-pedunculate to nearly sessile; phyllaries leaflike, equaling florets, frequently 5 large and 1 smaller; paleae equaling or exceeding corolla; ray flowers usually absent (if present, small and sterile); disk flowers yellow, mostly bisexual, ca 2 mm long, broadened above the narrow base, the lobes short, ovate, acute, bearing fleshy short trichomes inside, the filaments apparently at first syngenesious, becoming recurved and free, included, the style branches minutely bristled, slightly exerted and strongly recurved. Achenes turbinate, to 2.3(3) mm long, usually 4-sided, coarsely muricate and minutely pubescent; pappus cuplike, pubescent, brown. *Croat 7057*.

Seasonally abundant in clearings. Flowers and fruits primarily from June to December.

Texas south to Peru, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Herrera, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí, Coclé, and Panamá.

See Fig. 547.

EMILIA Cass.

Emilia sonchifolia (L.) DC., Prodr. 6:302. 1837

Tassel flower

Erect, weak-stemmed herb, 10–50 cm tall, glabrous or sparsely pubescent. Leaves alternate, to ca 12 cm long, the lower ones spatulate to lyrate-lobed, the upper ones narrowly triangular, sessile, and with the base sagittate-clasping. Panicles irregular, sparsely branched, terminal, slender-pedunculate, ca 1 cm long; heads few; phyllaries uniseriate, thin, somewhat shorter than the flowers; ray flowers usually lacking; disk flowers bisexual, the corolla tubular, 8–12 mm long, purplish, the stamens syngenesious, apparently remaining within corolla tube, the style very minutely papillate outside (apparently not emerging from anthers). Achenes brown, 5-angled, the angles minutely strigillose; pappus of numerous fine bristles. *Croat 9196*.

Common in clearings, especially at the laboratory. Apparently flowers year-round.

Florida and Mexico to Brazil; West Indies. In Panama, ecologically variable; known most commonly from tropical moist forest in the Canal Zone, Bocas del Toro, and Chiriquí; known also from tropical dry forest in Panamá, from premontane moist forest in Herrera, and from

premontane wet forest in the Canal Zone and Colón (mouth of Río Piedras).

ERECHTITES Raf.

Erechtites hieracifolia (L.) Raf. var. *cacalioides* (Fisch. ex Spreng.) Griseb., Fl. Brit. W. Ind. 381. 1861

Polygamous erect herb, to 1(3) m tall, hirsute to glabrate. Leaves alternate, sessile; blades lanceolate to linear-lanceolate, acute to acuminate at apex, auricled and clasping stem at base (especially the lower leaves), 4–12 cm long, 1–4 cm wide, coarsely dentate or incised-lobed. Corymbs pedunculate heads 1–2 cm long; phyllaries linear, ca 1 cm long, uniseriate, sometimes with a few shorter ones at base; ray flowers lacking; disk flowers greenish-yellow, heterogamous, the outer flowers pistillate, very slender, the inner flowers bisexual, tubular, the anthers syngenesious, the style slightly exerted. Achenes linear-oblong, ca 3 mm long, 10-ribbed or -striate, slightly pubescent; pappus of long, soft, white bristles. *Shattuck 757*.

Collected once by Shattuck; not seen in recent years, but to be expected in clearings. Flowering and fruiting to some extent all year, but mostly in the rainy season.

Canada to northern South America; Greater Antilles; central Europe; Hawaii. According to Adams (1972), the typical variety does not occur in Central America. In Panama, var. *cacalioides* is known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, and Darién, from tropical dry forest in Panamá, from premontane moist forest in Panamá, from premontane wet forest in Colón, Chiriquí, Panamá, and Darién, and from tropical wet forest in Panamá.

FLEISCHMANNIA Schultz-Bip.

Fleischmannia microstemon (Cass.) King & H. Robinson, Phytologia 19:204. 1970

Eupatorium microstemon Cass.

Annual herb, 15–100 cm tall; stems and petioles moderately short-villous. Leaves opposite; petioles 5–35 mm long; blades ± ovate, acute to acuminate at apex, abruptly attenuate at base, 1.5–5 cm long, 1–3 cm wide, sparsely strigillose on veins of both surfaces especially below, the surfaces (especially the lower) glandular-dotted, the margins crenate except along lower edge. Inflorescences of terminal or axillary, subcorymbiform panicles; peduncles 2–5 mm long; heads discoid, ca 4 mm long; phyllaries mostly oblong, 1.5–4.5 mm long, 3- or 4-veined, rounded to blunt, glabrous except sometimes weakly pubescent on midrib, usually ciliate and apiculate at

KEY TO THE SPECIES OF FLEISCHMANNIA

- Pedicels 2–5 mm long; heads in narrow corymbiform panicles *F. microstemon* (Cass.) King & H. Robinson
 Pedicels 3–15 mm long; heads in broad open panicles *F. sinclairii* (Benth.) King & H. Robinson

apex; ray flowers lacking; disk flowers bisexual, 5- or 6-lobed, lavender, to 2.5 mm long, slightly longer than pappus, the style branches thick. Achenes prismatic, scarcely constricted near apex, usually blackish with yellowish ribs, the ribs and distal lateral surfaces scabrid; pappus of 25–30 slender bristles. *Standley 31443*.

Collected once in the Laboratory Clearing. Flowers and fruits from June to December, especially in the middle of the rainy season.

Mexico to northern South America; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Panamá (Cerro Azul), and from tropical wet forest in Bocas del Toro and Panamá (Cerro Jefe).

Fleischmannia sinclairii (Benth. in Oerst.) King & H. Robinson, *Phytologia* 19:206. 1970

Eupatorium sinclairii Benth. in Oerst.

Herb, to 1 m tall; stems terete, often branched many times, bearing \pm uncinatate trichomes. Leaves opposite; petioles 1–3 cm long; blades \pm rhombic, mostly acute at apex, acute at base and decurrent onto petiole, 2–5 cm long, 1–3 cm wide, punctate, the upper surface with straight erect trichomes, the lower surface with recurved trichomes on veins, the margins crenate above middle. Panicles lax, open, terminal and upper-axillary; peduncles 3–15 mm long, slender; heads discoid, ca 4–6 mm high; phyllaries in several series, to 5 mm long, the outer acuminate, the inner acute, ciliate near apex; ray flowers lacking; disk flowers bisexual, the corolla ca 2.3 mm long, the tube white, the lobes and style lavender, the stamens syngenesious, included, the style exerted at anthesis. Achenes slender, weakly pubescent, ca 1.3 mm long, 5-striate, bearing a nipple-like projection at base; pappus of numerous awns, \pm equaling or shorter than corolla. *Croat 8934*.

Occasional in clearings. Flowers and fruits from December to June, especially throughout the dry season (December to April).

Mexico to Panama. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Colón, Veraguas, Herrera, Coclé, Panamá, and Darién (no doubt other provinces as well), from tropical dry forest in Darién (Punta Garachiné), from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, Los Santos (Loma Prieta), and Panamá, and from tropical wet forest in Colón.

HEBECLINIUM DC.

Hebeclinium macrophyllum (L.) DC., *Prodr.* 5:136. 1836

Eupatorium macrophyllum L.

Coarse herb, 1–2 m tall; branches striate; young parts densely short-pilose. Leaves opposite; petioles to 5 cm long; blades broadly ovate, acute to acuminate, truncate to cordate at base, 8–13 (15) cm long, 6–12 (20) cm wide, slightly pubescent above, densely woolly below, crenate. Panicles rounded, compact, corymbose; heads 6–7 mm

long, ca 5 mm wide, bearing many flowers; phyllaries lanceolate, to 5 mm long, in many series, the outer shorter; ray flowers lacking; disk flowers bisexual, the corolla greenish-white, ca 2 mm long, the anthers syngenesious; pistillate parts not seen. Achenes oblong, 5-angled, ca 1.2 mm long; pappus of long white bristles. *Aviles 5*.

Not seen in recent years on the island, but probably occurring periodically in clearings. Flowers and fruits from June to February, especially from the middle of the rainy season to the early dry season.

Mexico to Paraguay; West Indies. In Panama, occurring most commonly at middle elevations in premontane wet and tropical wet forests; known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in Panamá and Darién, and from tropical wet forest in Chiriquí, Los Santos, and Panamá.

HETEROCONDYLUS King & H. Robinson

Heterocondylus vitalbis (DC.) King & H. Robinson, *Phytologia* 24:391. 1972

Eupatorium vitalbae DC.

Arching shrub or vine, usually 2–3 (6) m tall; stems glabrous or sparsely pubescent, glabrous in age. Leaves opposite, short-petiolate; blades oblong-ovate, acuminate, obtuse to rounded at base, mostly 5–10 (12) cm long, 3–7 cm wide, glabrous above except on midrib, sparsely pubescent on veins below, entire or the margins remotely toothed in distal two-thirds; basal veins 3–5. Panicles terminal and upper-axillary, bearing few flowers; heads discoid, 1–1.5 cm long, widely spaced; phyllaries glandular, striate, lanceolate-oblong, 7–11 mm long, the outer series much broader than the inner series; ray flowers lacking; disk flowers bisexual, the corolla violet, ca 8 mm long, the anthers syngenesious, remaining in tube, the style long-exserted, white to lavender, minutely papillate outside. Achenes oblong, ca 3.5 mm long, sparsely hispidulous, 5-angulate; pappus of many white bristles \pm equaling corolla. *Croat 8776*.

Occasional, at the edges of clearings. Flowers and fruits principally during the dry season (January to April), rarely as late as June.

Honduras south to Peru, Bolivia, and Brazil. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Chiriquí, Veraguas, Herrera, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Chiriquí, Los Santos, and Panamá, from tropical wet forest in Chiriquí, Panamá, and Darién, and from premontane rain and lower montane moist forests in Chiriquí.

KOANOPHYLLON Arruda

Koanophyllum wetmorei (B. L. Robinson) King & H. Robinson, *Phytologia* 28:67. 1974

Eupatorium hypomalacum var. *wetmorei* B. L. Robinson

Slender erect shrub, 2–3 (5) m tall; stems crisp-pubescent and with viscid, \pm globular glands. Leaves opposite; petioles 10–20 cm long; blades broadly to narrowly



Fig. 547.
Eleutheranthera
ruderalis



Fig. 548.
Koanophyllon
wetmorei



Fig. 549.
Mikania
leiostachya

elliptic, long-acuminate, gradually tapered to base and decurrent onto petiole, 8–20 cm long, 2.6–5(6.5) cm wide, glabrate or weakly pubescent and densely covered with viscid, \pm globular glands on lower surface, sparsely serrate. Inflorescences paniculate, terminal, bearing many flowers; heads discoid, 5–6 mm high; phyllaries in several series, sharp-pointed, 2–5 mm long; ray flowers lacking; disk flowers bisexual, the corolla white, tubular, the lobes small, the anthers syngenesious, remaining in tube, the stigmas papillate outside, long-emergent after anthesis. Achenes narrowly turbinate, sharply angled, very sparsely pubescent, ca 2 mm long; pappus of numerous bristles. *Croat 13273.*

Uncommon along the shore and occasional southwest of Slothia Island on shaded shores. Flowers from the late rainy season through the dry season (November to April).

Panama and adjacent Costa Rica. In Panama, known from tropical moist forest in the Canal Zone (BCI) and in Bocas del Toro and from premontane wet forest in Panamá.

See Fig. 548.

MELAMPODIUM L.

Melampodium divaricatum (L. C. Rich.) DC., Prodr. 5:520. 1836

Polygamous annual herb, usually less than 1 m tall; stems sparsely pubescent, occasionally with purple longitudinal lines. Leaves opposite, petiolate; blades lanceolate to rhombic-ovate, acute to acuminate at apex, cuneate to attenuate and decurrent onto petiole at base, mostly 6.5–15 cm long, 2–7.5 cm wide, scabrous above, sparsely hispid below, the margins usually inconspicuously toothed; basal veins 2, arcuate, ascending, intersecting other lateral veins. Heads solitary, terminal, 10–17 mm wide; peduncles 2–8.5 cm long; flowers yellow; phyllaries in 2 series, the outer 4 or 5, rounded, imbricate, ciliate, the inner not bractlike, enveloping achene; ray flowers pistillate, rounded or emarginate at apex, 4.5–6 mm long, 3–3.5 mm wide, often with green lines on lower surface; disk flowers bisexual (the ovaries abortive), ca 2.7 mm long, each subtended by a fimbriate-margined palea. Achenes 2.8–4 mm long, the lateral surfaces with diagonal striations and enlarged margins; pappus lacking. *Croat 7680.*

Often abundant in the Laboratory Clearing, less frequent in other clearings. Flowers and fruits throughout the year.

According to T. Stuessy (pers. comm.), seeds may fall to the ground and germinate rapidly. Since plants are self-fertile, they are provided with the capability of rapid colonization of an area.

Southern Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Coclé and Panamá.

MELANTHERA Rohr

Melanthera aspera (Jacq.) Small, Bull. Torrey Bot. Club 36:164. 1909

Clavellina de monte, Julio, Sirvulaca

Widely branching herb, to ca 1 m tall; stems weakly ribbed, asperous, with appressed trichomes. Leaves opposite, petiolate; blades elliptic to ovate, acuminate, mostly 5–12 cm long, 2.5–6.5 cm wide, asperous, the trichomes \pm appressed, the margins crenate, the larger leaves abruptly narrowed and decurrent onto petiole, often hastate-lobed at base; basal veins 3. Heads solitary (or few), terminal or upper-axillary, discoid, long-pedunculate, bearing many flowers; phyllaries ovate, unequal, in 2 or 3 series; ray flowers lacking; disk flowers bisexual, developing centripetally, the outermost falling before the innermost open, ca 4.7 mm long, each subtended by an oblong, acute, keeled scale, the corolla white, ca 6 mm long, narrowed at base, the stamens syngenesious, the filaments free almost to base, the anthers black, shedding pollen in bud, emerging somewhat from tube, later receding as the filaments shrivel, the connective white, the style elongating simultaneously, carrying pollen with it on the bristled outer surface of stigmas, opening and recurving only after emerging from anthers, the nectary prominent, yellow. Achenes slender, angled, ca 3 mm long, glabrous, truncate at apex; pappus of a few, short, barbed awns. *Croat 12886.*

Probably once abundant, now uncommon, occurring sporadically in clearings. Flowers and fruits throughout the dry season (December to April).

The mature heads become loose, and the sharply pointed phyllaries, which often envelop the much shorter achenes at their base, may attach the seeds to passing animals.

Florida and Mexico to northern South America in areas bordering the Caribbean; West Indies. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Los Santos and Panamá, from premontane wet forest in Bocas del Toro (Río Guarumo), Colón, Chiriquí, Veraguas, Coclé, and Panamá, and from tropical wet forest in Bocas del Toro (Santa Catalina), Colón, and Coclé (Boca de Toabré).

MIKANIA Willd.

Mikania guaco H. & B., Pl. Aeq. 2:84. 1809

Herbaceous vine or slender liana. Leaves opposite, petiolate; blades ovate, acute or acuminate, acute and decurrent at base, 6–13(25) cm long, 3.5–10(15) cm wide, nearly glabrous or scabrous, \pm entire. Heads in large paniculate cymes, 4-flowered, ca 1 cm long; phyllaries 4, oblong, 4–6 mm long, rounded at apex, puberulent; ray flowers lacking; disk flowers bisexual, white or greenish-yellow, the anthers syngenesious, the style exserted, forked, its

KEY TO THE SPECIES OF MIKANIA

- Heads spicate, evenly disposed on the elongated branches of open panicles *M. leiostachya* Benth.
 Heads not spicate, conspicuously clustered in globular or flat-topped clusters:
 Blades cordate at base *M. micrantha* H.B.K.
 Blades not cordate at base:
 Phyllaries usually less than 3 mm high; heads in glomerulate, \pm globular corymbs
 *M. tonduzii* B. L. Robinson
 Phyllaries 4–5 mm high; heads in flat-topped or \pm globular corymbs:
 Heads almost all in groups of 3, often in flat-topped corymbs; style appendages hirsute with
 long papillae; style base papillose *M. guaco* H. & B.
 Heads not in groups of 3, in glomerulate, \pm globular corymbs; style appendages not hirsute,
 with short papillae; style base glabrous *M. hookeriana* DC.

branches long, hirsute. Achenes oblong, 4- or 5-angled, ca 2 (4) mm long, glabrous; pappus tan to reddish, of slender bristles ca 5 mm long. *Wilson 9 (F)*.

Not seen in recent years on the island, but to be expected. The species probably flowers and fruits in the dry season.

Widely distributed in tropical America from Mexico to Peru, Bolivia, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Chiriquí.

***Mikania hookeriana* DC.**, Prodr. 5:195. 1836

Slender liana; stems terete, striate, slightly puberulent to sparsely hirsute. Leaves opposite; petioles 1–5 cm long, canaliculate; blades ovate to broadly ovate or ovate-elliptic, rounded to acuminate at apex, rounded to cuneate at base, (3)6–10 (15) cm long, (1.5)3–7 (15) cm wide, sparsely puberulent to glabrate on upper surface, brownish-puberulent on lower surface; major lateral veins with 2 pairs prominent in the basal fourth of blade, the upper pair of these ascending to apex. Panicles terminal or upper-axillary, the branches short; heads 8–9 mm long, in small clusters at the tips of short branches, sessile; phyllaries 4, ca 4 mm long, ca 1 mm wide, sparsely puberulent and glandular on outside, glabrous and paler on inside; corolla whitish, fragrant, 4.5–5.5 mm long, the tube 1–1.5 mm long, the limb narrowly campanulate, the lobes glandular and short-pubescent near the tip; anther appendages ovate-triangular; style base glabrous, the style appendages short-papillate. Achenes 4- or 5-ribbed, ca 3.5 mm long; pappus bristles 40–50, mostly in one series, sharply angled. *Aviles 500, Bangham 597 (US)*.

Rare or perhaps no longer present. The species flowers and fruits mostly from July to September, but a few collections were made in flower and fruit in January and March. Possibly the species flowers twice per year.

Southern Mexico to Peru and Brazil. In Panama, known mostly from wetter forest life zones at medium elevations; known from tropical moist forest on BCI, from premontane wet forest in Colón, Coclé, and Panamá, from tropical wet forest in Colón and Panamá, and from premontane rain forest in Panamá (Cerro Jefe).

***Mikania leiostachya* Benth.**, Pl. Hartweg. 201. 1845

Slender vine; branches nearly perpendicular to axis; stems puberulent and glandular when young, glabrate in age. Leaves opposite; petioles ca 1.5 cm long, moderately puberulent; blades ovate, acuminate, obtuse to rounded (sometimes slightly subcordate) at base, 3.5–12 (18) cm long, 2–6 (11) cm wide, sparsely pubescent below and on veins above, entire. Panicles axillary, to ca 30 cm long, the branches long, strictly spicate; heads discoid, ca 5 mm long, arranged in spikes and evenly disposed on rachis; phyllaries 4, pubescent, ca 3 mm long; ray flowers lacking; disk flowers bisexual, with a strong sweet aroma, the corolla white, shallowly lobed, the tube bent somewhat outward above the phyllaries, the anthers syngenesious, not becoming exserted, the style well-exserted, the outer edges papillate near apex, the stigmas rolling inward after emerging. Achenes \pm oblong, 5-angled, glabrous; pappus bristles many, white, slightly exceeding corolla. *Croat 13245*.

Frequent in the canopy of the forest, occasionally over vegetation near the edge of the lake. Flowers and fruits principally in the dry season (January to April).

The sweet fragrance can be detected at considerable distances.

Honduras to Ecuador. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

See Fig. 549.

***Mikania micrantha* H.B.K.**, Nov. Gen. & Sp. 4:105. ed. fol. 1818

Slender vine; stem weakly pubescent. Leaves opposite; petioles 3–7 cm long; blades ovate-cordate, acuminate, 3.5–13 cm long, 2–8.5 (10) cm wide, glabrate or sparsely pubescent, often glandular-dotted below, coarsely serrate; palmate veins at base 5–7. Heads discoid, 4-flowered, 4–5 (8) mm long, in long-pedunculate, axillary, sub-corymbiform clusters; phyllaries 4, oblong, acute, 3–6 mm long; ray flowers lacking; disk flowers bisexual, the corolla white above constriction, green below, twisted outward above constriction, the stamens syngenesious, exserted at anthesis, the style long-emergent after anthesis, bending outward away from flower, the stigmas pubescent outside. Achenes oblong, ca 2 mm long, 4- or 5-ribbed, with viscid globular dots (at least on dried specimens); pappus of numerous barbellate bristles,

almost equaling corolla. *Croat 12949*.

Uncommon, usually over low vegetation near the edge of the lake and at the edges of clearings; locally very abundant. Flowers and fruits throughout the year, especially in the late rainy and early dry seasons.

The flowers are visited by two different species of *Trigona* bees.

Mexico to northern South America; West Indies. In Panama, widespread and ecologically variable; known from tropical moist forest in all provinces, from tropical dry forest in Los Santos, Herrera, Coclé, and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Colón, Chiriquí, Veraguas, Coclé, Panamá, and Darién, and from tropical wet forest in Bocas del Toro, Colón, Coclé, Panamá, and Darién.

Mikania tonduzii B. L. Robinson, Proc. Boston Soc. Nat. Hist. 31:256. 1904

Stout herbaceous vine climbing into canopy, glabrous to inconspicuously puberulent on stems, petioles, and lower leaf surfaces; internodes elongate. Leaves opposite; petioles 2–4.5 cm long; blades ovate, acuminate to caudate-acuminate, acute to rounded at base and decurrent onto petiole, 6–15 cm long, 3–10 cm wide, bicolorous, plicately veined, the veins 5. Panicles terminal, 30–50 cm long, branched many times, the branches 8–15 cm long; branches, pedicels, and at least the lower part of phyllaries densely and inconspicuously puberulent and glandular-puberulent; heads 7–8 mm long, sessile or nearly so, in branched semicircular clusters; phyllaries 4, rounded at apex, to 2.5 mm long; ray flowers lacking; disk flowers 4, bisexual, ca 4 mm long, greenish, the lobes 5, narrowly acute, the style exerted, its branches to ca 4 mm long. Achenes narrowly oblong, 1.5–2 mm long, prominently ridged; pappus bristles antrorsely barbed, slightly exceeding corolla. *Croat 7972*.

Apparently rare, in the canopy; collected once in February. Seasonal behavior uncertain. Probably flowers in the dry season.

The corolla of this species distinguishes it from other *Mikania* by being narrow and lacking a distinct tube.

Southern Mexico to Panama. In Panama, known only from BCI.

NEUROLAENA R. Br.

Neurolaena lobata (L.) R. Br., Trans. Linn. Soc. London 12:120. 1817
Contragavilana

Coarse herb, usually 1–3 m tall; stems ribbed, appressed-strigose. Leaves alternate; petioles 5–20 mm long; blades oblong-lanceolate, acute to acuminate, gradually tapered to a decurrent and sometimes inequilateral base, 8–23 cm long, 3–6.5 cm wide, appressed-strigose, the lower surface more densely pubescent, glandular, the glands numerous, viscid, round, the margins remotely and sharply toothed (more so on juveniles), the lower leaves deeply trilobate. Panicles large, terminal, corymbose; heads discoid, ca 7 mm long; phyllaries in several series, blunt, 3-veined;

ray flowers lacking; disk flowers yellow, bisexual, each subtended by a thin blunt bract, the tube constricted somewhat below the syngenesious anthers, the anthers and style emerging simultaneously from tube, the stigmas then emerging from anthers and recurving. Achenes oblong-turbinate, ca 1.5 mm long, black, with a constriction near base; pappus of numerous soft bristles in 1 series, shorter than corolla. *Croat 9112*.

Occasional, in brushy places and clearings; one collection from a tree stump in the lake. Flowers and fruits principally in the dry season, December to April (sometimes to June).

Southern Mexico to Colombia, Ecuador, and Peru; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Los Santos, Panamá, and Darién, from premontane moist forest in the Canal Zone (Ancón), from premontane wet forest in Colón, Chiriquí, Coclé, Panamá, and Darién, and from tropical wet forest in Colón, Chiriquí, Coclé, Panamá, and Darién.

PLUCHEA Cass.

Pluchea odorata (L.) Cass. in Levr., Dict. Sci. Nat. 42:3. 1826

P. purpurascens (Sw.) DC.

Polygamous annual herb, 20–90 (120) cm tall, ± granular-puberulent. Leaves alternate; petioles 2–7 mm long; blades ± oblanceolate-elliptic, acute or acuminate at apex, tapering to base, 4–8 cm long, 1.5–3 cm wide, irregularly and often markedly serrate. Inflorescences terminal, subcorymbiform; heads few, closely aggregated, ca 1 cm wide and 1.5 cm high; phyllaries in several series, 4–7 mm long, weakly pubescent outside, glabrous inside, the margins ± scarious and regularly ciliate, the outermost ± ovate, the inner ones mostly oblong-elliptic; flowers pinkish-purple; ray flowers pistillate, in several series, with the corolla filiform, shorter than the style; disk flowers bisexual but mainly sterile, ca 4 mm long, often with the style undivided, the fertile ones with the anthers exerted above the corolla tube at anthesis. Achenes 4- or 5-angled; pappus bristles many, uniseriate, basally united. *Woodworth & Vestal 611*.

Apparently rare, in marshes along the shore. Seasonal behavior not determined. Flowering plants have been collected on BCI in February and July.

Seeds are probably dispersed by both wind and water.

Atlantic and Gulf states in the United States south to Honduras; Panama and Colombia; West Indies. In Panama, adventive; known only from two collections on BCI.

PSEUDOELEPHANTOPUS Rohr

Pseudoelephantopus spicatus (B. Juss. ex Aubl.) C. F. Baker, Trans. Acad. Sci. St. Louis 12:45, 55. 1902

Escobilla blanca, Chicoria

Coarse herb, to 1 (1.2) m tall; stems dichotomously branched, with loose trichomes borne on the bulbous

base. Leaves alternate; petioles short, sheathing; blades narrowly elliptic to obovate, acute at apex, dilated and clasping at base, mostly 6–13 (21) cm long, 1–4 (6) cm wide, hispid above, glabrous to sparsely appressed-pubescent and resin-dotted below, sparsely serrate. Heads sessile, 4-flowered, usually in axillary clusters but often forming long terminal spikes; phyllaries ca 1 cm long, in 4 pairs, sharply pointed; ray flowers lacking; disk flowers bisexual, the corolla deeply 5-lobed, the tube white, 5–6 mm long, the lobes violet, the anthers syngenesious, the filaments united to the tube, the style with antrorse bristles, the stigmas curling up after emerging from anthers. Achenes narrowly obovoid, 5–7 mm long, 10-striate, hispidulous principally on ribs; pappus of 5–15 unequal bristles, 2 of them folded and refolded near apex. *Croat 8565.*

Very abundant in flower and fruit in the Laboratory Clearing, especially in the late rainy season and during the dry season.

Continental tropical America; West Indies; introduced in Africa and eastern Asia. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Los Santos, Panamá, and Darién; known also from tropical dry forest in Panamá, from premontane dry forest in Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá.

ROLANDRA Rottb.

Rolandra fruticosa (L.) O. Kuntze, *Rev. Gen. Pl.* 1:360. 1891
Niagurgin

Tall herb, to 1.5 m, mostly unbranched; stems with long, fine, white trichomes. Leaves alternate; petioles short; blades ovate to elliptic, acute at apex, obtuse to acute at base, 4–11 cm long, 1–5 cm wide, white-woolly below, nearly glabrous above in age, entire. Heads very numerous, glomerate in axils, sessile, the glomerules 1–1.5 cm wide, each head consisting of a single, bisexual disk flower subtended by usually 2 phyllaries, these unequal, coriaceous, straight, with spinelike awns; corolla white, ca 3.5 mm long, the lobes 4, sometimes with greenish tips; stamens 4; filaments united to tube below lobes, not elongating after anthesis; anthers syngenesious, ca 1 mm long, exposed after petals open; style barely forked, elongating and emerging after anthesis; stigmas recurved. Achenes oblong-turbinate, ca 1.5 mm long, 4- or 5-costate, resin-dotted; pappus a minute, lacerate crown. *Croat 8589.*

Occasional, locally common in clearings. Flowers and fruits in the dry season, December to March (sometimes November to April).

Honduras to the Guianas, Peru, and Brazil; West Indies. In Panama, ecologically variable, but principally in wetter areas especially on the Atlantic slope; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Herrera, Panamá, and Darién,

from tropical dry forest in Coclé (Penonomé), from premontane moist forest in the Canal Zone (Ancón Hill), from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, from tropical wet forest in Veraguas (Atlantic slope), Colón, and Panamá, and from premontane rain forest in Panamá (Cerro Jefe).

SCHISTOCARPHA Less.

Schistocarpa oppositifolia (O. Kuntze) Rydb., *N. Amer. Fl.* 34:306. 1927

Hermaphroditic or polygamous, coarse, erect herb, 1–1.5 (3) m tall; branches short-hirsute. Leaves opposite; petioles 3–15 cm long, wing-margined; blades broadly ovate, acuminate, abruptly narrowed to cuneate base and decurrent onto petiole, 10–20 cm long, 4–12 cm wide, densely hirsutulous, dentate, with mucronate teeth. Panicles cymose, terminal and upper-axillary; heads numerous, 6–9 mm high, very short-pedunculate; phyllaries in 3 or 4 series, imbricate, obtuse at apex; paleae 6–7 mm long; ray flowers lacking or minute and pistillate; disk flowers bisexual, yellowish or greenish-yellow, ca 5 mm long, the anthers syngenesious, the style forked. Achenes oblong, ca 1.5 mm long, glabrous, black and shiny; pappus of slender soft bristles ca 5 mm long. *Aviles 16.*

Collected once by S. Aviles; not seen in recent years, but to be expected. Flowering throughout the year, especially in the early rainy season (July and August).

Mexico to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, and Panamá, from premontane wet forest in Colón, Los Santos, Coclé, and Panamá, from tropical wet forest in Colón, and from lower montane wet forest in Chiriquí.

SPILANTHES Jacq.

Spilanthes alba L'Hér., *Stirp.* Nov. 7, t. 4. 1785

S. ocymifolia (Lam.) A. H. Moore f. *radiifera* A. H. Moore

Erect herb, usually to 60 cm tall (rarely less than 10 cm or more than 100 cm); stems spreading-pubescent. Leaves opposite; petioles 5–30 mm long; blades ovate, acute to acuminate, obtuse to rounded and decurrent at base, 1.5–9 cm long, 0.5–5 cm wide, nearly glabrous to sparsely ± appressed-pubescent on both surfaces, dentate to subentire, sparsely appressed-ciliate; lateral veins mostly in 3 pairs, from near base. Inflorescences of 1 or 2 heads emerging terminally, but later in the dichotomies of the stem; peduncles 1.5–10 cm long; heads lenticular to round and finally ovoid, 8–14 mm diam, bearing many flowers; phyllaries lanceolate, ca 8, in 1 or 2 series; paleae ± equaling corolla, yellowish at apex, folded longitudinally to envelop flower; ray flowers yellow, to 1.5 mm long, mostly lacking or few, pistillate; disk flowers numerous, bisexual, the corolla tubular, white, 4–5 mm long, with 5 oblique lobes, minutely papillate-granular inside and out; anthers syngenesious, ca 0.5 mm long, with deltoid appendages; ovary obovate, flattened; style base globose;

style branches yellow or orange. Achenes compressed, oval, black, with a hyaline margin, ca 2 mm long, bearing 2 caducous setae or awns at apex and a dense row of cilia on margin; pappus lacking, or of 2 or 3 weak bristles.

Croat 7782.

Occasional, in the Lighthouse Clearing. Flowers and fruits from November to May, especially during the dry season.

Mexico to Peru, Bolivia, and Brazil. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane dry forest in Los Santos, from tropical dry forest in Panamá, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón.

SPIRACANTHA H.B.K.

Spiracantha cornifolia H.B.K., Nov. Gen. & Sp. 4:28. 1820

Herb, 30–150 (200) cm tall; stems often maroon or streaked with maroon, covered with long loose trichomes. Leaves alternate; petioles 5–15 mm long, basally clasping; blades elliptic, acute, with a stiff spine at apex, obtuse to acute at base, 2–11 cm long, 1–4 cm wide, sparsely pubescent above (glabrate in age), densely woolly below with long straight trichomes on veins. Flower clusters dense, capitate, to 1.5 cm diam, mostly at ends of axillary branches, with 20–25 subsessile glomerules, the lowermost glomerules partially enclosed by leaflike bracts; bracts ovate, ca 2 cm long, membranaceous, with a sharp, horizontally directed mucro ca 1.5 mm long; heads 3–11 per glomerule, bearing 1 flower, developing centripetally, never more than 1 or 2 open at a time, soon falling; phyllaries about 6, imbricate, linear, thin and translucent, ca 4 mm long, unarmed at apex, with conspicuous, silky, white pubescence at base; ray flowers lacking; disk flowers bisexual, the corolla violet, to 4 mm long, deeply 4- or 5-lobed, the anthers syngenesious, 0.9 mm long, basally sagittate, the apical appendage ca 0.3 mm long; style branches 0.3 mm long, glabrate. Achenes obovate, ca 2 mm long (possibly immature), smooth, white; pappus with whitish resin dots on upper edge like those on phyllaries; scales narrow, brownish, ciliate, to 1 mm long. *Croat 11998.*

Locally abundant in the Rear #8 Lighthouse Clearing. Flowers and fruits principally during the dry season.

The plant has been confused with *Rolandra fruticosa*, which also has 1-flowered heads arranged in similar spiny clusters. *Rolandra* differs in having white flowers and usually two coriaceous phyllaries, with the outer one produced into a sharp acumen. *Spiracantha cornifolia* has violet flowers and about six membranaceous phyllaries, which are not spinescent. It is confused, however, because the lowermost glomerules of the inflorescences are partially enclosed by even spinier bracts turned outward.

Belize to Venezuela. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién; known also from tropical dry forest

in Herrera and Coclé, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in the Canal Zone and Panamá, and from premontane rain forest in Panamá.

See Fig. 550.

SYNEDRELLA Gaertn.

Synedrella nodiflora (L.) Gaertn., Fruct. & Sem. Pl. 2:456. 1791

Polygamous erect herb, to 75 (150) cm tall, with appressed white trichomes. Leaves opposite; petioles winged, ciliate, short; blades ovate, acute to acuminate, abruptly or gradually tapered to base and broadly decurrent onto petiole, mostly 2.5–7.5 (10) cm long, 1.5–5 cm wide, rugulose in age, crenate to subentire; basal veins 3. Heads 1 to few, nearly sessile, axillary, to 1 cm long, inconspicuous; phyllaries with the 2 outer pubescent, leaflike, to 1 cm long, exceeding flowers, the inner ones oblong, thin, ciliate; flowers yellow; ray flowers 3–5 (9), ca 5 mm long, inconspicuous, pistillate, anthers lacking, the style forked, equaling ligule; disk flowers bisexual, 6–10 (13), ca 4 mm long, yellow, the corolla lobes short, round, short-pubescent inside, the filaments fused to tube below middle, the anthers syngenesious, black, emerging somewhat from tube, the stigmas heavily antrorse-barbed outside, emerging from anthers. Achenes dimorphic, those of the ray flowers oblong to obovate, much flattened, the body black, 4–4.5 mm long, the margins pale green, the lateral and upper margins bearing 2 fin-shaped scales to 2 mm long; achenes of the disk flowers \pm turbinate, weakly 2-edged, one side with bumpy projections; pappus of 2 or 3 stiff bristled awns to 5 mm long. *Croat 9187.*

Seasonally abundant in clearings, especially at the laboratory. Flowers and fruits principally in the dry season (January to May).

Seeds are probably epizoochorous.

Widespread in the tropics. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Herrera, Panamá, and Darién, from tropical dry forest in Los Santos and Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Bocas del Toro, Colón, Coclé, and Panamá.

TRIDAX L.

Tridax procumbens L., Sp. Pl. 900. 1753

Polygamous, prostrate or erect herb, to 40 cm tall, hirsute, branched from the base, sometimes rooting at nodes. Leaves opposite; petioles short; blades \pm ovate to ovate-lanceolate, acute or acuminate, cuneate at base, 2–6 (12) cm long, 1–4 (6) cm wide, incised-dentate (the basal tooth sometimes very large). Heads to 1 cm diam, solitary, on long terminal peduncles; phyllaries with the 2 outer ovate, green, 6–10 mm long; flowers interspersed with paleae, these acute, maroon-tipped; ray flowers pistillate, white, few, the ligule to 7 mm long, 2- or 3-lobed; disk



Fig. 550. *Spiracantha cornifolia*



Fig. 551.
Verbesina gigantea

VERNONIA Schreb.**Vernonia canescens** H.B.K., Nov. Gen. & Sp.

4:35. 1820

Hierba de San Juan

Arching shrub, usually 2–3 m long, the stems densely \pm appressed-pubescent. Leaves alternate, short-petiolate; blades ovate to ovate-oblong, acuminate, obtuse to rounded at base, 4.5–11 (12) cm long, to 5 cm wide, rugulose and short-pubescent above, densely pilose below especially on veins, the margins entire or remotely denticulate. Panicles terminal or upper-axillary; branches usually long, recurving; heads bell-shaped, 6–7 mm high, widely spaced and chiefly on upper side of branches; phyllaries with the outer ones triangular-subulate, spinose-tipped, the inner ones lanceolate, acuminate, scarious; ray flowers lacking; disk flowers bisexual, developing centripetally, the corolla pale lavender (fading white), the lobes long and slender, tipped on outside with glandular droplets, loosely reflexed after anthesis, the filaments not elongating, the anthers syngenesious, the style densely barbed on outside, the stigmas usually not recurving until totally extended. Achenes narrowly turbinate, ca 2 mm long, 10-ribbed, with ascending white trichomes; pappus bristles many, weakly barbed, shorter than corolla. *Croat 8777.*

Common in clearings; occasional on the shore. Flowers and fruits throughout the dry season (January to May).

Mexico to Colombia, Venezuela, and Peru. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Los Santos, Herrera, and Panamá, from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón and Panamá, from tropical wet forest in Panamá, and from lower montane wet and rain forests in Chiriquí.

Vernonia cinerea (L.) Less., *Linnaea* 4:291. 1829

Erect herb, less than 75 cm tall (to 150 cm elsewhere); stems ribbed; pubescence whitish, \pm appressed, dense except on upper blade surface. Leaves alternate, often with 1 to several smaller leaves on a very short axillary branch; petioles less than 1 cm long; blades ovate or subrhombic, blunt at apex, obtuse at base and abruptly decurrent nearly to base of petiole, 1.5–5 cm long, 1–3 cm wide, weakly sinuate-dentate. Flowers in terminal panicles; heads discoid, ca 6 mm long, on short slender peduncles; phyllaries in several series, acuminate; ray flowers lacking; disk flowers bisexual, orchid, ca 4 mm long, the corolla lobes long and slender, spreading at anthesis

flowers bisexual, yellow, 6–7 mm long; anthers weakly exerted; style branches slender, flattened, with subulate tips. Achenes hispid, ca 2 mm long; pappus of 18–20 plumose bristle-like scales, on ray-flower achenes to ca 2 mm long, on disk-flower achenes ca 5 mm long. *Croat 7004.*

Very abundant locally in the Laboratory Clearing; occasional elsewhere. Flowers and fruits throughout the year.

Distinguished by the solitary pedunculate heads with few white ray flowers.

Native to Central America; now widespread in the tropics and subtropics. In Panama, ecologically variable, but chiefly from drier areas and mostly on the Pacific slope; known from tropical dry forest in Los Santos, Coclé, and Panamá, from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá, and from premontane wet forest in Chiriquí, and Coclé, and Panamá.

VERBESINA L.**Verbesina gigantea** Jacq., Coll. 1:53. 1787*V. myriocephala* Schultz-Bip.

Cerbatana, Lengua de muy

Polygamous, stout, usually unbranched herb, mostly 2.5–3.5 m tall; stems smooth, purplish, glabrous, pruinose when young. Leaves mostly alternate, sessile, the lowermost deciduous; blades deeply pinnatifid, narrowed at base and decurrent onto stem, 20–40 cm long, densely pubescent especially below, the margins sharply and irregularly toothed. Corymbs large, terminal, pubescent; heads ca 7 mm high; phyllaries keeled, pubescent, acuminate, similar to paleae subtending each flower of the head; flowers white, the tube with stiffly ascending trichomes near base; ray flowers 1–3, pistillate, the ligule small, weakly trilobate; disk flowers many, bisexual, the anthers syngenesious, the style emerging from tube simultaneously with anthers but continuing to elongate, the stigmas recurving, their outer surfaces weakly antrorsely barbed. Achenes 2-edged, ciliate; pappus of two barbed bristles, shorter than corolla tube. *Croat 4387.*

Occasional, in clearings. Flowers and fruits principally in the dry season (December to April).

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in the Canal Zone, Coclé, and Panamá, and from premontane wet forest in Colón and Panamá.

See Fig. 551.

KEY TO THE SPECIES OF VERNONIA

- Plants herbs, usually less than 1.5 m tall *V. cinerea* (L.) Less.
 Plants arching shrubs or small trees, more than 2 m tall:
 Plants erect shrubs or small trees; phyllaries green-tipped, bicolorous; blades mostly appressed-pubescent *V. patens* H.B.K.
 Plants arching shrubs or vines; phyllaries concolorous, their tips not dark green; blades with erect trichomes *V. canescens* H.B.K.



Fig. 552.
Vernonia patens



Fig. 553. *Wulffia baccata*

to expose syngenesious anthers, the style exerted, its branches bristled on outside. Achenes terete, ca 1.5 mm long, bristly pubescent; pappus of numerous barbed bristles, slightly shorter than corolla. *Croat 6879*.

Occasional in the Laboratory Clearing. Flowers and fruits throughout the year.

Native to the Old World, but naturalized in the New World and distributed widely in the tropics and subtropics. In Panama, known from tropical moist and premontane moist forests on both slopes of the Canal Zone and from tropical dry forest in Panamá (Taboga Island).

Vernonia patens H.B.K., Nov. Gen. & Sp. 4:41. 1820

Boton de pegapega, Lengua de buey o vaca, Palo blanco, Salvia, Sanalego, Tuete

Slender shrub or small tree, to 3.5(8) m tall; trunk mostly unbranched to near apex; stems moderately to densely pubescent with \pm viscid trichomes, 3-ribbed, the ribs originating below each petiole. Leaves alternate; petioles short; blades narrowly elliptic or lanceolate, acuminate, acute at base, 6–19 cm long, 1–5 cm wide, sparsely appressed-pubescent especially on veins, the margins with small apiculate teeth. Panicles 1-sided, scorpioid; heads sessile, ca 9 mm long; phyllaries in several series, acute, darker green at apex, the margins thin, ciliolate; ray flowers lacking; disk flowers bisexual, white (at least some flowers of the outer ring tinged with lavender), to 5.3 mm long, usually bent outward, the lobes long and slender, often remaining erect, the anthers syngenesious, becoming exerted, the style branches becoming long-exserted, antrorsely barbed outside. Achenes minutely pubescent, ca 1.5 mm long; pappus of many barbed bristles, equaling length of corolla on inner flowers, shorter than length of corolla on outer ring of flowers. *Croat 8778*.

Common in clearings. Flowers and fruits throughout the dry season (January to April).

Mexico to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in Panamá, from premontane wet forest in Colón, Chiriquí, and Panamá, from tropical wet forest in Chiriquí and Panamá, and from lower montane wet forest in Chiriquí.

See Fig. 552.

WEDELIA Jacq.

Wedelia trilobata (L.) Hitchc., Annual Rep. Missouri Bot. Gard. 4:99. 1893

Clavellin de playa

Polygamous low herb, often decumbent, sometimes rooting at lower nodes, to 2 m long; stems sparsely strigose or glabrous, weakly ribbed when dry. Leaves opposite, sessile or short-petiolate or perfoliate; blades obovate-elliptic to subrhombic, acute at apex, conspicuously narrowed in basal third and obtuse to rounded at base, 5–12 (18) cm long, 2.5–4.5 cm wide, sparsely scabrous above, less so below, broadly and irregularly serrate, sometimes shallowly trilobate. Heads ca 2.5 cm diam,

solitary from upper axils; peduncles and phyllaries strigose; peduncles 3–9 cm long; phyllaries in ca 3 series, the outermost foliaceous and longer than the inner ones; flowers yellow; ray flowers pistillate, ca 1 cm long, the style minutely trilobate; disk flowers bisexual, ca 4.7 mm long, the lobes pubescent inside, the anthers black, syngenesious, included, the style yellow, exerted, its lobes 2, recurved. Achenes ca 5 mm long, weakly pubescent, with a few glands; pappus minute, cup-shaped, the margins irregular. *Croat 11350*.

Locally abundant in clearings and on beaches of the lakeshore. Flowers and fruits in the rainy season (April to December).

Florida, Central and South America; West Indies; West Africa. In Panama, found in disturbed, wet places, principally on the Atlantic slope; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Los Santos, and Panamá, from tropical dry forest in Panamá, from premontane moist forest in Panamá, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón and Veraguas.

WULFFIA Neck. ex Cass.

Wulffia baccata (L.f.) O. Kuntze, Rev. Gen. Pl. 1:373. 1891

Vine or scrambling shrub, usually 2–4 m long, moderately strigose; branches perpendicular to axis; stems slightly angulate, asperous, mottled with purple. Leaves opposite; petioles 1–2 cm long; blades lanceolate-elliptic to ovate, falcate-acuminate, obtuse to acute and often inequilateral at base, 9–20 cm long, 3.5–9 cm wide, asperous below. Inflorescences terminal or upper-axillary, or 2 or 3 pedunculate heads, often on short lateral branches; peduncles 2–4 cm long; heads large, bearing many flowers; phyllaries in ca 2 series, green to orange, subequal, narrowly acute and recurved; ray flowers 8–15, yellow, sterile, irregular, oblong, weakly bifid at apex, 1–2 cm long; disk flowers bisexual, orange, each subtended by paleae, the paleae orange, to 7 mm long, longer than the disk flowers in bud but considerably shorter at anthesis, the corolla ca 6 mm long, shortly 5-lobed, the tube narrowed just above the base, the stamens syngenesious, the filaments fused to slender part of corolla, the anthers ca 2 mm long, black, the connective acute above, orange, the style branches exerted and spreading, orange, conspicuously antrorse-pubescent. Achenes \pm globose, ca 5 mm diam, minutely pubescent at apex, dark green and fleshy at maturity, contrasting sharply with the persistent orange palea; pappus lacking. *Croat 11466*.

Common at margins of the forest or in tree-fall areas within the forest. Flowers and fruits principally in the rainy season (July to December).

Panama south to Bolivia and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Colón, Coclé, Panamá, and Darién, and from tropical wet forest in Colón, Panamá, and Darién.

See Fig. 553.

A

Key to Sterile Woody Plants

Nearly 700 species are included in this key. Excluded are species that are both cultivated and known only from the Laboratory Clearing; species that are usually mostly herbaceous; and some species that are probably no longer on the island. Some of the more common coarse herbaceous vines in the forest *are* included, because they will be more frequently encountered and would otherwise be difficult to identify.

Approximately 60% of the woody plants can be identified with little difficulty, the remainder with varying degrees of difficulty. Species with excessive variation, or with juvenile forms that do not resemble the adult plants, may not key out. A few couplets terminate with two

species because no characters could be found that would adequately distinguish the species from each other in sterile condition.

Identifications should be thoroughly checked against the text descriptions and compared with herbarium specimens where possible. Troublesome couplets should be marked and the plant keyed out two or more ways, for even if the process yields several possibilities, it is faster and easier to check these in an herbarium than to attempt identification in most other ways.

Pairs of symbols were added before selected couplets to facilitate progress through the keys.

For further discussion of this key, see p. 53.

KEY TO STERILE WOODY PLANTS

Leaves simple:

Leaves opposite or whorled KEY 1, p. 861

Leaves alternate or spiraled:

Plants not lianas KEY 2, p. 877

Plants lianas KEY 3, p. 896

Leaves compound:

Leaves palmately compound with 4 or more leaflets KEY 4, p. 899

Leaves pinnately compound or with 3 or fewer leaflets:

Leaves compound more than once KEY 5, p. 899

Leaves pinnate or with 3 or fewer leaflets KEY 6, p. 901

KEY I: LEAVES SIMPLE, OPPOSITE OR WHORLED

- Blades with the major veins arising at or near base and \pm paralleling midrib for length of leaf, usually with tertiary veins perpendicular to and connecting these major laterals:
 - Blades maroon beneath *Miconia rufostellulata* (107. Melastomataceae)
 - Blades not maroon beneath:
 - ◆ Blades lacking stellate or densely branched trichomes and lacking fimbriate scales along lower midrib:
 - Blades essentially glabrous (possibly pubescent on veins or in axils below):
 - Plants lianas; blades entire:
 - Stems (at least older ones) armed; blades with white trichomes in small tufts in axils
 - *Strychnos brachistantha* (115. Loganiaceae)
 - Stems not armed; blades lacking tufts of white trichomes in axils:
 - Blades with tufts of long, brownish trichomes in axils at base; petioles glabrous or puberulent
 - *Strychnos darienensis* (115. Loganiaceae)
 - Blades not tufted in axils at base; petioles with long brownish or white trichomes
 - *Strychnos panamensis* (Fig. 447; 115. Loganiaceae)
- Plants shrubs or small trees:

A

- Blades usually with small tufts of trichomes in basal vein axils below; larger stems spiny
 *Strychnos brachistantha* (115. Loganiaceae)
- Blades lacking tufts in axils:
 Blades obscurely crenulate, with sparse stiff setae arising from vein ends near apex; plants shrubs . . .
 *Miconia lateriflora* (107. Melastomataceae)
- Blades entire, without marginal setae:
 Plants trees, usually 6–10 m tall *Miconia hondurensis* (107. Melastomataceae)
 Plants shrubs, usually less than 3.5 m tall (much shorter in parasitic *Oryctanthus*):
 Plants not epiphytic or parasitic; petioles ca 5 mm long
 *Conostegia cinnamomea* (Fig. 431; 107. Melastomataceae)
 Plants epiphytic or parasitic; petioles 1–2 cm long:
 Plants large epiphytic shrubs; leaves thin, deciduous in the dry season; tertiary veins conspic-
 uous, perpendicular to major veins *Topobaea praecox* (107. Melastomataceae)
 Plants small parasitic shrubs; leaves thick, not deciduous; tertiary veins not visible, not per-
 pendicular to major veins:
 Leaf blades obtuse to rounded at base (rarely subcordate)
 *Oryctanthus alveolatus* (42. Loranthaceae)
 Leaf blades broadly rounded to subcordate at base . . . *Oryctanthus cordifolius* (42. Loranthaceae)
- Blades pubescent:
 Petioles and stems glabrous or inconspicuously pubescent in age:
 Blades more than 10 cm wide, entire *Bellucia grossularioides* (107. Melastomataceae)
 Blades less than 5 cm wide, coarsely toothed:
 Blades asperous above, ovate to elliptic, shallowly toothed *Calea prunifolia* (133. Compositae)
 Blades smooth above, rhombic-ovate, usually coarsely toothed
 *Chromolaena odorata* (Fig. 546; 133. Compositae)
- Petioles and stems conspicuously pubescent:
 Plants lianas:
 Branches not paired and divaricate; blades minutely strigose below; petioles and stems near nodes
 short-rufous-pubescent *Adelobotrys ascendens* (107. Melastomataceae)
 Branches always paired and divaricate:
 Pubescence on stems and blades long, conspicuous; blades lacking axillary domatia below
 *Strychnos toxifera* (Fig. 448; 115. Loganiaceae)
 Pubescence short; blades with axillary tufts between inner pair of lateral veins below
 *Strychnos darienensis* (115. Loganiaceae)
- Plants shrubs or small trees:
 Lateral veins with the inner pair departing midrib 5 mm or more above basal pair:
 Blades ending abruptly at base, often inequilateral; trichomes on stems erect and spreading
 *Clidemia dentata* (Fig. 428; 107. Melastomataceae)
 Blades ± decurrent onto petioles; trichomes on stems appressed or acropetal; pairs of leaves often
 unequal *Miconia nervosa* (Fig. 436; 107. Melastomataceae)
- Lateral veins all departing midrib at or very near base (less than 5 mm above base):
 Trichomes on stems, petioles, veins below, and margins of blade brown, more than 5 mm long . . .
 *Clidemia collina* (107. Melastomataceae)
- Trichomes on stems and petioles less than 5 mm long:
 Larger blades with 7 veins from base; blades broadly rounded to subcordate at base, often with
 some stellate trichomes on upper surface
 *Leandra dichotoma* (Fig. 433; 107. Melastomataceae)
 Blades with 3–5 veins from base; trichomes on upper surface simple or lacking:
 Stems and petioles with purplish trichomes much longer than trichomes on midrib
 *Miconia lacera* (Fig. 435; 107. Melastomataceae)
 Stems and petioles with trichomes not purplish, ± the same size as trichomes on midrib:
 Blades conspicuously pubescent above and below, usually acute at base
 *Conostegia bracteata* (Fig. 430; 107. Melastomataceae)
 Blades ± glabrous above and minutely strigose below, usually ± rounded at base
 *Adelobotrys ascendens* (107. Melastomataceae)
- ◆ Blades with some stellate or densely branched trichomes or fimbriate scales below:
 ★ Major lateral veins departing midrib more than 5 mm above base:
 ▲ Stellate or densely branched trichomes below very minute (appearing merely granular in hand lens), ±
 restricted to veins:
 Blades less than 2.5 times longer than broad:
 Blades sparsely pilose above, the margins dentate, with ± irregular, pilose cilia
 *Ossaea quinquenervia* (107. Melastomataceae)
 Blades glabrous to granular-puberulent above, the margins ± entire, with sparse, short cilia
 *Clidemia septuplinervia* (107. Melastomataceae)
 Blades more than 2.5 times longer than broad:

- Petioles more than 1 cm long; blades long-decurrent onto petiole
 *Miconia lonchophylla* (107. Melastomataceae)
- Petioles usually less than 1 cm long; blades not conspicuously decurrent onto petiole:
 Blades usually less than 6 cm wide, often to 8 cm wide; lateral veins spaced mostly 3–5 mm apart,
 the smallest reticulate veins clearly visible, darker than surface
 *Conostegia cinnamomea* (Fig. 431; 107. Melastomataceae)
- Blades usually more than 8 cm wide, rarely less than 6 cm wide; lateral veins 5–12 mm apart, the
 smallest reticulate veins not clearly visible, not darker than surface
 *Miconia prasina* (Fig. 437; 107. Melastomataceae)
- ▲ Stellate or densely branched trichomes below very dense and/or conspicuous:
 Blades pubescent above at maturity:
 Blades with 3 veins from base; trichomes above sparse, \pm appressed; trichomes below with a single
 strong central axis and with many fine radial arms at base
 *Henriettea succosa* (Fig. 432; 107. Melastomataceae)
- Blades with 5–7 veins from base; trichomes above dense, erect; trichomes below of 2 types (simple
 and stellate) *Conostegia speciosa* (107. Melastomataceae)
- Blades glabrous above at maturity:
 Blades sessile, subcordate, often more than 10 cm wide
 *Miconia impetiolearis* (107. Melastomataceae)
- Blades petiolate:
 Petioles 1–1.5 cm long; blades usually less than 7 cm broad
 *Conostegia xalapensis* (107. Melastomataceae)
- Petioles more than 4 cm long; blades more than 10 cm wide
 *Miconia serrulata* (107. Melastomataceae)
- ★ Major lateral veins all departing midrib at or less than 5 mm above base:
 Blades densely pubescent above; plants with simple, glandular, and stellate trichomes:
 Blades cordate at base; trichomes on stem 5 mm long or more; blade surface smooth
 *Clidemia octona* (Fig. 429; 107. Melastomataceae)
- Blades obtuse at base; trichomes on stem short; blade surface bullate
 *Clidemia capitellata* (Fig. 427; 107. Melastomataceae)
- Blades glabrous or sparsely pubescent above; plants lacking gland-tipped trichomes (except *Miconia elata*):
 Lateral veins obscure or closely spaced (less than 2 mm apart):
 Plants shrubs or small trees, not epiphytic, usually on shore; blades narrowly ovate, long-acuminate;
 lateral veins obscure, not at all raised; stems slender, drying smooth
 *Miconia borealis* (107. Melastomataceae)
- Plants shrubs, epiphytic, usually in the forest, rarely on shore; blades \pm obovate, not long-acuminate;
 lateral veins distinctly raised; stems thick, drying wrinkled
 *Topobaea praecox* (107. Melastomataceae)
- Lateral veins prominent, more than 2 mm apart:
 Trichomes below long, stout, simple (densely branched at base); blades with 3 strong lateral veins . .
 *Henriettea succosa* (Fig. 432; 107. Melastomataceae)
- Trichomes not as above:
 Lower blade surface completely covered with minute stellate trichomes:
 Lower blade surface brownish, with many, minute, dark-brown, glandular areas scattered among
 the trichomes *Miconia elata* (107. Melastomataceae)
- Lower blade surface whitish, lacking dark-brown glandular areas
 *Miconia argentea* (Fig. 434; 107. Melastomataceae)
- Lower blade surface not completely covered with minute stellate trichomes:
 Lower blade surface often purple, sparsely pubescent
 *Miconia rufostellulata* (107. Melastomataceae)
- Lower blade surface green, sparsely to densely pubescent:
 Blades acute at base; stellate trichomes minute, inconspicuous
 *Miconia affinis* (107. Melastomataceae)
- Blades cordate at base:
 Trichomes below minute, stellate, restricted to veins
 *Clidemia purpureo-violacea* (107. Melastomataceae)
- Trichomes below simple or with long lateral branches, scattered on blade, more dense on
 midrib *Miconia shattuckii* (107. Melastomataceae)
- Blades with the major veins not arising at or near base and not \pm parallel to midrib for length of leaf:
 ○ Plants with interpetiolar stipules or their scars continuous between the petioles; milky sap lacking:
 ⊕ Stipules not entire, irregularly divided or slightly bifid at top to divided all the way to base and thus appearing
 as 2 separate lobes or caducous, leaving a row of interpetiolar setae or with the lobes aristate, with tri-
 chomes more than 2 mm long:
 □ Stipules bifid only at tip or divided less than two-thirds their length, otherwise entire (margins may be ciliate
 but not aristate), not represented by an interpetiolar line of stiff setae:

Young stems conspicuously pubescent, the trichomes brown, matted, spreading (not appressed), ca 0.5 mm long:

Upper blade surface densely short-pubescent, \pm scabrous *Psychotria micrantha* (Fig. 532; 130. Rubiaceae)

Upper blade surface essentially glabrous, smooth *Psychotria psychotriifolia* (Fig. 533; 130. Rubiaceae)

Young stems glabrous or with very closely appressed trichomes:

Lateral veins below \pm the same thickness and length throughout the blade; reticulate veins inconspicuous, often barely visible on young blades *Psychotria granadensis* (130. Rubiaceae)

Every second, or second and third, lateral vein below much thinner and shorter than the others; reticulate veins below conspicuous, connecting the lateral veins:

Stipules 8–15 mm long, foliaceous, caducous, bifid for less than one-fifth their length

..... *Psychotria capitata* (Fig. 527; 130. Rubiaceae)

Stipules 4–10 mm long, mostly persistent, usually bifid more than one-third their length:

Stipules coriaceous, their margins as durate as the body, the lobes usually flaring away from the stem, some of the stipules usually divided almost to base, the sinus between the lobes usually broadly U-shaped *Palicourea guianensis* (Fig. 524; 130. Rubiaceae)

Stipules \pm herbaceous, their margins \pm thin, usually dissipating before the main body, the lobes not flaring, not divided nearly to base, the sinus between the lobes usually V-shaped

..... *Psychotria brachiata* (130. Rubiaceae)

- Stipules divided completely to base or more than two-thirds their length or otherwise not entire or with conspicuous setae on margins ca 4 mm long or caducous and represented only by an interpetiolar line of stiff setae:

Young stems glabrous (sometimes with several widely dispersed trichomes):

Stipule margin with several, long, stiff setae ca 4 mm long; shrubs less than 50 cm tall

..... *Cephaelis ipecacuanha* (Fig. 516; 130. Rubiaceae)

Stipule margin lacking long stiff setae:

Stipules represented by a line of broad-based setae:

Setae ca 5 mm long *Mouriri myrtilloides* subsp. *parvifolia* (107. Melastomataceae)

Setae ca 0.5 mm long *Psychotria carthagenensis* (Fig. 528; 130. Rubiaceae)

Stipules not a line of setae:

Stipule lobes linear:

Petioles 1.5–4.5 cm long; leaves attenuate at base *Cephaelis discolor* (Fig. 515; 130. Rubiaceae)

Petioles 0.2–1 cm long; leaves \pm rounded at base:

Stipule lobes ca 10 mm long, their bases 1.5–2 mm wide

..... *Psychotria deflexa* (Fig. 529; 130. Rubiaceae)

Stipule lobes ca 3 mm long, their bases ca 1 mm wide

..... *Psychotria acuminata* (Fig. 526; 130. Rubiaceae)

Stipule lobes ovate to lanceolate:

Petioles to 3 cm long; leaves 12–25 cm long; stipule lobes usually \pm ovate and \pm rounded at apex, sometimes irregularly divided *Palicourea guianensis* (Fig. 524; 130. Rubiaceae)

Petioles 1–1.5 cm long; leaves 10–16 cm long; stipule lobes usually \pm lanceolate, \pm acute or apiculate at apex *Psychotria brachybotrya* (130. Rubiaceae)

Young stems variously pubescent, often inconspicuously so:

Trichomes on young stems densely spreading, ca 1.5 mm long; upper blade surface conspicuously pubescent *Cephaelis tomentosa* (Fig. 517; 130. Rubiaceae)

Pubescence not as above:

Plants lianas; stipules caducous *Trigonia floribunda* (72. Trigoniaceae)

Plants shrubs:

Stipules represented by a line of short bristles ca 0.5 mm long; stems and terminal buds densely sericeous with appressed trichomes; terminal buds conspicuous, ca 8 mm long [if only a line of short bristles are present and the plant does not fit the rest of this description, look for stipules at the very tips of the branches and return to ☉ on the preceding page]

..... *Amaioua corymbosa* (130. Rubiaceae)

Stipules not represented by a line of bristles, otherwise not as above:

Stipules 10–15 mm long or, if less than 10 mm, the lobes separated at base, persistent:

Stems cinereous, with dense appressed trichomes ca 0.5 mm long; blades 10–45 cm long; stipules ciliate, glabrous to appressed-pubescent *Iertia haenkeana* (130. Rubiaceae)

Stems merely puberulent to \pm cinereous, with appressed trichomes ca 0.1 mm long; blades 8–19 cm long; stipules not ciliate, glabrous to inconspicuously strigose with minute, black, slender trichomes *Psychotria racemosa* (Fig. 534; 130. Rubiaceae)

Stipules usually less than 10 mm long, the lobes not separated at base:

Blades usually 3.5–12 cm long and 1.2–4.5 cm wide:

Young stems conspicuously cinereous, with appressed, often matted trichomes ca 1 mm long;

lower midrib with dense appressed trichomes ca 0.5 mm long

..... *Psychotria pittieri* (130. Rubiaceae)

- Young stems minutely pubescent, with erect trichomes; lower midrib glabrous or puberulent, with appressed or spreading trichomes ca 0.1 mm long:
- Blades usually more than 12 cm long, at least the larger blades more than 3.5 cm wide; major lateral veins usually 10 or more on each side of midrib *Psychotria acuminata* (Fig. 526; 130. Rubiaceae)
 - Blades usually less than 10 cm long and 3.5 cm wide; major lateral veins usually 9 or fewer on each side of midrib *Psychotria furcata* (130. Rubiaceae)
- Blades usually 8–21 cm long and 2–10 cm wide:
- Younger parts of plant minutely puberulent, appearing almost glabrous, the trichomes scattered, less than 0.1 mm long *Psychotria acuminata* (Fig. 526; 130. Rubiaceae)
 - Younger parts of plant more conspicuously puberulent, sometimes appearing cinereous, the trichomes to ca 0.2 mm long:
 - Stipules 3–5 mm long, triangular, pliable *Psychotria pubescens* (130. Rubiaceae)
 - Stipules more than 6 mm long, slender-lanceolate, stiff *Psychotria racemosa* (Fig. 534; 130. Rubiaceae)
- ⊗ Stipules entire:
- Young stems densely pubescent, the trichomes 0.5 mm long or longer:
 - Stipules glabrous or with at least some part of the outer surface glabrous (may have dense trichomes only on midrib and/or at base):
 - Youngest blades with the upper surface bearing scattered, broad-based, appressed trichomes to ca 0.4 mm long:
 - Blades 3–6 (11) cm long and 1.5–3 cm wide; petioles obscure or to 1 cm long; stipules 1.5–3 mm long, triangular, often scoop-shaped and projecting away from stem *Randia formosa* (Fig. 535; 130. Rubiaceae)
 - Blades and petioles longer than above; stipules not as above:
 - Plants arching shrubs or lianas; blades briefly decurrent onto petiole; lower blade surface in dried specimens appearing finely wrinkled between lateral veins *Chomelia psilocarpa* (130. Rubiaceae)
 - Plants trees; blades rounded to obtuse at base, not at all decurrent onto petiole; lower blade surface not wrinkled *Guettarda foliacea* (Fig. 523; 130. Rubiaceae)
 - Youngest blades with the upper surface glabrous:
 - Plants trees, to 15 (25) m tall; blades blunt to rounded at apex; stipules ovate, to 1.8 cm long; trunk deeply involuted *Macrocnemum glabrescens* (130. Rubiaceae)
 - Plants shrubs, to 3 m tall; blades sharply acute at apex; stipules acute, to 0.5 (1) cm long; trunk not involuted:
 - Stipules joining above petiole; trichomes straight, slender *Bertiera guianensis* (130. Rubiaceae)
 - Stipules separate above petiole; trichomes ± curly, matted *Psychotria emetica* (Fig. 530; 130. Rubiaceae)
 - Stipules with the outer surface completely and evenly pubescent:
 - Lower blade surface (not veins only) conspicuously and permanently densely pubescent, the trichomes more than 0.5 mm long:
 - Plants trees, to 15 m tall; stipules long-attenuate; trichomes on upper blade restricted mostly to veins *Antirrhoea trichantha* (130. Rubiaceae)
 - Plants shrubs or vines, the younger parts herbaceous; stipules ovate and apiculate at apex; trichomes on upper blade scattered evenly over surface *Sabicea villosa* var. *adpressa* (130. Rubiaceae)
 - Lower blade surface ± glabrous to minutely puberulent (may have dense trichomes on veins or widely scattered trichomes less than 0.5 mm long):
 - Stipules densely brown-tomentose, to 1 cm long; lower stipule scars represented by a line of dark bristles ca 0.5 mm long; trees to 15 m tall *Amaioua corymbosa* (130. Rubiaceae)
 - Stipules and habit not as above:
 - Midrib of upper surface of young blades with dense, appressed trichomes ca 0.5 mm long *Guettarda foliacea* (Fig. 523; 130. Rubiaceae)
 - Midrib of upper surface of young blades essentially glabrous:
 - Plants usually 2–4 m tall; stems and veins of lower blade surface smoothly and densely appressed-pubescent (subsericeous), the trichomes whitish; stipules narrowly triangular, to 5 mm long, pubescent like stems *Bertiera guianensis* (130. Rubiaceae)
 - Plants usually less than 1 m tall, often less than 30 cm dbh; stems and veins of lower blade surface coarsely and sparsely strigose and with scattered debris fragments (appearing very dirty), the trichomes white or gray but not conspicuous; stipules inconspicuous, triangular, less than 2 mm long, strigose *Psychotria emetica* (Fig. 530; 130. Rubiaceae)
- Young stems glabrous to densely pubescent, the trichomes less than 0.3 mm long (or longer than 0.3 mm and widely scattered):
- Reticulate veins not directly visible; tertiary veins completely obscure; plants, if lianas, with persistent stipules:
 - Blades 2–5 (10) cm long and 1.3–4 (6) cm wide:

- Stipules ca 8–15 mm long, with the cusp \pm equaling the main stipular body; plants shrubs, frequent
 *Psychotria chagrensis* (130. Rubiaceae)
- Stipules to ca 4 mm long, with the cusp 3 or more times longer than the short, flaring base; plants
 shrubs, often climbing and vinelike, rare *Chiococca alba* (130. Rubiaceae)
- Blades 5–30 cm long and 2.5–14 cm wide:
- Blade apex rounded; stipules \pm obovate *Cosmibuena skinneri* (Fig. 518; 130. Rubiaceae)
- Blade apex acuminate to obtuse; stipules not obovate:
- Blades 5–10 (16) cm long and 2.5–5.5 cm wide; lower stipules represented by a dense line of setae ca
 0.7 mm long *Psychotria carthagenensis* (Fig. 528; 130. Rubiaceae)
- Blades larger than above, lacking setae:
- Stipules represented by a low, thick, forward-projecting ridge ca 1.5–3.5 mm high
 *Psychotria uliginosa* (130. Rubiaceae)
- Regular stipules present, 5–10 mm long *Psychotria limonensis* (Fig. 531; 130. Rubiaceae)
- Reticulate veins directly visible (may be very small); quaternary veins often also visible:
- Blades 30–65 cm long and 21–37 cm wide; stipules ca 7 cm long
 *Pentagonia macrophylla* (130. Rubiaceae)
- Blades and stipules smaller:
- Plants lianas, the stems with thick-based, recurved spines usually less than 10 mm long; blade base
 cordate to rounded. *Uncaria tomentosa* (Fig. 537; 130. Rubiaceae)
- Plants with the stems unarmed; blade base not cordate or rounded:
- ◇ Midrib on lower surface of young blades variously pubescent and/or the blades with tufts of
 trichomes in vein axils:
- Trichomes on midrib of younger blades below erect to vaguely appressed or less than 0.2 mm
 long:
- Lower surface of young (to half-mature) blades densely covered with short erect trichomes,
 giving the leaf a velvety feel *Genipa americana* (Fig. 520; 130. Rubiaceae)
- Leaf pubescence not as above:
- Branches with the 2–10 cm below the tips mostly glabrous, with conspicuous white lenticels:
- Lenticels roundish; vein axils below with conspicuous tufts of trichomes; blades acute to
 obtuse at apex *Coutarea hexandra* (Fig. 519; 130. Rubiaceae)
- Lenticels elongate, slender; vein axils not tufted; blades briefly acuminate at apex
 *Pogonopus speciosus* (130. Rubiaceae)
- Branches not as above:
- Lateral veins below usually somewhat enlarged, with pitlike domatia in axils, the trichomes
 on veins very short, granular, not densely pilose in axils
 *Psychotria horizontalis* (130. Rubiaceae)
- Veins and trichomes not as above:
- Blades with conspicuous flaplike projections on midrib near vein axils below
 *Psychotria micrantha* (Fig. 532; 130. Rubiaceae)
- Blades lacking axillary flaps:
- Stipules glabrous, usually \pm scoop-shaped, sharply acute, 5–10 mm long; branches
 often spinescent, usually stiff, with the bark peeling into small flakes; leaf scars
 often visible, shield-shaped *Randia armata* (130. Rubiaceae)
- Stipules and branches not as above:
- Trichomes on veins below curled, \pm matted and appressed, to ca 0.5 mm long;
 stems mostly pubescent and petioles to ca 1 cm long
 *Psychotria emetica* (Fig. 530; 130. Rubiaceae)
- Trichomes not as above and/or petioles longer than 1 cm:
- Petioles stout, less than 1 cm long; veins below mostly glabrous except for axil-
 lary tufts of trichomes; leaves acute at base
 *Alibertia edulis* (Fig. 511; 130. Rubiaceae)
- Leaves not as above:
- Stipules subpersistent, 2–37 mm long, slender-attenuate; midrib below on
 young blades glabrous to puberulent; plants not weak-stemmed and
 decumbent:
- Leaves 3 or 4 at each node *Hamelia patens* (130. Rubiaceae)
- Leaves 2 at each node *Hamelia axillaris* (130. Rubiaceae)
- Stipules and leaves not as above:
- Underside of veins on half-mature blades densely appressed-pubescent;
 plants trees *Chimarrhis parviflora* (130. Rubiaceae)
- Underside of veins on half-mature blades glabrous or puberulent; plants
 weak-stemmed, often decumbent shrubs
 *Hoffmannia woodsonii* (130. Rubiaceae)
- Trichomes on underside of midrib closely appressed and/or longer than 0.5 mm:

- Stipules 1.5–2 cm long, obovate, rounded at apex, not caducous
 *Macrocnemum glabrescens* (130. Rubiaceae)
- Stipules not as above:
- Stipules to ca 15 mm long; leaves 15–42 cm long, the underside covered with short erect trichomes, giving the surface a velvety feel . . . *Genipa americana* (Fig. 520; 130. Rubiaceae)
- Stipules and leaves not as above:
- Young branches with conspicuous, white, elongate lenticels; stipules persistent, to 2 mm long; leaf bases decurrent onto the short, obscure petiole
 *Pogonopus speciosus* (130. Rubiaceae)
- Branches and leaves not as above:
- Stipules 5 mm long or less:
- Stems usually mostly glabrous; trichomes, when present, usually ca 0.1 mm long
 *Hoffmannia woodsonii* (130. Rubiaceae)
- Stems usually \pm pubescent; trichomes at least 0.3 mm long:
- Stipules joining above petiole; trichomes straight, slender
 *Bertiera guianensis* (130. Rubiaceae)
- Stipules separate above petiole; trichomes \pm curled, matted
 *Psychotria emetica* (Fig. 530; 130. Rubiaceae)
- Stipules more than 5 mm long:
- Conspicuous lateral veins usually in 5–8 pairs per blade:
- Petioles usually 2–5 mm long; stipules subsistent, the pairs joined at base
 *Bertiera guianensis* (130. Rubiaceae)
- Petioles (7)10–25 mm long; stipules caducous, not joined at base:
- Terminal bud area with trichomes to ca 2 mm long
 *Calycophyllum candidissimum* (Fig. 514; 130. Rubiaceae)
- Terminal bud area lacking such long trichomes, at most densely sericeous:
- Blades with the midrib above densely short-appressed-pubescent; blades not long-attenuate at base *Guettarda foliacea* (Fig. 523; 130. Rubiaceae)
- Blades with the midrib above glabrous; blades long-attenuate at base
 *Chimarrhis parviflora* (130. Rubiaceae)
- Lateral veins usually in more than 12 pairs per blade:
- Stipules to 3 cm long, ca 7 mm wide at base, \pm persistent
 *Warszewiczia coccinea* (130. Rubiaceae)
- Stipules to 1.2 cm long, less than 5 mm wide at base, caducous:
- Half-mature blades with the trichomes on veins below less than 0.2 mm long, soft, \pm curled *Chimarrhis parviflora* (130. Rubiaceae)
- Half-mature blades with the trichomes on veins below appressed, straight, more than 0.7 mm long *Aseis blackiana* (Fig. 512; 130. Rubiaceae)
- ◇ Midrib on lower surface of young blades glabrous; blades lacking tufts of trichomes in vein axils (the pitlike domatia themselves may be pubescent inside in *Alibertia* and *Tocoyena*):
- Stipules 7–30 mm long:
- Midrib of blade below bearing conspicuous flaplike projections near each major lateral vein:
- Leaves clustered at branch tips, usually with less than 12 pairs of major lateral veins
 *Tocoyena pittieri* (Fig. 536; 130. Rubiaceae)
- Leaves not clustered at branch tips, usually with more than 12 pairs of major lateral veins
 *Psychotria marginata* (130. Rubiaceae)
- Midrib of blade below lacking flaps:
- Lateral veins at confluence with midrib below usually somewhat enlarged and with pitlike domatia, but lacking tufts of trichomes in the pits
 *Psychotria horizontalis* (130. Rubiaceae)
- Lateral veins lacking pitlike domatia or, if small pits present, the pits usually pubescent inside:
- Lower lateral vein axils with pubescent, pitlike axillary domatia:
- Leaf blades drying green or brown, the largest blades less than 17 cm long and 8 cm wide *Alibertia edulis* (Fig. 511; 130. Rubiaceae)
- Leaf blades drying black, the largest more than 25 cm long and 10 cm wide
 *Tocoyena pittieri* (Fig. 536; 130. Rubiaceae)
- Lower lateral vein axils not as above:
- Stipules with a cusp \pm as long as stipule body *Faramea occidentalis* (130. Rubiaceae)
- Stipules lacking a cusp or the cusp much shorter than stipule body:
- Stipules subsistent, to 12 mm long, 8–13 mm wide, ovate, with a cusp 2–3 mm long *Psychotria grandis* (130. Rubiaceae)
- Stipules not as above:
- △ Stipules caducous, not broadly triangular, usually densely cinereous; blades \pm cori-

- aceous, usually attenuate at base; plants rare
 *Chimarrhis parviflora* (130. Rubiaceae)
- △ Stipules and leaves not as above:
 Leaves appearing clustered at ends of branches, thin; midrib below often with
 flaps in the axils *Tocoyena pittieri* (Fig. 536; 130. Rubiaceae)
 Leaves not clustered at ends of branches, ± coriaceous; midrib lacking flaps
 *Posoqueria latifolia* (Fig. 525; 130. Rubiaceae)
- Stipules less than 7 mm long or, if longer, lacking conspicuous pits at base of secondary veins:
 Lateral veins with conspicuous pits in the side near axils below
 *Psychotria horizontalis* (130. Rubiaceae)
- Lateral veins lacking pits in the side:
 Lower leaf surface with conspicuous pits in the vein axils; petioles ca 5 mm long
 *Coussarea curvigemma* (130. Rubiaceae)
- Lower leaf surface lacking axillary pits; petioles may be much longer than 5 mm:
 Stems with conspicuous white lenticels 2–10 cm from tip, the twigs usually straight, stiff:
 Lenticels round, not more than 2 times longer than wide
 *Coutarea hexandra* (Fig. 519; 130. Rubiaceae)
- Lenticels elongate, several times longer than broad ... *Pogonopus speciosus* (130. Rubiaceae)
- Stems lacking white lenticels, the twigs various:
 Stipules ending in a conspicuous cusp about as long as the broadly flaring base:
 Blades abruptly acuminate, the acumen 7–10 mm long; lateral veins in 7–9 pairs per
 blade; major veins below ± sunken into the leaf matrix; plants in the forest ...
 *Faramea luteovirens* (130. Rubiaceae)
- Blades acute or with a slightly projecting acumen; lateral veins in more than 12 pairs
 per leaf; major veins below outstanding on the blade surface; plants cultivated at
 the Laboratory Clearing *Ixora coccinea* (130. Rubiaceae)
- Stipules lacking a long cusp:
 Plants trees; young branches usually ca 5 mm thick; stipules triangular, subpersistent,
 sharply acute, often somewhat projecting away from stem; blades 18–28 cm long
 and 7–14 cm wide *Tocoyena pittieri* (Fig. 536; 130. Rubiaceae)
- Plants not as above:
 Petioles to 1.5 cm long; blades 5–16 cm long; all veins arising from midrib of ±
 equal widths and lengths; stipular scars with a minute line of trichomes; stip-
 ules ± blunt at apex *Psychotria carthagenensis* (Fig. 528; 130. Rubiaceae)
- Petioles and blades longer than above; alternate veins arising from midrib much
 more slender and short than the others; stipule scars lacking a line of trichomes;
 stipules often sharp at apex:
 Stipules ± persistent, linear, ca 4 mm long; leaves often 3 or 4 per node; younger
 parts usually very minutely pubescent
 *Hamelia patens* var. *glabra* (130. Rubiaceae)
- Stipules caducous; leaves 2 per node:
 Plants trees, growing near the shore
 *Cassipourea elliptica* (104. Rhizophoraceae)
- Plants weak-stemmed shrubs, growing in the forest
 *Hoffmannia woodsonii* (130. Rubiaceae)
- © Plants lacking interpetiolar stipules (or if stipules or scars present, not continuous between petioles); milky sap
 often present:
 ☆ Leaf pairs markedly unequal (often subopposite):
 □ Blades lacking stellate trichomes below:
 Blades drying with prominent cystoliths; stems usually quadrangular in age; blades glabrous above and
 with scattered trichomes on veins below *Trichanthera gigantea* (129. Acanthaceae)
- Blades not drying with cystoliths:
 Blades with tufts of trichomes in vein axils below; most leaves alternate
 *Lycianthes synanthera* (124. Solanaceae)
- Blades lacking axillary tufts (except *Solanum antillarum*, with the leaves mostly opposite):
 Blades ± glabrous below, usually ± equilateral at base:
 Leaves arising opposite one another at nodes; branch tips with the terminal buds naked, reddish-
 brown *Neea amplifolia* (Fig. 227; 48. Nyctaginaceae)
- Smaller leaves arising from the axils of the larger, the leaves sometimes alternate; branch tips not as
 above:
 Blades with inconspicuous axillary tufts of trichomes *Solanum antillarum* (124. Solanaceae)
- Blades lacking axillary tufts *Solanum arboreum* (Fig. 484; 124. Solanaceae)
- Blades pubescent below, usually inequilateral at base:
 Plants armed in leaf axils *Pisonia aculeata* (Fig. 228; 48. Nyctaginaceae)
- Plants not armed:

- Blades pubescent only on midrib below, subcordate on one side at base *Rinorea sylvatica* (Fig. 397; 95. Violaceae)
- Blades densely pubescent below:
- Blades elliptic-oblong *Cordia panamensis* (121. Boraginaceae)
- Blades ovate-cordate *Cyphomandra hartwegii* (Fig. 481; 124. Solanaceae)
- Blades with stellate trichomes below:
- Blades armed on midrib with recurved prickles; prickles on stems recurved:
- Plants lianas; blades petiolate *Solanum lanciifolium* (124. Solanaceae)
- Plants shrubs; blades sessile or nearly so (larger blades may be petiolate) *Solanum jamaicense* (Fig. 486; 124. Solanaceae)
- Blades unarmed:
- Blades glabrous above in age; pubescence below so dense as to obscure surface; stems densely pubescent; plants often small trees *Solanum hayesii* (Fig. 485; 124. Solanaceae)
- Blades conspicuously pubescent above in age; pubescence below dense but surface visible; stems densely pubescent when young but sparsely so in age; plants small shrubs *Solanum subinerme* (124. Solanaceae)
- ☆ Leaf pairs ± equal:
- Blades, when held to light, with punctations or glandular or pellucid dots or lepidote scales below (may be on veins):
- Plants lianas; branch axils sometimes with long recurved spines:
- Most parts with stalked or sessile T-shaped trichomes; lower blade surface with a few, large, rounded glands near base (sunken into tissue, not at all free or peltate) *Tetrapteris macrocarpa* (Fig. 312; 71. Malpighiaceae)
- Plants lacking T-shaped trichomes; blades either lacking glands altogether or with glandlike peltate scales scattered over lower surface:
- Blades reddish-brown-pubescent on lower surface, the veins more densely pubescent; stems apparently lacking recurved axillary spines *Combretum laxum* var. *epiphyticum* (Fig. 420; 105. Combretaceae)
- Blades glabrous or nearly so on underside except on veins or in vein axils; stems sometimes with prominent axillary spines:
- Stems with axillary spines; underside of blades glabrous on veins, possessing axillary tufts, lacking conspicuous, pale, peltate scales over the surface *Combretum decandrum* (Figs. 416, 417, and fig. on p. 20; 105. Combretaceae)
- Stems lacking axillary spines; underside of blades pubescent on veins, lacking axillary tufts, possessing conspicuous, pale, peltate scales over the surface *Combretum fruticosum* (Fig. 418; 105. Combretaceae)
- Plants not as above:
- ◆ Blades pubescent at least on veins below:
- Blades with at least some stellate trichomes below:
- Blades mostly subcordate at base *Vismia macrophylla* (92. Guttiferae)
- Blades usually not subcordate at base:
- Blades sparsely pubescent below; sap clear *Siparuna guianensis* (57. Monimiaceae)
- Blade surface below obscured by dense (sometimes minute) pubescence; sap yellow or orange:
- Blades usually ovate, broadest near base; petioles more than 1.5 cm long; blades brown or whitish below, conspicuously stellate-pubescent, reddish-pellucid-punctate *Vismia baccifera* (Fig. 394; 92. Guttiferae)
- Blades elliptic, broadest near middle; petioles ca 1 cm long; blades usually green below, very inconspicuously pubescent, black-opaque-punctate *Vismia billbergiana* (Fig. 395; 92. Guttiferae)
- Blades lacking stellate trichomes below:
- Most blades less than 3 cm wide:
- Largest blades less than 6 cm long:
- Blade margins distinctly undulate *Eugenia nesiotica* (Fig. 424; 106. Myrtaceae)
- Blade margins not undulate *Eugenia principium* (106. Myrtaceae)
- Largest blades more than 6 cm long:
- Punctations opaque when dry *Adenaria floribunda* (102. Lythraceae)
- Punctations pellucid:
- Blades caudate-acuminate, the acumen to 1.5 cm long *Myrcia fosteri* (106. Myrtaceae)
- Blades acuminate but not caudate *Eugenia venezuelensis* (106. Myrtaceae)
- Most blades more than 3 cm wide:
- Plants lianas (*Aegiphila elata* sometimes a climbing shrub); blades ovate or broadly elliptic:
- Petioles less than 2 cm long; blades all simple; tendrils lacking *Aegiphila elata* (122. Verbenaceae)
- Petioles more than 3 cm long; adult plants with some blades bifoliate; tendrils simple *Cydista heterophylla* (Fig. 492; 126. Bignoniaceae)

- Plants shrubs or trees; blades oblong-elliptic to narrowly elliptic or lanceolate:
 - T-shaped trichomes restricted to midrib above and below; blades with a few round glands, especially at tip and base *Spachea membranacea* (71. Malpighiaceae)
 - Trichomes not T-shaped; blades lacking glands:
 - Younger parts with conspicuous orange punctations (black and opaque when dry); blades villous mostly on veins below, glabrate above *Adenaria floribunda* (102. Lythraceae)
 - Younger parts lacking orange (black or opaque when dry) punctations; blades with appressed, often minute trichomes on surface below:
 - Lateral veins in more than 12 pairs, prominently raised below; blades \pm thick, obtuse to short-acuminate *Psidium guajava* (106. Myrtaceae)
 - Lateral veins in fewer than 10 pairs; blades not thick, usually acuminate:
 - Blades glabrous above, with minute stellate trichomes below; sap yellow or orange *Vismia billbergiana* (Fig. 395; 92. Guttiferae)
 - Blades with trichomes at least on midrib above, with fine, simple, appressed pubescence below; sap clear:
 - Most blades less than 10 cm long and with a long blunt acumen *Eugenia galalonensis* (106. Myrtaceae)
 - Most blades more than 10 cm long, sometimes mucronate or with a sharp acumen *Aegiphila panamensis* (Fig. 478; 122. Verbenaceae)
- ◆ Blades essentially glabrous:
 - Petioles less than 5 mm long or lacking:
 - Blades sessile, less than 4 cm wide *Mouriri myrtilloides* subsp. *parvifolia* (107. Melastomataceae)
 - Blades petiolate:
 - Blades less than 7 cm long:
 - Young stems quadrangular or with 4 slender winglike ribs, glabrous or inconspicuously appressed-pubescent or minutely and inconspicuously puberulent:
 - Blades not noticeably glandular-punctate on surfaces, very sparsely pellucid-punctate, the youngest stems inconspicuously puberulent *Mouriri myrtilloides* subsp. *parvifolia* (107. Melastomataceae)
 - Blades conspicuously glandular-punctate on surfaces, densely pellucid-punctate, the youngest stems glabrous or appressed-pubescent:
 - Youngest stems wholly glabrous; tertiary venation of upper blade surface clearly visible, weakly raised, much less conspicuous than major lateral veins *Psidium friedrichsthalianum* (Fig. 425; 106. Myrtaceae)
 - Youngest stems sparsely appressed-pubescent; tertiary venation of upper blade surface obscure but scarcely less conspicuous than major lateral veins *Calycolpus warscewiczianus* (Fig. 423; 106. Myrtaceae)
 - Young stems terete, lacking wings, conspicuously short-puberulent or inconspicuously appressed-pubescent:
 - Young stems and petioles inconspicuously appressed-pubescent:
 - Leaf blades usually drying greenish (at least on lower surface), the veins all prominulous on upper surface (including the reticulate veins) *Myrcia gatunensis* (106. Myrtaceae)
 - Leaf blades usually drying brown (the upper surface usually dark brown), the veins of upper surface obscure, especially the collecting vein, the reticulate veins not at all visible *Calycolpus warscewiczianus* (Fig. 423; 106. Myrtaceae)
 - Young stems and petioles conspicuously short-puberulent:
 - Blades coriaceous, pale brown on drying, seldom more than 5 cm long, the midrib conspicuously puberulent on lower surface, glabrous on upper surface *Eugenia principium* (106. Myrtaceae)
 - Blades not coriaceous, drying green, frequently more than 5 cm long, the midrib glabrous on lower surface, sometimes inconspicuously puberulent along midrib on upper surface *Eugenia oerstediana* (106. Myrtaceae)
 - Blades more than 7 cm long:
 - Blades abruptly acuminate, with a short sharp cusp ca 1 mm long, the punctations below often brown, conspicuous *Combretum fruticosum* (Fig. 418; 105. Combretaceae)
 - Blades not as above:
 - ◇ Blades caudate-acuminate:
 - Blades more than 12 cm long *Psidium anglohondurense* (106. Myrtaceae)
 - Blades less than 10 cm long:
 - Leaf blades usually drying greenish (at least on lower surface), the veins all prominulous on upper surface (including the reticulate veins) *Myrcia gatunensis* (106. Myrtaceae)
 - Leaf blades usually drying brown (the upper surface usually dark brown), the veins of upper surface obscure, especially the collecting vein, the reticulate veins not at all visible *Calycolpus warscewiczianus* (Fig. 423; 106. Myrtaceae)

- ◊ Blades abruptly acuminate:
 - Blades less than 12 cm long *Psidium friedrichsthalianum* (Fig. 425; 106. Myrtaceae)
 - Blades more than 12 cm long:
 - Blades acute to abruptly and usually bluntly acuminate, drying \pm concolorous, usually brown; stems tending to be somewhat flattened near nodes *Eugenia coloradensis* (106. Myrtaceae)
 - Blades narrowly long and sharply acuminate, drying bicolorous, green, much paler beneath; stems terete; new leaves reddish *Psidium anglohondurense* (106. Myrtaceae)
- Petioles at least sometimes more than 5 mm long:
 - Blades more than 3 times longer than broad:
 - Blades toothed *Koanophyllon wetmorei* (Fig. 548; 133. Compositae)
 - Blades entire:
 - Plants lianas or small shrubs; blades with lepidote scales below *Combretum fruticosum* (Fig. 418; 105. Combretaceae)
 - Plants trees; blades lacking lepidote scales:
 - Reticulate veins connecting the major lateral veins very conspicuous, sinuate; blades to 9 cm wide *Marila laxiflora* (92. Guttiferae)
 - Reticulate veins not conspicuously sinuate; blades to 6 cm wide *Syzygium jambos* (Fig. 426; 106. Myrtaceae)
 - Blades less than 3 times longer than broad:
 - Sap copious, milky; stems with ridges:
 - Plants lianas; reticulate veins conspicuous; punctations restricted to veins, not raised *Odontadenia puncticulosa* (Figs. 458–60; 118. Apocynaceae)
 - Plants trees; reticulate veins obscure; punctations raised, not obviously associated with veins *Tabernaemontana arborea* (Fig. 464; 118. Apocynaceae)
 - Sap clear or the stems lacking ridges:
 - Basal vein axils with dense clusters of glands below *Cydista heterophylla* (Fig. 492; 126. Bignoniaceae)
 - Basal vein axils lacking dense clusters of glands below:
 - Reticulate veins connecting the lateral veins very conspicuous, sinuate *Marila laxiflora* (92. Guttiferae)
 - Reticulate veins very inconspicuous, not sinuate:
 - Lower blade surface with dense, conspicuous, peltate, usually concave scales *Combretum fruticosum* (Fig. 418; 105. Combretaceae)
 - Lower blade surface lacking peltate scales, with conspicuous, often raised glands but these never appearing at all free from the leaf tissue:
 - At least the younger stems with 4 ribs, appearing quadrangular *Psidium friedrichsthalianum* (Fig. 425; 106. Myrtaceae)
 - Stems not ribbed or quadrangular, sometimes flattened laterally so as to appear \pm 2-edged *Eugenia coloradensis* (106. Myrtaceae)
 - Blades lacking punctations, glandular and pellucid dots, and lepidote scales below:
 - Leaves often verticillate or congested at tips of branches:
 - Leaves not congested at apex of branches but verticillate with 4 or 5 leaves per node; sap milky *Allamanda cathartica* (118. Apocynaceae)
 - Leaves clustered at tips of branches; sap not milky:
 - Blades less than 10 cm long, with axillary domatia below; stipules lacking *Terminalia amazonica* (Figs. 421, 422; 105. Combretaceae)
 - Blades more than 15 cm long, lacking axillary domatia; interpetiolar stipules caducous *Aseis blackiana* (Fig. 512; 130. Rubiaceae)
 - Leaves not verticillate, not congested at apex of branches:
 - ▲ Plants parasitic shrubs or lianas, the blades generally coriaceous:
 - Stems square, or 2-edged at least near apex:
 - Stems square; blades less than 1.5 cm wide *Phoradendron quadrangule* (42. Loranthaceae)
 - Stems 2-edged at least near apex; blades more than 2 cm wide *Phthirusa pyrifolia* (42. Loranthaceae)
 - Stems terete:
 - Blades usually \pm elliptic, acuminate, \pm acute at base *Phoradendron piperoides* (Fig. 212; 42. Loranthaceae)
 - Blades ovate, usually rounded at apex, obtuse to subcordate at base:
 - Plants lianas, more than 1 m long; blades less than 5 cm long *Struthanthus orbicularis* (42. Loranthaceae)
 - Plants shrubby, less than 1 m long; blades more than 5 cm long:
 - Blades \pm cuneate, the petioles more than 5 mm long *Oryctanthus occidentalis* (Fig. 211; 42. Loranthaceae)
 - Blades rounded to subcordate at base, the petioles less than 5 mm long:

Leaf blades broadly rounded to subcordate at base . . . *Oryctanthus cordifolius* (42. Loranthaceae)

Leaf blades obtuse to rounded at base (rarely subcordate)

. *Oryctanthus alveolatus* (42. Loranthaceae)

▲ Plants not parasitic:

★ Plants lianas:

⊙ Blades pubescent below:

Trichomes simple, erect to ± appressed:

Young stems and blades below conspicuously and densely soft-pubescent:

Blades ± rounded or obtuse at base; midrib not arched

. *Aegiphila cephalophora* (122. Verbenaceae)

Blades often subcordate at base; midrib arched *Prestonia ipomiiifolia* (118. Apocynaceae)

Young stems and blades not conspicuously and densely pubescent:

Blades toothed:

Plants epiphytic lianas, often rooting at nodes; blades inequilateral at base

. *Drymonia serrulata* (Fig. 503; 127. Gesneriaceae)

Plants arching shrubs or lianas; blades equilateral at base:

Blades rounded to cordate, often with 3–5 palmate veins at base, less than 13 cm long

. *Heterocondylus vitalbis* (133. Compositae)

Blades obtuse to acute at base, not palmately veined, often more than 13 cm long

. *Wulffia baccata* (Fig. 553; 133. Compositae)

Blades entire:

Stems with stout axillary spines *Pisonia aculeata* (Fig. 228; 48. Nyctaginaceae)

Stems lacking spines:

Blades with reticulate venation not conspicuous (tertiary veins often visible on *Mandevilla villosa*); most blades less than 8 cm long:

Blades with major lateral veins obscure, the tertiary veins not visible; canopy lianas

. *Cynanchum recurvum* (119. Asclepiadaceae)

Blades with major lateral and secondary veins conspicuous

. *Mandevilla villosa* (Fig. 453; 118. Apocynaceae)

Blades with reticulate venation conspicuous without magnification (on dried specimens); at least some blades more than 8 cm long:

Petioles ca 1.5 cm or more long; blades with the lateral veins arising mostly from

basal half of midrib *Mikania leiostachya* (Fig. 549; 133. Compositae)

Petioles less than 1 cm long; blades with the lateral veins distributed evenly along midrib:

Stems usually with interpetiolar ridges; blade midribs and major lateral veins

bearing both pilose and puberulent trichomes

. *Forsteronia myriantha* (118. Apocynaceae)

Stems lacking interpetiolar ridges; blade midribs and major lateral veins glabrous

or merely sparsely pilose *Combretum cacocucia* (105. Combretaceae)

Trichomes T-shaped, often appearing as appressed, 2-ended trichomes but peltately attached (swivels on center):

Blades densely pubescent below:

Trichomes contiguous below, obscuring surface:

Blades ovate, broadly rounded at base, less than twice as long as broad

. *Stigmaphyllon hypargyrum* (71. Malpighiaceae)

Blades oblong-elliptic, narrowly rounded at base, more than twice as long as broad

. *Hiraea faginea* (71. Malpighiaceae)

Trichomes below not contiguous:

Trichomes below stalked:

Blades less than 10 cm wide, long-acuminate; petioles with 2 conspicuous, slender

glands at apex; stems sparsely pubescent *Hiraea quapara* (71. Malpighiaceae)

Blades more than 10 cm wide, cuspidate to short-acuminate; petioles lacking glands at

apex; stems densely ferruginous-tomentose

. *Hiraea grandifolia* (Fig. 308; 71. Malpighiaceae)

Trichomes below not stalked, appressed:

Petioles ca 1 cm long, with small, inconspicuous glands

. *Banisteriopsis cornifolia* (71. Malpighiaceae)

Petioles more than 1.5 cm long, with a conspicuous pair of glands at apex:

Blades broadly ovate, occasionally lobed, often palmately veined at base, less than

twice as long as broad . . . *Stigmaphyllon lindemanum* (Fig. 311; 71. Malpighiaceae)

Blades elliptic or ovate-elliptic, not lobed or palmately veined, more than twice as

long as broad *Stigmaphyllon puberum* (71. Malpighiaceae)

Blades not densely pubescent below:

⊕ Blades mostly obovate, the base narrow and subcordate . . . *Hiraea reclinata* (71. Malpighiaceae)

- ⊙ Blades ± ovate or elliptic, the base obtuse to rounded or subcordate:
 - Petioles with 2 glands at apex:
 - Blades elliptic, not palmately veined at base *Stigmaphyllon ellipticum* (71. Malpighiaceae)
 - Blades ovate, palmately veined at base *Stigmaphyllon lindenianum* (Fig. 311; 71. Malpighiaceae)
 - Petioles lacking glands:
 - Stems with sparse to dense, appressed, T-shaped trichomes, soon glabrate to glabrous; blades acuminate, obtuse to rounded at base *Mascagnia nervosa* (Fig. 309; 71. Malpighiaceae)
 - Stems tomentose with sessile and stalked T-shaped trichomes, at least the sessile ones persisting on stems; blades very short-acuminate or acute *Tetrapteris macrocarpa* (Fig. 312; 71. Malpighiaceae)
- ⊙ Blades essentially glabrous below (may have cystoliths appearing as trichomes):
 - Plants with milky sap:
 - Blades mostly less than 5 cm wide:
 - Blades with several (1–4) conspicuous glands at base of midrib above:
 - Blades lacking axillary pits below, often rounded at base *Mesechites trifida* (Fig. 454; 118. Apocynaceae)
 - Blades with pits in axils below, usually obtuse at base, coriaceous *Forsteronia viridescens* (118. Apocynaceae)
 - Blades lacking conspicuous glands at base of midrib, usually acute at base:
 - Blades with small pitlike domatia in axils below . . . *Forsteronia peninsularis* (118. Apocynaceae)
 - Blades lacking small pitlike domatia in axils:
 - Blades markedly bicolorous, the lateral veins inconspicuous, the apex gradually acuminate *Prestonia acutifolia* (118. Apocynaceae)
 - Blades not markedly bicolorous, the lateral veins conspicuous, the apex abruptly acuminate or mucronate *Rhabdadenia biflora* (118. Apocynaceae)
 - Blades mostly more than 5 cm wide:
 - Blades with pitlike axillary domatia below and 1–4 conic glands at base of midrib above *Forsteronia viridescens* (118. Apocynaceae)
 - Blades lacking pitlike axillary domatia and glands:
 - Stems corky, with many conspicuous lenticels *Prestonia obovata* (118. Apocynaceae)
 - Stems ± smooth:
 - Blades ovate-cordate; petioles ca 6 cm long *Cynanchum cubense* (119. Asclepiadaceae)
 - Blades not ovate-cordate; petioles less than 6 cm long:
 - Blades usually with 10 or more pairs of lateral veins *Odontadenia macrantha* (Figs. 455–57; 118. Apocynaceae)
 - Blades usually with 9 or fewer pairs of lateral veins:
 - Reticulate veins conspicuous below, the midrib lacking a raised ridge; veins with sessile, opaque, plate-shaped glands; apex of blades not markedly downturned *Odontadenia puncticulosa* (Figs. 458–60; 118. Apocynaceae)
 - Reticulate veins inconspicuous and/or the midrib with a raised ridge in center; veins lacking glands; apex of blades various:
 - Reticulate veins fine, distinct; blades usually obtuse but sometimes rounded at base *Prestonia portobellensis* (Fig. 461; 118. Apocynaceae)
 - Reticulate veins obscure, few; blades mostly rounded at base, becoming subcordate *Marsdenia crassipes* (119. Asclepiadaceae)
 - Plants lacking milky sap:
 - ▣ Blades broadly rounded at base:
 - Blades asperous:
 - Blades densely covered with minute lepidote scales especially below; margins often scabridulous *Petrea aspera* (Fig. 479; 122. Verbenaceae)
 - Blades lacking lepidote scales; margins glabrous *Prionostemma aspera* (Fig. 334; 78. Hippocrateaceae)
 - Blades not asperous:
 - Stems with very short, simple trichomes *Mikania tonduzii* (133. Compositae)
 - Stems glabrous or with T-shaped trichomes:
 - Petioles with 2 conspicuous glands 1–2 mm long at apex:
 - Petioles slender, 1–3 cm long . . . *Stigmaphyllon ellipticum* (Fig. 310; 71. Malpighiaceae)
 - Petioles thick, 0.7–1.5 cm long *Mascagnia hippocrateoides* (71. Malpighiaceae)
 - Petioles lacking 2 conspicuous glands:
 - Blades orbicular to very widely elliptic; young stems and buds golden-puberulent *Tetrapteris macrocarpa* (Fig. 312; 71. Malpighiaceae)
 - Blades elliptic; young stems and buds not golden-puberulent:

- Stipule scars lacking *Hylенаеа praecelsa* (78. Hippocrateaceae)
- Stipule scars present, sometimes encircling stem:
- Reticulate veins not obvious *Tontelea richardii* (Fig. 335; 78. Hippocrateaceae)
- Reticulate and even tertiary veins evident
- *Mascagnia nervosa* (Fig. 309; 71. Malpighiaceae)
- ▣ Blades ± acute at base:
- Blades somewhat toothed:
- Young stems densely puberulent, lacking wings below petiole when dry
- *Hippocratea volubilis* (Fig. 333; 78. Hippocrateaceae)
- Young stems glabrous, with minute wings below petiole when dry
- *Anthodon panamense* (Figs. 331, 332; 78. Hippocrateaceae)
- Blades entire:
- Blades with 3–5 palmate veins from near base *Mikania tonduzii* (133. Compositae)
- Blades pinnately veined throughout:
- Blades sometimes broadly ovate, with the lateral veins inconspicuous; plants large, much-branched lianas
- *Gnetum leyboldii* var. *woodsonianum* (Figs. 41, 42; 13. Gnetaceae)
- Blades ± elliptic to obovate, with the lateral veins distinct:
- Blades asperous and minutely lepidote below, the margins often scabridulous
- *Petrea aspera* (Fig. 479; 122. Verbenaceae)
- Blades not asperous below:
- Blades drying with linear cystoliths; largest blades less than 12 cm long; plants lianas on the forest floor *Justicia graciliflora* (Fig. 506; 129. Acanthaceae)
- Blades not drying with crystals or cystoliths; largest blades usually more than 12 cm long:
- Young stems puberulent, the trichomes erect, simple; blades often narrowly subcordate at base *Combretum laxum* var. *laxum* (Fig. 419; 105. Combretaceae)
- Young stems with appressed or stalked, T-shaped trichomes; blades not narrowly subcordate at base (usually acute to obtuse or subrounded):
- Blades subcoriaceous, drying brown, the reticulate venation raised, conspicuous; pubescence reddish-brown, the younger parts tomentose
- *Heteropteris laurifolia* (71. Malpighiaceae)
- Blades moderately thin, drying green or brownish, the reticulate venation scarcely raised, not conspicuous; pubescence whitish, ± sericeous but mostly soon deciduous:
- Blades usually long-acuminate, 2.5–3 times longer than wide; considerable pubescence persisting on stems *Tetrapteris discolor* (71. Malpighiaceae)
- Blades acute to short-acuminate, ca 2(2.5) times longer than wide; stems soon essentially glabrous *Tetrapteris seemannii* (71. Malpighiaceae)
- ★ Plants shrubs or trees, not lianas:
- Blades pubescent:
- Blades densely and conspicuously pubescent below:
- Blades with 10 or fewer pairs of lateral veins:
- Blades entire, smooth above; veins ± equidistant; stems with prominent leaf scars and stalked T-shaped trichomes *Byrsonima crassifolia* (71. Malpighiaceae)
- Blades conspicuously toothed, asperous above; veins closer to base than apex; stems lacking prominent leaf scars, the trichomes simple:
- Reticulate veins of lower leaf surface conspicuous, densely hispid (the trichomes stiffly erect) *Clibadium surinamense* (133. Compositae)
- Reticulate veins of lower leaf surface not raised, glabrate to strigose (the trichomes ± appressed or strongly leaning) *Clibadium asperum* (133. Compositae)
- Blades with 11 or more pairs of lateral veins:
- Stems ± square; trichomes on blades stellate
- *Siparuna pauciflora* (Figs. 246, 247; 57. Monimiaceae)
- Stems terete; trichomes on blades simple:
- Stems and lower blade surfaces brown; blades ending abruptly at base; plants trees, more than 6 m tall at maturity *Vochysia ferruginea* (73. Vochysiaceae)
- Stems and lower blade surfaces not brown; blades decurrent onto petioles; plants usually shrubs, less than 3 m tall *Aphelandra sinclairiana* (129. Acanthaceae)
- Blades not densely pubescent below:
- ◇ Trichomes T-shaped:
- Blades subsessile or with densely ferruginous young stems:
- Blades subsessile; plants shrubs, less than 2 m tall; young stems not densely ferruginous-pubescent *Malpighia romeroana* (71. Malpighiaceae)
- Blades conspicuously petiolate; plants trees, usually more than 10 m tall; young stems densely ferruginous-pubescent *Byrsonima spicata* (71. Malpighiaceae)

- Blades petiolate and not with ferruginous pubescence on young stems:
 Trichomes on underside of blades restricted to midrib, brownish
 *Spachea membranacea* (71. Malpighiaceae)
 Trichomes on underside of blades sparse to moderate, throughout surface (may be minute), whitish *Bunchosia cornifolia* (71. Malpighiaceae)
- ◊ Trichomes not T-shaped:
 Petioles mostly more than 1 cm long:
 Blades with conspicuous glands at base of midrib and sometimes along margins
 *Colubrina glandulosa* (81. Rhamnaceae)
 Blades lacking glands:
 Blades with 3–5 strong basal veins, often remotely toothed
 *Heterocondylus vitalbis* (133. Compositae)
 Blades pinnately veined, entire:
 Blades drying without prominent cystoliths; stems terete; blades \pm elliptic
 *Guapira standleyanum* (Fig. 226; 48. Nyctaginaceae)
 Blades drying with prominent cystoliths; stems often quadrangular; blades hetero-
 morphic, often \pm asymmetrical *Trichanthera gigantea* (129. Acanthaceae)
- Petioles mostly less than 1 cm long:
 Blades less than 1.5 cm broad or mostly more than 5.5 cm broad, entire, estipulate:
 Plants epiphytic shrubs; blades to 1.5 cm wide *Columnnea billbergiana* (127. Gesneriaceae)
 Plants shrubs or small trees; blades more than 3 cm wide (usually more than 5.5 cm) . .
 *Siparuna guianensis* (57. Monimiaceae)
 Blades 1.5–5.5 cm broad, usually toothed, stipulate:
 Blades oblique and rounded to slightly subcordate at base
 *Rinorea sylvatica* (Fig. 397; 95. Violaceae)
 Blades usually \pm equilateral, acute to obtuse at base:
 Blades caudate-acuminate, sparsely hirsute on veins below, less than 13 cm long . . .
 *Rinorea squamata* (95. Violaceae)
 Blades acuminate, not caudate, densely puberulent throughout below, to 17 cm long
 *Aegiphila panamensis* (Fig. 478; 122. Verbenaceae)
- Blades essentially glabrous (some with cystoliths):
 □ Petioles mostly more than 1 cm long:
 Lateral veins very closely spaced and/or inconspicuous:
 Blades oblong, emarginate at apex; lateral veins \pm perpendicular to midrib; plants not
 epiphytic *Calophyllum longifolium* (92. Guttiferae)
 Blades not oblong, not emarginate at apex:
 Blades obovate, rounded at apex; lateral veins ascending; plants epiphytic trees:
 Blades very thick and leathery, drying opaque *Clusia odorata* (Fig. 387; 92. Guttiferae)
 Blades thick but not leathery, drying translucent
 *Havetiopsis flexilis* (Fig. 388; 92. Guttiferae)
 Blades oblong-elliptic, acuminate at apex:
 Lateral veins very inconspicuous, ascending:
 Blades usually broadest above the middle, coriaceous, the midrib moderately indis-
 tinct, smooth, the primary lateral veins numerous and close, the reticulate vena-
 tion not visible *Clusia odorata* (Fig. 387; 92. Guttiferae)
 Blades usually broadest at about the middle, relatively thin, the midrib obviously
 raised beneath, bearing close minute projections under magnification, the primary
 lateral veins mostly in 8–12 pairs, ca 1 cm apart
 *Tovomitopsis nicaraguensis* (Fig. 393; 92. Guttiferae)
 Lateral veins conspicuous, \pm perpendicular to midrib:
 Blades dull on both surfaces (especially below); veins not raised, the marginal collect-
 ing vein not visible; sap in younger parts whitish-yellow; upper surface, when
 dry, with the reticulate veins not prominulous and the collecting vein obscure
 *Rheedia edulis* (Fig. 389; 92. Guttiferae)
 Blades at least weakly shiny; veins weakly raised, the collecting vein clearly visible
 on both surfaces; sap in younger parts bright yellow; upper surface, when dry,
 with the reticulate veins prominulous and the collecting vein evident
 *Rheedia acuminata* (92. Guttiferae)
- Lateral veins conspicuous and distant:
 △ Larger blades more than 15 cm long:
 ★ Plants shrubs, less than 2 m tall, or hemiepiphytic shrubs or small trees:
 Plants hemiepiphytic shrubs or small trees, usually restricted to higher canopy, rare;
 blades rounded to acute at apex *Hydrangea peruviana* (60. Saxifragaceae)
 Plants not hemiepiphytic; blades acuminate at apex:
 Younger branchlets ferruginous-pubescent, slender, lenticellate; blades lacking a
 marginal connecting vein *Neea amplifolia* (Fig. 227; 48. Nyctaginaceae)

- Younger branchlets glabrous, thick, not lenticellate; blades with a marginal connecting vein *Dendropanax stenodontus* (109. Araliaceae)
- ★ Plants trees, more than 3 m tall:
- Sap yellow:
- Trees ca 10 m tall with stilt-roots; largest blades usually more than 25 cm long *Tovomita longifolia* (Fig. 391; 92. Guttiferae)
- Trees ca 5 m tall, lacking stilt roots; largest blades usually less than 25 cm long (juveniles sometimes larger):
- Petioles less than 1.5 cm long; lateral veins below conspicuously loop-connected, with the secondary veins many, closely spaced, parallel, prominulous, connecting the lateral veins *Marila laxiflora* (92. Guttiferae)
- Most petioles more than 2 cm long; lateral veins below at most weakly loop-connected, with the secondary veins reticulate *Tovomitopsis nicaraguensis* (Fig. 393; 92. Guttiferae)
- Sap not colored:
- Petioles to 3 cm long, averaging ca 1.5 cm *Guapira standleyanum* (Fig. 226; 48. Nyctaginaceae)
- Petioles less than 1.5 cm long, averaging ca 0.7 cm *Petrea aspera* (Fig. 479; 122. Verbenaceae)
- △ All blades less than 15 cm long:
- Plants hemiepiphytic shrubs; blades usually rounded (sometimes acute) at apex; reticulate veins prominent below when dry *Hydrangea peruviana* (60. Saxifragaceae)
- Plants not hemiepiphytic; blades acuminate at apex:
- Blades somewhat palmately veined at base, with 2 glands at base on either side of petiole and with other glands scattered along blade margins *Colubrina glandulosa* (81. Rhamnaceae)
- Blades pinnately veined throughout, lacking glands:
- Young stems densely ferruginous-pubescent; older stems rough; sap clear; plants usually medium-sized trees; blades drying dark *Guapira standleyanum* (Fig. 226; 48. Nyctaginaceae)
- Young stems ± glabrous; older stems smooth; sap yellow; plants usually small trees; blades not drying dark *Tovomita stylosa* (Fig. 392; 92. Guttiferae)
- Petioles mostly less than 1 cm long:
- Plants with milky or yellow sap:
- Blades obovate or oblanceolate:
- Blades acuminate at apex, the veins inconspicuous; sap milky; plants not hemiepiphytic *Stemmadenia grandiflora* (Figs. 462, 463; 118. Apocynaceae)
- Blades rounded at apex, the veins obscure; sap yellow; plants hemiepiphytic trees:
- Blades very thick, leathery, drying opaque *Clusia odorata* (Fig. 387; 92. Guttiferae)
- Blades thick, not leathery, drying translucent *Havetiopsis flexilis* (Fig. 388; 92. Guttiferae)
- Blades oblong or elliptic:
- Sap milky; lateral veins more than 5 mm apart; stems not wrinkled when dry:
- Blades elliptic or lanceolate-elliptic, long-acuminate, with axillary domatia below *Malouetia guatemalensis* (Fig. 452; 118. Apocynaceae)
- Blades oblong, short-acuminate, lacking axillary domatia *Lacmellea panamensis* (118. Apocynaceae)
- Sap yellow; lateral veins either closely spaced or ± obscure; stems with longitudinal wrinkles when dry:
- Blades less than 8 cm long and 3 cm wide; plants very large trees with adventitious roots *Symphonia globulifera* (Fig. 390; 92. Guttiferae)
- Blades more than 8 cm long and 3 cm wide; plants small to medium-sized trees lacking adventitious roots:
- (Fresh) Blades dull on both surfaces, especially below; veins obscure, not at all raised; marginal collecting vein not visible; sap in younger parts whitish-yellow; (Dry) Reticulate veins not prominulous on upper surface; collecting vein obscure to lacking above *Rheedia edulis* (Fig. 389; 92. Guttiferae)
- (Fresh) Blades at least weakly shiny; veins weakly raised; collecting vein usually clearly visible on both surfaces; sap in younger parts bright yellow; (Dry) Reticulate veins prominulous on upper surface; collecting vein also prominulous on upper surface *Rheedia acuminata* (92. Guttiferae)
- Plants lacking yellow or milky sap:
- ☆ Plants hemiepiphytic:
- Plants small shrubs, less than 1 m tall; blades usually less than 3 cm wide *Codonanthe crassifolia* (Fig. 502), *C. uleana* (127. Gesneriaceae)
- Plants trees or large shrubs, more than 1 m tall; blades more than 3 cm wide:

- Blades gradually tapered to base, thick, the veins obscure; sap thick and copious; plants common *Clusia odorata* (Fig. 387; 92. Guttiferae)
- Blades ending abruptly at petiole, thin, the veins conspicuous; sap not thick or copious; plants rare *Hydrangea peruviana* (60. Saxifragaceae)
- ☆ Plants not hemiepiphytic:
- Mature blades mostly less than 7 cm long; at least the youngest stems winged when dry:
Plant a cultivated shrub at the Laboratory Clearing; most larger stems winged
..... *Thunbergia erecta* (129. Acanthaceae)
- Plants shrubs or trees, not cultivated; older stems not winged:
Blades mostly sessile, sharply acuminate, obtuse to rounded at base, lacking domatia;
plants usually shrubs
..... *Mouriri myrtilloides* subsp. *parvifolia* (107. Melastomataceae)
- Blades petiolate, with a rounded acumen, acute at base, bearing a small subterminal cavity; plants medium-sized trees
..... *Lafoensia puniceifolia* (Figs. 410, 411; 102. Lythraceae)
- Mature blades mostly more than 7 cm long or the younger stems not winged when dry
(*Calycolpus warscewiczianus* with leaves to only 8 cm long but the stems not winged):
Largest blades less than 3 cm wide; lateral veins many (more than 15 pairs) and closely spaced (less than 2 mm apart)
..... *Calycolpus warscewiczianus* (Fig. 423; 106. Myrtaceae)
- Largest blades more than 3 cm wide; lateral veins fewer and more widely spaced:
Blades estipulate, drying with prominent linear cystoliths
..... *Justicia graciliflora* (Fig. 506; 129. Acanthaceae)
- Blades stipulate, drying without linear cystoliths:
Stems and petioles essentially glabrous; blades inconspicuously toothed in apical half, the lateral veins loop-connected
..... *Cassipourea elliptica* (104. Rhizophoraceae)
- Stems and petioles with T-shaped trichomes:
Plants shrubs, usually less than 2 m tall; stipules interpetiolar
..... *Malpighia romeroana* (71. Malpighiaceae)
- Plants lianas or trees, usually more than 3 m tall; stipules axillary or lacking:
Plants lianas or scandent shrubs; mature blades glabrous above, coriaceous
..... *Heteropteris laurifolia* (71. Malpighiaceae)
- Plants trees, not scandent; mature blades pubescent on midrib above, not coriaceous:
Most blades with conspicuous glands near midrib at base below and often scattered on surface *Spachea membranacea* (71. Malpighiaceae)
- Most blades eglandular *Byrsonima spicata* (71. Malpighiaceae)

KEY 2: LEAVES SIMPLE, ALTERNATE OR SPIRALED; PLANTS NOT LIANAS

- Petioles with paired, usually stipitate glands near apex; sap milky; leaves very shallowly crenate or entire; plants not stellate-pubescent *Sapium aucuparium*, *S. caudatum* (Fig. 325; 75. Euphorbiaceae)
- Petioles lacking glands near apex or the sap not milky:
- Blades not entire (toothed or sinuate):
 - ◆ Blades essentially glabrous:
 - Petioles mostly more than 1 cm long:
 - Leaves nearly 1 m long, densely clustered at apices of stout stems; stems with numerous, persistent, imbricate, long stipules *Cespedezia macrophylla* (89. Ochnaceae)
 - Leaves and stems not as above:
 - Blades 5-lobed; petioles more than 20 cm long *Carica cauliflora* (Fig. 409; 99. Caricaceae)
 - Blades not lobed; petioles less than 10 cm long:
 - Petioles with a pair of large glands at apex; blades evenly pinnately veined, lacking axillary domatia below *Sapium caudatum* (Fig. 325; 75. Euphorbiaceae)
 - Petioles lacking glands at apex:
 - Blades with conspicuous glands at base:
 - Blades with axillary domatia below *Alchornea latifolia* (75. Euphorbiaceae)
 - Blades lacking axillary domatia:
 - Basal glands red on both surfaces when fresh, inconspicuous when dry; twigs tan, not pubescent; basal veins extending less than one-third the length of blade
..... *Alchornea costaricensis* (Fig. 318; 75. Euphorbiaceae)
 - Basal glands green above, not visible below, conspicuous when dry; twigs reddish-brown-pubescent when young; basal veins extending more than two-thirds the length of blade
..... *Hasseltia floribunda* (Fig. 399; 96. Flacourtiaceae)
 - Blades lacking glands:

- Plants shrubs, with slender trunks, usually less than 4 m tall:
 - Blades sparsely toothed, at most 20 teeth on each side of blade *Dendropanax stenodontus* (Fig. 443; 109. Araliaceae)
 - Blades with more than 30 teeth on each side of blade:
 - Leaves always broadest well above the middle, clustered at apex of stem; plants erect shrubs, usually more than 2.5 m tall; stems more than 1 cm diam *Gustavia fosteri* (103. Lecythidaceae)
 - Leaves broadest usually at or below the middle; plants shrubs, usually less than 1 m tall or vinelike; stems usually less than 7 mm diam:
 - Plants usually less than 1 m tall; blade margins with minute, subulate, regular teeth; petioles to 2 cm long *Ardisia pellucida* (112. Myrsinaceae)
 - Plants usually vinelike shrubs more than 2 m long; blades irregularly toothed; most petioles more than 3 cm long *Urera eggertii* (Fig. 210; 40. Urticaceae)
- Plants trees, with stout trunks:
 - Blades more than 30 cm long, oblanceolate; leaves densely spiraled at apices of branches:
 - Lateral veins apparent *Gustavia superba* (Figs. 414, 415; 103. Lecythidaceae)
 - Lateral veins obscure *Grias fendleri* (Fig. 413; 103. Lecythidaceae)
 - Blades less than 25 cm long, usually broadest near or below the middle; leaves not congested at apices of branches:
 - Blades \pm attenuate to acute at base, decurrent onto petiole; blades ovate *Roupala montana* (41. Proteaceae)
 - Blades obtuse to acute at base, ending abruptly at petiole:
 - Blades coarsely toothed, mostly with 6 or fewer pairs of lateral veins *Alchornea costaricensis* (Fig. 318; 75. Euphorbiaceae)
 - Blades finely toothed, with 7 or more pairs of lateral veins *Saurauia laevigata* (88. Dilleniaceae)
- Petioles mostly less than 1 cm long:
 - Blades nearly 1 m long, densely clustered at apices of stout stems; stems with numerous, persistent, imbricate, long stipules *Cespedezia macrophylla* (89. Ochnaceae)
 - Blades and stems not as above:
 - Blades with pellucid punctations or striations and/or conspicuous axillary domatia:
 - Blades not pellucid-punctate, rounded to subcordate at base and \pm inequilateral; domatia in axils below pocketlike, untufted *Tetrathylacium johansenii* (Fig. 400; 96. Flacourtiaceae)
 - Blades with pellucid punctations or striations, not both rounded and inequilateral at base:
 - Branchlets short, with terminal spines; blades less than 5.5 cm long *Casearia aculeata* (96. Flacourtiaceae)
 - Branchlets not short, lacking terminal spines; blades more than 5.5 cm long:
 - Petioles 1–4(6) mm long; blades \pm equilateral at base, usually with axillary domatia below *Casearia corymbosa* (96. Flacourtiaceae)
 - Petioles 5–10 mm long; blades often inequilateral at base, lacking axillary domatia:
 - Blade margins with 2–4 serrations per cm; blades elliptic *Laetia thammia* (96. Flacourtiaceae)
 - Blade margins with 5–8 serrations per cm; blades oblong *Laetia procera* (96. Flacourtiaceae)
 - Blades lacking pellucid punctations and axillary domatia:
 - Serrations mostly glandular-tipped; trunk spiny, the spines often branched:
 - Blades usually less than 2.5 times longer than wide, shallowly toothed *Xylosma oligandrum* (96. Flacourtiaceae)
 - Blades usually more than 2.5 times longer than wide, deeply toothed *Xylosma chloranthum* (Fig. 401; 96. Flacourtiaceae)
 - Serrations not glandular-tipped:
 - Lateral veins loop-connected:
 - Blades mostly more than 60 cm long *Grias fendleri* (Fig. 413; 103. Lecythidaceae)
 - Blades less than 25 cm long:
 - Largest blades less than 14 cm long *Mabea occidentalis* (75. Euphorbiaceae)
 - Largest blades more than 15 cm long:
 - Stipules amplexicaul *Olmedia aspera* (Fig. 205; 39. Moraceae)
 - Stipules lateral, paired:
 - Blades asperous *Trophis racemosa* (39. Moraceae)
 - Blades smooth *Sorocea affinis* (39. Moraceae)
 - Lateral veins not loop-connected:
 - Lateral veins not raised below; stipules subsistent; petioles slightly canaliculate, with sharp margins *Ouratea lucens* (89. Ochnaceae)
 - Lateral veins raised below:
 - Petioles canaliculate; blades with inconspicuous, flaplike axillary domatia below, rounded to subcordate at base and inequilateral. . . *Tetrathylacium johansenii* (Fig. 400; 96. Flacourtiaceae)
 - Petioles not canaliculate; blades lacking axillary domatia, acute and equilateral at base *Casearia commersoniana* (Fig. 398; 96. Flacourtiaceae)

- ◆ Blades pubescent, at least on veins:
 - ▲ Blades palmately veined at base:
 - Blades with simple trichomes:
 - Petioles less than 2 cm long:
 - Plants shrubs, often vinely, armed with recurved spines on stem (inconspicuously on juveniles) . . .
Celtis iguanaeus (38. Ulmaceae)
 - Plants shrubs or small trees, unarmed:
 - Blades somewhat cordate at base; stipules caducous:
 - Blades 5–15 cm long, 1.5–5 cm wide *Trema micrantha* (Fig. 193; 38. Ulmaceae)
 - Blades (10)15–33 cm long, 6–16 cm wide *Apeiba tibourbou* (84. Tiliaceae)
 - Blades not cordate at base; stipules caducous or persistent, slender:
 - Blades rounded onto petiole; tertiary veins prominent; petioles often more than 1 cm long; stipules persistent *Acalypha diversifolia* (Fig. 315; 75. Euphorbiaceae)
 - Blades acute at base; tertiary veins not prominent; petioles less than 1 cm long; stipules caducous *Casearia guianensis* (96. Flacourtiaceae)
 - Petioles more than 2 cm long:
 - Petioles ± glabrous; blades lobed or unlobed:
 - Blades 3–5-lobed *Cochlospermum vitifolium* (Fig. 396; 94. Cochlospermaceae)
 - Blades not lobed *Myriocarpa yzabalensis* (40. Urticaceae)
 - Petioles conspicuously pubescent with simple trichomes; blades unlobed:
 - Blades with conspicuous cystoliths above when dry, acute, obtuse, or rarely subcordate at base:
 - Blades often more than 20 cm long
Myriocarpa yzabalensis (40. Urticaceae)
 - Blades less than 18 cm long *Urera eggersii* (Fig. 210; 40. Urticaceae)
 - Blades lacking cystoliths, cordate or subcordate at base:
 - Plants shrubs to 2 m tall; blades less than 10 cm long *Melochia lupulina* (87. Sterculiaceae)
 - Plants trees or shrubs more than 3 m tall; blades more than 10 cm long:
 - Blades ovate, 10–20 cm long; stipules less than 13 mm long; petioles more than 4 cm long . . .
 *Acalypha macrostachya* (Fig. 316; 75. Euphorbiaceae)
 - Blades elliptic, more than 20 cm long; stipules more than 15 mm long; petioles less than 3 cm long *Apeiba tibourbou* (84. Tiliaceae)
 - Blades with stellate or arachnoid trichomes above or below:
 - Blades with the surface below obscured by dense arachnoid pubescence (some with stellate trichomes also):
 - Petioles more than 2 cm long, ferruginous; sap copious; twigs with large bud scales at apex
 *Coussapoa panamensis* (Fig. 198; 39. Moraceae)
 - Petioles less than 2 cm long:
 - Blades inequilateral at base, cordate on one side, ± acute on the other, usually less than 8 cm long; petioles less than 5 mm long *Muntingia calabura* (83. Elaeocarpaceae)
 - Blades ± equilateral at base, more than 10 cm long; petioles more than 8 mm long:
 - Lower blade surface with chiefly arachnoid, brownish pubescence
 *Luehea seemannii* (84. Tiliaceae)
 - Lower blade surface with both arachnoid and stellate pubescence
 *Luehea speciosa* (Fig. 359; 84. Tiliaceae)
 - Blades lacking arachnoid pubescence:
 - ★ Blades cordate or subcordate at base:
 - Trichomes on blade below a mixture of simple and stellate:
 - Blades lobed, armed with minute prickles *Hibiscus bifurcatus* (Fig. 363; 85. Malvaceae)
 - Blades unlobed, unarmed *Melochia lupulina* (87. Sterculiaceae)
 - All trichomes below stellate:
 - Blades with 4 or fewer pairs of lateral veins above the basal pair (usually arising in apical half of blade); blades often shallowly lobed:
 - Blades deeply cordate, the sinus of the larger leaves usually more than 1.5 cm deep; margins crenate (i.e., the teeth blunt) *Hibiscus sororius* (Fig. 364 and fig. on p. 12; 85. Malvaceae)
 - Blades not so deeply cordate, the sinus usually less than 1 cm deep; margins variously serrate with ± sharp teeth:
 - Upper blade surface with long, acicular trichomes interspersed with short, stellate, many-pointed ones *Heliocarpus popayanensis* (Fig. 358; 84. Tiliaceae)
 - Upper blade surface with trichomes of ± uniform size, either simple or few-pointed:
 - Blades 10–20 cm wide, cordate *Pavonia dasypetala* (85. Malvaceae)
 - Blades usually 4–10 cm wide, truncate or only very shallowly cordate
 *Pavonia paniculata* (85. Malvaceae)
 - Blades with 5 or more pairs of major lateral veins above the basal pair (usually ± equally spaced):
 - Blades ovate, broadest below the middle; petioles more than 3 cm long, with a row of glands at apex *Croton panamensis* (75. Euphorbiaceae)

Blades usually elliptic or oblong-elliptic; petioles less than 3 cm long, lacking glands:

- Blades softly rufous-pubescent below; stellate trichomes stalked; petioles and young branches long-pilose *Apeiba tibourbou* (84. Tiliaceae)
- Blades harshly grayish-pubescent below; stellate trichomes sessile:
 - Blades usually inequilateral at base; plants trees more than 3 m tall *Guazuma ulmifolia* (87. Sterculiaceae)
 - Blades \pm equilateral at base; plants shrubs less than 2.5 m tall *Waltheria glomerata* (87. Sterculiaceae)

★ Blades not cordate or subcordate at base:

- Lateral veins \pm uniformly spaced along midrib, sometimes lacking just above base:
 - Petioles more than 1.5 cm long; branchlets essentially glabrous; blades usually with 2 red glands at base *Alchornea costaricensis* (Fig. 318; 75. Euphorbiaceae)
 - Petioles less than 1 cm long; branchlets conspicuously stellate-pubescent; blades lacking glands *Waltheria glomerata* (87. Sterculiaceae)
- Lateral veins clustered in apical half of blade:
 - Blades more than twice as long as broad, often with tufts of trichomes in apical axils below, not lobed *Trichospermum mexicanum* (Fig. 360; 84. Tiliaceae)
 - Blades less than twice as long as broad, lacking tufts in axils below, the larger ones sometimes lobed:
 - Blades with 3–5 serrations per cm, the serrations ca 2 mm deep *Pavonia paniculata* (85. Malvaceae)
 - Blades with 6 or more serrations per cm, the serrations ca 1 mm deep:
 - Plants shrubs less than 2.5 m tall; upper blade surface with only stellate trichomes of various sizes *Triumfetta lappula* (Fig. 361; 84. Tiliaceae)
 - Plants trees more than 6 m tall; upper blade surface with long acicular trichomes interspersed with short stellate ones *Heliocarpus popayanensis* (Fig. 358; 84. Tiliaceae)

▲ Blades not palmately veined at base:

- Blades with pellucid dots:
 - Blades lacking sharp teeth, abruptly acuminate at apex:
 - Blades densely pubescent below, rounded to subcordate at base; petioles densely pubescent *Zuelania guidonia* (Figs. 403, 404; 96. Flacourtiaceae)
 - Blades sparsely pubescent below, acute at base; petioles glabrous or sparsely pubescent *Casearia aculeata* (96. Flacourtiaceae)
 - Blades sharply toothed, usually gradually acuminate at apex:
 - Blades less than 10 cm long, with conspicuous pellucid dots, the margins finely serrate *Casearia arborea* (96. Flacourtiaceae)
 - Blades more than 10 cm long:
 - Pellucid dots minute, red-orange; margins finely serrulate with subulate teeth; blades more than 20 cm long *Ardisia pellucida* (112. Myrsinaceae)
 - Pellucid dots usually clear, conspicuous or inconspicuous; margins coarsely serrate; blades less than 20 cm long:
 - Blades broadest above the middle, the pellucid dots conspicuous *Casearia guianensis* (96. Flacourtiaceae)
 - Blades broadest at or below the middle, the pellucid dots inconspicuous *Casearia arguta* (96. Flacourtiaceae)

Blades lacking pellucid dots:

- Lower blade surface densely and conspicuously pubescent (sometimes sparsely so in *Banara* but the petioles with glands at apex):
 - Blades either more than 10 cm wide and subcordate at base or \pm truncate at base with prominent glands at apex of petiole and on tips of serrations:
 - Blades with glands at apex of petiole and on serrations, less than 7 cm wide, never subcordate at base *Banara guianensis* (96. Flacourtiaceae)
 - Blades eglandular, more than 10 cm wide, often subcordate at base; teeth consisting of marginal tufts of trichomes *Castilla elastica* (39. Moraceae)
 - Blades less than 10 cm wide, lacking glands:
 - Blades mostly acute to attenuate at base; petioles often fused at base with a very short branch *Cordia spinescens* (121. Boraginaceae)
 - Blades obtuse to subcordate at base; petioles not as above:
 - Many leaves opposite or subopposite; blades sharply toothed, sometimes ovate *Clibadium surinamense* (133. Compositae)
 - Leaves all alternate; blades usually obscurely toothed *Vernonia canescens* (133. Compositae)

Lower blade surface not densely pubescent:

- ◎ Petioles more than 2 cm long:
 - Blades cordate at base; trunk armed *Hura crepitans* (75. Euphorbiaceae)
 - Blades acute to rounded at base; trunk unarmed:
 - Blades less than 12 cm long, toothed only in apical half *Roupala montana* (41. Proteaceae)

- Blades more than 20 cm long, obscurely toothed or sinuate to dentate throughout *Sloanea zuliensis* (83. Elaeocarpaceae)
- ⊙ Petioles less than 2 cm long:
- Blades toothed ± throughout, often prominently so:
- Serrations glandular-tipped; stipules subulate, persistent *Turnera panamensis* (Fig. 405; 97. Turneraceae)
- Serrations not glandular-tipped; stipules ovate and persistent, or caducous, or lacking:
- Stipules to 3 mm long, persistent, ovate, whitish; blades ± elliptic *Hybanthus prunifolius* (95. Violaceae)
- Stipules small and caducous or lacking:
- Blade margins with 8–12 serrations per cm; petioles 1–2.5 cm long *Ardisia pellucida* (112. Myrsinaceae)
- Blade margins with 4–6 shallow serrations per cm; petioles less than 0.8 cm long *Casearia arguta* (96. Flacourtiaceae)
- Blades toothed only near apex or obscurely toothed:
- Blades glabrous above:
- Lateral veins ascending; blades less than 12 cm long *Lozania pittieri* (37. Lacistemaceae)
- Lateral veins ± perpendicular to midrib; blades more than 12 cm long:
- Trees usually 5–15 m tall; stems greenish when dried, sparsely puberulent, the trichomes ca 0.5 mm long, the surface smooth, not with brownish structures like sand grains *Olmedia aspera* (Fig. 205; 39. Moraceae)
- Trees 8–25 m tall; stems brown, densely granular-puberulent, the trichomes to ca 0.2 mm long, the surface roughened with brown structures like sand grains *Trophis racemosa* (39. Moraceae)
- Blades pubescent above:
- Blades caudate-acuminate, gradually tapered to base; lateral veins often ± perpendicular to midrib; stipules amplexicaul *Olmedia aspera* (Fig. 205; 39. Moraceae)
- Blades acute to acuminate at apex, ± abrupt at base; lateral veins ascending:
- Stems rufous-tomentose *Couratari panamensis* (Fig. 412; 103. Lecythidaceae)
- Stems essentially glabrous:
- Plants trees or shrubs, often unbranched except near apex, growing only in clearings, estipulate; blades rugose above *Vernonia patens* (Fig. 552; 133. Compositae)
- Plants trees, usually branched, usually growing in the forest, stipulate; blades not rugose above *Trophis racemosa* (39. Moraceae)
- Blades entire (some lobed but the lobe margins not toothed, not sinuate):
- ⊙ Blades lobed:
- Blades deeply lobed, nearly to or beyond middle:
- Blades peltate:
- Blades smooth above, remaining intact and open after falling *Cecropia insignis* (Fig. 194; 39. Moraceae)
- Blades scabrous or rough above, rolling up after falling:
- Blades lobed more than three-fourths the way to base, flat or slightly folded *Cecropia obtusifolia* (Fig. 196; 39. Moraceae)
- Blades lobed to or slightly beyond middle, folded (not able to be flattened):
- Basal pulvinus of petiole with uniform velvetlike layer of trichomes; plants common *Cecropia peltata* (Fig. 197; 39. Moraceae)
- Basal pulvinus of petiole with brown, velvetlike layer of trichomes interspersed with dense, longer, white trichomes; plants rare *Cecropia longipes* (Fig. 195; 39. Moraceae)
- Blades not peltate:
- Blades densely grayish-white-arachnoid below or glabrous and waxy below (waxy lower surface sometimes appearing pubescent):
- Blades grayish-white-arachnoid below, more than 20 cm wide, asperous above; plants of the forest *Pourouma guianensis* (39. Moraceae)
- Blades glabrous and waxy below, less than 15 cm wide, smooth above; plants cultivated shrubs *Manihot esculenta* (75. Euphorbiaceae)
- Blades below not arachnoid-pubescent, not glabrous and waxy:
- Plants suffrutices; spines on stems, petioles, and blades below small, recurved; trichomes on blades below of 2 types (forked and simple) *Hibiscus bifurcatus* (Fig. 363; 85. Malvaceae)
- Plants large trees; spines lacking:
- Trichomes on blades below mostly stellate; trunk without swollen rings *Sterculia apetala* (Fig. 379; 87. Sterculiaceae)
- Trichomes on blades below mostly simple; trunk with swollen rings *Cavanillesia platanifolia* (Fig. 369; 86. Bombacaceae)
- Blades shallowly lobed:
- ▣ Blades glabrous or with simple trichomes:
- Blades uniform, almost all lobed; plants cultivated shrubs *Jatropha curcas* (75. Euphorbiaceae)
- Blades dimorphic, one leaf much smaller, in subopposite pairs, only the younger or lower blades lobed;

- plants of open areas in the forest *Cyphomandra hartwegii* (Fig. 481; 124. Solanaceae)
- ▣ Blades with stellate pubescence:
- At least the larger blades cordate or subcordate at base:
- Blades palmately veined, smooth above in age, sparsely puberulent or glabrous above; plants often medium-sized trees *Ochroma pyramidale* (Fig. 370; 86. Bombacaceae)
- Blades pinnately veined, densely pubescent above; plants shrubs
..... *Solanum ochraceo-ferrugineum* (124. Solanaceae)
- Blades acute to obtuse at base:
- Blades sessile *Solanum jamaicense* (Fig. 486; 124. Solanaceae)
- Blades conspicuously petiolate:
- Plants slender shrubs, 1.5–4 m tall; blades to 15 cm long and 9 cm wide, the margins usually weakly to strongly sinuate; branchlets armed with stout spines *Solanum subinerme* (124. Solanaceae)
- Plants stout trees, usually more than 5 m tall (on BCI); at least the largest blades 16 cm or more long, more than 10 cm wide, the margins usually entire, rarely sinuate; branchlets usually unarmed, the larger branches sometimes armed *Solanum hayesii* (Fig. 485; 124. Solanaceae)
- ⊕ Blades not lobed:
- Stems with conspicuous swollen nodes; sap not milky, often with pleasant aroma; plants shrubs or small trees, usually sterile only a short part of the year *Piper* (36. Piperaceae) [see fertile key]
- Stems and habit not as above:
- Fully formed blades pubescent, perhaps only on veins:
- ◇ Blades above glabrous or essentially so, even on midrib:
- Fully grown blades with the pubescence below chiefly restricted to veins:
- Blades conspicuously broadest above or below the middle:
- Blades broadest below the middle:
- Plants epiphytic trees; blades more than 10 cm wide, palmately veined at base; sap red or yellowish *Coussapoa magnifolia* (39. Moraceae)
- Plants suffruticose shrubs; blades less than 10 cm wide, pinnately veined at base; sap clear *Witheringia solanacea* (Figs. 488, 489; 124. Solanaceae)
- Blades broadest above the middle:
- Blades less than 10 cm long:
- Blades lacking axillary domatia *Ficus colubrinae* (39. Moraceae)
- Blades with axillary domatia:
- Vein axils below with tufts of brownish trichomes; leaves spiral in pseudovertilcils; plants large trees *Terminalia amazonica* (Figs. 421, 422; 105. Combretaceae)
- Vein axils below with flaplike pockets; leaves alternate; plants shrubs or small trees
..... *Annona acuminata* (55. Annonaceae)
- Blades usually more than 12 cm long (to 30 cm):
- Leaves scattered along branchlets, pubescent only on midrib below
..... *Ficus paraensis* (Fig. 203; 39. Moraceae)
- Leaves clustered at apex of branchlets, pubescent on midrib and lateral veins below and sometimes on surface:
- Blades with 12–20 pairs of major lateral veins *Pouteria fossicola* (113. Sapotaceae)
- Blades with 21–50 pairs of major lateral veins *Pouteria sapota* (113. Sapotaceae)
- Blades broadest at or near the middle:
- Plants with stipules:
- Blades lacking axillary domatia:
- Stipules amplexicaul, 5–10 mm long, leaving a distinct scar encircling the stem; major lateral veins of blade distinctly and regularly loop-connected, the lower surface drying brown, the reticulate veins lighter than the surface. . . *Perebea xanthochyma* (39. Moraceae)
- Stipules not amplexicaul, 1.5–3 mm long, not leaving a circumferential scar on stem; major lateral veins of blade only loosely and indistinctly loop-connected, the lower surface drying pale green, the reticulate veins darker than the surface
..... *Margaritaria nobilis* (75. Euphorbiaceae)
- Blades with axillary domatia:
- Stipules ocreate (encircling stem) *Coccoloba acuminata* (46. Polygonaceae)
- Stipules not ocreate (at most half encircling stem) *Lozania pittieri* (37. Lacistemaceae)
- Plants lacking stipules:
- Most blades less than 4.5 cm wide:
- Midrib prominently raised above; sap milky; blades lacking axillary domatia; plants trees to 10 m tall *Pouteria stipitata* (113. Sapotaceae)
- Midrib not prominently raised above; sap not milky; blades with axillary domatia; plants shrubs or trees usually less than 5 m tall *Annona acuminata* (55. Annonaceae)
- Most blades more than 5 cm wide:
- △ Petioles usually more than 1.5 cm long; leaves alternate or subopposite:
- Leaves subopposite *Neea amplifolia* (Fig. 227; 48. Nyctaginaceae)
- Leaves strictly alternate:

- Leaf blades membranaceous, the tertiary veins not at all raised; plants of clearings and clearing edges *Cestrum latifolium* (124. Solanaceae)
- Leaf blades coriaceous or subcoriaceous, the tertiary veins prominently raised (on dried specimens); plants of the forest:
- Blades ca 7 times longer than petioles; areoles of reticulate veins less than 1 mm diam; plants trees, more than 20 m tall *Ocotea pyramidata* (58. Lauraceae)
- Blades less than 4 times longer than petioles; areoles of reticulate veins mostly more than 1 mm diam; plants shrubs or trees, less than 15 m tall *Garcia nutans* (75. Euphorbiaceae)
- △ Petioles less than 1.5 cm long; leaves alternate:
- Plants scandent shrubs or vines; young stems glabrous *Tournefortia angustiflora* (Fig. 475; 121. Boraginaceae)
- Plants small trees; young stems rufous-pubescent:
- Blades usually broadest above the middle, the midrib usually raised or flat (rarely slightly sunken), relatively broad, usually densely and conspicuously pubescent, the trichomes long, curved, brownish *Annona hayesii* (55. Annonaceae)
- Blades usually broadest at the middle, the midrib deeply and narrowly sunken, relatively sparsely and inconspicuously pubescent or glabrous *Desmopsis panamensis* (Fig. 236; 55. Annonaceae)
- Fully grown blades pubescent on surface below (not just on veins):
- Blades stellate-pubescent or fimbriate-lepidote:
- Petioles mostly less than 1 cm long:
- Blades with 9 or fewer pairs of lateral veins; plants scandent shrubs *Solanum argenteum* (124. Solanaceae)
- Blades with 11 or more pairs of lateral veins:
- Blades with fewer than 15 pairs of lateral veins, stalked-stellate below; plants medium-sized trees *Virola sebifera* (Figs. 242, 243; 56. Myristicaceae)
- Blades with 20 or more pairs of lateral veins, sessile, stellate-pubescent below; plants tall trees *Virola surinamensis* (Figs. 244, 245; 56. Myristicaceae)
- Petioles mostly more than 1 cm long:
- Blades narrowly acuminate at apex or conspicuously cordate at base:
- Blades attenuate at base; plants shrubs, usually less than 2 m tall; trichomes restricted to a brownish band on either side of midrib on lower surface *Parathesis microcalyx* (Fig. 445; 112. Myrsinaceae)
- Blades cordate at base; plants small trees, more than 3 m tall; trichomes throughout blade on lower surface *Croton billbergianus* (75. Euphorbiaceae)
- Blades rounded to obtuse at apex, slightly subcordate at base:
- Blades with 11 or more pairs of major lateral veins *Virola sebifera* (Figs. 242, 243; 56. Myristicaceae)
- Blades with 5–7 pairs of major lateral veins:
- Blades inequilateral at base; stems densely stellate-pubescent; plants without a sweet odor *Solanum hayesii* (Fig. 485; 124. Solanaceae)
- Blades equilateral at base; stems fimbriate-lepidote; plants usually with a sweet odor:
- Plants usually trees less than 10 m tall; stems and lower blade surface densely stellate-pubescent *Quararibea pterocalyx* (Fig. 376; 86. Bombacaceae)
- Plants usually large trees (to 25 m tall); stems and lower blade surface fimbriate-lepidote *Quararibea asterolepis* (Figs. 374, 375; 86. Bombacaceae)
- Blades not stellate-pubescent, not fimbriate-lepidote:
- ☆ Petioles often more than 1 cm long:
- Trichomes on blade below so dense as to be contiguous:
- Lower blade surface reddish-brown; trichomes straight, T-shaped; blades broadly elliptic; sap usually not copious *Chrysophyllum cainito* (113. Sapotaceae)
- Lower blade surface grayish or light green; trichomes arachnoid; blades ovate; sap copious *Coussapoa panamensis* (Fig. 198; 39. Moraceae)
- Trichomes on blade below not contiguous:
- Pubescence of blades below conspicuous, erect, moderately long on veins; blades broadly ovate-elliptic; plants cultivated trees *Persea americana* (58. Lauraceae)
- Pubescence of blades below inconspicuous and/or appressed, the veins glabrous or appressed-pubescent:
- Axils below with tufts of trichomes:
- Blades conspicuously palmately 3-veined *Phoebe mexicana* (Fig. 251; 58. Lauraceae)
- Blades not palmately 3-veined:
- Largest blades less than 20 cm long, usually broadest above the middle, abruptly short-acuminate *Ocotea skutchii* (Fig. 250; 58. Lauraceae)
- Largest blades usually more than 20 cm long, usually broadest at middle or below, gradually long-acuminate *Nectandra globosa* (58. Lauraceae)

- Axils below lacking tufts of trichomes:
 - Sap copious, milky, reddish, or turbid:
 - Petioles more than 5 cm long; blades ovate-oblong, palmately veined; sap reddish or yellowish *Coussapoa magnifolia* (39. Moraceae)
 - Petioles less than 4 cm long:
 - Petioles and stems with long, arachnoid, deciduous trichomes; blades obovate, bluntly acuminate *Ficus colubrinae* (39. Moraceae)
 - Petioles and stems not with such pubescence:
 - Blades caudate-acuminate, asperous below with inconspicuous hirsute pubescence *Olmedia aspera* (Fig. 205; 39. Moraceae)
 - Blades not caudate-acuminate:
 - Petioles and stems with scurfy, brown, peeling outer bark, the petioles scurfy; stipules apical; blades often punctate below with short trichomes, conspicuously 3-veined at base *Ficus maxima* (Fig. 202; 39. Moraceae)
 - Petioles and stems smooth; stipules lacking; blades with T-shaped trichomes below, not 3-veined at base *Cynodendron panamense* (113. Sapotaceae)
 - Sap not colored, copious, or turbid:
 - Blades 3-veined near base, with the basal pair of lateral veins widely spaced from upper pairs *Phoebe mexicana* (Fig. 251; 58. Lauraceae)
 - Blades ± equally veined throughout, acute to narrowly acute at base:
 - Blades ± elliptic; reticulate veins conspicuous below; pubescence on petioles appressed; blades drying grayish below *Beilschmiedia pendula* (Fig. 248; 58. Lauraceae)
 - Blades slightly obovate; reticulate veins obscure below; pubescence on petioles usually ± erect; blades not drying grayish below *Ocotea oblonga* (58. Lauraceae)
- ☆ Petioles less than 1 cm long:
 - Largest blades less than 1.5 cm wide or more than 6 cm wide:
 - Largest blades less than 1.5 cm wide, lanceolate *Xylopia frutescens* (Figs. 240, 241; 55. Annonaceae)
 - Largest blades more than 6 cm wide, elliptic:
 - Petioles thick, swollen (scarcely so in *Perebea*), usually less than 5 mm long; plants small trees, lacking milky sap:
 - Plants with conspicuous amplexicaul stipules 5–10 mm long; stems with conspicuous, circumferential stipule scars *Perebea xanthochyma* (39. Moraceae)
 - Plants lacking stipules or conspicuous stipule scars:
 - Larger blades cordate, ± inequilateral at base *Guatteria amplifolia* (Figs. 237, 238; 55. Annonaceae)
 - Larger blades not cordate, ± equilateral at base *Desmopsis panamensis* (Fig. 236; 55. Annonaceae)
 - Petioles not swollen, usually more than 10 mm long; plants medium-sized trees, with milky sap at least in trunk; blades equilateral at base *Cynodendron panamense* (113. Sapotaceae)
 - Largest blades usually 1.5–6 cm wide:
 - Blades whitish, densely arachnoid below, the trichomes contiguous *Licania hypoleuca* (61. Chrysobalanaceae)
 - Blades not whitish, sparsely to densely pubescent below but the trichomes not contiguous:
 - Blades acute at base, with short trichomes on surface but not on veins; branches smooth, glabrous, divaricately branched, often with a leaf in the branch axil *Cordia lasiocalyx* (Fig. 474; 121. Boraginaceae)
 - Blades and branches not as above:
 - Blades verrucose above *Guatteria dumetorum* (55. Annonaceae)
 - Blades not verrucose above:
 - Blades densely brown-sericeous below *Chrysophyllum cainito* (113. Sapotaceae)
 - Blades not densely brown-sericeous below:
 - Plants with persistent, paired stipules *Margaritaria nobilis* (75. Euphorbiaceae)
 - Plants lacking stipules *Xylopia macrantha* (55. Annonaceae)
 - ◇ Blades pubescent above, at least on midrib or veins:
 - Blades pubescent above only on midrib or veins:
 - ▲ Blades below with the pubescence restricted to major veins or glabrous:
 - ★ Stipules ocreate (stipules or scars encircling stems):
 - Blades more than 2.5 times longer than wide; plants medium-sized trees, the trunk often to 30 cm dbh; stems hollow, inhabited by fiercely stinging ants *Triplaris cumingiana* (Fig. 223; 46. Polygonaceae)

- Blades less than 2 times longer than broad; plants small trees or vines, the trunk slender; stems not hollow:
- Most blades broadly ovate to suborbicular; plants often vinelike *Coccoloba parimensis* (46. Polygonaceae)
 - Most blades obovate; plants trees *Coccoloba manzanillensis* (Figs. 221, 222; 46. Polygonaceae)
- ★ Stipules lacking or not ocreate:
- Petioles usually less than 3 mm long:
 - Blades ± glabrous below, merely scabrid on midrib above *Phyllanthus acuminatus* (75. Euphorbiaceae)
 - Blades pubescent below, short- or long-pubescent above:
 - Leaves usually 8 or more per branchlet; trichomes of ± uniform length *Hirtella racemosa* (Fig. 252; 61. Chrysobalanaceae)
 - Leaves usually 7 or fewer per branchlet; trichomes of 2 types, long acropetal ones interspersed with short erect ones *Hirtella triandra* (Fig. 253; 61. Chrysobalanaceae)
 - Petioles more than 5 mm long:
 - Blades ovate, long-acuminate, solitary at the apex of short (ca 1 cm long) branches *Coccoloba acapulcensis* (Fig. 219; 46. Polygonaceae)
 - Blades not as above:
 - Blades more than 20 cm long; petioles short, swollen *Guatteria amplifolia* (Figs. 237, 238; 55. Annonaceae)
 - Blades less than 20 cm long; petioles not swollen:
 - Blades oblong-elliptic, ca 2.5 times longer than broad; petioles stout:
 - Blades usually acute to bluntly acuminate, obtuse to rounded at base; lateral veins in 13 or more pairs *Couratari panamensis* (Fig. 412; 103. Lecythidaceae)
 - Blades gradually acuminate, acute to attenuate at base; lateral veins usually in 9 or fewer pairs *Ocotea pyramidata* (58. Lauraceae)
 - Blades elliptic or obovate, ca 2 times longer than broad:
 - Blades rounded or obtuse at apex; petioles densely short-pubescent with appressed, brownish trichomes, slender *Sloanea terniflora* (83. Elaeocarpaceae)
 - Blades abruptly short-acuminate; petioles villous *Terminalia amazonica* (Figs. 421, 422; 105. Combretaceae)
- ▲ Blades pubescent throughout surface below:
- Blades stellate-pubescent:
 - Blades palmately veined at base *Croton billbergianus* (75. Euphorbiaceae)
 - Blades pinnately veined *Virola sebifera* (Figs. 242, 243; 56. Myristicaceae)
 - Blades with simple pubescence only:
 - Plants with stipules; blades with the midrib ± raised above:
 - Blades densely to moderately pubescent below *Hirtella americana* (61. Chrysobalanaceae)
 - Blades sparsely pubescent below:
 - Leaves usually 8 or more per branchlet; trichomes ± uniform in length *Hirtella racemosa* (Fig. 252; 61. Chrysobalanaceae)
 - Leaves usually 7 or fewer per branchlet; trichomes of 2 types, long acropetal ones interspersed with short erect ones *Hirtella triandra* (Fig. 253; 61. Chrysobalanaceae)
 - Plants lacking stipules; blades with the midrib raised above or not:
 - Blades with domatia in axils below:
 - Domatia pitlike; leaves narrowly elliptic to broadly oblanceolate, well scattered on stem *Ocotea oblonga* (58. Lauraceae)
 - Domatia consisting of tufts of trichomes in axils; leaves obovate, clustered at apices of branches *Terminalia amazonica* (Figs. 421, 422; 105. Combretaceae)
 - Blades lacking axillary domatia:
 - Lower leaf surface and stems densely rufous-pubescent *Chrysophyllum cainito* (113. Sapotaceae)
 - Lower leaf surface and stems not rufous-pubescent below:
 - Pubescence on lower surface uniform, sparse, appressed; blades drying verrucose (bumpy) *Guatteria dumetorum* (55. Annonaceae)
 - Pubescence on lower surface more dense on veins than on surface, not appressed; blades usually not drying verrucose:
 - Petioles mostly more than 1 cm long (to 4 cm) *Cestrum latifolium* (124. Solanaceae)
- Petioles 3–6 mm long:
 - Leaves mostly elliptic, the midrib above not densely pubescent *Desmopsis panamensis* (Fig. 236; 55. Annonaceae)
 - Leaves mostly lanceolate, the midrib above densely pubescent *Diospyros artanthifolia* (114. Ebenaceae)

- Blades pubescent above on surface as well as on veins:

Trichomes stellate on blade below:

Blades palmately veined at base, obtuse to rounded or cordate, equilateral:

Petioles less than 4 cm long; tufts of simple trichomes in vein axils below
 *Apeiba membranacea* (Fig. 375; 84. Tiliaceae)

Petioles more than 4 cm long; tufts lacking in vein axils below:

Lateral veins with only 1 or 2 pairs above the basal pair, near apex of leaf
 *Hampea appendiculata* var. *longicalyx* (Fig. 362; 85. Malvaceae)

Lateral veins with 3 or more pairs above the basal pair, \pm uniformly spaced along midrib:

Stellate trichomes below reddish-brown; petioles lacking glands
 *Ochroma pyramidale* (Fig. 370; 86. Bombacaceae)

Stellate trichomes below whitish; petioles with 2–4 glands at apex:

Stellate trichomes moderately dense throughout blade above; petioles more than 7 cm
 long *Croton panamensis* (75. Euphorbiaceae)

Stellate trichomes very sparse above except on veins; petioles less than 7 cm long
 *Croton billbergianus* (75. Euphorbiaceae)

Blades not palmately veined at base, obtuse to attenuate or rounded, inequilateral:

Blades ovate, less than 2.5 times longer than broad:

Blades lepidote, not actually stellate-pubescent, the scales appearing like branched
 trichomes *Hyeronima laxiflora* (Figs. 322, 323; 75. Euphorbiaceae)

Blades stellate-pubescent:

Plants not armed *Solanum hayesii* (Fig. 485; 124. Solanaceae)

Plants armed on stem and/or the petioles with recurved spines:

Blades densely, softly and conspicuously pubescent, with both sessile and stalked, stout,
 stellate trichomes, the individual trichomes often difficult to distinguish with the
 naked eye, the surface usually not dark, dull
 *Solanum ochraceo-ferrugineum* (124. Solanaceae)

Blades sparsely and inconspicuously pubescent with minute, sessile, stellate trichomes,
 the individual trichomes easily distinguishable with the naked eye, the surface
 drying dark, often semiglossy *Solanum subinerme* (124. Solanaceae)

Blades \pm oblanceolate or lanceolate, more than 2.5 times longer than broad:

Trichomes very minute, stellate under magnification; stems becoming sparsely pubescent,
 with conspicuous lenticels; plants trees usually more than 8 m tall; nodes of stems
 prominently enlarged *Cordia alliodora* (Fig. 473; 121. Boraginaceae)

Trichomes conspicuously stellate; stems densely pubescent, lacking lenticels; plants shrubs
 or small trees usually less than 5 m tall; nodes of stems not enlarged:

Most stellate trichomes on stems stalked, white
 *Solanum umbellatum* (Fig. 487; 124. Solanaceae)

Most stellate trichomes on stems \pm sessile, generally light brown:

Leaves mostly less than 5 cm wide *Solanum asperum* (124. Solanaceae)

Leaves mostly more than 5 cm wide *Solanum rugosum* (124. Solanaceae)

Trichomes not stellate on blade below:

- ◆ Mature blades densely pubescent below:

Stems conspicuously rufous-pubescent:

Plants lacking milky sap; stipules paired, persistent, linear
 *Hirtella americana* (61. Chrysobalanaceae)

Plants with milky sap; stipules apical, caducous, leaving prominent scars on stem:

Trichomes on upper midrib whitish, extending onto blade, variable in length, scarcely or
 only slightly longer than those on blade surface *Ficus popenoei* (39. Moraceae)

Trichomes on upper midrib rufous, mostly erect and in a \pm narrow line, considerably
 longer than those on blade surface *Ficus bullenei* (Fig. 200; 39. Moraceae)

Stems not conspicuously rufous-pubescent; sap not milky; plants lacking apical, caducous stip-
 ules, lacking prominent stipule scars on stem:

- Plants trees, with a large stout trunk, usually more than 6 m tall:

Pubescence below so dense as to totally obscure blade surface (less dense on juvenile
 leaves) *Cordia bicolor* (121. Boraginaceae)

Pubescence below dense but not obscuring surface:

Blades dimorphic, the larger \pm oblong-elliptic, subtended by a smaller ovate or
 rounded blade; young stems with both short and long, stiff, erect trichomes
 *Cordia panamensis* (121. Boraginaceae)

Blades \pm uniform; young stems sparsely to densely, uniformly crisp-villous or
 appressed-puberulent:

Lateral veins in 20 or more pairs, densely pubescent
 *Annona spraguei* (Fig. 235; 55. Annonaceae)

Lateral veins in 10 or fewer pairs, glabrous
 *Beilschmiedia pendula* (Fig. 248; 58. Lauraceae)

- ⊙ Plants shrubs or trees, vinelike or slender, without a stout trunk, seldom more than 3 m tall:
 - Blades deeply cordate at base, inequilateral, puberulent below and on midrib above; leaves with a large one often subtended by a smaller one, appearing subopposite
 - *Cyphomandra hartwegii* (Fig. 481; 124. Solanaceae)
 - Blades not as above; leaves strictly alternate:
 - Blades ± inequilateral at base; trichomes on smaller stems of 2 sizes:
 - Leaves dimorphic, acute to obtuse at base, the larger ones more than 9 cm wide; plants lacking stipules *Cordia panamensis* (121. Boraginaceae)
 - Leaves uniform, rounded to subcordate at base, less than 5 cm wide; plants with stipules *Pouzolzia obliqua* (Fig. 209; 40. Urticaceae)
 - Blades ± equilateral at base; trichomes on smaller stems ± uniform in length:
 - Blades less than 4.5 cm wide *Vernonia canescens* (133. Compositae)
 - Blades more than 4.5 cm wide:
 - Stems light brown, the trichomes of one type, 1–2 mm long, very dense, often conspicuously curved, the large swollen bases frequently contiguous or nearly so; blade surface usually glossy, lacking a dense layer of short puberulent trichomes *Tournefortia hirsutissima* (121. Boraginaceae)
 - Stems dark brown, the trichomes of 2 types, the longer 4–6 mm long, moderately sparse, straight, the bases never close to being contiguous; blade surface ± dull, densely covered with a layer of short puberulence *Tournefortia cuspidata* (Fig. 477; 121. Boraginaceae)
- ◆ Mature blades not densely pubescent below:
 - Blades conspicuously broadest above the middle; plants large trees; blades with axillary domatia below, obtuse at base and decurrent onto petiole; leaves clustered at tips of branches
 - *Terminalia amazonica* (Figs. 421, 422; 105. Combretaceae)
 - Blades broadest at or below the middle:
 - Blades ovate or ovate-oblong:
 - Petioles less than 1 cm long or the blades usually less than 5 cm wide:
 - Plants with stipules; petioles usually articulate at apex *Dalbergia brownei* (63C. Papilionoideae)
 - Plants lacking stipules; petioles not articulate at apex *Securidaca diversifolia* (Fig. 314; 74. Polygalaceae)
 - Petioles more than 1 cm long, the blades more than 5 cm wide; plants soft-wooded shrubs of forests and clearings, lacking stipules:
 - Blades not occasionally subopposite with a reduced opposing leaf, short-villous on lower surface, the trichomes jointed *Cestrum latifolium* (124. Solanaceae)
 - Blades occasionally subopposite with a reduced opposing leaf, puberulent or strigillose, the trichomes not jointed:
 - Blades puberulent throughout below *Cyphomandra hartwegii* (Fig. 481; 124. Solanaceae)
 - Blades strigillose only on veins below *Witheringia solanacea* (Figs. 488, 489; 124. Solanaceae)
 - Blades not ovate:
 - Blades caudate-acuminate, with a conspicuous collecting vein:
 - Blades elliptic-oblong; stipules 5 mm long, lateral *Trophis racemosa* (39. Moraceae)
 - Blades obovate; stipules 5–7 mm long, amplexicaul *Olmedia aspera* (Fig. 205; 39. Moraceae)
 - Blades not caudate-acuminate, lacking a prominent collecting vein; stipules less than 5 mm long or lacking:
 - Blades more than 20 cm long, more than 3 times longer than broad (*Annona hayesii* to more than 20 cm long, but less than 3 times longer than broad):
 - Blades rounded to subcordate at base; petioles very stout; some blades more than 30 cm long *Guatteria amplifolia* (Figs. 237, 238; 55. Annonaceae)
 - Blades tapered to an acute, decurrent base; petioles not stout; blades less than 25 cm long *Nectandra cissiflora* (58. Lauraceae)
 - Blades mostly less than 20 cm long:
 - Margins minutely toothed, revolute; blades more than 3 times longer than broad, usually less than 12 cm long *Vernonia patens* (Fig. 552; 133. Compositae)
 - Margins entire, not revolute; blades less than 3 times longer than broad:
 - Blades less than 4.5 cm wide *Hirtella triandra* (Fig. 253; 61. Chrysobalanaceae)
 - Blades usually more than 5 cm wide:
 - Blades abruptly acuminate, rounded at base *Annona hayesii* (55. Annonaceae)
 - Blades gradually acuminate, tapered to an acute, decurrent base *Nectandra cissiflora* (58. Lauraceae)
 - ⊙ Fully formed blades glabrous even on veins (some with tufts of trichomes in vein axils below):
 - ◆ Plants with both amplexicaul stipules and copious, clear, turbid, viscid, yellow-brown, or milky sap:

Lateral veins less than 1 cm apart along midrib of mature blades:

Stipules more than 2.5 cm long; plants tall trees with regular trunks:

Blades mostly less than 4.5 cm wide; stipules usually less than 5 cm long; lateral veins 2–4 mm apart *Ficus yoponensis* (39. Moraceae)

Blades mostly more than 4.5 cm wide; stipules usually more than 5 cm long; lateral veins 4–10 mm apart *Ficus insipida* (39. Moraceae)

Stipules less than 2.5 cm long; plants usually stranglers or with the base ± stilted:

Outer bark of young stems scurfy; blades ± obovate:

Leaves (including petioles) less than 11 cm long; petioles less than 1 cm long

. *Ficus perforata* (39. Moraceae)

Leaves (including petioles) more than 11 cm long; petioles mostly more than 1 cm long

. *Ficus paraensis* (Fig. 203; 39. Moraceae)

Outer bark of young stems smooth; blades elliptic to ovate, long-acuminate:

Lateral veins conspicuously straight and parallel, 1.5–2 mm apart, the reticulate veins very weak *Ficus yoponensis* (39. Moraceae)

Lateral veins not conspicuously straight and parallel, more than 2 mm apart, the reticulate veins evident:

Leaves distichous *Pseudolmedia spuria* (39. Moraceae)

Leaves spiral:

Blade margins not white, at least at apex; blades often narrowly rounded to subcordate at base *Ficus pertusa* (Fig. 204; 39. Moraceae)

Blade margins white all around; blades acute at base *Ficus retusa* (39. Moraceae)

Lateral veins more than 1 cm apart along midrib of mature blades:

Plants armed *Poulsenia armata* (Fig. 206; 39. Moraceae)

Plants unarmed:

Blades ovate, usually cordate, with 5 palmate veins at base:

Blades deeply cordate (the sinus narrow, more than 2 cm deep), abruptly short-acuminate at apex, smooth below *Ficus nymphiifolia* (39. Moraceae)

Blades slightly and broadly cordate (the sinus broad, less than 1 cm deep), obtuse to rounded at apex, asperous below *Coussapoa magnifolia* (39. Moraceae)

Blades not ovate-cordate:

Blade apex rounded or at most shortly and bluntly acuminate:

Blades with the lateral veins ± perpendicular to midrib at middle of blade or the leaves clustered densely at apex of stem and conspicuously broader beyond the middle; stipules glabrous:

Blades oblong-obovate, markedly tapered toward base; leaves clustered at apex of stem *Ficus obtusifolia* (39. Moraceae)

Blades broadly elliptic; leaves not clustered at apex of stem . . . *Ficus tonduzii* (39. Moraceae)

Blades and veins not as above; stipules pubescent (except in *Ficus citrifolia*):

Blades with 3 or fewer pairs of lateral veins *Ficus colubrinae* (39. Moraceae)

Blades with 6 or more pairs of lateral veins:

Submarginal collecting vein and outer ends of lateral veins below weaker than lateral veins near midrib; petioles sometimes more than 5 cm long; stipules glabrous; trees usually less than 12 m tall *Ficus citrifolia* (39. Moraceae)

Submarginal collecting vein and lateral veins below ± equally conspicuous throughout; petioles less than 5 cm long; stipules often pubescent; trees often more than 15 m tall:

Leaf blades generally broadest at the middle; stipules appressed-pubescent (sericeous), the stipular scars on younger stems with long trichomes

. *Ficus trigonata* (39. Moraceae)

Leaf blades often broadest above the middle; stipules patulous-pubescent (appearing almost villous), the stipular scars on younger stems with a few to many long trichomes *Ficus costaricana* (39. Moraceae)

Blade apex distinctly acuminate or sharp:

Petioles mostly less than 1 cm long:

Blades smooth; stipules lateral to half-amplexicaul

. *Brosimum alicastrum* subsp. *bolivarense* (39. Moraceae)

Blades asperous; stipules fully amplexicaul *Olmedia aspera* (Fig. 205; 39. Moraceae)

Petioles mostly more than 1 cm long:

Blades acute at base, asperous below:

Blades conspicuously caudate-acuminate at apex; petioles asperous but not scurfy

. *Olmedia aspera* (Fig. 205; 39. Moraceae)

Blades acuminate but not caudate at apex; petioles scurfy

. *Ficus maxima* (Fig. 202; 39. Moraceae)

- Blades obtuse to rounded at base or subcordate, not asperous below:
 Blades broader toward apex; stems scurfy; petioles generally less than 2.5 cm long
 *Ficus paraensis* (Fig. 203; 39. Moraceae)
 Blades generally not broader toward apex; stems smooth; petioles usually more than 2.5
 cm long:
 Trees usually less than 12 m tall; trunk grayish *Ficus citrifolia* (39. Moraceae)
 Trees often more than 15 m tall; trunk reddish-brown *Ficus dugandii* (39. Moraceae)
- Plants lacking amplexicaul stipules and/or the sap not copious, clear, turbid, viscid, yellow-brown, or
 milky:
 Leaves with large, overlapping, persistent stipules *Erythroxylum multiflorum* (66. Erythroxylaceae)
 Leaves lacking such stipules:
 Leaves with a large one subtended by a smaller one, appearing subopposite:
 Lacking tufts of trichomes in vein axils below *Solanum arboreum* (Fig. 484; 124. Solanaceae)
 Blades with tufts of trichomes in vein axils below *Lycianthes synanthera* (124. Solanaceae)
 Leaves not appearing subopposite and unequal:
 ● Petioles when fresh conspicuously terete-pulvinate for entire length or at apex (drying wrinkled
 in *Neea amplifolia*) or with a produced wing (sometimes small) at apex:
 Petioles swollen for entire length, either short (usually less than 1 cm long) or with a produced
 wing at apex:
 Blades less than 20 cm long; petioles with a produced wing (sometimes minute) at apex . . .
 *Swartzia simplex* var. *ochracea* (Fig. 280; 63B. Caesalpinioideae)
 Blades more than 20 cm long; petioles lacking a wing:
 Leaf blades usually rounded at base, sometimes obtuse, frequently with small lobes onto
 the petiole, these usually turned upward (i.e., at an angle to the remaining blade sur-
 face); petioles 4–6 mm diam; plants shrubs or small trees, (2.5)4–5(6) m tall
 *Guatteria amplifolia* (Figs. 237, 238; 55. Annonaceae)
 Leaf blades usually acute to obtuse at base, sometimes rounded, but never with small ±
 erect lobes; petioles 1–4 mm diam; plants usually trees more than 7 m tall (on BCI)
 or less than 3 m tall:
 Plants trees, usually more than 7 m tall; major lateral veins often conspicuously loop-
 connected; tertiary veins usually at least in part straight and connecting major
 lateral veins *Unonopsis pittieri* (Fig. 239; 55. Annonaceae)
 Plants shrubs, usually less than 2.5 m tall; major lateral veins free to the margins; ter-
 tiary veins almost always anastomosing, rarely straight and interconnecting major
 lateral veins *Neea amplifolia* (Fig. 227; 48. Nyctaginaceae)
 Petioles not swollen for entire length, lacking a produced wing:
 Blades lepidote below; petioles canaliculate
 *Hyeronima laxiflora* (Figs. 322, 323; 75. Euphorbiaceae)
 Blades not lepidote; petioles not canaliculate:
 Blades seldom exceeding 8 cm long, rounded to subcordate at base
 *Dalbergia brownei* (63C. Papilionoideae)
 Blades mostly (10)15–50 cm long:
 Blades at most acute at apex *Theobroma cacao* (87. Sterculiaceae)
 Blades mostly acuminate at apex *Capparis frondosa* (59. Capparidaceae)
- Petioles not terete-pulvinate and lacking a produced wing at apex:
 □ Most blades widest conspicuously beyond the middle:
 Larger blades more than 50 cm long, clustered at apex of branches; smaller leaves sessile
 *Grias fendleri* (103. Lecythidaceae)
 Blades less than 50 cm long:
 Blades rounded at apex:
 Plants hemiepiphytic, liana-like shrubs
 *Souroubea sympetala* (Fig. 385; 90. Marcgraviaceae)
 Plants trees, not hemiepiphytic:
 Trees less than 10 m tall; blades obovate, 6–15.5 cm long, to twice as long as wide
 *Anacardium occidentale* (76. Anacardiaceae)
 Trees 10–37 m tall; blades oblong-oblancoolate, 14–31 cm long, more than twice as
 long as wide *Anacardium excelsum* (Figs. 326, 327; 76. Anacardiaceae)
 Blades acute to acuminate at apex:
 Plants weak-stemmed shrubs, less than 2 m tall, lacking milky sap
 *Lycianthes maxonii* (124. Solanaceae)
 Plants shrubs or trees, more than 2 m tall, with or without milky sap:
 Mature blades more than 15 cm long; sap milky
 *Thevetia ahouai* (Fig. 465; 118. Apocynaceae)
 Mature blades less than 15 cm long; plants with or without milky sap:

- Lateral veins obscure *Ternstroemia tepezapote* (Fig. 386; 91. Theaceae)
- Lateral veins conspicuous:
- Young stems and blades with T-shaped trichomes ca 0.5 mm long; sap conspicuously milky; trunks not conspicuously buttressed
 *Pouteria stipitata* (113. Sapotaceae)
- Young stems and blades minutely rufous-pubescent, soon glabrous, lacking T-shaped trichomes; sap not milky; trunk usually with many buttresses
 *Terminalia chiriquensis* (105. Combretaceae)
- ▣ Most blades widest at or below the middle:
- Blades with conspicuous pellucid or black punctations or short striations or lepidote scales or axillary domatia:
- Blades with axillary domatia (i.e., thickened, pocketlike or flaplike structures, or tufts of glands or trichomes in axils of lateral veins below):
- Base of blade with 2–4 glands near midrib, obtuse to rounded
 *Alchornea latifolia* (75. Euphorbiaceae)
- Base of blade lacking glands, variable in shape:
- Domatia consisting of a flap in axils of lower surface; lateral veins sometimes prominent, flattened before joining midrib; blades glabrous to sparsely pubescent:
- Blades less than 3 cm broad *Annona acuminata* (55. Annonaceae)
- Blades more than 3 cm broad:
- Blades strictly pinnately veined *Annona muricata* (55. Annonaceae)
- Blades 3-veined from base *Celtis schippii* (38. Ulmaceae)
- Domatia consisting of tufts of trichomes in axils of lower surface; lateral veins not broadened before joining midrib, usually downturned:
- Base of blade ending abruptly, usually rounded or subcordate:
- Blades ± oblong, the sides often straight and parallel, not conspicuously narrowed at base; stipules large (17 mm long and 3 mm wide), foliaceous, caducous *Tetrathylacium johansenii* (Fig. 400; 96. Flacourtiaceae)
- Blades elliptic to obovate; stipules not as above:
- Blade tips minutely mucronate, rounded to subcordate at base
 *Adelia triloba* (Fig. 317; 75. Euphorbiaceae)
- Blade tips not mucronate, obtuse at base
 *Lycianthes synanthera* (124. Solanaceae)
- Base of blade obtuse to attenuate, continuous with margin of petiole:
- Lowermost pairs of veins much longer than those at the middle of the blade
 *Nectandra savannarum* (58. Lauraceae)
- Lowermost pairs of veins much shorter than those at the middle of the blade:
- Leaves, at least those near apex of stem, with a smaller subopposite leaf; some blades unequal at base *Solanum antillarum* (124. Solanaceae)
- Leaves strictly alternate, ± equal in size; blades usually equal at base:
- Reticulate veins conspicuous above . . . *Nectandra purpurascens* (58. Lauraceae)
- Reticulate veins not conspicuous above
 *Ocotea skutchii* (Fig. 250; 58. Lauraceae)
- Blades lacking axillary domatia:
- ◇ Lower blade surface lepidote, the scales round, peltate, easily removed, sometimes sparse and inconspicuous:
- Scales sparse:
- Blades generally oblong-lanceolate, acute at base, more than 3 times longer than broad *Mangifera indica* (76. Anacardiaceae)
- Blades variously shaped but not oblong-lanceolate, rounded to cordate at base, less than 2.5 times longer than broad:
- Petioles more than 3 cm long; stipules borne on stems
 *Hyeronima laxiflora* (Figs. 322, 323; 75. Euphorbiaceae)
- Petioles less than 3 cm long:
- Stipules ocreate; scales not fimbriate
 *Coccoloba coronata* (Fig. 220; 46. Polygonaceae)
- Stipules not ocreate; scales fimbriate
 *Quararibea asterolepis* (Figs. 374, 375; 86. Bombacaceae)
- Scales very dense, almost contiguous:
- Blades palmately veined at base, broadest well below middle, brown on lower surface; scales ± entire; plants small trees *Bixa orellana* (93. Bixaceae)
- Blades not palmately veined at base, broadest at or above middle, not brown on lower surface; scales fimbriate; plants usually large trees:
- Blades not lepidote on upper surface; plants with sweet aroma (even dried specimens) *Quararibea asterolepis* (Figs. 374, 375; 86. Bombacaceae)

- Blades lepidote on upper surface; plants lacking sweet aroma
 *Hyeronima laxiflora* (Figs. 322, 323; 75. Euphorbiaceae)
- ◇ Lower blade surface variously punctate, pellucid, or opaque, not lepidote:
 At least half the punctations lineate (i.e., many times longer than broad):
 Lower blade surface with a brownish band along midrib (composed of minute
 stellate trichomes) *Parathesis microcalyx* (Fig. 445; 112. Myrsinaceae)
- Lower blade surface concolorous:
 Blades with the visible punctations and lines reddish, darker than the remaining
 leaf tissue *Ardisia bartlettii* (112. Myrsinaceae)
- Blades with the visible punctations and lines clear, lighter than the remaining
 leaf tissue *Heisteria* (43. Olacaceae)
- Punctations all or chiefly round, not lineate:
 Punctations opaque:
 Plants moderately large trees with a stout trunk; punctations not obvious when
 held to light *Mangifera indica* (76. Anacardiaceae)
- Plants small trees with a slender trunk; punctations visible when held to light,
 dark and red *Ardisia fendleri* (Fig. 444; 112. Myrsinaceae)
- Punctations pellucid:
 Blades moderately thin or thick, the larger ones much more than 14 cm long;
 branches equally leafy throughout; stipules lacking:
 Blades not glaucous on lower surface, the major lateral veins in more than 20
 pairs, mostly less than 5 mm apart; tertiary veins prominulous; pellucid
 punctations reddish *Stylogyne standleyi* (112. Myrsinaceae)
- Blades glaucous on lower surface, the major lateral veins in fewer than 10
 pairs, mostly ca 1 cm or more apart; tertiary veins not prominulous;
 pellucid punctations ± clear *Crematosperma* sp. (55. Annonaceae)
- Blades moderately thin, less than 14 cm long; branches leafy mostly near apex;
 stipules caducous:
 One side of blade arising considerably above the other at base
 *Laetia thammia* (96. Flacourtiaceae)
- Both sides of blade arising at ± the same point at base:
 Stipules lanceolate, ocreate, more than 5 mm long at apex of twigs; blades
 inconspicuously pellucid-punctate when dry
 *Ficus pertusa* (Fig. 204; 39. Moraceae)
- Stipules not ocreate, small, caducous; blades conspicuously pellucid-
 punctate when dry *Casearia sylvestris* (96. Flacourtiaceae)
- Blades lacking conspicuous pellucid or black punctations, short striations, lepidote scales,
 and axillary domatia (*Unonopsis pittieri* and *Solanum arboreum* with small glandular
 white dots when dried; *Dendropanax arboreus* drying with indistinct dark spots):
 Leaves ± whorled, clustered at tips of branches, oblanceolate, ca 3 times longer than
 broad *Ternstroemia tepezapote* (Fig. 386; 91. Theaceae)
- Leaves not as above:
 □ Petioles usually more than 1 cm long:
 △ Petioles usually more than 3 cm long:
 At least some blades distinctly lobed:
 Blades with 5–7 lobes, to 25 cm long and 15 cm wide; plants cultivated in the
 Laboratory Clearing *Jatropha curcas* (75. Euphorbiaceae)
- Blades with 3 lobes, to 15 cm long and 7 cm wide; plants growing in the forest
 *Dendropanax arboreus* (Figs. 441, 442; 109. Araliaceae)
- Blades never lobed:
 Stipules ocreate (leaving scar encircling stem)
 *Coccoloba manzanillensis* (Figs. 221, 222; 46. Polygonaceae)
- Stipules not ocreate or lacking:
 Blades less than 15 cm long; petioles usually less than 5(8) cm long
 *Dendropanax arboreus* (Figs. 441, 442; 109. Araliaceae)
- Blades usually more than 15 cm long; petioles usually more than 5 cm long:
 Leaves crowded, some subopposite, usually broadly elliptic, tapered and
 acute at base *Oreopanax capitatus* (109. Araliaceae)
- Leaves well-spaced, alternate, variously shaped:
 Blades ovate *Roupala montana* (41. Proteaceae)
- Blades oblong-elliptic:
 Blades with 11 or more pairs of lateral veins
 *Mangifera indica* (76. Anacardiaceae)
- Blades with 10 or fewer pairs of lateral veins
 *Lindackeria laurina* (96. Flacourtiaceae)

△ Petioles usually less than 3 cm long:

Lateral veins inconspicuous; margins sometimes revolute; sap red (rarely yellow or white); plants large forest trees *Aspidosperma cruenta* (118. Apocynaceae)

Plants not as above:

Blades 2.5–3 times longer than broad, with a conspicuous collecting vein; sap viscid, becoming milky *Maquira costaricana* (39. Moraceae)

Blades and sap not as above:

Sap in trunk whitish; blades obtuse to narrowly and gradually attenuate at base, less than 5.5 cm wide:

Blades usually broadest well beyond middle, drying dark green
 *Pouteria stipitata* (113. Sapotaceae)

Blades usually broadest near the middle, drying brownish to light green:

Blades with 3–5 palmate veins; stipule rings often visible around stems
 *Ficus pertusa* (Fig. 204; 39. Moraceae)

Blades strictly pinnately veined; stipules not leaving ring around stem
 *Pouteria unilocularis* (Fig. 446; 113. Sapotaceae)

Sap not whitish; blades mostly obtuse to acute at base, often more than 5.5 cm wide:

Reticulate veins subparallel, ± perpendicular to midrib, prominulous on both surfaces when dry; sap red
 *Compsonaura sprucei* (56. Myristicaceae)

Reticulate veins not as above or the sap not red:

Lateral veins ± parallel from midrib to a distinct, conspicuous collecting vein; stipule rings inconspicuous
 *Maquira costaricana* (39. Moraceae)

Lateral veins not parallel; collecting veins lacking (except in *Coccoloba*); stipule rings, when present, sometimes conspicuous:

Petioles less than 12 mm long; blades caudate-acuminate, ca 2.5–3 times longer than broad, with inconspicuous axillary tufts of trichomes *Nectandra purpurascens* (58. Lauraceae)

Petioles mostly more than 12 mm long; blades acuminate to rounded, mostly less than 3 times longer than broad:

Twigs herbaceous; twigs and leaves drying black:

Blades membranaceous, usually drying blackish, often appearing punctate beneath with the minute bases of old trichomes . . .
 *Tournefortia angustiflora* (Fig. 475; 121. Boraginaceae)

Blades weakly coriaceous, usually drying brownish, not appearing punctate beneath
 *Tournefortia bicolor* (Fig. 476; 121. Boraginaceae)

Twigs woody (all but youngest); blades not drying black:

Blades more than 8 cm wide, with conspicuous collecting vein, ± bullate between veins
 *Coccoloba manzanillensis* (Figs. 221, 222; 46. Polygonaceae)

Blades less than 8 cm wide (except in *Oreopanax capitatus*):

Lateral veins numerous, mainly restricted to basal half of blade, the blades markedly coriaceous, sinuate to incised around apex *Roupala montana* (41. Proteaceae)

Lateral veins, if numerous, not restricted to basal half of blade: Petioles of irregular lengths, some more than 2.5 cm long (to 8 cm):

Blades less than 15 cm long
 *Dendropanax arboreus* (Figs. 441, 442; 109. Araliaceae)

Blades to 35 cm long *Oreopanax capitatus* (109. Araliaceae)

Petioles ± uniform in length, 1–3 cm long:

Veins more widely spaced along midrib near base than near apex; blades with weakly developed domatia in basal vein axils below
 *Phoebe mexicana* (Fig. 251; 58. Lauraceae)

Veins equally spaced along midrib; blades lacking domatia in vein axils below:

☆ Blades acute at base and decurrent onto petiole:

Margins drying conspicuously wavy; blades often with 5 or fewer pairs of lateral veins; midrib usually raised, the lateral veins not whitish on upper surface *Ocotea cernua* (58. Lauraceae)

- Margins not always drying wavy; blades usually with 6 or more pairs of lateral veins; midrib usually flat or sunken, the major lateral veins usually whitish on upper surface *Ocotea pyramidata* (58. Lauraceae)
- ☆ Blades obtuse to rounded at base, ± ending abruptly at petiole:
- Plants small trees of swamps and marshes . . . *Annona glabra* (Fig. 234 and fig. on p. 12; 55. Annonaceae)
- Plants forest trees, often more than 10 m tall:
- Blades shiny, coriaceous, the lateral veins not conspicuous *Heisteria concinna* (43. Olacaceae)
- Blades not shiny, subcoriaceous, the lateral veins conspicuous:
- Most blades elliptic to oblanceolate
 *Heisteria longipes* (43. Olacaceae)
- Most blades lanceolate
 *Cestrum racemosum* (124. Solanaceae)
- Petioles usually less than 1 cm long:
- Blades mostly more than 2.5 times longer than broad:
- Blades mostly more than 3 times longer than broad:
- Shrubs usually less than 1.5 m tall; young stems minutely ribbed
 *Heisteria costaricensis* (43. Olacaceae)
- Shrubs or trees more than 1.5 m tall; stems not ribbed:
- Plants with stipules:
- Stipules short, persistent, fused to base of petiole; stems and petioles reddish; sap red in time after being cut
 *Licania platypus* (Figs. 254, 255; 61. Chrysobalanaceae)
- Stipules not as above; stems, petioles, and sap not reddish:
- Blades shiny above:
- Blades acute at apex
 *Erythroxylum panamense* (Fig. 295; 66. Erythroxylaceae)
- Blades acuminate at apex *Mabea occidentalis* (75. Euphorbiaceae)
- Blades dull above:
- Blades lacking a prominent collecting vein, the acumen long but not caudate . . . *Lacistema aggregatum* (Figs. 191, 192; 37. Lacistemaceae)
- Blades with a prominent collecting vein, the apex abruptly caudate-acuminate:
- Stems granular-puberulent; leaf blades asperous on both surfaces
 *Trophis racemosa* (39. Moraceae)
- Stems almost or completely glabrous except perhaps when very young; leaf blades smooth to touch on both surfaces:
- Blades shiny when dried; stems smooth or scurfy but bearing few if any lenticels; pubescence on youngest parts ± appressed
 *Maquira costaricana* (39. Moraceae)
- Blades dull when dried; stems conspicuously and densely lenticellate; pubescence on youngest parts puberulent (short and stiffly erect)
 *Sorocea affinis* (39. Moraceae)
- Plants lacking stipules:
- Trees more than 10 m tall:
- Blades drying green, the lower surface glaucous; reticulate veins scarcely or not at all visible *Crematosperma* sp. (55. Annonaceae)
- Blades drying brown, the lower surface not at all glaucous; reticulate veins prominulous, close
 *Pouteria unilocularis* (Fig. 446; 113. Sapotaceae)
- Trees or shrubs less than 8 m tall:
- Blades oblanceolate, tapered to base; collecting vein obscure or ca 1 mm from margin *Cestrum megalophyllum* (Fig. 480; 124. Solanaceae)
- Blades narrowly elliptic, acute to obtuse at base; collecting vein usually conspicuous, 3–6 mm from margin
 *Anaxagorea panamensis* (Figs. 232, 233; 55. Annonaceae)
- Blades mostly 2.5–3 times longer than broad:
- ◆ Lateral veins ± parallel from midrib to a distinct, conspicuous, loop-connecting vein near margin (the distance between lateral veins nearly the same at the connecting vein as at midrib); blades long-acuminate:

- Largest blades less than 5 cm wide; margins often undulate
 *Mabea occidentalis* (75. Euphorbiaceae)
- Largest blades more than 5 cm wide; margins not distinctly undulate:
 Stems smooth, neither strongly lenticellate nor pubescent; blades smooth
 on both sides:
 Reticulate veins of blades not raised, the areoles (areas enclosed by the
 veinlets) minute, usually less than 0.2 mm diam, usually lighter than
 the surface (on dried plants); pubescence of youngest parts minute,
 uncinata, usually turned backward somewhat along the axis (but not
 appressed) *Brosimum alicastrum* subsp. *bolivarensis* (39. Moraceae)
- Reticulate veins of blades markedly raised, the areoles more than 1 mm
 diam, usually the same color as the surface (on dried plants); pubes-
 cence of youngest parts minute, appressed, not uncinata
 *Maquira costaricana* (39. Moraceae)
- Stems not smooth, either densely lenticellate or densely granular-
 puberulent; blades smooth or asperous:
 Blades smooth to the touch; stems essentially glabrous, conspicuously
 lenticellate *Sorocea affinis* (39. Moraceae)
- Blades asperous; stems densely granular-puberulent
 *Trophis racemosa* (39. Moraceae)
- ◆ Lateral veins lacking a distinct marginal collecting vein; blade apex various:
 Plants with conspicuous milky sap; blades ± obovate or elliptic:
 Blades ± elliptic, the major lateral veins in more than 15 pairs, the lower
 surface ± glaucous (at least when dried), the midrib sunken on upper
 surface *Aspidosperma megalocarpon* (118. Apocynaceae)
- Blades ± oblanceolate, the major lateral veins mostly in 5–7 pairs, the
 lower surface not glaucous, the midrib sharply raised on upper surface
 *Pouteria stipitata* (113. Sapotaceae)
- Plants lacking conspicuous, milky sap; blades mostly elliptic (obovate in
Cordia lasiocalyx):
 Stems divaricately branched, often with a leaf at branch nodes
 *Cordia lasiocalyx* (Fig. 474; 121. Boraginaceae)
- Stems not divaricately branched:
 Blades with a discolorous area on both sides of midrib below; plants
 shrubs or small trees usually less than 3 m tall; stems often with
 persistent inflorescence bases
 *Erythroxylum panamense* (Fig. 295; 66. Erythroxylaceae)
- Blades lacking a discolorous area along midrib below; plants shrubs or
 trees usually more than 3 m tall:
 Blades ± rounded and ending abruptly at base; blades ± lanceolate
 *Cestrum racemosum* (124. Solanaceae)
- Blades acute or at least not ending abruptly at base; blades ± elliptic:
 Plants stipulate; midrib of blade not arched:
 Stipules persistent, deltoid; young stems reddish-brown; blades
 with 7–12 pairs of lateral veins
 *Margaritaria nobilis* (75. Euphorbiaceae)
- Plants not as above:
 Stipules deciduous, linear, to 9 mm long, ciliate; blades with 3
 or 4 pairs of lateral veins; veins drying conspicuously
 wrinkled
 *Lacistema aggregatum* (Figs. 191, 192; 37. Lacistemaceae)
- Stipules caducous, linear-subulate; blades with 5–8 pairs of
 lateral veins; veins not drying conspicuously wrinkled
 *Casearia commersoniana* (Fig. 398; 96. Flacourtiaceae)
- Plants estipulate; midrib of blade prominently arched (not promi-
 nently arched on *Cestrum*):
 Blades with domatia in axils below
 *Nectandra purpurascens* (58. Lauraceae)
- Blades lacking axillary domatia:
 Blades with the acumen less than 1 cm long; young branchlets
 densely rufous-tomentulose
 *Terminalia chiriquensis* (105. Combretaceae)
- Blades with the acumen more than 1 cm long or the blades
 gradually acuminate, the acumen not distinct; young
 branchlets essentially glabrous:

- Leaf blades \pm coriaceous, abruptly acuminate, the acumen conspicuous, more than 1 cm long, the reticulate veins clearly visible without magnification; plants occurring in the forest *Ocotea cernua* (58. Lauraceae)
- Leaf blades membranaceous, gradually acuminate, the acumen not conspicuous, the reticulate veins not clearly visible; plants occurring in clearings and open areas *Cestrum nocturnum* (124. Solanaceae)
- Blades mostly less than 2.5 times longer than broad:
 - Blades less than 4.5 cm long, inconspicuously scabrid on midrib *Phyllanthus acuminatus* (75. Euphorbiaceae)
 - Blades more than 4.5 cm long:
 - Leaves borne at apex of very short (2–3 mm) branchlets; blades ovate, caudate-acuminate, 6–9 cm long; plants small trees *Coccoloba acapulcensis* (Fig. 219; 46. Polygonaceae)
 - Leaves and habit not as above:
 - ☆ Plants with stipules (some caducous):
 - Plants with the lateral veins \pm parallel with prominent collecting vein; blades generally more than 5 cm wide; stipules caducous; petioles scurfy; sap viscid:
 - Leaves usually less than 8 cm long, frequently less than 6 cm long, the primary lateral veins scarcely more conspicuous than the secondary lateral veins; stipules usually persistent (drying darker than stem) *Ficus pertusa* (Fig. 204; 39. Moraceae)
 - Leaves usually more than 10 cm long, frequently more than 12 cm long, the primary lateral veins much more conspicuous than the secondary lateral veins; stipules usually deciduous:
 - Reticulate veins of blade not raised, the areoles (areas enclosed by the veinlets) minute, usually less than 0.2 mm diam, usually lighter than the surface (on dried plants); pubescence of youngest parts minute, uncinata, usually turned backward somewhat along the axis (but not appressed) *Brosimum alicastrum* subsp. *bolivarensis* (39. Moraceae)
 - Reticulate veins of blade prominently raised, the areoles more than 1 mm diam, usually the same color as the surface (on dried plants); pubescence of youngest parts minute, appressed, not uncinata *Maquira costaricana* (39. Moraceae)
- Plants not as above:
- Petioles forked below base of blade, bearing 2 subulate appendages (vestigial leaflets) *Swartzia simplex* var. *ochracea* (Fig. 280; 63B. Caesalpinoideae)
 - Petioles not bearing subulate appendages:
 - Blades with lowermost major lateral veins stronger than any of the remaining lateral veins, arch-ascending to apical one-third to one-half of the blade *Celtis schippii* (38. Ulmaceae)
 - Blades with lowermost major lateral veins weaker or at least not stronger than the remaining lateral veins, ascending to no more than the basal one-third of the blade:
 - Blades moderately coriaceous, drying flat, the acumen blunt at tip, the reticulate veins not prominulous (at least not both close and prominulous):
 - Blades drying grayish, usually long-acuminate at apex; stipules subpersistent *Maytenus schippii* (77. Celastraceae)
 - Blades drying brownish, the acumen blunt, emarginate; stipules caducous *Vantanea occidentalis* (65. Humiriaceae)
 - Blades mostly membranaceous, the acumen very sharp at tip, the major lateral veins drying wrinkled or the reticulate veins both close and prominulous:
 - Basal pair of lateral veins reaching margin above the lower third of blade; stipules caducous, 5–9 mm long, marginally ciliate or pubescent *Lacistema aggregatum* (Figs. 191, 192; 37. Lacistemaceae)
 - Basal pair of lateral veins reaching margin in the lower fourth of blade; stipules subpersistent, 1.5–3 mm long, the margins glabrous *Margaritaria nobilis* (75. Euphorbiaceae)

☆ Plants stipulate:

At least the younger stems usually densely appressed-pubescent:

Pubescence on younger stems coarse, the trichomes not nearly contiguous and interspersed with many minute glandular globules; sap clear, not viscid; plants slender, erect or climbing shrubs
 *Tournefortia bicolor* (Fig. 476; 121. Boraginaceae)

Pubescence on younger stems fine, the trichomes often so dense as to be contiguous, lacking minute glandular globules; sap milky or clear; plants erect trees:

Leaf blades usually broadest at the middle, usually drying blackened, the tertiary veins anastomosing and running \pm parallel to the major lateral veins *Cynodendron panamense* (113. Sapotaceae)

Leaf blades often broadest above the middle, usually drying green, the tertiary veins often running straight between and perpendicular to the major lateral veins *Annona hayesii* (55. Annonaceae)

Younger stems glabrous or nearly so (at least not densely appressed-pubescent):

Stems \pm herbaceous; stems and leaves drying blackened
 *Tournefortia angustiflora* (Fig. 475; 121. Boraginaceae)

Stems woody; stems and leaves not drying blackened:

Leaf margins not revolute and not hyaline; midrib often \pm arched:

Leaves clustered at ends of branchlets in pseudowhorls, minutely verrucose *Terminalia chiriquensis* (105. Combretaceae)

Leaves alternate, not clustered at ends of branches, not verrucose:

Plants large forest trees, usually more than 20 m tall; leaves thick, the acumen thickened and often discolored at its tip
 *Drypetes standleyi* (Fig. 321; 75. Euphorbiaceae)

Plants shrubs or small trees, usually in clearings or at the edge of the forest, usually less than 5 m tall; leaves thin, the acumen not at all thickened or discolored
 *Cestrum nocturnum* (124. Solanaceae)

Leaf margins somewhat revolute and/or hyaline:

Acumen thickened near its apex and hyaline or discolored, the thickened area extending somewhat down either margin; blade margins weakly hyaline, not noticeably revolute, with a submarginal vein along much of its length
 *Drypetes standleyi* (Fig. 321; 75. Euphorbiaceae)

Acumen not as above; blade margins revolute, lacking a submarginal vein for all or most of its length:

Blades coriaceous, shiny, the lateral veins not conspicuous
 *Heisteria concinna* (43. Olacaceae)

Blades subcoriaceous, not shiny, the lateral veins conspicuous below *Heisteria longipes* (43. Olacaceae)

KEY 3: LEAVES SIMPLE, ALTERNATE OR SPIRALED; PLANTS LIANAS

Blades peltate, ovate:

Pubescence of sparse, long, spreading trichomes or puberulent *Cissampelos tropaeolifolia* (54. Menispermaceae)
 Pubescence long and sericeous or short and tomentose *Cissampelos pareira* (54. Menispermaceae)

Blades not peltate:

▣ Blades palmately veined at base (the 2–4 pairs of major lateral veins sometimes departing midrib 1–2 mm above base):

○ Petioles less than 1 cm long, the plants unarmed, or the blades deeply cleft at apex of midrib (juveniles so deeply cleft as to appear bifoliolate):

Blades deeply cleft at apex:

Trichomes on petioles and blades below obscure, appressed, less than 0.5 mm long
 *Bauhinia guianensis* (Fig. 274; 63B. Caesalpinioideae)

Trichomes on petioles and blades below ferruginous, erect to reclining, ca 1 mm long
 *Bauhinia reflexa* (63B. Caesalpinioideae)

Blades not cleft at apex:

Blades glabrous or nearly so:

Petioles swollen at apex *Abuta racemosa* (Fig. 230; 54. Menispermaceae)
 Petioles not swollen at apex *Smilax lanceolata* (26. Smilacaceae)

- Blades pubescent:
- Lower blade surface very densely pubescent with erect, crisp trichomes, the upper surface with sparse scabrous pubescence *Pouzolzia obliqua* (Fig. 209; 40. Urticaceae)
 - Lower blade surface sparsely to densely pubescent, the upper surface often glabrate:
 - Blades often shallowly cordate at base *Gouania lupuloides* (81. Rhamnaceae)
 - Blades obtuse to rounded at base *Securidaca diversifolia* (74. Polygalaceae)
- Petioles more than 1 cm long *or* the plants armed; blades not cleft at apex:
- Mature blades deeply 3–5-lobed:
 - Plants glabrous; leaves coriaceous, lacking teeth; tendrils trifid, branched from near base *Cayaponia granatensis* (131. Cucurbitaceae)
 - Plants pubescent; leaves not coriaceous, with \pm apiculate teeth; tendrils simple:
 - Pubescence dense, minute, ferruginous; blades with several round glands on margin at bases of sinuses between lobes *Passiflora vitifolia* (98. Passifloraceae)
 - Pubescence usually white-pilose or white-villous; blades eglandular:
 - Many mature blades 5-lobed, to 30 cm long and wide *Gurania makoyana* (131. Cucurbitaceae)
 - Mature blades mostly 3-lobed, to 20 cm long and wide *Gurania megistantha* (Fig. 540; 131. Cucurbitaceae)
 - Mature blades not lobed:
 - Most blades more than 3 times longer than wide, cordate at base, conspicuously punctate above when dry *Aristolochia chapmaniana* (Fig. 215, 216; 44. Aristolochiaceae)
 - Blades less than 3 times longer than wide:
 - Plants armed *or* with conspicuous glands at apex or base of petiole:
 - Plants armed:
 - Plants armed with recurved spines on stems, petioles, and midribs of blades *Byttneria aculeata* (Fig. 377; 87. Sterculiaceae)
 - Plants armed on stems only; blades toothed *Celtis iguanaeus* (38. Ulmaceae)
 - Plants unarmed:
 - Blades rounded at apex; petioles with 2 large glands at apex *Omphalea diandra* (Fig. 324; 75. Euphorbiaceae)
 - Blades long-acuminate; petioles with 2 protruding glands at base *Smilax lanceolata* (26. Smilacaceae)
 - Plants unarmed and lacking glands on petiole:
 - Lateral veins ending in a sharp tooth on margin:
 - Blades densely arachnoid below, the trichomes obscuring the surface *Vitis tiliifolia* (Figs. 355, 356; 82. Vitaceae)
 - Blades sparsely to densely pubescent below, not arachnoid, the surface not obscured:
 - Blades glabrous or with simple, villous pubescence, mostly ovate-oblong, monomorphic, the larger not cordate *Cissus sicyoides* (82. Vitaceae)
 - Blades pubescent at least on veins below with minute, close puberulence and often with appressed, T-shaped trichomes, ovate, dimorphic, the larger ones cordate *Cissus pseudosicyoides* (Fig. 354; 82. Vitaceae)
 - Lateral veins not ending in a sharp tooth on margin:
 - Blades densely short-white-pubescent below, the trichomes completely obscuring surface (less so on juveniles) *Chondrodendron tomentosum* (Fig. 231; 54. Menispermaceae)
 - Blades not so densely pubescent below:
 - Blades with domatia or nectaries in vein axils below at base of blade:
 - Domatia pocketlike *Fevillea cordifolia* (Fig. 538; 131. Cucurbitaceae)
 - Domatia flat, glandular areas or nectary pores:
 - Blades pubescent at least on veins below *Odontocarya tamoides* var. *canescens* (54. Menispermaceae)
 - Blades glabrous *Odontocarya truncata* (54. Menispermaceae)
 - Blades lacking domatia and nectaries in vein axils:
 - Petioles enlarged and usually curved and rugose at apex:
 - Petioles mostly less than 3 cm long *Abuta racemosa* (Fig. 230; 54. Menispermaceae)
 - Petioles mostly more than 4 cm long *Abuta panamensis* (54. Menispermaceae)
 - Petioles not enlarged or curved at apex:
 - Blade margins usually \pm crenate; blades longer than broad, drying with conspicuous cystoliths above *Urera eggersii* (Fig. 210; 40. Urticaceae)
 - Blade margins entire; blades nearly orbicular, lacking cystoliths *Ipomoea phillomega* (Fig. 471; 120. Convolvulaceae)
- Blades not palmately veined at base:
- ◇ Blades pubescent above on surface:
 - Plants with stellate trichomes and/or armed:
 - Plants armed with recurved spines on stems and midribs of blades *Solanum lanciifolium* (124. Solanaceae)
 - Plants unarmed:

- Petioles (5)10–20 mm long, the wings flaring upward at base *Tetracera volubilis* (88. Dilleniaceae)
 Petioles 3–10 mm long, the wings obscure or lacking at base
 *Tetracera portobellensis* (Fig. 383; 88. Dilleniaceae)
- Plants lacking stellate trichomes and unarmed:
 Stems essentially glabrous:
 Blades toothed and gradually acuminate (rarely entire); blade surface glabrous or with long, sparse, slender trichomes *Doliocarpus dentatus* (88. Dilleniaceae)
 Blades entire (or obscurely toothed at apex), rounded or bluntly acuminate at apex; blade surface scabridulous except for long, slender, ± appressed trichomes on veins *Davilla nitida* (88. Dilleniaceae)
- Stems conspicuously pubescent:
 Stems densely pubescent with T-shaped trichomes *Heteropteris laurifolia* (71. Malpighiaceae)
 Stems lacking T-shaped trichomes:
 Stems with 2 types of pubescence: very long (more than 4 mm), spreading trichomes and minute puberulence or the trichomes shorter with prominent bulbous bases:
 Trichomes on stems of 2 types, very long ones interspersed with short puberulence
 *Tournefortia cuspidata* (Fig. 477; 121. Boraginaceae)
 Trichomes on stems of a single type, bending toward apex with a prominent bulbous base
 *Tournefortia hirsutissima* (121. Boraginaceae)
- Stem pubescence of a single type, lacking bulbous bases:
 Stems lacking stipular glands at bases of petioles; blades ciliate, emarginate at apex with tufted apiculum *Isea luxurians* (120. Convolvulaceae)
 Stems with small, round, stipular glands at bases of petioles; blades ciliate or not:
 Pubescence on blades and stems appressed; blades usually acute to obtuse at apex, rounded to cuneate at base *Securidaca diversifolia* (Fig. 314; 74. Polygalaceae)
 Pubescence on blades and stems erect and spreading; blades obtuse to rounded at apex, broadly rounded or truncate at base *Securidaca tenuifolia* (74. Polygalaceae)
- ◇ Blades glabrous above or with trichomes on veins only:
 Plants parasitic lianas; lateral veins nearly invisible; blades usually less than 5 cm long
 *Struthanthus orbicularis* (42. Loranthaceae)
 Plants not parasitic; lateral veins visible:
 Stipules ocreate; blades with very minute peltate scales on both surfaces
 *Coccoloba parimensis* (46. Polygonaceae)
 Stipules lacking:
 Plants with long recurved spines in branch axils; vein axils with tufts of trichomes below; midrib raised and pubescent above *Combretum decandrum* (Figs. 416, 417, and fig. on p. 20; 105. Combretaceae)
 Plants lacking spines and axillary tufts:
 Midrib conspicuously sunken above:
 Midrib arched; lower blade surface smooth; lateral veins scarcely raised below
 *Mariipa panamensis* (120. Convolvulaceae)
 Midrib not arched; lower blade surface asperous or not; lateral veins very prominently raised below; petioles narrowly winged or sharply canaliculate below blade:
 Leaf blades broadest at or below middle, markedly asperous on lower surface, rounded or obtuse at base, drying grayish-green *Tetracera hydrophila* (88. Dilleniaceae)
 Leaf blades broadest somewhat above middle, smooth on lower surface, acute at base, drying dark brown *Doliocarpus multiflorus* (88. Dilleniaceae)
- Midrib flat or raised above (slightly sunken in *Doliocarpus dentatus* and *D. olivaceus*):
 Young stems usually 5-angulate and narrowly winged; blades with conspicuous punctations on both surfaces (inconspicuous on juveniles) *Doliocarpus major* (Fig. 380; 88. Dilleniaceae)
 Stems not markedly ribbed or winged; blades not punctate:
 Stems, except oldest parts, herbaceous, green; plants dark brown or black when dry, usually with minute, granular projections on young blades (bases of old trichomes):
 Blades membranaceous, usually drying blackish, often appearing punctate beneath with the minute bases of old trichomes *Tournefortia angustiflora* (Fig. 475; 121. Boraginaceae)
 Blades weakly coriaceous, usually drying brownish, not appearing punctate beneath
 *Tournefortia bicolor* (Fig. 476; 121. Boraginaceae)
- Stems woody, not green; plants not blackening and lacking granular projections on blades when dry:
 Stems densely pubescent with T-shaped trichomes *Heteropteris laurifolia* (71. Malpighiaceae)
 Plants lacking T-shaped trichomes:
 △ Lateral veins conspicuous; blades lacking rows of minute glands near margins, the margins frequently toothed, sometimes pubescent; petioles narrowly winged; plants not epiphytic:
 Blades essentially glabrous:
 At least some blades conspicuously dentate *Doliocarpus dentatus* (88. Dilleniaceae)
 Blades usually entire to obscurely dentate
 *Doliocarpus olivaceus* (Figs. 381, 382; 88. Dilleniaceae)

Blades pubescent:

- Blades scabridulous over surface, the trichomes on veins longer and \pm appressed; margins entire or dentate only at apex *Davilla nitida* (88. Dilleniaceae)
 Blades with long slender trichomes over surface; at least some blades markedly dentate *Dolioscarpus dentatus* (88. Dilleniaceae)

△ Lateral veins obscure; blades glabrous, with rows of minute glands near margins, the margins entire; petioles not winged; plants hemiepiphytic shrubs:

- Blades oblong to oblong-lanceolate, usually rounded or acute and ending abruptly at base, long-acuminate at apex; branches long-pendent *Marcgravia nepenthoides* (Fig. 384; 90. Marcgraviaceae)
 Blades not oblong or oblong-lanceolate:
 Blades ovate to obovate, acute to rounded at base; leaves irregular on stem, often subopposite *Markea ulei* (Figs. 482, 483; 124. Solanaceae)
 Blades usually obovate, gradually tapered to an acute base; leaves spirally arranged *Souroubea sympetala* (Fig. 385; 90. Marcgraviaceae)

KEY 4: LEAVES PALMATELY COMPOUND WITH FOUR OR MORE LEAFLETS

Blades pubescent below:

- Blades densely brown-sericeous, the trichomes simple, totally obscuring surface below *Didymopanax morototoni* (109. Araliaceae)
 Blades sparsely to densely pubescent below, the trichomes stellate, not obscuring surface:
 Leaves alternate; blades pubescent above only on veins; leaflets usually more than 25 cm long *Herrania purpurea* (Fig. 378; 87. Sterculiaceae)
 Leaves opposite; blades pubescent above throughout; leaflets less than 15 cm long *Tabebuia ochracea* var. *neochrysantha* (126. Bignoniaceae)

Blades glabrous or lepidote below:

- Leaflets conspicuously petiolulate, the petiolules usually more than 1.5 cm long; blades ending abruptly at petiole; leaves opposite or subopposite (except *Ceiba*):
 Blades with plate-shaped glands at least in lower vein axils *Tabebuia rosea* (Figs. 500, 501; 126. Bignoniaceae)
 Blades lacking plate-shaped glands in vein axils:
 Leaflets often more than 5 cm broad, tufted with stellate trichomes in axils below *Tabebuia guayacan* (Fig. 499; 126. Bignoniaceae)
 Leaflets less than 4.5 cm broad, not tufted in axils *Ceiba pentandra* (fig. on p. 10; 86. Bombacaceae)
 Leaflets sessile or the petiolules less than 1 cm long; blades tapered at base; leaves alternate:
 Older branches and trunk armed:
 Leaflets often more than 5 cm wide, usually obovate *Bombacopsis quinata* (Figs. 366, 367; 86. Bombacaceae)
 Leaflets less than 4.5 cm wide, usually oblong-lanceolate to oblong-elliptic:
 Leaflets glaucous on lower surface, drying pale bluish-green; reticulate veins not visible *Jacaratia spinosa* (99. Caricaceae)
 Leaflets not glaucous on lower surface, drying brownish; reticulate veins prominulous *Ceiba pentandra* (fig. on p. 10; 86. Bombacaceae)
 Branches and trunk not armed:
 Leaflets rounded to emarginate at apex *Bombacopsis sessilis* (Fig. 368; 86. Bombacaceae)
 Leaflets acute to acuminate or mucronate at apex:
 Leaflets articulate; trunk bark lacking green vertical bands *Pachira aquatica* (Fig. 371; 86. Bombacaceae)
 Leaflets not articulate; trunk bark with prominent, green, vertical bands *Pseudobombax septenatum* (Figs. 372, 373; 86. Bombacaceae)

KEY 5: LEAVES PINNATELY COMPOUND MORE THAN ONCE

☆ Leaves biternate or the basal set of leaflets ternate or with prominently winged rachis:

- All leaves biternate (i.e., with 3 sets of 3 leaflets each) or with the terminal set replaced by a tendril or tendril scar:
 Leaflets densely and softly rufous-pubescent below *Serjania cornigera* (Fig. 347; 80. Sapindaceae)
 Leaflets not rufous-pubescent:
 Blades with the midrib glabrous above:
 Leaves always biternate; stem unarmed; wood composite, consisting of a central woody core surrounded by 3 smaller peripheral bundles *Serjania paucidentata* (Fig. 349; 80. Sapindaceae)
 Leaves sometimes biternate at apex but always 2- or 3-pinnate lower on stem; stems usually armed with short prickles; wood simple, lacking peripheral bundles *Serjania mexicana* (Fig. 348; 80. Sapindaceae)
 Blades with the midrib pubescent above:
 Rachis not winged:
 Leaflets lacking axillary tufts; stems 5- or 6-costate *Serjania decapleuria* (80. Sapindaceae)

Leaflets with the axils conspicuously tufted below; stems terete to square:

Leaflets prominently toothed, the lateral leaflets nearly sessile *Serjania pluvialiflorens* (80. Sapindaceae)

Leaflets entire, all distinctly petiolulate *Pleonotoma variabilis* (126. Bignoniaceae)

Rachis narrowly winged:

Blades with black lines, especially below *Serjania atrolineata* (80. Sapindaceae)

Blades lacking black lines:

Stems terete; leaflets \pm glabrous below except for tufts of trichomes in axils *Paullinia fuscescens* (80. Sapindaceae)

Stems ribbed; leaflets pubescent below or lacking tufted axils:

Leaflets sparsely pubescent below, occasionally with tufts in axils; stems with simple wood *Serjania mexicana* (Fig. 348; 80. Sapindaceae)

Leaflets densely soft-pubescent below, lacking axillary tufts; stems with composite wood, having 3 peripheral bundles *Serjania rhombea* (80. Sapindaceae)

● Blades not strictly biternate, but with the basal set of leaflets ternate, or with more than 3 leaflets on the basal pinnae:

Terminal leaflets less than 4 cm long; leaves partially 3-pinnate; older stems 3-ribbed *Serjania trachygona* (Fig. 350; 80. Sapindaceae)

Terminal leaflets more than 4 cm long:

Stems terete; basal set of leaflets with 3 leaflets *Paullinia glomerulosa* (Fig. 343; 80. Sapindaceae)

Stems ribbed; basal set of leaflets with 3–8 leaflets; stems often armed *Serjania mexicana* (Fig. 348; 80. Sapindaceae)

☆ Leaves not biternate, simply bipinnate, the rachis unwinged:

Leaflets more than 5 mm wide:

Petioles or rachises with glands:

Petioles with a large conspicuous gland at apex (many times larger than other glands on leaf):

Gland at apex of petiole less than 3 mm high; leaflets 3–5 per pinna, acute at apex, ovate *Leucaena multicapitula* (Fig. 267; 63A. Mimosoideae)

Gland at apex of petiole ca 10 mm high; leaflets 7–12 per pinna, often rounded at apex, oblong *Pithecellobium macradenium* (Figs. 271, 272; 63A. Mimosoideae)

Petioles lacking a large gland at apex:

Each pinna with 8 or more pairs of leaflets *Schizolobium parahybum* (63B. Caesalpinoideae)

Each pinna with 7 or fewer pairs of leaflets:

Leaflets rounded at apex, narrowly ovate *Albizia guachapele* (Fig. 258; 63A. Mimosoideae)

Leaflets not rounded at apex, not ovate:

Pinnae with 2 leaflets, with recurved spines at base of leaf *Pithecellobium hymeneaeifolium* (Fig. 270; 63A. Mimosoideae)

Pinnae with 4–7 pairs of leaflets, lacking spines *Pithecellobium dinizii* (63A. Mimosoideae)

Petioles and rachises lacking glands:

Plants lianas:

Leaflets subsessile, the sides usually straight, broadest near apex *Adenopodia polystachya* (63A. Mimosoideae)

Leaflets petiolulate, the sides curved, broadest at middle . . . *Entada monostachya* (Fig. 259; 63A. Mimosoideae)

Plants trees:

Leaflets rounded at both ends, emarginate at apex, equilateral at base with the lateral veins inconspicuous; juveniles with resinous stems *Schizolobium parahybum* (63B. Caesalpinoideae)

Leaflets acuminate at apex:

Leaflets inequilateral at base and decurrent onto base of petiole, truly bipinnate; stipules lacking; plants large trees, usually more than 20 m tall *Jacaranda copaia* (Figs. 493, 494; 126. Bignoniaceae)

Leaflets \pm equal at base, the petioles distinct; blades simple, only appearing bipinnate due to deciduous branches; stipule at each leaf minute, triangular, persistent; plants shrubs or small trees, less than 8 m tall *Phyllanthus acuminatus* (75. Euphorbiaceae)

Leaflets less than 5 mm wide:

Stems unarmed:

Pinnae each with 14 or fewer pairs of leaflets; petioles, rachises, and lower leaflet surfaces tawny-tomentose *Pithecellobium barbourianum* (Fig. 269; 63A. Mimosoideae)

Pinnae each with 15 or more pairs of leaflets; leaflets not tawny-tomentose:

Leaflets less than 5 mm long; young stems, petioles, and rachises ferruginous *Enterolobium schomburgkii* (63A. Mimosoideae)

Leaflets more than 6 mm long; stems, petioles, and rachises usually glabrate, not ferruginous though sometimes \pm cinereous:

Stems, petioles, and rachises usually glabrate; leaflets in 3 or 4 pairs per cm along rachis *Enterolobium cyclocarpum* (Fig. 260; 63A. Mimosoideae)

Stems, petioles, and rachises \pm cinereous; leaflets in 5–7 pairs per cm along rachis *Acacia glomerosa* (63A. Mimosoideae)

Stems armed (often rachises also):

- Spines bullhorn-like, black, hollow, more than 3 cm long *Acacia melanoceras* (63A. Mimosoideae)
- Spines not as above:
- Stems and rachises densely rufous-pubescent; rachises armed throughout at each node *Mimosa pigra* (63A. Mimosoideae)
- Stems and rachises not densely rufous-pubescent; rachises sparsely armed:
- Plants large buttressed trees *Acacia glomerosa* (63A. Mimosoideae)
- Plants small trees or lianas or shrubs:
- Leaflets 3–7 mm long, glabrous or conspicuously pubescent on lower inner edge *Acacia riparia* (Fig. 257; 63A. Mimosoideae)
- Leaflets 9–14 mm long, glabrous or pubescent, but the trichomes never restricted to lower inner edge nearest rachis:
- Older stems usually deeply 4-sulcate *Acacia acanthophylla* (63A. Mimosoideae)
- Older stems usually subterete and with 5 prominent ribs but not 5-sulcate *Acacia hayesii* (63A. Mimosoideae)

KEY 6: LEAVES COMPOUND, PINNATE OR WITH THREE OR FEWER LEAFLETS

★ Leaves at most 2- or 3-foliolate:

Plants trees or shrubs:

Leaflets palmately veined at base; trunk spiny:

Plants large trees; spines on trunk broad, corky; leaflets rounded at apex, less than 8 cm broad, broadest near middle *Erythrina fusca* (Fig. 287; 63C. Papilionoideae)

Plants small, slender trees; spines short, small, not corky; leaflets acuminate, more than 10 cm broad, broadest near base *Erythrina costaricensis* var. *panamensis* (Figs. 285, 286; 63C. Papilionoideae)

Leaflets not palmately veined at base; trunk unarmed:

Leaflets 3, lacking wings on margin of petiole:

Leaflets sessile; axils of lower blade surface with tufts of pubescence *Allophylus psilospermus* (80. Sapindaceae)

Leaflets petiolulate, lacking axillary tufts on lower surface:

Leaflets thick, rounded at base, the petiolules with a terete pulvinus, not canaliculate; younger parts reddish-tomentose *Connarus panamensis* (Fig. 256; 62. Connaraceae)

Leaflets moderately thin, cuneate to attenuate at base, the petiolules canaliculate, not at all swollen; younger parts glabrate to puberulent. *Vitex cooperi* (122. Verbenaceae)

Leaflets 2 or petioles with produced winglike margins at apex:

Leaflets 3, ± equilateral, often with some simple leaves:

Leaflets ± elliptic, ending abruptly on petiolule, distinctly petiolulate, obtuse to rounded at base *Swartzia simplex* var. *grandiflora* (63B. Caesalpinioideae)

Leaflets oblanceolate, decurrent onto petiolule or sessile, acute and tapered at base (adults often with 5 leaflets) *Quassia amara* (68. Simaroubaceae)

Leaflets 2, inequilateral:

Petioles less than 5 mm long; leaflets usually emarginate at apex, sessile at apex of petiole *Cynometra bauhinifolia* (63B. Caesalpinioideae)

Petioles more than 10 mm long; leaflets usually not emarginate at apex:

Margins at base of leaflet not meeting petiolule at the same point, separated by 2–3 mm; leaflets not long-acuminate *Hymenaea courbaril* (63B. Caesalpinioideae)

Margins at base of leaflet joining petiolule at ± the same point; leaflets long-acuminate *Peltogyne purpurea* (63B. Caesalpinioideae)

Plants lianas:

◆ Leaflets toothed:

Blades with round, pellucid punctations throughout; stems hollow *Stizophyllum riparium* (126. Bignoniaceae)

Blades not pellucid-punctate throughout:

Tendrils coiled like a watchspring, axillary; leaflets irregularly, broadly toothed, usually crenate or not sharply toothed:

Leaflets lacking tufts of trichomes in axils below *Serjania circumvallata* (80. Sapindaceae)

Leaflets with tufts of trichomes in axils below:

Leaflets palmately veined at base *Thinouia myriantha* (80. Sapindaceae)

Leaflets not palmately veined at base *Paullinia turbacensis* (Fig. 346; 80. Sapindaceae)

Tendrils not coiled like a watchspring; leaflets ± regularly toothed and usually serrate-apiculate or closely irregularly crenate (*Cissus erosa*); leaves opposite:

Terminal leaflet rhombic; plants densely pubescent with glandular and/or eglandular trichomes; stipules on young branches lanceolate to linear-lanceolate, 3–6 mm long *Cissus rhombifolia* (82. Vitaceae)

Terminal leaflet elliptic to obovate; plants usually glabrous or with sparse eglandular trichomes; stipules on young branches broadly ovate to subrotund, 2–4 mm long or stipules lacking:

- Stems tetragonal, often winged, sometimes speckled with maroon at nodes *Cissus erosa* (82. Vitaceae)
- Stems terete to ribbed or subangulate, not winged, not speckled:
 - Petioles and petiolules conspicuously but sparsely white-pilose; terminal leaflet usually more than 12 cm long *Gurania coccinea* (131. Cucurbitaceae)
 - Petioles and petiolules not conspicuously pubescent; terminal leaflet usually less than 12 cm long *Cissus microcarpa* (Fig. 353; 82. Vitaceae)

◆ Leaflets entire:

- Leaflets 2, the tendrils arising from stems or axes of inflorescences:
 - Trichomes on petiole and lower blade surface obscure, appressed, less than 0.5 mm long *Bauhinia guianensis* (Fig. 274; 63B. Caesalpinioideae)
 - Trichomes on petiole and lower blade surface erect to reclining, ca 1 mm long *Bauhinia reflexa* (63B. Caesalpinioideae)
- Leaflets 3 or leaflets 2, the terminal (third) leaflet replaced by a tendril or tendril scar:
 - Young parts densely rufous-pubescent; lower petioles often more than 10 cm long; leaves trifoliolate, lacking both tendrils and stipels; plants often arching trees *Connarus panamensis* (Fig. 256; 62. Connaraceae)
 - Young parts not densely rufous-pubescent; all petioles usually less than 10 cm long; leaves trifoliolate, with tendrils and/or stipels, the terminal leaflet sometimes replaced by a tendril:
 - Plants lacking tendrils (except *Cymbosema*); stipels acicular; pseudostipules lacking:
 - Blades sparsely to densely pubescent above and below:
 - Trichomes on major veins below mostly more than 1.2 mm long, usually closely appressed *Dioclea reflexa* (Fig. 283; 63C. Papilionoideae)
 - Trichomes on major veins below mostly less than 1 mm long, spreading or vaguely appressed:
 - Plants often tendriled *Cymbosema roseum* (63C. Papilionoideae)
 - Plants lacking tendrils *Dioclea guianensis* (63C. Papilionoideae)
 - Blades sparsely pubescent to glabrate below, glabrous except on veins above:
 - Trichomes on veins below reddish, darker than those on surface *Dioclea wilsonii* (Fig. 284; 63C. Papilionoideae)
 - Trichomes concolorous:
 - Leaflets ± elliptic, with more than 10 pairs of lateral veins; stipels lanceolate and persistent, ca 5 mm long *Clitoria javitensis* (63C. Papilionoideae)
 - Leaflets ovate to ovate-elliptic, with fewer than 10 pairs of lateral veins; stipels acicular, caducous:
 - Terminal leaflet usually ± rhombic-ovate; leaflets glabrous below, at least the younger ones covered on underside with sessile, orange glands *Rhynchosia pyramidalis* (63C. Papilionoideae)
 - Terminal leaflet ovate-elliptic; leaflets lacking orange glands, sometimes with stiff, irritating trichomes on underside *Mucuna mutisiana* (Figs. 291, 292), *M. rostrata* (63C. Papilionoideae)
- Plants with tendrils; acicular stipels lacking; pseudostipules usually present; leaves 2- or 3-foliolate, mostly glandular-lepidote; stems usually with either interpetiolar ridges or interpetiolar glandular fields (except *Psiguria*, with tendrils opposite trifoliolate leaves):
 - Blades densely white- or grayish-pubescent below *Arrabidaea candicans* (126. Bignoniaceae)
 - Blades not whitish-pubescent below:
 - Stems (all but the largest) markedly 4-, 6-, or 8-angulate and ribbed:
 - Stems 6- or 8- angulate; lateral veins mostly arising from near base of leaf:
 - Blades stellate-pubescent in axils below, whitish below; lepidote scales dense, contiguous except on veins below; pseudostipules sickle-shaped, to 5 mm long *Amphilophium paniculatum* (126. Bignoniaceae)
 - Blades with plate-shaped glands in axils below, green above and below; lepidote scales sparse on both surfaces; pseudostipules spatulate, 7–19 mm long *Pithecoctenium crucigerum* (126. Bignoniaceae)
- Stems square:
 - Leaflets 3, the terminal one never replaced by a tendril; petiolules ± equal on a leaf; blades eglandular, not lepidote; plants mostly herbaceous vines lacking pseudostipules *Psiguria bignoniacea* (Fig. 542; 131. Cucurbitaceae)
 - Leaflets sometimes 2, the terminal one replaced by a sometimes deciduous tendril; petiolules of terminal leaflets (when present) longer than those of lateral leaflets; blades with few to many round glands and scurfy scales; plants lianas, often with pseudostipules:
 - Blades pellucid-punctate throughout; stems hollow *Stizophyllum riparium* (126. Bignoniaceae)
 - Blades with few round glands; stems solid:
 - Petioles with conspicuous glandular field at apex; pseudostipules vertically 3-seriate *Pachyptera kerere* (Fig. 496; 126. Bignoniaceae)
 - Petioles lacking glands at apex; pseudostipules small or lacking:

- Leaflets \pm elliptic, with few glands scattered below; pseudostipules small, clustered in leaf axils *Clytostoma binatum* (126. Bignoniaceae)
- Leaflets \pm ovate, with dense glands in basal vein axils below; pseudostipules lacking except on youngest stems *Cydista aequinoctalis* (Fig. 491; 126. Bignoniaceae)
- Stems terete or subterete, not ribbed (slightly ribbed in *Clytostoma*):
- Basal vein axils below with tufts of trichomes, domatia, or glands:
- Blades with a few round glands near midrib below:
- Stems with interpetiolar glandular fields; most parts drying reddish *Arrabidaea chica* (126. Bignoniaceae)
- Stems lacking interpetiolar glands; no parts drying conspicuously reddish:
- Axils of major lateral veins of lower blade surface with small, pitlike, pubescent domatia; stems lacking interpetiolar ridges; leaf blades obtuse to broadly rounded at base; tendrils simple *Callichlamys latifolia* (Fig. 490; 126. Bignoniaceae)
- Axils of major lateral veins lacking domatia; stems with interpetiolar ridges; leaf blades truncate to asymmetrically cordate at base; tendrils trifid *Martinella obovata* (Fig. 495; 126. Bignoniaceae)
- Blades mostly lacking glands:
- Blades often orbicular or ovate, abruptly acuminate, with sunken axillary domatia below *Ceratophytum tetragonolobum* (126. Bignoniaceae)
- Blades \pm elliptic, \pm gradually acuminate, with tufted axils below:
- Midribs below markedly pubescent (villous); stems lacking interpetiolar glands *Arrabidaea patellifera* (126. Bignoniaceae)
- Midribs below inconspicuously pubescent; stems with interpetiolar glands at some nodes *Arrabidaea verrucosa* (126. Bignoniaceae)
- Basal vein axils below lacking long trichomes, domatia, and glands:
- Mature blades conspicuously pubescent, the trichomes at least 0.5 mm long *Cymbosema roseum* (63C. Papilionoideae)
- Mature blades glabrous or with trichomes less than 0.5 mm long:
- Blades with very conspicuous yellow glands ca 0.1 mm diam on lower surface *Stizophyllum riparium* (126. Bignoniaceae)
- Blades lacking such glands:
- Stems with conspicuous interpetiolar glandular fields, often with a thin, raised ridge on stem above the field; pseudostipules of several subulate scales 3–4 mm long, \pm persistent *Pachyptera kerere* (Fig. 496; 126. Bignoniaceae)
- Stems and pseudostipules not as above:
- Pseudostipules \pm persistent, foliaceous, not longitudinally striate, 4 at each node, 3–13 mm long, 1.5–10 mm wide *Anemopaegma chrysoleucum* (126. Bignoniaceae)
- Pseudostipules not present or, if present, less than 3 mm long or longitudinally striate:
- Pseudostipules ca 5 mm long, longitudinally striate; tendrils trifid and clawlike; phloem rays irregular, many-armed *Macfadyena unguis-cati* (126. Bignoniaceae)
- Pseudostipules, tendrils, and phloem rays not as above:
- Blades lepidote above and below, yielding a sweet odor when freshly crushed; petioles with a glandular field at apex; pith with 4 phloem arms; pseudostipules of 2 or 3 subulate scales, appressed to twig; young branchlets usually with conspicuous, raised, warty lenticels ca 0.6 mm long *Paragonia pyramidata* (126. Bignoniaceae)
- Plants not with the above combination of characters:
- Tendrils trifid; pith strongly 4-angular; blades usually broadly ovate, attenuate at apex, bicolorous; fresh vegetative parts with odor of cloves; pseudostipules lacking *Tynnanthus croatianus* (126. Bignoniaceae)
- Plants not with the above combination of characters:
- ▲ Pith 4-angular:
- Blades drying very reddish, \pm ovate, sharply long-attenuate at apex, not subcordate at base *Arrabidaea chica* (126. Bignoniaceae)
- Blades not drying reddish, variously shaped:
- Blades usually truncate to subcordate at base, not drying with a conspicuous white margin, lacking branched trichomes on midrib below; petiolules abruptly and conspicuously expanded at apex *Adenocalymna arthropotiolatum* (126. Bignoniaceae)
- Blades not as above:
- Blades drying with a conspicuous white margin and a dark pewter color; pseudostipules small, pointed, \pm ovate *Adenocalymna apurensis* (126. Bignoniaceae)
- Blades not drying with a white margin, usually drying olive-green to olive-gray; pseudostipules inconspicuous or lacking:

- Midribs below with branched trichomes to ca 0.3 mm long
 *Xylophragma seemannianum* (126. Bignoniaceae)
 Midribs below lacking such trichomes
 *Arrabidaea florida* (126. Bignoniaceae)

▲ Pith 8–16-angulate:

- Leaves simple to bifoliolate, usually strongly 3-veined from base; petioles usually less than 3 cm long
 *Cydista heterophylla* (Fig. 492; 126. Bignoniaceae)

Leaves all bifoliolate; petioles often more than 3 cm long:

- Conspicuous glandular area restricted to basal axils on underside of blade; lateral veins in 3–5 pairs
 *Cydista aequinoctalis* (Fig. 491; 126. Bignoniaceae)

Dense glandular area in basal axils lacking; lateral veins often in more than 5 pairs:

- Pseudostipules conspicuous, appearing as small bromeliads; blades elliptic, sharply acuminate, acute at base
 *Clytostoma binatum* (126. Bignoniaceae)

- Pseudostipules lacking or very inconspicuous; blades ± ovate, not sharply acuminate, rounded to subcordate at base
 *Phryganocydia corymbosa* (Fig. 497; 126. Bignoniaceae)

★ Some leaves with 4 or more leaflets:

⊙ Petioles or rachises bearing conspicuous raised glands:

⊗ Rachis winged:

Blades glabrous above except possibly on veins:

Blades pubescent below at least on veins:

- Stipules persistent, striate, to 10 mm long; largest leaflets usually more than 5.5 cm wide; rachis winged throughout or only near apex; young parts ferruginous-pubescent; stems light, not conspicuously lenticellate
 *Inga sapindoides* (63A. Mimosoideae)

- Stipules caducous, not striate, 5–6 mm long; largest leaflets less than 5.5 cm wide; rachis winged only at apex; young parts not ferruginous-pubescent; stems dark brown, conspicuously lenticellate
 *Inga pezizifera* (63A. Mimosoideae)

Blades essentially glabrous below:

- Leaflets obovate *Inga fagifolia* (63A. Mimosoideae)

Leaflets elliptic:

- All leaves with 2 pairs of leaflets; rachis wing tapering to base. *Inga marginata* (63A. Mimosoideae)

Some leaves with more than 2 pairs of leaflets:

- Leaves with 2 or 3 pairs of leaflets (usually 3); rachis wings becoming obsolete well before base
 *Inga umbellifera* (Fig. 266; 63A. Mimosoideae)

- Leaves with 3–5 pairs of leaflets (usually 4); rachis wings narrow
 *Inga pezizifera* (63A. Mimosoideae)

Blades pubescent above on surface and veins:

Stems conspicuously pubescent with long, dense, reddish-brown trichomes:

- Leaflets with gland on upper surface of midrib ca 1–2 cm from base; stipules ovate
 *Inga goldmanii* (Fig. 261; 63A. Mimosoideae)

Leaflets lacking gland on midrib; stipules apiculate:

- Branchlets densely ferruginous-velutinous; terminal leaflets at least 7 cm wide or visibly pubescent above
 *Inga mucuna* (Fig. 263; 63A. Mimosoideae)

- Branchlets glabrous in age; terminal leaflets less than 7 cm wide and not visibly pubescent above (may be densely puberulent)
 *Inga pauciflora* (Fig. 264; 63A. Mimosoideae)

Stems not conspicuously pubescent with reddish-brown trichomes, at least in age:

Petioles usually more than 2 cm long:

- Lower leaflet surface densely pubescent, the trichomes on veins contiguous; glands on rachis ca 2.5–3 mm diam; stems ribbed between leaves; stipules 2–3 mm long, caducous
 *Inga minutula* (Fig. 262; 63A. Mimosoideae)

- Lower leaflet surface sparsely pubescent, the trichomes on veins not contiguous; glands on rachis 1–2 mm diam; stems not ribbed; stipules to 10 mm long, persistent
 *Inga sapindoides* (63A. Mimosoideae)

Petioles usually less than 2 cm long:

- Apical leaflets usually more than 9 cm wide, glabrous or sparsely pubescent above even when young (few appressed trichomes); leaves with 2 or 3 pairs of leaflets (usually 2)
 *Inga spectabilis* (63A. Mimosoideae)

Apical leaflets less than 9 cm wide, moderately to densely pubescent above (at least when young) with erect trichomes; leaves with 3–6 pairs of leaflets:

- Leaves usually with more than 4 pairs of leaflets; rachis glands more than 1 mm diam
 *Inga vera* (63A. Mimosoideae)

- Leaves with 4 or fewer pairs of leaflets; rachis glands less than 1 mm diam:

- Blades softly puberulent below *Inga pauciflora* (Fig. 264; 63A. Mimosoideae)
 Blades glabrate or scabrous below *Inga hayesii* (63A. Mimosoideae)
- ⊗ Rachis not winged:
- At least some leaves with more than 4 pairs of leaflets:
 - All leaves with 5 or fewer pairs of leaflets:
 - Blades densely pubescent below with appressed trichomes, scabrid above with the midrib densely appressed-pubescent *Inga thibaudiana* (63A. Mimosoideae)
 - Blades sparsely pubescent or glabrate below, the trichomes chiefly erect (or at least not markedly acropetal), not scabrid above, the midrib not densely appressed-pubescent:
 - Glands on rachis more than 1.5 mm wide; blade margins undulate *Pithecellobium rufescens* (Fig. 273; 63A. Mimosoideae)
 - Glands on rachis less than 1.5 mm wide; blade margins not markedly undulate:
 - Rachis margined to narrowly winged; blades not noticeably puberulent on veins below *Inga pezizifera* (63A. Mimosoideae)
 - Rachis not margined, not winged; blades puberulent on veins below *Inga ruiziana* (Fig. 265; 63A. Mimosoideae)
 - At least some leaves with more than 5 pairs of leaflets:
 - Some leaves with more than 8 pairs of leaflets; blades sparsely pubescent above except more densely so on midrib, shiny above, pubescent below especially on veins, the trichomes on midrib acropetal; apical leaflets less than 5 cm wide *Inga multijuga* (63A. Mimosoideae)
 - All leaves with 8 or fewer pairs of leaflets:
 - Upper surface glabrous or very sparsely puberulent on midrib; leaves predominately narrowly obovate *Inga ruiziana* (Fig. 265; 63A. Mimosoideae)
 - Upper surface villous on midrib; leaves predominately elliptic or lanceolate:
 - Leaf rachis often with linear appendage ca 4 mm long at apex; basal leaflets usually somewhat asymmetrical *Inga thibaudiana* (63A. Mimosoideae)
 - Leaf rachis without a linear appendage at apex; basal leaflets usually \pm symmetrical *Inga cocleensis* (63A. Mimosoideae)
 - All leaves with 4 or fewer pairs of leaflets:
 - Petioles longer than rachises; rachis glands subulate to oblong-conic, not at all cupulate; leaflets 4:
 - Leaflets less than 3.5 cm wide; rachis with glands between both pairs of leaflets *Cassia undulata* (Fig. 276; 63B. Caesalpinioideae)
 - Leaflets more than 3.5 cm wide; rachis with only one gland (between lower pair of leaflets) *Cassia fruticosa* (63B. Caesalpinioideae)
 - Petioles shorter than rachises; rachis glands subcupulate:
 - Rachis conspicuously pubescent:
 - Blade surface above softly puberulent with reddish-brown trichomes, softly puberulent to hirtellous below; blades acute or obscurely acuminate at apex; stems densely rufous-pubescent *Pithecellobium rufescens* (Fig. 273; 63A. Mimosoideae)
 - Blade surface not softly puberulent with reddish-brown trichomes; blades short- to long-acuminate:
 - Young stems essentially glabrous; internodes with ribs extending down from stipule scars *Inga punctata* (63A. Mimosoideae)
 - Young stems moderately pubescent; internodes lacking ribs *Inga quaternata* (63A. Mimosoideae)
 - Rachis glabrous or inconspicuously pubescent:
 - Internodes with ribs extending down from stipule scars *Inga punctata* (63A. Mimosoideae)
 - Internodes lacking ribs:
 - Leaves mostly with 2 pairs of leaflets; leaflets obovate, broadly acuminate or blunt at apex *Inga fagifolia* (63A. Mimosoideae)
 - Leaves with 3 or 4 pairs of leaflets; leaflets \pm elliptic or lanceolate, long-acuminate at apex *Inga pezizifera* (63A. Mimosoideae)
- ⊗ Petioles and rachises lacking glands:
- ▣ Rachis winged:
 - Plants trees or shrubs:
 - Plants large trees; leaves with 12–14 pairs of leaflets; rachis continuously winged *Dipteryx panamensis* (63C. Papilionoideae)
 - Plants shrubs or trees less than 4 m tall; leaves with 2–5 pairs of leaflets; rachis wing interrupted at leaflets:
 - Rachis wing sharply toothed at apex; stipules acicular, ca 3 mm long *Swartzia simplex*, juvenile (63B. Caesalpinioideae) [see fertile key]
 - Rachis wing flat or rounded at apex; stipules lacking *Quassia amara* (68. Simaroubaceae)
 - Plants lianas; leaflets 5:
 - Stems terete; leaflets usually \pm entire, with the axils below tufted with trichomes *Paullinia fibrigera* (Fig. 342; 80. Sapindaceae)
 - Stems angulate or ribbed; leaflets usually toothed:
 - Stems and petioles hispid, the trichomes conspicuous, long, brown, more than 2 mm long; petioles not winged *Paullinia baileyi* (80. Sapindaceae)
 - Stems and petioles not conspicuously hispid:

- Axils of veins below shortly tufted; leaflets with few appressed trichomes *Paullinia pinnata* (Fig. 344; 80. Sapindaceae)
- Axils of veins not tufted; leaflets with conspicuous erect trichomes below; petioles winged; stipules more than 4 cm long, persistent, usually brown *Paullinia bracteosa* (Fig. 341; 80. Sapindaceae)
- Rachis not winged:
- Leaflets opposite (or slightly subopposite on basal pairs of leaflets but no pairs alternate):
- Leaves paripinnate:
- Petioles pulvinate at base, the pulvinus terete; stipules acicular or foliaceous:
- Stipules paired, deciduous, compound, leaflike; stems ribbed; leaves with more than 12 pairs of leaflets *Tachigalia versicolor* (63B. Caesalpinioideae)
- Stipules not as above:
- Blades pellucid-punctate at least on margins (punctations visible when leaf held to light):
- Leaflets 2 or 4 (1 or 2 pairs), glabrous; plants often large trees *Prioria copaifera* (Figs. 277, 278; 63B. Caesalpinioideae)
- Leaflets 6 or more, glabrous or pubescent; plants small to large trees *Zanthoxylum* [see key to 67. Rutaceae]
- Blades not pellucid-punctate; plants shrubs or small trees:
- Leaflets densely soft-pubescent below; stems and petioles soft-pubescent *Cassia reticulata* (Fig. 275; 63B. Caesalpinioideae)
- Leaflets not densely soft-pubescent; stems and petioles sometimes densely tomentose *Brownia macrophylla* (63B. Caesalpinioideae)
- Petioles not pulvinate at base with a terete pulvinus, the pulvinus (when present) usually flat and ± ribbed on upper side (except *Cedrela odorata*, with petioles often subterete at base and not ribbed); stipules lacking:
- Lateral veins markedly widened at base before joining midrib; plants large forest trees, the bark dark, very deeply and coarsely fissured on adults; vein axils sometimes with pocketlike domatia *Cedrela odorata* (Fig. 305; 70. Meliaceae)
- Lateral veins not widened before joining midrib, either joining at right angles or turning basally before joining; plants usually small trees, the bark not coarsely fissured:
- Leaves large, to 2 m long, often with more than 7 pairs of leaflets; petioles and young stems usually densely ferruginous-pubescent *Guarea multiflora* (Figs. 306, 307; 70. Meliaceae)
- Leaves less than 0.5 m long, usually with less than 7 pairs of leaflets; petioles and young stems not densely ferruginous-pubescent:
- Leaflets less than 3 cm wide, usually sparsely ciliate and revolute *Trichilia hirta* (70. Meliaceae)
- Leaflets more than 4 cm wide, not ciliate *Guarea glabra* (70. Meliaceae)
- Leaves imparipinnate:
- Leaves opposite; plants glabrous:
- Leaflets toothed; stipules not interpetiolar *Turpinia occidentalis* subsp. *breviflora* (Figs. 336, 337; 79. Staphyleaceae)
- Leaflets entire; interpetiolar stipules leaving scar *Platymiscium pinnatum* (63C. Papilionoideae)
- Leaves alternate:
- Leaflets toothed:
- Leaflets more than 5; plants shrubs or trees:
- Leaflets pellucid-punctate *Zanthoxylum* [see key to 67. Rutaceae]
- Leaflets not pellucid-punctate *Astronium graveolens* (76. Anacardiaceae)
- Leaflets 5; plants lianas:
- Blades with dense simple pubescence on lower surface; stipules large, suborbicular, fimbriate *Paullinia rugosa* (Fig. 345; 80. Sapindaceae)
- Blades ± glabrous throughout; stipules lanceolate-linear *Paullinia pterocarpa* (80. Sapindaceae)
- Leaflets entire:
- ◇ Petioles pulvinate at base with a terete pulvinus; petiolules pulvinate and articulate at base; plants with stipules (these sometimes caducous); sap seldom distinctly aromatic:
- Stems with prominent ribs:
- Leaflets often more than 5 cm wide; stipules, when present, deltoid, 1–2 mm long *Ormosia coccinea* var. *subsimplax* (Fig. 293; 63C. Papilionoideae)
- Leaflets less than 5 cm wide; young stems reddish; stipules deciduous, paired, looking like reduced compound leaves *Tachigalia versicolor* (63B. Caesalpinioideae)
- Stems lacking ribs:
- Leaves mostly with more than 7 leaflets:
- Leaflets each subtended by a stipel, the margins subrevolute, the surfaces glabrous except on midrib below *Andira inermis* (63C. Papilionoideae)
- Leaflets lacking stipels, the margins not revolute, the lower surface glabrous to densely puberulent:
- Lateral veins on one side of midrib 4–6 per leaflet; leaflets mostly glabrous below *Ormosia macrocalyx* (63C. Papilionoideae)

Lateral veins on one side of midrib 8–18 per leaflet; leaflets densely but minutely pubescent below *Lonchocarpus pentaphyllus* (63C. Papilionoideae)

● Leaves mostly with 3, 5, or 7 leaflets:

Reticulate veins all raised and closely anastomosing below:

Lower surface with the trichomes usually appressed, not raised higher than veinlets, the reticulate veins inconspicuous *Lonchocarpus pentaphyllus* (63C. Papilionoideae)

Lower surface with the trichomes \pm erect, raised higher than veinlets, the reticulate veins conspicuous *Lonchocarpus velutinus* (Fig. 288; 63C. Papilionoideae)

Reticulate veins not raised and closely anastomosing below; leaves mostly with 3 or 5 leaflets (*Connarus turczaninowii* with 7):

Petioles and petiolules densely pubescent; blades densely rufous-pubescent below *Cnestidium rufescens* (62. Connaraceae)

Petioles glabrous or sparsely pubescent except possibly on pulvinus:

Plants lianas; blades \pm glabrous, usually with fewer than 8 pairs of lateral veins, not caudate-acuminate *Connarus turczaninowii* (62. Connaraceae)

Plants trees; blades not as above:

Blades moderately golden-pubescent below, with 10–16 pairs of lateral veins *Ormosia panamensis* (63C. Papilionoideae)

Blades glabrous or with trichomes only on veins, with 9 or fewer pairs of lateral veins, caudate-acuminate *Swartzia panamensis* (Fig. 279; 63B. Caesalpinioideae)

◇ Petioles and petiolules not pulvinate and not articulate at base (or, if pulvinate, the pulvinus not terete); plants lacking stipules; sap usually distinctly aromatic:

At least some leaves with 6 or more pairs of lateral leaflets, the leaflets less than 3.5 cm wide:

Leaflets at most bluntly short-acuminate, often acute or even rounded at apex, the midrib on upper surface thick, prominently raised, densely pubescent; reticulate veins obscure *Mosquitoxylum jamaicense* (Fig. 328; 76. Anacardiaceae)

Leaflets narrowly long-acuminate, the midrib flat or very slender and weakly raised, usually in a sunken trough, glabrous; reticulate veins conspicuously visible *Trichilia hirta* (70. Meliaceae)

All leaves with fewer than 6 pairs of lateral leaflets or the leaflets more than 3.5 cm wide:

Leaflets pubescent below (trichomes may be restricted to veins):

Leaflets asperous on upper surface; petioles flat on upper surface, usually more than 7 mm broad near base, the margin prominently raised *Trattinnickia aspera* (Fig. 304; 69. Burseraceae)

Leaflets not asperous on upper surface; petioles not markedly flattened on upper surface with a raised margin:

Stems glabrous, the stems and trunk with paper-thin, brown, peeling bark; trichomes on lower blade surface \pm erect but not stiff and straight *Bursera simaruba* (69. Burseraceae)

Stems densely pubescent, the bark not as above; trichomes on lower blade surface stiffly erect, straight *Protium costaricense* (69. Burseraceae)

Leaflets \pm glabrous or sparsely pubescent below:

Petiolules mostly less than 1 cm long:

Terminal leaflet often more than 8 cm wide; leaflets (3)5–7 per pinna *Trichilia montana* (70. Meliaceae)

Terminal leaflet usually less than 7 cm wide; leaflets 7–11 per pinna *Tetragastris panamensis* (Fig. 303; 69. Burseraceae)

Petiolules mostly more than 1 cm long:

Largest leaflets usually more than 8 cm wide, not papillose; lateral veins not raised below *Protium panamense* (Fig. 302; 69. Burseraceae)

Largest leaflets usually less than 8 cm wide:

Leaflets minutely papillate below; lateral veins conspicuously raised below (a fingernail run down the blade catches on them) *Protium tenuifolium* var. *sessiliflorum* (69. Burseraceae)

Leaflets not papillate; lateral veins not conspicuously raised below:

Plants villous to velutinous (the trichomes either not straight or long and very dense); leaves usually drying blackened; blades lacking a submarginal collecting vein *Spondias radlkoferi* (76. Anacardiaceae)

Plants glabrous or pubescent, some parts merely puberulent (the trichomes short and straight); leaves not drying blackened; blades with a conspicuous submarginal collecting vein *Spondias mombin* (Figs. 329, 330; 76. Anacardiaceae)

○ Leaflets alternate (or subopposite on apical pairs but definitely alternate near base):

□ Plants lianas (or scandent shrubs or trees when young):

△ Leaf nodes on mature plants armed with \pm recurved spines:

- Most leaves with more than 20 leaflets:
 Largest leaflets more than 5 mm wide *Machaerium milleflorum* (63C. Papilionoideae)
 Largest leaflets less than 5 mm wide *Machaerium microphyllum* (63C. Papilionoideae)
- Most leaves with fewer than 20 leaflets:
 All leaves with 7 or fewer leaflets *Machaerium arboreum* (63C. Papilionoideae)
 At least some leaves with 8 or more leaflets:
 Leaflets all less than 3 cm wide:
 Leaflets rounded to retuse at apex *Machaerium riparium* (63C. Papilionoideae)
 Leaflets acuminate at apex, the acumens blunt *Machaerium seemannii* (63C. Papilionoideae)
- Largest leaflets often more than 3 cm wide:
 Stems (except nearest apex) densely covered with erect spiny trichomes; leaflets \pm glabrous below (at least in age), long-acuminate
 *Machaerium kegelii* (Figs. 289, 290; 63C. Papilionoideae)
 Stems lacking dense spiny trichomes; leaflets densely appressed-pubescent below, obtuse to short-acuminate *Machaerium floribundum* (63C. Papilionoideae)
- △ Leaf nodes on mature plants lacking spines:
 Leaves mostly with 4 or 5 leaflets (never more than 5):
 Leaflets ovate; petioles mostly less than 3 cm long; rachis usually flexuous in apical half
 *Dalbergia monetaria* (63C. Papilionoideae)
 Leaflets \pm elliptic; petioles usually more than 4 cm long; rachis straight
 *Connarus turczaninowii* (62. Connaraceae)
- Leaves mostly with 3 leaflets or some leaves with more than 5 leaflets:
 Leaves mostly with 3 leaflets (rarely 5); blades glabrous above
 *Connarus panamensis* (Fig. 256; 62. Connaraceae)
 At least some leaves with more than 5 leaflets; blades pubescent at least on midrib above:
 Leaflets densely rufous-pubescent below *Cnestidium rufescens* (62. Connaraceae)
 Leaflets inconspicuously puberulent to glabrous below except on veins:
 Leaflets with the reticulate veins somewhat to markedly prominent on both surfaces
 *Rourea glabra* (62. Connaraceae)
 Leaflets with the reticulate veins scarcely or not at all visible
 *Connarus turczaninowii* (62. Connaraceae)
- Plants trees or shrubs:
 Leaflets pellucid-punctate, at least on margins:
 Pellucid punctations round *Zanthoxylum* [see key to 67. Rutaceae]
 Some pellucid punctations elongate *Myroxylon balsamum* var. *pereirae* (63C. Papilionoideae)
 Leaflets not pellucid-punctate:
 ☆ Leaves usually with 9 or fewer leaflets:
 Leaflets conspicuously pubescent at least on veins below:
 Leaflets toothed, round or acute at apex:
 Leaflets densely reddish-brown-pubescent along midrib above; stems with long reddish-brown trichomes; some leaves simple *Cupania rufescens* (Fig. 339; 80. Sapindaceae)
 Leaflets \pm glabrate above or the pubescence not reddish-brown; stems glabrous or with short trichomes:
 Blades below whitish, densely tomentose with contiguous trichomes
 *Cupania cinerea* (80. Sapindaceae)
 Blades below green, glabrate to sparsely pubescent and papillate; some leaves simple; some leaflets subopposite *Cupania latifolia* (80. Sapindaceae)
- Leaflets entire, acuminate at apex:
 Rachis densely pubescent, the trichomes erect or appressed but not stiff and straight:
 Plants small trees less than 4 m tall; petiolules not equally pulvinate throughout, not articulate at base; stipules lacking *Cupania sylvatica* (Fig. 340; 80. Sapindaceae)
 Plants large trees to 25 m tall; petiolules equally pulvinate throughout, articulate at base; stipules minute *Pterocarpus rohrii* (63C. Papilionoideae)
- Rachis glabrate to short-puberulent:
 Midrib flat or sunken above when dry *Trichilia verrucosa* (70. Meliaceae)
 Midrib raised above (markedly in apical half) *Trichilia cipo* (70. Meliaceae)
- Leaflets essentially glabrous:
 Petiolules pulvinate:
 Leaflets long-acuminate, often falcate; plants lacking stipules
 *Picramnia latifolia* (68. Simaroubaceae)
 Leaflets acute or short-acuminate; plants with stipules
 *Ormosia coccinea* var. *subsimplex* (Fig. 293; 63C. Papilionoideae)
- Petiolules not pulvinate:
 Terminal leaflets more than 8 cm wide *Trichilia montana* (70. Meliaceae)
 Most terminal leaflets less than 8 cm wide:

- Midrib flat or sunken above (when dry); minute, aborted leaflets often at base; most leaves with 5 leaflets (not including aborted leaflets) *Trichilia verrucosa* (70. Meliaceae)
- Midrib prominently raised in apical half; minute leaflets lacking, most leaves with 7 leaflets *Trichilia cipo* (70. Meliaceae)
- ☆ At least some leaves with more than 9 leaflets:
- Leaflets mostly more than 5 cm wide:
- Leaves usually with more than 9 pairs of leaflets; all leaflets usually less than 6.5 cm wide, lacking a prominent collecting vein; stems often with reduced, leaflike structures at apex *Talisia princeps* (80. Sapindaceae)
- Leaves usually with 8 or fewer pairs of leaflets; at least the terminal leaflets often more than 6.5 cm wide; lateral veins with a conspicuous submarginal collecting vein; stems lacking reduced leaflike structures *Talisia nervosa* (80. Sapindaceae)
- Leaflets mostly less than 5 cm wide:
- Lateral veins mostly obscure; leaflets not acuminate (some acute to retuse at apex) or the petioles and leaflets pilose below:
- Most leaflets retuse at apex *Platypodium elegans* (63C. Papilionoideae)
- Leaflets not retuse at apex:
- Lateral veins obscure; leaflets oblong to oblanceolate *Simarouba amara* (Figs. 300, 301; 68. Simaroubaceae)
- Lateral veins conspicuous, at least below:
- Leaflets widest below the middle; reticulate venation conspicuous *Dalbergia retusa* (Fig. 282; 63C. Papilionoideae)
- Leaflets widest above the middle; reticulate venation obscure *Mosquitoxylum jamaicense* (Fig. 328; 76. Anacardiaceae)
- Lateral veins conspicuous; leaflets acuminate:
- Rachis ridged or minutely winged toward apex; lateral veins raised below more than above:
- Plants glabrous or pubescent, parts merely puberulent (the trichomes short and straight); leaves not drying blackened; blades with a conspicuous submarginal collecting vein *Spondias mombin* (Figs. 329, 330; 76. Anacardiaceae)
- Plants villous to velutinous (the trichomes either not straight or long and very dense); leaves usually drying blackened; blades lacking a submarginal vein *Spondias radlkoferi* (76. Anacardiaceae)
- Rachis not ridged or winged; lateral veins, if raised below, then about the same below and above:
- Petiolules not pulvinate, less than 4 mm long *Astronium graveolens* (76. Anacardiaceae)
- Petiolules pulvinate, to 4 mm or more long:
- Leaflets acute to obscurely acuminate, short-pilose below, sometimes becoming glabrous with age *Dalbergia retusa* (Fig. 282; 63C. Papilionoideae)
- Leaflets shortly and abruptly acuminate, glabrous below or with minute appressed trichomes *Pterocarpus officinalis*, *Vatairea erythrocarpa* (63C. Papilionoideae)
-

Species Excluded

A total of 138 names have been excluded from the flora. Most of these are the result of misidentification by Standley at the time of the writing of the *Flora* (1933), but some reflect the different interpretations of later workers. Others are cultivated plants that no longer grow on the island. A few species, such as *Bidens pilosa*, *Porophyllum ruderale*, and *Lemna cyclostasa*, are species for which no BCI specimens have been found. I believe that Standley reported some of these names merely because he thought they would be found on the island.

The following species and specimens were reported by Standley for BCI unless otherwise indicated.

Acalypha villosa Jacq. (75. Euphorbiaceae): *Shattuck 843* is *A. macrostachya*.

Aeschynomene hispida Sw. (63C. Papilionoideae): *Bailey 763* is *A. ciliata*.

Albizia adinocephala (Donn. Sm.) Britt. & Rose (63A. Mimosoideae): *Bailey 281* is *Leucaena multicapitula*.

Alsophila ternerifrons H. Christ (9. Cyatheaceae): Based on misidentification of *Nephelea cuspidata*.

Annona purpurea Moc. & Sesse ex Dunal (55. Annonaceae): Reported in the *Flora of Panama*. *Bangham 610 (US)* carries a BCI label that is marked out and replaced with "Government Reservation—Ancón."

Anthurium crassinervium (Jacq.) Schott (21. Araceae): One of several species confused by Standley with *A. tetragonum*. *A. crassinervium* is a species restricted to South America.

A. maximum (Desf.) Engler: Confused with *A. tetragonum* by Standley. *A. maximum* is a Colombian species of higher elevations.

A. ramonense Engler & Krause: Reported in the *Flora of Panama*. *Standley 41149* is *A. littorale*.

A. schlechtendalii Kunth: No specimen was cited by Standley. *Shattuck 638*, cited in the *Flora of Panama*, is *A. tetragonum*.

A. turrialbense Engler: Reported in the *Flora of Panama*. *Standley 31386* and *40887* are probably *A. littorale*.

A. undatum Schott: Based on misidentification of *A. bombacifolium*.

Aphelandra tetragona (Vahl) Nees (129. Acanthaceae): Based on a sterile collection of *Alseis blackiana* (130. Rubiaceae).

Apodanthes flacourtiiae Karst. (45. Rafflesiaceae): Based on misidentification of *A. caseariae*.

Ardisia compressa H.B.K. (112. Myrsinaceae): Confused by Standley with *A. bartlettii*.

Bauhinia purpurea L. (63B. Caesalpinioideae): A cultivated species no longer present on the island.

Bellucia costaricensis (L.) Tr. (107. Melastomataceae): A synonym of *B. axinantha* Tr., which does not occur on the island. The report for the island by Gleason in the *Flora of Panama* (1958) was based on *Shattuck 1119*, which is *B. grossularioides*.

Bidens pilosa L. (133. Compositae): No specimen has been seen and none was cited by Standley.

Blechnum panamense Lindau (129. Acanthaceae): Based on misidentification of the narrow-leaved form of *B. costaricense*.

Borreria suaveolens G. Meyer (130. Rubiaceae): *Shattuck 421* is *B. densiflora*.

Bunchosia nitida (Jacq.) DC. (71. Malpighiaceae): Probably based on *Bangham 508*, which is *Malpighia romeroana*.

Byrsonima coriacea (Sw.) Kunth (71. Malpighiaceae): *Starry 129* is *B. spicata*. According to Cuatrecasas (1958), *B. coriacea* is confined to Jamaica.

Calathea altissima Koern. (33. Marantaceae): Confused by Standley and others with *C. inocephala*. *C. altissima*, which does not occur in Panama, differs in having a smaller head with clavigulate bracteoles and capsule walls that are not fleshy.

C. violacea (Rosc.) Lindl.: Based on misidentification of *C. latifolia*. *C. violacea* is restricted to Brazil.

Casearia javitensis H.B.K. (96. Flacourtiaceae): Confused by Standley with *C. commersoniana*. *C. javitensis*, a South American species, does not occur in Panama.

Cassia tora L. (63B. Caesalpinioideae): Confused with *C. obtusifolia*. *C. tora* is an Old World species.

Celosia argentea L. (47. Amaranthaceae): Reported by Standley as a probable escapee from cultivation. The species no longer occurs on the island.

- Centrosema virginianum** (L.) Benth. (63C. Papilionoideae): All BCI specimens originally determined as this species are *C. pubescens*.
- Chaetochlamys panamensis** Lindau (129. Acanthaceae): No specimen has been cited, and the plant has not been seen growing on the island in recent years.
- Citrus medica** L. (67. Rutaceae): *Shattuck 861*, determined by Standley as this species, is *C. limon*.
- Clidemia petiolata** (Rich.) DC. (107. Melastomataceae): No specimen has been seen. This species is a narrow endemic (*vide* J. Wurdack, pers. comm.) and definitely does not occur on the island.
- Clusia rosea** L. (92. Guttiferae): No specimen has been seen. Possibly reported on the basis of *Shattuck 684* (685?), which is probably a juvenile collection of *C. odorata*.
- Coccoloba changuinola** Standl. (46. Polygonaceae): This is a synonym of *C. lehmannii* Lindau, which is not known for BCI. Probably reported on the basis of misidentification of *C. coronata*.
- Combretum punctulatum** Pitt. (105. Combretaceae): A synonym of *C. spinosum* Bonpl. *Wilson 128* is *C. decandrum*.
- Cordia nitida** Jacq. (121. Boraginaceae): *Wilson 69* and *Shattuck 813* and *853* are *C. lasiocalyx*.
- C. sericalyx** A. DC.: This name was used by Standley for *C. panamensis*. It is similar to *C. panamensis* and ranges from western Colombia to Trinidad and Surinam, but has not been collected in Panama.
- Costus spicatus** (Jacq.) Sw. (32. Zingiberaceae): No specimen has been seen. *C. spicatus* is a West Indian species.
- Croton glandulosus** L. (75. Euphorbiaceae): Confused with *C. hirtus*. *C. glandulosus* does not occur in Panama.
- Cucurbita pepo** L. (131. Cucurbitaceae): Cultivated on the island at one time, but no longer present.
- Cuphea wrightii** Gray (102. Lythraceae): Apparently based on misidentification of *C. carthagenensis*.
- Dalbergia ecastophyllum** (L.) Taub. (63C. Papilionoideae): Probably based on *Kenoyer 387* and *629*, which are *D. brownii*.
- Davilla kunthii** St.-Hil. (88. Dilleniaceae): A synonym of *D. aspera* (Aubl.) Ben., which does not occur on the island. Based on misidentification of *D. nitida* (*Woodworth & Vestal 331*).
- D. rugosa** Poir.: Based on misidentification of *D. nitida*.
- Dichromena pubera** Vahl (18. Cyperaceae): *Standley 40831*, reported in the *Flora of Panama*, is *Rhynchospora nervosa*.
- Dieffenbachia aurantiaca** Engler (21. Araceae): *Bailey 335* is *D. oerstedii*.
- Dillenia indica** L. (88. Dilleniaceae): Reported by Standley as planted at the laboratory. It no longer occurs there.
- Diphysa robinoides** Benth. (63C. Papilionoideae): *Shattuck 869* is *Platymiscium pinnatum*.
- Epidendrum fragrans** Sw. (35. Orchidaceae): *Shattuck 551* is *Encyclia chimborazoensis*.
- Epiphyllum pittieri** Britt. & Rose (101. Cactaceae): *Shattuck 603* is *E. phyllanthus* var. *columbiense*. *E. phyllanthus* var. *pittieri* does not occur on the island.
- Eriochloa punctata** (L.) Desv. (17. Gramineae): *Shattuck 323* is *Brachiaria mutica*.
- Eschatogramme furcata** (L.) Trev. (10. Polypodiaceae): Based on misidentification of *Dicranoglossum panamense*.
- Eugenia sericiflora** Benth. (106. Myrtaceae): A synonym of *E. bicolor* L. No specimen was cited and none has been seen. The species is not easily confused with any other, but it is not believed to occur on the island.
- Eupatorium billbergianum** Beurl. (133. Compositae): Based on misidentification of *Koanophyllum wetmorei*.
- Ficus crassiuscula** Warb. (39. Moraceae): Based on misidentification of *F. insipida*.
- F. glabrata** H.B.K.: Based on misidentification of *F. insipida*.
- F. hemsleyana** Standl.: A synonym of *F. goldmanii* Standl., which does not occur on the island. Many specimens of *F. citrifolia* were annotated by Standley as *F. hemsleyana*.
- F. involuta** (Liebm.) Miq.: Based on misidentification of *F. obtusifolia*, a distinct species.
- F. padifolia** H.B.K.: This is a highland species from western Panama and Costa Rica that was confused by Standley with *F. pertusa*.
- F. velutina** Willd.: A species occurring in Panama only at higher elevations in Chiriquí. *Bailey 408* is a juvenile form of *F. bullenei*.
- Gossypium barbadense** L. (85. Malvaceae): This is *G. mexicanum* sensu Standl. non Todaro. Probably originally planted near the laboratory, but no longer growing on the island.
- Guarea guarea** (Jacq.) P. Wils. (70. Meliaceae): *Woodworth & Vestal 747* is *G. multiflora*.
- Guatteria dolichopoda** Donn. Sm. (55. Annonaceae): *Kenoyer 359* is *G. dumetorum*.
- Hampea panamensis** Standl. (85. Malvaceae): A synonym of *H. appendiculata* Donn. Sm. var. *appendiculata*, which occurs in western Panama, Costa Rica, and Honduras.
- Heisteria macrophylla** Oerst. (43. Olacaceae): *Standley 40877*, also listed in the *Flora of Panama*, is *H. costaricensis*.
- Heliconia acuminata** A. Rich. (31. Musaceae): Based on misidentification of *H. vaginalis*.
- H. pendula** Wawra: Based on misidentification of *H. irrasa*. *H. pendula* does not occur in Panama.
- H. platystachya** Baker: Reported by both Standley and the *Flora of Panama*. This South American species has been confused with *H. catheta*.
- H. subulata** R. & P.: Reported in the *Flora of Panama*, on the basis of misidentification of *H. vaginalis*. *H. subulata* is a Peruvian species.
- H. villosa** Klotzsch: Restricted to South America. Reported in the *Flora of Panama*, on the basis of misidentification of *H. irrasa*.
- Hiraea fagifolia** (DC.) Adr. Juss. (71. Malpighiaceae): Probably based on misidentification of *Mascagnia nervosa*. No specimen was cited, but *Shattuck 1057* and *1156* and *Bangham 602* (all *F*), originally deter-

- mined by Standley as *H. fagifolia*, are *Mascagnia nervosa*.
- Hyeronima alchorneoides** Allem. (75. Euphorbiaceae): According to Webster and Burch in the *Flora of Panama* (1967), a species from Brazil that does not occur in Panama. Probably based on misidentification of *H. laxiflora*.
- Hymenocallis littoralis** (Jacq.) Salisb. (28. Amaryllidaceae): Called *Pancratium littorale* Jacq. in the *Flora of Panama*. Both based on misidentifications of *H. pedalis*.
- Ichnanthus nemorosus** Doell. (17. Gramineae): Apparently confused by Standley with *I. brevivaginat*.
- Ipomoea triloba** L. (120. Convolvulaceae): *Bailey 673* and *Starry 121* are *I. tiliacea*. *I. triloba* does not occur in Panama.
- Lasiacis divaricata** (L.) Hitchc. (17. Gramineae): *Bailey 285* is *Chusquea simpliciflora*.
- L. ruscifolia** (H.B.K.) Hitchc.: *Shattuck 528* is *L. sorghoidea*.
- Lemna cyclostasa** (Ell.) Chev. (Lemnaceae): A synonym for *L. valdiviana* Phil. Reported by Standley on the basis of someone else's report. However, no specimens have been seen on BCI and I have not seen it growing there. It could easily occur in the water of Gatun Lake.
- Luffa cylindrica** (L.) Roem. (131. Cucurbitaceae): No longer cultivated on the island.
- Machaerium darienense** Pitt. (63C. Papilionoideae): Reported in the *Flora of Panama* by Dwyer (1965) for BCI on the basis of *Killip 40014* (misspelled *M. dariense* Pitt.). The Killip collection does not differ from other collections of *M. arboreum* and the key characters used to separate the two taxa are quite variable. *M. darienense* is now considered a synonym of *M. striatum* J. R. Johnston.
- Malpighia glabra** L. (71. Malpighiaceae): *Shattuck 511* is *M. romeroana*.
- Monstera pertusa** (L.) DeVr. (21. Araceae): Confused with *M. dubia*.
- M. pittieri** Engler: Based on misidentification of a juvenile specimen of *M. dilacerata*.
- Mucuna urens** (L.) Medic. (63C. Papilionoideae): Probably based on *Bailey & Bailey 348* and *Shattuck 286*, which are both *M. mutisiana*.
- Musa paradisiaca** L. (31. Musaceae): No longer cultivated at the Laboratory Clearing.
- Myrosma panamensis** Standl. (33. Marantaceae): Standley apparently confused this plant with *Calathea panamensis*. *Myrosma panamensis* is a synonym of *Hylaeanthus panamensis* (Standl.) H. Kenn., which does not occur on the island.
- Nectandra glabrescens** Benth. (58. Lauraceae): A species that occurs in Panama only along the Caribbean coast and most closely resembles *N. globosa*. Confused by Standley with *N. purpurascens*.
- Neea psychotrioides** sensu Standl. non Donn. Sm. (48. Nyctaginaceae): This is *N. laetevirens* Donn. Sm., which does not occur on the island. *Shattuck 121* is *N. amplifolia*.
- Ossaea micrantha** (Sw.) Macfad. (107. Melastomataceae): No specimen has been cited, and the plant has not been seen growing on the island.
- Ouratea nitida** (Sw.) Engler (89. Ochnaceae): *Shattuck 243* is *O. lucens*. The two names may be synonymous.
- Paullinia alata** Don. (80. Sapindaceae): *Standley 31281 (US)* is *P. bracteosa*.
- Peltophorum** sp. (63B. Caesalpinioideae): *Woodworth & Vestal 743* is a fruit of *Tachigalia versicolor*.
- Peperomia viridispica** Trel. (36. Piperaceae): Reported by Standley on the basis of a single sterile and possibly juvenile specimen (*Shattuck 207*). This specimen does not appear to be any of the other reported species but cannot be assigned to any species with certainty.
- Petrea volubilis** Jacq. (122. Verbenaceae): Reported by Moldenke for BCI in the *Flora of Panama* (1973). *Aviles 14* and *Shattuck 412* are *P. aspera*.
- Pharus glaber** H.B.K. (17. Gramineae): Apparently confused by Standley with *P. parvifolius*.
- Phaseolus vulgaris** L. (63C. Papilionoideae): This garden bean is no longer cultivated on the island.
- Philodendron wendlandii** Schott (21. Araceae): Based on misidentification of *P. inconcinnum*.
- Pilea serpyllacea** (H.B.K.) Liebm. (40. Urticaceae): *Shattuck 196* represents a cultivated plant that no longer grows on the island.
- Piper breve** C. DC. (36. Piperaceae): A synonym for *P. pseudo-fuligineum* C. DC., which does not occur on the island. Possibly Standley confused this with *P. dilatatum*.
- P. frostii** Trel.: An unpublished name. The specimens cited are *P. aequale*.
- P. lucigaudens** C. DC.: Reported in the *Flora of Panama*. *Standley 31288* and *31387* are *P. hispidum*.
- P. polyneurum** C. DC.: A synonym for *P. augustum* var. *cocleanum* (Trel.) Yunck. Though this species has been collected near Frijoles, no specimen has been seen for BCI. *Starry 63* is *P. grande*. Neither *Aviles 36* nor *Starry 95*, also cited by Standley, has been located.
- P. pseudo-cativalense** Trel.: Confused by Standley with *P. dilatatum*.
- Polybotrya caudata** Kunze (10. Polypodiaceae): Probably based on misidentification of *P. villosula*. The two species are doubtfully distinct.
- P. osmundacea** H. & B.: No collection of this species has been seen at lower elevations in Panama.
- P. tectum** Kaulf.: *Bailey 513* is an aberrant specimen of *P. ciliatum*.
- Porophyllum ruderale** (Jacq.) Cass. (133. Compositae): No specimen has been seen from the island, and the plant has not been seen growing there.
- Pouzolzia occidentalis** Wedd. (40. Urticaceae): Based on *Aviles 24*, which has not been located. *Aviles 24b* is *P. obliqua* and was originally determined as *P. occidentalis*.
- Prestonia exserta** (A. DC.) Standl. (118. Apocynaceae): *Woodworth & Vestal 498* is *P. acutifolia*.
- Psychotria calophylla** Standl. (130. Rubiaceae): No specimen has been seen for the island. All collections are from areas near the Atlantic coast or from areas of

- higher elevation, usually premontane wet or tropical wet forest.
- Randia lisiantha** Standl. (130. Rubiaceae): *Starry 8* is *R. armata*.
- Renealmia occidentalis** (Sw.) Sweet (32. Zingiberaceae): This species was treated as a synonym of *R. aromatica* (Aubl.) Griseb. in the *Flora of Panama*, where *Kenoyer 238* was listed for BCI. Presumably this is the same collection on which Standley based his report. *Kenoyer 238* is *R. alpinia*.
- Rivea campanulata** (L.) House (120. Convolvulaceae): A synonym of *Stictocardia campanulata* (L.) Merr., which Standley reported on the basis of misidentification of *Ipomoea phillomega*.
- Rudgea cornifolia** (H. & B.) Standl. (130. Rubiaceae): Apparently based on *Standley 41058* (found unlabeled with other *R. cornifolia* specimens). This is *Coussarea curvigemma*.
- Salvinia auriculata** Aubl. (11. Salviniaceae): No specimen has been seen from the island. Other specimens identified as *S. auriculata* are *S. radula*.
- Schomburgkia** sp. (35. Orchidaceae): *Shattuck 500* is *Caularthron bilamellatum*.
- Scleria bracteata** Cav. (18. Cyperaceae): *Shattuck 144* is *S. secans*.
- Securidaca coriacea** Bonpl. (74. Polygalaceae): *Woodworth & Vestal 505* is *S. tenuifolia*.
- Sicydium tannifolium** (H.B.K.) Cogn. (131. Cucurbitaceae): Apparently confused by Standley with *S. coriaceum*.
- Simarouba glauca** DC. (68. Simaroubaceae): *Starry 144* has not been located. It is probably *S. amara*.
- Solanum bicolor** Willd. (124. Solanaceae): The species is probably not found in Panama. The name is applied to several other species, including *S. rugosum*, *S. umbellatum*, *S. asperum*, and *S. erianthum* D. Don. No BCI specimen has been found that originally bore the name.
- S. nigrum** L.: No specimen has been found. Probably (according to W. G. D'Arcy, pers. comm.) Standley was referring to *S. americana* P. Mill., which is a common garden weed in Panama. Neither *S. americana* nor any of its close relatives occurs on the island.
- Spathiphyllum patinii** (Hogg) N. E. Brown (21. Araceae): Reported from Colombia and probably confused by Standley with *S. phrynifolium*, though no collection bearing the name *S. patinii* from BCI has been found.
- Stachytarpheta cayennensis** (L. C. Rich.) Vahl (122. Verbenaceae): *Woodworth & Vestal 739* is *S. jamaicensis*.
- Stenorrhynchus** sp. (35. Orchidaceae): Reported by Standley on the basis of an undesignated Kenoyer collection. None has been found, but according to R. Dressler, the specimen probably was confused with *Spiranthes lanceolata*.
- Stigmaphyllon humboldtianum** A. Dr. Juss. (71. Malpighiaceae): Based on misidentification of *S. lindonianum*.
- Stylogyne laevis** (Oerst.) Mez (112. Myrsinaceae): Probably based on misidentification of *Ardisia fendleri*.
- S. ramiflora** (Oerst.) Mez: A synonym of *S. laevis* (Oerst.) Mez, which does not occur on the island. Probably based on misidentification of *S. standleyi*.
- Tetracera oblongata** DC. (88. Dilleniaceae): Apparently based on misidentification of *T. portobellensis*.
- T. sessiliflora** Tr. & Planch.: A synonym of *T. portobellensis*, according to the *Flora of Panama*. Probably based on misidentification of *T. hydrophila*.
- Tillandsia melanopus** E. Morr. (22. Bromeliaceae): *Starry 101* is a juvenile plant that cannot be determined (*vide* L. B. Smith). Since no mature plants of *T. melanopus* have been found, I am assuming that *Starry 101* is a juvenile of another *Tillandsia*.
- T. usneoides** L.: Reported by Standley on the basis of a sterile fragment (*Shattuck 414*). There is reason to believe that the species could occur on BCI, since it occurs in tropical moist forest in Bocas del Toro and Darién; but *Shattuck 414* has roots and an indumentum different from those of *T. usneoides*, and therefore it cannot be this species. Mason Hale (pers. comm.) has ruled it out as a lichen. It remains undetermined.
- Tradescantia cumanensis** Kunth (23. Commelinaceae): A synonym of *Tripogandra multiflora*, which does not occur in Panama. Probably confused with *Tripogandra serrulata*.
- Triplaris americana** L. (46. Polygonaceae): Based on misidentification of *T. cumingiana*.
- Tripogandra elongata** (G. Meyer) Woods. (23. Commelinaceae): *Standley 41079*, reported in the *Flora of Panama* (Woodson & Schery, 1944), is *Callisia ciliata*.
- Vigna repens** (L.) O. Kuntze (63C. Papilionoideae): A synonym of *V. luteola* (Jacq.) Benth. *Bailey & Bailey 299* has not been located, but it is probably *Phaseolus trichocarpus*.
- Vincetoxicum dubium** (Pitt.) Standl. (119. Asclepiadaceae): A synonym of *Gonolobus dubium* Woods. *Wetmore & Abbe 202* is *G. allenii*.
- Virola guatemalensis** (Hemsl.) Warb. (56. Myristicaceae): *Shattuck 694* and *Wetmore & Abbe 155* are *V. surinamensis*.
- Vismia guianensis** (Aubl.) Pers. (92. Guttiferae): Based on misidentification of *V. baccifera*.
- Xylosma hemsleyana** Standl. (96. Flacourtiaceae): A synonym of *X. flexuosa* (H.B.K.) Hemsl. This species apparently occurs only at higher elevations in Chiriquí. Kenoyer (1929) confused this with *Casearia guianensis* and Standley may have done the same.
- X. intermedia** (Tr. & Planch.) Griseb.: This species is known for certain only from Chiriquí. Confused by Standley with *X. chloranthum*.
- Zanthoxylum microcarpum** Griseb. (67. Rutaceae): Known only from Panamá Province, but not from BCI. Confused by Standley with *Z. belizense*.
- Zea mays** L. (17. Gramineae): No longer cultivated on the island.

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