PSYGMORCHIS Dods. & Dressl.

Psygmorchis pusilla (L.) Dods. & Dressl., Phytologia 24:288. 1972

Oncidium pusillum (L.) Reichb.f.

Dwarf epiphyte, to 8 cm tall; pseudobulbs lacking. Leaves ± dense, spreading like a fan, equitant, ± linear, 2–6 cm long, to 1 cm wide. Inflorescences 1–6 from base of leaves, about equaling leaves, consisting of long scapes, the apices with several acute, strongly compressed, imbricating sheaths; flowers produced in succession from axils of sheaths; flowers 2–2.5 cm long; sepals free, spreading, bright yellow, keeled and apiculate, the dorsal sepal ca 5 mm long, nearly as wide, the lateral sepals 4–5 mm long, 1–1.5 mm wide, hidden by lateral lobes of lip; petals to 8 mm long and 4 mm wide, bright yellow streaked with reddish-brown, the margins undulate; lip trilobate, to 2 cm long and broad, bright yellow, the lateral lobes ± orbicular, the middle lobe deeply emarginate, the base with an elaborate subquadrate process; column ca 3 mm long, with prominent, denticulate, lateral wings. Fruits ellipsoid, ca 1.5 cm long, with slender ridges. *Croat 4157.*

Rare on BCI, more common elsewhere in Panama. Flowers during most of the year, but principally in the dry season. Known to flower more than once per season since plants often bear both flowers and fruits on separate inflorescences.

Often found in large colonies (especially on *Citrus,* 66. Rutaceae, trees) covering many of the branches.

Mexico to Venezuela and south to Brazil and Bolivia; Trinidad. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, Panamá, and Darién.

SCAPHYGLOTTIS Poepp. & Endl.

Scaphyglottis graminifolia (R. & P.) Poepp. & Endl., Now. Gen. Sp. Pl. 1:59. 1836

S. behrii (Reichb.f.) Benth. & Hook. ex Hemsl.

Caespitose epiphyte, to 45 cm tall; stems densely clustered and slender, consisting of several superimposed, weakly swollen, finely ridged segments (the lower segments most slender), occasionally branched, the old leafless stems persisting. Leaves usually 2, near apex of each segment, usually only the uppermost persisting, linear, 5–25 cm long, 1.5–4.5 mm broad, obscurely emarginate at apex. Inflorescences single flowers or more commonly few-flowered fascicles or abbreviated, few-flowered racemes, borne at apex of stems; flowers white, 3.5–4.5 mm long; sepals 3–4.5 mm long, 1–2 mm wide; petals as long as sepals, 0.5–1 mm wide; lip 3.5–5 mm long, 2–3.5 mm wide, entire or obscurely trilobate; column narrowly winged. Fruits oblong-elliptic, ca 1 cm long (including the long narrowly tapered base), ca 2 mm wide. *Croat 8079.*

Common in the forest, usually high in trees. Flowers in the early dry season (December to March), especially in January and February. The fruits mature in the middle to late dry season.

Confused with *S. longicaulis,* which is usually a much smaller plant bearing mostly solitary flowers.

Guatemala to Venezuela, Brazil, Peru, and Ecuador. In Panama, no doubt widespread; known from tropical moist forest in the Canal Zone and adjacent Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Veraguas (Bahía Honda).

Scaphyglottis longicaulis S. Wats., Proc. Amer. Acad. Arts 23:286. 1888

S. unguiculata Schlechter

Epiphyte, to 30 cm tall; stems densely clustered, usually short, slender, less than 4 mm diam, consisting of a few swollen, superimposed segments, occasionally somewhat maroon, the old leafless stems persisting; stem sheaths (or their scars) restricted to base. Leaves usually 2 near apex of each segment, usually only the uppermost persisting, linear, 4–16 cm long, 2–7 mm wide, obscurely emarginate at apex. Flowers white, 5–7 mm long, usually solitary at apex of the short upper stem segment; sepals 5–7 mm long, 1–2 mm wide, the laterals united at base; petals 5–7 mm long, ca 1 mm wide; lip prominently trilobate, 5–7 mm long, 3–4 mm wide, acute, usually tinged with maroon; column winged laterally, tinged with purple especially on pollinia. Fruits narrowly ellipsoid, ca 7 mm long. *Croat 10098.*

Common in the forest, usually high in trees. Apparently flowers irregularly throughout the year, possibly with two flowering seasons; flowering has been observed in March, April June, September, November, and December.

KEY TO THE SPECIES OF SCAPHYGLOTTIS

Leaves linear-lanceolate, relatively short and broad (usually no more than 8 times longer than broad), mostly less than 6 cm long ..... *S. prolifera* Cogn.

Leaves linear, many times longer than broad, most more than 6 cm long (if less only 1–2 mm wide):

Lip trilobate, the lobes of ± equal length; flowers usually 1 per stem (at least only 1 open); stems usually less than 10 cm long, bearing only 1 or 2 sheaths, the sheaths usually near the base, often loose and spreading ..... *S. longicaulis* S. Wats.

Lip entire or obscurely trilobate (if lobed, the lateral lobes shorter than the middle lobe); flowers usually several in fascicles or racemes; stems often more than 10 cm long, bearing numerous, closely fitting sheaths (or with numerous sheath scars) ..... *S. graminifolia* (R. & P.) Poepp. & Endl.

Fig. 173. *Scaphyglottis longicaulis*

Fig. 174. *Sobralia suaveolens*

Most easily confused with *S. graminifolia.* See the genus key for distinctions.

Guatemala to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién.

See Fig. 173.

Scaphyglottis prolifera Cogn. in Mart., Fl. Brasil. 3(5):15. 1898

S. cuneata Schlechter

Small caespitose epiphyte, 7–25 cm tall; stems slender with slender, fusiform segments superimposed along their length. Leaves usually 2 at apex of each segment, all but the lowermost persisting, linear-lanceolate, 1–6 cm long, 1–7 mm wide, emarginate at apex. Flowers white, ± sessile, solitary or few in fascicles at apex of stem segments; sepals 3.5–5 mm long, 1–2.5 mm wide; petals as long as lateral sepals, 0.5–0.6 mm wide; lip entire or trilobate, 4–6 mm long, 2.5–4 mm wide. Fruits not seen. *Shattuck 549.*

Uncommon, high in trees. Flowering season undetermined. Seen flowering in both the late rainy season (October) and the dry season (December and February).

Guatemala to Brazil and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in Coclé (El Valle), from tropical wet forest in Panamá (Cerro Campana), and from premontane rain forest in Coclé Cerro Pilón) and Panamá (Cerro Jefe).

SIEVEKINGIA Reichb.f.

Sievekingia suavis Reichb.f., Beitr. Syst. Pfl. 3. 1871

Dwarf epiphyte; pseudobulbs ovate, 1.5–3 cm long, with 2 or 3 papery bracts at base. Leaves solitary at apex of pseudobulb, elliptic-lanceolate, 8–25 cm long, 1.5–3 cm wide, plicate. Racemes short, few-flowered, pendent, from base of pseudobulb; sepals subequal, 10–17 mm long, 4–8 mm wide, pale yellow; petals orange, 10–15 mm long, 3–6 mm wide; lip concave, orange, with purplish spots, 8–11 mm long, nearly as wide; column 6–8 mm long, green with broad orange wings. Fruits not seen.

Not seen on BCI, but Dressler has collected the pollinia from bees on the island and is certain that the species occurs there. Seasonal behavior uncertain. Costa Rican plants are known to flower in March.

Pollinated by *Euglossa dodsoni* bees (Dressler, 1968a).

Costa Rica and Panama. In Panama, known from tropical moist forest on BCI and reported from Colón and the Atlantic slope of central Panama.

SOBRALIA R. & P.

Sobralia fragrans Lindl., Gard. Chron. 598. 1853

Small epiphyte (rarely terrestrial), 15–25(45) cm tall; pseudobulbs lacking; stems reedlike but flattened, usually with only 1 leaf (to 3). Leaves narrowly elliptic to oblong-elliptic, narrowly acute to acuminate at apex, (6)9–12(23) cm long, 1.5–3.5 cm wide, plicate, articulated at base with a conduplicate, persistent, sheathing base. Flowers solitary at apex of stem; sepals ± equal, linear to oblong-lanceolate, acute or apiculate apically, 3–4 cm long, 4–7 mm wide, white to cream or pale lavender (at least externally), connate at base; petals ± equaling sepals, white or cream with a yellow throat; lip oval to obovate, 3–3.5 cm long, 1.5–2 cm wide, white with raised yellow ridges, the central ridge terminating in ragged, hairlike projections, the base of the lip with several thickened veins and 2 callus thickenings; column 16–18 mm long. Fruits slender, to ca 6 cm long and 5 mm wide, closely ribbed.

Reported by Dressler; one specimen was seen from the island and transferred to the epiphyte house, but no collection was made. The species flowers throughout the rainy season (June to November), especially in July and August. Fruiting plants are common in the dry season.

Guatemala to Colombia (Chocó) and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién, from premontane wet forest in Chiriquí and Veraguas, and from premontane rain forest in Panamá (Cerro Jefe).

Sobralia panamensis Schlechter, Feddes Repert. Beih. 17:11. 1922

Epiphyte, to 1.5 m tall; stems reedlike, terete, simple or branching, lepidote or furfuraceous. Leaves spaced along stem, elliptic to broadly elliptic-lanceolate, acuminate, obtuse at base, 5–22 cm long, 2–7.5 cm wide, plicate; leaf sheaths pubescent, closely clasping stem. Flowers solitary

KEY TO THE SPECIES OF SOBRALIA

Plants usually less than 50 cm tall; most leaves less than 4.5 cm wide; sepals less than 4 cm long:
- Flowers borne from bract at apex of stem, the distance to the next lower leaf at least 7 cm; stems markedly flattened, often with a single leaf; sepals 3–4 cm long ..... *S. fragrans* Lindl.
- Flowers borne in axil of uppermost leaf, the distance to the next lower leaf usually less than 5 cm; stems ± terete, usually bearing 3 or more leaves; sepals less than 2.8 cm long ..... *S. suaveolens* Reichb.f.

Plants usually more than 75 cm tall; most leaves at least 5 cm wide; sepals more than 4.5 cm long:
- Stems and leaf sheaths minutely furfuraceous or scurfy; flowers lavender to red-violet, enclosed at base by narrowly acute bracts; fruits to ca 2 cm wide ..... *S. panamensis* Schlechter
- Stems and leaf sheaths glabrous; flowers yellow, borne between the uppermost leaf and a leaflike bract; fruits less than 1 cm wide ..... *S. rolfeana* Schlechter

at apex of stems, lavender to red-violet or whitish; sepals ± equal, ligulate to lanceolate, 4.5–6 cm long, 12–16 mm wide, the laterals ± oblique; petals slightly shorter than sepals, broader, to 2 cm wide, obtuse or acute; both sepals and petals weakly recurved near apex; lip colored as petals but much darker, 4–6 cm long, 3–4 cm wide, forming a tube around the column, flaring abruptly at apex, undulate on the margin, with 2 small calluses at base; column to 3 cm long. Fruits elongate, ca 12 cm long and 2 cm wide, the ribs stout and widely spaced. *Croat 4314.*

Occasional, in the forest, usually on tree trunks in deep shade above 3 meters. Flowering season uncertain. Seen in flower in December and March, and both flowers and mature-sized fruits have been seen in February.

The species can easily be distinguished by its scurfy stems. It is similar in other aspects to *S. rolfeana,* which has yellow flowers and lacks the scurfy stems. *S. panamensis* appears to be most similar to *S. decora* Batem., a species ranging from Mexico to Panama, and is perhaps not separable from it.

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

Sobralia rolfeana Schlechter, Feddes Repert. Beih. 17:12. 1922

Epiphyte, 75–100 cm tall; stem reedlike, terete, unbranched, glabrous. Leaves spaced along stem mostly above the middle, elliptic to oblanceolate-elliptic, acute to very abruptly acuminate and downturned at apex, obtuse at base, 7–21 cm long, 2.5–7.5 cm wide, glabrous and smooth, plicate, the sheath often somewhat flattened. Flowers solitary at apex of stem, creamy yellow with a lemon-yellow throat, arising from between a reduced leaf and a much smaller, leaflike bract; sepals 5.5–7.5 cm long, 8–16 mm broad, ligulate to ellptic or elliptic-lanceolate, acute, the laterals ± oblique; petals 5.5–6.5 cm long, 0.8–1.4 cm wide, ligulate to oblong-ligulate, obtuse or acute; lip obovate, retuse, 5.5–7 cm long, 2.5–4.7 cm wide, lacerate-dentate at apex, obscurely bilamellate at base; column 2–3 cm long. Fruits to 12 cm long and 7 mm wide, closely ribbed, light brown. *Croat 6259.*

Apparently rare, in the forest. Flowering more than once during the rainy season; flowers have been seen in August and September borne on an inflorescence with a fruit of mature size.

Collections of the species from Cerro Campana are often much shorter (to as little as 20 cm tall) than those found on BCI and in other lowland areas.

Known only from Panama, principally from tropical moist forest in the Canal Zone and Bocas del Toro (probably also in Darién); known also from premontane wet forest in Panamá (Cerro Campana).

Sobralia suaveolens Reichb.f., Gard. Chron. n.s. 9:622. 1878

Epiphyte, 20–50 cm tall; stems reedlike, few-leaved. Leaves narrowly elliptic, 5–19 cm long, 2–4.5 cm wide, plicate; leaf sheaths glabrous, not verrucose. Flowers 2 or 3 from axil of terminal leaf; sepals and petals ± equal, 2–2.5 cm long, 4–5 mm wide, white to pale yellow; lip as long as petals, darker yellow, 1–1.5 cm wide, trilobate, the longitudinal lamellae several, becoming lacerated at apex and branching into 2 groups at base; column about 8 mm long. Fruits slender, 4–7 cm long, ca 4 mm wide, closely ribbed, the stout ribs forming a cagelike structure persisting long after seeds are dispersed. *Croat 6788, 8253, 12639.*

Occasional, in the forest; common on tree stumps at the edge of the lake and often forming the dominant element of the tree-stump vegetation. Flowers chiefly from October to December. The fruits attain full size by February and March and probably dehisce in the late dry season.

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

See Fig. 174 and fig. on p. 14.

SPIRANTHES L. C. Rich.

Spiranthes lanceolata (Aubl.) León, Contr. Ocas. Mus. Hist. Nat. Colegio "De La Salle," 8:358. 1946
S. orchiodes (Sw.) A. Rich.

Terrestrial, 20–70 cm tall; stem unbranched, stiffly erect, slender, pubescent, leafless at flowering, sheathed in thin bracts. Leaves few, basal, appearing after flowering, elliptic to elliptic-lanceolate, 15–21 cm long, 2.5–4 cm wide, thin; scape bracts lanceolate, to 1.5 cm long. Spikes terminal, many-flowered; sepals unequal, connivent or spreading at tip, yellow-green, often flushed with pink or white on inner surface, pubescent on outer surface; dorsal sepal 13–21 mm long, 3–6 mm wide, the lateral sepals 18–27 mm long, 3–4.5 mm wide; petals salmon-pink, 12–15 mm long; lip lanceolate, clawed, 15–23 mm long, 5.5–9 mm wide, the lateral margins erect, the margins of the claw fleshy and pubescent. Fruits not seen. *D'Arcy 4292.*

Collected once in Rear #8 Lighthouse Clearing. Flowers in the late dry season and the early rainy season (April to May, rarely as late as August).

Stenorrhynchus sp., as reported by Standley from a collection by Kenoyer, was apparently this species, although no such collection annotated by him has been located.

Scattered throughout tropical America. In Panama, known principally from tropical moist forest in the Canal Zone, Chiriquí, and Panamá (the Chiriquí collection near Remedios could have been made in premontane wet forest).

STELIS Sw.

Stelis crescentiicola Schlechter, Feddes Repert. 16:442. 1920

Small, caespitose epiphyte; thickened pseudobulbs lacking; stems short, slender, bearing a single leaf. Blades oblanceolate, mostly rounded or emarginate at apex, attenuate at base, 3.5–10 cm long, 0.6–1.5 cm wide, glabrous, coriaceous (prominently striate longitudinally when dried). Inflorescences densely flowered, terminal

racemes 10–22 cm long; flowers pale violet-purple, persisting in fruit, minute (to 2.7 mm long); sepals ± ovate, acute or obtuse, to 1.3 mm long, papillate to minutely glandular; petals minute, much smaller than sepals, broader than long, held to either side of the minute trilobate lip. Fruits obliquely 3-sided, ± ellipsoid, 4–6 mm long, green. *Croat 14938.*

Apparently uncommon, though because of its habit in trees it is often overlooked. Flowers in the late dry season (April) and the early rainy season (May). The fruits develop by June.

In habit the plant is similar to *Pleurothallis* and may occur in the same places as *P. brighamii* and *P. grobyi.*

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest and tropical wet forest in Colón (Santa Rita Ridge and Portobelo, respectively).

TRICHOCENTRUM Poepp. & Endl.

Trichocentrum capistratum Linden & Reichb.f., Gard. Chron. 1257. 1871

T. panamense Rolfe

Dwarf epiphyte, 3–12 cm tall; pseudobulbs minute. Leaves very fleshy, solitary at apex of pseudobulbs, narrowly elliptic-lanceolate, acute, 2.5–10 cm long, 0.8–2.5 cm wide. Scapes pendent, arising from base of leaf, 1–4 cm long, elongating and successively producing solitary flowers; sepals and petals subequal, spreading, 10–12 mm long, 3–4 mm wide, pale yellowish-green; lip 10–12 mm long, ca 6 mm wide, white with purplish blotch at base, adnate at base to base of column and expanded into an obscurely 4-lobed spur; column about 5 mm long. Fruits not seen.

One specimen seen in the epiphyte house, the specimen having been collected by Dressler on the island. Seasonal behavior unknown.

The species is variable in the size and shape of its leaves and the length of its inflorescence.

Pollinated by the bee *Euglossa cordata* (Dodson, 1967a).

Costa Rica to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone (both slopes) and from premontane wet forest in Coclé (Río Antón, 500–600 m) and Panamá (Cerro Campana).

TRICHOPILIA Lindl.

Trichopilia maculata Reichb.f., Bonplandia 3:215. 1855

Small epiphyte, 7–20 cm tall; pseudobulbs oblong-elliptic, strongly flattened, 2–5 cm long, densely clustered and inserted at an acute angle on a short rhizome, enveloped at base by several densely dark-spotted, imbricate, papery bracts. Leaves solitary at apex of pseudobulb, ± oblong-elliptic, 5–12 cm long, 2–3.5 cm wide. Scapes solitary, 1-flowered, to 6 cm long, from base of pseudobulb; sepals and petals lanceolate, acuminate, free and spreading, subequal, 3–4 cm long, ca 5 mm wide, greenish-yellow; lip forming a tube around the column, flared at apex, ca 3.5 cm long and 1.7 cm wide, white to pale yellow with orange-red streaks, contracted and adnate at base to base of column; column slender, with a tripartite, minutely denticulate hood at apex covering the anther. Fruits not seen. *Shattuck 555.*

Not seen on BCI in recent years. Apparently flowering more than once during the rainy season (September to December). Moderately well-developed fruits have been seen in early December on a flowering plant; full-sized fruits have been seen in January.

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

Trichopilia subulata (Sw.) Reichb.f., Flora 48:278. 1865

Caespitose epiphyte, 5–25 cm tall; pseudobulbs cylindrical, inconspicuous, 1–2.5 cm long, less than 5 mm wide, enclosed in papery deciduous sheaths. Leaves leathery, solitary on pseudobulb, linear to subterete, 5–22 cm long, less than 1 cm wide. Racemes ± erect or pendulous, 2.5–6 cm long, from base of pseudobulb; flowers 5 or 6 on slender pedicels subtended by spathaceous bracts; sepals and petals subequal, linear-lanceolate, acuminate, 18–23 mm long, 2.5–4 mm wide, translucent white to pale yellow; lip ± obovate, concave, 15–20 mm long, nearly as wide, white spotted with rose-purple, the margin denticulate to prominently lacerate, adnate at base to base of column; column 7–9 mm long with an entire, denticulate to fimbriate hood at apex covering the anthers; anthers terminal and caplike. Fruits narrowly-ellipsoid, ca 2 cm long. *Croat 8500.*

Rare, in the forest. Probably flowers in the rainy season. Mature-sized fruits have been seen in March.

Known from Panama to Peru; Trinidad and Cuba. In Panama, known principally from premontane wet and tropical wet forests in Coclé (El Valle) and Panamá (Cerro Campana); known also from tropical moist forest in the vicinity of the Canal Zone.

TRIGONIDIUM Lindl.

Trigonidium egertonianum Batem. ex Lindl., Edward's Bot. Reg. n.s. 1, misc. 73. 1838

Epiphyte; pseudobulbs ± ovoid, compressed and ridged, densely clustered, ca 5 cm long and 3.5 cm wide, sub-

KEY TO THE SPECIES OF TRICHOPILIA

Pseudobulbs elliptic-oblong, strongly flattened; leaves subcoriaceous, elliptic-lanceolate, 2–3.5 cm wide; lip tubular ..... *T. maculata* Reichb.f.

Pseudobulbs subcylindrical; leaves fleshy, narrowly linear to semiterete, 10 mm or less wide; lip not tubular ..... *T. subulata* (Sw.) Reichb.f.

Fig. 175. *Trigonidium egertonianum*

Fig. 176.
Triphora gentianoides

tended by imbricating bracts; the bracts weathering into fibers. Leaves 2, from apex of pseudobulb, linear-lanceolate, 20–60 cm long, 1–3 cm wide, conduplicate at base. Inflorescences 1 to several, erect bracteated scapes bearing 1 flower, ± the same height as leaves, arising from base of pseudobulb; sepals free, mostly acute, 3–4 cm long, faintly brown- to purple-striped, usually tan to yellow, the dorsal sepal erect, the laterals recurved at apices; petals much smaller, more prominently striate, purple and with a glandlike thickening near apex; lip thick, trilobate, recurved at apex, about a third as long as petals, the sides closely fit around the smaller column; column canaliculate on inner surface, the margins purple; anther solitary near apex; pollinia orange. Fruits narrowly ellipsoid, ca 5 cm long. *Croat 8414.*

Abundant on tree stumps at the margin of the lake. Flowers from December to July, chiefly in the dry season months of January to March. Some fruits develop to mature size by late February and have been found unopened as late as early April.

Mexico to Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, and Panamá; known also from tropical wet forest in Veraguas (Bahía Honda) and Colón (Cerro Santa Rita, 400 m).

See Fig. 175.

TRIPHORA Nutt.

Triphora gentianoides (Sw.) Ames & Schlechter in Ames, Orchid. 7:5. 1922

Pogonia cubensis Reichb.f.; *T. cubensis* (Reichb.f.) Ames

Apparently saprophytic, terrestrial herb, to 15 cm tall; stem usually solitary, slender, arising from one end of a tuber. Leaves few, lanceolate to suborbicular, reduced to sheathing bracts above, 1–2 cm long, 0.5–1 cm wide. Flowers several, solitary from upper axils, forming corymbiform racemes; petals and sepals 7–8 mm long, 1–1.5 mm wide, obtuse to acute, green, the sepals tinged with maroon; lip lanceolate-obovate, clawed, trilobate, 7–8 mm long, ca 3 mm wide, white with light green on 3 crested keels, the middle lobe subrotund. Fruits not seen. *Kenoyer 250.*

Rare. Flowering season unknown; the plant seems to appear at irregular intervals.

Reported by Dunsterville and Garay (1965) to have cleistogamous flowers.

Florida and Mexico, Guatemala, Panama, Venezuela, and Ecuador; the Antilles; probably in the intervening areas also. In Panama, known only from tropical moist forest on BCI.

See Fig. 176.

Triphora mexicana (S. Wats.) Schlechter, Feddes Repert. 17:139. 1921

Pogonia mexicana S. Wats.

Terrestrial, to ca 15 cm tall; stem single, slender, ± fleshy, arising from a small tuber. Leaves few, alternate, narrowly to broadly ovate, obtuse to abruptly short-acuminate, obtuse to rounded at base, 8–20 mm long, 5–17 mm wide, thin, 5-veined, the uppermost and lowermost usually much reduced. Pedicels to 12 mm long; flowers 1–3, borne in axils of upper leaves or leaflike bracts; sepals and petals white, narrowly acute at apex; dorsal sepal narrowly lanceolate, to 2 cm long, the lateral sepals linear to narrowly elliptic, subfalcate, to 1.7 cm long; petals similar to lateral sepals; lip ± obovate, trilobate, slightly shorter than lateral sepals, white, with 3 green medial lines, the terminal lobe rounded, marked along the margin with red-violet, the lateral lobes turned upward along the column, infused submarginally with red-violet; column free, thickened somewhat laterally, slightly shorter than lateral lobes of lip; anther red-violet. Fruits not seen. *Croat 15567.*

Rare; seen only once in the forest on BCI. Known to flower in July.

According to R. Dressler, the species may be somewhat saprophytic and, as a consequence, may go for long periods without producing a vegetative shoot.

Mexico, Guatemala, and Panama. In Panama, known only from tropical moist forest in the Canal Zone.

VANILLA P. Mill.

Vanilla fragrans (Salisb.) Ames, Sched. Orch. 7:36. 1924

V. planifolia Andr.

Vanilla

Scandent epiphytic vine; stems thick, often branched, 10–15 mm long. Leaves oblong-elliptic to oblong-oblanceolate, usually acuminate, 8–20(26) cm long, 2–4.5(8) cm wide, fleshy. Racemes axillary (rarely terminal), 5–7 cm long, bracteate at nodes; bracts oblong, usually obtuse, to 1 cm long, persistent at nodes; pedicels 2–4 cm long; flowers white; sepals linear to oblanceolate, 4–7 cm long, 1–1.5 cm wide; petals similar to sepals but smaller; lip obscurely trilobate, curved around sides of column, 4–5 cm long, 1.5–3 cm wide, with a tuft of trichomes at base and streaked with longitudinal, verrucose lines, the middle lobe ± recurved at apex; column ca 3 cm long, pubescent on outer surface. Capsules terete, linear, very aromatic, to 25 cm long, 8–15 mm diam, pendent. *Croat 4528.*

Occasional, in the forest, often climbing to 10 m or more in the canopy. Flowering in March and April; the

KEY TO THE SPECIES OF TRIPHORA

Leaves usually lanceolate; sepals and petals 7–8 mm long .... *T. gentianoides* (Sw.) Ames & Schlechter
Leaves narrowly or broadly ovate; sepals and petals 10–20 mm long ..... *T. mexicana* (S. Wats.) Schlechter

KEY TO THE SPECIES OF VANILLA

Lip with verrucose lines or papillae, somewhat trilobate, not visibly longer than sepals and petals ..... *V. fragrans* (Salisb.) Ames

Lip without verrucose lines or papillae, not at all trilobate, visibly longer than sepals and petals ... . *V. pompona* Schiede

plant rarely flowers and when it does the flowers perish so quickly that they are seldom seen. The fruit set appears to be exceedingly poor also since the fruits are not seen any more frequently than the flowers.

Flowers are pollinated by the bee *Melipona beechii* (Dodson, 1967a).

Mexico to Panama; cultivated throughout the tropics of the world (Boriquet, 1954). In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Panamá.

Vanilla pompona Schiede, Linnaea 4:573. 1829
Vanilla

Epiphytic vine; stems thick, fleshy. Leaves variable in shape, mostly ± oblong-elliptic, often oblique, acute or obtuse at apex, acute to rounded at base, 10–30 cm long, 3.5–14 cm wide. Racemes axillary, to 16 cm long, several-flowered; floral bracts lanceolate to ovate, concave, ca 1 cm long, persistent; petals and sepals greenish-white; sepals ± linear-oblanceolate, obtuse or acute, 7–8.5 cm long, ca 1 cm wide; petals similar to sepals but somewhat smaller and with a midrib outside; lip slightly longer than petals, clawed, to 4 cm wide, enveloping the column and adnate to it, mostly orange-yellow, the outer margin crenulate; column ca 6 cm long. Fruits fusiform capsules to 1.5 cm long, 1.5–2 cm diam. *Wilson 119.*

Not seen in recent years on BCI. Seasonal behavior undetermined. The few flowering collections seen were made in March and April.

Southeastern Mexico to Colombia, Venezuela, the Guianas, Brazil, Paraguay, and Ecuador; Trinidad; probably occurring as an escaped cultivar throughout part of this range. In Panama, known only from tropical moist forest in the Canal Zone.

XYLOBIUM Lindl.

Xylobium foveatum (Lindl.) Nich., Dict. Gard. 4:225. 1887

Epiphyte; pseudobulbs ovoid or subconic, mostly about 8 cm long and 3 cm wide, tapered to apex, ± smooth, enveloped in fibrous imbricating sheaths. Leaves 2 or 3 at apex of pseudobulb, lanceolate to oblanceolate, acute or acuminate, plicate (often weakly so), tapering to a conduplicate petiole, to 50 cm long (including petiole) and 7 cm wide. Inflorescences erect, bracteated, many-flowered racemes from base of pseudobulb, 12–30 cm long; flowers creamy-white, the lip with reddish veins, pedicellate, fragrant, ca 1.5 cm long; sepals subequal, free, the dorsal sepal free, the laterals produced below the pedicel and adnate to foot of column; petals ± equaling dorsal sepal; lip trilobate, the lateral margins twined upward; apex of column with a hooded cavity bearing the anther on its inner margin. Fruits not seen. *Aviles 32.*

Rare; collected only once. Flowering from November to March, principally in the dry season.

Mexico to Peru, the Guianas; Jamaica. In Panama, known from tropical moist forest in the Canal Zone and Panamá. Ospina (1958) reported that the species usually occurs in Colombia at 1,200–1,500 m elevation!

ANTHOPHYTA
Dicotyledoneae

KEY TO THE DICOTYLEDONEAE

All families in Key 5 are also keyed out in Keys 6–9. Key 5 is included so that decisions based on floral characters of minute flowers can be avoided.

Plants aquatic ..... KEY 1
Plants not aquatic:
  Leaves compound:
    Leaves pinnately or bipinnately compound with more than 3 leaflets ..... KEY 2
    Leaves palmately compound or with only 2 or 3 leaflets ..... KEY 3
  Leaves simple or lacking:
    Plants lacking leaves and/or chlorophyll ..... KEY 4
    Plants with both leaves and chlorophyll:
      Flowers individually inconspicuous, minute, usually crowded, the perianth often lacking or undifferentiated into calyx and corolla ..... KEY 5
      Flowers as above or not:
        Leaves opposite, ternate, or quaternate:
          Ovary inferior ..... KEY 6
          Ovary superior ..... KEY 7
        Leaves alternate, spiraled or whorled:
          Ovary inferior ..... KEY 8
          Ovary superior ..... KEY 9

KEY 1: PLANTS AQUATIC

Petals 5 (rarely 4), yellow or white with yellow spots at base, caducous; stamens 10, in 2 series; ovary inferior; capsules cylindrical ..... 108. ONAGRACEAE (*Ludwigia,* in part)
Petals not as above, either not yellow or white with yellow spots or not 5; stamens not 10 in 2 series; ovary inferior or superior; fruits not capsular or, if capsular, then not cylindrical:
- Blades or blade segments narrow, at least 3 times longer than wide, ligulate, filiform or grasslike:
  Leaves simple, alternate or basal, not submerged:
    Leaves succulent, basal ..... 28. AMARYLLIDACEAE (*Crinum erubescens* Ait.)*
    Leaves not succulent, alternate ..... 17. GRAMINEAE (in part)*
  Leaves dissected or verticillate, primarily submerged:
    Blades simple ..... 16. HYDROCHARITACEAE (*Hydrilla verticillata* (L.f.) Royle)*
    Blades dissected or forked (also inconspicuous in Lentibulariaceae):
      Plants free-floating, at or near surface ..... 128. LENTIBULARIACEAE
      Plants rooted ..... 53. CERATOPHYLLACEAE (*Ceratophyllum demersum* L.)

*Not a dicotyledon; included here because of superficial similarity.

• Blades broad, not dissected, less than 3 times as long as wide:
Blades ± orbicular, often floating on surface, conspicuously palmately veined below:
Largest blades more than 20 cm long, deeply dentate . . . . . 52. NYMPHAEACEAE
Largest blades less than 20 cm long, generally entire to undulate:
Blades more than 8 cm long, purplish beneath; flowers bisexual; petals fimbriate . . . . . 117. MENYANTHACEAE (*Nymphoides indica* L.)
Blades less than 7.5 cm long, not purplish beneath; flowers unisexual or bisexual; petals not fimbriate:
Flowers unisexual, 1–3, subtended by 1 or 2 spathes . . . . . 16. HYDROCHARITACEAE (*Limnobium stoloniferum* (G. Meyer) Griseb.)*
Flowers bisexual, borne solitary in leaf axils or in dense, long-pedunculate umbels:
Flowers regular, white, numerous, in dense, long-pedunculate umbels; leaves with the petioles many times longer than blades, the blades peltate . . . . . 110. UMBELLIFERAE (*Hydrocotyle umbellata* L.)
Flowers bilabiate, blue, solitary in leaf axils; leaves sessile, not peltate . . . . . 125. SCROPHULARIACEAE (*Bacopa salzmannii* Edw.)
Blades not orbicular, not floating on surface, not conspicuously veined below:
Blades entire:
Blades more than 20 cm long; petioles not inflated . . . . . 15. ALISMATACEAE (*Sagittaria lancifolia* L.)*
Blades less than 20 cm long; petioles often inflated . . . . . 24. PONTEDERIACEAE
Blades serrate:
Blades peltate . . . . . 110. UMBELLIFERAE (*Hydrocotyle umbellata* L.)
Blades basifixed:
Blades ± equilateral at base; flowers minute, clustered in axils . . . . . 40. URTICACEAE (*Boehmeria cylindrica* (L.) Sw.)
Blades inequilateral at base; flowers showy, in terminal inflorescences . . . . . 100. BEGONIACEAE (*Begonia patula* Haw.)

KEY 2: BLADES PINNATELY OR BIPINNATELY COMPOUND WITH MORE THAN THREE LEAFLETS

Leaves opposite:
Petals and sepals 5, free; stamens 5; pistil 1, with 3 free carpels . . . . . 79. STAPHYLEACEAE (*Turpinia occidentalis* subsp. *breviflora* Croat)
Petals and sepals united; stamens 4 or 10; pistil of 1 or 2 united carpels:
Stamens 10, united into a staminal tube which is open on one side; fruits indehiscent, 1-seeded . . . . . 63C. PAPILIONOIDEAE (*Platymiscium pinnatum* (Jacq.) Dug.)
Stamens 4, borne on corolla tube, the filaments not united; fruits dehiscent, many-seeded . . . . . 126. BIGNONIACEAE (in part)
Leaves alternate:
Flowers with the petals lacking, the calyx 6-lobed in 2 series; stamens 3; blades simple, the branchlets only appearing as pinnately compound leaves, the branchlets deciduous . . . . . 75. EUPHORBIACEAE (*Phyllanthus*)
Flowers with the calyx and corolla each 4- or 5-lobed or 4- or 5-parted (segments 3 in some Burseraceae, sometimes 6 in Connaraceae; *Prioria* (Leguminosae) with 5 petaloid sepals and 2 calyx-like bracts also included here); stamens 4 to many; leaves pinnately or bipinnately compound:
◆ Style 1, the stigma simple or obscurely lobed:
Calyx with the sepals united, variously lobed (or obsolete in some *Mimosa*):
Ovary 1-carpellate, 1-locular; fruits usually ± elongate, 2-valved capsules, rarely drupes or samaras; flowers actinomorphic, densely congested in heads or umbels or spikes, with usually many (as few as 4 in *Mimosa*) exserted stamens giving the inflorescences a fluffy appearance (Mimosoideae) *or* flowers weakly to strongly zygomorphic (Caesalpinioideae, Papilionoideae) . . . . . 63. LEGUMINOSAE (in part)
Ovary with 2 or more carpels and locules (*Trattinnickia* 1-seeded by abortion); fruits usually capsular, fleshy or with more than 2 valves; flowers actinomorphic, the stamens to twice as many as petals, but flowers not congested with the stamens exserted giving the inflorescence a fluffy appearance:
Stamens united into a tube or attached to the gynophore . . . . . 70. MELIACEAE
Stamens free, in 2 whorls . . . . . 69. BURSERACEAE

*Not a dicotyledon; included here because of superficial similarity.

Calyx with the sepals free or nearly so:
Flowers with the corolla sympetalous or markedly zygomorphic; seeds not arillate ..... 63. LEGUMINOSAE (in part)
Flowers actinomorphic and with the petals free (weakly zygomorphic in *Paullinia* and *Serjania*); seeds arillate or not:
Petals bearing petaloid scales on inner surface; stamens 8; stipules present on lianas ..... 80. SAPINDACEAE (in part)
Petals lacking scales; stamens 5 or 10(12) or more in 2 or more series; stipules lacking:
Plants lianas ..... 62. CONNARACEAE (*Connarus*)
Plants trees or shrubs:
Rachis conspicuously winged; leaves imparipinnate ..... 68. SIMAROUBACEAE (*Quassia amara* L.)
Rachis not winged; leaves paripinnate ..... 63B. CAESALPINIOIDEAE (in part)
◆ Styles 2 or more or parted 2 or more times:
Plants lianas lacking tendrils; flowers lacking a disk; seeds arillate .. 62. CONNARACEAE (in part)
Plants shrubs, trees, or tendriled lianas; flowers with a disk (except Oxalidaceae); seeds arillate or not:
Ovary inferior; leaflets conspicuously serrate, usually white-margined; plants cultivated ..... 109. ARALIACEAE (*Polyscias guilfoylei* (Cogn. & Marchal) Bailey)
Ovary superior; leaflets not white-margined; plants cultivated or not:
Leaves glandular-punctate; plants frequently armed; ovary lobed and elevated on a disk; sap often aromatic; fruits of usually several follicles with a shiny seed ..... 67. RUTACEAE (*Zanthoxylum*)
Leaves not punctate; plants unarmed; ovary usually not lobed and not elevated on a disk; sap usually not distinctively aromatic; fruits various:
Petals bearing petaloid scales on inner surface; stamens 8; plants tendriled lianas or trees; fruits capsular, the seeds arillate ..... 80. SAPINDACEAE (in part)
Petals not appendaged; stamens 5, 10, or more; plants not scandent; fruits not capsular, the seeds not arillate:
Plants cultivated trees in the Laboratory Clearing; stamens 5 with 5 more reduced to staminodia; ovules many per locule ..... 65. OXALIDACEAE (*Averrhoa carambola* L.)
Plants not cultivated; stamens 5 or 10, equal or unequal, but never 5 and 5; ovules 1 or 2(3) per locule:
Flowers in leaf-opposed spikes (*Picramnia*) *or* flowers greenish, in terminal panicles (*Simarouba*) ..... 68. SIMAROUBACEAE
Flowers white (except *Astronium* with the flowers greenish-yellow, the styles 3, the stamens 5, and the drupes carried in winglike, accrescent sepals), in terminal panicles ..... 76. ANACARDIACEAE (in part)

KEY 3: BLADES PALMATELY COMPOUND OR WITH ONLY TWO OR THREE LEAFLETS

Leaves opposite:
Flowers blue; blades with simple trichomes (at least when young); fruits ± globose berries; seeds few, not winged ..... 122. VERBENACEAE (*Vitex cooperi* Standl.)
Flowers yellow, pinkish, or whitish; blades glabrous or with stellate trichomes; fruits elongated capsules; seeds usually many, usually winged ..... 126. BIGNONIACEAE (in part)
Leaves alternate:
Ovary inferior:
Plants large trees; flowers in compound umbels; leaflets densely rufous-pubescent beneath; styles 2; seeds 2 ..... 109. ARALIACEAE (*Didymopanax morototoni* (Aubl.) Dec. & Planch.)
Plants vines; flowers solitary or in cymose panicles; leaflets not rufous-pubescent; style 1; seeds usually many ..... 131. CUCURBITACEAE (in part)
Ovary superior (sometimes subinferior in *Ceiba*):
■ Most leaves with more than 3 leaflets:
Plants herbs to 60 cm tall .... 59. CAPPARIDACEAE (*Cleome parviflora* H.B.K. subsp. *parviflora*)
Plants shrubs or trees:
Plants shrubs or small trees; flowers and fruits borne on trunk ..... 87. STERCULIACEAE (*Herrania purpurea* (Pitt.) R. E. Schult.)
Plants large trees; flowers borne on branches:
Flowers usually large, with many exserted anthers (5 in *Ceiba*); fruits capsules, the seeds embedded in kapok (except *Pachira*) ..... 86. BOMBACACEAE (in part)
Flowers with 8 stamens; fruits berries, the seeds enveloped in a fleshy matrix ..... 99. CARICACEAE (*Jacaratia spinosa* (Aubl.) A. DC.)

■ Most leaves with 2 or 3 leaflets:
Stipules lacking:
Plants herbs to 60 cm tall; stamens 6; fruits fusiform siliques borne on a gynophore . . . . . 59. CAPPARIDACEAE (*Cleome parviflora* H.B.K. subsp. *parviflora*)
Plants shrubs, lianas, or trees; stamens 8–12; fruits not as above:
Leaves with 2 leaflets; flowers in small conelike inflorescences . . . . . 63B. CAESALPINIOIDEAE (*Cynometra bauhiniifolia* Benth.)
Leaves with 3 or more leaflets:
Sepals and petals 4; plants shrubs or small trees, never scandent; fruits of 1(2) obovoid, fleshy cocci; petals with scales appendaged on inner surface . . . . . 80. SAPINDACEAE (*Allophylus psilospermus* Radlk.)
Sepals and petals 5; plants usually lianas; fruits leathery follicles with a single, shiny, arillate seed; petals not appendaged . . . . . 62. CONNARACEAE (*Connarus panamensis* Griseb.)
Stipules present:
Styles 3:
Inflorescences subtended by and partially enclosed by a pair of large bracts; flowers apetalous, distinctly unisexual; stamens many . . . . 75. EUPHORBIACEAE (*Dalechampia*)
Inflorescences not partially enclosed in large bracts; flowers at least appearing bisexual, the petals 4; stamens usually 8 . . . . . 80. SAPINDACEAE (in part)
Style 1, simple:
Inflorescences leaf-opposed; flowers 4-parted; stamens 4 . . . . 82. VITACEAE (*Cissus,* in part)
Inflorescences axillary or terminal; flowers 5-parted; stamens 5 or more . . . . . 63. LEGUMINOSAE (in part)

KEY 4: PLANTS LACKING LEAVES AND/OR CHLOROPHYLL

Plants growing on the ground, saprophytic:
Flowers zygomorphic; perianth 6-parted, appendaged; stamens 6 . . . . . 34. BURMANNIACEAE (*Thismia panamensis* (Standl.) Jonk.)*
Flowers actinomorphic; perianth 5-parted, not appendaged; stamens 5 . . . . . 116. GENTIANACEAE (*Voyria*)
Plants growing on trees, epiphytic or parasitic:
Plants parasitic, consisting only of flowers less than 1 cm diam . . . . . 45. RAFFLESIACEAE (*Apodanthes casearíae* Poit.)
Plants epiphytic, consisting of green, angular or flattened stems and large flowers . . 101. CACTACEAE

KEY 5: BLADES SIMPLE; FLOWERS INCONSPICUOUS, MINUTE, USUALLY CROWDED; PERIANTH OFTEN LACKING OR UNDIFFERENTIATED INTO CALYX AND COROLLA

All families in this key are also keyed out in Keys 6–9. This key is included so that decisions based on floral characters of minute flowers can be avoided.

Leaves opposite:
Flowers obscured by bracts *or* flowers in dense heads subtended by a series of bracts:
Flowers in dense heads subtended by a series of greenish bracts; corolla tubular at least at base; seeds usually with bristles or scales borne at apex . . . . . 133. COMPOSITAE (in part)
Flowers individually hidden by whitish scarious bracts; corolla lacking; seeds shiny, black, lacking appendages . . . . . 47. AMARANTHACEAE (in part)
Flowers not obscured by bracts and not in dense heads subtended by a series of bracts:
Plants parasitic shrubs or vines with thick leathery leaves . . . . . 42. LORANTHACEAE
Plants herbs, the leaves not thick and leathery:
Flowers with a perianth, usually of 3–5 tepals, with 3–5 stamens or with a simple style; leaves often opposite on stem but alternate on branches (opposing leaves unequal in *Pilea*) . . . . . 40. URTICACEAE (in part)
Flowers lacking a perianth, consisting of a single stamen or 3 styles, subtended by a conspicuous stalked gland; leaves all opposite, or alternate at base and opposite above . . . . 75. EUPHORBIACEAE (in part)
Leaves alternate:
□ Stipules lacking:

*Not a dicotyledon; included here because of superficial similarity.

Plants scandent; blades palmately veined:
Flowers bisexual, congested in pencil-like spikes ..... 36. PIPERACEAE (in part)
Flowers unisexual, in panicles or racemes, often fasciculate ..... 54. MENISPERMACEAE
Plants not scandent; most blades not palmately veined:
Flowers in pencil-like spikes; plants epiphytic herbs (*Peperomia*), terrestrial herbs (*Pothomorphe*), or shrubs or trees with leaf-opposed spikes (*Piper*) ..... 36. PIPERACEAE (in part)
Flowers not in pencil-like spikes:
Plants forest trees with red sap ..... 56. MYRISTICACEAE
Plants shrubs or herbs (if treelike, never in forest), the sap not red:
Flowers with tubular corollas, in dense heads surrounded by series of bracts ..... 133. COMPOSITAE (in part)
Flowers with free sepals and corolla lacking, hidden by scarious white bracts ..... 47. AMARANTHACEAE (in part)

□ Stipules present:
Plants small herbs (less than 20 cm tall), with fleshy leaves and yellow flowers crowded in the axils ..... 50. PORTULACACEAE (*Portulaca oleracea* L.)
Plants large herbs, shrubs, vines, or trees:
Petioles with conspicuous glands at apex ..... 75. EUPHORBIACEAE (in part)
Petioles lacking glands:
Blades lobed ..... 39. MORACEAE (in part)
Blades not lobed:
Blades palmately veined at base, the strong basal vein extending ca half the length of the blade or more:
Style 1; fruits green achenes less than 4 mm long, usually hidden in bracts ..... 40. URTICACEAE (in part)
Styles 2; fruits drupes either green and more than 1 cm long or red at maturity ..... 38. ULMACEAE
Blades not palmately veined at base or weakly so, the basal veins not extending halfway into blade:
Flowers not in spikelike racemes; trees usually with milky or colored, viscid sap; stipules often large and amplexicaul ..... 39. MORACEAE (in part)
Flowers in spikelike racemes; sap milky or not; stipules lateral, not encircling stems:
Styles 2 or bifid; stamens 4; fruits drupes, the seeds not arillate; sap milky ..... 39. MORACEAE (in part)
Styles 3; stamen 1; fruits fleshy 3-valved capsules, the seeds arillate; sap not milky ..... 37. LACISTEMACEAE

KEY 6: LEAVES SIMPLE, OPPOSITE (OR TERNATE OR QUATERNATE); OVARY INFERIOR

Flowers with the corolla tubular or the perianth undifferentiated into calyx and corolla:
Stipules interpetiolar; calyx and corolla usually 4- or 5-lobed, usually regular ..... 130. RUBIACEAE
Stipules lacking or, if present, not continuous between petioles; perianth undifferentiated into typical calyx and corolla or bilabiate and zygomorphic:
Corolla bilabiate, zygomorphic; stems juicy; plants epiphytic or loosely rooted in soil ..... 127. GESNERIACEAE (in part)
Corolla not bilabiate or lacking; stems not juicy; plants terrestrial or parasitic (Loranthaceae):
Flowers with tubular corollas in dense bracteate heads, the calyx reduced to bristles or scales ..... 133. COMPOSITAE (in part)
Flowers lacking a corolla or with free, undifferentiated tepals, not in dense bracteate heads:
Plants parasitic shrubs or vines; tepals free; blades thick, leathery ..... 42. LORANTHACEAE
Plants terrestrial shrubs, trees, climbing shrubs, or lianas; calyx cupular, 5-lobed, the corolla lacking; blades not thick; ovary appearing inferior ..... 48. NYCTAGINACEAE
Flowers with the petals free, the calyx present and ± typical:
Plants herbs ..... 110. UMBELLIFERAE (in part)
Plants not herbs:
▲ Plants lianas or hemiepiphytic shrubs, often somewhat scandent:
Plants lianas; fruits winged or prominently angled, more than 10 mm long ..... 105. COMBRETACEAE (*Combretum*)
Plants hemiepiphytic shrubs; fruits small, winged capsules to 2 mm long or fleshy berries:
Fruits fleshy, many-seeded berries to 10 mm long; style 1; inflorescences with all flowers alike ..... 107. MELASTOMATACEAE (*Topobaea praecox* Gleason)
Fruits small, winged capsules to 2 mm long; inflorescences with some neuter flowers consisting of showy calycine lobes, the bisexual flowers with 2 styles ..... 60. SAXIFRAGACEAE (*Hydrangea peruviana* Moric.)

▲ Plants trees or shrubs, never hemiepiphytic or scandent:
Stamens equal in number to petals and ± hidden by petals; leaves with large glands at base below ..... 81. RHAMNACEAE (*Colubrina glandulosa* Perk.)
Stamens more than petals; leaves lacking large basal glands:
Stamens many; most parts pellucid-punctate ..... 106. MYRTACEAE
Stamens twice as many as petals; plants not pellucid-punctate:
Leaves pliveined or nearly so (except *Mouriri,* which is not epiphytic); flowers all bisexual; plants terrestrial (except *Topobaea*); fruits berries ..... 107. MELASTOMATACEAE (in part)
Leaves not pliveined; inflorescences with neuter flowers consisting only of enlarged calycine lobes; plants epiphytic; fruits small capsules ..... 60. SAXIFRAGACEAE (*Hydrangea peruviana* Moric.)

KEY 7: LEAVES SIMPLE, OPPOSITE (OR TERNATE OR QUATERNATE); OVARY SUPERIOR

Plants dioecious lianas with opposite, decussate leaves and swollen nodes; flowers with naked ovules, in bracteate strobili; seeds oblong, drupelike, reddish; leaves broadly ovate, coriaceous, glabrous ..... 13. GNETACEAE (*Gnetum leyboldii* Tul. var. *woodsonianum* Markg.)*
Plants not as above:
★ Petals united at least at base; perianth differentiated into calyx and corolla:
Flowers zygomorphic, the corolla bilabiate (except *Trichanthera,* Acanthaceae); stamens 4 and didynamous or 2:
Ovary 4-celled (2-carpellate, 2-loculate) with 1 ovule per cell; stems usually square; plants often aromatic; herbs of open areas ..... 123. LABIATAE
Ovary 1- or 2-celled (except *Clerodendrum,* Verbenaceae, with red flowers, cultivated at the Laboratory Clearing); stems usually not square; plants not distinctly aromatic; herbs or shrubs in open areas or forest:
Ovary 1-locular with more than 4 ovules; stems juicy; plants epiphytic or loosely rooted; corolla often gibbous at base ..... 127. GESNERIACEAE
Ovary not 1-celled or if so with 1 or 2 ovules:
Ovules borne on hooklike funicle, flattened at maturity and forcibly ejected by funicle; inflorescences usually prominently bracteate; leaves with cystoliths (except *Mendoncia,* with 1 cell and 2 ovules) ..... 129. ACANTHACEAE
Ovules sessile or on short, not hooked funicles, ± round at maturity, not ejected; inflorescences not bracteate; leaves lacking cystoliths:
Plants small herbs; ovules many per locule ..... 125. SCROPHULARIACEAE
Plants trees, shrubs, lianas, or large herbs; ovules 1 per locule ..... 122. VERBENACEAE (in part)
Flowers regular (weakly zygomorphic in *Lantana,* Verbenaceae); stamens usually alternate with the petals or corolla lobes or stamens 5 (except *Chelonanthus,* with green flowers):
Sap milky; pistil apocarpous, with 1 style and 2 separate, unicarpellate, unilocular ovaries, each with few to many ovules (except *Allamanda cathartica,* Apocynaceae, which has quaternate leaves, large yellow flowers, and spiny fruits); plants frequently herbaceous vines:
Corolla twisted in bud; stamens and style held within corolla tube, blocking entrance; anther sacs normal ..... 118. APOCYNACEAE (in part)
Corolla not twisted in bud; stamens and style joined in a column at the center of the flaring corolla tube; anther sacs formed into a pollinium, connected in pairs ..... 119. ASCLEPIADACEAE
Sap not milky; pistil simple; style 1:
Flowers distinctly unisexual, with one of the sexes greatly reduced; calyx-like structure beneath perianth of 1–3 free parts (these actually bracts, not true sepals) ..... 48. NYCTAGINACEAE
Flowers usually bisexual or at least not distinctly unisexual; calyx typical or at least not of 1–3 free bractlike structures:
Stipules interpetiolar or with stipular lines or scars; plants lianas with pliveined leaves *or* plants herbs ..... 115. LOGANIACEAE
Stipules lacking; plants herbs, lianas, shrubs, or trees, the leaves never pliveined:
Leaf pairs usually very unequal; corolla usually plicate ..... 124. SOLANACEAE (in part)
Leaf pairs ± equal; corolla not plicate:
Ovary 2-carpellate, 1-locular, with many ovules per locule; fruits 2-valved capsules with many, minute, wind-dispersed seeds ... 116. GENTIANACEAE (in part)
Ovary 2–4-carpellate and 2–4-locular, with 1 ovule per locule; fruits of several nutlets or drupes of several pyrenes ..... 122. VERBENACEAE (in part)

*Not a dicotyledon; included here because of superficial similarity.

★ Petals free or lacking *or* perianth not differentiated into calyx and corolla:
Petals lacking *or* perianth undifferentiated into calyx and corolla:
Plants herbs:
Perianth lacking; inflorescences cyathia . . . . . 75. EUPHORBIACEAE (in part)
Perianth present; inflorescences lacking glands:
Flowers not obscured by scarious bracts; cystoliths linear or punctiform in blades; blades less than 5 mm long or strongly palmately veined at base . . . . . 40. URTICACEAE (in part)
Flowers obscured by scarious bracts; cystoliths lacking; blades more than 1 cm long, not palmately veined at base . . . . . 47. AMARANTHACEAE (in part)
Plants trees, shrubs, or lianas:
Leaf blades with numerous, closely parallel veins; tertiary veins lacking; sap yellow; plants large trees . . . . . 92. GUTTIFERAE (*Calophyllum longifolium* Willd.)
Leaf blades lacking numerous, closely parallel veins; tertiary veins present; sap not yellow; plants shrubs or small trees:
Inflorescences terminal, corymbose; calyx 5-lobed, the corolla lacking; stamens 6–10; fruits achenes enclosed in the accrescent calyx; seed 1, not arillate; sap not aromatic . . . . . 48. NYCTAGINACEAE
Inflorescences axillary or cauliflorous cymes; tepals 4–8, borne on a hypanthium; stamens many; fruits drupelike aggregates enclosed in the hypanthium; seeds several, arillate; sap aromatic . . . . . 57. MONIMIACEAE
Petals free, the calyx present:
Plants trees or shrubs:
Styles or stigmas usually 3 or more (2 in *Spachea*, Malpighiaceae):
Stamens 5, hidden by petals; leaves with large basal glands below . . . . . 81. RHAMNACEAE (*Colubrina glandulosa* Perk.)
Stamens 4, 8, 10, or more:
Calyx lobes with pairs of conspicuous glands; sap not colored . . . . . 71. MALPIGHIACEAE (in part)
Calyx lacking glands; sap yellow, orange, or red . . . . . 92. GUTTIFERAE
Style and stigma 1:
Stamens as many as petals *or* stamen 1 with 2 staminodia; flowers frequently zygomorphic:
Petals 3, orange; plants large trees; seeds winged; stamens not appendaged . . . . . 73. VOCHYSIACEAE (*Vochysia ferruginea* Mart.)
Petals 5, white; plants shrubs or small trees; seeds not winged; stamens appendaged . . . . . 95. VIOLACEAE (*Rinorea*)
Stamens more numerous than petals; flowers actinomorphic:
Flowers with calyx and corolla fused into a hypanthium at base, petals crumpled in bud; ovary 1- or 2-locular, 2-carpellate, with many ovules per locule; seeds not arillate . . . . . 102. LYTHRACEAE (except *Cuphea*)
Flowers lacking a hypanthium; petals not crumpled; ovary 3-locular, 3-carpellate, with 2 ovules per locule; seeds arillate . . . . . 104. RHIZOPHORACEAE (*Cassipourea elliptica* (Sw.) Poir.)
Plants herbs, vines, or lianas:
Plants herbs:
Leaves pliveined or nearly so . . . . . 107. MELASTOMATACEAE (in part)
Leaves pinnately or palmately veined:
Plants tiny prostrate herbs; blades reniform to ovate; petals bifid; styles 3 . . . . . 51. CARYOPHYLLACEAE (*Drymaria cordata* (L.) R. & S.)
Plants erect herbs; blades lanceolate to oblanceolate; petals entire; style 1, simple:
Flowers with ± zygomorphic, tubular hypanthium and 6 violet petals; stamens 11 or 12 . . . . . 102. LYTHRACEAE (*Cuphea carthagenensis* (Jacq.) Macbr.)
Flowers lacking a hypanthium and with 4 white petals; stamens 4 and didynamous . . . . . 125. SCROPHULARIACEAE (*Scoparia dulcis* L.)
Plants vines or lianas:
Leaves pliveined . . . . . 107. MELASTOMATACEAE (*Adelobotrys adscendens* (Sw.) Tr.)
Leaves not pliveined:
Flowers zygomorphic and white; stamens united into a cleft tube; fruits single capsules . . . . . 72. TRIGONIACEAE (*Trigonia floribunda* Oerst.)
Flowers actinomorphic or yellow or red and zygomorphic; stamens not united into a cleft tube; fruits not capsular or fruits of 3 capsular mericarps:
Sepals with conspicuous glands; stamens 10 (sometimes with 4 reduced); disk lacking; styles or stigmas 3; fruits of 2 separable cocci, schizocarps of 3 samaras, or drupes of 1–3 pyrenes . . . . . 71. MALPIGHIACEAE (in part)
Sepals eglandular; stamens 3, strap-shaped, inserted on a prominent disk; style and stigma 1; fruits usually of 3 capsular mericarps (drupes in *Tontelea*) . . . . . 78. HIPPOCRATEACEAE

KEY 8: BLADES SIMPLE, ALTERNATE, SPIRALED OR WHORLED; OVARY INFERIOR

Perianth segments undifferentiated *or* flowers with calyx and/or corolla lacking *or* flowers very zygomorphic or in bracteate heads:
- Plants vines or lianas:
  - Flowers solitary or in short racemes; flowers zygomorphic, modified into a large, complex, fly-trapping structure ..... 44. ARISTOLOCHIACEAE
  - Flowers in bracteate heads; flowers actinomorphic, tubular ..... 133. COMPOSITAE (in part)
- Plants not vines or lianas:
  - Stipules present:
    - Plants herbs or suffrutices; sap clear, not viscid; blades conspicuously inequilateral at base; tepals of staminate flowers 2, or 4 in unequal pairs, those of pistillate flowers 4 or 5 ..... 100. BEGONIACEAE
    - Plants trees; sap usually colored, viscid; blades ± equilateral; tepals not as above ..... 39. MORACEAE (in part)
  - Stipules lacking:
    - Perianth parts free; flowers in a corymb ..... 103. LECYTHIDACEAE (*Gustavia*)
    - Perianth tubular; flowers solitary or in heads or spikes:
      - Flowers solitary; pedicels more than 3.5 cm long ..... 132. CAMPANULACEAE (*Centropogon cornutus* (L.) Druce)
      - Flowers in heads or spikes; pedicels much shorter:
        - Flowers in dense bracteate heads; corolla present; calyx reduced to bristles or scales; stamens 5 ..... 133. COMPOSITAE (in part)
        - Flowers in long spikes; corolla lacking; calyx tubular, 5-lobed; stamens 8 or 10 ..... 105. COMBRETACEAE (*Terminalia*)

Perianth differentiated into a ± typical calyx and corolla:
- Plants herbs or suffrutescent herbs, not vines:
  - Flowers solitary in leaf axils:
    - Flowers with the corolla tubular, zygomorphic, 6–8 cm long, red or pink ..... 132. CAMPANULACEAE (*Centropogon cornutus* (L.) Druce)
    - Flowers of free petals, actinomorphic, less than 2 cm long, yellow ..... 108. ONAGRACEAE
  - Flowers not solitary:
    - Flowers congested in leaf axils; stipules present; blades succulent ..... 50. PORTULACACEAE
    - Flowers in spicate heads or umbels; stipules lacking; blades not succulent ..... 110. UMBELLIFERAE (*Hydrocotyle umbellata* L.)
- Plants vines, lianas, or trees:
  - Plants vines or lianas:
    - Flowers unisexual, with the corolla tubular; fruits many-seeded pepos ..... 131. CUCURBITACEAE (in part)
    - Flowers bisexual, with the petals free; fruits winged:
      - Tendrils present; spines lacking; stamens 4 or 5; stipules present; fruits with the 3 mericarps 2-winged ..... 81. RHAMNACEAE (*Gouania*)
      - Tendrils lacking; spines on stems; stamens 8–10; stipules lacking; fruits 5-winged ..... 105. COMBRETACEAE (*Combretum*, in part)
  - Plants shrubs or trees:
    - Flowers more than 10 mm long:
      - Flowers solitary; style exceeding staminal column ..... 86. BOMBACACEAE (*Quararibea*)
      - Flowers in clusters on trunks or in corymbs or panicles; style very short ..... 103. LECYTHIDACEAE (in part)
    - Flowers less than 5 mm long:
      - Blades with large glands at base below; flowers in axillary thyrses 1–5 cm long; fruits explosively dehiscent capsules ..... 81. RHAMNACEAE (*Colubrina glandulosa* Perk.)
      - Blades eglandular; flowers in terminal panicles with ultimate divisions in umbels or heads; fruits berries ..... 109. ARALIACEAE (in part)

KEY 9: BLADES SIMPLE, ALTERNATE, SPIRALED OR WHORLED; OVARY SUPERIOR

- Perianth undifferentiated into calyx and corolla *or* flowers apetalous:
  - Stipules or tendrils present:
    - Blades markedly palmately veined, the veins extending nearly midway or further from base into the blade:
      - Blades lobed:
        - Blades large, usually more than 20 cm long:
          - Blades peltate ..... 39. MORACEAE (*Cecropia*)
          - Blades basifixed:

Flowers more than 10 mm long, greenish with violet-purple markings; petioles not hollow; stipules axillary ..... 87. STERCULIACEAE (*Sterculia apetala* (Jacq.) Karst.)
Flowers less than 5 mm long, greenish; petioles hollow; stipules amplexicaul ..... 39. MORACEAE (*Pourouma aspera* Trec.)

◇ Blades less than 20 cm long:
Leaves conspicuously pubescent:
Plants shrubs; most parts stellate-pubescent; flowers bisexual; stamens 5 or 15 (rarely 10) ..... 84. TILIACEAE (*Triumfetta lappula* L.)
Plants vines; trichomes not stellate; flowers unisexual (plants monoecious); stamens more than 20 ..... 75. EUPHORBIACEAE (*Dalechampia*)
Leaves essentially glabrous:
Blades peltate, usually trilobate, not glaucous below; plants vines; sap not colored; flowers bisexual ..... 98. PASSIFLORACEAE (*Passiflora coriacea* Adr. Juss.)
Blades basifixed, usually with more than 3 lobes, glaucous below; plants herbs or shrubs, not climbing; sap milky; flowers unisexual (plants monoecious) ..... 75. EUPHORBIACEAE (*Manihot esculenta* Crantz)

○ Blades not lobed:
Stipules amplexicaul, large and conspicuous; sap thick, usually colored ..... 39. MORACEAE (in part)
Stipules not amplexicaul, usually inconspicuous or reduced; sap usually not thick and colored (violet-purple in *Omphalea,* Euphorbiaceae):
Stems usually conspicuously swollen at nodes; flowers naked, closely aggregated in firm, peltate-bracteate pencil-like spikes ..... 36. PIPERACEAE (*Piper*)*
Stems not swollen at nodes; flowers with the perianth usually present, variously arranged but not as above:
Styles 3; stamens usually more than or fewer than perianth lobes; fruits 3-valved, explosively dehiscent capsules (except *Omphalea*) .... 75. EUPHORBIACEAE (in part)
Styles 2 or 1; stamens equal in number to and opposite perianth lobes (perianth lacking in staminate *Myriocarpa,* Urticaceae); fruits indehiscent:
Styles 2; fruits drupes, either green and more than 1 cm long or red at maturity ..... 38. ULMACEAE
Style 1; fruits achenes, green and less than 4 mm long, hidden in bracts ..... 40. URTICACEAE (in part)

■ Blades not palmately veined:
Pistillate inflorescences of numerous flowers congested into dense, capitate, bracteate clusters developing into fleshy aggregate fruits (*Ficus* flowers contained within fleshy receptacles) ..... 39. MORACEAE (in part)
Pistillate inflorescences not as above *or* flowers bisexual:
Pistil with 1 simple style and 1 ovule (2 ovules in *Licania,* Chrysobalanaceae); fruits 1-seeded:
Plants herbs; stamens 8; blades inconspicuously pubescent ..... 49. PHYTOLACCACEAE (*Petiveria alliacea* L.)
Plants shrubs; stamens 3 or 4; blades glabrous above, densely white-arachnoid-pubescent below or with linear cystoliths visible on both surfaces:
Flowers 4-parted, in long slender spikes to 60 cm long; leaves nearly glabrous beneath with conspicuous linear cystoliths radiating from areoles ..... 40. URTICACEAE (*Myriocarpa yzabalensis* (Donn. Sm.) Killip)
Flowers 5-parted, in terminal panicles 10–20 cm long; leaves densely white-arachnoid-pubescent beneath .. 61. CHRYSOBALANACEAE (*Licania hypoleuca* Benth.)
Pistil with 2 or more styles or with 2 or more ovules; fruits various:
Stipules ocreate (encircling stem and forming sheath around stem); styles 3 and mostly free (2 in *Polygonum acuminatum*); stamens 6–9; fruits usually shiny, trigonous or lenticular achenes ..... 46. POLYGONACEAE
Stipules not ocreate; styles or stigmas 1–3, connate or free; stamens 1 to many; fruits not as above:
Stems usually conspicuously swollen at nodes; flowers naked, closely aggregated in firm, peltate-bracteate, pencil-like spikes ..... 36. PIPERACEAE (*Piper*)
Stems not swollen at nodes; flowers with perianth usually present, variously arranged but not as above:
▲ Styles 3, free or connate *or* stigma trifid:
Stamen 1; flowers bisexual, lacking staminodia ..... 37. LACISTEMACEAE
Stamens 2 or more; flowers bisexual or unisexual:
Blades pellucid-punctate; staminodia conspicuous, alternating with stamens; flowers bisexual ..... 96. FLACOURTIACEAE (*Casearia*)
Blades not pellucid-punctate; staminodia lacking; flowers unisexual (monoecious or dioecious) ..... 75. EUPHORBIACEAE (in part)

*Included here because of stipule-like structures.

▲ Styles 1 or 2:
Sap often milky; styles 2 or conspicuously bilobed or style 1 and agglutinated to stamens:
Flowers unisexual; corolla never contorted in bud; styles 2 or conspicuously bilobed; plants trees or shrubs ..... 39. MORACEAE (in part)
Flowers bisexual; corolla contorted in bud; style 1, agglutinated to stamens (except *Ervatamia*); plants lianas (*Ervatamia* a cultivated shrub) ..... 118. APOCYNACEAE (in part)
Sap clear; style 1 and simple:
Blades usually pellucid-punctate or with gland-tipped teeth; fruits drupes or unarmed capsules; seeds 1 or many ..... 96. FLACOURTIACEAE (in part)
Blades not pellucid-punctate, not with glandular teeth; fruits spiny capsules with 1 or 2 seeds *or* fruits drupes:
Fruits drupaceous, fleshy when mature, the outside smooth, never armed; seed 1 ..... 61. CHRYSOBALANACEAE (*Licania hypoleuca* Benth.)
Fruits capsular, hard at maturity (usually woody), the outside spiny; seeds 1 or 2 ..... 83. ELAEOCARPACEAE (*Sloanea*)

◆ Stipules and tendrils lacking:
Perianth lacking; spikes leaf-opposed, solitary, pencil-like; plants mostly epiphytic herbs or shrubs with swollen leaf nodes ..... 36. PIPERACEAE
Perianth present (except *Poinsettia,* Euphorbiaceae); spikes not pencil-like, not leaf-opposed or solitary; plants not epiphytic, usually lacking swollen leaf nodes:
Filaments completely united into a tube; sap in trunk and branches reddish; fruits 2-valved, the seed arillate ..... 56. MYRISTICACEAE
Filaments free or partly free; sap not reddish; fruits and seeds various:
Carpels simple or compound and united; styles 3 (free or connate) or conspicuously bifid or trifid:
Flowers unisexual; pistillate flowers with 1 petal; fruits small red drupes less than 7 mm long ..... 54. MENISPERMACEAE (*Cissampelos*)
Flowers unisexual or bisexual; perianth lobes 2 or more; fruits shiny achenes or explosively dehiscent capsules (rarely fleshy and more than 8 cm broad):
Stamens and perianth lobes 3 or 5, the stamens alternate with lobes; fruits shiny achenes ..... 47. AMARANTHACEAE (in part)
Stamens and perianth lobes unequal or 2, 4, or 8 of each; fruits usually explosively dehiscent capsules, rarely drupes ..... 75. EUPHORBIACEAE (in part)
Carpels free, each with 1 style, *or* carpels simple or compound and united; styles 1, 2, or many:
Gynoecium of 1–6, ± free carpels; plants vines or lianas; blades palmately veined; petals sometimes present but minute; sepals in whorls ..... 54. MENISPERMACEAE (in part)
Gynoecium not of ± free carpels; plants of variable habit; blades variously veined; petals lacking or indistinguishable from sepals; perianth not in whorls:
Perianth parts 6; stamens in 3 series of 3 each, at least the outer series alternating with conspicuous glands; fruits 1-seeded, usually subtended by a conspicuous cupule (accrescent, persistent calyx tube) ..... 58. LAURACEAE
Perianth parts 3–5; stamens not in series, lacking glands; seeds 1 to many, fruits not subtended by cupule:
Plants herbs or vines; flowers bisexual:
Flowers hidden by scarious bracts; style 1 ..... 47. AMARANTHACEAE (in part)
Flowers not hidden by bracts; styles 1, 2, or many .. 49. PHYTOLACCACEAE (in part)
Plants trees or shrubs; flowers bisexual or unisexual:
Stamens many; blades usually glandular-toothed or pellucid-punctate ..... 96. FLACOURTIACEAE (in part)
Stamens 10 or fewer; blades not with gland-tipped teeth or pellucid punctations:
Stamens 4, opposite 4 free sepals; flowers more than 6 mm long, bisexual; juvenile leaves compound ..... 41. PROTEACEAE (*Roupala montana* Aubl.)
Stamens 3–10, not opposite lobes of calyx; plants dioecious, the flowers less than 4 mm long; juvenile leaves simple ..... 56. MYRISTICACEAE

● Perianth differentiated into calyx and corolla:
★ Corolla fused into a tube at least at base, actinomorphic (flowers of *Browallia,* Solanaceae, zygomorphic, and those of Marcgraviaceae appearing zygomorphic owing to nectaries and calyx):
Stamens as many as and alternate with petals *or* stamens fewer than petals; flowers bisexual:
Flowers markedly zygomorphic, with a prominent, external, club-shaped nectary more than 1.5 cm long ..... 90. MARCGRAVIACEAE (*Souroubea sympetala* Gilg.)
Flowers not zygomorphic, lacking prominent external nectaries:
✪ Plants lianas or vines:
Plants armed on stems and blades *or* plants hemiepiphytic .... 124. SOLANACEAE (in part)

Plants unarmed, not hemiepiphytic:
Corolla more than 2 cm long, pleated vertically, usually unlobed ..... 120. CONVOLVULACEAE
Corolla less than 1 cm long, not pleated, usually lobed ca one-third its length ..... 121. BORAGINACEAE (*Tournefortia*)

✪ Plants shrubs, trees, or herbs:
Corolla twisted in bud; sap milky; pistil with carpels free .... 118. APOCYNACEAE (in part)
Corolla not twisted in bud; sap not milky; pistil with the carpels united:
Ovary with many ovules ..... 124. SOLANACEAE (in part)
Ovary with 2 or 4 ovules ..... 121. BORAGINACEAE (in part)

Stamens equal in number to and opposite the corolla lobes *or* stamens more numerous than corolla lobes *or* plants dioecious:
Plants vines, lianas, or scandent hemiepiphytic shrubs:
Flowers with conspicuous nectaries; plants hemiepiphytic shrubs; fruits berries with many seeds ..... 90. MARCGRAVIACEAE (*Marcgravia nepenthoides* Seem.)
Flowers lacking nectaries; plants vines, not hemiepiphytic; fruits drupaceous ..... 54. MENISPERMACEAE (*Cissampelos*)
Plants not scandent:
Plants unbranched trees; leaves with petioles more than 30 cm long; blades more than 20 cm long, palmately lobed ..... 99. CARICACEAE (*Carica*)
Plants normally branched trees or shrubs; leaves with petioles less than 15 cm long; blades usually less than 20 cm long, unlobed (except *Jatropha*):
Flowers with many stamens and a single, simple style; capsules irregularly dehiscent, with bright red seeds .... 91. THEACEAE (*Ternstroemia tepezapote* Schlecht. & Cham.)
Flowers with stamens equal to or double the number of corolla lobes *or* flowers with many stamens and more than 1 style:
Stamens twice as many as corolla lobes, in 2 series ..... 43. OLACACEAE
Stamens as many as corolla lobes *or* stamens many:
Stamens as many as corolla lobes; style 1:
Flowers orange, more than 1 cm diam; blades coriaceous, stiff, with a sharp apiculum ..... 111. THEOPHRASTACEAE (*Jacquinia macrocarpa* Cav.)
Flowers not orange, less than 1 cm diam; blades not stiff, lacking a sharp apiculum:
Blades pellucid-punctate or opaque-punctate or opaque-lineate; sap not milky; corolla deeply lobed to near base; stamens with the free part of filaments evident; plants mostly shrubs ..... 112. MYRSINACEAE
Blades not punctate; sap milky; corolla shallowly lobed; stamens with the anthers sessile and borne at apex; plants mostly large trees more than 10 m tall ..... 113. SAPOTACEAE
More stamens than corolla lobes; styles several:
Blades palmately veined and usually palmately lobed; plants monoecious; corolla 5-lobed; fruits capsules ..... 75. EUPHORBIACEAE (*Jatropha curcas* L.)
Blades pinnately veined and unlobed; plants dioecious or flowers bisexual; corolla 4-lobed or mostly 6-lobed; fruits berries:
Corolla 4-lobed; blades with stellate trichomes; berries white at maturity ..... 88. DILLENIACEAE (*Saurauia laevigata* Tr. & Planch.)
Corolla mostly 6-lobed; blades with simple trichomes; berries not white at maturity ..... 114. EBENACEAE (*Diospyros artanthifolia* Mart.)

★ Corolla of free petals (Papilionoideae sometimes with keel petals united), zygomorphic or actinomorphic:
⊙ Stamens as many as petals:
Plants scandent and unarmed:
Petals large, more than 1 cm long, showy; flowers solitary or paired in axils; tendrils axillary; fruits berries with many seeds ..... 98. PASSIFLORACEAE (in part)
Petals small, less than 5 mm long:
Flowers bisexual, in cymose inflorescences; petals easily visible; tendrils leaf-opposed; fruits with 1 or 2 seeds ..... 82. VITACEAE (in part)
Flowers unisexual, in racemose inflorescences; petals minute, hidden; tendrils lacking; gynoecium of usually 6 free carpels, developing into 6 drupes (or fewer by abortion) ..... 54. MENISPERMACEAE (in part)
Plants not scandent (except *Byttneria,* Sterculiaceae, which is conspicuously armed):
Blades palmately veined at base:
Flowers zygomorphic, 3–4 cm long; stipules small, triangular, persistent, white; stamens appendaged ..... 95. VIOLACEAE (*Hybanthus prunifolius* (Schult.) Schulze)
Flowers actinomorphic, less than 1 cm long; stipules usually caducous:
Blades with prominent glands at base; flowers with a conspicuous disk; plants ± glabrous, with simple pubescence on young parts ..... 81. RHAMNACEAE (*Colubrina glandulosa* Perk.)

Blades eglandular; flowers lacking a disk; plants usually with stellate or branched trichomes ..... 87. STERCULIACEAE (in part)
Blades not palmately veined:
Plants with blades and sepals usually pellucid-punctate ..... 112. MYRSINACEAE
Plants not pellucid-punctate:
Flowers solitary or few, in condensed axillary inflorescences less than 3 cm long:
Petals bright orange, more than 20 mm long; calyx of 5 free sepals; blade margins glandular-crenate ..... 97. TURNERACEAE (*Turnera panamensis* Urban)
Petals cream-colored, less than 5 mm long; calyx weakly lobed; blades entire ..... 77. CELASTRACEAE (*Maytenus schippii* Lund.)
Flowers many, in racemes or panicles more than 5 cm long:
Flowers white, in large terminal panicles more than 20 cm long ..... 76. ANACARDIACEAE (*Mangifera indica* L.)
Flowers lavender, in slender racemes usually less than 20 cm long ..... 61. CHRYSOBALANACEAE (*Hirtella racemosa* Lam.)

⊙ Stamens not equal in number to petals:
Stamens twice as many as petals:
Stamens 10 or 12, ± equal, in 2 series of 5 or 6 each:
Stipules conspicuous; blades with a brownish band of minute trichomes along midrib beneath; petals with ligulate appendage inside; calyx not accrescent in fruit ..... 66. ERYTHROXYLACEAE
Stipules lacking; blades lacking discolored band; petals not appendaged; calyx accrescent, red and showy in fruit ..... 43. OLACACEAE
Stamens 6 or 10, equal or unequal or united, not in 2 series of 5 or 6 each:
Plants large trees or shrubs, in the forest; stamens 10, equal or with 1 or 4 longer and fertile:
Plants large forest trees; stamens unequal; pedicels expanding into fleshy hypocarps in fruit; fruits solitary ..... 76. ANACARDIACEAE (*Anacardium*)
Plants shrubs; stamens equal; pedicels not expanding; fruits of 5 elliptic drupelets ..... 89. OCHNACEAE (*Ouratea lucens* (H.B.K.) Engler)
Plants herbs, scandent shrubs, vines, or lianas (*Dalbergia brownei,* Leguminosae, sometimes an erect shrub, but always occurring along the shore); stamens 6 or 10:
Petals 3; flowers actinomorphic; stamens 6; fruits drupaceous ..... 54. MENISPERMACEAE (except *Cissampelos*)
Petals 5; flowers zygomorphic; stamens 10; fruits legumes with 1–4 seeds ..... 63. LEGUMINOSAE (in part)
Stamens not twice as many as petals:
Stamens conspicuously united in 1 or more clusters:
Plants herbs, vines, lianas, or scandent shrubs; flowers zygomorphic (except staminate flowers of *Cissampelos*); petals 1, 3, or 4; stamens 4 or 8:
Flowers bisexual, zygomorphic, the petals 3; stamens 8, connate most of their length ..... 74. POLYGALACEAE
Flowers unisexual, the pistillate flowers with 1 petal and sepal; stamens 4, the anthers sessile on filament tube ..... 54. MENISPERMACEAE (*Cissampelos*)
Plants shrubs, trees, or suffruticose herbs, not scandent; flowers actinomorphic; petals 4 or 5; stamens 15 to many, variously united into 1 or 5 clusters:
Petals with bifid, ligulate appendage ca 5 mm long (petal ca 4 mm long excluding appendage); blades very unequal at base; fruits nearly globose capsules with short, ± pyramidal tubercles ..... 87. STERCULIACEAE (*Guazuma ulmifolia* Lam.)
Petals lacking apical appendages; blades equilateral or only slightly unequal at base; fruits not as above:
Anthers 2-celled, dehiscent by 2 pores; capsules transversely elliptic (*Apeiba*) or seeds winged (*Luehea*) ..... 84. TILIACEAE (in part)
Anthers 1-celled, dehiscent by 1 pore or slit:
Blades usually toothed (sometimes also lobed); fruits dehiscent capsules or schizocarps separating into mericarps ..... 85. MALVACEAE
Blades not toothed (sometimes lobed); fruits capsules with seeds enveloped in kapok *or* fruits broadly 5-winged, to 15 cm long and 8 cm wide *or* fruits drupaceous ..... 86. BOMBACACEAE (in part)
Stamens apparently free (weakly connate at base in *Vantanea,* Humiriaceae):
Petal 1, more than 3 cm long and wider than long; stamens of 2 sizes ..... 63B. CAESALPINIOIDEAE (*Swartzia simplex* (Sw.) Spreng. var. *ochnacea* (A. DC.) Cowan)
Petals 2 or more:
□ Blades deeply lobed; calyx with 2 outer and 3 inner sepals; fruits capsules with wind-dispersed seeds in a cottony mass ..... 94. COCHLOSPERMACEAE (*Cochlospermum vitifolium* (Willd.) Spreng.)

□ Blades not lobed or shallowly so; flowers and fruits not as above:
Plants lianas ..... 88. DILLENIACEAE (in part)
Plants not scandent, herbs, shrubs, or trees:
Blades palmately veined at base:
Blades very unequal at base, one side cordate and ± overlapping stem .....
..... 83. ELAEOCARPACEAE (*Muntingia calabura* L.)
Blades ± equilateral:
Pedicels with 5 conspicuous glands below the calyx .....
..... 93. BIXACEAE (*Bixa orellana* L.)
Pedicels eglandular:
Calyx tubular:
Calyx barely lobed; style 1, slightly tripartite ..... 85. MALVACEAE (*Hampea appendiculata* (J. D. Sm.) Standl. var. *longicalyx* Fryx.)
Calyx lobed to middle; styles 3, bifid .....75. EUPHORBIACEAE (in part)
Calyx with the sepals free or nearly so:
Sepals 4 or 5; plants usually stellate-pubescent; fruits mostly capsular; ovary with 2 to many cells; placentation axile .....
..... 84. TILIACEAE (in part)
Sepals 3 (except 4 in *Hasseltia*); plants usually lacking stellate pubescence, often pellucid-punctate (except *Lindackeria*); fruits baccate (except *Lindackeria*); ovary with 1 cell; placentation parietal
..... 96. FLACOURTIACEAE (in part)
Blades not palmately veined:
Blades pellucid-punctate; petioles usually winged ..... 67. RUTACEAE (*Citrus*)
Blades not pellucid-punctate; petioles not winged:
Petals 3, 4, 6, or more (5 or 6 in staminate flowers, lacking in pistillate flowers of *Codiaeum,* Euphorbiaceae):
Petals 4, thin; petioles variable in length on the same plant, 1–20 cm long; fruits purple schizocarps .....
..... 59. CAPPARIDACEAE (*Capparis frondosa* Jacq.)
Petals 3, 6, or more, thin or fleshy; petioles ± uniform; fruits monocarpic berries or fleshy aggregates or capsules:
Petals (5)6–13, not fleshy; fruits capsular....75. EUPHORBIACEAE (in part)
Petals 3 or 6, usually fleshy; fruits monocarpic berries or fleshy aggregates; sepals 3, regular ..... 55. ANNONACEAE
Petals 5:
Flowers bright yellow; leaves to 1 m long; fruits capsules .....
..... 89. OCHNACEAE (*Cespedezia macrophylla* Seem.)
Flowers greenish-white or white; fruits drupes:
Stamens to ca 80; drupes ca 3.5 cm long, the endocarps hard, ovoid-ellipsoid, with 5 broad ribs alternating with 5 oblong valves ....
.....65. HUMIRIACEAE (*Vantanea occidentalis* Cuatr.)
Stamens 3–15; fruits not as above ..... 61. CHRYSOBALANACEAE (in part)

36. PIPERACEAE

Small trees, shrubs, or epiphytic or terrestrial herbs, rarely vines, often fleshy, usually with swollen nodes. Leaves alternate; petioles often sheathing the stem, those at flowering nodes also with stipule-like prophylls; blades simple, entire, basifixed or sometimes peltate; venation pinnate or palmate; stipules adnate to petiole when present. Flowers bisexual, in dense, axillary, leaf-opposed, or rarely terminal spikes (compound in *Pothomorphe*); flowers subtended by a peltate bract; perianth lacking; stamens 2–5; anthers 2-celled, dehiscing longitudinally; pistal 1; ovary superior, 1-locular, 2–5-carpellate; placentation basal; ovule 1, orthotropous; styles 1–4; stigma lobes 1–4. Fruits tiny drupes; seed with endosperm.

Distinguished by the slender spikes with the flowers usually so closely congested as to be continuous. In addition, *Piper* may be distinguished by the woody stems with swollen nodes and *Peperomia* by the epiphytic or loosely terrestrial habit and the fleshy stems.

Flowers are apparently protandrous, and the stamens are exserted above the bracts. *Trigona* bees are important pollinators of *Piper* (R. Dressler, pers. comm.). In Costa Rica, *Piper* species are often visited by *Trigona* and *Exomalopsis* bees and by *Strangalia* (Cerambycidae), galerucine, and galemud beetles (Chrysomelidae) (Heithaus, 1973).

The tiny fruits of *Piper* are probably endozoochorous through small birds (Ridley, 1930) and bats (Bonaccorso, 1975; Wilson, 1971; Heithaus, Fleming & Opler, 1975). Seeds of several species of *Piper,* including *P. auritum* and *P. hispidum,* were gathered by the bat *Artibeus jamaicensis* in Mexico (Yazquez-Yanes et al., 1975). Fruits of *Peperomia* are dispersed perhaps in part in the same manner, but some species have very tiny, sticky fruits that are probably dispersed on the beaks and feathers of birds also. *Peperomia macrostachya* is often associated with ant nests and it may be that its seeds are dispersed in part by ants.

Ten to twelve genera with more than 2,000 species;

KEY TO THE TAXA OF PIPERACEAE

Plants moderately small epiphytic herbs; stamens 2; stigma 1 ..... *Peperomia*
Plants shrubs, trees, or herbs (*Pothomorphe*), rooted in soil; stamens 2–5; stigmas 2–4:
  Inflorescences axillary, with several spikes on a common peduncle; plants chiefly herbaceous, in clearings ..... *Pothomorphe peltata* (L.) Miq.
  Inflorescences leaf-opposed, each with a single spike; plants shrubs or trees ..... *Piper*

mostly in the tropics. Although the family is represented in the Old World also, it is espeeially well developed in Latin America.

PEPEROMIA R. & P.

Plants of the genus are distinguished by being epiphytic or weakly terrestrial herbs with usually fleshy stems and leaves. Flowers are sessile and perfect with two stamens. Each flower is subtended by a triangular or rhombic bract, which usually hides the flower and ovary until maturity of the fruit. The minute, one-seeded, drupelike fruits are well exserted from the rachis at maturity; they are sticky and probably epizoochorous.

Peperomia ciliolibractea C. DC., Candollea 1:360, 383. 1923

Stoloniferous herb, epiphytic (or terrestrial where there is considerable debris); stems usually decumbent but soon ascending, thick, rooting profusely at lower nodes; stems, petioles, and peduncles densely puberulent. Leaves deciduous below, crowded toward apex; petioles 2–5(8) cm long; blades oblong-ovate to subobovate, shortly sharp-acuminate, rounded to subcordate or acute at base, 5–14 cm long, 2–7 cm wide, puberulent on both surfaces, especially on veins below, 9–11-pliveined mostly in basal half, drying membranaceous with moderately strong glandular dots below, the margins ciliate. Spikes 10–18 cm long, from upper leaf axils, ca 4 mm wide in fruit; bracts round, reddish, glandular-dotted, sparsely short-ciliate. Fruits subglobose, ca 1 mm diam, the lower two-thirds of each fruit yellowish, the upper part reddish with glandular dots, the apex pointed and oblique; stigma essentially apical. *Croat 6309, 6848.*

Infrequent, in the forest, usually near the ground. Flowering chiefly in the middle of the rainy season (September to October). Fruiting chiefly in the late rainy season and the earliest part of the dry season (October to January).

Known only from Panama, from tropical moist forest around Gatun Lake and in eastern Panamá.

Peperomia cordulata C. DC., J. Bot. 4:137. 1866

Glabrous, pendent, epiphytic herb, to ca 75 cm long; stems and leaves thick and succulent; internodes 2–6 cm long. Leaves peltate within ca 1 cm of the margin; petioles stout, 1–5 cm long; blades broadly ovate to round-ovate, acute to acuminate at apex, rounded at base, 3–11 cm long, 2.5–8.5 cm wide, drying thin but firm, palmately veined, the veins obscure. Spikes 12–19 cm long, on short, bracteate, leaf-opposed branches; peduncles 1–2.5 cm long, the subtending bract lanceolate; floral bracts round. Fruits subglobose, ca 1 mm diam, only slightly exserted; stigma central on an oblique, bluntly tongue-shaped style. *Croat 7770, 8386.*

Infrequent, at the margin of the lake, generally low over the lake surface. Beginning to flower mostly with the onset of the dry season. The fruits develop by the middle to late dry season and the early rainy season.

Commonly associated with *Trigona* bee nests, often on tree stumps in the lake.

Known only from Panama, from tropical moist forest in the Canal Zone (around Madden Lake) and in Colón.

See Fig. 177.

Peperomia ebingeri Yunck., Ann. Missouri Bot. Gard. 53:263. 1966

Creeping epiphyte; stems weak, puberulent. Petioles 1–3 mm long, usually perpendicular to blade; blades ± orbicular, to 11 mm long, usually broader than long, puberulent to glabrous but minutely ciliate, the upper surface dark green, minutely and densely papillate with the few veins lighter green, the lower surface light green, smooth. Spikes less than 1 cm long; peduncles 3–8 mm long;

KEY TO THE SPECIES OF PEPEROMIA

Spikes in large paniculate inflorescences 20–40 cm long; blades elliptic to oblanceolate, 15–27 cm long, 4–10 cm wide ..... *P. mameiana* Schroed.
Spikes solitary or few on a common peduncle; leaves not as above:
  Leaves peltate, broadly ovate to round-ovate ..... *P. cordulata* C. DC.
  Leaves basifixed:
    Leaf blades orbicular or nearly so, all less than 1.5 cm long:
      Veins of leaf lighter in color, clearly visible; plants forming appressed mats usually on tree trunks ..... *P. ebingeri* Yunck.
      Veins of leaf very obscure; plants loosely clinging to trees, usually on small branches ..... *P. rotundifolia* (L.) H.B.K.

Leaf blades seldom if ever orbicular, mostly more than 1.5 cm long:
All leaf blades rounded to emarginate at apex; fruits ellipsoid, tapered to a slender hooked beak at apex ..... *P. obtusifolia* (L.) A. Dietr.
Leaf blades seldom, if ever, rounded at apex:
Blades often subcordate at base; petioles mostly more than 2.5 cm long; plants stoloniferous, stiffly ascending; stems usually short and unbranched:
Blades pinnately veined; stems, petioles, and lower blade surfaces densely puberulent; rachis of inflorescence not densely papillate ..... *P. ciliolibractea* C. DC.
Blades palmately veined; stems, petioles, and lower blade surfaces glabrous or nearly so; rachis of inflorescence densely papillate ..... *P. killipi* Trel.
Blades seldom if ever subcordate at base; petioles less than 2.5 cm long; plants usually sprawling, erect to pendent; stems often long and branched:
Fruits cylindrical, more than 1.5 mm long; style tongue-shaped, flat; leaves mostly more than 4 cm long; plants frequently long-pendent .... *P. macrostachya* (Vahl) A. Dietr.
Fruits subglobose to broadly ovate; style mammilliform (not flattened); leaves generally less than 4 cm long; plants sprawling to erect, never long-pendent:
Plants with prominent dark glandular dots (when dried) on all parts but especially on underside of blade; stems pubescent only along 2 lines below petiole, if at all ..... *P. glabella* (Sw.) A. Dietr.
Plants lacking prominent, dark, glandular punctations; stems densely pubescent all over ..... *P. obscurifolia* C. DC.

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bracts round, thick, usually puberulent on upper surface in apical half. Fruits subglobose, less than 0.5 mm diam; stigma a small brown tuft of trichomes. *Croat 10802, 11456, Ebinger 165* (type).

Fairly common throughout the forest, often on trunks of trees near the ground. Flowering and fruiting during the dry season and the early rainy season, with the fruits occurring chiefly in the early rainy season. Some populations remain sterile during much of the rainy season.

The species is distinguished by its small round leaves, minutely puberulent bracts, and short inflorescences. It is similar to *P. rotundifolia,* but never with such a scandent habit as that species.

Guatemala, Costa Rica, and Panama. In Panama, known only from tropical moist forest on BCI.

Peperomia glabella (Sw.) A. Dietr., Sp. Pl. 1:156. 1831
P. conjungens Trel.; *P. glabella* var. *nervulosa* (C. DC.) Yunck.

Epiphyte, nearly glabrous, weak-stemmed, sprawling or erect, to 25 cm high; punctations obscure or lacking when fresh but prominent red to black on most parts when dry; stems often somewhat reddish, flexuous near apex. Petioles 1–11 mm long, often ciliate, the pubescence usually continuing in 2 lines on stem; blades ovate-elliptic to lanceolate-elliptic, acuminate and often downturned at apex, acute at base, (1.5)2.5–5(8) cm long, (0.5)1–2(3) cm wide, thick, weakly 3-veined. Spikes to 15 cm long, solitary or few at apex of stem or from upper axils; peduncles to 1 cm long when fresh; bracts round; anthers 2, exposed between bract and style. Fruits globose-ovoid, ca 1 mm diam, sticky, covered (except style) with glands, exserted on stalk at maturity, the stalk conical, about as long as fruit; style persistent, oblique, tongue-shaped; stigma subapical. *Croat 5478, 8625.*

Abundant in the forest at most levels. Flowering mostly in the dry season and the earliest part of the rainy season; flowering plants sometimes are seen in the very late rainy season. The fruits develop rapidly, but most mature during the early rainy season. Burger (1971) reported the species to flower and fruit all year in Costa Rica.

About as common as *P. obscurifolia* and confused with that species, but may be distinguished by its nearly glabrous stem and dark punctations when dry. The variety *nervulosa* (C. DC.) Yunck. is not considered distinct because leaf shape and size are quite variable. Burger (1971) reported the species to range from sea level to 2,400 m.

Guatemala to Colombia, Venezuela, the Guianas, and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Colón and Chiriquí.

Peperomia killipi Trel., Bot. Gaz. (Crawfordsville) 73:143. 1922

Erect, short-stemmed epiphyte, 15–30 cm tall (including spikes); stems subrhizomatous, decumbent then ascending, rooting at lower nodes, glabrous. Leaves mostly clustered near apex; petioles 2.5–9 cm long, usually as long as or longer than blade, the stout base persisting on stem; blades broadly ovate and cordate, acute or bluntly acuminate at apex, 3–7 cm long, 1.5–4.5 cm wide, bicolorous when fresh, inconspicuously appressed-pubescent above, glabrous beneath, palmately 7-veined. Spikes often several, from upper axils, extending well above leaves, 5–15 cm long, to ca 2.5 mm wide (1.5 mm dry); peduncles to 7 cm long, glabrous; rachis conspicuously papillate; bracts round, minute. Fruits ovoid, ca 0.5 mm diam, black; stigma subapical on an oblique, bluntly tongue-shaped style. *Croat 12857, Shattuck 596.*

Rare; seen once on Wheeler Trail growing on rotting wood. Flowering and fruiting mostly in the late rainy season (October to December), perhaps to the earliest part of the dry season (January).

The species is similar to *P. pseudo-dependens* C. DC. and *P. lignescens* C. DC. of Costa Rica. See Burger (1971) for a discussion of the differences.

Known only from Panama, from tropical moist forest

Fig. 178. *Peperomia killipi*

Fig. 177. *Peperomia cordulata*

Fig. 179. *Peperomia macrostachya*

in the Canal Zone, Panamá, and Darién and from premontane wet forest in Chiriquí.

See Fig. 178.

Peperomia macrostachya (Vahl) A. Dietr. in L., Sp. Pl. ed. 6, 1:149. 1831

P. caudulilimba C. DC. var. *longependula* C. DC.; *P. gatunensis* C. DC.; *P. caudulilimba* C. DC. var. *cylindribacca* (C. DC.) Yunck.

Epiphytic herb, variable in habit, seldom erect, commonly pendent or creeping vertically or horizontally over larger tree branches, to 1.5 m long; larger plants often associated with ant nests; stems, petioles, and peduncles glabrous to puberulent or villous; stems 4–7 mm diam. Leaves variable; petioles 1–27 mm long (short near apex of stem, longer below); blades ovate to ovate-elliptic or lance-elliptic, gradually or abruptly acuminate to rarely acute at apex (often downturned), obtuse to acute at base, 3.5–15 cm long, 0.8–5.5 cm wide, usually ± succulent (drying papyraceous to moderately thick), the veins 2–5, obscure, from near base, the midrib sunken above, the margin sometimes minutely ciliate. Spikes usually 1–3 at apex of stems, mostly 10–15 cm long in flower, less than 2 mm wide, to 22 cm long in fruit; peduncles 1–2.5 cm long, sometimes violet-purple; bracts round. Fruits subcylindrical, narrowed toward apex, 2–3 mm long (as little as 1.5 mm on drying), usually flesh-colored, covered with numerous, sticky globules; style oblique, tongue-shaped; stigma central on style. *Croat 13805.*

Frequent in the forest, especially the older forest, generally high in trees but below the canopy. Flowering chiefly in the dry season and the early rainy season. The fruits develop rapidly, but most mature in the late dry and early rainy seasons; most fruits are gone by the middle of the rainy season.

No doubt the most variable *Peperomia* on BCI. The habit differences indicate that more than one species is included, but no characters are sufficiently uniform to separate the material. The species is similar to and probably not separable from *P. portobellensis* Beurl., described from Portobelo (Colón Province). Standley (1933) misspelled *P. caudulilimba* as *P. cordulilimba.*

Sometimes associated with *Aechmea tillandsioides* var. *kienastii* (22. Bromeliaceae) on the same ant nest.

Mexico to South America; sea level to 1,800 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in Coclé, and from premontane wet forest in Colón and Chiriquí.

See Fig. 179.

Peperomia mameiana C. DC. ex Schroed., Candollea 3:128. 1926

Rhizomatous, glabrous, epiphytic herb; stems and leaves succulent; stems to 1 cm or more thick when fresh, rooting at nodes; internodes 1–3 cm long. Petioles 5–10 cm long, stout, reddish at least at base; blades elliptic, lanceolate-elliptic to oblanceolate, acute to bluntly acuminate at apex, gradually tapered at base, 15–27 cm long, 4–10 cm wide, the veins on each side 5–7, pinnate, the midrib stout below, the margin weakly revolute. Inflorescences terminal or axillary, 20–40 cm long, paniculate, the major axes of the inflorescences and peduncles reddish; peduncles 0.6–5 cm long; spikes 6–15 cm long, ca 3 mm thick, white at anthesis; bracts round; stigma centrally disposed on style. Fruits ellipsoid, ca 1 mm long. *Croat 9015, Kenoyer 303.*

Apparently rare on BCI; usually occurring on rocks or trees near the ground. Flowers chiefly from the middle to late rainy season (August to December). The fruits apparently develop soon after flowering.

Costa Rica and Panama; at elevations less than 800 m. In Panama, known from tropical moist forest in the Canal Zone (vicinity of Gatun Lake), Bocas del Toro, and eastern Panamá. Collected from tropical wet forest on the Osa Peninsula of Costa Rica.

See Fig. 180.

Peperomia obscurifolia C. DC., Candollea 1:357. 1923

P. baileyae Trel.; *P. chrysleri* Yunck.

Epiphyte; stems creeping or erect, to ca 25 cm high, flexuous near apex; internodes sometimes reddish; stems, petioles, peduncles, and sometimes midribs of lower surfaces sparsely to densely pubescent with straight, usually appressed trichomes. Petioles 1–10 mm long; blades elliptic to lance-elliptic, acute or rarely acuminate at apex, acute to cuneate at base, 1–5.5 (6.5) cm long, 0.6–2.5 cm wide, bicolorous, the veins 3–5, the basal 1 cm coalesced with midrib on larger leaves. Spikes 5–16 cm long, ca 2 mm thick; peduncles 1.5–2.5 cm long; bracts round, ca 0.8 mm wide. Fruits globose, sticky, ca 0.5 mm diam, brown, exserted at maturity; style oblique, tongue-shaped, as broad as fruit body; stigma punctiform on center of style. *Croat 9792, 10178.*

Abundant in the forest, most frequently on lower vegetation or on large rocks. Flowers chiefly in the late dry season and the early rainy season. The fruits develop quickly. Both flowering and fruiting spikes may be present on the same plant.

Similar to *P. glabella,* but differing by having pubescence throughout on the stems and by lacking black punctations when dry (obscure but light punctations may appear). Leaf blades are extremely variable. Some blades are so thick as to be lenticular in cross section, while others on the same plant, usually higher on the stem, are thin. Some plants of the species lack the very thick leaves.

Known only from central Panama, from tropical moist forest in the Canal Zone, from premontane moist forest in Colón and Coclé, and from premontane wet forest in Coclé.

See Fig. 181.

Peperomia obtusifolia (L.) A. Dietr. in L., Sp. Pl. ed. 6, 1:154. 1831

Fleshy, stoloniferous herb, epiphytic or terrestrial, nearly glabrous; stems thick, decumbent-ascending, to 15 cm or more high, rooting at lower nodes. Petioles 0.5–4 cm long;

Fig. 180. *Peperomia mameiana*

Fig. 182. *Peperomia obtusifolia*

Fig. 181. *Peperomia obscurifolia*

blades ± obovate, obtuse to emarginate (usually rounded) at apex, cuneate at base, 4–12 cm long, 2.5–6 cm wide, thick, sometimes weakly pubescent on lower surface, pliveined mostly below middle, the veins obscure. Spikes densely flowered, solitary or paired on a 1-bracted, terminal, leaf-opposed, or axillary stalk, 5–15 cm long, to 5 cm wide in fruit; peduncles and stalks weakly puberulent, together 3–5 cm long; floral bracts round. Fruits ellipsoid, ca 1 mm long, tapered at apex into a slender, terminally hooked beak; stigma on upper side at base of beak. *Croat 6610.*

Rare, in the forest. On the basis of the few observations and herbarium collections of the species, it appears that flowering and fruiting occur in the middle to late rainy season, perhaps extending into the early dry season.

When terrestrial, the plant is usually rooted in soil composed of a considerable amount of debris.

Throughout tropical regions of the Western Hemisphere; tropical Africa and Madagascar; usually between sea level and 1,200 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá and from tropical wet forest in Coclé.

See Fig. 182.

Peperomia rotundifolia (L.) H.B.K., Nov. Gen. & Sp. 1:65. 1816

Poleo

Small, creeping, epiphytic herb; stems scarcely 1 mm wide, glabrous or pubescent. Petioles to 5 mm long, basal, usually perpendicular to blade; blades orbicular, to 12 mm diam, fleshy, bicolorous, often sparsely crisp-pubescent above. Spikes to 2 cm long, little more than 1 mm wide, often on short lateral branches; peduncles short; bracts round-peltate, glabrous. Fruits globose-ovoid, less than 1 mm long; stigma subapical. *Croat 9446.*

Common in the forest, usually creeping or pendent from slender branches and within 6 m of the ground. Flowering chiefly in the dry season and the early rainy season, though it has been seen in flower in the middle of the rainy season; perhaps less seasonal than most *Peperomia.*

The species is apparently closely related to *P. ebingeri.* See that species for discussion.

Throughout the tropics of the Western Hemisphere; from sea level to 2,200 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién and from premontane wet forest in Colón and Chiriquí.

PIPER L.

(Gusanillo, Hinojo, Cordoncillo, Barbasco, Canotillo)

The genus is distinguished by its swollen nodes and leaf-opposed, cylindrical spikes with minute, usually sessile, perfect flowers. Each flower has two to five stamens (usually four) and is subtended by a round to triangular, usually ciliolate, peltate bract; styles are present or absent, the stigmas two, three, or four. Fruits are minute (usually 1–3 mm long), one-seeded, and drupelike; they are usually exserted from the bracts at maturity.

A noteworthy feature of the genus is the development of a modified prophyll in those leaf axils that form an inflorescence. Nodes that do not form inflorescences protect the new growth by a sheathing leaf base. The prophyll may be confused with a stipule (Burger, 1972).

Piper aequale Vahl, Eclog. Amer. 1:4, pl. 3. 1796

Glabrous shrub, 1–3 m tall; branches widely spreading. Petioles 5–25 mm long (shortest on ovate leaves); blades lanceolate-ovate to ovate, gradually to abruptly long-acuminate, subinequilaterally obtuse to rounded at base, 10–27 cm long, 4.5–9 cm wide, the major lateral veins usually 4 or 5 pairs, chiefly in basal half; prophylls prominent, slender and pointed. Spikes erect in flower and fruit, 8–10 cm long, 2–4 mm wide in fruit; peduncles equaling or slightly shorter than petiole; bracts inconspicuously fringed. Fruits green, glabrous, bluntly 3-sided, papillate, the small round stigmatic area weakly depressed; stigmas 3, undifferentiated. *Croat 12213.*

Very common in the forest. Juvenile inflorescences appear with new leaf formation during the middle to late rainy season, with the flowers occurring chiefly during the dry season and in the earliest part of the next rainy season. The fruits begin to develop in the rainy season; most fruits mature in the middle to late rainy season and are still present when the new spikes begin appearing.

The species normally has gradually long-acuminate leaves that are broadest well below the middle of the blade. It is in this condition that the leaves of the species differ from the otherwise similar leaves of *P. darienense* and *P. perlasense,* which also have lateral veins extending into the upper three-fourths of the blade. Some specimens differ, however, in having ovate-elliptic leaves that are broadest at about the middle and have shorter petioles and peduncles. Though they are included here with *P. aequale,* these collections (*Croat 8719, 10096, 16577*) may prove to represent another species. Standley (1933)

KEY TO THE SPECIES OF PIPER

Leaves palmately veined or parallel-veined from the lowermost 5 mm:
- Plant a twining vine ..... *P. aristolochiifolium* (Trel.) Yunck.
- Plants shrubs or trees:
  - Shrubs or trees to 8 m tall in the forest; leaves usually more than 15 cm wide, the margins glabrous; fruits papillate, with a prominent, glabrous, apical disk ..... *P. reticulatum* L.
  - Shrubs to 2 m in clearings; leaves usually less than 15 cm wide, without prominent punctations, the margins pubescent; fruits lacking any evident apical disk .... *P. marginatum* Jacq.

Leaves pinnately veined:
Major lateral veins arising along at least three-fourths of blade:
Leaf bases strongly unequal, one side usually 5–15 mm shorter ..... *P. arboreum* Aubl.
Leaf bases ± equal or sometimes oblique with one side only slightly shorter (to 5 mm):
Petioles strongly vaginate-winged to blade; leaves bronzed beneath when dry, bicolorous fresh; veins prominently loop-connected ..... *P. cordulatum* C. DC.
Petioles usually not vaginate-winged (weakly so in *P. grande* and *P. arieianum*); leaves usually greenish beneath:
Bracts cupulate, glabrous; fruits free on rachis, exserted, very short-styled; plants usually less than 1 m tall; leaves without glandular dots ..... *P. darienense* C. DC.
Bracts ± peltate; fruits congested on rachis; plants usually more than 1 m tall:
Blades mostly more than 8 cm wide, ± glabrous beneath except for narrow band between margin and collecting vein ..... *P. grande* Vahl
Blades mostly less than 6 cm wide:
Leaves glandular-dotted on underside ..... *P. arieianum* C. DC.
Leaves not obviously glandular-dotted ..... *P. perlasense* Yunck.
Most lateral veins arising in basal half of blade (to basal two-thirds):
Leaves mostly 20–25 cm long or more, 10–20 cm wide or more:
Leaves scabrous ..... *P. peracuminatum* C. DC.
Leaves not scabrous:
Leaf margins densely ciliolate, drying thin ..... *P. auritum* H.B.K.
Leaf margins glabrous or essentially so:
Young twigs, nodes, and/or petioles and midribs below ± fleshy-warty (particularly younger petioles) ..... *P. imperiale* (Miq.) C. DC.
Stems glabrous, not fleshy-warty:
Leaves minutely puberulent on all major veins, gray when dry; fruits short-papillate; bracts glabrous ..... *P. carrilloanum* C. DC.
Leaves either glabrate or with sparse loose pubescence (particularly between margin and collecting vein); fruits not papillate; bracts ciliate with a prominent papilla ..... *P. grande* Vahl
Leaves mostly less than 20 cm long and 10 cm wide or, if larger, not lobed at base:
Leaves at least somewhat scabrous or markedly asperous above:
Pubescence of stems conspicuously long, the trichomes of smaller stems often longer than the width of the stem on which they are borne; plants usually less than 1.5 m tall, uncommon, apparently restricted to ravines in the forest:
Leaves dark glandular-dotted, smooth to only slightly scabrous; petioles to ca 5 mm long ..... *P. pseudo-garagaranum* Trel.
Leaves not glandular-dotted, markedly scabrous above; petioles to 5 mm long at apex of plant, grading to 2.5 cm long nearer base ..... *P. viridicaule* Trel.
Pubescence of stems not conspicuously long, the trichomes of smaller stems not longer than the width of the stem on which they are borne; plants common in the forest or occurring in clearings only (those in forest more than 2 m tall):
Upper blade surface not markedly asperous; trichomes of lower veins ± appressed-ascending; plants found in clearings, usually 1.5–2 m tall ... *P. dilatatum* L. C. Rich.
Upper blade surface markedly asperous; trichomes of lower veins erect, at least not appressed-ascending:
Lower blade surface with prominent reddish-brown glandular dots (visible when fresh or dried); intervenous areas with many long trichomes; plants found in clearings, usually less than 2 m tall ..... *P. villiramulum* C. DC.
Lower blade surface without prominent glandular dots (sometimes obscure black dots visible when dried); intervenous areas glabrous or with very few small trichomes (elsewhere in Panama with longer trichomes in intervenous areas); blades drying dark gray; plants found in the forest, usually 3–6 m tall ..... *P. hispidum* Sw.
Leaves not noticeably scabrous:
Spikes short, usually less than 2 cm long and 5 mm wide at anthesis, to 3 cm long in fruit; stems and petioles hirsute; plants usually about 1.5 m or less tall ..... *P. pubistipulum* C. DC.
Spikes 6 cm long or longer at anthesis; otherwise not as above:
• Stems glabrous; leaves nearly glabrous:
Leaves totally glabrous below ..... *P. aequale* Vahl
Leaves either puberulent on veins below or with short sparse trichomes between margin and collecting vein:
Leaves puberulent beneath on major veins below, gray when dried; fruits short-papillate; floral bracts minute, lacking a dome-shaped apex, glabrous ..... *P. carrilloanum* C. DC.

Leaves mostly glabrous below except for band of coarse short trichomes between margin and collecting vein; fruits not papillate; bracts large, dome-shaped, ciliate ..... *P. grande* Vahl

- Stems and leaves pubescent:
  Leaves (especially older ones) smooth and ± glabrous above ..... *P. culebranum* Schroed.
  Leaves pubescent above, at least on midrib:
    Upper leaf surface glabrate or with shorter scabrous trichomes over surface, the longer pubescence restricted to veins ..... *P. dilatatum* L. C. Rich.
    Upper leaf surface sparsely long-villous and glabrescent, the pubescence not restricted as above ..... *P. pseudo-garagaranum* Trel.

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treated *P. aequale* as *P. frostii* Trel., a name that was never published.

Honduras to northern South America; West Indies; sea level to 2,000 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Colón, Coclé, and Darién.

See Fig. 183.

Piper arboreum Aubl., Hist. Pl. Guiane Fr. 1:23. 1775
P. subnudispicum Trel.

Glabrous shrub, 2–7 m. Petioles 2–20 mm long, those at branching nodes vaginate-winged almost to blade; blades lanceolate-elliptic, gradually acuminate to short-acuminate, acute to subcordate and markedly unequal at base (one side 5–15 mm shorter), 14–26 cm long, 3.5–10 (12) cm wide, very dark green and shiny above, duller beneath, veined throughout, the veins all prominent, with 7–10 pairs of major lateral veins. Spikes erect when juvenile, usually pendent in fruit, 5–14 cm long in fruit, and to 5 mm diam; peduncles 5–17 mm long; bracts sharply triangular (appearing round in bud), densely ciliate marginally, often more conspicuously so on upper margin. Fruits compressed laterally and much longer in the direction of the rachis, truncate but depressed at the style, sparsely puberulent to papillate-puberulent; stigmas 3, short, deltoid, persistent. *Croat 6685, 12605.*

Infrequent, in the forest. Probably flowers mostly in the dry season and the early rainy season, with most fruits maturing in the early rainy season. Burger (1971) reported the species to flower and fruit from November to May in Costa Rica.

Distinguished by having the leaves veined throughout and inequilateral at base. BCI specimens show no sign of the verrucose-warty stems reported by Yuncker (1950).

Guatemala to northern South America; West Indies; sea level to 1,500 m. In Panama, known from tropical moist forest in the Canal Zone, Darién, and Panamá, but more common from premontane wet forest in Panamá and Chiriquí, from tropical wet forest in Colón, and from premontane rain forest in Chiriquí.

Piper arieianum C. DC., Anales Inst. Fís.-Geogr. Nac. Costa Rica 9:166. 1897
P. acutissimum Trel.
Cordoncillo

Glabrous shrub, usually 1–1.5 m tall. Petioles 5–10 mm long near apex of plant, to 3.3 cm long below; blades lanceolate-elliptic, sharply and narrowly acuminate at apex, mostly subequilaterally acute at base, somewhat decurrent, 10–19 cm long, 2.5–6 cm wide, the major lateral veins 6–10 pairs, extending to apex, often weakly loop-connected, glabrous or sparsely pubescent beneath, drying with glandular dots. Spikes 3–9 cm long; peduncles very slender, 7–20 mm long, glabrate to puberulent; bracts peltate, triangular, sparsely short-ciliate. Fruits bluntly trigonous, ± granular-papillate, truncate and concave at apex; stigmas 3, short, strap-shaped, often persisting in fruit. *Croat 14574.*

Occasional, apparently preferring moist areas of gulleys. Seasonal behavior uncertain. Inflorescences develop during the late rainy season and flower mostly in the dry season. The fruits probably mature in the early rainy season.

Shorter plants may be confused with *P. darienense,* but have longer petioles and short-ciliolate bracts. The species is perhaps most easily confused with *P. perlasense,* but that species lacks the dark glandular dots and has leaf blades more prominently inequilateral with one side obtuse or rounded. It may also be confused with *P. cordulatum* but differs in having prominent reticulate veins on fresh leaves and glandular dots on dried leaves.

Nicaragua to Colombia; Trinidad; usually less than 500 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Herrera, Panamá, and Darién and from premontane wet forest in Panamá (Chimán).

Piper aristolochiifolium (Trel.) Yunck., Ann. Missouri Bot. Gard. 37:18. 1950

Twining vine; stems and petioles densely and inconspicuously short-puberulent; internodes elongate, to 15 cm or more long. Petioles 3.5–4.5 cm long, invaginate; blades ovate-cordate, abruptly acuminate, 9–17 cm long, 6–13 cm wide, drying dark, ± glabrous above, glabrous to sparsely puberulent on veins below, the veins 5–7, palmate, the reticulate veins prominulous. Inflorescences unknown. *Croat 12929, 13245a.*

Apparently rare in the forest, though surely more common than it would appear; it has been collected only in the forest in the vicinity of the Laboratory Clearing.

The collections are sterile but closely match the type, which was also sterile. The plant was described as a shrub by Yuncker in the *Flora of Panama,* but the BCI plants are clearly vinelike.

Known only from the Canal Zone (BCI and the Frijoles type collection).

Fig. 183. *Piper aequale*

Fig. 184. *Piper auritum*

Piper auritum H.B.K., Nov. Gen. & Sp. 1:54. 1816
Cowfoot, Cordoncillo, Santa María

Tree, 2.5–8 m tall, the trunk to ca 10 cm diam; wood soft; cut parts sweetly aromatic; stems ± glabrous. Petioles 4–12 cm long, conspicuously winged-vaginate much of their length; blades ± ovate, acute to short-acuminate at apex, cordate at base with very unequal lobes and one side 1–2 cm shorter on petiole, mostly 20–40 cm long, 12–27 cm wide, pinnately veined above the sinus, sparsely short-pubescent above, especially on veins, densely so below, densely white-ciliolate. Spikes stout, 10–27 cm long, to 8 mm or more thick in fruit; peduncles 2–8 cm long; bracts ± round and densely ciliate with long white trichomes. Fruits small, obpyramidal-trigonous; stigmas 3, sessile. *Croat 6976.*

Uncommon; occurring sporadically, usually at the edge of clearings. Apparently not markedly seasonal in flowering behavior, but perhaps with more flowering activity in the rainy season. Plants tend to have more fruiting spikes in the dry season.

Mexico to Colombia; West Indies; sea level to 1,200 m. In Panama, known from tropical moist forest all along the Atlantic slope and in the Canal Zone, Chiriquí, Panamá, and Darién; known also from tropical dry forest in Coclé, from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

See Fig. 184.

Piper carrilloanum C. DC., Bull. Soc. Roy. Bot. Belgique sér. 2, 30(1):209. 1891
P. paulowniifolium C. DC.

Shrub, 2–4 m tall; glabrous but with the veins of lower leaf surface puberulent. Petioles usually 2–5(21) cm long, winged-vaginate about halfway on some larger leaves; blades subequilaterally ovate, abruptly acuminate at apex, rounded at base, the lower ones subcordate, becoming cordate on larger lowermost leaves, usually 14–21 cm long, 6–12 cm wide (to 38 cm long and 30 cm wide on largest leaves), the pairs of major lateral veins usually 4–6 (more on large cordate leaves), chiefly in lower half, often pinkish on fresh leaves, the blade drying more or less grayish. Spikes 6–20 (25) cm long, 2–4 mm thick, scarcely thicker in fruit than in flower; peduncles 5–20 mm long; bracts small, ± triangular, glabrous. Fruits short-papillate; stigmas 3, sessile, recurved. *Croat 6319.*

Abundant in the forest. Flowering spikes are present during the late rainy season and throughout most of the dry season. The fruits mature in the late dry season and throughout the rainy season (to December).

May be confused with *P. grande,* but distinguishable by the dense, short puberulence on all the veins; *P. grande* is glabrous except along the margin of the blade.

Hladik and Hladik (1969) reported that fruits of this species are eaten by the tamarin (*Sanguinus geoffroyi*) during January and February. Probably only juvenile fruits or flowers were eaten, since the fruits do not mature until later than this.

Nicaragua to Colombia and Ecuador; sea level to 1,500 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Colón and Chiriquí.

See Fig. 185.

Piper cordulatum C. DC., J. Bot. 4:217. 1866

Glabrous shrub, usually less than 2 m tall. Petioles 1–2 cm long, prominently vaginate-winged throughout; blades moderately thick, lanceolate or lanceolate-oblong, sharply acuminate, rounded to acute at base (one side often slightly shorter), 10–22 cm long, 3–6.5 cm wide, markedly bicolorous especially when fresh, the lower surface pale green becoming brown on drying, the veins obscure above, only moderately prominent below, forming collecting vein. Spikes apiculate, green, to 8.5 cm long and 6 mm wide and pendent in fruit; peduncles nearly 1 cm long in fruit; bracts triangular and cupulate beneath. Fruits ovoid, glabrous, the apex depressed at center; stigmas 3(4), short, strap-shaped. *Croat 7307, 11537.*

Abundant in the forest. Though both flowering and fruiting plants may be found throughout the year, young inflorescences generally begin to appear near the middle of the rainy season (chiefly in September and October). The first flowering inflorescences appear in the latter part of the rainy season and in the early dry season, as early as November but chiefly from December to February. The fruits develop as early as March, chiefly from May to August, with some persisting until late in the rainy season.

Easily distinguished by its narrow, bicolorous leaves and sparsely fruited, pendent spikes. The fruits are so large that there are fewer than ten around the circumference of the spike.

Known only from Panama, from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Panamá (Cerro Azul).

Piper culebranum C. DC. ex Schroed., Candollea 3:136. 1926

Shrub or small tree, usually 1.5–4 m tall; stems sometimes warty with lenticels; all parts except upper surface of older leaves sparsely to moderately villous (at least when young), the trichomes long, mostly erect and straight (crisp and crinkled when dry). Petioles 4–22 mm long; blades elliptic to elliptic-oblanceolate or elliptic-obovate, abruptly long-acuminate, unequal at base, one side 1–5 mm shorter and acute to obtuse, the longer side obtuse to subcordate, the blades 12–20 cm long, 4.5–8(9.5) cm wide, the upper side smooth, sparsely villous when young, becoming smooth, glabrate, and often ± rugulose in age (drying gray-green), the lower surface villous throughout but especially on the veins, the major lateral veins usually in 4 or 5 pairs arising mostly in basal half of blade. Spikes 7–9.5 cm long, pendent when juvenile, erect at anthesis, ca 3 mm thick at maturity; peduncles 8–15 mm long; bracts very densely fringed, obscuring apex and overlapping in flower, the cilia longer than width of bract proper. Fruits subcylindrical, truncate, ± depressed medially, glabrous; styles

Fig. 185. *Piper carrilloanum*

Fig. 186. *Piper culebranum*

usually 3, short and thick, deciduous. *Croat 5179, 7733.*

Occasional, in the forest, apparently preferring ravines, most commonly a tree 3–3.5 m tall. Flowers in the dry season and the early rainy season. The fruits begin to mature by the late dry season, but are dispersed chiefly in the rainy season. Plants may go for a considerable portion of the rainy season in totally sterile condition, putting on the first juvenile spikes as early as September.

Because of similar height and leaves of the same size and shape, *P. culebranum* may be easily confused with *P. hispidum,* which has short scabrous pubescence and leaves with glandular dots. In contrast, *P. culebranum* has long-villous pubescence (crisp-villous when dry), inflorescence bracts with long, dense cilia, and no glandular dots on the leaves.

Piper culebranum was treated as a synonym of *P. colonense* C. DC. by Burger (1971) in *Flora Costaricensis.* He believes, however, that he may have overclumped (pers. comm.) and that *P. culebranum* should be separate from *P. colonense.*

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Panamá (Cerro Jefe).

See Fig. 186.

Piper darienense C. DC. in DC., Prodr. 16(1):374. 1869

P. laxispicum Trel.

Duerme boca

Shrub, mostly less than 60 cm tall (occasionally to 120 cm), glabrous, mostly unbranched and leafless in basal one-half to three-fourths. Petioles usually less than 6 mm long (to 13 mm); blades mostly oblong to lanceolate-elliptic, long-acuminate, subequilaterally acute to rounded at base, 10–19 cm long, 2–7 cm wide, the lateral veins in 6–9 pairs, loop-connected, extending to the apex. Spikes 1.5–5 cm long, white at anthesis, irregular, to 8 mm thick in fruit; peduncles ca 5 mm long; stamens 4 per flower; pistil conical, much longer than stamens; stigmas 3 or 4; bracts cupulate, glabrous, usually partly enclosing the lowermost anther of each flower, much smaller than fruits. Fruits mostly exserted, rounded, to 3 mm long including style, weakly papillate-puberulent, weakly ribbed, becoming tetragonous on drying; seeds brown, with 4 ribs. *Croat 6550, 8582.*

Common in the forest. Flowers chiefly in the dry season and the earliest part of the rainy season. The fruits mature mostly in the middle to late rainy season, by the time the next season's spikes are beginning to develop.

Leaf shape is similar to that of *P. aequale,* and the blade is especially similar to that of *P. perlasense.*

Nicaragua to northern Colombia; usually sea level to 200 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Panamá, and Darién.

Piper dilatatum L. C. Rich., Actes Soc. Hist. Nat. Paris 1:105. 1792

P. leptocladum C. DC.; *P. diazanum* Trel.

Shrub, to 3 m tall, usually 1.5–2 m; upper internodes short, sparsely crisp-pubescent. Petioles villous, 5–10 mm long; blades subrhombic-elliptic or subovate, gradually acuminate, often unequal and obtuse to subcordate at base, mostly 10–19 cm long, 3.5–7 cm wide, usually drying thin, puberulent to scabrous above (trichomes longer on veins), often glabrate or the trichomes restricted to veins in age, crisp or appressed-villous below, especially on veins, the glandular dots obscure when fresh, inconspicuous when dry, the lateral veins in 4 or 5 pairs, arising in basal half of blade; prophylls lunate. Spikes whitish in flower, 6–9 cm long in fruit, ca 3 mm wide; bracts densely white-ciliate, contiguous. Fruits brown or black, obpyramidal, 3-sided and truncate at apex with sparse white pubescence; styles usually 3, slender, short, deciduous. *Croat 12263.*

Occasional in clearings, open areas in the forest, and exposed areas on the lakeshore, particularly abundant in the Laboratory Clearing. Lacking strong seasonal flowering behavior, it can be seen with flowers or fruits most of the year. A flush of flowering occurs with the beginning of the dry season; flowering then continues through most of the rainy season. Most fruits mature at the end of the rainy season and in the early dry season.

This species was mistaken for *P. pseudo-cativalense* Trel. by Standley in his *Flora of Barro Colorado Island.* It may be confused with both *P. hispidum* and *P. culebranum,* but can be distinguished by having short and appressed trichomes on the lower leaf surface, a leaf scar, and a lunate prophyll. The other species are usually much taller and are restricted to the forest.

Mexico throughout continental tropical America; Lesser Antilles and Trinidad; sea level to 200 m. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, and Panamá, from tropical dry forest in Coclé, and from tropical wet forest in Colón.

Piper grande Vahl, Eclog. Amer. 2:3, pl. 11. 1798

P. pseudo-variabile Trel.

Shrub or small tree, 1.5–5 m tall, nearly glabrous. Petioles 1–3(7) cm long and winged-vaginate on larger leaves; blades ovate, somewhat inequilateral, abruptly acuminate, acute or subacute at base of upper leaves, obtuse to subcordate or occasionally cordate at base of the larger lower leaves, 16–31 cm long, 8–23 cm wide, glabrous or with scattered trichomes on the veins but usually with a narrow band of coarse trichomes between margin and collecting vein, the major lateral veins usually in 4–6 pairs, mostly in the basal half. Spikes to 16 cm long, 4–6 mm wide; peduncles 5–10 mm long; bracts large, round, with a prominent dome-shaped apex, the margin densely and obscurely short-ciliate (may be hidden), the stalk of the bract villous. Fruits cushion-shaped, very bluntly trigonous, borne on a slender, ± flattened stalk at maturity, obscured by bracts until maturity; styles 3, moderately long, slender, their thick bases persisting. *Croat 4591, 6501.*

One of the most abundant species of *Piper* on the island, usually in the forest. Though spikes in various stages of development may be present throughout most of the year, most flowering occurs during the dry season when plants may have only flowering spikes; some

flowering continues through most or all of the rainy season. The fruits mature chiefly during the rainy season, mostly from June to December, but some plants still have fruits until just before flowering resumes in January.

Easily confused with *P. carrilloanum,* but that species is densely puberulent on the veins. Yuncker (1950) was perhaps referring to the persistent style bases when he called the stigmas sessile.

Nicaragua to northern South America; usually less than 800 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Colón, Veraguas, Coclé, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Colón, Chiriquí, Coclé, and Panamá.

Piper hispidum Sw., Prodr. Veg. Ind. Occ. 15. 1788

Shrub, usually 3–6 m tall; stems inconspicuously hispid or glabrate in age basally, the trichomes moderately short, rigid, mostly directed outward or ascending, often more dense about the nodes, of varying lengths. Petioles usually 3–8 mm long; blades mostly elliptic to elliptic-ovate, acuminate, obliquely inequilateral, one side 2–5 mm shorter at base and mostly acute, the longer side usually obtuse to rounded at base, the blades mostly 8–20 cm long, 3.5–9 cm wide, drying very dark, pustular-scabrous above with longer stiff trichomes on veins, the lower surface usually with obscure glandular dots and with long straight trichomes mostly restricted to veins (remaining straight on drying), the intervenous areas glabrous or with shorter, less conspicuous trichomes (elsewhere in Panama with many long trichomes), the major lateral veins in 4–6 pairs, mostly in basal half. Spikes mucronate, mostly 9–12 cm long in fruit, ca 3 cm wide; peduncles usually 10 mm long; bracts triangular to round, sparsely short-ciliolate, the cilia shorter than width of bract. Fruits glandular-dotted, obovoid, ± truncate and usually puberulent at apex; stigmas 3, minute, sessile. *Croat 10191.*

Occasional, in the forest. Flowering mostly in the dry season and the early rainy season. Fruiting in the rainy season. Plants are usually completely sterile during the late rainy season.

The species is confused with *P. dilatatum* and *P. culebranum,* which are pubescent and have leaves of similar shape. Yuncker (1950) recognized two varieties of the species on BCI in addition to the typical variety. The variety *trachyderma* (Trel.) Yunck. differs in having the short stout trichomes on the upper internodes curved upward and more or less appressed. Considering the extreme variability in species of *Piper,* the character is hardly worthy of recognition.

Range is uncertain, owing to the confusion in the taxonomy of this complex taxon. The species is described from the West Indies and probably occurs throughout the tropics of the Western Hemisphere. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from premontane wet forest in Chiriquí and Coclé, and from lower montane wet forest in Chiriquí. Burger (1971) reported the species to be absent below 500 m elevation on the Pacific slope in Costa Rica.

See Fig. 187.

Piper imperiale (Miq.) C. DC. in DC., Prodr. 16(1):339. 1869

Shrub or small tree, 2–5 m tall; upper internodes stout, with warty excrescences especially on nodes, these extending onto petiole and midrib. Petioles usually 4–8 cm long, vaginate nearly to blade; blades broadly ovate-cordate, acute or short-acuminate, unequal[1v] lobed at base, mostly 30–50 cm long, 20–29 cm wide, glabrate or minutely puberulent above, glabrate to appressed-puberulent below, short-crisp-villous along veins. Spikes 30–50 cm long or more, to 1 cm thick; peduncles 4–6 cm long or more; bracts ± triangular, the apex prominently raised, densely ciliate, the cilia long, irregular, often denser on apical side; stamens 4, conspicuous. Fruits obovoid to oblong, glabrous; styles 3, slender, soon deciduous, the stout, raised, stylar base persisting in fruit. *Croat 12195.*

Apparently rare, known only from the stream north of the Laboratory Clearing, probably occurring in ravines elsewhere. Spikes have been seen beginning to develop in the middle of the rainy season, flowering usually in the late rainy season or the early dry season. The fruits probably require several months to develop; mature fruits have been collected in other areas in March and June.

Easily distinguished by its cordate leaves and the warty excrescences on the stems and petioles.

Costa Rica and Panama; sea level to 2,000 m, but usually 1,000–2,000 m. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Coclé, and from tropical wet forest in Colón, Panamá, and Darién.

Piper marginatum Jacq., Icon. Pl. Rar. 2:2, pl. 215. 1786

P. san-joseanum C. DC.

Shrub or small tree, usually ca 2(3) m tall, ± glabrous; branches often black when dry. Petioles to 6 cm long, vaginate-winged to blade; blades thin, round-ovate, sharply acuminate, usually cordate at base, 8–20 cm long, glabrous except at margin, drying with pellucid dots, the veins 9–13, palmate. Spikes usually 10–16 cm long, 2–4 mm thick in fruit; peduncles ca 1 cm long; bracts rounded, densely ciliate with long white trichomes (± contiguous in spiral arrangements). Fruits obpyramidal, smooth, depressed-truncate at apex; stigmas 3, linear, deciduous. *Croat 4582, 6908.*

Occasional, in clearings. Showing little seasonal flowering behavior, which is no doubt beneficial to its weedy, invading nature. Most flowering commences sometime after the first rains (usually in July) and continues into the earliest part of the dry season, occasionally to the end of the dry season. The fruits develop quickly, most maturing in the late rainy and early dry seasons.

Cut parts are strongly and pleasantly aromatic.

Guatemala to Ecuador and Brazil; West Indies; usually sea level to 1,200 m. In Panama, known from tropical moist forest all along the Pacific slope and on the Atlantic slope in the Canal Zone and San Blas, from tropical dry forest in Herrera, Coclé, and Panamá, from premontane moist forest in the Canal Zone and Veraguas, from pre-

Fig. 187. *Piper hispidum*

Fig. 188. *Piper marginatum*

montane wet forest in Colón, Veraguas, Los Santos, Coclé, and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 188.

Piper peracuminatum C. DC., Smithsonian Misc. Collect. 71(6):9. 1920

Shrub or small tree, 2–3 m tall; stems with hirsute trichomes of varying lengths; stems and lower leaf surface with stiff, erect trichomes of different lengths as well as longer flexuous trichomes. Petioles usually 5–10 mm long, vaginate-winged; blades elliptic-obovate, abruptly acuminate, cordate at base, inequilateral (the longer side 2–4 mm shorter at petiole and covering petiole), 16–27 cm long, 8–14 cm wide, scabrous above, the major lateral veins usually in 6 or 7 pairs, mostly in basal half. Spikes 10–13 cm long, ca 5 mm wide; peduncles about 2 cm long; bracts with short, stiff cilia. Fruits oblong; stigmas 3, recurved.

Rare or no longer present on the island. The species was reported by Standley, but no specimens were cited nor have any specimens been located. No plant resembling this species has been seen recently on BCI, though the species does occur in the isthmus on the Atlantic slope and could be on BCI. Seasonal behavior uncertain; fertile plants have been seen in March in other parts of Panama.

Costa Rica and Panama on the lowland Caribbean coastal plain. In Panama, known only from tropical moist forest in the Canal Zone (around Gatun Lake) and in Colón.

Piper perlasense Yunck., Ann. Missouri Bot. Gard. 37:67. 1950

Glabrous shrub, 2–3 m tall; branches slender, usually widely branched. Petioles 4–10 mm long (usually ca 5 mm); blades mostly lanceolate, gradually long-acuminate, somewhat falcate, subequilateral at base, one side slightly shorter and acute, the longer side obtuse to rounded, the blades 6–16 cm long, 2–4.7 cm wide, the major lateral veins in 6–8 pairs, to all but perhaps apical fourth of blade, strongly ascending. Spikes erect, 5–8 cm long, 2–3 mm wide in fruit; peduncles ca 5 mm long; bracts rhombic or rounded, fringed. Fruits glabrous, obtusely 3-sided, slightly beaked; stigma single, round, sessile. *Croat 8069, Tyson 4203.*

Occasional, in the forest. Flowering mostly in the dry and early rainy seasons. The fruits mature in the rainy season, mostly from June to September.

Leaves are similar in shape to *P. aequale,* but may be distinguished by having the major lateral veins extending into at least three-fourths of the blade. The leaves of this species resemble those of *P. darienense,* but that species is distinguished by having cupulate, glabrous floral bracts.

Known only from Panama, from tropical moist forest in the Canal Zone and Panamá (San Jose Island).

Piper pseudo-garagaranum Trel., Contr. U.S. Natl. Herb. 26:28. 1927

Shrub, 1–2 m tall; flowering internodes short and slender, villous, the trichomes appearing jointed or multicellular, directed outward, the stem glabrate downward. Petioles usually 2–4 mm long; blades thin, lanceolate-elliptic, gradually very long-acuminate, inequilateral at base, one side 2–4 mm shorter and obtuse, the longer side rounded to subcordate, the blades 9–15 cm long, 3–5 cm wide, sparsely long-villous on both sides, particularly on veins beneath, the trichomes occasionally more than 4 mm long, both surfaces but especially the lower with obscure to prominent reddish glandular dots, the major lateral veins in the basal half in 4 pairs. Spikes to 7.5 cm long at maturity; peduncles less than 1 cm long, with red glandular dots. Fruits 3-sided, truncate at apex, red-glandular; stigma sessile, unlobed or obscurely 2–3-lobed. *Croat 10829, Standley 41164.*

Apparently rare; it has been collected in Creek #7 on Shannon Trail. Seasonal behavior is uncertain.

Distinguished by its narrow, long-pointed leaves with long, villous trichomes and glandular dots. Similar to and possibly not distinct from *P. viridicaule.*

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

Piper pubistipulum C. DC., Smithsonian Misc. Collect. 71(6):5. 1920

P. pubistipulum C. DC. var. *estylosum* Trel.

Shrub, 1–1.5 m tall; internodes short; stems and petioles densely, retrorsely hirsute, often matted with debris. Petioles 3–12 mm long, deeply vaginate at base; blades oblong-lanceolate to narrowly ovate (drying firm, grayish), gradually acuminate, narrowed and inequilateral at base (one side 2–4 mm shorter), 10–20 cm long, 3.5–7 cm wide, dark green and glabrous above (except sometimes at base of midrib), duller and hirsute below especially on the raised veins, the lateral veins in lower half usually 4 pairs, the intercostals prominent and raised. Spikes very small in flower, mucronate, to 3 cm long and 6 mm wide at maturity; peduncles 5–9 mm long, hirsute; bracts cupulate, triangular. Fruits 4-angled, irregularly ridged; styles 2, prominent, deciduous. *Croat 8502.*

Rare; found in ravines and low areas in the forest. Flowering chiefly in the dry season and the early rainy season. Fruiting from the early to middle rainy season. Juvenile spikes may begin to develop before the previous year's fruits have shed.

Fruiting inflorescences are sometimes quite irregular, owing to unequal development of fruits. The species is easily recognized by its short stature, its dingy, densely pubescent stem, and its short spikes.

Known only from central Panama, from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Panamá (Cerro Campana).

See Fig. 189.

Piper reticulatum L., Sp. Pl. 29. 1753

P. smilacifolium H.B.K.

Canotillo

Shrub or tree, to 8 m tall, ± glabrous. Petioles mostly 1–2 cm long, channeled above; blades ovate-elliptic to broadly ovate, abruptly acuminate and usually downturned at apex with arched midrib, subequilateral and

Fig. 189. *Piper pubistipulum*

Fig. 190. *Piper reticulatum*

acute to rounded or truncate below (rarely cordate except often so on juveniles), 10–32 cm long, 5–27 cm wide (juvenile blades to 36 cm long and 32 cm wide), the lower surface often sparsely puberulent, the veins 5–9, palmate, prominently raised. Spikes erect, as little as 4 cm long at anthesis, ca 2–2.5 mm wide, to 16 cm long in fruit and 4–6 mm thick; peduncles slender, 1–2 cm long; bracts small, their stalk and margin bearded. Fruits obovoid, papillate, with a broad, smooth apical disk; styles 3 or 4, short and thick. *Croat 14651.*

Occasional, in the forest. Flowering mostly from the middle of the dry season into the rainy season. The fruits develop throughout the rainy season, perhaps chiefly in the early rainy season, particularly in June and July.

Because of its peltate venation it could be confused with *P. marginatum,* a species with smaller, thinner, more cordate leaves occurring in clearings and at the margins of the forest. The species is distinguished from all others on BCI by the prominent apical disk on its fruit. Standley listed this taxon as *P. smilacifolium* C. DC., which is not a valid name.

Nicaragua to northern South America; West Indies; sea level to 700 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Panamá, and Darién.

See Fig. 190.

Piper villiramulum C. DC., Smithsonian Misc. Collect. 71(6):11. 1920

Shrub, 2–3 m tall; stems villous (crisp-villous when dry), glandular-pubescent and sometimes gland-dotted. Petioles 5–10 mm long; blades ovate-elliptic, sharply long-acuminate, unequal at base with one side 1–6 mm shorter and acute to obtuse (the longer side rounded to subcordate), 8–17 cm long, 3–7 cm wide, densely scabrous above, interspersed with longer straight trichomes, the surface rugulose in age, densely villous below, prominently dotted with reddish-brown glands, the major lateral veins chiefly in basal half, in 5 or 6 pairs. Spikes to 9 cm long and 4 mm diam; peduncles 5–10 mm long; bracts small, round, densely ciliolate with short white trichomes especially on upper edge. Fruits dark brown, obovoid, ± flattened and puberulent with white glands at apex; stigma small, sessile. *Croat 9400, 12812.*

Uncommon, in clearings. Flowering and fruiting to some extent throughout the year. Flowering is initiated mostly in the late rainy season, with the fruits maturing mostly in the dry and early rainy seasons.

Distinguished by the scabrous leaves, often rugose in age, bearing prominent, brown, glandular dots.

Nicaragua to Panama; sea level to 1,000 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Panamá, and Darién, from tropical dry forest in Los Santos, from premontane wet forest in Colón, and from tropical wet forest in Colón, Panamá, and Darién.

Piper viridicaule Trel., Contr. U.S. Natl. Herb. 26:32. 1927

Slender shrub, usually 1–1.5(2) m tall; stems slender; plants pubescent, the stems, petioles, and midrib below with conspicuous trichomes to ca 2 mm or more long and appearing jointed. Petioles short near apex of plant, 4–5 mm long, grading to 2.5 cm long near base; blades lanceolate-elliptic to ovate-elliptic, sharply long-acuminate, moderately to prominently inequilateral and rounded to subcordate at base, 9–12 cm long, 3–7 cm wide, thin, lacking glandular dots, with long slender trichomes on the lower surface and with both long slender and scabrous trichomes on upper surface, the major lateral veins in 3–5 pairs, in basal half of blade. Spikes unknown. *Croat 11282.*

Rare, occurring in steep ravines along Shannon Trail in the same habitat as *P. pseudo-garagaranum.* Seasonal behavior not determined.

The species is very similar to *P. pseudo-garagaranum,* and additional material may prove them inseparable. However, *P. viridicaule* differs in its longer petioles, its lack of glandular dots, and its prominently scabrous upper blade surface.

Known only from BCI.

POTHOMORPHE Miq.

Pothomorphe peltata (L.) Miq., Comm. Phyt. 37. 1840
Piper peltatum L.
Santa María, Hinojo

Herb, usually to 1.5 m tall, glabrous except for sparse to dense short white trichomes on veins of blade, especially below. Petioles 9–22 cm long, the sheaths prominent; blades peltate ca one-third from base, suborbicular, short-acuminate, cordate at base, to 28 cm diam, whitish below with minute, dense, glandular dots, the major veins usually 9–15, palmate. Spikes several on an axillary stalk to 10 cm long; peduncles to 15 mm long; bracts triangular to round, prominently white-ciliate. Fruits small, obpyramidal, sharply 3-sided, truncate; stigmas 3. *Croat 4051.*

Abundant locally in the Laboratory Clearing and occasionally growing along trails. An exceedingly weedy plant showing little seasonal variation in flowering.

Throughout the tropics of the world. In Panama, usually below 1,000 m; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from tropical wet forest in Colón, and from premontane rain forest in Chiriquí (Boquete), Colón, and Coclé (El Valle).

37. LACISTEMACEAE

Shrubs or trees. Leaves alternate, petiolate; blades simple, entire or serrate; venation pinnate; stipules present, caducous. Flowers bisexual, apetalous, ± zygomorphic, in axillary, bracteate spikes or racemes; perianth 4-lobed, the lobes subequal; disk present, prominent, hypogynous; stamen 1; anther 2-celled; thecae separated by a forked connective, dehiscing longitudinally; ovary superior, 1-locular, 3-carpellate; placentation parietal; ovules 1 or 2 per placenta, anatropous; styles 3 or stigma trifid. Fruit a 3-valved, loculicidal capsule (berrylike at first); seeds 3 or by abortion 1, arillate, with endosperm.

Lacistemaceae are trees or shrubs distinguished by

KEY TO THE SPECIES OF LACISTEMACEAE

Inflorescences less than 3 cm long; capsules more than 5 mm diam; axils of lower lateral veins not tufted ..... *Lacistema aggregatum* (Berg) Rusby

Inflorescences more than 4 cm long; capsules less than 4 mm diam; axils of lower lateral veins usually conspicuously tufted (axils glabrous elsewhere) .... *Lozania pittieri* (S. F. Blake) L. B. Smith

their reduced flowers bearing a single stamen and by their small, fleshy, capsular fruits with arillate seeds. The family will be treated by H. Sleumer (pers. comm.) as Flacourtiaceae in his revision of that family.

Flowers are minute and clustered, each with a single anther. Pollination system is unknown.

The fruits display arillate seeds, and though dispersed principally by birds, they are also taken by monkeys (Oppenheimer, 1968).

Two genera and about 27 species; tropical America.

LACISTEMA Sw.

Lacistema aggregatum (Berg) Rusby, Bull. New York Bot. Gard. 4:447. 1907

Tree, usually 6–20 m tall, glabrate or with sparse puberulence on young stems and underside of leaf. Petioles 5–10(20) mm long; blades lanceolate, oblong-elliptic or oblanceolate-acuminate, acute to rounded at base, 10–16 cm long, 4.5–7 cm wide, entire or remotely crenate, the veins drying wrinkled, usually barbate in the axils of lateral veins on the lower surface, often pubescent all along midrib at least when young; stipules to 1 cm long, caducous. Flowers greenish, sessile, in narrow, cylindrical, bracteated spikes, the spikes 1–3 cm long, 4–12 per axil; bracts cupulate, broader than long, one subtending each flower; perianth segments 4, ca 0.5 mm long, unequal, erose; ovary and stamen centrally situated on a broad fleshy disk, the disk subtended by free bracteoles (usually 3) exceeding width of disk; stamen solitary, ca 2 mm long, exceeding pistil, the connective bifurcate; styles 3, short. Capsules ovoid, ca 1 cm long, red, short-stalked, splitting ± irregularly into 2 or 3 valves; seed 1, ca 7 mm long, surrounded by a fleshy, bitter, white aril. *Croat 5691, 8402.*

Common in the forest, especially in the young forest. Flowers in the dry and early rainy seasons, from January to May (rarely to July), usually in the latter half of the dry season. The fruits mature from April to June (sometimes August).

The inner wall of one of the valves of the capsule becomes free and folds along the median. After being forced out, the seed is suspended on a slender white fiber from near the apex of the inner wall. Though the seeds are no doubt principally dispersed by birds, Oppenheimer (1968) reported that white-faced monkeys eat the white aril associated with the seed.

Mexico to Colombia, Venezuela, the Guianas, and Peru; Trinidad, Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Los Santos, Herrera, and Darién, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón (Guásimo). Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Figs. 191 and 192.

LOZANIA Mutis ex Cald.

Lozania pittieri (S. F. Blake) L. B. Smith, Phytologia 1(3):138. 1935

L. pedicellata (Standl.) L. B. Smith

Shrub or small tree, to 8 m tall; stems and twigs brittle; younger stems, petioles, and axes of inflorescences strigose. Petioles 3–8 mm long; blades elliptic to obovate-elliptic, acuminate, acute at base, 8–14 cm long, 2.5–4.5 cm wide, entire to obscurely toothed, glabrous above, the veins below weakly strigose and often pilose as well, especially in axils of lateral veins; stipules 1.5–2 mm long, caducous, the scar at most half-encircling stem. Flowers green, ca 1.5 mm diam, in solitary, axillary racemes to 9 cm long; axis and bracts pubescent; bracts minute; pedicels ca 1.5 mm long; perianth oblique, 4-lobed, the lobes ± rounded, concave, the uppermost at first erect and ± enclosing the pistil, later spreading to expose the pistil, the others ± spreading, subtending the fleshy reniform disk; stamen 1, to 1 mm long, at first held near the upper perianth lobe with the anthers unopened, the filament later elongating, spreading away from the pistil, the anthers opening; anthers longitudinally dehiscent, broader than long, the thecae distinct, directed upward; ovary minute, pubescent; styles 3, recurved (appearing as 3 hooks). Capsules globose, ca 4 mm diam, sparsely puberulent; seeds 3, minute, with a red aril. *Foster 2364.*

Apparently rare, but at least locally common. Collected by R. Foster on Balboa Trail 10 (*Foster 2364*) and by O. Shattuck at Gross Point (*Shattuck 972*). Flowering on BCI mostly in July and August. The fruits mature in August and September (mostly in August). Rarely flowering elsewhere in Panama in March, with the fruits maturing in April. Allen (1956) reported the species to flower in December on the Osa Peninsula in Costa Rica.

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

38. ULMACEAE

Trees and shrubs, sometimes scandent and armed. Leaves alternate, petiolate; blades simple, generally serrate, palmately veined at base; stipules present, caducous. Flowers

Fig. 191. *Lacistema aggregatum*

Fig. 192. *Lacistema aggregatum*

Fig. 193. *Trema micrantha*

KEY TO THE SPECIES OF ULMACEAE

Plants lianas or climbing shrubs, the stems armed ..... *Celtis iguanaeus* (Jacq.) Sarg.
Plants unarmed trees:
Leaf blades ± glabrous except for midrib, not cordate at base; fruits more than 1 cm long .....
..... *Celtis schippii* Standl.
Leaf blades pubescent, asperous especially above, cordate at base; fruits less than 5 mm long ...
..... *Trema micrantha* (L.) Blume

unisexual or bisexual (monoecious or polygamomonoecious), apetalous, sometimes obscurely zygomorphic, solitary or in axillary cymes; sepals 5, basally connate; stamens 5, free, opposite the sepals; anthers 2-celled, dehiscing longitudinally; ovary superior, 1-locular, 2-carpellate; placentation apical; ovule 1, anatropous, pendulous; styles 2, basally fused (in *Celtis,* the stigmas bifurcate). Fruits drupes; seed lacking endosperm.

Members of the family resemble both the Moraceae (39), from which they differ by lacking milky or viscid sap and by having usually inequilateral leaf bases, and the Urticaceae (40), from which they differ by having a two-carpellate ovary and two styles. Some Urticaceae also have unequal leaf bases.

Pollination system unknown. Wind pollination is common in the order Urticales (Faegri & van der Pijl, 1966).

Fruits are probably all animal dispersed. *Trema micrantha* has small red fruits and is probably bird dispersed. Van der Pijl (1968) reported that the seeds of *Celtis iguanaeus* are eaten by iguanas.

Sixteen genera and about 300 species; widely distributed.

CELTIS L.

Celtis iguanaeus (Jacq.) Sarg., Silv. North Amer. 7:64. 1895
Hackberry, Cagalara

Andromonoecious (with staminate and bisexual flowers on the same plant) liana or climbing shrub, 10–25 m long, the trunk usually less than 10 cm diam, at least the smaller branches armed with recurved spines. Petioles 5–10 mm long; blades ± ovate, acute to acuminate at apex, obtuse to subcordate, 3-veined, and sometimes inequilateral at base, 3–11 cm long, 1.5–4.5 cm wide, sparsely pubescent to glabrous, serrate, the veins on underside prominently raised. Inflorescences cymose, axillary, the smaller branches and often pedicels and calyces minutely puberulent; flowers usually 5-parted, pedicellate, 1.5–2 mm long, green or greenish-yellow; sepals ± oblong, the margins scarious, ± ciliate; petals lacking; staminate flowers with a rudimentary pistil ca 1.5 mm long, the stamens opposite the sepals, the filaments at first curved inward, ca 1.7 mm long, the anthers attached apically near the base of the pistillode, becoming free, the filament then straightening rapidly to fling pollen from the anthers; pollen powdery; bisexual flowers similar to staminate flowers, the ovary 1-locular. Drupes ovoid, ca 1 cm long, ± 2-edged, yellow, orange, or red. *Croat 14649.*

Occasional, in the forest, climbing high into the canopy. Flowers in the early rainy season. The fruits mature in the middle to late rainy season.

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

Celtis schippii Trel. ex Standl., Field Mus. Nat. Hist., Bot. Ser. 12:409. 1936

Tree to 30 m tall, to 60 cm dbh, often buttressed 1.5 m; bark thin, planar, unfissured or with minute cracks; inner bark thick, with brown streaks; sparsely short-pubescent on young stems and leaves, ± glabrous in age except for midrib above and below. Petioles 5–9 mm long; blades ovate-elliptic to elliptic or ovate, acuminate, obtuse and slightly inequilateral at base, ± decurrent onto petiole, 6–14 cm long and 3.5–7 cm wide (to 24 cm long and 10 cm wide on juveniles), 3-veined at base, the larger lateral veins with inconspicuous cavelike domatia in axils beneath (especially the apical axils) with 2–4 pairs of major laterals above the basal pair. Flowers axillary, solitary; pedicels to 7 mm long in fruit; sepals 5, suborbicular, to 1 mm long, persistent, ciliate. Drupes narrowly ovoid, with a pungent odor, green at maturity, to 1.8 cm long, glabrous; pericarp leathery, ca 1 mm thick; seed with a brown testa, ca 1 cm long. *Croat 16212.*

Rare; known from a few individuals in the old forest. Flowering unknown. Fruits in July; elsewhere in Central America mature-sized fruits have been seen in March and September.

Belize, Costa Rica, and Panama. In Panama, known only from tropical moist forest on BCI.

TREMA Lour.

Trema micrantha (L.) Blume, Mus. Bot. Lugduno-Batavum 2:58. 1856
T. integerrima (Beurl.) Standl.
Capulín macho, Capulín, Jordancillo

Monoecious tree, 2–20 m tall, the trunk to ca 16 cm dbh; bark light brown, thin, prominently lenticellate; inner bark moderately thick, tan; pubescent all over with erect trichomes, the branchlets becoming glabrate; sap ± pungent, somewhat foul-smelling. Petioles 5–10(18) mm long; blades narrowly lanceolate, long-acuminate, cordate and often inequilateral at base, 5–15 cm long, 1.5–5 cm wide, asperous especially above, serrate to subentire; stipules lanceolate, minute. Cymes axillary, to 1.5 cm long; flowers minute, 5-parted, green, greenish-yellow, or whitish; sepals to 1.3 mm long, minutely pubescent

outside; petals lacking; anthers of the staminate flowers contained within the boat-shaped tepal in bud, the tension of the elongating filament released when the anther slips from the sepal and springs upward, the thecae directed upward; pollen white, powdery; pistillode columnar; pistillate flowers similar to staminate flowers, the ovary globose, with 2 bifid styles, the stylar bases persisting in fruit. Fruits ovoid or subglobose, 3–4 mm long, red. *Croat 6242.*

Occasional at the edges of clearings, rare in the forest. Flowers and fruits principally in the rainy season.

Superficially similar to *Pouzolzia obliqua* (40. Urticaceae), which has four-parted flowers and an achene with a single long style.

In Ecuador and some other areas, *Trema integerrima* (Beurl.) Standl. is recognized as a distinct species, being a larger tree occurring in forests rather than in disturbed areas. The differences on BCI seem insignificant, though two collections, *Aviles 58a* and *Hayden 4,* have the short erect pubescence and the entire thin leaves attributed to *T. integerrima.* Both are considered here to be only forms of *T. micrantha.*

Widely distributed in the tropics and subtropics of the Western Hemisphere. In Panama, ecologically variable and widespread in cutover areas; known from tropical moist forest throughout Panama, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, Coclé, and Panamá, from tropical wet forest in Colón and Veraguas, and from premontane rain and lower montane wet forests in Chiriquí.

See Fig. 193.

39. MORACEAE

Trees, shrubs, or herbs (*Dorstenia*), sometimes buttressed, often epiphytic or hemiepiphytic (ultimately free-standing in usually strangling *Ficus*); sap viscid, usually milky, brown, black, or merely turbid; stems sometimes hollow. Leaves alternate, usually basifixed (peltate in *Cecropia*); blades usually simple and pinnately veined (deeply palmately lobed or divided and palmately veined in *Cecropia* and *Pourouma,*), entire to serrate; stipules present, usually conspicuous and ensheathing bud, leaving a scar encircling the stem. Flowers unisexual (dioecious or monoecious), actinomorphic, in cymes, spathaceous catkins, or hollow receptacles; perianth obsolete, tubular or (2)4(5)-lobed; stamens 1, 2, or 4 (numerous in *Castilla*), free; anthers 2-celled, versatile, dehiscing longitudinally (circumscissile in *Brosimum*); ovary 1, superior to inferior, 1-locular, 1- or 2-carpellate; stigmas usually 2 (1 in *Ficus, Coussapoa,* and *Cecropia*); ovule 1, anatropous and pendulous from near the apex of the locule or campylotropous (basal and erect in *Cecropia, Coussapoa,* and *Pourouma*). Fruits diverse, basically drupes or achenes (1-seeded drupes in *Trophis, Pourouma, Sorocea,* and *Maquira*; false drupes in *Brosimum,* consisting of a single pistillate flower surrounded by a receptacle and all old staminate flowers; fleshy syncarps in *Artocarpus, Castilla, Poulsenia,* and *Coussapoa*; achenes closely aggregated into fleshy, catkinlike structures in *Cecropia* or encased in the receptacle, completely in *Ficus,* partially in *Dorstenia*).

Members of the family are most easily distinguished by the latex, by the paired stipules often forming a cap over the bud and leaving a cylindrical scar, and by the unisexual flowers, the pistillate ones having only two styles.

Most species of Moraceae, including *Brosimum, Coussapoa, Poulsenia,* and *Cecropia,* have numerous aggregated flowers with exserted anthers ideally suited to pollen-feeding insects. *Olmedia* and *Trophis* are possibly wind pollinated. In both cases, stamens are spring-loaded. When the stamens are released from the tepals, the pollen is catapulted from the anthers. Also possibly wind pollinated are *Cecropia, Artocarpus, Brosimum, Castilla, Coussapoa, Pourouma, Poulsenia,* and *Maquira.* Bawa and Opler (1975) reported that *Cecropia* offers no nectar, which further indicates that it may be wind pollinated. *Ficus* pollination is treated at length in the genus discussion.

The seeds of all species of Moraceae are animal dispersed. Most species, especially *Cecropia* (Leck, 1972), *Coussapoa, Olmedia* (Chapman, 1931), *Maquira, Sorocea,* and *Trophis,* are dispersed by birds. All species, however, are also dispersed by other animals, particularly arboreal frugivores. *Olmedia aspera, Maquira costaricana,* all *Cecropia,* and nearly all *Ficus* species were reported to be taken by white-faced monkeys (Oppenheimer, 1968). Most species of *Cecropia* and *Ficus* and *Brosimum alicastrum* (Hladik & Hladik, 1969) are also taken by spider and howler monkeys. *Cecropia longipes* and *Olmedia aspera* are taken by tamarins (Hladik & Hladik, 1969). *Cecropia peltata* is eaten by coatis (Kaufmann, 1962). *Ficus* is an important part of the diet of bats. In addition to *Piper* (36. Piperaceae) and *Cecropia,* bats depend heavily on *Ficus* for food (E. Tyson, pers. comm.). Of the 23 species of plants found in bat detritus of *Artibeus jamaicensis* Leach in Mexico (Yazquez-Yanes et al., 1975), 28 percent were Moraceae, including seeds of *Pseudolmedia, Cecropia obtusifolia, Ficus insipida, F. obtusifolia, Poulsenia armata,* and *Brosimum alicastrum.* Bonaccorso (1975) also reported *Brosimum* and *Poulsenia* to be dispersed by bats. Fruits of *Cecropia peltata* are also bat dispersed (Goodwin & Greenhall, 1961). R. Foster (pers. comm.) believes bats are the principal dispersing agent for *Cecropia* and green-fruited figs. *Cecropia obtusifolia* was the most well-represented plant species in studies of bat detritus samples made in Mexico (Yazquez-Yanes et al., 1975).

Birds may take small colored figs. Since most species of *Ficus* must germinate high in the canopy of the forest and develop as true epiphytes, fruits that fall to the ground and are further dispersed by forest floor inhabitants are wasted. Enders (1935) reported that oppossums, squirrels, spiny rats, and collared peccaries eat figs.

Despite their close association with *Cecropia,* ants of

KEY TO THE TAXA OF MORACEAE

Plants herbs; inflorescences cup-shaped ..... *Dorstenia contrajerva* L.
Plants trees or shrubs; inflorescences various:
  Flowers borne on the inner surface of a ± globose, hollow receptacle, its apex a small opening closed by scales; stems solid; stipules fully amplexicaul, usually conspicuous ..... *Ficus*
  Flowers not borne on inner surface of a ± closed receptacle; stems often hollow; stipules fully amplexicaul or lateral:
    Leaves conspicuously lobed:
      Leaves pinnately lobed; sap white ..... *Artocarpus altilis* (Park.) Fosb.
      Leaves palmately lobed; sap brown or black:
        Flowers in spikes; leaves peltate ..... *Cecropia*
        Flowers in cymes; leaves basifixed ..... *Pourouma guianensis* Aubl.
    Leaves not lobed:
      Plants armed; staminate flowers in dense globose heads 1–2.3 cm diam; pistillate flowers more than 5 mm long, 5–9 in ovoid heads ..... *Poulsenia armata* (Miq.) Standl.
      Plants unarmed; flowers various:
        Flowers in spikes or racemes:
          Staminate spikes densely flowered; pistillate flowers and fruits sessile; leaves asperous ..... *Trophis racemosa* (L.) Urban
          Staminate spikes loosely flowered; pistillate flowers and fruits pedicellate; leaves smooth ..... *Sorocea affinis* Hemsl.
        Flowers solitary or in globose or discoid heads:
          Leaves ovate, spirally arranged; petioles more than 3 cm long; staminate inflorescences dichotomously branched 2–4 times with several ± globose heads ca 5 mm diam:
            Leaves usually cordate at base, the major lateral veins in 6–8 pairs above base; pistillate inflorescences (heads) 2–4-lobed ..... *Coussapoa magnifolia* Trec.
            Leaves usually obtuse to truncate at base, the major lateral veins in 10–20 pairs above base; pistillate inflorescences (heads) not lobed ..... *Coussapoa panamensis* Pitt.
          Leaves not ovate, distichous; petioles less than 2 cm long; staminate inflorescences not compound:
            Inflorescences bisexual, globular, ca 5–10 mm diam with many staminate flowers and 1 or 2 pistillate flowers at center of cluster ..... *Brosimum alicastrum* Sw. subsp. *bolivarense* (Pitt.) C. C. Berg
            Inflorescences unisexual:
              Staminate inflorescences fan-shaped; pistillate flowers in discoid heads; perianth lacking; fruits syncarps (all carpels united); blades strongly cordate, dentate ..... *Castilla elastica* Sessé
              Staminate inflorescences not fan-shaped; pistillate flowers solitary or in discoid heads; perianth distinct; fruits solitary or the carpels ± free; blades cuneate to narrowly rounded at base, mostly entire (undulate-serrate in *Perebea*):
                Pistillate flowers dense in discoid heads:
                  Leaves and stems glabrous or the stems inconspicuously puberulent; blades entire; fruiting heads to 5 cm diam; fruits to 2 cm long ..... *Maquira costaricana* (Standl.) C. C. Berg
                  Leaves (at least on midrib) and stems conspicuously hispidulous; blades undulate-serrate toward apex; fruiting heads ca 2 cm diam; fruits less than 1 cm long ..... *Perebea xanthochyma* Karst.
                Pistillate flowers solitary, small, bracteate at base:
                  Leaves asperous; staminate flowers with a distinct perianth and 4 stamens; ovary superior; leaves remotely undulate-serrate at apex ..... *Olmedia aspera* R. & P.
                  Leaves smooth; staminate flowers with vestigial perianth, the heads unorganized; ovary inferior to semi-inferior; leaves entire ..... *Pseudolmedia spuria* (Sw.) Griseb.

the genus *Azteca* do not function in pollination of flowers or dispersal of seeds (Wheeler, 1910). These ants are beneficial to the plant, however, in warding off predators such as leaf-cutter ants (*Atta*) (Janzen, 1969).

Reportedly 53 (Willis, 1966) to 73 (Lawrence, 1964) genera and 1,000–1,500 species. The family is worldwide in distribution, principally in tropical or subtropical areas with comparatively few species in temperate areas.

ARTOCARPUS Forst. & Forst.f.

Artocarpus altilis (Park.) Fosb., J. Wash. Acad. Sci. 31:95. 1941.

A. communis Forst. & Forst.f.

Breadfruit

Monoecious tree, usually less than 12(20) m tall; trunk lenticellate; outer bark thin; inner bark thick, granular, with copious milky sap; wood yellowish. Petioles stout, (2)4–7 cm long; blades ovate in outline, deeply pinnately lobed, acuminate at apices of lobes, the blades acute at base, 30–80(100) cm long, 15–40(65) cm wide, thick and leathery, scabrous, usually pubescent below and on veins above; stipules fully amplexicaul, to 15 cm long, conspicuously appressed-pubescent, deciduous. Peduncles stout, 5–8 cm long; staminate spikes club-shaped, 20–40 cm long, ca 3 cm diam at apex, narrower at base, the staminate flowers dense; perianth 2- or 4-lobed, ca 3 mm long; stamen solitary; anther exserted, oblong, bilobed. Pistillate flowers in globular or oblong spikes; perianth tubular, embedded in the fleshy rachis; style exserted; stigmas entire, 2- or 3-lobed; fruiting pedicels to 7.5 cm long, 1.5–2 cm wide. Syncarp ellipsoid or rounded, 10–30 cm long, green and soft at maturity, the surface asperous with numerous round or isodiametrical segments or echinate; seeds many. *Croat 10121.*

Cultivated in the Laboratory Clearing. Flowers in the late dry season. The fruits mature in the middle to late rainy season.

Native to the South Pacific islands; cultivated throughout the tropics of the world and in various places in Panama.

BROSIMUM Sw.

Brosimum alicastrum Sw. subsp. **bolivarense** (Pitt.) C. C. Berg, Acta Bot. Neerl. 19:326. 1970.

B. bernadetteae Woods.; *Helicostylis latifolia* Pitt.

Berba

Monoecious tree, 3–35 m tall; bark thin, with prominent leaf scars and irregular horizontal raised lines; inner bark smooth, thick, tan; sap forming milky droplets. Petioles stout, 4–14 mm long; blades elliptic-obovate to elliptic, acuminate to mucronate at apex, broadly cuneate to rounded at base, 6–15(20) cm long, 3–6.5(8) cm wide, glabrous, coriaceous, the major lateral veins raised below, with a conspicuous submarginal collecting vein and prominulous reticulate veins; stipules nearly encircling stem, 5–9(15) mm long, deciduous. Flowers dense, in globular clusters 4–9 mm diam, completely concealed before anthesis by short-stipitate, round, peltate bracts; peduncles obsolete or to 5 mm long; perianth obsolete; staminate flowers many, the stamen solitary, the anther circular, eccentrically peltate, ca 1 mm diam, dehiscing by 2 basal valves; pistillate flowers 1 or 2 at center of clusters, the stigmas deeply 2-lobed, the lobes exserted 4–7 mm before staminate flowers open, spreading, subulate. Fruit a false drupe, ± globose, 1–1.5(2) cm diam, with minute round protuberances, with an apical depression; seed 1. *Croat 10306, 11647.*

Common in the forest. Seasonal behavior uncertain. Apparently flowers from November to May, mostly during the dry season. The fruits mature from May to October and are eaten when ripe by monkeys (Hladik & Hladik, 1969).

Carpenter (1934) reported that fruits of this species are second only to *Ficus* as food for most animals of the forest. Bats play a principal role in their dispersal (R. Foster, pers. comm.). The outer shell of the fruit is often thrown to the ground.

The subspecies *bolivarense* is distinguished from the subspecies *alicastrum* by having anthers with free thecae; anthers of the subspecies *alicastrum* are peltate with the thecae fused.

The typical subspecies ranges from Mexico to Costa Rica and the West Indies. The subspecies *bolivarense* ranges from Costa Rica through the Andes to Guyana and Brazil (Acre Territory). In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién. Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

CASTILLA Sessé

Castilla elastica Sessé in Cerv., Gaz. Lit. Mexico, Suppl. 7. 1794

C. panamensis Cook

Rubber tree, Mastate blanco, Caucho, Hule, Ule

Monoecious or dioecious tree, 10–30 m tall, with low buttresses; young parts densely yellowish-pubescent; stems hollow; sap white. Leaves pendulous, deciduous; petioles to 1 cm long; stipules fully amplexicaul, 3–9 cm long, densely golden, appressed-pubescent, deciduous; blades oblong to oblong-obovate, acuminate at apex, cordate at base, 20–45(55) cm long, 8–18(25) cm wide, minutely ciliate-denticulate, asperous especially below with short, spreading, often golden trichomes. Flowers inserted on large, flattened, unisexual receptacles covered with imbricate bracts, the receptacles axillary or at defoliated nodes, involucrate; primary staminate inflorescences (2)4(6) per axil, fan-shaped, conduplicate, to 15 mm long and 25 mm wide; peduncles 3–10 mm long; bracts in 10–12 series; perianth absent; stamens numerous, scattered among the bractlets; filaments to 3.5 mm long; anthers oval, ca 1 mm long; complemental staminate inflorescences (accompanying pistillate inflorescences) usually 2, similar to primary ones or funnel-shaped to cup-shaped. Pistillate receptacles usually solitary, thickly discoid, 1–2 cm diam, 1–2 cm thick, nearly sessile; involucral bracts in 5–10 series; flowers mostly 15–30; perianth tubular, (1.5)2–3 mm long, shallowly 4(5)-lobed, fleshy, short-velutinous, accrescent; ovary subinferior; styles dimorphic, to 1.5 mm long with stigmas 3–6 mm long or 2–3 mm long with stigmas less than 3 mm long; stigmas 2, rarely 3. Fruits thick, discoid syncarps 2.5–4.5

cm wide; seeds many, ca 1 cm long and enclosed in the orange, fleshy, accrescent perianth. *Croat 5335.*

Occasional in the forest on the western side of the island. Probably flowers in the late dry and early rainy seasons (April and May). Berg (1972) reported that the species flowers all year. The fruits are mature in May and June. The leaves are lost in the dry season.

Widespread on both coasts from Mexico to Panama and along the western coasts of Colombia and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Coclé (El Valle), and from tropical wet forest in Colón (Guásimo).

CECROPIA L. (Guarumo, Trompy, Trumpet tree)

Cecropia is distinguished by its slender, pendent, unisexual catkins; staminate catkins fall soon after anthesis. Flowers have a minute tubular perianth, the staminate with two stamens, the pistillate with a barely exserted, pencil-shaped style. Each flower produces a tiny achene. Leaves are peltate and spirally arranged on stout, hollow branches, which frequently house myrmecophilous ants. The leaves are a favorite food of sloths. The genus is characteristic of secondary areas and usually has soft wood and black sap.

Cecropia insignis Liebm., K. Danske Vidensk. Selsk. Skr. Naturvidensk. Math. Afd., ser. 5, 318. 1851

C. eximia Cuatr.

Guarumo blanco

Dioecious tree, to about 40 m high and 70 cm dbh, broadly branched; trunk with prominent lenticels and often stilt-rooted; outer bark thin; inner bark reddish. Petioles stout, arachnoid-villous and longitudinally striate, the basal pulvinus brown; stipules commonly red when falling, mostly 17–26(40) cm long and 5–8 cm broad, densely hirtellous on outer surface, with 2 prominent ridges; mature leaves prominently clustered at ends of branches, up to 90 cm wide, divided more than three-fourths of the way to center, the lobes 7–9, acute to obtuse at apex, conspicuously narrowed at base, to 22 cm broad, the margins held conspicuously upward, the upper surface smooth and shiny, glabrous except for sparse arachnoid trichomes deciduous in age, the lower surface paler and minutely canescent beneath (at least between veins). Staminate spathes oblong, 10–12(16) cm long, 5–6.5 cm wide, rounded at apex with long apiculate tip, the spadices held erect in clusters of usually 6 or 7, 12–15 cm long, 8–10 mm wide, whitish or green, the basal stipes

KEY TO THE SPECIES OF CECROPIA

Leaves smooth above, remaining intact after falling to ground; basal stipe of spadices glabrous, purplish, pruinose (covered with thin, waxy layer); pistillate spadices yellow (except when very young) ..... *C. insignis* Liebm.

Leaves scabrous or rough on upper surface, usually rolling up after falling to ground; basal stipe of spadices not pruinose, variously pubescent; pistillate spadices white or greenish:

Leaves often divided more than three-fourths of the way to base, usually flat or only slightly folded; staminate spadices usually in clusters of less than 10; pistillate spadices 25–30 cm long when fully expanded ..... *C. obtusifolia* Bertol.

Leaves usually divided about halfway to base or less, the surface of the blade much folded, not able to be flattened; staminate spadices in clusters of 12–60; pistillate spadices less than 12 cm long when fully expanded:

Pistillate spadices in clusters of 4–6, the common peduncle not more than twice as long as spadix; basal pulvinus of petiole with uniform trichomes, the velvetlike layer of trichomes not interspersed with longer white trichomes ..... *C. peltata* L.

Pistillate spadices in clusters of 6–12, the common peduncle 5–8 times as long as spadix; basal pulvinus of petiole with the brown velvetlike layer of trichomes interspersed with dense, longer, white trichomes ..... *C. longipes* Pitt.

KEY TO THE SPECIES OF CECROPIA
(ON THE BASIS OF STAMINATE SPADICES)

The following key is provided because staminate inflorescences fall soon after anthesis and are often found on the ground.

Staminate spadices less than 10 per peduncle:

Spadices 4 mm thick; basal stipes ± green, puberulent, to 10 mm long; leaves scabridulous above, flat to somewhat pleated ..... *C. obtusifolia* Bertol.

Spadices ca 1 cm thick; basal stipes glabrous, purple, pruinose, 12–16 mm long; leaves smooth above, much pleated ..... *C. insignis* Liebm.

Staminate spadices 12 or more per peduncle:

Spadices usually less than 6 cm long ..... *C. peltata* L.

Spadices usually more than 6 cm long ..... *C. longipes* Pitt.

Fig. 194. *Cecropia insignis*

Fig. 195. *Cecropia longipes*

purplish, broad, 12–16 mm long, pruinose, the common peduncles 5–10 cm long; pistillate spathes as those of staminate, the spadices in clusters of 4–7, pale yellow, 8–10 cm long and ca 8 mm thick at anthesis, becoming bright yellow in fruit and to 15 cm long and 1.3 cm thick, the basal stipes thick, pruinose, ca 1 cm long, the common peduncles 8–13 cm long, gray-hirtellous. Achenes ovate-elliptic, somewhat flattened, 1.7–2.3 mm long, ca 1 mm wide, conspicuously muricate, reddish-brown. *Croat 7023* ♂.

Common in the forest, even in the older forest. Many individuals grow in the vicinity of the Laboratory Clearing. Flowers in the dry season (December to April). The fruits mature from April to August with a peak in July.

Easily distinguished by the large, smooth, very deeply divided blades and the spadices with pruinose stipes.

Nicaragua to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Los Santos and from tropical wet forest in Colón (Salúd). Reported from premontane wet and rain forests in Costa Rica (Holdridge et al., 1971).

See Fig. 194.

Cecropia longipes Pitt., Contr. U.S. Natl. Herb. 18:227. 1917

Guarumo poludo

Dioecious tree, to 15 m tall; branches stout, 4–5 cm diam at apex. Petioles gray-hirtellous, 30–75 cm long, the brown velutinous trichomes interspersed with longer white trichomes; stipules ca 7–9 cm long; mature leaves to ca 90 cm wide, usually divided less than halfway to center, dark green and scabridulous above, paler and subarachnoid-puberulent below; lobes 9–13, broadly rounded at apex, not narrowed at base. Staminate spathes carrot-shaped before anthesis, pendent, reddish-brown, densely hirsute, 9–12 cm long, the spadices in clusters of 16–50, to 13 cm long and 2–3 mm diam, the stipes 1–2 cm long, gray-hirtellous, the common peduncles 7–12 cm long, densely hirsute; perianth tubular; stamens 2. Pistillate spathes reddish, 2-ribbed, the spadices in clusters of 6–12, 8–9 cm long and 5 mm diam at anthesis, 10–12 cm long and ca 1 cm diam in fruit, the stipes hirtellous, to 1 cm long, the common peduncles greatly accrescent in fruit, 50–80 cm long, moderately covered with sharp and stiff, somewhat urticating trichomes. Achenes tan, ellipsoid to narrowly ovate, smooth when fresh, ca 2.3 mm long, to 1.3 mm wide. *Croat 15248a.*

Apparently rare; known only from the vicinity of the Laboratory Clearing. In the Canal Zone, the plant is uncommon, growing as isolated plants in open areas. Both of the pistillate plants growing in the Laboratory Clearing set an abundance of fruit. Flowers at the beginning of the rainy season (April to June). The fruits mature from July to September (sometimes November).

Known only from Panama, from tropical moist forest on both slopes of the Canal Zone and in Darién and from premontane moist forest on the Pacific slope of the Canal Zone (Fort Kobbe).

See Fig. 195.

Cecropia obtusifolia Bertol., Fl. Guat. 39. 1840

C. mexicana Hemsl.; *C. panamensis* Hemsl.

Guarumo, Trumpet tree

Dioecious tree, mostly 5–10 m tall; trunk moderately slender, the young branches stout, ferruginous-hirtellous to glabrate. Petioles densely short-pubescent; stipules 7–11 cm long; mature leaves usually divided more than halfway to center, scabridulous and minutely arachnoid above, paler and minutely cinereous below; lobes usually 9–15, rounded to shortly acuminate at apex, somewhat to moderately narrowed at base, the lower free margin held ± flat to moderately erect, the leaves thus ± pleated, the area surrounding the petiole flat to 3–4 cm in all directions from center; veins, petioles, and spathes often ± maroon. Staminate spathes (11)12–20 cm long, ca 2 cm wide at anthesis, gradually acuminate, the spadices usually in clusters of 3–9, (10)12–18 cm long, 3–4 mm thick, subsessile or with puberulent stipes to 1 cm long, the common peduncle 8–12 cm long; pistillate spathes 16–20 cm long at anthesis, usually arachnoid on outside, villous inside, the spadices in clusters of 2–4, 17–30 cm long, ca 5 mm diam at anthesis, 6–9 mm diam and fleshy in fruit, the common peduncle 8–20(24) cm long, usually rough with short erect trichomes. Achenes ovate to broadly oblong, somewhat flattened, the edges acute, 3.3–3.7 mm long, to 2.7 mm broad, tan to white. *Croat 11716, 11800.*

Very common along the edge of the lake, particularly the northern and the eroded eastern shorelines; occasional in the forest, especially in tree-fall areas, some trees being found in the older forest. Flowers and fruits throughout the year.

Most easily confused with *C. peltata,* which has leaves conspicuously pleated to the center with shorter, broader lobes and shorter spadices.

Fruits are taken by spider monkeys from April to August (Hladik & Hladik, 1969).

Southern Mexico to Panama, Ecuador, and probably Colombia. In Panama, a wide-ranging and ecologically variable species and a characteristic tree of tropical moist forest (Holdridge & Budowski, 1956); known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién (no doubt elsewhere also), from premontane wet forest in Panamá, from tropical wet forest in Colón and Darién, and from premontane rain forest in Panamá (summit of Cerro Jefe).

See Fig. 196.

Cecropia peltata L., Syst. Nat. ed. 10, 1286. 1759

C. arachnoidea Pitt.

Guarumo, Trumpet tree

Dioecious tree, 6–20 m tall. Petioles densely hirtellous and arachnoid, the basal pulvinus a uniform mass of dense trichomes; stipules 6–9 cm long; leaves lobed less than three-fourths of the way to middle, usually about halfway; lobes 9–11, obtuse to rounded at apex, scarcely or not at all contracted at base, the lateral margins held prominently upward and prominently pleated between

lobes to almost center of leaf, scabridulous above, paler and densely arachnoid-villous to glabrate below, the veins green. Staminate spathes usually 4–7 cm long, softly arachnoid outside, glabrous inside, the spadices in clusters of 12–46, 2.5–6 cm long and 3–4 mm diam, the stipes short, minutely hirtellous to glabrate, the common peduncle puberulent, 3.5–13 cm long, minutely hirtellous; perianth tubular; stamens two. Pistillate spathes mostly less than 7 cm long but sometimes to 10 cm at anthesis, broadly conic, mucronate, the spadices in clusters of 4–6, 3–5 cm long and ca 5 mm wide at anthesis, to 15 cm long and 1 cm wide in fruit, subsessile or with an inconspicuous sparsely pubescent stipe, the common peduncle 4.5–12(17) cm long, hirtellous. Achenes oblong, acute at apex, ca 1.7 mm long, to 1 cm wide, muricate, greenish. *Croat 11749, 11831.*

Common along the shore and in the old tree-fall areas of the older forest. Flowering seems to begin in the dry season and continue nearly all year. The fruits mature all year, possibly with a peak in the early rainy season.

Closely related to and perhaps inseparable from *C. obtusa* Trec., which ranges from the Guianas to Peru, Brazil, and Paraguay.

Mexico to Colombia, Venezuela, and the Guianas; West Indies. In Panama, characteristic of tropical moist and premontane moist forests (Tosi, 1971); known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from tropical wet forest in Colón, Veraguas, and Darién. Reported from premontane wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Fig. 197.

COUSSAPOA Aubl.

Coussapoa magnifolia Trec., Ann. Sci. Nat. Bot., sér. 3, 8:98. 1847

C. nymphiifolia Standl.

Dioecious trees, to 10 m tall, usually hemiepiphytic; branches hollow; young parts minutely ferruginous-tomentulose, glabrate in age. Leaves spiral; petioles 5–15 cm long; blades broadly oval, rounded at apex, usually cordate at base, 15–30(36) cm long, 10–25 cm wide, somewhat asperous on both surfaces, entire or indefinitely sinuate on margin; venation palmate at base, the major lateral veins in 6–8 pairs above base; stipules fully amplexicaul, 3–5 cm long. Inflorescences upper-axillary, shorter than subtending petioles; staminate heads many, globular, 4–10 mm diam, the inflorescences dichotomously branched 3 or 4 times, the flowers with 4 free tepals and 2 fused stamens; pistillate heads 3–5 cm broad, obscurely compound or lobed with 2 to 4 lobes, the flowers with a short style, the stigma barely exserted. Syncarps loosely coherent, quite fleshy. *Croat 5125, 15064.*

Rare; known from areas along the shore of the bay south of Orchid Island, usually epiphytic on submerged trees in the lake. Possibly also occurring in the canopy of the forest. Probably begins to flower in the early dry season and continues for much of the year.

Panama to Peru and Brazil. In Panama, known only from tropical moist forest on the Atlantic slope of the Canal Zone.

Coussapoa panamensis Pitt., Contr. U.S. Natl. Herb. 18:226. 1917

Dioecious tree, usually to 13 m tall, usually hemiepiphytic, attached to host at least when young by circumferal grasping roots; young stems and petioles reddish-brown, scurfy, glabrate, or puberulent; sap viscid, clear, reddish or yellowish. Leaves spiral; petioles 3–7 cm long; stipules fully amplexicaul, 1–7 cm long, usually pubescent; blades ovate, obtuse and often apiculate at apex, subcordate to rounded or truncate at base, 10–20 cm long, 6.5–12 cm wide, glabrous above, whitish below with dense, appressed, arachnoid trichomes, the margins sinuate to crenate; venation palmate at base, the major lateral veins in 10–20 pairs above base. Inflorescences of pedunculate globular heads ca 5 mm broad, the staminate inflorescences dichotomously compounded 2–4 times, equaling or shorter than subtending petiole, the flowers with 4 free tepals and 2 fused stamens; pistillate inflorescences simple, usually 2 per node, the peduncles 4–6 cm long, the heads ca 1 cm diam at anthesis, the style very short, the stigma barely exserted, the peduncle and ovary minutely pubescent. Syncarps ± globose, fleshy at maturity, orange, ca 2 cm diam. *Croat 5698, 7839.*

Occasional, along the shore and in the forest. Flowers mostly in the dry season (February to June), with the fruits maturing in late rainy season.

Southern Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá and from premontane wet and tropical wet forests in Colón.

See Fig. 198.

DORSTENIA L.

Dorstenia contrajerva L., Sp. Pl. 121. 1753

Herb, usually less than 30 cm tall; stems short, the plants often appearing acaulescent; leaves and stems juicy. Leaves crowded, spirally arranged; petioles 7–25 cm long; blades extremely variable in shape and size, commonly deeply pinnatifid, basifixed, 8–24 cm long, 9–20 cm wide, scrabridulous or inconspicuously puberulent, the lobes acuminate, often contracted toward base, the leaf base truncate to cordate. Peduncles usually longer than petioles, to 36 cm long; receptacles yellowish, centrally peltate, variously radiate to ± quadrangular, 1.5–3.5 cm diam, accrescent and to 5 cm diam in fruit. Seeds ca 1 mm long, ± rounded, weakly tuberculate. *Foster 2791.*

Collected once at Shannon Creek. Plants are fertile from May to August.

Southern Mexico to Peru and the Guianas; the Antilles. In Panama, known from tropical dry forest in Panamá (Taboga Island), from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, and from premontane wet forest in Coclé.

Fig. 196. *Cecropia obtusifolia*

Fig. 198. *Coussapoa panamensis*

Fig. 197. *Cecropia peltata*

FICUS L. (Higo, Higueron)

The genus is recognized by its fruitlike inflorescence (the fig), by its usually viscid milky sap, and by its prominent amplexicaul stipules. The minute, unisexual, naked flowers of both sexes are interspersed on the inner surface of the receptacle, which becomes fleshy when the fig is mature. Pistillate flowers consist of both functional pistillate flowers, which are generally sessile and mature into viable achenes, and sterile pistillate flowers (gall flowers), which are generally stalked and function as incubators for the larvae of the wasp that pollinates the flower.

Ficus is pollinated by tiny, specialized wasps. *Ficus* flowers are unisexual, borne on the inner surface of a globose receptacle, with the receptacle having an apical pore closed by a series of interlocking bracts. Pistillate flowers are of two kinds, long-styled and short-styled. Flowers are pollinated by usually host-specific female agaonid wasps (Ramirez B., 1970), which enter the fig through the ostiole (carrying pollen from another tree) when the ostiolar scales loosen and the pistillate flowers are ready for pollination. All pistillate flowers in a receptacle mature synchronously. Wasps probably pollinate both long- and short-styled pistillate flowers, then lay eggs in the short-styled flowers and later die within the fig. The long-styled flowers that are pollinated develop normally and produce seeds, while the short-styled flowers that also received agaonid eggs become "gall" flowers, each nourishing a single wasp larva. The period of time between fertilization of the pistillate flowers and maturation of the staminate flowers, when the wasps reach the adult stage, is called the interfloral phase. Maturation of staminate flowers occurs synchronously with the emergence of the adult wasps from the gall flowers. The interfloral phase varies greatly from species to species. Copulation takes place before the female wasps leave their galls. Once they leave the galls they go directly to the anthers, collect pollen, then leave through holes in the fig wall made by the males. The females fly to a tree of the same species that is ready for pollination. Fig development on any tree is usually highly synchronized so that pollination of all figs of a single tree occurs on the same day. There is also usually a more or less synchronous ripening of figs on a single tree. This occurs only after the fig wasps have emerged from the fig and ensures that they are not eaten by frugivores. The activity of different individuals of a species is not synchronized, however, and the species may be found in all stages at any one time. Recent studies by A. S. Rand (pers. comm.) on *Ficus yoponensis* and *F. insipida* indicate that although there is no synchronization of flowering between different individuals of a species, an individual tree may show some degree of fidelity to a particular pattern of flowering on consecutive years. Rand has found that these two species have one period of flowering sometime between November and January and may have a second or third period of flowering later in the year. Because no mention can be made of flowering and fruiting behavior in a seasonal sense, the length of the interfloral phase will be given when it is known.

The two New World subgenera of *Ficus,* which both occur on BCI, are morphologically and ecologically distinct:

Pharmacosyce: Free-growing trees, the result of a seed that germinated on the ground; figs solitary in axils with three or three-lobed basal bracts; flowers pollinated by *Tetrapus* wasps; stamens two; anthers dehisce and pollen comes out naturally from thecal sacs; ovary pale, unspotted; tepals of pistillate flowers narrowly deltoid or lanceolate; seeds usually dry, not sticky.

KEY TO THE SPECIES OF FICUS

Leaves ovate-cordate ..... *F. nymphiifolia* P. Mill.
Leaves not ovate-cordate:
  Young stems bearing dense, reddish-brown, spreading pubescence; leaves usually asperous above; figs conspicuously pubescent:
    Figs cylindrical (conspicuously longer than broad); leaves puberulent or hispidulous below with straight trichomes; ostioles not wide-tubular ..... *F. popenoei* Standl.
    Figs globose; leaves softly villous below; ostioles wide-tubular ..... *F. bullenei* I. M. Johnston
  Young stems not densely rufous-pubescent; leaves smooth above; figs glabrous or pubescent, usually not conspicuously pubescent:
  • Figs solitary in leaf axils; trees not strangling; trunk terete, often buttressed:
    Petioles with thin, scurfy, brown periderm; stipules less than 2.5 cm long; leaves often very minutely puberulent below; figs asperous ..... *F. maxima* P. Mill.
    Petioles not scurfy; stipules mostly more than 2.5 cm long; leaves glabrous on both surfaces:
      Major lateral veins in less than 15 pairs, rather distant; collecting vein below as prominent as lateral veins or nearly so; trees usually less than 15 m tall; figs usually sessile, depressed-globose ..... *F. tonduzii* Standl.
      Major lateral veins in 15–30 pairs, close; collecting vein below usually more obscure than lateral veins; trees usually 25 m or more tall:
        Figs to 1.8 cm diam, the slender, tubular ostiole to 3 mm long; major lateral veins less than 4 mm apart ..... *F. yoponensis* Desv.
        Figs to 4 cm diam, the ostiole only slightly raised; major lateral veins mostly more than 5 mm apart ..... *F. insipida* Willd.

- Figs paired in axils (sometimes with one aborted); trees usually strangling; trunks often contorted, buttressed or not:
  - Figs on a distinct peduncle:
    - Leaves less than 5 cm wide:
      - Figs less than 7 mm diam; ostioles mammillate; leaf blades rounded to bluntly acuminate at apex ..... *F. perforata* L.
      - Figs more than 7 mm diam; ostioles sunken; leaf blades long-acuminate ... *F. pertusa* L.f.
    - Larger leaves more than 5 cm wide:
      - Figs more than 15 mm diam, reddish to purplish when ripe; stipules usually pubescent with long appressed trichomes; figs few, usually restricted to leafy axils ..... *F. trigonata* L.
      - Figs less than 15 mm diam, greenish or yellowish when ripe (except purplish in *F. citrifolia*); stipules glabrous or minutely puberulent; figs numerous, often at leafless axils (except *F. dugandii*):
        - Small epiphytic trees; trunks gray; sap clear; leaf blades acuminate, coriaceous; figs ± globose, the ostiole flat, not prominent; peduncles 4–15 mm long ..... *F. citrifolia* P. Mill.
        - Large buttressed trees; trunks brownish; sap milky; leaf blades thin, long-acuminate; figs turbinate, the ostiole mammillate; peduncles less than 4 mm long ..... *F. dugandii* Standl.
  - Figs sessile or nearly so (*F. obtusifolia* rarely with peduncles to 8 mm long, but usually at least appearing sessile):
    - Bracteoles at base of figs 3; leaf margins conspicuously white, matching midrib when dry; plants cultivated at the Laboratory Clearing ..... *F. retusa* L.
    - Bracteoles at base of figs 2; leaf margins not conspicuously white; plants not cultivated:
      - Figs less than 8 mm diam; leaves 3-veined near base (sometimes 5-veined), the major lateral veins in fewer than 5 pairs, long-appressed-pubescent below ..... *F. colubrinae* Standl.
      - Figs more than 10 mm diam; leaves not 3-veined near base, the major lateral veins in more than 5 pairs, glabrous or pubescent:
        - Figs conspicuously velvety pubescent, maturing green; leaves and figs densely clustered at apex of stem; bracts more than 1 cm long ..... *F. obtusifolia* H.B.K.
        - Figs not velvety pubescent, maturing reddish or green with red, purple, or brown spots; leaves and figs not clustered at apex of stem; bracts less than 1 cm long:
          - Leaves distinctly acuminate; stipules glabrous or puberulent:
            - Figs with purplish vertical stripes, the ostioles purplish; small trees usually less than 10 m tall; petioles less than 3.5 cm long ..... *F. paraensis* (Miq.) Miq.
            - Figs not marked with purple; usually large trees more than 10 m tall; petioles often more than 4 cm long ..... *F. dugandii* Standl.
          - Leaves rounded to obscurely acuminate; stipules with long trichomes when young:
            - Figs less than 14 mm wide, whitish or yellowish-green, becoming reddish to red, the ostiole not prominently raised (the surface often forming a few, small, radial ridges on drying); stipules subpersistent ..... *F. costaricana* (Liebm.) Miq.
            - Figs more than 14 mm wide (when mature), usually green with reddish spots or entirely violet-purple, the ostiole raised and buttonlike (the surface not drying with radial ridges); stipules deciduous ..... *F. trigonata* L.

Urostigma: Epiphytic or hemiepiphytic and usually with the strangling habit (i.e., roots coalescing around host tree), the result of a seed that germinated on another tree; figs paired in axils, their basal bracts two or two-lobed; flowers pollinated by *Blastophaga* subg. *Pegoscapus* wasps; stamen one; anthers dehisce but pollen does not come out naturally; ovary with a red spot at base of style; tepals of all flowers hooded; seeds usually sticky, thus sticking to trees where they are deposited by bats, which eat them, and birds, often no doubt as they clean their beaks. See Fig. 199 and fig. on p. 23.

I am indebted to William Ramirez B. for the information given here concerning length of the interfloral phase, fruit dispersal agents, and ecology.

Ficus bullenei I. M. Johnston, Sargentia 8:113. 1949

Tree, to 21 m tall, usually a strangler; trunk to 60 cm dbh, grayish or reddish, with many close pustular lenticels, buttressed at base, some buttresses stiltlike (perhaps only by erosion); young stems and petioles densely reddish-brown spreading-pubescent; sap copious, milky. Petioles 1–3 (4) cm long; stipules triangular, 1–2 cm long, deciduous, the pubescence densely appressed, reddish-brown; blades broadly elliptic to obovate, short-acuminate, rounded to subcordate and sometimes inequilateral at base, 7.5–26 cm long, 4.5–13 cm wide, entire to ± erose, asperous above, the pubescence dense, reddish-brown (lighter than stems and petioles), spreading, especially

Fig. 199. *Ficus*, showing the void once occupied by the host

Fig. 200. *Ficus bullenei*

Fig. 201. *Ficus costaricana*

below and on major veins above; juvenile leaves with coarsely crenate margins. Figs paired, globose, to 1.7 cm diam, subsessile, bearing conspicuous, ± spreading pubescence, greenish at maturity; ostioles surrounded by a wide, tubular, erect to spreading ring to 3 mm high; basal bracts 2, ovate, 4–5 mm long, bearing dense reddish-brown pubescence. *Croat 5557.*

Rare in the forest; occasional on shore. Interfloral phase is 37 days.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone and Panamá (San José Island).

See Fig. 200.

Ficus citrifolia P. Mill., Gard. Dict. ed. 8, *Ficus* no. 10. 1768

Tree, to 12(20) m tall, originally epiphytic, usually rather short and forming a solid trunk in exposed areas (such as along the shore); bark grayish; twigs minutely puberulent, smooth except for small lenticels; sap copious, watery. Leaves glabrous; petioles slender, 5–13 cm long; stipules narrowly triangular, 1–3 cm long, glabrous, deciduous; blades ovate, elliptic, oblong, or rarely obovate, acuminate, mostly obtuse to rounded or subcordate at base, 10–25 cm long, 4–9 cm wide, more or less coriaceous, folded along midrib, the veins in 4–12 pairs. Figs ± globose, 8–14 mm diam at maturity, borne in pairs (one frequently falling) in dense clusters among and below leaves, green with many pale green dots or becoming violet-red; peduncles 4–15 mm long, glabrous; ostioles flat; basal bracts 2, usually bluntly rounded, 2–3 mm long. *Croat 7891.*

Common, at least along the shore; rare or possibly absent from the older forest.

Occasionally visited by bats.

Florida to Paraguay; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá (San José Island) and from premontane dry forest in Coclé (Santa Clara Beach).

Ficus colubrinae Standl., Contr. U.S. Natl. Herb. 20:16. 1917

Hemiepiphytic tree, usually less than 6 m tall, probably never a strangler, the trunk to 20 cm diam; stems sparsely long-pubescent to glabrate in age; sap copious, milky. Petioles 5–25 mm long, often conspicuously long-appressed-pubescent; stipules 5–20 mm long, ovate, with long stiff trichomes, sometimes glabrate in age; blades obovate to (less frequently) ovate, abruptly short-acuminate, acute to rounded at base, 6.5–10.5 cm long, 3–7 cm wide, glabrous or long-pubescent especially on veins below, the veins at base 3(5), palmate, the major lateral veins in usually 2 pairs above base (sometimes 3 or 4). Figs paired, globose, 5–8 mm diam, glabrous, sessile, red at maturity; ostioles slightly raised; basal bracts 2, semicircular, to 2 mm long, with long stiff trichomes. *Croat 6822.*

Collected mostly along the shore; occasional in the forest.

Ficus colubrinae was considered synonymous with *F. hartwegii* (Miq.) Miq. by DeWolf (1960) in the *Flora of Panama.* W. C. Burger (pers. comm.) believes the two species are distinct, with *F. colubrinae* found only from sea level to 800 m and *F. hartwegii* from 900 m to 1,600 m.

Guatemala and Belize to central Panama; sea level to 800 m. In Panama, known from tropical moist forest on the Atlantic slope of the Canal Zone and in Bocas del Toro, Colón, and Darién, from tropical wet forest in Colón, and from premontane wet forest in Coclé (El Valle).

Ficus costaricana (Liebm.) Miq., Ann. Mus. Bot. Lugduno-Batavum 3:298. 1867

Tree of conspicuously strangling habit, to 30 m tall, glabrous except the stipules and floral bracts densely pubescent and the young stems, petioles, and leaf blades below or midribs above sometimes with long trichomes; bark often reddish-brown; sap milky. Petioles 1–4 cm long; stipules lanceolate, 1.5–3 cm long, densely pubescent (possibly glabrate in age), subpersistent; blades obovate or less frequently elliptic, rounded or obtuse at apex (acuminate on juveniles), rounded to subcordate at base, 8–20(32) cm long, 4.5–11(13) cm wide, the veins in 6–10 pairs, usually 3(5)-veined at base. Figs paired, depressed-globose, 12–14 mm diam, borne among leaves, glabrous, sessile, yellowish-green to pale yellow becoming reddish with darker red spots, finally entirely red at maturity; basal bracts 2, usually with long appressed trichomes, to 1 cm long. *Croat 9505.*

Common in the forest, occasional along the shoreline; a large tree occurs at Zetek Trail 310. The species is one of the most well-developed stranglers on the island.

The fruits are eaten by birds. Ants often form permanent trails on the branches to patrol the figs against predators. Escaping female wasps jump downward soon after emerging from the ostiole of the fig to prevent being eaten by the ants (W. Ramirez B., pers. comm.).

Guatemala to Panama. In Panama, known from tropical moist forest on BCI and in Chiriquí (Davíd) and from premontane wet forest in Chiriquí (Caldera). Reported from tropical dry forest in Costa Rica (Holdridge et al., 1971).

See Fig. 201.

Ficus dugandii Standl., Trop. Woods 32:20. 1932
F. turbinata Pitt. non Willd.

Hemiepiphytic tree, to 30 m tall, apparently not a strangler, the trunk ca 1.5 m dbh, buttressed; stems and leaves glabrous; bark pale reddish-brown, lenticellate; sap copious, milky. Petioles 2.5–7 cm long; stipules minutely puberulent to glabrate, ca 7 mm long; blades ovate-elliptic, acuminate, obtuse to rounded or truncate at base, 9–18 cm long, 5–8 cm wide, moderately thin, the major veins in 10–13 pairs, often appearing 3-veined at base, the reticulate veins of lower surface very distinct. Figs paired, turbinate, to 14 mm diam, puberulent, green with brownish spots at maturity; peduncles obsolete or to 4 mm long; ostioles raised; basal bracts 2, semicircular, puberulent, to 3 mm long. *Croat 12863.*

Adults rare, seen north of Zetek Trail 1300 and on

Barbour Trail. Seedlings more common, seen both along the shore and in the forest, always epiphytic and near the ground, such as on rotting fallen trees.

The species was considered to be a synonym of *F. citrifolia* by DeWolf (1960) in the *Flora of Panama,* but the two have been shown to be distinct by Ramirez B. (1970), who has made detailed studies of their pollination systems. Though they are morphologically similar and often difficult to distinguish in the herbarium, they are much easier to distinguish in the field. *F. dugandii* frequently grows along river banks in the Canal Zone, where it is a large tree with the solid trunk indicative of plants that grow from the ground up (or, in the case of fig trees, as epiphytes from near the ground) rather than from the treetops down as in the case of stranglers.

Costa Rica to Colombia and Venezuela. In Panama, known only from tropical moist forest in the Canal Zone (BCI and Gamboa).

Ficus insipida Willd., Sp. Pl. 4:1143. 1806

Free-growing tree, 30(40) m tall and ca 70 cm dbh, prominently buttressed; bark light gray, ± smooth; essentially glabrous but the fig puberulent; sap milky, copious. Petioles 2–5.5 cm long; stipules linear, 1–12 cm long, glabrous, deciduous; blades ± elliptic, obtuse to short-acuminate at apex, obtuse to rounded at base, 10–20 cm long, 5–9 cm wide (juvenile leaves to 40 cm long and 16 cm wide), the veins in 15–30 pairs, 2–4 veins arising sharply at base. Figs solitary, to 4 cm diam, borne among leaves, glabrous or minutely pubescent, yellowish-green at maturity with lighter spots; peduncles mostly 5–15 mm long; ostioles mammillate; basal bracts 3, to 3 mm long, semicircular, glabrous or pubescent. *Croat 8220.*

Abundant at least in younger areas of the forest; seedlings of this species have been seen growing in marshes on the south side of the island. One of the most abundant figs on the island. Interfloral phase is 15 days.

Seedlings require a tree fall or clearing to have sufficient light to grow. This species has been confused with *F. glabrata* H.B.K., which always occurs in riparian habitats. *F. crassiuscula* Warb. was considered a synonym by DeWolf in the *Flora of Panama,* but this species has been shown to be distinct by Burger (1974), who said it occurs only at elevations greater than 1,100 m in Costa Rica and Panama, whereas *F. insipida* occurs only at elevations less than 500 m. Ramirez B. (1970) also reported that the two species have different pollinators.

Southern Mexico to Brazil. In Panama, from tropical moist forest in the Canal Zone, Panamá, and Darién.

Ficus maxima P. Mill., Gard. Dict. ed. 8, *Ficus* no. 6. 1768

Free-growing tree, to 20(30) m tall, to 1 m dbh; outer bark thin, light brown, coarse but planar; inner bark thick, light, marbled; smaller twigs and petioles with a scurfy brown periderm; sap clear or turbid, copious. Petioles 1–3(4) cm long; stipules lanceolate, 1–2.5 cm long, usually glabrous; blades obovate to elliptic, usually abruptly short-acuminate, cuneate and 3-veined at base, ending abruptly on petiole, 9–16.5(25) cm long, 5–8(11) cm wide, stiff, asperous and very inconspicuously pubescent beneath or glabrous. Figs solitary, globose, 2–3 mm diam, reddish inside before maturity, green outside at maturity, the surface ± punctate and asperous with stiff, short trichomes; peduncles 5–10(25) mm long, minutely pubescent; ostioles inconspicuous, ± flat; basal bracts 3, short, rounded. *Croat 8363.*

Occasional, in the forest. Interfloral phase is 30 days.

The species is not very conspicuous because the trunk is not light-colored, as are many other figs, nor is it conspicuously buttressed.

Southern Mexico to the Amazon basin; Cuba, Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién and from premontane moist forest in the Canal Zone.

See Fig. 202.

Ficus nymphiifolia P. Mill., Gard. Dict. ed. 8, *Ficus* no. 9. 1768

Tree, usually less than 15 m tall, of inconspicuously strangling habit; stems minutely puberulent near apex, otherwise glabrous; sap milky. Petioles to 14 cm long, commonly more than three-fourths as long as blade, occasionally longer; stipules narrowly triangular, mostly 12–30(40) mm long; blades ovate, abruptly acuminate and downturned at apex, deeply cordate at base, mostly 9–20 cm long, 7–15 cm wide, palmately veined at base, the major lateral veins in 4–6 pairs above base; juvenile leaves reddish when young. Figs globose, 15–28 mm diam, minutely puberulent, somewhat glaucous, borne in pairs among leaves (one often aborting), green at maturity, with a faint sweet odor; ostioles flat or weakly raised; basal bracts 2, connate, usually rounded (sometimes acute) at apex. *Croat 12708.*

Rare; seen both in the forest and along the shore. Often epiphytic on palms. It has been seen epiphytic at 30 m in the canopy on *Sapium caudatum* (75. Euphorbiaceae). Interfloral phase is 20 days.

Figs of this species (and apparently most others that are green at maturity) have a pleasant odor and are eaten by bats.

Costa Rica to the Guianas and Brazil. In Panama, known from tropical moist forest in the Canal Zone and Darién and from tropical wet forest in Colón (Salúd). Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

Ficus obtusifolia H.B.K., Nov. Gen. & Sp. 2:49. 1817, non Roxb. 1814

Tree, to 40 m tall, usually a conspicuous strangler (juveniles especially), usually glabrous; trunk often unbuttressed; sap milky, copious. Leaves clustered near ends of stems; petioles 2–4 cm long; stipules 2–3 cm long, ovate, caducous; blades obovate or oblanceolate, rounded to obtuse at apex, cuneate at base, 15–25 cm long, 6–12 cm wide, often drying grayish above, the veins in 8–11 pairs. Figs paired, globose, 1.5–3 cm diam, green, borne among leaves, glabrous or minutely velvety pubescent;

Fig. 202. *Ficus maxima*

Fig. 203. *Ficus paraensis*

peduncles obsolete or to 8 mm long; ostioles usually slightly raised; basal bracts 2, to 2 cm long, semicircular, minutely pubescent, sometimes split. *Croat 8276.*

Common; the most abundant and conspicuous strangler on the island. Interfloral phase is 45 days.

Visited by bats but generally not visited by birds. Juvenile plants are usually conspicuously strapped to the host tree with their roots enveloping the tree's trunk.

This species was reported by Standley as *F. involuta* (Liebm.) Miq., which was considered a synonym of *F. obtusifolia* by DeWolf (1960) in the *Flora of Panama* and by Burger (1975) in his *Flora Costaricensis.* However, W. Ramirez B. (pers. comm.) considers *F. obtusifolia* a distinct species from *F. involuta,* which does not occur on BCI.

Mexico to Peru. In Panama, known from tropical moist forest in the Canal Zone and San Blas and from premontane wet forest in Panamá (Cerro Campana).

Ficus paraensis (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavum 3:298. 1867

F. panamensis Standl.

Hemiepiphytic tree, to 10(20) m tall, apparently not a strangler; branches conspicuously roughened with lenticels and pedicel scars; sap copious, often not very milky. Petioles 5–35 mm long; stipules 1.5–2.5(3.5) cm long, glabrous or minutely puberulent; blades oblong to oblong-oblanceolate, abruptly acuminate and markedly downturned at apex; rounded to subcordate at base, 9–18 cm long, 4–8 cm wide, glabrous or minutely puberulent, the major lateral veins in 9–18 pairs, the reticulate veins prominent. Figs paired, globose, 10–18 mm diam, borne among leaves, green with maroon streaks becoming yellow with violet-purple streaks; peduncles short and stout or lacking; ostioles violet-purple, raised; basal bracts 2, ovate, puberulent, often somewhat maroon. *Croat 12680.*

Frequent, especially on the shore. Interfloral phase is 60 days.

Ant nests are nearly always on the branches of this species, often with aerial roots in them.

Southern Mexico to the Guianas, Peru, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Colón (Nombre de Dios).

See Fig. 203.

Ficus perforata L., Pl. Surin. 17. 1775

F. oerstediana (Miq.) Miq.

Hemiepiphytic tree, to 15(30) m tall, apparently not a strangler, the trunk slender; stems glabrous in age, often pubescent when young; sap milky. Petioles 5–10 mm long, sometimes pubescent; stipules 5–12 mm long, ovate, glabrous or minutely puberulent; blades obovate, obtuse to very shortly blunt-acuminate at apex, cuneate to narrowly rounded at base, 4–9 cm long, 2–4.5 cm wide, the major lateral veins not raised below, faint above. Figs paired, globose, to 7 mm diam, borne among leaves, reddish at maturity; peduncles to 12 mm long, minutely puberulent or glabrous; ostioles mammillate; basal bracts 2, to 2 mm long, ovate. *Croat 6693.*

Possibly restricted to the shoreline or in the younger forest. Interfloral phase is 30 days.

A tree planted at the north of the library (*Croat 9009*) is an introduced species from the Old World (*F. retusa* L.), which can easily be confused with *F. perforata,* especially when sterile.

Guatemala and Belize to Colombia; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Darién and from premontane wet forest in Panamá (Cerro Campana).

Ficus pertusa L.f., Suppl. Pl. Syst. Veg. 442. 1781

Hemiepiphytic tree, 8–25 m or more tall; trunk smooth, sometimes with somewhat stilted roots; branches spreading, the youngest (including petioles and stipules) often puberulent. Petioles usually 5–15(30) mm long; stipules 5–13 mm long, slender, sharp-pointed; blades elliptic to oblong-lanceolate, abruptly long-acuminate, cuneate to rounded at base, mostly 3.5–7 cm long, 2–3.5 cm wide, pellucid-punctate when fresh, glabrous or with puberulence on midrib near base. Figs paired (one usually aborting), globose, usually 10–18 mm diam, puberulent, green with lighter flecks becoming greenish-yellow at maturity; peduncles 2–7 mm long; puberulent; ostioles prominently sunken; basal bracts 2, semicircular, to 4 mm long. *Croat 12274.*

Apparently rare; seen along the shortcut of Lutz Trail behind the Animal House and on the shore of Fuertes Cove.

Distinguishing characters are small leaves and figs usually greater than 8 mm diam. The species may be confused with two other small-leaved species, *Ficus perforata,* which has fruits less than 8 mm diam, and *F. retusa,* which has sessile fruits.

Mexico to Paraguay; West Indies. In Panama, known from tropical moist forest on BCI and in Bocas del Toro and Darién.

See Fig. 204.

Ficus popenoei Standl., Publ. Field Columbian Mus., Bot. Ser. 4:301. 1929

A conspicuous strangler, occasionally forming a solid but gnarled trunk, to 17(25) m tall; young stems with dense, rufous, spreading pubescence, the stems glabrate in age; sap milky. Petioles 1–2 cm long, rufous-pubescent; stipules 6–15 mm long, densely rufous-pubescent; blades obovate to broadly elliptic, rounded at apex, rounded or subcordate at base, 9–21 cm long, 5.5–10.5 cm wide, tawny-pubescent below and on veins above, asperous. Figs paired, cylindrical, about twice as long as broad, to 2.5 cm long and 1.5 cm wide, densely tawny-pubescent, green at maturity; peduncles 2–5 mm long, pubescent; ostioles flat or slightly raised; basal bracts 2, ovate, to 5 mm long. *Croat 11768.*

Occasional. A tree near Zetek Trail 600 has a trunk ca 1 m diam. Interfloral phase is 43 days.

Fruits dispersed by bats.

Belize to Colombia. In Panama, known from tropical moist forest in the Canal Zone (BCI) and Panamá (San José Island) and from premontane wet forest in Coclé (El Valle).

Ficus retusa L., Mant. Pl. 129. 1767
F. nitida Thunb.

Glabrous tree, 8 m tall, the trunk ca 30 cm dbh; bark on twigs whitish, peeling; sap milky. Petioles 1–2 cm long, drying reddish-brown; stipules lanceolate, ca 5 mm long, drying reddish-brown; blades obovate to elliptic, acuminate, acute at base, 7–10 cm long, 2.5–4 cm wide, minutely pellucid-punctate, the margin thickened, whitish (at least when dry). Figs paired, sessile, globose, 6–10 mm diam; ostioles ± flat; basal bracts 3, ± ovate, ca 2 mm long. *Croat 10116.*

Planted at the north edge of the Laboratory Clearing.

Ficus retusa can be confused with *F. perforata,* which has similar leaves but which also has figs borne on a distinct peduncle, whereas those of *F. retusa* are sessile.

Native to lowland tropics of Southeast Asia.

Reported by Standley in *Flora of the Panama Canal Zone* and planted in Balboa and Panamá City. Known from Darién in areas where cultivars are not expected (*Duke & Bristan 413, Stern et al. 785*).

Ficus tonduzii Standl., Contr. U.S. Natl. Herb. 20:8. 1917

Free-growing tree, 3–10(20) m tall, usually rather small; trunk buttressed, to 50 cm dbh; bark planar, brown, with many round, raised lenticels; sap milky, copious. Petioles to 5 cm long; stipules ovate, 1–3(6) cm long; blades mostly broadly elliptic, rounded or acuminate at apex, obtuse to rounded or truncate at base, 6–19(30) cm long, 5–12(17) cm wide, glabrous, stiff, the major lateral veins in 7–12 pairs, branching from midrib at ca 90° angle, loop-connected, the reticulate veins distinct. Figs solitary, depressed-globose, 2.5–3.5 cm diam, glabrous or minutely scabrid, depressed at apex, borne among leaves, green with lighter spots; peduncles obsolete or very short; ostioles flat or beaked; basal bracts 3, to 6 mm broad, ± rounded at apex. *Croat 8621.*

Occasional, chiefly in the older forest. Many of the trees in the forest are relatively small, mostly less than 10 m tall; at least some produce fruit. Elsewhere in Panama, at least on the Atlantic slope, the species is often riparian and taller than is commonly encountered on BCI (usually to 15 m). Interfloral phase is 31 days.

Easily distinguished by the leaves.

The fruits are distributed by bats.

Honduras to Ecuador. In Panama, known from tropical moist forest in the Canal Zone and Chiriquí and from premontane wet forest in the Canal Zone.

Ficus trigonata L., Pl. Surin. 17. 1775

Commonly a strangler but often a large tree, to 30(40) m tall, ca 4 m wide at base, 80–150 cm wide above buttresses; stems ± glabrous; bark brownish; buttressing roots to 3 m in open areas or along the shore; sap copious, milky. Petioles 2–5 cm long; stipules 1.5–3 cm long with long silky trichomes, deciduous; blades ± elliptic to ovate-elliptic, infrequently obovate, abruptly short-acuminate (sometimes rounded) at apex (the acumen sharp or blunt), obtuse, rounded, or subcordate at base, mostly 13–25 cm long and 7–10 cm wide, glabrous, the midrib above white, 3–5-veined at base, the major veins in 5–11 pairs, the smallest reticulate veins distinct. Figs paired, globose, 1.5–3 cm diam, puberulous, sparsely covered with round reddish dots; peduncles obsolete or to 7 mm long; ostioles raised and buttonlike, flat on top, ca 5 mm wide; basal bracts 2, rounded, 1–5 mm long, 4–7 mm broad, becoming brown, bilobed. *Croat 12719.*

Uncommon, in the forest and along the shore. Interfloral phase is 27 days.

Distinguished by the fig with red spots and buttonlike ostiole. Most easily confused with *F. costaricana;* see the genus key for distinguishing characters.

Figs are distributed by bats.

Southern Mexico to Colombia on the Caribbean slope; Greater Antilles. In Panama, known from tropical moist forest on both slopes in the Canal Zone and in Panamá (San José Island) and Darién; known also from premontane dry forest (Penonomé) and premontane wet forest (El Valle) in Coclé.

Ficus yoponensis Desv., Ann. Sci. Nat. Bot., sér. 2, 18:310. 1842

Free-growing tree, to 40(50) m tall; trunk buttressed, ca 1 m diam, light gray, somewhat smooth; stems and leaves glabrous; outer bark planar with weak fissures and rows of lenticels; inner bark tan, in inverted V-shaped bands; sap copious, milky. Petioles 1–2.5 cm long; stipules linear, 3–5 cm long, caducous; blades elliptic to oblong-elliptic, acuminate, acute to obtuse at base, 6–11 cm long and 2.5–4 cm wide (juveniles with blades to 28 cm long and 5 cm wide), the major lateral veins in 15–30 pairs, mostly less than 4 mm apart, forming obscure collecting vein. Figs solitary, globose, to 1.8 cm diam, green at maturity, often purplish at apex, mottled with irregular, lighter green, weakly pustular areas; peduncles 3–11 mm long; ostioles narrowly tubular, to 3 mm long; basal bracts 3, free, ca 1 mm long. *Croat 15060.*

Common, especially in the younger forest. Seedlings require considerable light to survive, which explains their greater abundance in the younger forest.

Figs are distributed by bats.

Mexico (Chiapas) to Colombia and Venezuela; sea level to 1,600 but usually at 500 to 1,200 m. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Chiriquí (Boquete).

MAQUIRA Aubl.

Maquira costaricana (Standl.) C. C. Berg, Acta Bot. Neerl. 18:463. 1969

Dioecious tree, ca 20 m tall, the trunk mostly 10–20 cm diam, with narrow buttresses ca 1 m high, glabrous but with puberulent stems; bark thin, brown; sap in trunk

Fig. 204. *Ficus pertusa*

Fig. 205. *Olmedia aspera*

copious, light brown, viscid, at first not obvious, becoming milky. Petioles to 1.5 cm, stout, callous; stipules paired, lateral, ovate, ca 5 mm long, caducous; blades oblong-elliptic, abruptly long-acuminate, obtuse to slightly rounded at base, 11–20 cm long, 4–8 cm wide, with a conspicuous collecting vein. Staminate inflorescences discoid, 1–3 per axil, 5–10 mm diam; peduncles 2–8 mm long; involucral bracts in ca 5 series; flowers free; perianth to 1 mm long, 4-lobed, puberulent, the lobes obtuse; stamens 4, to ca 1.5 mm long. Pistillate involucrate heads solitary in axils, discoid, 7–10 mm long and 10–17 mm wide at anthesis, subsessile or pedunculate; bracts ovate to rounded, acute to obtuse at apex, in 3–6 series, to 2.5 mm wide, minutely pubescent, their margins scarious, ciliate; perianth 2–2.5 mm long, fleshy, tubular, truncate or obscurely 4-lobed, minutely pubescent outside, tightly enclosing and eventually adnate to ovary; stigmas sessile, bilobed, the lobes flat, strap-shaped, densely puberulent, persisting in fruit. Fruiting heads to 5 cm diam; fruits oblong-elliptic to obovate, to 2 cm long and 1.8 cm wide, with a depression around the style at apex (often with minute ridges when immature), nearly glabrous, red at maturity; exocarp thin; mesocarp sweet, fleshy, to 3 mm thick; seed obovate, smooth, brown, ca 1.3 cm long. *Croat 9786, 15248.*

Occasional, but locally common. Flowers from January to May, with the fruits maturing mostly from May to July.

The fruits are eaten by toucans (label on *Duke 12280*).

Nicaragua to Peru; to 850 m elevation. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién.

OLMEDIA R. & P.

Olmedia aspera R. & P., Syst. Veg. 257. 1798

Dioecious shrub or tree, to ca 6(20) m tall; younger stems, petioles, and peduncles with coarse, erect or appressed trichomes; stems eventually glabrate or puberulent; sap whitish, watery, becoming clear with white clots. Leaves alternate; petioles 5–7(15) mm long; stipules fully amplexicaul, small; blades variable, mostly oblanceolate-elliptic, subcaudate-acuminate at apex, remotely serrate-undulate toward apex, cuneate at base, mostly 10–25 cm long, 2.5–9 cm wide, often somewhat falcate, glabrate and weakly asperous above, asperous below with short inconspicuous trichomes. Staminate flowers numerous, in involucrate discoid heads to ca 1 cm diam; perianth green, apiculate in bud, 4-lobed, the lobes acuminate, scabrid outside; stamens 4, inflexed in bud, springing out violently upon the bursting open of the thin perianth lobes, becoming strongly reflexed; pollen white, powdery. Pistillate inflorescences small, axillary, solitary or clustered, ovoid, consisting of a solitary flower surrounded by involucrate bracts, the bracts orange within at maturity, opening broadly to expose fruit; ovary superior; ovule and style pubescent at apex; stigmas with 2 filiform exserted lobes. Fruits sweet, orange, false (?) drupes ca 8 mm diam; seed rounded, ca 5 mm diam. *Croat 5073, 10168.*

Common in both the young and the old forests. Flowers and fruits throughout the year.

The flowers are visited by small bees.

Costa Rica through the Andes to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Los Santos, Panamá, and Darién; known also from premontane wet forest in Coclé and Panamá.

See Fig. 205.

PEREBEA Aubl.

Perebea xanthochyma Karst., Fl. Columb. 2:23, t. 112. 1861

Dioecious or monoecious tree, to 10(35) m tall, usually to ca 15 cm dbh; branches slender, slightly flexuous, conspicuously but sparsely hispidulous (except densely so when young), sometimes becoming glabrate, the trichomes usually acropetal; sap yellowish, turning brown or reddish. Leaves alternate, distichous; petioles 3–5 mm long; petioles and midrib of blades pubescent like the stems; stipules fully amplexicaul, lanceolate, 5–10 mm long, densely hispidulous; blades oblong-elliptic to narrowly obovate, abruptly and narrowly long-acuminate to subcuspidate at apex, obtuse to rounded at base, (6)16–28(48) cm long, (2)4–10(20) cm wide, glabrate on upper surface except on midrib, glabrate to sparsely hispidulous on smaller veins below, densely hispidulous on midrib below, the lateral veins in 7–23 pairs, the margins entire to ± coarsely undulate-serrate toward apex. Inflorescences axillary, solitary or clustered, involucrate, discoid; staminate inflorescences 3–6(10) mm diam, the peduncles 1–3(6) mm long, the bracts ca 25–60, deltoid to ovate, acute at apex, in 4–8 series, the flowers 10 or more; perianth to 1.1 mm long; tepals 4, free, cucullate, obtuse, yellowish-puberulent; stamens 4, free, nearly included; anthers broadly oval. Pistillate inflorescences solitary or accompanied by staminate ones, 4–15 mm diam, subsessile to pedunculate, the peduncles slender, to 3 mm long, the bracts 20–90, deltoid to ovate, in 4–10 series, the flowers numerous, all fertile; perianth entire to 4-lobed, to ca 2 mm long, hispidulous, accrescent and ± pulpy in fruit but essentially free; ovary superior to subinferior; style central; stigma lobes short, broad. Fruiting heads subsessile, 1–2 cm diam; fruits ovoid, orange, hispidulous, to ca 9 mm long, together forming a weakly united syncarp. *Knight 3502, 1510.*

Apparently rare; known only from the forest near Standley Trail 1000 and along AMNH Trail. Seasonality uncertain. Flowers principally from August to April. The fruits mature mostly from January to June.

Costa Rica to Peru. In Panama, restricted to the Atlantic Coast; known from wetter areas of tropical moist forest in the Canal Zone and Bocas del Toro, from premontane wet forest in the Canal Zone (Pipeline Road) and Bocas del Toro (Punta Peña, vicinity of Chiriquicito), and from tropical wet forest in Colón (Portobelo) and Panamá.

POULSENIA Eggers

Poulsenia armata (Miq.) Standl., Trop. Woods 33:4. 1933

Cucuá, Cocuá, Maragua, Mastate, Namaqua

Monoecious tree, to 27 m tall and 90 cm dbh, with low buttresses; outer bark thick; stems, petioles, stipules, and lower midrib of leaf armed with short sharp spines 1–3 mm long; sap copious, yellowish-brown. Leaves alternate; petioles stout, 1–4 cm long, armed; stipules amplexicaul, 1.5–3 cm long, armed; blades variable, obliquely ovate to oblong-elliptic, obtuse to short-acuminate at apex, obtuse to rounded and inequilateral at base, 10–40(70) cm long, 6–25(35) cm wide, usually glabrous in age, coriaceous. Staminate inflorescences globose, 1–2.3 cm diam, bearing many dense flowers; tepals 4, barely united; stamens 4, slightly exserted. Pistillate inflorescences ovoid, 1–1.5 cm diam, yellowish with (3)5–9 flowers; perianth 4-dentate; stigmas deeply 2-lobed, exserted. Fruiting heads subglobose or ovoid, to 2.5 cm long, the individual carpels conic, irregularly angulate, sharply pointed at apex, the involucral bracts sharply pointed; seeds 1 per carpel, ovoid, shiny, brown, to 4 mm long. *Croat 8533, 9280.*

Abundant throughout the forest. Flowers and fruits throughout the year, especially during the dry and early rainy seasons. The leaves, which are somewhat resistant to decay, are usually lost and replaced during the dry season.

Red spider monkeys have been seen eating the syncarp.

Mexico to Bolivia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién, from premontane wet forest in the Canal Zone, and from tropical wet forest in Colón and Darién.

See Fig. 206.

POUROUMA Aubl.

Pourouma guianensis Aubl., Hist. Pl. Guiane Fr. 2:892, t. 341. 1775

Mangabé, Guarumo macho, Viranjo

Dioecious tree, 10–25(30) m tall; trunk light brown, with irregular, horizontal rings; branchlets stout, hollow, defoliate except near apex; young parts bearing dense reddish-brown pubescence with minute branched trichomes (appearing papillate) and usually also golden, pilose, deciduous pubescence especially around stipule scars and on stipules; bark soft; sap clear or light yellow in trunk, turbid or milky usually turning black in younger parts. Leaves spiral, crowded at apex of branchlets; petioles mostly 10–25 cm long, terete, hollow, longitudinally striate or grooved, with minute reddish-brown trichomes interspersed with longer, ± hispid pubescence; stipules amplexicaul, 7–15 cm long, caducous, the pubescence dense, minute, reddish-brown, often also golden-pilose; blades ovate in outline, entire to irregularly sinuate with (3)5(7) deep lobes, usually abruptly short-acuminate at apex, deeply cordate at base, mostly 20–45(50) cm long and 20–50 cm wide, asperous above with minute trichomes on surface and longer hispid pubescence on midribs of lobes, the pubescence below dense, white, arachnoid-tomentose interspersed with sparse hispid bristles especially on veins, the veins parallel, raised and darker than surface below, the parallel tertiary veins connecting the major lateral veins prominulous below. Inflorescences upper-axillary, repeatedly cymose; inflorescence branches, pedicels, and pistillate flowers reddish-brown granular-pubescent; flowers unisexual, sessile; staminate flowers sessile or borne on a thick pedicel; perianth deeply 3- or 4-lobed, ca 1 mm long; stamens 3 or 4; anthers ovate, yellowish. Pistillate flowers borne on a stout pedicel about as long and as broad as the flower; perianth ovoid-tubular, 3.5–4 mm long, with a small opening at apex; stigmas peltate-discoid, papillate, exserted. Drupes ovoid, 1–1.5 cm long, bearing minute reddish-brown pubescence, capped by the persistent, discoid stigma, purplish-black and juicy at maturity. *Croat 8097, 8100.*

Mature plants uncommon; seedlings common in the forest. Mature plants are locally common along Conrad Trail. Flowers in the early dry season. The fruits mature in the late dry season.

Belize to Colombia, Venezuela, and the Guianas. In Panama, a characteristic tree species in tropical moist forest (Tosi, 1971), known from BCI and in Darién; known also from premontane wet forest in the Canal Zone (Pipeline Road) and from tropical wet forest in Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 207.

PSEUDOLMEDIA Trec.

Pseudolmedia spuria (Sw.) Griseb., Fl. Brit. W. Ind. 152. 1859

Caciqui, Cucuá

Dioecious tree, 8–20(30) m tall; branchlets slender, weakly flexuous, soon glabrous; sap white. Leaves alternate, distichous; petioles 3–10 mm long; stipules very narrowly lanceolate, long-acuminate, fully amplexicaul, mostly 5–7 mm long, rarely to 2 cm; blades ± oblong-elliptic, acuminate to caudate-acuminate at apex, acute to obtuse at base, 9–15(17) cm long, 3–5(6) cm wide, glabrous or nearly so. Flowers unisexual; staminate inflorescences in discoid, usually paired, sessile or subsessile heads 8–10 mm diam, the bracts broadly obtuse, minutely puberulent, in 2–4 series, the bracteoles interspersed with flowers; perianth vestigial; stamen solitary, to 3 mm long; anthers ± oblong, basifixed, apiculate. Pistillate flowers ovoid, solitary, sessile, involucrate, ca 2 mm diam, the bracts in 3–6 series, imbricate, softly puberulent; perianth tubular, 2–2.5 mm long, minutely 4-lobed; ovary inferior to semi-inferior; style to 1.5 mm long; stigmas 2, 4–6 mm long, widely exserted. Fruits false drupes, globose to cylindroid, 9–14 mm long, red; mesocarp thin. *Croat 11935.*

Rare; seen only once. The BCI collection is sterile, but almost certainly represents this species. Descriptions of

Fig. 206. *Poulsenia armata*

Fig. 207. *Pourouma guianensis*

the flowers and fruits were based on the *Flora of Panama* (Woodson & Schery, 1960) and on herbarium material from Central America. Flowers elsewhere from January to May, with the fruits maturing from February to June.

Mexico (Chiapas) to Panama; Greater Antilles; sea level to 900 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién (Duke, 1968).

SOROCEA St.-Hil.

Sorocea affinis Hemsl., Biol. Centr.-Amer. Bot. 3:150. 1883
Cauchillo

Dioecious tree, usually less than 6 m tall (to 15 m), glabrous but the leaves occasionally puberulent; branchlets grayish, sometimes lenticellate; sap milky. Leaves alternate; petioles 5–10 mm long; stipules lateral, ovate, paired, 2–5 mm long, caducous; blades oblong to oblong-obovate, caudate-acuminate at apex, narrowing to acute or rounded base, 7–16(18) cm long, 2.5–5.5(7.2) cm wide, entire or rarely bluntly serrate, the major lateral veins conspicuous below, loop-connected. Racemes puberulent, axillary; staminate racemes soon falling, 2–8 cm long, cream-colored, puberulent, the flowers numerous, bowl-shaped, ca 2 mm long, equaling length of pedicel, not dense, interspersed with minute peltate bracts; tepals 4, fleshy, broadly oval, concave; stamens 4, opposite and as long as tepals; filaments arched. Pistillate racemes usually 1–8 cm long in flower (to 6 cm in fruit), the flowers to 3 mm long, numerous, not dense, interspersed with many small bracts; pedicels pink and elongating to 6–10 mm in fruit; perianth depressed-globose, thick, ca 1.5 mm long and to 2.3 mm wide, the upper margin held tightly around the style; style bifid, with short, stout, flattened lobes spreading and recurving above throat of perianth; ovary ovoid, weakly pubescent. Drupes subglobose, ca 8 mm diam, green with an orange or red tip, becoming bright red and finally purple at maturity; seed 1. *Croat 4106, 5765.*

Frequent in the forest. Flowers sometimes starting in April, but mostly June to November, with the fruits maturing from September to December (sometimes February).

Guatemala to Panama. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá, from premontane wet forest in Coclé (El Valle), and from tropical wet forest in Colón.

TROPHIS P. Browne

Trophis racemosa (L.) Urban, Symb. Ant. 4:195. 1905
Breadnut, Gallote, Lechosa, Morillo, Ojocho macho, Ramón

Dioecious tree, to 17 m tall, to 25 cm dbh; trunk with broad, horizontal leaf scars; outer bark thin, sometimes reddish; inner bark thick, granular, tan; glabrous all over or sparsely puberulent on young stems, petioles, leaf veins below, and fruit; sap thin, copious, milky. Leaves alternate; petioles to 1(1.6) cm long; stipules lanceolate, lateral, minute, subpersistent; blades mostly oblong-elliptic to obovate, abruptly long-acuminate, rounded to obtuse at base, 7–15(23) cm long, 2.5–6(10) cm wide, entire or minutely serrate near apex, slightly asperous above and below. Staminate spikes pendent, 4–6.5 cm long, ca 5–6 mm wide, very densely flowered; tepals 4, broadly oval, to ca 1.7 mm long, densely and minutely pubescent; stamens 4, 2–3 mm long, strongly inflexed in bud; filament elongating, the anther springing free to fling the powdery white pollen into the air; pistillode ca 0.5 mm long. Pistillate spikes densely grayish-velutinous, usually less than 2 cm long, the flowers 4–15 per spike, sessile, ovoid, or conic; perianth minutely 4-lobed at the narrowly opened apex, 2–4.5 mm long; style branches 2, 2–5.5 mm long, long-exserted. Drupes sessile, ovoid to globular, ca 1 cm diam, densely and minutely velutinous, red becoming purple at maturity. *Croat 15247, Shattuck 1164.*

Occasional in both the young and the old forests. Seasonal behavior uncertain. Flowers principally from June to August, sometimes as early as April or as late as December, with the fruits maturing from October to December. Allen (1956) reported that the species flowers in February on the Osa Peninsula in Costa Rica.

Mexico to Peru and Brazil; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién and from premontane moist forest in the Canal Zone.

40. URTICACEAE

Trees, shrubs, or herbs (succulent in *Pilea*), sometimes scandent or epiphytic. Leaves alternate or opposite, petiolate; blades simple, serrate to entire (*Pilea*), sometimes palmately veined at the base; stipules present. Flowers unisexual (monoecious or dioecious), actinomorphic, in generally axillary, bracteate cymes or glomerules, sometimes spicate; tepals 3–5, biseriate, undifferentiated (or perianth lacking); stamens 3–5, opposite the tepals, free, springing out elastically at anthesis to throw pollen; anthers 2-celled, dehiscing longitudinally; ovary superior, 1-locular, 1-carpellate; placentation apical; ovule 1, falsely orthotropous; style and stigma 1; stigma penicillate. Fruits achenes; seed solitary, with endosperm.

Members of the family are distinguished by the frequently stinging trichomes, the minute greenish flowers, and the ovary with one carpel and one style.

Flowers are wind pollinated (Faegri & van der Pijl, 1966). The dry powdery pollen is catapulted by the elastic movement of the stamens at anthesis. G. Frankie (pers. comm.) reports that in Costa Rica stingless bees may aid in the opening of staminate flowers of *Myriocarpa* by their persistent probing of unopened flowers.

Dispersal of the minute achenes may be by birds, wind, or water. *Boehmeria cylindrica* and *Myriocarpa yzabalensis* usually grow in swampy areas or along water-

KEY TO THE SPECIES OF URTICACEAE

Leaves opposite, at least along main stem:
- Leaves less than 1 cm long, one leaf of a pair ca half the size of the other; blades entire; plants often minute, always less than 30 cm tall ..... *Pilea microphylla* (L.) Liebm.
- Leaves more than 2 cm long, pairs ± equal; blades serrate-dentate; plants more than 50 cm tall ..... *Boehmeria cylindrica* (L.) Sw.

Leaves alternate:
- Flowers in long slender spikes; leaves often more than 8 cm wide ..... *Myriocarpa yzabalensis* (Donn. Sm.) Killip
- Flowers not in slender spikes; leaves less than 8 cm wide:
  - Petioles less than 1 cm long; blades unequal at base ..... *Pouzolzia obliqua* (Poepp.) Wedd.
  - Petioles 1–7 cm long; blades ± equal at base ..... *Urera eggersii* Hieron.

courses, and their seeds may be water dispersed. *Pilea microphylla* somehow finds itself in every concrete crack in shady areas; possibly its minute seeds are carried around by ants or rain wash. Van der Pijl (1968) reported that in some species of *Pilea* the staminodia eject the entire fruit.

Some 49 genera with about 2,000 species; widespread but mostly in the tropics.

BOEHMERIA Jacq.

Boehmeria cylindrica (L.) Sw., Prodr. Veg. Ind. Occ. 34. 1788

Monoecious herb, sometimes epiphytic, erect, to 1.5 m high. Leaves opposite on stem, alternate on any branches; petioles 5–25 mm long, sparsely pubescent; blades narrowly ovate or lanceolate, acuminate, rounded to subcordate at base, 4.5–11(18) cm long, 2.5–4(7) cm wide, serrate-dentate, glabrous or with inconspicuous pubescence on lower surface of veins. Flowers minute, pinkish, in discrete, unisexual, globular clusters along axillary spikes 2–8 cm long and often leafy near the tip; staminate perianth 4-lobed; pistillate perianth 4-toothed, ca 2 mm long, nearly sessile. Achenes ± round, compressed, ca 1 mm diam, brown. *Croat 12691.*

Uncommon, usually occurring in swampy areas along the shore. Flowers and fruits in the rainy season.

Canada south to southeastern Brazil; West Indies. In Panama, known only from tropical moist forest in the Canal Zone and Bocas del Toro.

See Fig. 208.

MYRIOCARPA Benth.

Myriocarpa yzabalensis (Donn. Sm.) Killip, Proc. Biol. Soc. Wash. 40:29. 1927
Cow itch

Dioecious shrub or small tree, 3–8(10) m tall; stems ribbed below petioles, with harsh pubescence. Leaves alternate; petioles one-fourth to as long as blade; blades ovate to ovate-elliptic, abruptly acuminate, mostly rounded at base, 15–40 cm long, 10–25 cm broad, punctate, with linear cystoliths conspicuous when dry, glabrous above, sparsely pubescent on veins below. Staminate spikes to 10 cm long, erect or ± pendent, bracteate, the flowers to 1.2 mm diam; tepals 4; stamens spring flowers open and throw pollen. Pistillate spikes 30–60(90) cm long, slender, pendent; perianth lacking; style oblique on short stalk; stigma brushlike, straight and divergent at anthesis, later curling. Achenes scabrid, ca 1 mm long, soon falling. *Croat 4196, 8048.*

Frequent along creek banks in the younger forest. Flowers in the early dry season. The fruits mature in the middle to late dry season.

The achenes are light enough to be blown and probably are carried downstream by water currents. Their scabrid trichomes no doubt play a role in dispersal.

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Los Santos, Panamá and Darién, from premontane wet forest in Panamá (Cerro Campana), and from tropical wet forest in Darién.

PILEA Lindl.

Pilea microphylla (L.) Liebm., K. Danske Vidensk. Selsk. Skr. Naturvidensk. Math. Afd., ser. 5, 2:296. 1851

Monoecious (rarely dioecious), glabrous, succulent herb, often minute but to 30 cm high. Leaves opposite, one of each pair smaller; petioles to 2 mm long; blades obovate, mostly obtuse at apex, decurrent at base, the larger to 1 cm long and 5 mm wide, the smaller to ca 3 mm long and 1.5 mm wide, with linear cystoliths. Flowers white, in minute, globular, axillary, ± sessile clusters; staminate flowers mostly 4-parted; pistillate flowers usually 3-parted, the middle segment larger than lateral ones. Achenes ovate, ca 0.5 mm long, brown. *Croat 12966.*

Locally abundant in shady or moist places in the Laboratory Clearing, especially on sidewalks, concrete, or rock walls; rare elsewhere. Flowers and fruits throughout the year.

Throughout the American tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, and Panamá, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón (Portobelo).

Fig. 208. *Boehmeria cylindrica*

Fig. 209. *Pouzolzia obliqua*

Fig. 210. *Urera eggersii*

POUZOLZIA Gaud.

Pouzolzia obliqua (Poepp.) Wedd., Arch. Mus. Hist. Nat. 9:405. 1857

Monoecious liana or climbing shrub, to 2(5) m tall; most parts densely hirsute. Leaves alternate; petioles less than 1 cm long; stipules paired, lanceolate, 3–10 mm long, persistent; blades oblong-lanceolate to oblong, acuminate, rounded to subcordate and inequilateral at base, 2–12(15) cm long, 1.5–4.5(5) cm wide, scabrous above with dense punctiform cystoliths. Flowers minute, white or greenish, in small, globular, androgynous (bisexual with staminate flowers at apex) or unisexual clusters; staminate flowers 4-parted; pistillate perianth tubular, 2- or 4-toothed, strongly veined. Achenes ovoid-ellipsoid, acute at apex, 2–4 mm diam, light brown and shiny. *Croat 11773.*

Occasional, along the shore. Flowers and fruits during the rainy season.

Guatemala to Venezuela and Peru. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Coclé, and Panamá.

See Fig. 209.

URERA Gaud.

Urera eggersii Hieron., Bot. Jahrb. 20, Beibl. 49:3. 1895
Ortiga, Palo ortigo

Dioecious liana or vine, sometimes pendent from trees (elsewhere in Panama sometimes a small tree); young stems densely hirsute, glabrous in age. Leaves alternate; petioles 1–7 cm long, sparsely pilose; stipules acute, 1.5–2 mm long, caducous; blades ovate-oblong to obovate-oblong (rarely ovate elsewhere), acuminate, obtuse to subcordate at base, 9–17 cm long, 3.5–7.5 cm wide, short-hirsute on veins below or glabrate, entire to obscurely sinuate or crenate-dentate, the linear cystoliths of the upper surface mostly radiating from scattered, pellucid-punctations, those of the lower surface aligned mostly parallel to secondary and tertiary veins. Inflorescences dichotomously branched cymes, 1–5 cm long, about as long as wide; peduncles to 2 cm long, usually less than 1 cm long; peduncles and branches of inflorescence puberulent. Flowers unisexual, minute, white or greenish, inconspicuous; staminate flowers 4- or 5-parted, sessile, in glomerules; pistillate flowers 4-parted, usually solitary, short-pedicellate, the style very short, the stigma ± capitate, densely pubescent. Achenes ± globular, to ca 3 mm diam, orange, partially covered by fleshy, enlarged perianth. *Croat 12179.*

Uncommon, in the forest. Flowers in the late dry and early rainy seasons, from April to September, especially in July and August. The fruits mature mostly from September to December, but sometimes in the early dry season.

Possibly several species are involved. In the *Flora of Panama* (Killip, 1960), this species was treated as *U. elata* Griseb., which is endemic to the West Indies. *Urera eggersii* is extremely variable throughout its range; it is described as being a shrub or tree in other regions. The description here reflects mostly material collected on BCI. Plants from BCI differ from the type specimen from Ecuador in drying darker, in having much less pubescence, and in having conspicuous cystoliths. It is possible that the BCI plants represent a new species, but the problem warrants much more field work before a decision can be made. *Urera boliviensis* Herz. and *U. killipii* Standl. & Steyerm. may also be synonymous with *U. eggersii.*

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

See Fig. 210.

41. PROTEACEAE

Trees with aromatic wood. Leaves alternate, petiolate; blades heteromorphic, the juvenile ones pinnate, the adult ones simple with pinnate venation; stipules lacking. Flowers bisexual, apetalous, actinomorphic, in terminal or axillary, bracteate racemes; sepals 4, free, petaloid; disk present; stamens 4, opposite the sepals; anthers 2-celled, longitudinally dehiscent; ovary 1, superior, 1-locular, 1-carpellate; placentation pendulous; ovules 2; style 1; stigma 1, bulbous. Fruits 2-valved follicles; seeds 2, winged.

The family is represented on BCI only by the genus *Roupala,* which is distinguished by its dimorphic leaves and by the spikelike racemes of flowers with four tepals and a slender, exserted, clublike style.

Inflorescences are brush-type pollination units in the sense of Faegri and van der Pijl (1966). Seeds are winged and apparently wind dispersed.

Some 62 genera and 1,400 species; mainly in the drier regions of the Southern Hemisphere.

ROUPALA Aubl.

Roupala montana Aubl., Hist. Pl. Guiane Fr. 1:83. 1775
R. darienensis Pitt.

Tree, to 20 m tall; wood aromatic when cut; young stems ferruginous-strigillose. Leaves alternate, heteromorphic; juvenile leaves pinnately compound, imparipinnate, the leaflets to ca 19, coarsely serrate; adult leaves simple; petioles 1–6 cm long; blades ovate, mostly acute or acuminate at apex, obtuse to cuneate at base, 5–12 cm long, 2–9 cm wide, subcoriaceous to coriaceous, grayish-green, mostly entire to undulate, rarely serrate, glabrous but the midvein above ferruginous-strigillose. Flowers cream-colored, on multi-flowered, terminal or axillary racemes; rachis 9–18 cm long, ferruginous-strigillose; pedicels ca 3 mm long, strigillose; sepals 4, linear-oblanceolate, ca 8 mm long, widely reflexed, strigillose outside, gla-

brous inside; petals lacking; stamens 4, inserted about midway on sepals, strap-shaped, ca 3 mm long, nearly sessile; disk of 4 hypogynous glands alternate with sepals; ovary densely strigose; style and stigma linear-oblanceolate, together ca 5.5 mm long, glabrous. Follicles flattened, elliptic to obovate, 2.5–4 cm long, ca 1.5 cm wide, glabrous, often obscurely spurred at base; seeds 2, oval, winged, ca 1.5 mm long and 8 mm wide. *Croat 14647.*

Seen only once at the junction of Snyder-Molino and Barbour trails. Flowers January to May. The fruits reported in June.

Mexico to Peru, Bolivia, and Brazil. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet and lower montane rain forests in Darién.

42. LORANTHACEAE

Glabrous, parasitic shrubs or vines; nodes usually swollen, the internodes with scalelike cataphylls. Leaves opposite, sessile or petiolate; blades simple, entire, leathery; venation generally obscure (may be palmately veined at base); stipules lacking. Flowers bisexual or unisexual (dioecious or monoecious), actinomorphic, borne on a cupular receptacle (the calyculus) in axillary spikes of few to many flowers; perianth in 1 or 2 similar series, the outer series truncate or 4- or 6-parted, the inner series (lacking in ours) 6-parted; stamens equal in number to perianth lobes and borne on them; anthers 2-celled, generally introrse, dehiscing longitudinally, often with a connective extending above the thecae; ovary inferior, formed by the receptacle, 1-locular (obscurely so), presumably 3- or 4-carpellate; placental area central, basal; ovule 1; style 1, simple; stigma capitate or lacking in staminate flowers. Fruits berries; seeds few, with endosperm.

This family of parasitic shrubs with brittle stems is not confused with any other. Plants are particularly conspicuous in the dry season if their host happens to be a deciduous tree. All species are photosynthetic and attached firmly by modified roots (haustoria), which connect directly to the vascular system of the host. No systematic study has been made with regard to host preference but, if any exists, it is not apparent. The *Citrus* species (67. Rutaceae) of the Laboratory Clearing abound with a number of species of Loranthaceae, especially *Oryctanthus* and *Phthirusa pyrifolia,* but this is perhaps due to the fact that these trees are roosts for a multitude of birds. Sexual parts of the opposite sex for species with unisexual flowers may be absent altogether as in *Phoradendron* or merely reduced and sterile as in *Struthanthus.*

The minute greenish flowers are pollinated by small insects (Kuijt, 1969).

The sticky-seeded berries are typically bird dispersed (Ridley, 1930; Kuijt, 1969). Seeds are frequently seen germinating on tree branches where birds have roosted. Van der Pijl (1968) reported that some Loranthaceae have seeds with a built-in water reserve, which allows them to germinate on dry branches in the absence of water.

About 30–40 genera with 1,000–1,400 species; mainly in the tropics.

KEY TO THE SPECIES OF LORANTHACEAE

Rachis of the spike with depressions in which the flowers and fruits are attached:
- Spikes of several joints with bracteoles beneath each joint; stems with paired scales (cataphylls) on some of the internodes, at least on the lowermost internode of each branch; tepals 3:
  - Scales present at the base of each internode; stems terete; leaves more than 2.5 cm wide, acuminate ..... *Phoradendron piperoides* (H.B.K.) Trel.
  - Scales present only on the lowermost internode of each branch; stems 4-angled when young; leaves less than 2.5 cm wide, not acuminate ..... *Phoradendron quadrangule* (H.B.K.) Krug & Urban
- Spikes lacking joints or bracteoles; stems lacking paired scales; tepals 6:
  - Leaves more or less cuneate; fruits attached perpendicularly to and entirely exposed from rachis; rachis glabrous, less than 2 mm wide ..... *Oryctanthus occidentalis* (L.) Eichl.
  - Leaves rounded or cordate at base; fruits attached antrorsely to and partly sunken into cavities of rachis; rachis scaly, more than 2 mm wide:
    - Leaves petiolate, rounded at base; stems terete ..... *Oryctanthus alveolatus* (H.B.K.) Kuijt
    - Leaves usually sessile, cordate at base; stems usually sharply 2(4)-angled ..... *Oryctanthus cordifolius* (Presl) Urban

Rachis lacking depressions:
- Plants herbaceous vines, usually much more than 1 m long; leaves orbicular, less than 5 cm long; flowers more than 5 mm long; fruits ca 10 mm long ..... *Struthanthus orbicularis* (H.B.K.) Blume
- Plants shrubs, to ca 1 m long; leaves ovate-elliptic, more than 5 cm long; flowers less than 2 mm long; fruits ca 5 mm long ..... *Phthirusa pyrifolia* (H.B.K.) Eichl.

ORYCTANTHUS Eichl.

Oryctanthus alveolatus (H.B.K.) Kuijt, Bot. Jahrb. Syst. 95(4):504. 1976
Mato palo

Erect, parasitic shrub; stems terete, to 70 cm long; periderm rufous-scaly but glabrescent. Leaves glabrous; petioles short, to 5 mm long; blades ± ovate, rounded at apex and base, slightly decurrent on petiole, not at all clasping stem, 4–9 cm long, 3–5.5 (rarely 9) cm wide, coriaceous, drying brownish; venation palmate, the midvein not reaching apex, the principal vein usually branching. Spikes axillary, usually 2 per axil, 2–3.5 cm long, sessile or on rufous peduncles to 5 mm long; rachis becoming more than 3 mm wide in fruit, reddish, scaly; flowers sunken into pockets in rachis, oblique to the rachis; margins of bracteoles united with rachis, appearing indistinct from rachis; flowers minute, bisexual, greenish; tepals 6; stamens 6, the filaments fused to tepals; anthers strongly dimorphic, the 2 inner pollen sacs much smaller than the outer ones; style 1. Fruits ovoid-oblong, ca 5 mm long, greenish, sometimes with yellowish base, the apex exceeded by the margin of the persistent, oily calyculus; seed 1, obdeltoid, ca 2 mm long, drying black. *Croat 6566.*

Frequent along the shore and at the edges of clearings. Flowers and fruits throughout the year.

This species was confused with *O. spicatus* (Jacq.) Eichl. in the *Flora of Panama* by Rizzini (1960) and by Standley in the *Flora of Barro Colorado Island* (1933). *O. spicatus* ranges from Guatemala to Venezuela, Brazil, and Peru. It has not been reported from Panama, but is to be expected, since it occurs in Colombia (Chocó).

Costa Rica to Colombia, Venezuela, the Guianas, Brazil, and Bolivia; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, 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.

Oryctanthus cordifolius (Presl) Urban, Bot. Jahrb. Syst. 24:30. 1898

Erect, parasitic shrub; stems prominently 2(4)-angled, especially when young. Leaves sessile, thick, ovate, obtusely acute to rounded at apex, rounded to cordate at base, 7–12 cm long, 4–8 cm wide, the lateral veins from near the base 7–9, obscure, visible when dried. Spikes axillary, solitary, 1–8 cm long; peduncles 5–15 mm long; bracteoles with margins free; flowers and buds red, sunken obliquely into rachis in 4 distinct rows; tepals 6, ca 2 mm long. Fruits ellipsoid to obovoid, 5 mm long, 2.5 mm wide, perpendicular to axis, 1-seeded, purplish-black when mature (Kuijt, 1976). *Shattuck 425.*

The Shattuck collection has not been located but it is assumed to have been properly identified; the species has been collected elsewhere in the Canal Zone. Apparently flowers and fruits all year.

The species is similar to *O. occidentalis* except for its usually two-sided stem and cordate leaf blades.

Mexico to Caribbean and Pacific Colombia, Guyana (based on a single collection). In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón and Panamá, from tropical dry forest in Coclé (Penonomé), from premontane moist forest in Panamá (Punta Paitilla), and from premontane wet forest in Coclé (El Valle).

Oryctanthus occidentalis (L.) Eichl. in Mart., Fl. Brasil. 5(2):89. 1868

Erect, parasitic shrub; stems terete, usually less than 60 cm long; periderm rufous, scaly. Leaves glabrous; petioles lacking or to 5 mm long; blades ovate (may be lanceolate when young), acute to rounded at apex, ± obtuse at base and decurrent on petiole but not clasping stem, 7–11 cm long, 2–7 cm wide, coriaceous, shiny, green (bronze when young), drying chestnut and green, the veins purple. Spikes axillary, usually 2 or 3 per axil, conelike, to 3 cm long; peduncles rufous, 5–10 mm long; rachis to 2 mm wide (rarely to 3 mm), green, glabrous; flowers bisexual, sunken in rachis, perpendicular to the rachis and arranged in 4 rows; margins of the bracteoles distinct from the rachis; tepals 6, dimorphic, green, acute at apex, ca 1.2 mm long; stamens 6, each fused to lower part of tepal; filaments red; anthers dimorphic, both types at or above middle of tepal, each with 4 locules or with 2 locules, or both these types alternating, then the 4-celled anthers lower than the 2-celled anthers, the connective extending above thecae; style simple; stigma capitate, held at about the level of the anthers; nectariferous disk surrounding style at base (Kuijt, 1976). Fruits cylindrical, to 4 mm long and 2 mm wide, yellow- and green-striped, drying dark; seed 1, ellipsoid, ca 1 mm long, brown. *Croat 6443.*

Common, often in exposed, sunny areas, especially along the shore. Even individual plants may flower throughout the year.

The fruits are taken by a variety of birds, including pigeons, manakins, flycatchers, tanagers, and finches (Leck, 1972).

Costa Rica to Ecuador, Venezuela, the Guianas, Brazil, and Peru; Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Panamá, and Darién and from premontane wet forest in Bocas del Toro, Coclé, and Panamá.

See Fig. 211.

PHORADENDRON Nutt.

Phoradendron piperoides (H.B.K.) Trel., Monogr. Phoradendron 145. 1916

Monoecious, parasitic shrub; stems terete, branched, green when fresh (drying rugose with a yellowish cast), a pair of cataphylls on almost every internode, the lower internodes usually with 2–5 pairs of cataphylls. Petioles less than 5 mm long; blades obliquely ovate, bluntly acuminate, ± cuneate at base, 6–13 cm long, 2.5–5.5 cm wide, coriaceous, green when fresh, drying rugose and brownish to almost black if young, glabrous, often marginally crisped, the veins lacking or obscurely pinnate on underside. Inflorescences of axillary, jointed spikes

Fig. 211. *Oryctanthus occidentalis*

Fig. 212. *Phoradendron piperoides*

2.5–4.5 cm long, the spikes 4–6(8) per node, the joints 4–6 per spike, each subtended by two small, perfoliate bracts to 2 mm long; peduncles obscure or lacking; flowers unisexual, yellow, generally 12–20 per joint, 4-ranked, minute; tepals 3. Fruits attached from depressions in the rachis, ellipsoid, ca 4 mm long when mature, pale yellow to orange-brown. *Croat 8408.*

Occasional, in open areas and along the shore. Flowers and fruits from January to August.

The proper name for this species cannot be *P. piperoides* (H.B.K.) Trel. J. Kuijt (pers. comm.), who has studied the type of *Loranthus piperoides* H.B.K., reports that it is not the same species as that going by the name *P. piperoides.* Until someone can study the types of other old synonyms, however, the name will be used.

Mexico to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Coclé, Panamá, and Darién, from premontane wet forest in Bocas del Toro and Chiriquí, and from premontane rain forest in Chiriquí.

See Fig. 212.

Phoradendron quadrangule (H.B.K.) Krug & Urban, Bot. Jahrb. Syst. 24:35. 1897

P. seibertii Rizz.; *P. venezuelense* Trel.

Mahoho, Mongreo

Monoecious, parasitic shrub, ± glabrous, only the inflorescence obtaining a yellowish cast when dry; stems square at least when young, a pair of cataphylls on only the lower internode of each branch. Petioles ca 2 mm long; blades elliptic-oblong, somewhat asymmetrical, mostly rounded at apex, sometimes mucronulate, attenuate to the base, 3–6 cm long, 0.7–2.5 cm wide, coriaceous, drying green to brown, rugulose, glabrous, the veins 3 and parallel or lacking. Spikes axillary, jointed, 1 or 2 per node, 1.5–4 cm long, the joints 3 or 4 per spike, each subtended by 2 minute bracts to 15 mm long; peduncles 3–10 mm long; flowers yellowish-green, generally 10–24 per joint, minute; tepals 3. Fruits attached from depressions in the rachis, globose, ca 3 mm long, yellow. *Croat 7398.*

Occasional, in the Laboratory Clearing. Flowers and fruits throughout the year.

Panama, Colombia, and Venezuela; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Panamá, and Darién, from tropical dry forest in Herrera and Coclé, and from premontane moist forest in the Canal Zone, Los Santos, and Panamá.

See Fig. 213.

PHTHIRUSA Mart.

Phthirusa pyrifolia (H.B.K.) Eichl. in Mart., Fl. Brasil. 5(2):36. 1868

Parasitic shrub, sometimes to about 1 m long; branches flattened, 2-edged (especially the younger ones), the scurfy margins extending onto midrib of blades. Leaves glabrous; petioles 3–10 mm long; blades ovate-elliptic, obtuse to rounded at apex, rounded at base, 5–10 cm long, 3–5 cm wide, coriaceous, the veins often visible. Spikes 1 or 2 per axil, to 15 cm long; flowers bisexual, 4–6-parted, maroon, 1–2 mm long, in sessile ternations, these widely spaced along the furfuraceous, lenticellate spikes; calyculus truncate; tepals valvate, oblong, acute; stamens shorter than tepals; filaments thick, fused to lower half of tepal; anthers about as broad as long, held at the level of the style; ovary red; stigma sessile; nectary prominent, the nectar rather copious. Fruits oblong, ca 5 mm long, becoming yellow or orange at maturity, drying gray to brown; exocarp thin but leathery; mesocarp sticky, white; seed 1. *Croat 6812, 7919.*

Common in trees of the Laboratory Clearing; frequent elsewhere. Flowers and fruits throughout the year.

The fruits are a favorite of small birds.

Belize to Peru, Bolivia, and Brazil. In Panama known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Veraguas, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí, Panamá, and Darién.

STRUTHANTHUS Mart.

Struthanthus orbicularis (H.B.K.) Blume in R. & S., Syst. Veg. 7(2):1731. 1830

Mata rama, God bush

Dioecious, somewhat woody, glabrous, parasitic vine; stems terete with thick adventitious roots at the nodes. Petioles ca 1 cm long, sometimes twining, if so their blades reduced; blades suborbicular, rounded at apex, obtuse at base, 3–5 cm long, 2.5–4 cm wide, coriaceous, the veins generally apparent. Flowers with strong, sweet aroma, greenish or greenish-yellow, fairly conspicuous, 5–7 mm long, in sets of 3 on slender spikelike inflorescences to 15 cm long, the ternations ± sessile; tepals 6, slender, free, acute, spreading above middle; stamens of staminate flowers fused to lower half of tepals, exserted at anthesis (above recurving tepals); filaments thickened just below anther (providing some protection to nectary), 3 filaments somewhat longer than the others; anthers introrse, about as broad as long; stigma held midway between upper and lower sets of anthers; nectary small, the nectar not copious. Fruits ellipsoid, ca 1 cm long, faintly orange to rust-red or purple, with copious milky latex; seed solitary. *Croat 12620, White 121.*

Uncommon, on trees near the edge of the lake in the vicinity of Colorado Point and Gigante Bay. Flowers and fruits from January to September.

Mexico to Peru and western Brazil. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Panamá, and Darién, from premontane dry forest in Herrera and Coclé, 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 and Coclé, and from premontane rain forest in Darién (Cerro Pirre).

43. OLACACEAE

Glabrous trees or shrubs. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, in axillary, cymose clusters; calyx 5(6)-lobed, accrescent and colorful in fruit; petals 5(6), briefly connate at very base, valvate; stamens 10(12), in two whorls, free; anthers 2-celled, longitudinally dehiscent; ovary superior, 3-locular, 3-carpellate; placentation apical; ovules solitary in each locule, pendulous; style 1, short; stigma 1, trilobate. Fruits drupes borne on the showy, accrescent, red calyx; seed solitary, with copious endosperm.

Flowers of *Heisteria,* the only genus of the family on BCI, are very small and inconspicuous. Distinguishing features of the flower include the superior ovary, the stamens numbering twice the petals, and the freely pendulous ovules. The colorful accrescent calyx of the fruiting plant is the most distinctive feature of the genus.

The system for pollination of the minute greenish flowers is unknown.

The fruits are clearly suited for bird dispersal. *Heisteria* fruits are dispersed by pigeons in Martinique (Ridley, 1930).

Some 27 genera with about 250 species; tropics.

HEISTERIA Jacq.

Heisteria concinna Standl., Publ. Field Columbian Mus., Bot. Ser. 8:137. 1930

Naranjillo, Ajicillo, Chorola

Glabrous tree, to 20 m tall, to ca 30 cm dbh; outer bark thin, minutely fissured (often bumpy below), peeling off easily after slash; inner bark ± thin, granular, its outer surface reddish with irregular green strips; sap with a foul, pungent odor. Leaves shiny; petioles 9–16 mm long; blades ovate, acuminate, obtuse at base, 10–15(23) cm long, 3.5–8(14.5) cm wide, coriaceous, the primary lateral veins not conspicuous, scarcely lighter than the surrounding tissue. Flowers greenish-white, ca 2 mm long; pedicels ca 5 mm long, clustered in axillary fascicles, 8–12 mm long in fruit; calyx shallow, accrescent in fruit, the lobes 5, acute; petals 5, valvate, floccose within, boat-shaped; stamens 10; anthers 0.2–0.3 mm long and wide; ovary oblate-spheroid. Fruiting calyces conspicuously 5-lobed, shorter than drupe, ca 2 cm broad, red; drupes ± globose (or broadly ellipsoid), 10–15 mm diam, white at maturity. *Croat 12559, Foster 1491.*

Common in the forest. Flowers more than once per season, apparently mostly in the late rainy season (November and probably earlier as well), with the fruits developing from January to April. A second flowering may occur in the early rainy season, but it is apparently smaller; the fruits of the second flowering have been seen mature in October and November.

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

Heisteria costaricensis Donn. Sm., Bot. Gaz. (Crawfordsville) 19:254. 1894

Slender glabrous shrub, to 2.5 m tall; young stems weakly flexuous, the internodes with 2 ribs. Petioles 5–11 mm long; blades linear-lanceolate, tapered to apex, rounded at base, 14–25 cm long, (1)2.5–5.5 cm wide, chartaceous, the primary lateral veins many and variable in number. Flowers greenish-white; pedicels clustered in axillary fascicles, ca 1 mm long, 6–12 mm long and jointed in fruit; calyx accrescent in fruit, the lobes 5, shallow; petals 5, valvate; stamens 10, free; anthers to 0.5 mm long. Fruiting calyces becoming bright red, longer than drupe, crateriform, to 2 cm diam, shallowly 5-lobed, spreading; drupes ovoid, ca 8 mm long, vertically ribbed, black with a single white seed. *Croat 4190, 11131a.*

Occasional, in the younger forest, particularly east and south of the laboratory. Flowers mostly from April to July. The fruits mature principally from July to December.

The leaves of this species are quite variable, the broadest leaves of some specimens approaching those of *H. macrophylla* Oerst. *Standley 40877* was originally identified as *H. macrophylla* for the *Flora of Panama* (Nevling, 1961) and apparently formed the basis for Nevling's report of this species for BCI.

Costa Rica and Panama. In Panama, growing mostly on the Atlantic slope at low and middle elevations; known from tropical moist forest in the Canal Zone and San Blas, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Colón and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 214.

Heisteria longipes Standl., J. Wash. Acad. Sci. 17:8. 1927

Naranjillo colorado, Coloradito

Glabrous shrub or small tree, to 10(20) m tall; inner bark red; wood pinkish, hard; younger stems olive-green, the internodes weakly ribbed. Petioles 5–15 mm long, cana-

KEY TO THE SPECIES OF HEISTERIA

Leaves linear-lanceolate, more than 3 times as long as wide ..... *H. costaricensis* Donn. Sm.
Leaves more or less ovate, less than 3 times as long as wide:
  Leaves shiny, coriaceous, the primary lateral veins not conspicuous; fruiting calyces conspicuously 5-lobed; drupes white ..... *H. concinna* Standl.
  Leaves not shiny, subcoriaceous, the primary lateral veins conspicuous below; fruiting calyces at most shallowly 5-lobed; drupes black ..... *H. longipes* Standl.

Fig. 213. *Phoradendron quadrangule*

Fig. 214. *Heisteria costaricensis*

liculate; blades ovate, elliptic or obovate, acute to acuminate at apex, acute at base, 3.5–18 cm long, 2–7.5 cm wide, subcoriaceous, the major lateral veins in 6–9 pairs, conspicuous below, distinctly lighter than the surrounding tissue. Flowers greenish, ca 2.5 mm long; pedicels ca 5 mm long, clustered in axillary fascicles; calyx shallow, accrescent in fruit, the lobes 5, acute; petals 5, greenish, valvate, boat-shaped; stamens 10, shorter than petals, included; filaments strap-shaped, narrowed just below anther; anthers ca 0.3 mm long and wide; ovary ovate. Fuiting calyces about as long as drupe, ca 2 cm broad, red, shallowly 5-lobed or undulate; drupes ellipsoid, ca 1 cm long, black. *Croat 4532, 6052.*

Common in the forest, especially the old forest. Flowers principally from April to July (especially in May and June). The fruits develop to mature size by July, but mostly in August and September.

Costa Rica to Colombia. In Panama, widespread; most common at low to middle elevations; known from tropical moist forest in the Canal Zone, Colón, Chiriquí, and Darién, from premontane wet forest in Veraguas, Coclé, Panamá, and Darién, and from tropical wet forest in Colón and Coclé.

44. ARISTOLOCHIACEAE

Lianas, the younger stems herbaceous. Leaves alternate, petiolate, simple; blades entire, somewhat pubescent; venation pinnate (may be subpinnate at base); stipules lacking; pseudostipules lacking (in ours). Flowers protogynous, bisexual, apetalous, zygomorphic, solitary in the leaf axils or on short racemes; calyx tubular, consisting of 3 united sepals, inflated at the base (the inflated part called the utricle), expanded at the limb, showy, the tube forming an annulus where it meets the limb and also forming an inverted narrowed structure on the lower end (the syrinx), which extends into the utricle; petals lacking; styles, stigmas, and stamens united in a crownlike gynostegium; stamens 6, adnate to the style; anthers 4-celled, extrorse, dehiscing longitudinally; ovary inferior, 6-loculate; placentation axile; ovules several to many per placenta, anatropous; styles 6, forming subcapitate, stigmatic lobes. Fruits capsules; dehiscence acropetal, septifragal; seeds numerous, flat, with copious endosperm.

Distinguished by their unusual flowers and fruits. The complex flower is a greatly modified calyx. For a descriptive account of flower morphology refer to Pfeifer (1966).

Pollinated by insects, usually flies (Diptera), which are attracted to the flowers by a carrionlike odor and the intense colors (usually purplish). The corolla tube has rigid retrorse trichomes on the first day after opening when the stigmas are receptive (Petch, 1924; Corner, 1964). The pollinators are prevented from leaving the flower by these trichomes, so they find their way to the utricle. The following day the anthers dehisce, shedding pollen on the insect, and the retrorse trichomes wilt, allowing the insect to escape carrying the pollen.

For a description of typical seed dispersal, see the discussion of *Aristolochia chapmaniana.*

Ten genera and about 450 species; primarily in the tropics but extending to most temperate regions.

ARISTOLOCHIA L.

Aristolochia chapmaniana Standl., Contr. Arnold Arbor. 5:60. 1933

Twining liana, sparsely hispidulous; trunk corky and deeply fissured near ground, to ca 5 cm diam. Leaves alternate; petioles 8–22 mm long; blades oblong-spatulate, acute to obtuse at apex, deeply cordate at base, 10–20 cm long, 3–6 cm wide, glabrate above, inconspicuously short-pubescent below. Flowers solitary, axillary, usually slightly arched, dark purple-brown; calyx expanded into a narrow ellipsoid balloon ca 6 cm long, then constricted into a tube ca 3.5 cm long, the tube split on one side to form an oblong-lanceolate limb to 7 cm long; corolla lacking; stamens 6, the anthers sessile and adnate to style; styles 6, connate; stigmas capitate. Capsules ovate-cylindrical, prominently 6-ribbed, 10–12 cm long, ca 5 cm wide, on a long stipe, dehiscing from apex to base, the 6 valves spreading widely to disperse seeds but remaining attached on both ends, the inner valves diverging through outer valves at apex and attached to outer valves by a ladderlike series of fibers, the fibers acting to slow dispersal of seeds; seeds very numerous, flattened, stacked in 6 vertical rows, the seminiferous part cordate, ca 5 mm diam, bearing 2 unequal pairs of lateral wings ca 2 cm wide, the sides of the wings ± rounded, the longer pair ca 1.2 cm long, the shorter pair ca 0.8 cm long. *Croat 5958, Shattuck 413* (type).

Occasional, in the forest and along the shore. Flowers from at least November to January. The fruits, with some seeds, reported from April to September. Capsules may hang on all year.

Central America and northern South America. In Panama, known from tropical moist forest in the Canal

KEY TO THE SPECIES OF ARISTOLOCHIA

Plants conspicuously pilose on most parts; limb of calyx less than 3 cm long; capsules ovoid, ca 6 cm long ..... *A. pilosa* H.B.K.
Plants not pilose; limb of calyx more than 3 cm long; capsules ± cylindrical:
  Blades deeply and narrowly cordate at base, scarcely if at all broader at base; calyx limb narrow, ca 7 cm long ..... *A. chapmaniana* Standl.
  Blades truncate or shallowly and broadly cordate at base, conspicuously ovate; calyx limb 10–20 cm long ..... *A. gigantea* Mart. & Zucc.

Fig. 215. *Aristolochia chapmaniana*

Fig. 217. *Aristolochia pilosa*

Fig. 216. *Aristolochia chapmaniana*

Zone and Panamá and from premontane wet forest in Coclé.

See Figs. 215 and 216.

Aristolochia gigantea Mart. & Zucc., Nov. Gen. Sp. Pl. 1:75, t. 48. 1824

A. sylvicola Standl.

Zaragosa

Twining liana, glabrous but the leaf blade below arachnoid-pubescent. Leaves alternate; petioles slender, ca 4–6 cm long; blades ovate, acuminate, truncate to shallowly cordate at base, 10–15(20) cm long, 7–11(12) cm wide, grayish below with arachnoid trichomes. Flowers in short racemes of few flowers, white, densely speckled with pink and maroon; calyx expanded into a ± campanulate balloon to 8 cm long, constricted into a short, reflexed tube opening into a large limb to 20 cm long; corolla lacking; stamens 6, the anthers sessile and adnate to style; styles 6, ± connate; stamens capitate. Capsules cylindrical, to 13 cm long and ca 3 cm wide, dehiscing from base, bearing many seeds; seeds 7–8 mm long, flattened, elliptic, the margins bordering a prominent medial rib, very revolute, the dehisced valves ca 1.5 cm wide. *Croat 11260, Shattuck 640.*

Rare, in the forest. Some flowers have been seen in September and December. Maturity time of the fruits is uncertain, probably in the dry season.

Known only from Panama, in tropical moist forest in the Canal Zone and Bocas del Toro and from tropical wet forest in Darién.

Aristolochia pilosa H.B.K., Nov. Gen. & Sp. 2:146, t. 113. 1817

A. costaricensis (Klotzsch) Duch.

Slender, twining liana, conspicuously pilose on most parts. Leaves alternate; petioles slender, to 7 cm long; blades ovate, acute at apex, deeply cordate at base, 6–25 cm long, 5–15 cm wide, glabrescent above. Flowers solitary in axils, speckled white and brownish-purple; calyx expanded into a short ellipsoid balloon to 3 cm long, then constricted obliquely into a campanulate tube ca 2.5 cm long, finally opening into a narrow, fringed limb 1.5–2.5 cm long; corolla lacking; stamens 6, the anthers sessile and adnate to style; styles 6, connate; stigmas capitate. Capsules ovoid, ca 6 cm long and 4 cm wide, dehiscing from base, bearing many seeds; seeds disk-shaped, ca 1 cm diam. *Croat 9011.*

Occasional, around the Laboratory Clearing. Flowers mostly from January to May, sometimes later in the rainy season also. The fruits have not been seen on the island.

Central America and northern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

See Fig. 217.

45. RAFFLESIACEAE

Parasitic herbs lacking chlorophyll, growing (on BCI) on the wood of *Casearia* spp. (96. Flacourtiaceae). Leaves lacking. Flowers unisexual, apetalous, actinomorphic, solitary, subtended by 2 series of bracts, the lower of 2 bracts, the upper of 4; sepals 4, free, imbricate, subequal, caducous; stamens indefinite, usually many, in 2 series, epigynous; ovary subinferior, 1-locular, 4-carpellate; placentation parietal; ovules many; style 1; stigma apparently an annulus around the style apex. Fruits berries; seeds many, with endosperm.

Apodanthes may be difficult to recognize as a flowering plant because of its leafless habit. It may appear to be simply a cauliflorous flower of the host plant.

About 8 genera and 50 species; tropics, primarily in the Old World.

APODANTHES Poit.

Apodanthes casearіae Poit., Ann. Sci. Nat. (Paris) 3:422. 1824

A. flacourtiae Karst.; *A. panamensis* Vatt., nomen nudum

Small, leafless, parasitic herb, emerging from the bark on trunk and larger branches of *Casearia* (96. Flacourtiaceae). Flowers solitary; pistillate flowers white to cream, sitting in a cuplike receptacle formed in the outer bark of the host plant, the receptacle 1–2 mm high and 2–3 mm wide; basal bracts 2, ± orbicular, concave, thick, 2–2.7 mm long; upper bracts 4, narrowly rounded at apex, to 5 mm long, fused to lower one-half or one-third of the ovary and pressed inward against the ovary; calyx segments 4, obovate, imbricate, white, slightly inequilateral, spreading at about the middle, narrowed at the base and borne in a minute depression near the apex of the ovary; petals lacking; ovary ovoid, orange, ca 3.5 mm long; ovules numerous, white, minute, borne on several weak invaginations in the outer walls of the unilocular ovary; style thick and stout, to ca 2 mm long, broader at apex; stigma minutely papillate; staminate flowers (Gentry, 1973a) "with a short central stylar column terminating in a hemispheric stigma-like cap; stamens inserted around the stylar column below the cap in 2 series of ca 19 each, subsessile. Fruit a berry." *Croat 17021.*

Infrequent; known from several locations in the young forest. Perhaps more frequently encountered on *Casearia aculeata* than on *C. guianensis.* Apparently not noticeable the rest of the year, plants have been seen only during August and September.

Plants are inconspicuous and easily could be missed, but the species is not confused with any other. Vattimo (1971) used the name *A. panamensis* for Panamanian populations, but the name was invalidly published. It is listed as a synonym here only to avoid future misunderstandings about the name.

Flowers were seen visited by a small, yellowish-brown bee. R. Foster (pers. comm.) also reports that the flowers are visited by small butterflies and even mosquitos.

Fruits are seemingly adapted to bird dispersal, but if so it is uncertain how the seeds find themselves on only the two species of *Casearia* on which they occur—surely birds aren't so particular where they perch! This unexplained fidelity of host and parasite indicates a more

KEY TO THE TAXA OF POLYGONACEAE

Herbs; leaves long and narrow, less than 3.5 cm wide; flowers perfect ..... *Polygonum*
Trees, shrubs, or woody vines; leaves more than 3.5 cm wide (if less, then ovate); plants usually dioecious or the flowers functionally unisexual:
  Tree more than 10 m tall and more than 12 cm dbh, the stems hollow, usually inhabited by fiercely stinging ants; achenes contained within enlarged, papery, reddish, 3-winged calyx more than 4 cm long ..... *Triplaris cumingiana* Fisch. & C. Meyer
  Woody vines, shrubs, or small trees usually less than 10 m tall or less than 12 cm dbh, usually lacking hollow stems (as adults) and not inhabited by stinging ants; achenes drupelike, enveloped in fleshy perianth lobes ..... *Coccoloba*

complex system of fruit dispersal. A host-dependent phytophagous insect might be suspected.

Range is difficult to determine because of the inconspicuous habit of the plant. Probably ranging from Belize to Brazil. In Panama, known from tropical moist forest in the Canal Zone and from premontane wet forest in Coclé (El Valle).

See Fig. 218.

46. POLYGONACEAE

Trees, shrubs, lianas, or succulent-stemmed herbs (stems hollow in *Triplaris*). Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules present as sheathing ocreae. Flowers bisexual or unisexual (functionally monoecious in *Coccoloba,* dioecious in *Triplaris*), actinomorphic, on terminal spikes, racemes, or panicles in ocreolate fascicles of 1 to few flowers; tepals 4–6, free, in 1 series (in *Triplaris,* 6, connate, in 2 series), accrescent in fruit, becoming winged or bladdery; stamens 6–9, in basically 2 series, free or adnate; anthers 2-celled, at least the outer introrse, dehiscing longitudinally; ovary superior, 1-locular, 2–4-carpellate, subtended by an annular, nectar-secreting disk; placentation seemingly basal; ovule 1, orthotropous; styles and stigmas 2 or 3. Fruits achenes (enveloped by the fleshy perianth lobes and drupelike in *Coccoloba*); seed with mealy endosperm.

Polygonaceae are distinguished by their ocreate stipules.

Pollination systems are unknown. Some members of the family have dimorphic heterostyly (Faegri & van der Pijl, 1966).

The seeds of *Triplaris cumingiana* are wind dispersed, but those of probably most Polygonaceae are principally bird dispersed. *Coccoloba* generally has a thin fleshy mesocarp and a well-protected seed, but in the case of *C. acuminata* the shiny dark seed is displayed against the greatly accrescent, fleshy, white sepals. The achenes of *Polygonum* are probably similarly displayed, but since most occur in aquatic habitats they are perhaps in part water dispersed as well. Van der Pijl (1968) suggested that seeds of *Polygonum* may be dispersed on the feet of shore birds. Despite their close association with *Triplaris,* ants of the genus *Pseudomyrmex* do not function in pollination or fruit dispersal (Wheeler, 1910). They do benefit the plant, however, by warding off predators such as leaf-cutter ants (*Atta*). The sting of the genus *Pseudomyrmex* is severe and no doubt provides *Triplaris* with considerable protection.

About 40 genera with some 800 species; mostly of North Temperate distribution.

COCCOLOBA P. Browne

Coccoloba acapulcensis Standl., Proc. Biol. Soc. Wash. 33:66. 1920

Monoecious tree, 4–8 m tall, glabrous but with the lower midrib of leaf minutely hirtellous; trunk slender, sometimes forming adventitious roots. Leaves borne individually at apex of short shoots to ca 1 cm long; blades ovate, narrowly very long-acuminate at apex, rounded at base, 4–10 cm long, 2–6 cm wide, the midrib raised above; major lateral veins in 3 or 4 pairs. Flowers brownish-purple, borne in racemes to 2 cm long from near apex of short shoot before leaves appear; rachis hirtellous; bracts ± lanceolate, ca 0.5 mm long; pedicels ca 1 mm long; staminate flowers borne individually along rachis (usually less than 12 per inflorescence); tepals usually 5, oblong-obovate, rounded at apex, ca 1.5 mm long, ± spreading; stamens usually 9, to 4.5 mm long; pistillate flowers not seen. Fruits narrowly ovoid, red, to 9 mm long and 6 mm wide (dried), often moderately well developed before leaves appear. *Croat 8339, 14991.*

Apparently rare on the island; collected on Standley Trail 1340 and north of Zetek Trail on the escarpment in the old forest. Flowers in early April before the leaves appear. The fruits usually develop by late April, and the trees have leaves by the time the fruit fully matures (see *Gentry 5163,* Madden Lake).

KEY TO THE SPECIES OF COCCOLOBA

Midrib sunken above (at least with respect to blade surface) and usually pubescent with conspicuous, brown, hispid or puberulent pubescence (the trichomes sometimes deciduous in age) ..... *C. manzanillensis* Beurl.

Midrib raised above, usually glabrous or inconspicuously puberulent (never with conspicuous long trichomes):
Leaves less than 10 cm long, ovate, narrowly very long-acuminate at apex, rounded at base, borne on a short shoot about 1 cm long; inflorescences ca 1–2 cm long ..... *C. acapulcensis* Standl.
Leaves usually more than 10 cm long, not shaped as above; inflorescences much longer:
Leaves lanceolate to ovate-lanceolate, gradually acuminate, often less than 5 cm wide, with prominent axillary tufts on lateral veins of lower surface; inflorescences spicate; fruiting perianths red or white; plant usually a shrub ..... *C. acuminata* H.B.K.
Leaves not as above, often more than 5 cm wide, generally lacking axillary tufts below; inflorescences racemose; fruiting perianths never red or white; plants usually a tree or vine:
Plant usually a vine; blades often subrounded, broadly rounded at base, usually blunt to rounded at apex, the midrib often with some short puberulence above; lepidote scales on blades reddish-brown ..... *C. parimensis* Benth.
Plant a tree; blades acuminate at apex, not subrounded; midribs usually glabrous above; lepidote scales usually pale, easily seen under magnification ..... *C. coronata* Jacq.

Panamanian material, though identified as *C. acapulcensis* by R. A. Howard, differs radically from specimens elsewhere in Central America. However, the species is quite variable.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone (BCI and near Madden Lake) and from tropical wet forest in adjacent Colón (Río Piña–Río Media divide). The species tends to grow only in regions where there are extensive outcrops of limestone.

See Fig. 219.

Coccoloba acuminata H.B.K., Nov. Gen. & Sp. 2:176. 1817

Slender, functionally monoecious shrub or tree, 2–8 m tall; stems glabrous to puberulent, with sparse round lenticels; ocreae to 1 cm long. Petioles from base of ocrea, 4–15 mm long; blades mostly oblong-lanceolate or oblong-elliptic, acuminate, cuneate to nearly rounded at base, mostly 6–18 (22) cm long, 2–5 (8) cm wide, glabrous above, glabrous to weakly pubescent on midrib and veins below, the vein axils tufted, the midrib arched. Inflorescences terminal, spicate, slender, mostly 15–25 cm long; rachis ridged, swollen at each flower cluster; staminate flowers red, ca 2 mm long, appearing successively from the apex of a very short, stout, bracteated stalk; perianth lobes 5, ovate, imbricate, 6–8 mm long, fleshy, accrescent, reddish turning white at maturity; stamens 8 (9), included, the filaments fused into a tube ca half their length; anthers blocking entrance to nonfunctional ovary. Pistillate flowers usually borne singly at each nodule of rachis; ovary 3-sided; styles 3, short, held somewhat below anthers; nectar stored within staminal tube. Fruits subglobose, 6–8 mm wide, the achene strongly 3-sided, shiny black or brown, enveloped by 3 of the 5 perianth lobes and contrasting sharply with them in color, protruding at maturity. *Croat 15101.*

Common along some areas of the shore. Flowers and fruits throughout the year.

Panama to Ecuador, Peru, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical wet forest in Darién.

Coccoloba coronata Jacq., Enum. Syst. Pl. Ins. Carib. 19. 1760

C. obovata H.B.K.

Peña blanca, Papaturra blanca

Apparently dioecious tree, 4–13 m tall, the trunks mostly less than 15 cm diam and clustered, usually producing sucker shoots from near base, the internodes often hollow; branches glabrous, the younger parts with lepidote scales (striate when dry); bark smooth. Petioles ± terete, 1–2.5 cm long, inserted above base of stipule (about midway on stipule); blades ± ovate to obovate, abruptly to gradually acuminate at apex, acute to obtuse or subcordate and sometimes inequilateral at base, 8–24 cm long, 3–9.5 cm wide, glabrous but with both surfaces bearing ± prominent lepidote scales; midrib raised above; juvenile leaves red to wine-colored, to 28 cm long and 14 cm wide or larger. Inflorescences slender, solitary, erect, on short lateral branches; flowers numerous, white, ca 2 mm long, subtended by brown ocreolae; staminate inflorescences to 25 cm long; stamens usually 8, exserted. Pistillate inflorescences 16–20 cm long, the flowers sessile or short-pedicellate; staminodia usually 8, short; styles 3; stigmas spatulate, flattened. Fruits sessile or short-stalked, ovate, ± terete in cross section when fresh (prominently striate when dry), to 12 mm long and 8 mm wide. *Croat 11962.*

Occasional, in the forest. Usually flowering from late June to August, less frequently in September. The fruits mature from September to December.

The hollow stems may be inhabited by small ants.

Guatemala to Colombia and Venezuela; Trinidad, southern Windward Islands. In Panama, known principally from tropical moist forest in the Canal Zone, San Blas, Chiriquí, Veraguas, Panamá, and Darién; known also from tropical dry forest in Herrera (Pesé) and from premontane wet forest in Chiriquí, Coclé, and Panamá.

See Fig. 220.

Coccoloba manzanillensis Beurl., Prim. Fl. Portobello in K. Vetensk. Acad. Handl. 142. 1854 (1856)

C. nematostachya (Griseb.) Lindau

Hueso

Monoecious tree, usually less than 13 m tall; branchlets densely appressed-pubescent; stems at first grayish-

Fig. 218. *Apodanthes casearíae*

Fig. 219. *Coccoloba acapulcensis*

Fig. 220. *Coccoloba coronata*

Fig. 221. *Coccoloba manzanillensis*

Fig. 222. *Coccoloba manzanillensis*

pubescent, soon becoming glabrous, gray, conspicuously lenticellate (striate when dried); ocreae divided to middle or below, to 4.5(9) cm long. Petioles 1–2 cm long (to 4.5 cm on juveniles), inserted at base of ocrea, puberulent (also with longer trichomes near base); blades oblong-elliptic to obovate, short-acuminate (often downturned) to rounded at apex, narrowing below middle, narrowly cordate or rounded at base, mostly 9–28 cm long, 4.5–19 cm wide, young, thin, and often reddish when in flower, mature, thick, and bullate in fruit, ± glabrous above but with the veins densely brown-hirsute (trichomes sometimes deciduous in age), the veins sunken above, conspicuously raised and puberulent to hirsute below. Inflorescences spikelike racemes to 40 cm long, pendent from the ends of the main stem or from short lateral branches near apex; flowers greenish, ovate, ca 1.5 mm long, functionally unisexual; staminate flowers in clusters of 3 or 4; tepals 4 or 5, green; stamens 6–8, long-exserted, spreading; pollen white, moderately tacky; pistillode with 2 or 3 styles. Pistillate flowers densely congested on racemes, borne singly at each nodule. Fruits globose (beaked and striate on drying), ca 6 mm diam, reddish to violet-purple at first, fleshy, sweet, and purple when mature; achenes ovoid, beaked, dark brown, ca 4 mm long, drying trigonous. *Croat 9558, 15071.*

Adult plants common along the shore but uncommon within the forest; juveniles are abundant within the forest, especially in the younger forest. Juveniles are typically unbranched with hollow, densely pubescent stems and leaves that are very large (usually 35–50 cm long and 18–27 cm wide), short-petiolate, elliptic to obovate or oblanceolate, with pilose, deeply divided stipules to 11 cm long. Plants lose their leaves shortly before flowering and generally flower as new leaves are emerging. Flowers from late rainy season into the dry season. The fruits are mature in the rainy season, mostly from June to September.

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

See Figs. 221 and 222.

Coccoloba parimensis Benth., London J. Bot. 4:626. 1845

C. leptostachya Standl.

Monoecious liana, extending into top of canopy (juvenile sometimes appearing to be suberect shrub; plant reportedly a tree elsewhere); stems minutely puberulent, becoming glabrous (striate when dry), often ± flattened. Petioles mostly 2–3 cm long, (to 5 cm on juveniles) weakly canaliculate above; stipules ocreate, 2.5–5 cm long, subpersistent; blades broadly ovate to elliptic or obovate, rounded to acuminate at apex, rounded to subcordate and sometimes inequilateral at base, mostly (5)10–25 cm long and (3)5–16 cm wide (juveniles to 33 cm long and 22 cm wide), both surfaces with minute, reddish-brown, lepidote scales, the midrib raised, ± glabrous to minutely puberulent above, all veins conspicuously raised below, usually loop-connected. Inflorescences axillary or terminal on short, lateral, leafy branches, usually solitary; all parts puberulent; flowers greenish, ca 2 mm long, each surrounded by a thin brown ocreola; staminate inflorescences to 16 cm long, the flowers clustered in distinct, somewhat spiral whorls; stamens slightly exserted; pistil rudimentary. Pistillate inflorescences usually less than 10 cm long, the flowers solitary at each nodule; stamens rudimentary; pistil 2 mm long; styles 3. Fruiting pedicels usually 3–4 mm long; fruits ovoid to globose, to 1 cm long, black, with a thin, fleshy mesocarp; seed 1, ovoid, ca 7 mm long, brown. *Croat 4777, 15161.*

Frequent in the forest. Flowers at the beginning of the rainy season in May and June. The fruits usually mature by September and November, sometimes as early as August.

Less common than *C. manzanillensis.*

Known from Panama, Colombia, Peru, and Brazil. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

POLYGONUM L.

Polygonum acuminatum H.B.K., Nov. Gen. & Sp. 2:178. 1817

Robust herb, to 3 m tall (usually less), often growing in water; moderately to densely strigose on most parts. Leaves sessile or subsessile; blades linear-lanceolate, long-acuminate at apex, abruptly decurrent at base, 10–30 cm long, 1–3.5 cm wide, strigose-ciliate, inconspicuously pellucid-punctate; ocreae 2–3 cm long, apically ciliate with long strigose pubescence 1–1.5 cm long. Inflorescences terminal, spikelike racemes or panicles of few branches; flowers continuous on rachis, fasciculate, whitish, subtended by ciliate, imbricate ocreolae 2–3.5 mm long; pedicels exceeding ocreolae ca 1 mm, conspicu-

KEY TO THE SPECIES OF POLYGONUM

Leaves conspicuously strigose all over; ocreae with long apical cilia to 1.5 cm long ..... *P. acuminatum* H.B.K.

Leaves glabrous or pubescent on veins only; ocreae with apical cilia lacking or less than 1 cm long:

Leaves, ocreae, and tepals conspicuously dark-punctate; midribs of leaves subglabrous ..... *P. punctatum* S. Elliott

Leaves, ocreae, and tepals inconspicuously pellucid-punctate; midribs of leaves strigose ..... *P. hydropiperoides* Michx.

ously articulate at apex; tepals 4(5), ovate, 2.5–3.5 mm long; stamens usually 6, exserted, ca 3.5 mm long; ovary lenticular; styles 2, 2–3 mm long. Achenes lenticular, 2–2.5 mm long, 1.5–2 mm wide, brown to black, beaked. *White 142.*

Rare, in marshy habitats. Seasonal behavior uncertain. Probably flowers and fruits throughout the year.

Mexico to Argentina; West Indies. In Panama, known only from tropical moist forest in the Canal Zone.

Polygonum hydropiperoides Michx., Fl. Bor. Amer. 1:239. 1803

Slender herb, to ca 1 m tall, often ± reclining, subglabrous. Petioles usually less than 5 mm long; blades linear-lanceolate, long-acuminate at apex, acute and decurrent on petiole at base, 4–15 cm long, 0.5–1.5 cm wide, inconspicuously pellucid-punctate, usually strigose on midrib and veins below, minutely ciliate; ocreae 1–3 cm long, with strigose apical cilia to 8 mm long. Inflorescences terminal, spikelike racemes or panicles of few branches; flowers interrupted along rachis, fasciculate, light purplish to greenish, subtended by ciliate ocreolae 2–3 mm long; pedicels exceeding ocreolae ca 1 mm, articulate at apex; tepals usually 5, ovate, 2–3 mm long; stamens usually 9, ca 1.5 mm long; ovary trigonous; styles 3, ca 1 mm long. Achenes trigonous, 2–3 mm long, brown to black, inconspicuously beaked. *Shattuck 840.*

Collected once by Shattuck at Gigante Bay. Apparently flowering and fruiting throughout the year.

Canada to South America. In Panama, known only from BCI.

Polygonum punctatum S. Elliott, Bot. S. Carolina & Georgia 1:455. 1817

Chilillo, Chili de perro

Slender herb, to 70 cm tall, nearly glabrous. Leaves, ocreae, and tepals conspicuously dark-punctate; petioles less than 5 mm long; blades linear-lanceolate, acuminate at apex, narrowly decurrent on petiole at base, 2–10 cm long, 0.5–2 cm wide, glabrous but minutely ciliate and sometimes with the midrib near base sparsely strigose; ocreae 5–15 mm long, with strigose cilia at apex usually 7–10 mm long. Inflorescences terminal, spikelike racemes or panicles of few branches; flowers interrupted along rachis, fasciculate, white or greenish, subtended by ciliate ocreolae 2–3 mm long; pedicels exceeding ocreolae 1–2 mm, articulate at apex; tepals 5, ovate, 3–4 mm long; stamens usually 8, 1.5–2 mm long; ovary trigonous; styles 3, ca 1 mm long. Achenes trigonous, 2.5–4 mm long, brown to black, somewhat beaked. *Croat 5247.*

Rare, in marshy places, especially sandbars. Flowers throughout the year, possibly with a peak in the late rainy and early dry seasons.

Canada to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from tropical dry forest in Coclé, and from premontane wet forest in Chiriquí and Coclé.

TRIPLARIS Loefl.

Triplaris cumingiana Fisch. & C. Meyer, Mém. Acad. Imp. Sci. Saint-Pétersbourg, Sér. 6, 6:149. 1840

Palo santo, Guayabo hormiguero, Vara santa

Dioecious tree, usually 10–20 m tall; trunk smooth, 12–30 cm dbh; bark light brown, thin, peeling off; stems hollow. Petioles very short or to 2 cm long, canaliculate; blades mostly oblong-elliptic, acuminate, obtuse at base, 15–30 cm long, 4–12 cm wide, glabrous but with the veins below strigose (especially midrib). Inflorescences from upper axils; staminate inflorescences of spikes to 35 cm long and 1.5 cm wide; flowers subsessile, usually in pairs, emerging one at a time from densely pubescent, spathaceous ocreolae; perianth greenish, in one series of 3 linear and 3 narrowly triangular tepals 3–4 mm long, connate for about half their length; stamens 9, exserted; anthers introrse, versatile. Pistillate inflorescences of racemes to ca 20 cm long (to 30 cm in fruit); pedicels 2–9 mm long; calyx sericeous, ca 1 cm long at anthesis (greatly accrescent and becoming red in age), the lobes narrowly triangular to linear, 2–3 times the length of the tube and spreading at anthesis; petals ± linear, exceeding tube, fused to base of tube; styles 3, the inner surface stigmatic in upper two-thirds. Achenes sharply trigonous (the surfaces ± flat), 8–12 mm long, shiny, brown, persistent within and dispersed by the enlarged calyx, the calyx to 6 cm long, pubescent, 3-winged, the wings pinkish, spreading, 3.5–4.5 cm long, 6–7 mm wide. *Croat 4633, 8165.*

Usually locally common; otherwise only occasional in both the young and old forests. Plants may begin to flower when as little as 11 m tall and 12 cm dbh. Flowers from February to April, chiefly in March. The fruits begin to mature by February and are dispersed chiefly in March and April but also in May. Plants lose their leaves in July and August.

Stems are inhabited by very aggressive ants (*Pseudomyrmex triplaridis* Forel.), whose sting is quite severe.

Costa Rica to Ecuador; cultivated in the West Indies and elsewhere. In Panama, known from tropical moist forest in the Canal Zone, San Blas (Permé), Los Santos, Panamá, and Darién and from tropical wet forest in Panamá (Cerro Campana).

See Fig. 223.

47. AMARANTHACEAE

Erect or decumbent herbs, vines, or clambering shrubs. Leaves alternate or opposite, petiolate, simple; blades entire to somewhat irregular; venation pinnate; stipules lacking. Flowers bisexual or unisexual, apetalous, in bracteate panicles, spikes, or axillary glomerules; sepals 5 (or by reduction 3), free, overlapping, scarious; stamens 5 (or by reduction 3), alternate with petals, united below into a tube, filamentous; staminodia present or absent; anthers 2- or 4-celled, introrse, with dorsal-median at-

KEY TO THE SPECIES OF AMARANTHACEAE

Leaves alternate:
- Sepals 5; flowers bisexual; leaf blades usually more than 7 cm long; plants occasional ..... *Chamissoa altissima* (Jacq.) H.B.K.
- Sepals 3; flowers monoecious or polygamomonoecious; leaf blades less than 6 cm long; plants rare or no longer present on the island ..... *Amaranthus viridis* L.

Leaves opposite:
- Inflorescences ± globose, not more than 2 cm long:
  - Mature leaves pilose; stigmas 2 ..... *Gomphrena decumbens* Jacq.
  - Mature leaves at most sparsely villous; stigma 1:
    - Sepals longer than utricle, 3–5-veined ..... *Alternanthera ficoidea* (L.) R. Br.
    - Sepals shorter than utricle, 1-veined ..... *Alternanthera sessilis* (L.) R. Br.
- Inflorescences not globose, usually more than 2 cm long:
  - Inflorescence a simple spike, the flowers in glomerules, becoming reflexed and hooked ..... *Cyathula prostrata* (L.) Blume
  - Inflorescence a panicle of spikes, the flowers not reflexed and not associated with hooks:
    - Leaf blades near base of plant ovate ..... *Iresine celosia* L.
    - Leaf blades near base of plant lanceolate to linear ..... *Iresine angustifolia* Euphr.

tachment, dehiscing by longitudinal slits; ovary superior, unilocular; ovule solitary (in ours), basal, campylotropous; style single, conspicuously trifid; stigma capitate or long-bifurcate or trifurcate. Fruits indehiscent or circumscissily dehiscent utricles (1-seeded, with a loose pericarp); seed usually with a shiny testa and abundant endosperm.

Distinguished by their small, densely bracteate, usually greenish inflorescences with inconspicuous apetalous flowers and small shiny seeds.

The flowers are probably wind pollinated or self-pollinated (H. Baker, pers. comm.).

Seeds are dispersed chiefly by small birds. Ridley (1930) reported that seeds of some genera, including *Gomphrena,* are possibly wind dispersed by means of the plumelike pubescence of the achene or the glumaceous flower and broad persistent bracts. Some seeds are eaten by browsing animals and passed unharmed (Ridley, 1930), and some are harvested by ants (Wheeler, 1910).

About 50–65 genera with 500–850 species; mostly in the tropics of Africa and America.

ALTERNANTHERA Forssk.

Alternanthera ficoidea (L.) R. Br., Prodr. 1:417. 1810

Decumbent, sprawling perennial herb; stems branching, to ca 1 m long; stems velutinous above and on nodes below, the trichomes antrorsely hispidulous. Leaves opposite; petioles 2–10 mm long; blades broadly ovate to elliptic or obovate, acute and mucronulate at apex, cuneate at base, to 6 cm long and 3 cm wide, villous when young, becoming sparsely villous to glabrate. Inflorescences of sessile, whitish, axillary, ovoid or globose tufts to 1 cm long; bracts and bracteoles ± equal, ± ovate, to 3 mm long, acuminate; flowers bisexual; sepals 5, similar to bracts but the outer 3 broader, 3-veined, 3–5 mm long; stamens 5, united below, exceeded by pseudostaminodia; style 2–3 times longer than the single, capitate stigma. Utricles indehiscent, suborbicular, membranaceous, to 1.5 mm long, shorter than sepals; seeds reddish-brown, to 1.2 mm long. *Croat 9240.*

Abundant in the Laboratory Clearing, usually growing over and supported by other low vegetation. Flowers and fruits all year though probably with a peak of activity in the dry season.

BCI plants apparently intergrade with *A. halimifolia* (Lam.) Standl., as they show characters intermediate with that species, especially the moderate to dense, plumose pubescence.

Florida and central Mexico south to Paraguay; West Indies. In Panama, an occasional weed growing in clearings and along streams; known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Coclé, and from tropical wet forest in Colón.

See Fig. 224.

Alternanthera sessilis (L.) R. Br., Prodr. 1:417. 1810

Sanguinaria

Similar to *A. ficoidea* except the petioles 1–5 mm long; the blades to 4 cm long and 1.5 cm wide; the inflorescences of axillary tufts to 4 mm long; the bracts and bracteoles 1 mm long or less; the sepals 5, 1-veined, to 1.5 mm long; the utricles 1.5–2 mm long, slightly exceeding the sepals. *Standley 40948.*

Perhaps no longer present on the island, but reported by Standley to have been frequent. Probably flowers all year, but especially during the rainy season.

Honduras to Brazil; West Indies. In Panama, the few collections are widely scattered and the plant occasionally extends to aquatic habitats; known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién.

Fig. 223.
Triplaris cumingiana

Fig. 224.
Alternanthera ficoidea

Fig. 225. *Chamissoa altissima*

AMARANTHUS L.

Amaranthus viridis L., Sp. Pl. ed. 2, 1405. 1763
A. gracilis Desf.
Bledo, Calalú

Polygamomonoecious or monoecious annual herb, to ca 1 m tall, glabrous; stems branched. Leaves alternate; petioles 0.5–4 cm long; blades ± deltoid, emarginate to rounded and mucronate at apex, truncate to subacute at base, 1.5–6 cm long, 1–4 cm wide. Flowers in closely congested, ± cylindrical thyrses ca 5 mm wide, arranged in racemes; bracts and bracteoles ca 1 mm long; sepals 3, rounded and mucronate at apex, 1–1.5 mm long; stamens 3, equaling sepals; ovary compressed-globose; style 1, minute; stigmas 3, longer than style. Utricles indehiscent, strongly rugose; seed 1, cochleate-orbicular, ca 1 mm broad, dull, dark. *Kenoyer 348.*

Collected once and not seen recently, but it could be expected in clearings. Flowers and fruits most of the year, especially in the rainy season.

Presumably native to the Old World tropics, but introduced into the New World tropics and subtropics. In Panama, known only from tropical moist forest in the Canal Zone.

CHAMISSOA Kunth

Chamissoa altissima (Jacq.) H.B.K., Nov. Gen. & Sp. 2:197. 1817

Suffruticose vine or clambering shrub, glabrous but with the fertile parts stellate-villous. Leaves alternate; petioles 0.5–3.5 cm long; blades lanceolate to ovate, broadly acuminate and mucronate at apex, ± obtuse at base, 7–15 cm long, 3–6 cm wide, villous when young, becoming glabrous. Inflorescences of glomerules arranged in axillary spikes to 10 cm long or in terminal or upper-axillary, often leafy panicles to 20 cm long; flowers bisexual, subtended by membranaceous-margined bracts to 1.5 mm long; sepals 5, subequal, ovate, acute, 5-veined, the central vein more conspicuous; stamens 5; filaments to 3 mm long, the lower third united; ovary ovate, crowned by a narrow circular ring; style to 1 mm long; stigmas 2, less than half the length of style. Utricles ovate, thin-walled, 4–5 mm long, exserted from bracts at maturity, weakly crowned at apex, circumscissily dehiscent; seed rounded and flattened, ca 2 mm diam, shiny, round, enveloped in an aril, the aril foamy, glistening, transparent, 2-valved, extruding from lower valve and becoming somewhat enlarged. *Croat 7082.*

Occasional in clearings. Flowers principally throughout the dry season, from December to April, but sometimes as late as June and elsewhere in Panama as early as September.

Central Mexico to northern Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Los Santos, and Darién, from tropical dry forest in Los Santos, Coclé, and Panamá, from premontane wet forest in Coclé, and from tropical wet forest on the Atlantic slope in Coclé.

See Fig. 225.

CYATHULA Blume

Cyathula prostrata (L.) Blume, Bijdr. Ned. Ind. 549. 1826
Cadillo

Erect or decumbent herb, to 1 m tall, usually rooting at lower nodes, sparsely puberulent to strigose on most parts. Leaves opposite; petioles to 2 cm long; blades ovate to obovate, often rhombate, acuminate, acute at base, 3–10 cm long, 1.5–5.5 cm wide. Flowers bisexual, in glomerules (often in 3s) to 5 mm long in axillary or terminal, deflexed spikes to 20 cm long, the spikes interrupted along more than half their length when mature, the glomerules at maturity with ca 20 flowers modified into hooks to 1.5 mm long; sepals 5, subequal, lanceolate, ca 2 mm long, pubescent, the veins to 3; stamens 5, united basally into a short tube projected into 5 pseudostaminodia; pseudostaminodia alternate with stamens, regularly bifurcate when young, trifurcate when mature; style 1; stigma capitate, slightly longer than stamens. Utricles ellipsoid, conspicuously operculate, irregularly circumscissily dehiscent, the cap chartaceous, the remainder hyaline; seed ovate, ca 1 mm long, tan to reddish-brown. *Croat 4072.*

Very abundant on slopes in the Laboratory Clearing; rare on forest trails. Flowers and fruits throughout the year, probably peaking in the dry season.

Widely scattered in Central America and northern South America; West Indies; common and widespread throughout the Old World tropics, where it is probably native. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Coclé, and from tropical wet forest in Colón.

GOMPHRENA L.

Gomphrena decumbens Jacq., Hort. Schoenbr. 4:41. 1804
G. dispersa Standl.

Decumbent herb, to 50 cm long, rooting at nodes and often forming dense mats, pilose on most parts. Leaves opposite; petioles obsolete or to 5 mm long; blades oblong-obovate to oblong-ovate, acute and mucronate at apex, rounded to attenuate at base, 2–5(10) cm long, 0.5–1.5(5) cm wide. Inflorescences of terminal or axillary, ± globose, pedunculate heads ca 1–1.5 cm diam; peduncles very short; flowers bisexual, subtended by whitish bracts, the largest bract to 6 mm long; sepals 5, to 5 mm long, mostly woolly-pubescent from base, becoming indurate; stamens 5, sessile, alternate with bilobed pseudostaminodia; stigmas 2; style persistent. Utricles to 2 mm long, indehiscent; seed reddish-brown, ca 1.5 cm diam. *Shattuck 633.*

Collected once on the island; rare or no longer present but to be expected. Flowers essentially all year elsewhere in Panama.

Florida and Texas to northern Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas,

Panamá, and Darién and from premontane moist forest in the Canal Zone.

IRESINE P. Browne

Iresine angustifolia Euphr., Beskr. St. Barth. 165. 1795

Erect or reclining suffruticose herb, 1 m tall; stems with several light ridges; young parts strigilose. Leaves opposite; petioles 0.5–1.5 cm long; blades lanceolate to linear-lanceolate in lower part of plant, linear in upper flowering part, acuminate and mucronate at apex, acute to attenuate at base, 5–9 cm long, 1.5–3 cm wide. Inflorescences spicate, ovoid to linear, usually ca 1 cm long and 5 mm wide, pedunculate, alternate, subtended by linear leaves, in panicles merging with vegetative part of plant, the reproductive part to 50 cm long or more; flowers bisexual, subtended by transparent, mucronate bracts to 1 mm long; sepals 5, acute, 1–1.5 mm long, pilose and subtended by dense woolly pubescence; stamens 5; stigmas 2, not much longer than style. Utricles fragile, indehiscent, capped, falling with sepals; seed lens-shaped, ca 0.7 mm diam, reddish-brown to dark brown. *Croat 8710.*

Infrequent, in the Laboratory Clearing. Flowers and fruits mostly in the dry season (February to May).

Baja California and Mexico south to Brazil; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone and Darién, from premontane dry forest and tropical dry forest in Coclé, from premontane moist forest in the Canal Zone, from premontane wet forest in Colón and Panamá, and from tropical wet forest in Colón.

Iresine celosia L., Syst. Nat., ed. 10, 1291. 1759

Dioecious herb, clambering or erect, to 3 m long, glabrate but with the young parts sometimes densely puberulent, particularly lower leaf surface. Leaves opposite; petioles 0.5–3 (6) cm long; blades ovate, acuminate and mucronate at apex, rounded to cuneate at base, 1.5–9 (15) cm long, 0.5–4 (7) cm wide. Flowers in panicles of spikes, the spikes ± sessile, filiform when young, becoming linear, to 1 cm long and 3 mm wide; bracts and sepals membranaceous, pinkish-green when fresh; sepals 5, acute at apex, 0.5–1 mm long, pilose and subtended by dense woolly tufts in the pistillate flowers; stamens 5; stigmas 2, much longer than style. Utricles fragile, indehiscent, capped, falling with sepals; seed lens-shaped, ca 5 mm diam, varying from reddish-brown to dark brown. *Shattuck 738.*

Not seen on the island in recent years but to be expected in clearings. Flowers and fruits principally from January to May, sometimes as early as December or as late as July.

Florida, Texas, and Mexico south to northern Argentina; West Indies. In Panama, ecologically variable; known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Los Santos, Coclé, Panamá, and Darién, also from tropical dry forest in Herrera and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from premontane rain, lower montane wet, and lower montane rain forests in Chiriquí.

48. NYCTAGINACEAE

Trees, shrubs, or lianas (if lianas, with axillary spines); young branchlets often ferruginous-pubescent. Leaves opposite or nearly so, petiolate; blades simple, entire; venation pinnate; stipules lacking. Flowers unisexual (dioecious), apetalous, in terminal, bracteate, corymbose clusters; calyx 5-lobed, petaloid; stamens 6–10; filaments united near the base; anthers 2-celled, dorsifixed, dehiscing longitudinally; ovary superior, 1-locular, 1-carpellate; placentation basal; ovule solitary, anatropous or campylotropous; style 1, slender; stigma divided and appearing brushlike. Fruits achenes, enclosed in the persistent, modified calyx (i.e., the anthocarp); seed 1, with endosperm.

Members of the family are distinguished by the simple, often subopposite leaves, which usually dry darkened, by the distinctive anthocarpic fruit, and by the unisexual apetalous flowers, which usually have an undulate perianth limb and a brushlike or much-divided style.

Pollination systems are unknown.

Fruits of *Neea* and *Guapira* are endozoochorous. Those of *Neea* are chiefly bird dispersed but are also taken by monkeys. Oppenheimer (1968) reported that white-faced monkeys usually remove the pulp and discard the seed. Fruits of *Guapira* are probably dispersed in part by birds, but white-faced monkeys eat them as well. *Pisonia aculeata* has sticky fruits that appear suited for

KEY TO THE SPECIES OF NYCTAGINACEAE

Plants lianas with stout axillary spines ..... *Pisonia aculeata* L.
Plants shrubs or trees, unarmed:
  Shrubs usually less than 2 m tall (to 7 m); staminate flowers tubular-urceolate, the stamens included; pistillate flowers with ovary sessile, the style included; anthocarps reddish to violet-purple at maturity, usually less than 10 mm long, the surface drying smooth ..... *Neea amplifolia* Donn. Sm.
  Trees to 20 m or more tall; staminate flowers campanulate, the stamens ca half-exserted; pistillate flowers with ovary stipitate, the style exserted; anthocarps dark blue-violet at maturity, mostly more than 10 mm long, drying with prominent longitudinal grooves ..... *Guapira standleyanum* Woods.

epizoochory by becoming attached to the fur of animals or to the feathers or beaks of birds.

About 30 genera with 300 species; mostly in the American subtropics and tropics.

GUAPIRA Aubl.

Guapira standleyanum Woods., Ann. Missouri Bot. Gard. 48:404. 1961

Dioecious tree, to 20(35) m tall and 70 cm dbh, sometimes buttressed, often ribbed near base; outer bark very thin, flaking in minute pieces; inner bark tan; sap moderately strong and somewhat foul-smelling; glabrous but with the branchlets and inflorescences densely ferruginous-tomentose and the petioles and midribs puberulent. Leaves opposite, crowded; petioles 1–3 cm long, variable on same stem; blades variable, ovate to elliptic to obovate, acute to blunt or long-acuminate at apex with tip downturned, acute to rounded at base, 5.5–20 cm long, 2.5–9 cm wide, often inequilateral, broadly undulate, drying gray-brown. Inflorescences terminal, corymbose-thyrsiform, 4–13 cm long, all exposed parts minutely ferruginous-pubescent; flowering peduncles to 8 cm long; flowers unisexual, greenish-yellow, 3–7 mm long, densely tomentose; perianth campanulate, flared abruptly above base, the rim undulate, not flared; staminate flowers campanulate; stamens 7–10, about half-exserted; filaments united near base. Pistillate flowers with the perianth accrescent and persistent in fruit; ovary stipitate; style exserted, whitish at anthesis; stigma with many divisions. Anthocarps oblong-ellipsoid, 12–16 mm long, minutely ferruginous-pubescent, becoming dark blue-violet at maturity, longitudinally striate when dry; seed 1, whitish, ribbed, oblong-ellipsoid, to 13 mm long; mesocarp fleshy, purple, to 2 mm thick. *Croat 5555, 5704.*

Frequent in the forest. Flowers from February to June. The fruits mature mostly from May to July.

More field work is necessary on this species before the name can be certain. *Guapira standleyanum* does not differ appreciably from the type of *G. costaricana* Standl. from the Nicoya Peninsula of Guanacaste Province in Costa Rica. Nor does it differ greatly from *G. itzana* Lund. from Guatemala or from the following species of *Torrubia,* which are also to be considered *Guapira: T. uberrima* Standl. (Colombia), *T. rusbyana* (Heim.) Standl. (Venezuela), and *T. myrtiflora* Standl. (Peru). Probably the species is much more widespread, but currently it should be considered to be endemic to Panama.

Differing considerably from *Guapira standleyanum,* however, are plants going by the name *Guapira costaricana* Standl. from premontane wet forest at higher elevations such as El Valle in Coclé and Loma Prieta in Los Santos (e.g., *Lewis et al. 2199*). This is possibly a new species.

Known only from Panama, where it is ecologically variable; known from tropical dry forest in Panamá, from tropical moist forest in the Canal Zone and Darién, and from probably premontane wet forest in Colón (Santa Rita Ridge).

See Fig. 226.

NEEA R. & P.

Neea amplifolia Donn. Sm., Bot. Gaz. (Crawfordsville) 61:386. 1916

N. pittieri Standl.

Dioecious shrub, usually less than 2 m tall (to 7 m); younger branches densely ferruginous-pubescent, becoming glabrate in age. Leaves opposite or nearly so; petioles 0.5–5 cm long, canaliculate, often somewhat reddish; blades ± elliptic, ovate to obovate-elliptic, abruptly to gradually long-acuminate, obtuse to attenuate at base, 7–36 cm long, 3–15 cm wide, entire, glabrous above, glabrate to puberulent below. Inflorescences terminal, obscurely dichasial thyrses, essentially glabrous to densely ferruginous-pubescent, 4–15 cm long, bearing few to many flowers; staminate flowers narrowly tubular-urceolate, 5–10 mm long, about 2.5 mm wide, the perianth with 5 short lobes, the limb weakly spreading; stamens 8, to 5.5 mm long, included, attached near base of tube; filaments of different lengths, united into a short tube around the sessile pistillode. Pistillate flowers similar to staminate flowers but with a prominent constriction about one-third of the way down the perianth tube, thickened within at point of constriction; style and staminodia (usually 9) fitting tightly through the constriction, included, later exposed when the upper third of perianth above the constriction withers and falls; staminodia held just above constriction; ovary narrowly elliptic, sessile, at first loosely enveloped by perianth, by maturity completely filling it; style slender; stigma with few divisions. Anthocarp elliptic-oblong, ca 1 cm long, at first reddish, becoming violet-purple at maturity, the persistent perianth fleshy and sweet; seed solitary, somewhat shorter than fruit. *Croat 4213, 5626.*

Frequent in the forest. Flowers throughout the year, most commonly from March to September. The fruits are most common from June to December.

Standley (1933) also reported *N. psychotrioides* Donn. Sm., which is a Costa Rican species earlier confused with *N. laetevirens* Standl. of the Atlantic slope of Panama. *N. laetevirens* probably does not occur on BCI. Most of the material from BCI assigned the name *N. psychotrioides* is *N. amplifolia.* A single sterile collection, *Shattuck 121,* is in doubt; it does not appear to be typical of *N. amplifolia.* However, it can be stated with confidence that a second species of *Neea* does not now occur on the island. Leaves of the species are consistently host to various cryptogamic epiphytes, including mosses and lichens.

Costa Rica and Panama. In Panama, known principally from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Darién; known also from premontane wet forest in Colón, Chiriquí, and Coclé and from tropical wet forest in Colón.

See Fig. 227.

PISONIA L.

Pisonia aculeata L., Sp. Pl. 1026. 1753

Dioecious, climbing shrub or liana, growing into canopy, its climbing aided by stout, recurved, axillary spines on

Fig. 226. *Guapira standleyanum*

Fig. 228. *Pisonia aculeata*

Fig. 227. *Neea amplifolia*

smaller stems, nearly glabrous to sparsely villous, especially on younger parts, underside of leaves, and axes of inflorescences; trunk to 12 cm diam, unarmed; branching divaricate. Leaves opposite to subopposite, the pairs often markedly unequal; petioles 0.5–3 cm long; blades variable, mostly obovate to obovate-elliptic, acute to short-acuminate at apex, rounded to acute at base, 2–10 cm long, 1.5–5 cm wide, usually glabrate above except midrib. Inflorescences usually terminal on condensed short shoots; flowers greenish-yellow, numerous, in dense, ± globular, short-pedunculate clusters to 4 cm diam; pedicels short, bearing few bracts; pedicels and perianth densely and coarsely short-pubescent; staminate flowers campanulate, ca 3 mm long, the limb 5–7 mm diam, the lobes 5, acute; stamens 6–8 (often 7), unequal, widely exserted, to 8 mm long; anthers as broad as or broader than long, longitudinally dehiscent, dorsifixed at base; pistillode with a slender style and brushlike stigma, usually held to one side and above rim. Pistillate flowers tubular, ca 2.5 mm long; style short-exserted; stigma brushlike; staminodia reduced. Fruiting inflorescences usually much expanded; anthocarps club-shaped and 5-sided, to 1.5 cm long, densely short-pubescent, bearing a longitudinal row of prominent stalked glands on the angles, the glands sticky. *Croat 5390, 8313.*

Occasional, in the canopy of the forest, sometimes hanging down over the edge of the lake. Plants may lose their leaves just before flowering. Flowering usually occurs from January to April, with the fruits maturing as early as February.

The sticky, stipitate glands on the fruit presumably function in distribution by adhering to the feathers of birds.

Widely distributed in the American tropics. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane moist forest in Panamá, and from premontane wet forest in Coclé.

See Fig. 228.

49. PHYTOLACCACEAE

Herbs or weak shrubs, sometimes with a garlic odor. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules minute or lacking. Flowers bisexual, actinomorphic, in terminal or extra-axillary racemes, bracteate; tepals 4 or 5, briefly united; stamens 4 to many, free, inserted on the hypogynous disk; anthers 2-celled, dorsifixed, dehiscing longitudinally; ovary superior, 1-carpellate (*Rivina* and *Petiveria*), 2-carpellate (*Microtea*), or many-carpellate (*Phytolacca*); locules the same number as carpels; ovules 1 per locule, on axile placentas; styles the same number as carpels. Fruits many-celled berries (*Phytolacca*), drupes (*Rivina, Microtea*), or uncinate achenes (*Petriveria*); seeds with much endosperm.

The species of Phytolaccaceae on BCI are individually distinct, but there is relatively little that typifies them as a family.

Pollination systems are unknown.

The fruits are chiefly ornithochorous in *Phytolacca rivinoides* and *Rivina humilis* and epizoochorous in *Microtea debilis* and *Petiveria alliacea.* In *Petiveria* fruits are attached by the hooked apices of the achene. In *Microtea debilis* the fruits are attached to animals by the numerous viscid protuberances on the exocarp. Seeds of *Rivina humilis* have been found in the gut of ducks (Ridley, 1930).

Seventeen genera with over 120 species; widespread but mostly in the American subtropics and tropics.

MICROTEA Sw.

Microtea debilis Sw., Prodr. Veg. Ind. Oec. 53. 1788

Decumbent herb, 15–50 cm long; stems sharply angled. Petioles 5–20 mm long, winged nearly to base; blades variable in shape, commonly ovate, elliptic, or rhomboid, acute at apex, long-attenuate at base, 1–4 cm long, 1–2.8 cm wide, glabrous. Racemes terminal or upper-axillary, 1.5–4 cm long; bracts lanceolate, ca 1 mm long, very thin, persistent; pedicels ca 1 mm long; tepals 5, lanceolate, less than 1 mm long, white; stamens 5, ca 0.5 mm long; ovary globose, ca 0.5 mm diam; stigmas 2. Drupes ± globose, 1–1.5 mm diam, with ± viscid tubercles often united into a honeycomb pattern; seed black, closely filling the capsule.

Reported by Standley (1933) for BCI, but no specimens have been seen. The species occurs in weedy areas of the Canal Zone and may appear from time to time on the island. Flowers and fruits principally in the dry season.

Guatemala to Peru and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone,

KEY TO THE SPECIES OF PHYTOLACCACEAE

Racemes less than 15 cm long:
- Tepals 4, more than 2 mm long; fruits red drupes more than 4 mm diam; leaves usually more than 4 cm long ..... *Rivina humilis* L.
- Tepals 5, less than 1 mm long; fruits achenes less than 2 mm diam; leaves less than 4 cm long ..... *Microtea debilis* Sw.

Racemes more than 15 cm long:
- Flowers subsessile; tepals 4; fruits linear achenes less than 1 cm long, bearing 4 uncinate green appendages at apex ..... *Petiveria alliacea* L.
- Flowers with pedicels more than 5 mm long; tepals 5; fruits globose berries 2–6 mm diam, black and juicy ..... *Phytolacca rivinoides* Kunth & Bouché

Bocas del Toro, Panamá, and Darién and from tropical dry forest in Panamá (Taboga Island).

PETIVERIA L.

Petiveria alliacea L., Sp. Pl. 342. 1753
Garlic weed, Anamú

Herb, to ca 1 m tall, woody at base in age; cut parts with a foul aroma; inconspicuously appressed-pubescent on stems, axes of inflorescences, and leaves, especially on veins. Petioles 5–20 cm long; blades narrowly elliptic to obovate, acuminate or acute at apex, acute at base, 5–16 cm long, 2–6 cm wide. Flowers white, in sparsely flowered, terminal or upper-axillary racemes 15–40 cm long; pedicels ca 1 mm long; tepals 4, white or greenish-white (sometimes pinkish), spreading, united at base, 3–5 mm long, erect, green and persistent in fruit; stamens 8, fully exposed at anthesis, to ca 3 mm long; filaments unequal; anthers linear, dorsifixed; ovary densely pubescent, bearing 4 uncinate green appendages at apex, the hooks becoming enlarged and prominent in fruit (probably aiding in epizoochorous dispersal); stigma finely dissected, subapical. Achenes linear, bilobed at apex, to 8 mm long, each lobe bearing hooks to 4 mm long. *Croat 17051.*

Uncommon, in the forest beyond the Tower Clearing. Flowers and fruits throughout the year, principally in the rainy season.

Southern United States to Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Panamá, and Darién, from tropical dry forest in Los Santos, Herrera, and Panamá, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí and Coclé.

PHYTOLACCA L.

Phytolacca rivinoides Kunth & Bouché, Ind. Sem. Hort. Berol. 15. 1848
Pokeberry, Jaboncillo, Calalú

Robust, glabrous herb, often woody at base, usually 1–2 m tall, sometimes treelike and to as much as 4 m tall; branches angulate. Petioles 1–4.5 cm long; blades elliptic, oblong-elliptic, or lanceolate, acuminate and often mucronate at apex, decurrent at base, 9–17 cm long, 4.5–7 cm wide. Racemes terminal or upper-axillary, 15–50(70) cm long; rachis and pedicels often reddish; pedicels 7–13 mm long; basal bracts 1.5–2 mm long; bracteoles 2, ca 0.5 mm long; tepals 5, ovate, ca 2 mm long and 1.5 mm wide, white to reddish; stamens 9–17(22), 2–3 mm long, in 2 whorls on a hypogynous disk; ovary globose, 10–16-carpellate, united; styles connivent at base, free above. Berries ± globose, 2–6 mm diam, purple-black and juicy at maturity, ribbed when dry. *Hladik 110, Shattuck 1150.*

The species was once common on the island, judging from collections made, but now is apparently rare along the shore in clearings. Probably flowers and fruits throughout the year.

Mexico to Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, Panamá, and Darién, from premontane wet forest in Colón, Chiriquí, and Panamá, and from premontane rain forest in Coclé and Darién.

RIVINA L.

Rivina humilis L., Sp. Pl. 121. 1753

Herb, sometimes woody at base, usually to ca 1 m tall; stems ribbed. Petioles 1–6 cm long; blades mostly ovate, acuminate, rounded to truncate at base, 2.5–12 cm long, 1.5–6 cm wide, glabrous to finely pubescent. Racemes terminal or axillary, 6–15 cm long; pedicels to 3 mm in flower, to 8 mm long in fruit; tepals 4, spatulate, 2–3.5 mm long, greenish in bud, white or pinkish at anthesis; stamens 4, alternate with tepals and inserted at base of perianth, 1–2 mm long; anthers held at level of stigma; ovary ellipsoid to obovoid, 1-carpellate; style ca 0.5 mm long; stigma capitate. Drupes red, broadly ovoid, 4–6 mm long, 3.5–5 mm broad; mesocarp juicy; seed ca 2.5 mm wide, round, weakly flattened, the pubescence dense, stiff.

Reported by Standley (1933), but no specimens have been seen. A weedy species in the Canal Zone, it can be expected on BCI. Flowers and fruits throughout the year, principally in the dry season.

Southern United States to Argentina; West Indies (Cayman Islands); Africa, Asia, and Australia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Panamá, and Darién, from tropical dry and premontane wet forests in Coclé, and from tropical wet forest in Chiriquí.

50. PORTULACACEAE

Succulent, glabrous, prostrate herbs. Leaves alternate, petiolate, fleshy, succulent; blades simple, entire; venation obscure; stipules minute. Flowers bisexual, actinomorphic, crowded in the axils; sepals 2, briefly united, subequal; petals 4, briefly united, yellow; stamens 6–15, inserted at base of petals; anthers 2-celled, longitudinally dehiscent; ovary half-inferior, 1-locular, 2- or 3-carpellate; placentation basal; ovules many, campylotropous; styles and stigmas 4–6. Fruits circumscissile capsules; seeds many, with copious endosperm.

Members of the family can usually be distinguished by having fleshy leaves and flowers with two sepals. *Portulaca oleracea*, the only species on BCI, is native to northern Africa and distributed throughout the world. For centuries it was a medicinal plant and pot herb. (Ridley, 1930).

Pollination system is unknown.

Seeds are apparently dispersed by the wind or merely spilled locally. Elsewhere, ants of the genus *Pheidole* harvest seeds (Wheeler, 1910).

Nineteen genera with more than 500 species; widely distributed in the subtropics and tropics.

PORTULACA L.

Portulaca oleracea L., Sp. Pl. 445. 1753
Pusley, Verdolaga

Glabrous herb, usually less than 20 cm long, prostrate and radially spreading. Petioles 1–8 mm long; stipules minute, fimbriate; blades elliptic to obovoid, obtuse at apex, cuneate at base, 1–3 cm long, 0.5–1 cm wide. Inflorescences near apex of stems; flowers sessile, yellow; sepals 2, ovate, 3–4.5 mm long, connate below, unequal, ± persistent; petals 4, 3–4.5 mm long; stamens 6–15; anthers globose; style 4–6-lobed. Capsules ovoid to fusiform, ca 2.5 mm diam; seeds minute.

Reported by Standley as "a rare weed in open places." No specimens from the island have been seen, but the species should be expected there. Elsewhere in Panama apparently flowers and fruits throughout the year.

A weed in temperate and tropical regions of the New World; native to the Old World tropics. In Panama, known from disturbed areas of tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Los Santos, Coclé, Panamá, and Darién; known also from premontane wet forest in Chiriquí (Boquete).

51. CARYOPHYLLACEAE

Annual herbs. Leaves opposite, petiolate; blades simple, entire, palmately veined at base; stipules present. Flowers bisexual, actinomorphic, in bracteate, terminal, axillary cymes of 5 to many flowers (rarely 1); sepals 5, free; petals 5, free, bifid, white; stamens 2–5, slightly connate at base; anthers 2-celled, versatile, dehiscing longitudinally; ovary superior; placentation free central; ovules numerous, campylotropous; styles 3, united at base. Fruits longitudinally dehiscent capsules; seeds usually several to many; endosperm hard.

Caryophyllaceae are of relatively little consequence in tropical regions. They can be distinguished by a combination of opposite leaves, connate leaf bases, free central placentation, and unilocular capsules.

About 80 genera with over 2,000 species; mostly in North Temperate regions.

DRYMARIA Willd.

Drymaria cordata (L.) Willd. ex R. & S., Syst. Veg. 5:406. 1819

Weak herb; stems prostrate and spreading or erect, 10–30 cm long, rooting at lower nodes, branching along length of stem. Petioles wing-margined, 2.5–5 mm long, connected by stipules; stipules scarious, laciniate, to 2.5 mm long; blades reniform to ovate, rounded to acute at apex, subcordate to rounded at base, 5–25 mm long, 5–30 mm wide, palmately veined, crenulate. Inflorescences of terminal or axillary dichasial cymes of few to many flowers or rarely the flowers solitary in axils; pedicels canescent-glandular, to 5 mm long; sepals 5, elliptic, scarious-margined, ca 3 mm long, 3 (5)-veined; petals 5, white, deeply bifid and Y-shaped, the rounded sinus between lobes ca 2 mm deep, the lobes linear; stamens 2 or 3 (to 5); filaments flattened, 2–2.5 mm long; anthers suborbicular, ca 0.2 mm long; ovary ellipsoid, ca 2.5 mm long; styles 3, free nearly to bases. Capsules ovoid, 1.5–2.5 mm long, the 3 valves entire; seeds 1–12, 1–1.5 mm broad, dark, reddish-brown, tuberculate. *Croat 4163.*

Frequent in clearings. Flowering and fruiting from May to January.

Pollination system is unknown. Seeds are probably spilled locally.

Pantropical. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane wet forest in Coclé, from tropical wet forest in Panamá, and from lower montane wet forest in Chiriquí.

52. NYMPHAEACEAE

Aquatic, rhizomatous, perennial herbs, the leaves and flowers floating. Leaves alternate or basal, long-petiolate; blades simple, entire or more often serrate, with a deep basal sinus; venation palmate; stipules lacking. Flowers bisexual, actinomorphic, often fragrant; sepals 4–8, mostly free; petals several to many, white; stamens many; anthers 2-celled, introrse, dehiscing longitudinally; pistils many, immersed in the receptacle; ovary thus semi-inferior, 1-locular; placentation parietal; ovules many per ovary, anatropous; style 1; stigmas many, radiate. Fruits baccate, ripening under water and dehiscing irregularly; seeds many, arillate, operculate, with little endosperm.

These large floating-leaved aquatics are confused only with Menyanthaceae (117), which have a similar habit but have five-parted flowers in umbels and are easily separated.

Nymphaea ampla, with flowers opening by day, are visited by pollen feeders; *Trigona* bees visit them in large numbers. Pollination of *Nymphaea blanda,* whose flowers open at night, has never been observed, but it should be by a completely different group of pollinators. At least some species of *Nymphaea* are trap flowers. In greenhouse studies *N. citrina* Peter had a definite pistillate and staminate phase (Faegri & van der Pijl, 1966). During the pistillate phase, the stigma secretes nectar. Later the stamens of the inner whorls close over the stigma and thus the flowers present only pollen. The flowers are thus considered protogynous. It is not known if the same or similar activities are carried out by *Nymphaea* species on BCI. According to Schulthorpe (1967) most Nymphaeaceae are nectarless and are pollinated by beetles, small flies, and "sweat" bees, which "crawl indiscriminately over flowers." He reported that *N. ampla* L. is mostly odorless and homogamous (stamens and style developed at the same time) and that the species is largely self-pollinated.

Seeds are probably mostly water dispersed, though those of *N. blanda,* which is often found in isolated and

seasonal swamps, must also be carried around by birds or other animals. Van der Pijl (1968) reported that in other areas species of *Nymphaea* are sometimes distributed by ducks. He also reported that the seeds of *N. alba* L. are heavier than water but float because of a transformed arilloid.

Eight genera with about 80 species; cosmopolitan.

NYMPHAEA L.

Nymphaea ampla (Salisb.) DC., Reg. Veg. Syst. Nat. 2:54. 1821
Waterlily

Aquatic, glabrous herb. Leaves with very long petioles, arising from a rhizome rooted in soil; blades floating on water, suborbicular, 10–45 cm long, green above, usually purple-mottled below, the veins raised on lower surface, the margin prominently toothed, the sinus deep. Flowers to ca 15 cm diam at anthesis, long-pedunculate, opening diurnally, held somewhat above surface of water (buds below surface); sepals 4–8, greenish with purple striations, 6–10 cm long; petals white, slightly shorter and more numerous than sepals, blunt at apex; stamens numerous, the outer progressively longer, the connective produced above, the innermost stamens usually folded over the bowl-shaped surface of carpels; stigmas slender, radiating from center, 5–7 mm long. Fruits 2–3 cm broad, maturing beneath water, irregularly dehiscent; seeds many, subglobose, ca 1 mm diam, strigillose, indurate. *Croat 5715.*

Uncommon, in quiet waters on the south edge of the island. Flowers seen from February to July on BCI; elsewhere in Central America no seasonal variation is obvious from specimens. Fruit maturity time uncertain.

Development of the flower primordia is very slow and may require three to four years for flowers to develop fully (Cutter, 1957).

The bee *Trigona cupira* have been seen in great numbers collecting pollen from this species.

Throughout tropical and subtropical regions of the New World. In Panama, known from wet places in tropical moist forest in the Canal Zone and adjacent Panamá.

See Fig. 229.

Nymphaea blanda G. Meyer, Prim. Fl. Esseq. 201. 1818

Rhizomatous, aquatic herb, nearly glabrous, floating. Petioles 15–50 cm long; blades suborbicular, blunt to rounded at apex, subcordate (the sinus 1–5 cm deep), 5–15 cm long, 3–10 cm wide, entire, green below. Flowers long-pedunculate, floating on water, opening at night, mostly 7–9 cm broad; sepals 4, lanceolate-ovate to acute, 3–5 cm long, green outside, greenish-white inside; petals to 14, lanceolate-oblong, acute at apex, white, the outermost often tinged with green at apex, about as long as sepals, the innermost much shorter; stamens numerous; flattened, 1–2.5 cm long, arched inward, the outermost thicker and longer, gradually reduced in length inward; anthers introrse, comprising about half of stamen, the connective rounded at apex; carpels ca 20, connate laterally, the entire unit to 1.2 cm diam. Fruits 1.5–2.5 cm broad, 1–2 cm long, maturing under water, pulpy, irregularly dehiscent; seeds many, globose, operculate, ca 1.5 mm long, strigillose. *Croat 12232.*

Rare; known to occur intermittently in swamps. The species has been collected in the swampy area between Armour Trail 900 and Zetek Trail 300. Flowers in the rainy season. The plants disappear during the dry season.

Guatemala to northeastern South America. In Panama, known from wet areas of tropical moist forest in the Canal Zone, Coclé, Panamá, and Darién.

KEY TO THE SPECIES OF NYMPHAEA

Leaves often more than 20 cm long, usually purplish beneath, toothed on margin, the veins coarse, prominently raised on lower surface ..... *N. ampla* (Salisb.) DC.
Leaves less than 15 cm long, usually green beneath, entire, the veins fine, not raised on lower surface ..... *N. blanda* G. Meyer

53. CERATOPHYLLACEAE

Submerged, perennial aquatics. Leaves whorled, sessile; blades linear, dichotomously divided; stipules lacking. Flowers unisexual (monoecious), apetalous, actinomorphic, solitary at the nodes; sepals 6–15, basally connate; stamens 10–20, spirally arranged on a flat receptacle; anthers subsessile, 2-celled, dehiscing longitudinally, with a colored connective; ovary superior, 1-locular, 1-carpellate; placentation parietal; ovule 1, pendulous, anatropous; style 1, slender; stigma undifferentiated. Fruits nuts; seed lacking endosperm.

The family is represented by a single species on BCI, which may easily be recognized by its aquatic habit and whorled, dichotomously branched leaves.

Flowers are pollinated under the surface of the water (hyphydrophily of Faegri & van der Pijl, 1966). After the staminate flowers open, anthers float to the surface by means of their expanded connective, where they dehisce. The pollen eventually sinks and comes in contact with the filiform style of the axillary pistillate flowers (Schulthorpe, 1967).

The fruits are dispersed by water currents or aquatic birds. Plants may rely more on vegetative reproduction than on sexual reproduction. According to Ridley (1930), the widespread distribution of *Ceratophyllum demersum* is due to epizoochory by birds of its minute spiny fruits.

One genus, with 4 or more species; cosmopolitan.

CERATOPHYLLUM L.

Ceratophyllum demersum L., Sp. Pl. 992. 1753

Monoecious, submerged, aquatic herb, rootless, to about 1 m long, dark green, unbranched or branched, with a single lateral branch produced at a node. Leaves whorled, 6–12 per node, 1–1.5 cm long, dichotomously dissected once or twice, the divisions mostly filiform, minutely denticulate, the whitish teeth on a broad base of green tissue. Flowers rare, unisexual, sessile, solitary in axil of one leaf of a whorl, ca 1 mm long; staminate flowers with sepals 10–15, basally connate; corolla lacking; stamens 10–20, spirally arranged on a flat receptacle; filaments very short; anthers linear-oblong, with a thickened, produced connective. Pistillate flowers with perianth similar to staminate flowers; ovary gradually tapered to slender style; pistil longer than sepals; stigma 1, undifferentiated from style. Nuts also rare, axillary, tuberculate, with 2 spines at base, ca 4 mm long, tipped by the long persistent style. *Croat 5738.*

Occasional, in coves around the island, occurring with but much less common than *Hydrilla verticillata* (L.f.) Royle (16. Hydrocharitaceae). Seasonal behavior unknown.

This distinctive aquatic is not confused with any other in Panama.

Cosmopolitan distribution. In Panama, it occurs probably in all lakes or slow-moving, freshwater habitats.

54. MENISPERMACEAE

Lianas or vines. Leaves alternate, petiolate; blades simple, entire or crenate (may be slightly lobed in *Odontocarya*); venation palmate or blades only palmiveined at base; stipules lacking. Flowers unisexual (dioecious), generally actinomorphic, in axillary, bracteate, often fasciculate panicles or racemes; sepals and petals 3 or 6 (1 or 4 in *Cissampelos;* petals lacking in *Abuta*), the sepals free, in 1 or 2 series; petals often connate; stamens 6 (or 4 in *Cissampelos*), opposite the petals; anthers 2- or 4-celled, the thecae often separated by a connective, dehiscing longitudinally; gynoecium of 1–6 free pistils; ovary superior, 1-locular; placentation parietal; ovules 2, aborting to 1, anatropous; style 1, very short, or the stigma sessile; stigma lobed or incised. Fruits drupaceous; seed usually lacking endosperm.

These uncommon vines or lianas are distinguished by unisexual and usually three-parted flowers, often bearing a double whorl of sepals, leaves palmately veined (at the base), and curved seeds.

Pollination systems are unknown. Plants are both dioecious and not very common.

Species with known fruits (and certainly *Cissampelos* species) are probably eaten by birds. *Cissampelos* are also eaten by white-faced monkeys (Oppenheimer, 1968).

About 65–70 genera and 350–400 species; mostly in the tropics.

ABUTA Aubl.

Abuta panamensis (Standl.) Kruk. & Barn., Mem. New York Bot. Gard. 20:22. 1970

Hyperbaena panamensis Standl.

Dioecious liana to 35 m high or tree to 6 m tall; trunk not known, probably flattened; stems terete, the older stems lenticellate. Leaves alternate; petioles (1)4–6(9) cm long, usually curved and enlarged near apex; blades variable, elliptic to oblong or ovate, acute and apiculate or short-acuminate at apex, obtuse to rounded or truncate at base,

KEY TO THE SPECIES OF MENISPERMACEAE

Blades peltate; staminate flowers with 4 sepals and 4 stamens, the petals connate; pistillate flowers with 1 sepal and 1 petal:
- Inflorescence bracts to 1.5 cm long and wide; carpels glabrous; drupes 5–7 mm long; leaves and stems sparsely pubescent, the trichomes long and spreading .... *Cissampelos tropaeolifolia* DC.
- Inflorescence bracts usually less than 1 cm long; carpels densely pubescent; drupes 4–5 mm long; leaves and stems moderately to densely pubescent, the trichomes long and sericeous or short and tomentose ..... *Cissampelos pareira* L.

Blades basifixed; staminate flowers with 6–16 sepals and 6 stamens; petals various; pistillate flowers with 6 sepals and 6 petals or petals lacking:
- Blades densely white-woolly beneath ..... *Chondrodendron tomentosum* R. & P.
- Blades not densely white-woolly beneath:
  - Plants herbaceous vines; blades broadly ovate, usually conspicuously cordate, with domatia or glands at base; sepals 6; petals 6:
    - Blades short-pubescent at least on veins below; drupes ca 1 cm long ..... *Odontocarya tamoides* (DC.) Miers var. *canescens* (Miers) Barn.
    - Blades glabrous; drupes ca 2 cm long..... *Odontocarya truncata* Standl.
  - Plants woody lianas; leaf blades mostly elliptic, rarely subcordate, lacking domatia or glands at base; sepals 6 in 2 series; petals lacking:
    - Petioles mostly more than 4 cm long; staminate inflorescences more than 10 cm long; flowers obviously pedicellate ..... *Abuta panamensis* (Standl.) Kruk. & Barn.
    - Petioles usually less than 3 cm long; staminate inflorescences less than 10 cm long; flowers sessile or nearly so ..... *Abuta racemosa* (Thunb.) Tr. & Planch.

Fig. 229. *Nymphaea ampla*

Fig. 230. *Abuta racemosa*

Fig. 231. *Chondrodendron tomentosum*

6–24 cm long, 3–14 cm wide, glabrous above, sparsely puberulent or glabrous below; veins at base 3–5. Staminate inflorescences racemose, to 10–15 cm long, the branches reduced to short-stalked, 3-flowered cymes; branches and pedicels appressed-pubescent; pedicels to 3 mm long; outer sepals 3, narrowly ovate, ca 1 mm long, the inner sepals 3, broadly ovate to obovate, 2–2.8 mm long, fleshy, granular-puberulent on inside, ± strigose on outside; petals lacking; stamens 6, 1.5–2.2 mm long; filaments somewhat flattened, pubescent at least on one margin, connate into a column toward the base; anthers ca 0.2 mm long, dehiscent longitudinally; pistillode lacking. Pistillate inflorescences racemose, axillary, pedunculate or subsessile, 7–12 cm long, with few flowers; sepals and petals similar to staminate flowers; staminodia 6, 2–2.3 mm long, short-pilose in basal half, glabrous above; ovary densely pubescent; styles 3. Fruiting peduncles stout, ca 2 mm long; fruits of 3 drupes, the drupes oblong, ca 2.5 cm long and 1.3 cm diam, yellow-orange, densely short-pubescent, sessile. *Bangham 484, Bailey 101, Standley 28417.*

A number of collections exist, but the plant has not been seen recently on the island. Seasonality not determined. Flowers mostly from July to September elsewhere in Central America, with the fruits maturing from March to May. Some flowers have also been seen in November and February.

Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone and Veraguas.

Abuta racemosa (Thunb.) Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 17:48. 1862

Dioecious liana, growing into canopy; trunk flattened, 5–20 cm diam; stems puberulent when young, becoming glabrous, the apices often attenuated and twining. Leaves alternate; petioles 0.7–4.5 cm long, usually curved and enlarged near apex; blades oblong-elliptic to oblanceolate, acuminate to bluntly acuminate, rounded, truncate, or subcordate at base, 5–15.5 cm long, 2–8.5 cm wide, stiff, glabrous but with sparse appressed pubescence below and stiff erect trichomes on major veins above, the margins entire to obscurely crenulate; veins at base 3–5, the midrib arched. Staminate inflorescences narrowly pseudoracemose, 5–10 cm long, the branchlets reduced to short-stalked, 3-flowered cymules; pedicels to 1.7 mm long; pedicels and sepals with dense, erect or appressed puberulence; outer sepals 3, narrowly triangular or lanceolate, ciliate, ca 1.3 mm long, the inner sepals 3, ovate, thick, valvate, held closely together in basal half, somewhat spreading above the middle, acute at apex, ± glabrous to granular-puberulent on inside, with appressed grayish pubescence on outside; petals lacking; stamens 6, included, slightly more than 1 mm long, in 2 series, the inner 3 somewhat larger with the filaments connate into a column and the anthers swollen, the thecae apical, widely separated by a swollen connective, the outer 3 with the filaments free and the anthers minute. Pistillate inflorescences similar to staminate but apparently shorter; pistil 3-carpellate; ovary densely sericeous, curved; styles apical and possibly fused to each other in flower but free at least in juvenile fruit, curved outward, pointed at apex. Fruits 3-parted, the carpels drupaceous, oblong-obovate, orange to black at maturity, 2–2.3 cm long, 1.1–1.2 cm diam, tomentulose when young, glabrate; seeds 1 per carpel, each surrounded by a fleshy white mesocarp. *Croat 15004.*

Occasionally seen, though likely to be common in the canopy; the flowers are small and difficult to see. Most collections have been made in tree-fall areas. Flowers in the early rainy season (May to July), with the fruits probably maturing from August to October.

Panama, Colombia, and Bolivia. In Panama, known only from tropical moist forest on BCI and in Darién.

See Fig. 230.

CHONDRODENDRON R. & P.

Chondrodendron tomentosum R. & P., Syst. Veg. 261. 1798

C. hypoleucum Standl.

Large dioecious canopy liana; trunk near the ground to ca 10 cm diam; stems terete, puberulent to tomentose (striate when dry). Petioles 4–14 cm long, puberulent to tomentose; blades ovate to suborbicular, blunt to apiculate (rarely emarginate) at apex, truncate to cordate at base, 10–20 cm long, 9–18 cm wide, subcoriaceous, glabrous above, white-woolly below; veins at base 5, palmate, with 2–4 additional pairs of major lateral veins above. Staminate inflorescences paniculate; panicles fascicled in leaf axils, often on older stems, to 10 cm long, the branches short; all axes densely tomentose; flowers greenish-white; sepals 9–16, the outermost reduced, tomentose or ciliolate, the inner 6–8 much larger, to 3 mm long, oblong-obovate to obovate, recurved, glabrate or inconspicuously pubescent, ciliolate; petals usually 6, minute and obscured by sepals, less than 1 mm long; stamens 6, ca 1.5 mm long; anthers ± horizontal, affixed subbasally, the connective produced beyond the thecae and usually directed inward. Pistillate inflorescences and flowers similar to staminate but with gynoecium of 6 pistils, the pubescence dense, short-appressed; style 1 per carpel, simple, ca 0.5 mm long, slightly curved. Drupes oblong-ovoid, ca 1.5 mm long, narrowed at base into a short stipe, tomentose to glabrous in age. *Croat 13801.*

Uncommon. Known to flower in late July and early August.

Panama to Peru and Bolivia. In Panama, known from tropical moist forest on BCI and in Darién.

See Fig. 231.

CISSAMPELOS L.

Cissampelos pareira L., Sp. Pl. 1031. 1753

Bejuco de cerca, Alcotán

Generally a slender twining vine; stems, petioles, and lower surface of leaves loosely pubescent with long and

sericeous or short and puberulent trichomes, the upper leaf surface glabrate or sparsely pubescent. Leaves obscurely peltate; petioles 3.5–7 cm long, slender; blades broadly ovate, usually obtuse and mucronate at apex, truncate to cordate at base, 2–12 cm long and wide; venation palmate. Staminate inflorescences lacy and branched many times, usually axillary, often at leafless nodes; bracts less than 1 cm long; flowers greenish, ca 3 mm diam; sepals 4, much longer than the cone-shaped corolla; stamens united, the apex flaring; anthers 4. Pistillate flowers fasciculate along axillary branches, the branches often several at a node, the fascicles each subtended by a small, ovate or reniform, leaflike bract; sepals and petals each 1 per flower, caducous, borne at the gibbous base of the carpel; carpel 1, densely pubescent; stigma deeply trilobate. Drupes suborbicular, ± flattened, red, 4–5 mm long, pubescent; seed brown, flattened, verrucose, 3–4 mm long, the embryo horseshoe-shaped. *Croat 4397, 11997.*

Generally abundant in clearings; rare in the forest. Flowers and fruits throughout the year.

Throughout tropics of the world. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Los Santos, Panamá, and Darién, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, Los Santos, Coclé, and Panamá, and from tropical wet forest in Coclé and Darién.

Cissampelos tropaeolifolia DC., Reg. Veg. Syst. Nat. 1:532. 1818

Twining vine; stems, leaves, and inflorescence branches usually with long whitish trichomes. Leaves peltate; petioles slender, 3–7 cm long; blades ovate to suborbicular, rounded to obtuse or acuminate and mucronate at apex, truncate to cordate at base, 5–11 cm long and wide, glabrous to sparsely long-pubescent above, paler and usually long-pubescent or puberulent below; venation palmate. Staminate inflorescences of fasciculate dichasia in leaf axils or on short axillary branches in the axils of reduced leaves or bracts, the bracts to 1.5 cm long and 2.5 cm wide; flowers minute; sepals 4, 1–1.5 mm long, ca 1 mm wide, usually pubescent on outside; corolla greenish, campanulate, 0.5–1 mm diam, glabrous; stamens with filaments united into a tube; anthers 4, borne on filament tube, glabrous. Pistillate flowers fasciculate in the axils of bracts on secondary branches; sepal 1, ovate to obovate, ca 1 mm long, glabrous or puberulent; petal 1, greenish, suborbicular, ca 0.5 mm long and to 1 mm wide; carpel 1, gibbous, sessile, glabrous; stigma trilobate. Drupes obovoid, flattened, 5–7 mm long, 4–5 mm wide, red, pubescent; seed verrucose, the embryo horseshoe-shaped. *Croat 9265.*

Rare in the forest. Flowers and fruits throughout the year.

Southern Mexico to northern South America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, and Darién, from premontane wet forest in the Canal Zone and Chiriquí, and from tropical wet forest in Darién.

ODONTOCARYA Miers

Odontocarya tamoides (DC.) Miers var. **canescens** (Miers) Barn., Mem. New York Bot. Gard. 20:89. 1970

O. paupera (Griseb.) Diels

Slender vine; older stems lenticellate. Leaves alternate; petioles slender, 3–8.5 cm long; blades ovate to subhastate, obtuse to acuminate and mucronulate at apex, usually shallowly cordate at base (acute on juveniles), 3–10 cm long, 3–8.5 cm wide, glabrous above, with conspicuous glandular areas at base of blades near petiole, pubescent below with short, spreading trichomes especially on veins; venation at base palmate. Inflorescences axillary or supra-axillary, solitary; rachis glabrous or puberulent; staminate inflorescences pseudoracemose, to 22 cm long, with flowers in fascicles of 2–6, occasionally with several short branches; pedicels 3–6 mm long; sepals 6, membranaceous, the outer 3 ± ovate, to 1.5 mm long and 1 mm wide, the inner 3 ± oblanceolate, 2–4 mm long, 1.5–2.5 mm wide; petals 6, the outer 3 greenish, somewhat fleshy, bowl-shaped, 2–2.5 mm long, 1.5–2 mm wide, the inner 3 similar but smaller; stamens 6, 1–2 mm long, the filaments connate about half their length; anthers 6, ca 0.5 mm long. Pistillate inflorescences strictly racemose, with 6–12 loosely spaced flowers; pedicels to 1.4 cm in fruit; sepals and petals as in staminate flowers; staminodia 6; ovary glabrous. Fruits of 1–3 drupes, ellipsoid, ca 1 cm long and 7 mm diam, reddish-orange, drying blackish. *Croat 5631, 5640.*

Rare in clearings and occasional in the canopy of the forest. Seasonal behavior uncertain. Known to flower and fruit from May to October.

Southern Mexico to Colombia, Venezuela, the Guianas, and northeastern Brazil; Lesser Antilles. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from tropical dry forest in Panamá.

Odontocarya truncata Standl., J. Arnold Arbor. 11:121. 1930

Glabrous, slender vine. Leaves alternate; petioles 4.5–7.5 cm long; blades ovate, acuminate, truncate to shallowly cordate at base, 8–13 cm long, 5–9 cm wide, with sunken, discolored domatia in axils on lower surface; venation palmate at base. Inflorescences racemose, axillary (sometimes at leafless nodes), solitary; sepals of staminate flowers 6, membranaceous, the outer 3 ovate, ca 0.5 mm long and wide, the inner 3 obovate, concave, ca 2 mm long and 1.5 mm wide; petals of staminate flowers 6, narrowly oblanceolate, ca 1.5 mm long and 0.5 mm wide; stamens 6, ca 1.3 mm long; filaments ca 1 mm long, the outer 3 connate to the middle, the inner 3 connate their entire length. Pistillate infructescences 10–20 cm long; fruiting pedicels 1–1.5 cm long; pistillate flowers unknown. Fruits

of 1–3 drupes, these oblong-ellipsoid, ca 2 cm long and 1–2 cm diam, orange-yellow, drying blackish, with a small ridge around the margin. *Croat 4945.*

Rare, at the edge of clearings. Seasonal behavior uncertain. Known to flower in January and fruit from April to September.

Costa Rica to northern Colombia. In Panama, known from tropical moist forest in the Canal Zone (on and adjacent to BCI).

55. ANNONACEAE

Trees or shrubs. Leaves alternate, petiolate, simple, entire; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, solitary or several in a cluster; sepals 3, free or connate, valvate; petals 6, in 2 series (the outer may be reduced or lacking), free or connate, imbricate or valvate; stamens numerous, free; anthers 4-celled, introrse, dehiscing longitudinally, the connective expanded above the anther; gynoecium of numerous, separate pistils; ovary superior, 1-locular; placentation parietal (may seem basal); ovules 1 to several, anatropous; style 1 and short or lacking; stigma 1, simple. Fruits monocarpic berries or fleshy aggregates (*Annona*); seeds with copious, ruminate endosperm.

Annonaceae are confused with no other family when in flower or fruit. The flowers are usually large and greenish, with thick petals and many stamens and ovules. The fruits are either fleshy aggregates or composed of several monocarps. The ruminate endosperm of the seeds is also diagnostic of the family.

The open flowers provide no access problems. They also offer little or no nectar and are probably pollinated by a wide variety of insects, especially pollen feeders with chewing mouth parts such as beetles (Corner, 1964).

KEY TO THE SPECIES OF ANNONACEAE

Inflorescences in leaf axils:
- Most blades more than 20 cm long:
  - Petals imbricate; fruits ellipsoid, ca 1 cm long, pointed at both ends ..... *Guatteria amplifolia* Tr. & Planch.
  - Petals valvate; fruits globose, ca 1.5–2 cm diam ..... *Unonopsis pittieri* Saff.
- All blades less than 20 cm long:
  - Blades less than 6 cm long, lanceolate; flowers nearly sessile; branches conspicuously arcuate-ascending ..... *Xylopia frutescens* Aubl.
  - Blades more than 6 cm long, ± elliptic; flowers pedicellate; branches not arcuate:
    - Sepals united to above middle; monocarps reniform, several-seeded, 3 or more cm long in dense globular clusters ..... *Xylopia macrantha* Tr. & Planch.
    - Sepals free; monocarps not as above:
      - Outer petals imbricate, densely pubescent; monocarps ellipsoid, indehiscent, to 2.5 cm long, with 1 seed ..... *Guatteria dumetorum* Fries
      - Outer petals valvate, glabrate; monocarps golf-club-shaped, dehiscent, more than 3 cm long, with 2 orange seeds ..... *Anaxagorea panamensis* Standl.

Inflorescences not axillary, usually ± opposite leaves or internodal:
- Petals 6, ± equal in size, narrowly lanceolate, more than 3 times longer than broad; fruits of several monocarps, stipitate, ± cylindrical, red, with several disk-shaped seeds ..... *Desmopsis panamensis* (Rob.) Saff.
- Petals with the 3 outer much larger than the 3 inner (or 3 inner petals rudimentary), the outer usually ovate (except *A. hayesii*), less than 3 times longer than broad; fruits with mericarps united into a single many-seeded mass:
  - Petals 6:
    - Outer petals connate ca 5 mm above base with a long narrow acumen; fruits less than 8 cm long, densely pubescent, lacking spines ..... *Annona hayesii* Standl.
    - Outer petals free, valvate, ovate; fruits more than 8 cm long, glabrous or spiny:
      - Plants cultivated at Laboratory Clearing; fruits spiny ..... *Annona muricata* L.
      - Plants restricted to swamps at edge of lake; fruits smooth, glabrous ..... *Annona glabra* L.
  - Petals with the 3 inner lacking or rudimentary:
    - Flowers less than 2.5 cm long and 2.5 cm wide (petal size assumed from size of other species and size of calyx); fruits of many 1-seeded, stipitate monocarps ..... *Crematosperma* sp.
    - Flowers either longer or wider than 2.5 cm; fruits not of 1-seeded, stipitate mericarps, either globose or ± ellipsoidal aggregates (1 aggregate fruit per flower):
      - Leaves glabrous; blades mostly less than 9 cm long; petals less than 15 mm long; fruits to 3 cm wide with very short protuberances, explosive at maturity ..... *Annona acuminata* Saff.
      - Leaves densely tomentose below; blades more than 10 cm long; petals more than 18 mm long; fruits to 6 cm wide, shaggy with long-attenuate protuberances, not explosive at maturity ..... *Annona spraguei* Saff.

Fig. 232. *Anaxagorea panamensis*

Fig. 233.
Anaxagorea panamensis

Fig. 234.
Annona glabra

Guatteria, Annona, and *Xylopia* are pollinated by small beetles of the families Nitulidae and Curculionidae (Gottsberger, 1970). Gottsberger reported that the flowers are protogynous, with anthesis lasting a long time, and usually somewhat closed at the end of anthesis to prevent the entry of larger beetles, which would completely destroy the flowers. Beetles are apparently attracted to the flowers by a strong foul aroma (Faegri & van der Pijl, 1966); Gottsberger (1970) likened the smell to rotting fruit.

The fruits are dispersed chiefly by birds (Ridley, 1930) and mammals, except *Anaxagorea,* which has mechanically dispersed fruits. Bats are also listed as fruit dispersers by Ridley (1930). Seeds of *Guatteria* and *Xylopia* are bird dispersed (Gottsberger, 1970). *Annona muricata* is eaten by the bat *Artibeus jamaicensis* (Phyllostomidae) in Trinidad (Goodwin & Greenhall, 1961) and by a woodpecker in Jamaica (Ridley, 1930). Fruits of *Annona acuminata* are eaten by coati (Kaufmann, 1962). Several species of *Annona,* as well as *Desmopsis panamensis,* are eaten by the white-faced monkey (Oppenheimer, 1968); the seeds and pericarp of *Desmopsis* were often spit out. *Annona spraguei* is also eaten by spider monkeys, and fruits of *Guatteria dumetorum* and *G. amplifolia* are eaten by howler monkeys (Carpenter, 1934).

About 100–120 genera and 2,000 or more species; mostly in the tropics.

ANAXAGOREA St.-Hil.

Anaxagorea panamensis Standl., J. Wash. Acad. Sci. 15:101. 1925

Shrub, to 3 m tall; parts puberulent when young, glabrous in age. Petioles 5–9 mm long; blades oblong-elliptic to lanceolate-oblong, acuminate, acute to obtuse at base, 10–16 cm long, 2.5–5 cm wide. Flowers pale yellow, solitary in axils; pedicels 1.5–2.5 cm long, with a minute bracteole near apex; sepals 3, ovate, ca 8 mm long; petals valvate, the outer 3 narrowly oblong, ca 2 cm long, the inner 3 ovate, ca 1 cm long. Monocarps obliquely club-shaped, 3–4 cm long, apiculate at apex; seeds 2 per carpel, ± elliptic, flat, shiny, orange, forcibly expelled by contraction of walls of monocarp (*fide* R. Foster). *Croat 11158, 12569.*

Rare; known from a single area in the old forest north of Zetek Trail 600. Flowers in July and January. Mature fruits were seen from November to January.

Known only from Panama, from tropical moist forest in the Canal Zone (on and adjacent to BCI) and Panamá.

See Figs. 232 and 233.

ANNONA L.

Annona acuminata Saff., Contr. U.S. Natl. Herb. 16:274, pl. 97. 1913

Camaron

Small tree, (3)4–5(7) m tall; young stems, petioles, and lower surface of blades with sparse appressed-ferruginous pubescence, soon glabrous. Petioles to 6 mm long; blades lanceolate to oblong-elliptic or oblanceolate, acuminate, acute and decurrent at base, 4–11.5 cm long, 1.5–3.5 cm wide. Flowers solitary, on stems opposite leaves; pedicels to 1.6 cm long, bearing a small bracteole near base; flower buds depressed-globose; calyx ca 5 mm long, saucer-shaped with 3 minute lobes, with appressed-ferruginous pubescence; petals 3, valvate, white, green in bud, ovate-rounded, thick, obtuse at apex, 10–15 mm long; stamens 2.5 mm long, numerous. Fruits fleshy aggregates, green, 2–3 cm wide, 1.8–2.3 cm long, rounded above, flat below, the surface covered with prominent projections 1–2 mm high, subtended by the thick, flattened, 3-sided calyx, bursting open irregularly from apex at maturity to expose bright orange interior; seeds 1 per carpel, broadest at apex, gradually tapered to base, weakly angulate, ca 1 cm long, tan. *Croat 4379, 11757.*

Frequent in the forest. Flowers from May through August. The fruits mature from November to March, sometimes beginning in October.

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

Annona glabra L., Sp. Pl. 537. 1753

Pond apple, Anón de puerco, Anón

Glabrous tree, to 10 m tall, usually to about 6 m and 15(25) cm dbh; trunk swollen below water level. Petioles canaliculate, brownish above, 1–2 cm long; blades ovate-elliptic to oblong-elliptic, acute at apex, rounded and ± decurrent at base, 5–16 cm long, 3–8 cm wide. Flowers solitary, supra-axillary (rarely opposite leaves); pedicels 1.5–3 cm long; sepals 3, short, minutely apiculate; petals valvate, thick, ovate, white, the outer 3 larger, red inside at base and often spotted with red, to 3 cm long, the inner 3 somewhat shorter, often red nearly all over the inside; stamens numerous, 3–4 mm long, the connective thickened, papillose; stigmas many, ca 1 mm long. Fruits fleshy aggregates, ovoid, rounded at apex, to 15 cm long and 9 cm wide, green, densely speckled, glabrous; seeds numerous, 1 per carpel. *Croat 5019, 7791.*

Frequent in and restricted to shoreline marshes, chiefly on the south and west sides of the island, often in association with *Acrostichum* (10. Polypodiaceae). Flowers mainly in the dry season (February to June). The fruits are probably mature from December to May, but hang on the tree all year.

Mexico to Ecuador and Brazil; West Indies, western Africa. 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.

See Fig. 234 and fig. on p. 12.

Annona hayesii Saff. ex Standl., J. Wash. Acad. Sci. 15:102. 1925

Slender tree or shrub, to 4 m tall, less than 8 cm dbh; stems puberulent when young, glabrate in age. Leaves puberulent when young, glabrous except on veins in age; petioles less than 1 cm long; blades obovate to oblong-elliptic, abruptly acuminate, rounded to obtuse at base,

10–23 cm long, 5–9 cm wide. Flowers greenish, 1 to few, opposite leaves or internodal; pedicels to 1.5 cm long; sepals 3, ovate, to ca 4 mm long, acuminate; petals valvate, the outer 3 to 3.2 cm long, connate to 5 mm at base, abruptly narrowed ca 1 cm above base, dark violet-purple inside at base, the inner three 5–7 mm long, connate with outer petals at base; stamens numerous, 1–1.5 mm long. Fruits fleshy aggregates, oblong-ellipsoid, 4–6 cm long, ca 3 cm diam, densely pubescent, smooth or with slightly raised anastomosing lines, these forming irregular isodiametric cells; seeds numerous, 1 per carpel. *Croat 11428, 14879.*

Occasional to locally common in the forest. Numerous trees grow beyond Snyder-Molino Trail 300, at Shannon Trail 0, and along Miller and Lake trails. Flowers from April to July. The fruits mature probably from July to September (sometimes to October).

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

Annona muricata L., Sp. Pl. 536. 1753
Soursop, Guanábana

Tree, to 7 m tall; young stems and sometimes petioles ferruginous-tomentose. Petioles ca 5 mm long; blades oblong-elliptic to oblong-obovate, acuminate, obtuse to rounded at base, 6–12 cm long, 2.5–5 cm wide, glabrous. Flowers solitary along stems; pedicels 2–3 cm long; sepals 3, ovate, less than 5 mm long; petals valvate, the outer 3 ovate, free, thick, 2–3 cm long, the inner 3 thinner and smaller than the outer; stamens numerous. Fruits fleshy aggregates, ovoid-ellipsoid, to 20(25) cm long and 10(12) cm diam, with white juicy pulp, dark green, bearing stout fleshy spines; seeds numerous, 1 per carpel. *Croat 5176, 5898.*

Cultivated at the Laboratory Clearing near the dock. Flowers from January to August. The fruits, which hang on all year, are known to mature in July and August, but probably in the dry season also.

Cultivated throughout tropical America; introduced into West Africa. In Panama, collections exist from tropical moist forest in the Canal Zone and San Blas, but the plant is cultivated in many places.

Annona spraguei Saff., Contr. U.S. Natl. Herb. 16:270. 1913
Chirimoya, Negrito

Tree, to 15 m tall; outer bark thin, with broad shallow fissures in young trees; inner bark thin; branchlets tomentose when young, glabrous in age; sap at first with pungent odor, soon fading. Leaves deciduous, short-pilose all over, more sparsely above; petioles 5–15 mm long; blades oblong-lanceolate to narrowly elliptic, acuminate, rounded to obtuse at base, 15–30 cm long, 6–11 cm wide. Flowers solitary, arising between nodes, globose in bud, on pedicels 1–2 cm long; sepals 3, connate at base, the lobes deltoid, to 1.3 cm long; petals 3, valvate, to 6 mm thick, broadly ovate, acute at apex, to 3 cm long, moderately pubescent outside with a purple spot inside near base; stamens numerous, ca 4 mm long. Fruits fleshy aggregates, ± globose, to 6 cm diam, green, shaggy with dense, long-attenuate protuberances; seeds many, 1 per carpel, oblong, to 1 cm long. *Croat 5070, 6750.*

Frequent in the forest, especially in the young forest. Leaves are lost in the middle of the dry season. The flowers often appear at the same time as the new leaves, usually from February to June. The fruits are probably mature from June to October.

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

See Fig. 235.

CREMATOSPERMA R. E. Fries

Crematosperma sp.

Tree, to ca 15 m; stems weakly appressed-pubescent when young, soon glabrous, lenticellate. Leaves glabrous, firm; petioles 2–4 mm long, canaliculate on upper surface; blades oblong-lanceolate, narrowly acute to acuminate at apex, acute at base, 8.5–15 cm long, 1.7–3.5 cm wide, green and shiny on upper surface, paler below, weakly glaucous; major lateral veins 10–14 pairs, weakly loop-connected 2–5 mm from margin. Mature flowers not known; flower buds suborbicular, the sepals broadly ovoid-rounded, ciliate. Fruiting inflorescences interaxillary; fruiting pedicels ca 9 mm long, 2.5 mm thick, articulate near the middle, bearing a bract above the articulation, the bract deltoid, ca 1 mm long, ciliate, the old sepals broadly triangular, ca 4 mm long; monocarps numerous, oblong-ellipsoid, 1.5–1.8 mm long, obtuse on both ends, red at maturity; seed 1, only slightly smaller than monocarp. *Garwood & Foster 442.*

Apparently rare, in the old forest; collected once recently on Wheeler Trail.

The species may be new to science, but owing to the difficulty of the group I am reluctant to describe it from a fruiting collection.

Known only from Panama on BCI.

DESMOPSIS Saff.

Desmopsis panamensis (Rob.) Saff., Bull. Torrey Bot. Club 43:185, pl. 7. 1916

Tree, usually 4–6(8) m tall; young branches densely ferruginous-pubescent. Petioles to 6 mm long; blades ± elliptic to elliptic-lanceolate, acuminate, obtuse to acute at base, 8–22 cm long, 3–10 cm wide, ± glabrous above except on midrib, brownish-puberulent beneath, especially on veins. Flowers 1 or 2, opposite leaves, with short brownish pubescence; peduncles short with an ovate-cordate bract 4–16 mm long near apex; pedicels to 7 cm long; sepals 3, small, triangular; petals 6, ± equal, free, at first green, becoming greenish-yellow at maturity, narrowly triangular, to 3 cm long, valvate or slightly imbricate at apex, the margins revolute, the apex curled inward; anthers many, sessile, to 1.7 mm long; carpels

Fig. 235. *Annona spraguei*

Fig. 236. *Desmopsis panamensis*

Fig. 237. *Guatteria amplifolia*

Fig. 238. *Guatteria amplifolia*

Fig. 239. *Unonopsis pittieri*

Fig. 241. *Xylopia frutescens*

Fig. 240. *Xylopia frutescens*

numerous, the styles held tightly together and exceeding anthers; ovules 2–8 per carpel. Monocarps densely short-pubescent, cylindrical, rounded on both ends, longer than broad, to 25 mm long, becoming soft and brick red at maturity on stipes to 1 cm long; seeds usually 4–6, disk-shaped. *Croat 7361, 8793.*

Abundant in the forest, especially in the old forest. Flowers mostly during the dry season (January to April), rarely during the rainy season. Fruit maturity time uncertain, but the fruits are eaten by white-faced monkeys from October to May (J. Oppenheimer, pers. comm.).

Known only from Panama, from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién.

See Fig. 236.

GUATTERIA R. & P.

Guatteria amplifolia Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 17:35. 1862

Tree, to 8 m tall; branches often long and arching; branchlets glabrous. Petioles short, ± curved, thick; blades moderately thick, elliptic to oblong-elliptic, abruptly or gradually acuminate, rounded or emarginate at base, mostly 20–35 cm long and 7–13 cm wide, glabrous but with inconspicuous pubescence on veins below; lateral veins impressed above, raised below, loop-connected, some reticulate veins prominent. Flowers usually solitary in axils, covered with dense short pubescence; pedicels ca 1 cm long, articulate, with 1 to several small bracts below the articulation; calyx lobes 3, acute, divided nearly to base, ca 1 cm long, often persisting in fruit; petals 6, imbricate, ± equal, triangular-oblong, ca 2 cm long, to 14 mm wide, green or yellowish; stamens very numerous, ca 2 mm long, forming a dense, round, cushion-shaped mass around style; style somewhat longer than stamens, its many stigmas held tightly together, ca 1 mm long. Monocarps ellipsoid, short-pubescent, ca 1 cm long, purple, on red stipes 10–15 mm long, 1-seeded, usually on older branches. *Croat 12216, 12693a.*

Occasional in the young forest; abundant on Orchid Island (R. Foster, pers. comm.). The flowers are seen throughout the year, less commonly from April through June. Fruit maturity time uncertain.

Mexico to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Panamá, from premontane moist forest in Panamá, and from premontane wet forest in the Canal Zone and Panamá. Reported from tropical wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Figs. 237 and 238.

Guatteria dumetorum Fries, Kongl. Svenska Vetenskapsakad. Handl., ser. 3, 24(10):12. 1948

Tree, 20–35 m tall, to 80 cm dbh, sparsely buttressed; outer bark coarse, dark, flaky; inner bark tan, unmarked; younger branchlets appressed-pubescent, becoming glabrate; sap with sweet aroma. Petioles 6–10 mm long, pubescent; blades narrowly elliptic, acuminate, acute at base and decurrent onto petiole, 6.5–15 cm long, 2.5–5 cm wide, glabrate above, sparsely appressed-pubescent below, the surfaces smooth when fresh, minutely warty when dry. Flowers greenish-yellow, 1 or 2 in leaf axils; pedicels 2–2.5 cm long, sparsely to moderately pubescent, articulate ca 5 mm above base; sepals and petals densely sericeous to tomentosc; sepals 3, valvate, 3–4 mm long, recurved; petals 6, imbricate, ± equal, rounded at apex, ca 1 cm long; staminal cluster ca 6 mm wide, somewhat 3-sided, burnt orange to tan; anthers ca 1 mm long. Monocarps 6–30, ellipsoid, acute at both ends, 1–2.5 cm long, purplish, 1-seeded, on a stipe to 12 mm long. *Croat 7738, 14040.*

Frequent in the old forest. Flowers throughout the year, mainly from February through August, with some individuals flowering more than once a year. Time of fruit maturity not known.

Known only from Panama, from tropical moist forest on BCI and in Darién and from premontane wet forest in the Canal Zone (Pipeline Road) and Colón.

UNONOPSIS Fries

Unonopsis pittieri Saff., J. Wash. Acad. Sci. 15:102. 1925

Yava blanca

Slender tree, to 20 m tall, with pyramidal crown; stems dark, often lenticellate; parts minutely sericeous when young, glabrate in age. Petioles swollen, stout, ca 6 mm long; blades elliptic to obovate-elliptic, obtuse to acuminate at apex, obtuse to rounded at base, 20–30 cm long, 6–9 cm wide. Flowers solitary in axils on leafless branches; pedicels slender, 2–4 cm long, articulate near middle with small bracteoles above and below the articulation; sepals 3, valvate, 1.5–3 mm long, triangular, connate; petals 6, valvate, sericeous, broadly ovate, thick, the outer three 8–9(20) mm long, the inner 3 thicker, 5–6(15) mm long; stamens ca 1.5 mm long. Monocarps 11 or 12, globose, 1.5–2 cm diam, brown or black at maturity, 1-seeded, on a stipe 1–1.5 cm long. *Croat 9577.*

Infrequent, in the forest, especially the old forest. Seasonal behavior uncertain; probably flowering and fruiting intermittently all year. The flowers have been seen in February, July, and August. Full-sized fruits have been seen throughout the year.

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

See Fig. 239.

XYLOPIA L.

Xylopia frutescens Aubl., Hist. Pl. Guiane Fr. 1:602, t. 292. 1775

Malagueto hembra

Slender tree, to 19(25) m tall; branches clustered toward apex of tree, arcuate, ascending; stems when young pilose, in age dark, glabrate, and lenticellate. Petioles pilose, 3–5 mm long; blades lanceolate, acuminate, acute to ob-

Fig. 242. *Virola sebifera*

Fig. 243. *Virola sebifera*

tuse at base, 3–6 cm long, 8–10(15) mm wide, stiff, glabrous above, sericeous below. Flowers ca 1 cm long, in short axillary clusters of 1–5 each, sweetly aromatic; pedicels very short, bracteate; sepals 3, ovate, to 2.3 mm long, connate at base, sericeous outside, glabrous inside; petals 6, valvate, greenish-white and ± erect at anthesis, oblong, blunt at apex, the outer 3 to 11 mm long and 2.5 mm wide, sericeous outside, the inner 3 slightly shorter and much narrower; stamens greenish, ca 1.3 mm long; style triangular-conic, to 5.3 mm long, white, fleshy, soon deciduous; stigma simple. Monocarps irregular, ca 1.5 times longer than wide, to 1.2 cm long and 7 mm wide, rounded at both ends, orange to red, (1)2(3)-seeded, the short stipe off-center; seeds ovoid, black, ca 6 mm long. *Croat 4868, 8418.*

Occasional to locally common along the margin of the lake and in the young forest. Flowers mainly from April to June. The fruits are mature mostly in the dry season, from January to April (sometimes from November).

Guatemala to southern Brazil. In Panama, ecologically variable; a typical component of tropical dry forest (Holdridge & Budowski, 1956) and tropical moist forest (Tosi, 1971), but known also from premontane dry forest in Coclé, from premontane moist forest in Panamá, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Coclé.

See Figs. 240 and 241.

Xylopia macrantha Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 17:38. 1862

Corobá, Rayado

Small tree, to 10 m tall and 10 cm dbh; stems sericeous-villous when young, glabrous and lenticellate in age. Petioles ca 5 mm long, sericeous to glabrate; blades oblong-elliptic, acuminate, rounded at base, 6–14 cm long, 2–5 cm wide, glabrous above, sericeous below when young, becoming glabrate in age. Flowers solitary at sometimes defoliated leaf axils; pedicels stout, sericeous, to 9 mm long, bracteate; sepals 3, connate to above middle, 1–1.5 cm long, sericeous; petals 6, valvate, thick, the outer 3 oblong, 2–2.5 cm long, ± tomentose, the inner 3 quadrangular-prismatic, 1–1.5 cm long, ca 3 mm thick. Monocarps 10–27, reniform to oblong, 3–4.5 cm long, puberulent, dehiscing along one side and opening out flat to expose seeds, the valves thick and fleshy, red-orange within; seeds several. *Croat 6236.*

Occasional, in the old forest and along the shore on Burrunga Point. Flowers from May to October. The fruits probably mature from February through May.

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

56. MYRISTICACEAE

Trees or shrubs with red sap. Leaves alternate, petiolate; blades simple, entire, sometimes stellate-pubescent; venation pinnate; stipules lacking. Flowers unisexual (dioecious), actinomorphic, in axillary panicles, subspicate racemes, or fascicles; perianth 3- or 4-lobed; stamens 3–8, equal or double the number of lobes; filaments partly or completely connate in a column; anthers 2-celled, extrorse, dehiscing longitudinally; ovary superior, 1-locular, 1-carpellate; placentation parietal (seemingly basal); ovule 1, anatropous; style 1; stigma 1. Fruits 2-valved, dehiscent drupes; seed 1, arillate, with ruminate endosperm.

Recognized by the tiny, unisexual flowers with fused stamens, the red sap in the trunk and branches, and the two-valved fruits each with a large arillate seed having ruminate endosperm.

Pollination systems are unknown.

The endozoochorous fruits are taken principally by arboreal frugivores, though many are found on the ground and may be dispersed by rodents and other animals. The aril around the seed of *Virola sebifera* is eaten by white-faced, spider, and howler monkeys (Hladik & Hladik, 1969; Carpenter, 1934). Oppenheimer (1968) reported that white-faced monkeys sometimes swallow the seed. Birds, including motmots, toucans, and trogons, are also fond of *Virola sebifera* (Chapman, 1931).

Eighteen genera and about 300 species; tropics.

VIROLA Aubl.

Virola sebifera Aubl., Hist. Pl. Guiane Fr. 2:904. 1775

V. panamensis (Hemsl.) Warb.; *V. warburgii* Pitt.

Velario colorado, Copidijo, Wild nutmeg, Bogamani, Fruta dorada, Gorgoran, Malaguela de montaña, Tabegua, Mancha

Dioecious tree, to 30(40) m tall, to 30 cm dbh; outer bark hard, dark, minutely fissured vertically (flaking off when slashed); inner bark moderately thick, with ± viscid, acrid sap forming near the wood; branches often clustered in distinct whorls on the trunk; younger branches, underside of leaves, inflorescences and fruits densely pubescent with reddish-brown stellate trichomes; sap reddish, with a sweet aroma. Petioles 8–25 mm long, stout, terete; blades mostly ± oblong to obovate-oblong, long-acuminate, cordate to truncate or rounded at base, mostly 20–40 cm long, 6–15 cm wide, glabrous above. Staminate flowers in much-branched supra-axillary panicles 6–12 cm long; pedicels 1–4 mm long; perianth 1.5–3 mm long, 3- or 4-lobed about one-third of its length; stamens 3(4), equaling number of lobes, fused into a column. Pistillate flowers solitary or clustered in racemes 3–7 cm long; stigma sessile, obscurely bilobed. Capsules globose to

KEY TO THE SPECIES OF VIROLA

Older leaves densely pubescent below with stalked trichomes; fruits 10–30 per inflorescence, dark reddish-brown, usually less than 2 cm wide ..... *V. sebifera* Aubl.

Older leaves glabrate, the trichomes (if any) sessile; fruits 3–8 per inflorescence, light orange, usually 3–3.5 cm wide ..... *V. surinamensis* (Rol.) Warb.

Fig. 244. *Virola surinamensis*

Fig. 245. *Virola surinamensis*

ellipsoid, ca 3 cm long, dark reddish-brown, dehiscing by 2 thick woody valves to expose a single seed; valves bearing scars on the inside made by the aril; seed ca 2 cm long, ellipsoid, the endosperm markedly ruminate, the aril red, irregularly laciniate. *Croat 4275, 4539.*

Frequent, especially in the old forest. Apparently flowering twice a year, from December to April, especially in January and February, and again from June to August. Mature-sized fruits are seen nearly all year, but the length of the fruit maturation period is unknown.

Nicaragua to Peru, Bolivia, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Figs. 242 and 243.

Virola surinamensis (Rol.) Warb., Nova Acta Acad. Caes. Leop.-Carol. German. Nat. Cur. 68:208. 1897
V. nobilis A. C. Smith

Dioecious tree, to 30 m or more tall, to ca 60 cm dbh, often moderately buttressed; outer bark coarse, hard, shallowly fissured, reddish-brown; inner bark tan, reddish on its outer surface; branches often spiraled or clustered, extending nearly horizontally; parts when young bearing ferruginous, sessile, stellate pubescence, glabrate in age; sap red, lacking distinctive odor. Petioles canaliculate, 5–10 mm long; blades oblong, acuminate, rounded to acute at base, 9–16 cm long, 1.5–4.5 cm wide, coriaceous; major lateral veins in 20–30 pairs. All parts of inflorescences densely short-pubescent, the trichomes mostly stellate; pedicels ca 1.5 mm long; perianth ca 2 mm long, 3- or 4-lobed usually to middle or beyond, the lobes thick, acute to rounded at apex, spreading at anthesis; staminate flowers in fascicles on panicles to 4 cm long; anthers mostly (2)3(6), connate to apex. Pistillate flowers in clusters of 3 to many, in racemes to 5 cm long; ovary 1-carpellate, ± ovate; stigma sessile, 2-cleft. Capsules ovoid-ellipsoid, thick-walled, light orange, 3–3.5 cm long, bearing dense, short, stellate pubescence; valves 2, woody, ca 5 mm thick, splitting widely at maturity; seed 1, ellipsoid, ca 2 cm long, the aril deeply laciniate, red at maturity (white until just before maturity), fleshy, tasty but becoming bitter soon after being chewed. *Croat 7488, 8090.*

Common in the forest, especially in the older forest; probably less abundant than *V. sebifera.* Flowers from June to March, especially November to February. The fruits mature from April to August (sometimes from February).

Costa Rica and Panama, the Guianas, and Brazil; Lesser Antilles. In Panama, known from tropical moist forest on BCI and in adjacent parts of the Canal Zone and from premontane wet forest in Panamá (Cerro Azul). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Figs. 244 and 245.

57. MONIMIACEAE

Strongly scented shrubs or small trees. Leaves opposite, petiolate; blades simple, generally entire, sometimes stellate-pubescent; venation pinnate; stipules lacking. Flowers unisexual (monoecious or dioecious), actinomorphic, in axillary or cauliflorous cymes; tepals 4–8, connate, borne on a hypanthium; stamens many; anthers 2-celled, basifixed, dehiscing longitudinally; pistils many, 1-carpellate; ovaries superior, 1-locular; placentation parietal; ovule 1 per locule, anatropous; styles simple, basally connate. Fruits drupelike aggregates, enclosed in the hypanthium, opening irregularly; seeds arillate, several, with copious oily endosperm.

The family is represented on BCI only by *Siparuna,* which can be distinguished by the very aromatic sap, by the greenish dioecious flowers having a conspicuous hypanthium and no obvious tepals, and by the aggregate, berrylike fruits, which rupture irregularly at maturity to expose the colorful interior.

Pollination system is unknown.

The hypanthium dehisces like a fruit, and the arillate seedlike fruitlets are probably bird dispersed. Though the fleshy hypanthium might be eaten by larger animals, it is not tasty.

Twenty genera and 150 species (Willis, 1966) or 32 genera and 350 species (Lawrence, 1964); chiefly in the Southern Hemisphere tropics, especially Madagascar, Polynesia, and Australia.

SIPARUNA Aubl.

Siparuna guianensis Aubl., Hist. Pl. Guiane Fr. 2:865. 1775
Hierba de pasmo, Pasmo

Monoecious shrubs or small trees, mostly to 5 m tall but occasionally taller; stems reddish, stellate-puberulent particularly when young, malodorous. Leaves opposite; petioles 5–8 mm long; blades elliptic-oblong, acuminate, round to obtuse at base, 8–18 cm long, 4–8 cm wide, densely and minutely pellucid-glandular, sparsely strigillose and stellate-puberulent above, sparsely stellate-

KEY TO THE SPECIES OF SIPARUNA

Blades sparsely stellate-puberulent below, not soft to the touch; petioles less than 1 cm long . . . . . *S. guianensis* Aubl.

Blades densely stellate-pubescent below, soft to the touch; petioles more than 1 cm long . . . . . *S. pauciflora* (Beurl.) A. DC.

Fig. 246. *Siparuna pauciflora*

Fig. 247. *Siparuna pauciflora*

Fig. 248. *Beilschmiedia pendula*

puberulent below, densely yellowish-puberulent when young; major lateral veins in 7–9 pairs. Flowers greenish, in axillary cymes, the cymes 1 or 2 on each side of stem, to 1.5 cm long (to 3 cm long in fruit), mostly unisexual, with 5–15 flowers, the puberulence yellowish, stellate; flowers to 2 mm long on pedicels to 3 mm long; tepals 4–6, deltoid; staminate flowers with 10–14 stamens; pistillate flowers with basally connate styles. Fruits several per cyme, drupaceous, aggregate, enclosed in the hypanthium, ± globose, to 1.5 cm diam, reddish-yellow when mature, bursting irregularly; seeds about 6, tuberculate, grayish. *White 250.*

Not collected in recent years on the island; several earlier collections were made, but the species may have been replaced in the course of succession in recent years. Elsewhere in the Canal Zone, the plant is occasional in disturbed areas. Flowers in April and May. The fruits mature from August to October. What is referred to as seeds within the hypanthium are the fruits of individual flowers, but it seems best to think of them as seeds of a single fruit.

Costa Rica to Colombia, Peru, and Brazil. In Panama, known from low to middle elevations in all regions of tropical moist forest (except in Bocas del Toro) and from premontane wet forest in Chiriquí (Tolé) and Panamá (Lago Cerro Azul).

Siparuna pauciflora (Beurl.) A. DC. in DC., Prodr. 16(2):696. 1868

Limoncillo, Pasmo, Pasmo tetano

Dioecious shrub or small tree, usually 4–6(10) m tall, shortly stellate-pubescent all over, densely so except on upper leaf surfaces; upper branches quadrangular or flattened; sap aromatic. Leaves opposite; petioles 1.5–4 cm long; blades broadly elliptic-obovate (may be narrowly elliptic elsewhere), generally short-acuminate to acute at apex, ± obtuse at base, 15–32 cm long, 7–17 cm wide, thin, obscurely pellucid-punctate, strigillose above but with densely stellate-pubescent veins, densely stellate-pubescent below; lateral veins in 12–15 pairs. Flowers usually many, in cymes congested in axils or borne on stems below leaves; pedicels 2–10 mm long; tepals 4–8, connate to form a broadly flattened annulus with a small central orifice, pale orange at anthesis; staminate inflorescences often short-pedunculate; stamens usually 12–30, ca 1 mm long, in several series, the filaments flattened laterally; pistillate inflorescences ± sessile, the styles many, short, densely papillate, exserted through the central orifice. Fruits drupaceous, aggregate, enclosed in the hypanthium, globose, with a crateriform depression at apex, 1.5–2 cm diam, light green at maturity, bursting irregularly to display usually fewer than 10 seeds; seeds ± oblong, verrucose, enveloped at least on one side by a thin, fleshy, rose-colored aril. *Croat 6284, 13216.*

Frequent in the forest. Flowers regularly from January to April. The fruits may reach full size by June, but do not mature until September or October.

Costa Rica to Peru; mostly at low elevations. In Panama, widespread and common throughout tropical moist forests; known also from premontane wet forests in Panamá (Cerro Azul) and Chiriquí (Tolé) and from tropical wet forest in Coclé (above El Valle), Panamá (slopes of Cerro Jefe), and Darién.

See Figs. 246 and 247.

58. LAURACEAE

Trees or shrubs, usually with weakly aromatic sap. Leaves alternate, petiolate; blades simple, entire or undulate; venation pinnate; stipules lacking. Flowers bisexual, or unisexual and dioecious (in *Ocotea*), actinomorphic, in terminal or axillary panicles, often clustered; perianth undifferentiated, arising from a hypanthium, deeply 6-lobed, the lobes unequal or subequal, generally white, often fragrant, the tubular part persisting in fruit; stamens free, epipetalous, in 3 series of 3 each, variously modified, the outer and middle series of 3 each subtended by and alternating with glands, the inner series usually bearing glands and alternating with staminodia (these ideally a fourth series of stamens), their filaments usually longer than those of the outer series, the glands usually conspicuous; anthers 2- or 4-celled (if 4, usually superimposed, but arclike in *Nectandra*), basifixed, dehiscing by flaplike valves opening upward, the outer 2 series introrse, the inner series extrorse, usually longer than the style; ovary superior, 1-locular, seemingly 1-carpellate; placentation parietal; ovule 1, anatropous, pendulous; style 1; stigma simple. Fruits drupes, often surrounded at the base by the cupular, persistent perianth tube; seed 1, lacking endosperm.

Certainly one of the most poorly known families of tropical America. Individuals of the family are among the principal components of the most poorly known lowland

KEY TO THE TAXA OF LAURACEAE
(ON THE BASIS OF TRADITIONAL SEXUAL CHARACTERS)

Anthers 2-celled; fruits lacking cupule; lower leaf surface with dense, minute, very appressed, whitish trichomes and prominulous, very closely spaced reticulate veins, the major lateral veins essentially glabrous ..... *Beilschmiedia pendula* (Sw.) Hemsl.

Anthers 4-celled; fruits with or without cupule; lower leaf surface glabrous, with erect trichomes, or if with dense appressed trichomes then lacking closely spaced prominulous reticulate veins with glabrous lateral veins:

Fruits very large, usually 10–12 cm long at maturity, lacking a cupule; staminodia large, cordate, stipitate (also true of *Phoebe*); lower leaf surface bearing conspicuous, erect pubescence ... . *Persea americana* Mill.

Fruits small, less than 6 cm long, borne in a cupule; staminodia inconspicuous and sessile or lacking; lower leaf surface glabrous or nearly so or bearing ± appressed pubescence (± erect but ascending in *Nectandra cissiflora*):
Blades 3-veined, the lateral veins prominently pliveined at base, extending to near apex; cupule of fruit conspicuously lobed ..... *Phoebe mexicana* Meisn.
Blades not 3-veined, not pliveined, the lateral veins not extending to near apex; cupule of fruit truncate:
Perianth lobes reflexed or spreading, usually fleshy; outer series of anthers fan-shaped, the 4 thecae arranged in a gradual arc; flowers bisexual ..... *Nectandra*
Perianth lobes erect, often thin; outer series of anthers broadly oblong, the 4 thecae arranged in 2 distinct or only slightly overlapping planes; flowers unisexual ..... *Ocotea*

KEY TO THE TAXA OF LAURACEAE
(CHIEFLY ON THE BASIS OF STERILE CHARACTERS)

Leaf blades definitely pubescent on lower surface:
Pubescence of lower blade surface erect or at least not closely appressed:
Blades usually broadly rounded at apex or with an abrupt, short acumen, the upper surface glabrous; flowers ca 10 mm wide; fruits more than 8 cm long ..... *Persea americana* Mill.
Blades usually gradually long-acuminate at apex, the upper surface moderately pubescent at least on midrib; flowers less than 7 mm wide; fruits less than 6 cm long .....
..... *Nectandra cissiflora* Nees
Pubescence of lower blade surface mostly appressed:
Axils of lower blade surface bearing distinct domatia (pits or tufts of trichomes):
Axillary domatia of elongated slitlike pits; blades usually broadest above the midlle .....
..... *Ocotea oblonga* (Meisn.) Mez
Axillary domatia of ± rounded tufts of villous pubescence, never of slitlike pits:
Flowers 10 mm or more wide, the perianth lobes broadly spreading; fruits ca 1 cm long
..... *Nectandra globosa* (Aubl.) Mez
Flowers less than 10 mm wide, the perianth lobes ± erect; fruits 4–6 cm long .....
..... *Ocotea skutchii* C. K. Allen
Axils of lower blade surface usually lacking domatia ..... *Beilschmiedia pendula* (Sw.) Hemsl.
Leaf blades essentially glabrous (sometimes with axillary tufts of trichomes):
Blades 3-veined or with the lower pairs of lateral veins longer than the middle and upper pairs:
Blades 3-veined, markedly pliveined at base, the lateral veins extending nearly to apex; calyx lobes persistent in fruit ..... *Phoebe mexicana* Meisn.
Blades with several pairs of lateral veins, not pliveined, the lateral veins not extending to near apex; calyx lobes deciduous, forming a truncate cup at maturity:
Perianth lobes erect, ca 1 mm long, glabrous; peduncles usually less than 1.5 cm long; blades usually prominently arched along midrib ..... *Ocotea cernua* (Nees) Mez
Perianth lobes spreading, ca 1.5–2 mm long, densely pubescent; peduncles usually more than 2 cm long; blades usually not prominently arched along midrib .....
..... *Nectandra savannarum* (Standl. & Steyerm.) C. K. Allen
Blades not 3-veined, the lower pairs of lateral veins shorter than the middle and upper pairs:
Blades bearing domatia in axils of at least lowermost lateral veins:
Blades widest at or below middle, markedly arched along midrib; reticulate venation of upper surface prominulous; flowers bisexual; perianth lobes spreading; fruits rounded, to 1.5 cm long ..... *Nectandra purpurascens* (R. & P.) Mez
Blades widest at or above middle, not arched along midrib; reticulate venation of upper surface not prominulous; flowers unisexual; perianth lobes erect; fruits ± oblong or ellipsoid, 4–6 cm long ..... *Ocotea skutchii* C. K. Allen
Blades lacking axillary domatia ..... *Ocotea pyramidata* Brandegee

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forest regions. They are often widely dispersed and difficult to distinguish and collect. Nearly three times as many Lauraceae are now known from BCI as when Standley wrote his flora; this increase is probably greater than for any other group, and no doubt even more species will still be found.

Lauraceae are easily recognized by their unusual primitive flowers, with stamens generally in two or three series alternating with the glands, and especially by the flaplike valves over the thecae of the anthers. The fruits are equally distinctive, frequently being subtended by or set in an often colorful cupule. The plants are often large trees, usually with pleasant-smelling sap. The leaves have lateral veins that usually extend downward along the side of the midrib before finally merging with it. Many other tropical species have this "lauraceous veining" but none have the characteristic as frequently or conspicuously as do the Lauraceae.

The flowers are primitive and open. Pollination systems are unknown.

Smaller-fruited species, such as *Nectandra globosa, N. purpurascens, Phoebe mexicana,* and *Ocotea cernua,* are at

least in part bird dispersed, whereas the larger-fruited species are probably dispersed chiefly by arboreal mammals. Both *Ocotea skutchii* and *Beilschmiedia pendula* fruits have been found on the forest floor with the thin exocarp scraped off, apparently the work of monkeys or birds. Large birds often regurgitate seeds after they have removed the outer layer. This may explain how many Lauraceae fruits, suited to bird dispersal but with seeds poorly protected, can survive being eaten by birds.

Some 45 genera with 2,000–2,500 species; mostly in the subtropics and tropics of Asia and America.

BEILSCHMIEDIA Nees

Beilschmiedia pendula (Sw.) Hemsl., Biol. Centr.-Amer. Bot. 3:70. 1882

Hufelandia pendula (Sw.) Nees

Tree, 13–40 m tall, to 75 cm dbh; buttresses ± lacking or to 1 m; outer bark reddish-brown and scarcely fissured on younger trees, becoming loosened in squarish patches in age, the older parts becoming marked with shallow depressions; inner bark granular with darker lines in tangential section; stems with dense, short, brown, appressed pubescence, the younger stems ribbed; sap sweet, with pleasant aroma. Petioles 8–15(25) mm long, canaliculate; blades elliptic to oblong-elliptic, abruptly short-acuminate (rarely with a long acumen), cuneate to attenuate at base, decurrent onto petiole, mostly 10–20 cm long, 5–9 cm wide, ± glabrous above, the pubescence below short, whitish, appressed; reticulate veins prominulous, very closely spaced. Panicles terminal and from axils of older leaves, 10–15 cm long; flowers bisexual, greenish-yellow, ca 3 mm long; hypanthium lobes 6, ovate, thin at margin, pubescent inside and out; stamens 9, 2-celled, the connective produced and ± fleshy at apex, the outer series of 6 somewhat shorter than the inner 3, 1.3–1.7 mm long, pubescent and ciliate, subtended by and alternating with 6 fleshy yellow glands; filaments stout, fused to perianth lobes, the inner series of 3 stamens alternating with shorter ovate staminodia; ovary glabrous; style simple, shorter than inner stamens. Fruits lacking a cupule, oblong or ellipsoid, shiny, to 5.5 cm long and 2 cm diam, purple-brown, with a single embryo and 2 large yellow-green cotyledons surrounded by a thin green pericarp ca 1.5 mm thick. *Croat 12928, 14063.*

Common in the old forest. Flowers in the early dry season (December and January). The fruits attain full size by March, but ripen during May and June. Leaves are replaced slowly at about the time of flowering.

Not confused with any other species.

Wilson (1971) reported that the fruits are taken by the bat *Micronycteris hirsuta.* Monkeys eat the thin outer skin and the scant mesocarp, discarding the remainder. Seeds germinate soon after falling.

Costa Rica and Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone and from tropical wet forest in Los Santos (Coabal). Possibly also in Ecuador (*Little 6294*).

See Fig. 248.

NECTANDRA Rol. ex Rottb.

The genus *Nectandra* is easily confused with *Ocotea.* On BCI, *Nectandra* may be distinguished by having bisexual flowers with the perianth lobes fleshy to membranaceous and spreading to reflexed. The outer series of anthers is ovate and more or less flattened, with their four thecae arranged in an arc on the inner surface. The inner series of anthers is more or less quadrangular, the four cells arranged in two overlapping planes, the upper ones laterally dehiscent, the lower ones extrorsely dehiscent.

Nectandra cissiflora Nees, Syst. Laur. 296. 1836

Tree, to 27 m tall and 30 cm dbh; trunk weakly involute throughout much of its length, with warty protuberances (probably deciduous branch bases); outer bark unfissured, thin, obscurely lenticellate; inner bark thin, granular; young stems densely rufous-tomentose, with a flat-topped rib extending below each petiole, these persisting on older stems; sap with faint sweet aroma. Petioles 1–2 cm long, densely tomentose; blades oblong-elliptic to oblanceolate, gradually long-acuminate and often twisted at apex, attenuate to acute and decurrent at base, 10–24 cm long, 4–8 cm wide, moderately pubescent above at least on midrib (the trichomes more dense on veins, brownish, straight, leaning forward), tomentose on veins below (the trichomes not completely appressed), otherwise the surface below moderately appressed-pubescent, the margins ± revolute; midrib arched. Panicles from upper axils, to 20 cm long, with a slender axis, branched mostly in the upper two-thirds; axes, peduncles, and pedicels

KEY TO THE SPECIES OF NECTANDRA

Lower leaf surface distinctly pubescent:
- Pubescence of major veins of lower leaf surface mostly closely appressed; flowers usually more than 1 cm wide ..... *N. globosa* (Aubl.) Mez
- Pubescence of major veins of lower leaf surface mostly erect, never closely appressed; flowers usually less than 7 mm wide ..... *N. cissiflora* Nees

Lower leaf surface essentially glabrous:
- Blades usually with fewer than 6 pairs of lateral veins, the lowermost pairs much longer than those at middle of blade ..... *N. savannarum* (Standl. & Steyerm.) C. K. Allen
- Blades usually with more than 7 pairs of lateral veins, the lowermost pairs usually much shorter than those at middle of blade ..... *N. purpurascens* (R. & P.) Mez

densely short-pubescent; flowers bisexual, mostly clustered at ends of branches; pedicels 1–3 mm long in flower, 5–12 mm long in fruit, densely grayish-puberulent; flowers cream-colored, ca 5 mm wide; perianth lobes sessile, subequal, spreading at anthesis, ovate-triangular, acute at apex, weakly grayish-pubescent outside, granular-puberulent inside; stamens 9, the 6 outer ones opposite perianth lobes, sessile, the outer side weakly pubescent, the subtending glands fused into a ring around the ovary, about half as high as the outer stamens, the 3 inner stamens apparently fused to the glandular ring; ovary ovoid; style short; stigma simple. Fruits fleshy, 1-seeded, round, to 1.3 cm diam, the cupule green, obconical, 9–13 mm long and ca 1 cm wide at apex, glabrous to weakly pubescent. *Croat 14989.*

Rare; known above the escarpment north of Zetek Trail and on the slope northwest of the laboratory. Saplings are seen in the old forest. Seasonal behavior uncertain; probably fruits in the early rainy season.

The plant north of Zetek Trail has sucker shoots near the base with densely rufous-tomentose stems.

Panama to Peru and Brazil. In Panama, known only from tropical moist forest on BCI.

Nectandra globosa (Aubl.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5:415. 1889

Sigua, Sweetwood

Tree, usually 3–10 (15) m tall; wood soft, light in weight; branchlets and inflorescences minutely and densely pubescent. Petioles stout, to 1.5 cm long; blades elliptic to oblong-elliptic, acuminate and often ± twisted to one side, rounded to acute at base, 10–32 cm long, 3–9 cm wide, ± glabrous (sparsely and obscurely pubescent) and shiny above, dull below and densely and minutely appressed-pubescent, often with tufts in axils. Panicles axillary, usually at end of branches, mostly 7–20 cm long; flowers bisexual, white, with sweet odor, to 13 mm wide; perianth lobes 6, acute to obtuse, broadly spreading, fleshy, pubescent outside, papillose inside; stamens almost sessile, about as broad as long, topped by a broad, white, papillose connective about half their height, the outer 6 subtended by and alternate with fleshy rounded glands, the inner 3 held above the stigma, affixed to a thick disk, alternating with staminodia, the disk about as high as ovary; ovary glabrous, round; style about as long as ovary; stigma globular, probably receptive before pollen is released. Fruits ellipsoid, ca 1 cm long, black at maturity. *Croat 4888, 7847.*

Frequent along the shore, at least in some areas of the northern part of the island and on Orchid Island; occasional elsewhere along the shore. Flowers from late November to early April, chiefly from December to March. The fruits mature mostly during April and May.

Distinguished from all other Lauraceae on BCI by the large flowers. *Nectandra globosa* is uniformly and persistently pubescent on the lower leaf surface. It can be confused with *N. glabrescens* Benth., which occurs along the Atlantic slope of Panama and in South America to the Guianas, Bolivia, and Brazil (Planalto). *N. glabrescens* has leaves much less pubescent, at least in age, and flowers principally from July through October. It also differs from *N. globosa* in having a depressed-globose ovary with a very short style.

Mexico to Panama, the Guianas, and Peru; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

Nectandra purpurascens (R. & P.) Mez, Jahrb. Königl. Bot. Gart. Berlin 5:443. 1889

N. latifolia (H.B.K.) Mez

Sigua blanca, Sigua negra

Small tree, to 17 m tall and 27 cm dbh, glabrous except young parts with short appressed trichomes. Petioles 1–1.5 cm long, slightly canaliculate; blades ovate to elliptic or lanceolate-elliptic, long-acuminate and sometimes falcate at apex, acute to rounded at base, 6–20 cm long, 3–6 cm wide, usually bearing weak tufts of trichomes (domatia) in lower vein axils on underside of leaves; midrib arched, the reticulate venation conspicuous on both surfaces. Panicles 6–12 cm long, terminal or in upper axils; flowers bisexual, white, ca 5 mm wide, with sweet aroma, in usually subcorymbiform panicles; perianth lobes 6, fleshy, spreading, densely short-pubescent, the inner 3 usually narrower; stamens exserted, the outer 6 with short filaments and the anthers ± reniform, the glands white or orange, subtending and alternating with outer stamens (often larger than anthers), the 3 inner stamens closely surrounding and ± equaling the length of the style, alternating with 3 shorter staminodia; ovary glabrous. Fruits fleshy, 1-seeded, ± rounded, green and speckled, becoming black at maturity, to 1.5 cm diam, the pedicel and cupule conical, bright red, together ca 1 cm long. *Croat 9556.*

Frequent along the shore, especially on the north side of the island; occasional in the younger forest. Some flowers may be seen in all months of the year, but flowering occurs principally in two waves, one at the beginning of the dry season (December to March) and one at the beginning of the rainy season (May to July). The fruits usually develop within a few months, but some have been seen as late as October. Individual plants flowering in March were seen again with both flowers and fruits in the rainy season.

Standley mistakenly reported this species as *N. glabrescens* Benth., which has affinities with *N. globosa* and occurs in Panama only along the Atlantic slope.

Nicaragua to Panama, south to Ecuador, Peru, and Brazil; at low elevations. In Panama, known principally from tropical moist forest in the Canal Zone, but also from tropical wet forest in Colón.

See Fig. 249.

Nectandra savannarum (Standl. & Steyerm.) C. K. Allen, J. Arnold Arbor. 26:382. 1945

Tree, 7 m tall; stems obscurely and densely strigillose. Petioles pubescent, 5–9 mm long, canaliculate; blades narrowly ovate to lanceolate-elliptic, gradually acuminate

to caudate-acuminate, acute to attenuate at base, 5–17 cm long, 1.5–5 cm wide, moderately thin, essentially glabrous above, nearly glabrous below but with inconspicuous tufts in axils, the margins weakly undulate; lateral veins usually in 4–6 pairs, the reticulate venation inconspicuous especially above. Inflorescences 2–10 cm long, slender; peduncles 1.5–4.5 cm long, the branches short; pedicels ca 3 mm long; inflorescence branches, pedicels, and hypanthia tomentulose especially the terminal parts; flowers bisexual, 5–6 mm wide; perianth lobes 6, spreading, ca 1.5–2 mm long, glandular-tomentose to villous inside and out, hispid outside toward base; outer stamens 6, obovate, ca 0.5 mm long, the short filaments and outer surface of anthers pubescent, the inner stamens 3, spatulate, ca 0.7 mm long, the filaments almost equaling anthers, pubescent, the anthers pubescent to near apex; staminodia club-shaped, shorter than and alternating with inner stamens; glands subglobose, glabrous, ca 0.5 mm high; ovary ovoid, ca 1 mm long, glabrate, tapered abruptly to style; style equaling inner stamens. Fruits subglobose, apiculate, the cupule coral-orange, to 4 mm long, ca 8 mm diam and 3–4 mm deep. *Foster 960.*

Rare; collected once along the shore on the east side of Peña Blanca Peninsula southwest of Orchid Island. Seasonal behavior uncertain. *Foster 960* had flowers in early June; elsewhere in Central America flowering specimens have been collected principally in the dry season.

Description of the fruits, which are incompletely known, is based on Allen (1945).

The BCI material differs only slightly from specimens from other areas in Central America that usually have leaves more coriaceous and frequently much more pubescent on the stems and underside of leaves, rarely also on the midrib and veins above.

Guatemala, Belize, Honduras, and Panama; no doubt in areas between Honduras and Panama. In Panama, known only from tropical moist forest on BCI.

OCOTEA Aubl.

The genus *Ocotea* is easily confused with *Nectandra.* On BCI, *Ocotea* can be distinguished by having unisexual flowers (dioecious) with the perianth lobes usually thin and erect at anthesis. The outer series of anthers is more or less fan-shaped with the four thecae arranged in two distinct horizontal planes on the inner surface. The inner series of anthers is more or less quadrangular with the four thecae arranged in two distinct planes. The two upper thecae are laterally dehiscent, and the two lower extrorsely dehiscent.

Ocotea cernua (Nees) Mez, Jahrb. Königl. Bot. Gart. Berlin 5:377. 1889
O. caudata (Nees) Mez
Sigua, Encibe

Dioecious tree, to 12 m tall, glabrous but sometimes with sparse pubescence on young stems, petioles, and midribs below and dense pubescence at tips of stems; stems weakly ribbed below petioles. Petioles 8–20 mm long; blades elliptic to oblong-elliptic, usually long-acuminate, acute to obtuse at base, 4.5–18 cm long, 2–7 cm wide, the margins minutely undulate; midrib arched and raised, the veins in 3–5 pairs. Flowers cream-white, unisexual, with aroma of fresh peaches, 3–4 mm wide, in solitary axillary panicles usually 3–7 cm long; peduncles to ca 1 cm long; pedicels 1–4 mm long; perianth lobes 6, slightly unequal, ovate, blunt to acute, slightly more than 1 mm long, erect at anthesis, glabrous outside, hispidulous inside near base, borne on a campanulate hypanthium; stamens of staminate flowers in 2 series, the anthers of the outer 6 sessile, ca 0.8 mm long, opposite and fused to base of perianth lobes, subtended by and alternating with glands, the glands broader than long, the inner stamens 3, ca 1 mm long, hispidulous on inner surface, bearing 2 small yellowish glands on outer side at base, the filaments short, the anthers oblong; pistillode cylindrical, ca 0.5 mm long; pistillate flowers similar to staminate flowers but with smaller, apparently nonfunctional stamens (about half as high as pistil); ovary and style together to 1.5 mm long, the style short; stigma conspicuous, tripartite. Fruits ellipsoid, apiculate, to 1.5 cm long and 1 cm wide, black, the lower third tightly set into cupule, the cupule to 6 mm long and 11 mm wide, brownish. *Croat 15559* ♂, *8116* ♀, *Shattuck 1140.*

Uncommon, along the shore, especially on the north side of the island and in the young forest. Flowers from

KEY TO THE SPECIES OF OCOTEA

Leaves definitely pubescent:
- Leaf blades with slitlike pits in axils of major lateral veins ..... *O. oblonga* (Meisn.) Mez
- Leaf blades with ± rounded villous tufts in axils of major lateral veins..... *O. skutchii* C. K. Allen

Leaves glabrous or essentially so:
- Leaf blades bearing tufts of trichomes in axils of major lateral veins ..... *O. skutchii* C. K. Allen
- Leaf blades lacking axillary tufts:
  - Leaves with fewer than 5 pairs of lateral veins, the blades usually less than 5 cm wide, usually markedly arched along the midrib and caudate-acuminate at apex; midrib usually raised; major lateral veins not whitish on upper surface; perianth lobes ca 1 mm long ..... *O. cernua* (Nees) Mez
  - Leaves with more than 7 pairs of lateral veins, the blades usually more than 5 cm wide, usually not markedly arched along midrib, merely acuminate, not caudate-acuminate; midrib usually sunken or flat; major lateral veins whitish on upper surface; perianth lobes 2–2.7 mm long ..... *O. pyramidata* Brandegee

Fig. 249. *Nectandra purpurascens*

Fig. 250. *Ocotea skutchii*

Fig. 251. *Phoebe mexicana*

February to March (sometimes to May and rarely as late as July). The fruits mature mostly in August and September.

The species is not separable from *O. caudata* (Nees) Mez, which ranges widely in South America. The character used by Mez, i.e., degree of prominence of reticulate veins, is not adequate for separation of the South American material.

Southern Mexico to Panama, Guyana, Peru, and Brazil (Mato Grosso); Windward Islands. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Darién. Known from premontane wet forest in Costa Rica (Holdridge et al, 1971).

Ocotea oblonga (Meisn.) Mez, Jahrb. Königl. Bot. Gart. Berlin. 5:366. 1889
Sigua

Dioecious tree, to 30 m tall, to 45 cm dbh, conspicuously buttressed; bark coarse, conspicuously lenticellate, becoming moderately fissured on exposed parts above; branches mostly from near apex, widely spreading; young stems densely ferruginous-tomentose, with 2 ribs below the petioles; sap with ± pungent odor. Leaves drying blackened; petioles mostly 1–2 cm long, densely appressed-puberulent; blades narrowly elliptic to broadly oblanceolate, acute to acuminate with the acumen broadly rounded, narrowly acute to attenuate at base, 10–22 cm long, 3–6 cm wide, glossy and glabrous above except along the prominently raised, squarish midrib, densely and obscurely appressed-pubescent below, with slitlike pit domatia near the axils, the domatia usually puberulent within, directed at a sharp angle to the lateral veins; major lateral veins in about 7 pairs, the reticulate veins obscure. Panicles axillary or terminal, to 13 cm long; flowers, pedicels, and inflorescence branches densely short-pubescent; flowers unisexual; staminate flowers not available; pistillate flowers to 1.7 mm long, about as wide as long, greenish-white at anthesis; perianth lobes 6, erect to spreading, ovate, ca 1.5 mm long, densely papillose-puberulent on inside; outer series of stamens 6, ca 0.7 mm long, the filaments short, weakly pubescent on outside near base, the glands ± orbicular and flattened, the inner stamens 3, the filaments about half as long as anthers, pubescent; anthers ± quadrangular, pubescent inside on basal half; ovary ovoid, ± glabrous; style short; stigma conspicuous, held just above the inner stamens. Fruits ellipsoid, to 14 mm long and 8 mm wide, the basal cupule subflattened, ca 5 mm wide. *Aviles 9, Croat 16201, 16515.*

Rare; a few individuals known in the old forest south of the big trees on Armour Trail. The flowers have been seen on BCI during July and August.

Determination of the BCI plants was made by C. K. Allen. Staminate flowers remain unknown.

Characters of the fruits are taken from the type description.

Bolivian specimens bearing this name may be the same, but the leaves lack the slitlike domatia in the axils of the lateral veins.

Panama and the Guianas, but no doubt more widespread in South America. In Panama, known only from tropical moist forest on BCI.

Ocotea pyramidata Blake ex Brandegee, Univ. Calif. Publ. Bot. 7:326. 1920
Sigua

Dioecious tree, to ca 27 m tall and ca 50 cm dbh; outer bark unfissured, with numerous raised lenticels; inner bark inconspicuous; branchlets minutely and densely puberulent, becoming glabrous, conspicuously flattened, with a rib extending downward from each petiole. Petioles 1–3 cm long, canaliculate above; blades elliptic to lanceolate-elliptic, acuminate, somewhat falcate and downturned apically, acute at base, 7–20 cm long, 2.5–6.5 cm wide, glabrous or minutely appressed-pubescent on lower surface especially on veins; midrib arched, usually sunken above, at least apical part of midrib and the major lateral veins whitish, the major lateral veins in 7–10 pairs, the reticulate venation prominulous on both sides, especially below, and whitish above. Panicles axillary or subterminal, to 7 cm long, usually in upper axils (rarely from older branches); flowers unisexual; staminate flowers greenish-white, ca 5 mm long; pedicels ca 1.5 mm long; perianth lobes 6, thin, blunt, ca 2.7 mm long and 2 mm wide, puberulent inside near base; stamens included, the outer series of 6 opposite perianth lobes, 2–2.5 mm long, subtended by and alternating with glands, the filaments ± flattened, about equaling anthers, fused toward base to perianth lobes, the anthers ovate, the glands ca 0.7 mm wide, cushion-shaped, glabrous, the 3 inner stamens slightly shorter than the outer series, surrounded by the glands, their anthers narrowly ovate, held closely around style, shedding pollen after lengthening and overtopping stigma; pistillode slender, glabrous, merging imperceptibly with style; stigma held at or just above the level of the anthers of inner stamens; pistillate flowers not available. Fruits unknown. *Croat 12805.*

Rare; known only from Fairchild Trail 1675, on the shore south of Colorado Point, and in the young forest above the escarpment. All the plants seen were staminate. Flowers at the beginning of the dry season.

The BCI plants are a perfect match for the type (*Purpus 8456*) from Zacuapan, Veracruz, Mexico. The species probably also occurs all along the Atlantic slope of Central America.

The three individual plants known to me from BCI are very distant from one another. Though there are undoubtedly more individuals on the island, their infrequency and the relatively short flowering season make pollination a difficult and interesting phenomenon.

Known only from BCI and Veracruz, Mexico.

Ocotea skutchii C. K. Allen, J. Arnold Arbor. 26:352. 1945
O. williamsii P. H. Allen

Dioecious tree, 15–30 m tall; branchlets slender, ± terete, grayish-sericeous when young, glabrate in age; sap with sweet aroma. Petioles short and obscure or to 1.5 cm long; blades oblong-obovate to oblong-elliptic, moderately

acuminate to long-acuminate (the acumen blunt), narrowly acute to attenuate at base, 7–15 cm long, 3–6 cm wide, weakly coriaceous, the upper surface glabrous, the lower surface inconspicuously and ± densely appressed-pubescent, in age glabrous but with well-developed villous axillary tufts; midrib flat or slightly raised above, the lateral veins mostly in 7–9 pairs, mostly branching from midrib at ca 30° angle, the reticulate venation prominulous below. Panicles upper-axillary or subterminal, 6–15 cm long, branched several times, the branches grayish-puberulent, the trichomes becoming appressed on the upper parts of the branchlets; pedicels and hypanthium lobes gray-sericeous; pedicels ca 2 mm long; flowers unisexual, ca 3 mm long, whitish; perianth 6-lobed nearly to base, deciduous from the hypanthium usually as a unit, the lobes ± equal, imbricate, ovate-elliptic, moderately thick, narrowly rounded at apex, papillate-puberulent within; outer stamens 6, suborbicular, somewhat flattened, ca 1 mm long, the filaments very short, merging almost imperceptibly with anthers, papillate-puberulent on outside and along medial part of connective on inside, the glands globose, about half as high as stamens, glabrous except near base, the inner stamens 3, to ca 1.5 mm long, the filaments papillate-pubescent, the anthers as long as filaments, narrowly ovoid, papillate-pubescent on outside at base; pistil ca 1.5 mm long; ovary ovoid, glabrous, about twice as long as style; stigma ± triangular. Fruits ± ellipsoid to narrowly ovoid, 4–6 cm long, 2–2.5 cm wide, minutely apiculate at apex, at first dark green with minute speckles of lighter green, becoming black at maturity; exocarp thin, black; mesocarp less than 2 mm thick, the 2 large cotyledons red; cupule 1.5–2.5 cm long, the upper part saucer-shaped, 1.1–1.4 cm wide at apex, 2–4 mm deep, green to brown or reddish-brown at maturity of fruit. *Croat 8150, 9780, 14846.*

Occasional or rare, in the older forest. Flowers in the late dry season (April). The fruits mature in the early rainy season (late May to July). One collection tentatively determined as this species (*Shattuck 535*) has juvenile fruits in early December. Allen (1956) reported the species (as *O. williamsii* P. H. Allen) to flower in May in Costa Rica.

As the leaves of this species age, they become increasingly darkened on drying and the appressed pubescence of the lower leaf surface almost disappears. In addition, axillary domatia become better developed on mature leaves. Fruits of the species fall at about the same time as those of *Beilschmiedia pendula,* which are the same size and shape, but *B. pendula* differs in having yellowish-green cotyledons rather than the red ones of *O. skutchii.*

Costa Rica and Panama. In Panama, known only from tropical moist forest on BCI.

See Fig. 250.

PERSEA P. Mill.

Persea americana P. Mill., Gard. Dict. ed. 8. 1768
Aguacate, Avocado, Avocado pear

Tree, to 15(20) m tall. Leaves falling shortly before or during time of flowering, soon replaced; petioles 1.5–5 cm long; blades ovate to obovate-oblong, abruptly acuminate to rounded at apex, usually obtuse at base, mostly 10–30 cm long and 6–16 cm wide, glabrous above, softly pubescent below; veins all prominent. Panicles axillary or subterminal; flowers fragrant, bisexual, greenish-white or greenish-yellow, ca 1 cm wide, weakly puberulent all over, 6–7 mm long; perianth lobes 6, acute, spreading at anthesis; stamens 9, ± erect; filaments distinct, puberulent, the outer 6 ca 2.5–3.5 mm long, the inner 3 longer, ± equaling the slender style; anthers with 4 thecae in 2 planes; staminodia prominent, yellow, short-stipitate; ovary ovoid, pubescent; style short; stigma discoid. Fruits ovoid or pear-shaped drupes, usually 10–12 cm long; exocarp thin, leathery; mesocarp thick; seed ovoid, to 5 cm long. *Croat 4162, 7491.*

Cultivated at the Laboratory Clearing and rarely encountered in the forest, presumably persisting from old settlement sites. Flowers mostly in the early dry season. The fruits mature in the early rainy season.

Probably native to Mexico; widely cultivated in Panama and elsewhere in the tropics and subtropics. Reported from premontane wet, tropical wet, premontane rain, lower montane wet, and lower montane rain forests in Costa Rica (Holdridge et al., 1971).

PHOEBE Nees

Phoebe mexicana Meisn. in DC., Prodr. 15(1):31. 1864
Sigua blanca

Tree, to 25 m tall and 30 cm dbh; outer bark planar, minutely lenticellate; inner bark tan, granular, moderately thin; glabrous but with fine, minute trichomes on younger stems, petioles, axes of inflorescences, and pedicels; smaller stems angulate with prominent ribs extending below petioles; sap with a faint sweet odor. Petioles stout, broadly canaliculate, to 2.5 cm long; blades ± elliptic to oblong-elliptic, rounded or bluntly to narrowly acuminate at apex, often falcate and downcurved, obtuse to acute or attenuate at base, 9–29 cm long, 4–14.5 cm wide, conspicuously 3-veined from above base, pliveined at base, coriaceous, the lower axils often weakly tufted with trichomes. Flowers greenish-white, bisexual, 2–3 mm long, in numerous axillary or subterminal racemose panicles 12–20 cm long; pedicels 3–5 mm long; perianth lobes 6, unequal (the outer 3 shorter), ovate, obtuse to rounded at apex, glabrous or weakly pubescent outside, ± sericeous inside, erect at anthesis, persistent in fruit; stamens 9, subequal, usually longer than outer perianth lobes, shorter than inner ones; filaments longer than anthers, the outer 6 fused to perianth lobes in basal half, ca 1.7 mm long; anthers with 4 thecae in 2 definite planes, the inner 3 anthers extrorse, to 2 mm long or more, adjacent to and equaling or longer than style, alternating with 3 cordate stipitate staminodia; glands longer than and alternating with filaments between the outer and inner whorl of stamens; ovary glabrous, ± equaling length of style; style ± simple. Fruits obovoid to ellipsoid, 1–1.5 cm long and 7–10 mm wide, dark green with light green spots, the cupule campanulate, with the enlarged perianth lobes ca 2 mm long, glabrous. *Croat 14819.*

Occasional, along the shore, uncommon in the old forest, and rare in the young forest. Flowers mostly in

May and June. The fruits mature by July and August.

Monographic work will probably show that this species is much more wide ranging. The species is variable and should probably include *P. elongata* (Vahl) Nees of the West Indies, *P. costaricana* Mez & Pitt. of Costa Rica and western Panama, and *P. cinnamomifolia* (H.B.K.) Nees of South America from Colombia and Venezuela to Peru.

Mexico to Panama, Colombia, and Venezuela. In Panama, occasional in tropical moist forest in the Canal Zone, Panamá, and Darién, especially on the Atlantic slope, or at medium elevations of the Pacific slope such as in Panamá (lower slopes of Cerro Campana).

See Fig. 251.

59. CAPPARIDACEAE

Small trees, shrubs, or annual herbs often with spines at nodes. Leaves alternate, sessile or petiolate; blades simple or palmately compound, entire; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, in terminal or upper-axillary, bracteate racemes of few flowers; sepals 4, free; petals 4, free; receptacle elongated into a discoid androgynophore; stamens 6 or many; anthers 4-celled, dorsifixed near base, dehiscing longitudinally; ovary superior, 1-locular, 2-carpellate; placentas 2, parietal; ovules few to many, campylotropous; style 1 or the stigma sessile. Fruits dry or fleshy siliques (2 valves falling away from a central frame on which the seeds are attached), dehiscing regularly or irregularly lengthwise; ovules numerous, lacking endosperm.

Recognized by their slender gynophore, which bears the ovary.

Corner (1964) implied that the family is principally bird pollinated, but characteristics of bat-pollinated flowers are present. Some species of *Cleome* (*C. anomala* H.B.K.) are known to be bat pollinated (Vogel, 1958). *Capparis frondosa* is animal dispersed. Its purplish fruit with whitish seeds suggest possible bat dispersal. At least some species of *Cleome* have eliasomes associated with their seeds and are ant dispersed; this is true of *C. pilosa* Benth. and *C. aculeata* L. and is possibly true of *C. parviflora* as well (H. Iltis, pers. comm.).

Some 46 genera and 700–800 species; mostly in the drier parts of the subtropics and tropics.

CAPPARIS L.

Capparis frondosa Jacq., Enum. Syst. Pl. Ins. Carib. 24. 1760

C. baducca sensu auct. non Rheed. ex L.

Shrub or small tree, to 5 m tall. Leaves simple; petioles quite variable in length, very short or to 20 cm long (variable even on the same branch), pulvinate at both ends; blades oblong-lanceolate to oblong-oblanceolate, mostly acuminate, acute to obtuse at base, 4.5–22 cm long and 1.8–9 cm wide (variable in size even on the same branch); midrib raised above. Flowers in short racemes of few flowers in the upper leaf axils; pedicels 1–3 cm long (2–4 cm long in fruit); sepals 4, bluntly triangular, ca 1.5 mm long, open in bud, each with a minute disk gland at base within; petals 4, ovate, ca 1 cm long, obtuse at apex, white; stamens ca 100, 1.5 cm long; pistil oblong, ca 3 mm long, on a gynophore ca 1 cm long (ca 3 cm long in fruit). Fruits oblong, fleshy, tardily dehiscent siliques to 9 cm long, becoming maroon when mature, ca 1.5 cm wide, dehiscing irregularly lengthwise to expose seeds, the seeds ca 20, sticky, ± spherical, ca 8 mm diam. *Croat 5861, 7802.*

Common throughout the forest. Seasonality uncertain. Flowers in January and February and from July to September. White-faced monkeys eat the fruits from November to February (Oppenheimer, 1968), but fruits are also seen from March to May.

The species is distinguished by a combination of many-staminate flowers, petioles of greatly differing lengths, and purple siliques borne on a gynophore.

Southern Mexico to Peru and Brazil; West Indies. In Panama, ecologically variable; known from tropical moist forest on both slopes in the Canal Zone and in Los Santos, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Panamá, and from premontane rain forest in Darién (Cerro Pirre).

CLEOME L.

Cleome parviflora H.B.K. subsp. **parviflora,** Nov. Gen. & Sp. 5:83. 1821

C. houstoni sensu Standl. (1933) non R. Br.; *C. panamensis* Standl.

Weak, annual herb, to 60 cm tall; stems at most sparsely pubescent, the nodes with retrorse spines to 2 mm long. Leaves palmately compound (or simple near base of plant); petioles 3–6 mm long; leaflets 3(5), ± lanceolate, acuminate, 3–6 cm long, strigillose and becoming glabrous above, occasionally with minute spines on midrib below. Inflorescences terminal racemes of few flowers, mostly less than 15 cm long in flower but to 30 cm long; pedicels 1–1.5 cm long, very slender, subtended by foliaceous bracts; sepals lanceolate, (2)3–5 mm long; petals pale to deep pink, greenish-purple, green, or white, 3–6 mm long, with a claw about one-third as long as blade; stamens 6; gynophore 1–9(11) mm long. Fruits narrowly fusiform siliques, 2–8 cm long and ca 3 mm wide, dehiscing regularly lengthwise; seeds numerous, reniform, 1.5–2.3 mm long. *Croat 6403.*

KEY TO THE SPECIES OF CAPPARIDACEAE

Plants shrubs or small trees; leaves simple ..... *Capparis frondosa* Jacq.
Plants herbs; leaves palmately compound ..... *Cleome parviflora* H.B.K. subsp. *parviflora*

Infrequent; known only from sandbars in coves around the edge of the island. Seasonal behavior undetermined. Flowers and fruits at least from May to September.

The species can be recognized by a combination of palmately compound leaves, four clawed petals much exceeded by the stamens, and siliques borne on a gynophore. The species was mistakenly reported by Standley (1933) as *Cleome houstoni* R. Br., a species endemic to Cuba.

Mexico to the Guianas (Surinam), Ecuador, northern Peru, and Amazonian Brazil; usually at elevations of 10 to 250 m, usually in marshes. In Panama, known from tropical moist forest in the Canal Zone on the Atlantic slope and in Darién.

60. SAXIFRAGACEAE

Woody climbers. Leaves opposite, petiolate; blades simple; venation pinnate; stipules lacking. Flowers bisexual or neuter (sterile), actinomorphic, in generally terminal, bracteate cymes; calyx 4-toothed; petals 4, free, showy; stamens 8, free; anthers 2-celled, dehiscing longitudinally; ovary inferior, of 2(3) locules and carpels; placentation axile; ovules many, anatropous; styles 2; stigmas capitate; neuter flowers consisting only of short, broadly expanded, deeply divided calyces. Fruits septicidally dehiscent capsules; seeds many, with abundant endosperm.

The family is represented on the island only by *Hydrangea,* which is distinguished by being a climbing shrub, somewhat hemiepiphytic, with showy, sterile flowers and less conspicuous fertile flowers in the same inflorescence.

Hydrangea is probably pollinated by insects in the orders Hymenoptera, Diptera, Coleoptera, and Lepidoptera (McClintock, 1957).

The tiny seeds are possibly wind dispersed.

About 80 genera and 1,200 species; primarily in temperate North America.

HYDRANGEA L.

Hydrangea peruviana Moric. in DC., Prodr. 4:14. 1830

Climbing liana-like shrub, usually tightly fastened to supporting tree; older stems with a flaky brown periderm; younger stems and inflorescences with scalelike stellate pubescence. Leaves subcoriaceous; petioles 1–2 cm long; blades oval to elliptic, round to acute at apex, obtuse at base, 6–15(23) cm long, 3–7(14) cm wide, bicolorous, both surfaces sparsely covered with brown stellate scales, those of the upper surface often ± sunken, the margins ± entire; midrib usually arched, the reticulate venation visible only on lower surface. Inflorescences at or near apex, open and spreading; branches 4–7 cm long, at first enclosed in a large bud 1.5–2 cm broad of several spathe-like bracts; sterile flowers at first white, becoming pale green, to 1.5 cm diam, of 4 rounded sepals, the pedicels mostly 1.5 cm long; fertile flowers maroon, short-pedicellate; calyx obscurely 4-toothed; petals 4, ca 1.7 mm long, caducous; stamens 8, inconspicuous, to 0.7 mm long, shorter than style; styles 2, spatulate; stigmas marginal, 2 mm long at maturity. Capsules ca 2 mm long, splitting open at apex between styles; seeds less than 1 mm long, linear, very numerous. *Croat 11850.*

Rare, occurring high in the canopy. Juvenile plants with their small, more or less ovate leaves and densely rooted, closely appressed stems are usually common climbing trees in the vicinity of the adult plants. Flowers principally from July to September (elsewhere often flowering in January). The fruits develop quickly and are usually present on all but the youngest inflorescences.

H. oerstediana Briq., reported in the *Flora of Panama* (McClintock, 1950), may be merely a form of *H. peruviana.*

Costa Rica to Peru, possibly as far north as Mexico. In Panama, known principally at high to middle elevations from lower montane wet forest in Chiriquí, from tropical wet forest in Coclé, and from premontane wet forest in the Canal Zone (Pipeline Road), Chiriquí, and Coclé; known much less frequently from tropical moist forest at lower elevations in the Canal Zone and Panamá.

61. CHRYSOBALANACEAE

Trees or shrubs; sap sometimes colored. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules present. Flowers bisexual, ± actinomorphic, in terminal or axillary panicles or racemes; receptacles present; calyx 5-lobed, the lobes imbricate; petals 5 (rarely lacking), imbricate, free, inserted on the margin of the disk at the top of the hypanthium; stamens 3–15, free, sometimes unilateral; anthers 2-locular, longitudinally dehiscent; ovary superior, with 1 fertile carpel (and 2 aborted carpels), 1-locular; placentation basal; ovules 2; style filiform, basally attached at one side of ovary; stigma truncate or slightly lobed. Fruits drupaceous; seed exalbuminous.

Distinguished by having their styles attached basally to the ovary. Though no other clearly defined morphological features distinguish them, all the BCI species are distinctive and are not easily confused with members of any other family.

The flowers of the family are open. Pollinators are unknown.

The fruits of *Hirtella* are dark-colored and fleshy. They are possibly dispersed chiefly by bats, but are also

KEY TO THE GENERA OF CHRYSOBALANACEAE

Stamens more than 8 mm long; inflorescences narrow racemose panicles or racemes; leaf blades pubescent but never arachnoid-tomentose ..... *Hirtella*

Stamens less than 5 mm long; inflorescences ± pyramidal panicles; leaf blades white arachnoid-tomentose on lower surface or completely glabrous ..... *Licania*

taken by monkeys. *H. triandra* is taken by the white-faced monkey, which eats the fleshy part and spits out the seed (Oppenheimer, 1968). *Licania platypus* is also probably bat dispersed (R. Foster, pers. comm.). A *Licania* species was among those whose seeds were found in bat detritus of *Artibeus jamaicensis* in Mexico.

Seventeen genera and about 420 species; lowland tropics of Western and Eastern hemispheres.

HIRTELLA L.

Hirtella americana L., Sp. Pl. 34. 1753
Pigeon plum

Tree, to 20 m tall, to 30 cm dbh; young branchlets and petioles densely rufous-tomentulose. Petioles stout, very short; stipules subulate, paired, velutinous, 5–9 mm long, subpersistent; blades oblong to oblong-elliptic, short-acuminate, rounded at base, 7–15 cm long, 2.5–6.5 cm wide, glabrous to sparsely pubescent above, velutinous below especially on veins, the trichomes denser on veins, with a few round glands near base below. Inflorescences narrow terminal panicles 10–20 cm long, densely pubescent except on petals and inner flower parts; branches with rounded or oval, gland-tipped bracts, the glands sessile or short-stipitate; pedicels 1–2 mm long; calyx lobes 5, oval, rounded at apex, often tinged with purple; petals 5, oval, ca 4 mm long, white to reddish, spreading at anthesis; stamens 3, ca 1 cm long, mounted on a whitish disk (2 aborted stamens sometimes visible as subulate trichomes); filaments white, straight and divergent at anthesis; style erect, ± equaling ovary, violet-purple near apex, villous near base. Drupes ellipsoid, 1.5–2 cm long, sparsely pubescent to glabrous, black, shiny; pericarp thin, fleshy. *Croat 4866, 7751.*

Occasional, in the forest, especially the younger forest. Flowers from February to May. The fruits probably mature in the early to middle rainy season.

Southern Mexico to northern Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién and from tropical dry forest in Coclé (Penonomé).

Hirtella racemosa Lam., Encycl. Méth. Bot. 3:133. 1789
H. americana sensu Aubl. non L.

Small tree or arching shrub, 1–5 m tall, usually less than 10 cm dbh; young branches usually moderately pubescent. Petioles 1–3 mm long, densely hispid to glabrous; stipules paired, linear, 2–5 mm long, persistent; blades elliptic to oblong, bluntly acuminate at apex, obtuse to subcordate at base, 4–12(19) cm long, 1.5–5(7) cm wide, sparsely appressed-pubescent on midrib above and below and sometimes on surface below. Racemes axillary or terminal, 5–15(29) cm long; rachis and pedicels puberulent; bracts and bracteoles 1–3 mm long, narrowly triangular, appressed-pubescent, usually with 1 or more round, sessile glands near base; pedicels slender, (1.5)4–11 mm long, perpendicular to rachis; calyx lobes 5, ovate, 2–3 mm long, sparsely puberulent; petals 5, obovate to elliptic, 3–5 mm long, lavender; stamens 5–7; filaments 1–2 cm long, lavender; ovary densely pilose-tomentose; style to 1.5 cm long. Drupes oblong-obovoid, to 1.5 cm long, ca 6 mm diam, purplish-brown turning black, sparsely pubescent. *Croat 9518.*

Frequent in the forest and along the shore. Flowers from November to June, principally in the dry season. The species may flower more than once a year. The fruits probably mature in a few months, mostly in the late dry and early rainy seasons.

Panama through Colombia, Venezuela, and the Guianas to Peru, northern Bolivia, and Amazonian Brazil. In Panama, known from tropical moist forest in the Canal Zone, Colón, Los Santos, Panamá, and Darién and from tropical dry forest in Coclé (Penonomé) and Panamá (Taboga Island). Reported from premontane moist, premontane wet, and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Fig. 252.

Hirtella triandra Sw., Prodr. Veg. Ind. Occ. 51. 1788
Camaroncillo, Carapoto, Chicharron, Conejo, Wild pigeon plum

Tree or shrub, to 20 m; trunk to 23 cm dbh; outer bark thin, fissured, weakly flaky; inner bark reddish-brown, granular; wood light brown, hard, heavy; youngest stems pubescent; sap inconspicuous. Petioles to 5 mm long, moderately pubescent; stipules paired, subulate, to 5 mm long, subpersistent; blades elliptic-oblong, acuminate at apex, acute to rounded or subcordate at base, 4–12(14.5) cm long, 1.5–5 cm wide, glabrous above except on midrib, sparsely pubescent below, the trichomes denser on veins. Flowers in terminal racemose panicles to 8 cm long; rachis, branches, and pedicels tomentulose; pedicels slender, 2–3 mm long (appearing longer since flowers are often solitary at apices of branches); bracts and bracteoles narrowly lanceolate, 1–3.5 mm long, pubescent, lack-

KEY TO THE SPECIES OF HIRTELLA

Inflorescences strict racemes (pedicels ± perpendicular to axis); stamens 5–7; flowers lavender . . . . . *H. racemosa* Lam.

Inflorescences short-branched panicles; stamens 3; flowers white:

- Branches of inflorescences and younger stems very densely golden-brown tomentose; panicles usually more than 10 cm long, many times longer than broad; bracteoles of inflorescence bearing conspicuous glands; drupes black, shiny, sparsely pubescent . . . . . *H. americana* L.
- Branches of inflorescences and younger stems not very densely golden-brown tomentose; panicles less than 8 cm long, often about as broad as long; bracteoles of inflorescence lacking conspicuous glands; drupes brownish-purple, densely golden-brown tomentose . . . . . *H. triandra* Sw.

Fig. 252. *Hirtella racemosa*

Fig. 253. *Hirtella triandra*

ing glands; calyx lobes 5, ovate, 3–4 mm long, rounded at apex, reflexed at anthesis, puberulent on both sides; petals 5, broadly elliptic, ca 5 mm long, rounded at both ends, white; stamens 3, long-exserted, arising from side of flower; filaments purplish above, 1–2 cm long, fused into a low ring arising from rim of hypanthium (remnants of a 4th and a 5th stamen persisting as sharp lobes on this ring); style ± equaling stamens and opposite them at anthesis, pilose and white below middle, purple above; ovary pilose-tomentose; stigma small, capitate. Drupes ovoid-oblong to rounded, ca 2.3 cm long, densely short-pubescent; exocarp thin, brownish-purple; mesocarp fleshy, sweet, tasty; seed ± ovate, ca 1.7 cm long, with irregular longitudinal grooves, abruptly narrowed at base. *Croat 7171, 10969.*

Common in the forest, mostly in the old forest. Flowers sporadically throughout the year, principally from November to May. Individuals flower more than once a year, possibly as many as three times. The fruits mature throughout the year; white-faced monkeys eat the fruits in June and July (Oppenheimer, 1968).

Unusual growths were found on *Croat 6010,* which consisted of long-stipitate, obovate, greenish-white, fruitlike structures covered with short erect trichomes. The structures were regularly disposed on the stems and were at first believed to be fruits. Dr. Ghillean Prance (New York Botanical Garden), who made sections of the structures, has confirmed that they are not fruits. They are possibly due to gall insects.

Central Mexico to northern and western South America, Bolivia, and Brazil; West Indies. In Panama, known from tropical moist forest all along the Atlantic slope and in Chiriquí, Panamá, and Darién and from premontane wet forest in Colón.

See Fig. 253.

LICANIA Aubl.

Licania hypoleuca Benth., Bot. Voy. Sulphur 91, t. 32. 1844

Garapata

Tree, to 15 m tall; trunk ca 20 cm dbh; outer bark unfissured, minutely roughened, thin; inner bark reddish-brown, thin, hard; branches enlarged at base; young branchlets and petioles puberulent; sap with faint, pungent odor. Petioles 0.5–1 cm long; stipules minute, paired, subpersistent; blades ovate, acuminate at apex, obtuse to rounded at base, 5.5–10 cm long, 2.5–5 cm wide, glabrous above, whitish below with dense, minute, arachnoid trichomes. Flowers minute, in terminal or upper-axillary panicles 10–20 cm long, the branches and pedicels densely and minutely puberulent; hypanthium campanulate or turbinate, to 2 mm long; calyx lobes 5, minute, ovate, acute; petals lacking; stamens 3, less than 1 mm long; anthers about half as long as filaments; ovary white-hirsute; style to 2 mm long, adjacent to the 2 stamenless calyx lobes. Fruits pyriform to obovate, to 2.5 cm long and 2 cm diam, at first pink to red, becoming white and soft at maturity, usually with a minute depression at apex; mesocarp thick, fleshy, sweet, somewhat pithy; seed obovate, ca 1 cm diam. *Croat 14648.*

Infrequent, in both the younger and older forests. Probably flowers in the early dry season. The fruits are mature mostly from April to June.

Southern Mexico to Colombia, Venezuela, the Guianas, and Amazonian Brazil. In Panama, known from tropical moist forest on BCI and in Darién and from premontane wet forest in Panamá (Cerro Azul).

Licania platypus (Hemsl.) Fritsch, Ann. K.K. Naturhist. Hofmus. 4:53. 1889

Sangre, Wild pear, Zapote

Tree, 10–30(50) m tall; trunk to 75 cm dbh (sometimes buttressed to 1–2.5 m elsewhere); branches and leaves glabrous; branchlets often reddish; sap red in age. Petioles ca 1 cm long; stipules ovate, ca 2.5 mm long, stiff, adnate to petiole at base, persistent; blades mostly narrowly oblong-elliptic, shortly acuminate at apex, acute to rounded at base, 10–20(30) cm long, 3–6(8) cm wide, lustrous above, pale and ± glaucous below, with small round flattened or sunken glands below, especially near margin. Panicles terminal or upper-axillary, 10–25(35) cm long, the branches gray-tomentose, flattened at base; flowers minute, white, fragrant, sessile or very short-pedicellate; hypanthium, sepals, and edges of petals gray-tomentose; hypanthium ± turbinate, ca 1.5–2 mm diam; sepals 5, triangular, ca 1 mm long and wide, spreading; petals 5, obovate, 2–3 mm long; stamens 15, glabrous; filaments ca 3 mm long, attached separately to disk; style 5–6 mm long. Drupes variable in size, reported to 20 cm long and 14 cm diam, green turning brown; mesocarp granular, yellow, juicy, sweet; seed usually 1, ovate-oblong, flattened, to 5 cm or more long. *Croat 8695, 11851.*

Frequent in the forest, especially the old forest. Flowers principally in the dry season, especially from February to April. Time of fruit maturation is uncertain, since fruit size is so variable, but fruits believed to be mature were falling in June and late August. Some fruits probably persist on the tree much longer.

At maturity, the mesocarp smells much like fresh pumpkin.

Southern Mexico (both coasts) south to Colombia; reported also from the valley of the Magdalena (Jimenez S., 1970). In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién; Allen (unpublished) reported the species to be very common

KEY TO THE SPECIES OF LICANIA

Stamens 15; petals 5; leaves glabrous; sap red; fruit to 20 cm long; branchlets reddish ..... *L. platypus* (Hemsl.) Fritsch

Stamens 3; petals lacking; leaves densely whitish-arachnoid below; sap not colored; fruits to 2.5 cm long; branchlets not reddish ..... *L. hypoleuca* Benth.

Fig. 254. *Licania platypus*

Fig. 256. *Connarus panamensis*

Fig. 255. *Licania platypus*

on the dry Pacific coast, and Johnston (1949) reported that it appears to prefer growing on well-drained terraces in ravines.

See Figs. 254 and 255.

62. CONNARACEAE

Lianas or climbing shrubs. Leaves alternate, petiolate, imparipinnate; leaflets entire; T-shaped trichomes may be present; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, often glandular and fragrant, in axillary or terminal panicles; sepals 5, free or connate at base, imbricate or valvate, persistent in fruit; petals 5(6), free or connate at base, imbricate, white; stamens 10(12), in 2 series, briefly united at base, the shorter series opposite petals; anthers 2-celled, dehiscing longitudinally; pistils 1 (*Connarus*) or 5 (*Cnestidium, Rourea*); ovaries superior, 1-locular, 1–5-carpellate; placentation subbasal from the inner angle; ovules 2, orthotropous or anatropous; style 1 per carpel; stigma simple, capitate. Fruits dehiscent, sessile or stalked follicles (in 5-pistillate flowers only 1 develops) with a single seed; seed black, arillate, the aril yellow or orange; endosperm lacking.

Members of this family may be easily mistaken for Leguminosae (63) because of their imparipinnate leaves, swollen pulvini on petiolules, and legume-like follicles. Connaraceae are distinguished from the legumes by their arillate seed.

Flowers are small, white, and open, especially in *Rourea* and *Cnestidium*, and appear well suited for pollination by small insects, especially bees.

Seeds are black and shiny and are enveloped at the base by an aril of contrasting color, usually yellow, orange, or red. They are bird dispersed.

Some 24 genera with over 300 species; pantropical.

CNESTIDIUM Planch.

Cnestidium rufescens Planch., Linnaea 23:440. 1850

Liana, usually slender; younger branches, petioles, rachises, lower midribs, axes of inflorescences, pedicels, and calyces densely ferruginous-pubescent. Leaves imparipinnate, 10–25 cm long; leaf scars prominent; petioles 2–6 cm long; petiolules to 3 mm long; leaflets 7–11, alternate to opposite, obovate-oblong to elliptic, acute to bluntly acuminate, obtuse to rounded at base, persistently ferruginous-pubescent, especially below, the terminal leaflet 3.5–12 cm long, 1.5–6 cm wide, the others somewhat smaller. Flowers 5–6 mm diam, numerous, slightly aromatic, in upper-axillary panicles 6–15 cm long; pedicels very short; sepals 5, oblong-ovate, acute to blunt, to 1.5(3) mm long, slightly accrescent in fruit; petals 5, white, oblong, acute to rounded at apex, to 3.5 mm long, spreading to recurved; stamens 10, in alternate cycles of 2 lengths, united briefly at base, the longest to 2.5 mm; ovary and base of styles densely pubescent with stiff white trichomes; ovary of usually 5 free carpels; styles to 2.5 mm long, erect; stigmas simple. Follicles sessile, solitary, densely ferruginous-tomentose, ca 1.5 cm long; seed 1, oblong, black, shiny, ca 1 cm long, the basal aril orange. *Croat 7878, 16701.*

Infrequent, along the shore and at the margin of the forest in clearings. Flowers from July to September. The fruits mature by the early dry season (December to March).

Southern Mexico to Colombia; Cuba. Common in most of Panama at lower elevations; known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Herrera, Panamá, and Darién; known also from premontane moist forest in the Canal Zone and Panamá, from tropical dry forest in Coclé and Panamá (Taboga Island), and from premontane wet forest in Chiriquí and Panamá.

CONNARUS L.

Connarus panamensis Griseb., Bonplandia 6:6. 1858

Liana or climbing shrub, erect when juvenile, growing into lower part of canopy; trunk less than 2 cm dbh, with soft, thin, flaking bark; sap red with faint sweet aroma. Leaves weakly pubescent to glabrate; petioles 5–14 cm long, swollen and wrinkled at base; petiolules enlarged, wrinkled; leaflets 3(5), elliptic, acuminate at apex,

KEY TO THE SPECIES OF CONNARACEAE

Stems, leaves, and follicles densely ferruginous-pubescent ..... *Cnestidium rufescens* Planch.
Stems, leaves, and follicles weakly pubescent to glabrous in age:
  Flowers with 5 carpels; follicles sessile, ± terete, less than 8 mm diam; inflorescences never ferruginous-tomentose; leaflets ± appressed-pubescent on veins below .... *Rourea glabra* H.B.K.
  Flowers with 1 carpel; follicles stipitate, somewhat compressed, more than 12 mm diam; at least younger parts of inflorescence densely ferruginous-tomentose; leaflets glabrous or nearly so:
    Leaflets mostly 3, never 7, the margins often erose (as though eaten); flowers sessile, in dense clusters along branches; axes of inflorescences and young fruits bearing very dense, pile-like tomentum of erect simple trichomes; inflorescence branches usually stout, moderately short, and stiffly spreading (sometimes slender and dangling) ..... *Connarus panamensis* Griseb.
    Leaflets 3 or 7, the margins usually smooth; flowers pedicellate, in small clusters or solitary along branches of inflorescence; axes of inflorescences and young fruits bearing mostly appressed pubescence of obscurely T-shaped trichomes (sometimes with erect trichomes on younger parts but these soon deciduous); inflorescence branches slender, usually long and dangling ..... *Connarus turczaninowii* Tr.

rounded at base with petiolule often attached slightly above base, 10–25 cm long, 3–10 cm wide (juveniles to 35 cm long and 18 cm wide). Inflorescences spicate-paniculate, terminal, densely ferruginous-tomentulose, the pubescence eventually deciduous, the axis simple or branched; flowers sessile or subsessile, sweetly aromatic; sepals 5, ovate, 1.5–2.3 mm long, often about as broad as long; petals 5, white, to 3 mm long, often with red glandular dots; stamens 10, in 2 whorls, the inner whorl much shorter, the longer filaments to 2.3 mm long, often with stipitate glands near apex; carpel 1; ovary erect-pubescent; style 1, short, conic, off-center in fruit. Follicles compressed-obovoid, 1.5–2.5 cm long, red-orange, the stalk off-center, ca 5 mm long, the valves nearly glabrous at maturity (any remaining pubescence, usually on stipe, dense and erect), dehiscing along one side to expose a single seed; seed shiny, black, arillate, ca 1.5 cm long, the aril thin, yellow, to about midway on seed, its margins ± fimbriate. *Croat 7986, 11100.*

Abundant along the shore; less common in the canopy of the forest, especially the young forest. Seasonal behavior uncertain. Some flowers and fruits have been seen throughout much of the year, but individuals flower at least twice a year, mostly at the beginning of the dry season, with their fruits developing within 3 months. Another and possibly even larger surge of flowering occurs during the early rainy season (July to September), but with other plants flowering even later in the rainy season. The latter part of the dry season and the earliest part of the rainy season (April to June) appear to show the least flowering activity.

Costa Rica to Colombia. In Panama, known principally from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí.

See Fig. 256.

Connarus turczaninowii Tr., Ann. Sci. Nat. Bot., sér. 5, 16:364. 1872

Liana or climbing shrub, ± glabrous except inflorescences; trunk often stout, growing into lower part of canopy. Leaves compound; petioles pulvinate at base; petiolules stout, callous; leaflets 3 or 7, opposite or subopposite (rarely alternate), lanceolate-elliptic to oblanceolate, acuminate and often downturned at apex, acute to rounded at base, 4–15 cm long, 2–7 cm wide, stiff. Inflorescences terminal, usually branched only once, the branches slender, drooping, 8–45 cm long; branches, pedicels, and calyces rufous-tomentose at least when young, the simple erect trichomes usually soon deciduous, leaving mostly appressed, T-shaped trichomes, these also eventually deciduous; flowers 5-parted, 4–5 mm long, with a definite but short pedicel and a strong, sweet aroma; sepals to 2.5 mm long, usually much longer than broad; petals white, ± oblong, about twice as long as sepals; stamens 10, in 2 whorls, the inner 5 shorter, the longer 5 nearly equaling petals; filaments and connective with gland-tipped trichomes; carpel 1; ovary narrowly ovoid, with dense, ± appressed pubescence (the trichomes obscurely T-shaped); style 1, short. Fruits nearly identical to those of *C. panamensis* but with any remaining pubescence (often persisting on stipe) short, appressed, often whitish, and T-shaped. *Croat 8397, 12599.*

Common along the lakeshore; less common in the canopy of the forest. Seasonal behavior uncertain. Some flowers have been seen throughout most of the year; individuals clearly flower more than once a year, but perhaps no more than twice a year. Mature fruits are frequently found on plants at the time of their next flowering.

The flowers are visited by the bee *Trigona tataira.*

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

ROUREA Aubl.

Rourea glabra H.B.K., Nov. Gen. & Sp. 7:41. 1824
R. adenophora S. F. Blake
Mata negro

Liana. Leaves imparipinnate; petioles 2–6 cm long, terete with swollen basal pulvinus; petiolules pulvinate, 2–4 mm long; leaflets 3–7(9), alternate or subopposite, ovate-elliptic to oblong-elliptic, usually acuminate at apex, rounded to obtuse at base, 3–14 cm long, 1.5–6 cm wide, glabrous above except on midrib, glabrate to puberulent below especially on veins; midrib often arched. Panicles 5–15 cm long, from upper axils; branches and pedicels usually puberulent; flowers white, fragrant, ovoid in bud; calyx to ca 3.5 mm long at anthesis, larger and much thickened in fruit, glabrate or puberulent, with or without minute glands, the 5 lobes imbricate, divided to beyond middle; petals 5(6), ± oblong and rounded at apex, strongly reflexed at anthesis, usually 5–6 mm long, soon falling; stamens 10(12), alternating long and short, the longer to 4.5 mm long, the shorter to 3 mm long; filaments fused in a ring at base; anthers about as broad as long, opening in bud, the thecae opening broadly; pollen removed soon after anthesis; ovary of 5(6) carpels, pubescent; styles ca 4 mm long, pubescent on base. Follicles 1–1.5 cm long, cylindrical, slightly curved, orange-red to bittersweet at maturity (at least at apex), splitting open on one side to expose a single seed; seed shiny, black, slightly shorter than follicle, the aril yellow to orange, ca 5 mm long, about one-third as long as seed. *Croat 17030.*

Occasional, along the shore and in advanced clearings; also in the canopy, but usually on trunks below the top of the canopy. Flowers twice a year, once at the beginning of the dry season (December to February) and again from July to September. The fruits usually develop within 3 months, but some may persist until the next flowering.

In my opinion *R. adenophora* S. F. Blake is not a good species. It is supposed to differ from *R. glabra* by having the calyces and pedicels glandular. Presence or absence of pubescence on the upper midrib has also been used as a character to separate these taxa, but my investigations show the pubescence to be variable even on the same plant, often deciduous on some leaves and present on others.

Seeds are reportedly poisonous (Blohm, 1962).

KEY TO THE SUBFAMILIES OF LEGUMINOSAE

Flowers radially symmetrical, usually valvate in bud, usually sympetalous, the lobes equal; stamens usually many and long-exserted; leaves bipinnate (pinnate in *Inga* and a few *Pithecellobium*) ..... 63A. MIMOSOIDEAE

Flowers bilaterally symmetrical, imbricate in bud, polypetalous, the petals unequal; stamens usually 10 or fewer (except *Brownea* and *Swartzia* in Caesalpinioideae), usually not exserted; leaves simple, trifoliolate, or pinnate (rarely bipinnate, in *Caesalpinia* and *Schizolobium*):

Flowers with the odd petal innermost (inside the others in bud); stamens usually free or nearly so; leaves simple, pinnate, or bipinnate, never trifoliolate ..... 63B. CAESALPINIOIDEAE

Flowers with the odd petal outermost (outside the others in bud); stamens usually united below, monadelphous or diadelphous; leaves simple, trifoliolate, or pinnate, never bipinnate ..... 63C. PAPILIONOIDEAE

Southern Mexico to the Guianas and Brazil; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, San Blas, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón and Panamá.

63. LEGUMINOSAE (FABACEAE)

Trees, shrubs, or herbs, sometimes scandent, tendriled, and/or armed. Leaves alternate (opposite in *Platymiscium*), petiolate; blades simple, pinnate or bipinnate, entire or subentire; venation pinnate (palmate in *Bauhinia* and the blades bilobed); stipules usually present. Inflorescences terminal or axillary, paniculate, racemose, spicate, or sometimes globose heads; flowers bisexual, actinomorphic or zygomorphic; calyx 5-lobed, the lobes subequal, rarely free, rarely obsolete; petals 5, equal or unequal, free, or the 2 anterior petals united, usually showy; stamens 10 to many, free, monadelphous or diadelphous; anthers 2-celled, dehiscing longitudinally; ovary superior, 1-locular, 1-carpellate; placentation parietal; ovules 2 to many, in 2 rows on the ventral suture, anatropous; style 1, simple; stigma 1. Fruits legumes, loments, follicles, or drupes; seeds generally lacking endosperm.

An exceedingly diverse, large, and important tropical family most easily confused with the Connaraceae (62), which differ in having follicles with arillate seeds.

Because of the nature of the leguminous fruit, which generally offers little in the way of a meal for larger animals, most endozoochorous diaspores of the family are bird dispersed. A smaller number are dispersed by larger animals. Large-seeded legumes are hoarded by agoutis and spiny rats (N. Smythe, pers. comm.). The next most important type of dispersal for the family is anemochory. Fewer are hydrochorous, epizoochorous, or autochorous.

About 600 genera and 12,000–14,000 species; worldwide.

63A. MIMOSOIDEAE

Leaves bipinnate (merely pinnate in *Inga* and *Pithecellobium rufescens*); stipules present. Flowers actinomorphic, in cylindrical spikes or globose heads; floral bracteoles present in *Mimosa;* calyx cupular, rarely obsolete, the lobes imbricate or valvate; corolla lobes usually valvate; stamens many, often polyadelphous, equal, considerably longer than corolla.

Members of the subfamily Mimosoideae are most easily distinguished by their bipinnate leaves (except *Inga* and *Pithecellobium rufescens,* which usually have conspicuous glands at the apex of their petioles) and by their actinomorphic flowers with numerous stamens (at least twice the number of petals).

The flowers of the Mimosoideae are open with exserted sexual parts. In most cases the pollination unit includes the entire inflorescence; in all cases the pollen is easily accessible. Flowers may be pollinated by unspecialized pollen feeders, which crawl over the surface of the inflorescence, or by fluttering or hovering insects or birds. In general, the larger flowers or inflorescences, which provide nectar in quantity, are probably visited by bats or birds. *Inga vera* is known to be pollinated by several

KEY TO THE TAXA OF MIMOSOIDEAE

Leaves pinnate:

Inflorescences racemose or spicate ..... *Inga* (in part)

Inflorescences umbelliform to globose (short capituliform racemes in *Inga quaternata*):

Leaf rachis winged at least near apex ..... *Inga umbellifera* (Vahl) Steud.

Leaf rachis not winged:

Heads small, globular, less than 3 cm diam; flowers sessile; legumes moniliform, reddish with black seeds ..... *Pithecellobium rufescens* (Benth.) Pitt.

Heads (including stamens) more than 3 cm diam; flowers pedicellate; legumes not as above ..... *Inga quaternata* Poepp.

Leaves bipinnate:
- Inflorescences various, not globular or subglobular; flowers arising from an elongated rachis more than 2 cm long; leaflets at least in part 1 cm or more wide:
  - Pinnae bifoliolate; stems with paired, recurved, nodal thorns; corollas ca 10 mm long; legumes reddish, linear-moniliform, less than 3 cm wide ..... *Pithecellobium hymeneaefolium* (H. & B.) Benth.
  - Pinnae with 3 or more pairs of leaflets; stems unarmed; corollas less than 5 mm long; legumes more than 5 cm wide:
    - Inflorescences terminal racemes of spikes; legumes less than 7 cm wide; seeds ellipsoid, less than 1.5 cm long, dispersed with transverse segments of legume ..... *Adenopodia polystachya* (L.) J. Dixon
    - Inflorescences in supra-axillary spikes; legumes more than 8 cm wide; seeds disk-shaped, 5–6 cm diam, not dispersed with transverse segments of legume ..... *Entada monostachya* DC.
- Inflorescences globular or with very brief floral rachises less than 5 mm long:
  - Leaflets more than 1 cm wide:
    - Peduncles more than 3 cm long; flowers pedicellate; petioles bearing large cupular gland 1 cm long at apex; legumes curled:
      - Pedicels less than 2.5 mm long; gland between basal pair of pinnae ca 1 cm long, the others at successively higher nodes small; mature fruits curved into nearly complete circle ..... *Pithecellobium macradenium* Pitt.
      - Pedicels more than 8 mm long; gland between all pairs of pinnae minute; mature fruits oblong-linear, never curved into circle ..... *Albizia guachapele* (Kunth) Dug.
    - Peduncles less than 2 cm long; flowers sessile; petioles bearing small gland at apex:
      - Inflorescences paniculate with many globose heads ca 1 cm wide; individual flowers tiny, difficult to distinguish without magnification; pinnae usually in (2)4 pairs ..... *Leucaena multicapitula* Schery
      - Inflorescences of several spikes issuing from nodes along stem; individual flowers clearly visible, the corolla ca 5 mm long; pinnae usually in 2(3) pairs ..... *Pithecellobium dinizii* Ducke
  - Leaflets less than 1 cm wide:
    - Plants conspicuously armed:
      - Petiole and rachis eglandular; stamens fewer than 10; legumes armed ..... *Mimosa*
      - Petiole or rachis with small glands; stamens more than 10; legumes unarmed ..... *Acacia*
    - Plants unarmed:
      - Flowers on pedicels usually more than 1 cm long; legumes flat, straight, more than 15 cm long ..... *Albizia guachapele* (Kunth) Dug.
      - Flowers sessile or on pedicels less than 3 mm long, in small globular heads (less than 2 cm diam); legumes curled:
        - Leaflets in fewer than 15 pairs per pinna; leaves with petiole, rachis, and lower leaflet surface tawny-tomentose; legumes less than 2 cm wide, reddish inside ..... *Pithecellobium barbourianum* Standl.
        - Leaflets usually in more than 15 pairs per pinna; leaves not tawny-tomentose; legumes more than 2 cm wide, not reddish inside ..... *Enterolobium*

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bat species (Heithaus, Fleming & Opler, 1975).

Sphingid moths have been seen visiting the flowers in the early morning and early evening in Costa Rica (G. Frankie, pers. comm.). R. Heithaus (pers. comm.) also suggests hummingbirds and large trap line bees as pollinators.

Evidence exists of specialization in the pollen arrangement in the Mimosoideae. Different taxa form polyads with varying numbers of pollen grains per polyad (Guinet, 1969; Sorsa, 1969). The number of pollen grains per polyad usually correlates very well with the number of ovules per carpel (T. Elias, pers. comm.). This probably indicates a specialization in pollinators, and clusters of pollen are probably carried by nectar feeders rather than by the relatively unspecialized pollen feeders.

The largest dispersal category of Mimosoideae is endozoochory, especially mammalian. Examples are *Enterolobium cyclocarpum, E. schomburgkii,* and possibly all species of *Inga.* Oppenheimer (1968) reported that fruits of perhaps all species of *Inga* are eaten by the white-faced monkey. Some *Inga* may be water dispersed as well, especially those occurring only along the lakeshore. Quite likely these species of *Inga,* as well as similar shoreline species of *Pithecellobium,* are dispersed in part by fish or reptiles as is suggested by van der Pijl (1968).

Birds are probably the chief agents of dispersal for seeds of all *Pithecellobium* but especially for those of *P. barbourianum* and *P. rufescens,* which have well-developed arilloids clearly suited to bird dispersal. Seeds of some species of *Acacia,* such as *A. hayesii* and *A. riparia,* as well as those of *Leucaena multicapitula,* may also be bird dispersed, because the fruits open at maturity and the dark seeds are then displayed against the light inner valve surface.

Seeds of all *Mimosa* on BCI are chiefly epizoochorous. They are perhaps also wind dispersed, since they are

much flattened and break up into small segments. Water may also play a part in the dispersal of *M. casta* and *M. pigra*, since these generally occur near water; water currents play an important role in the dispersal of *Entada monostachya*. Van der Pijl (1968) suggested that *Albizia*, which lacks arilloids, is frequently wind and water dispersed; the seeds themselves sink but are dispersed while enclosed in the buoyant pod (Ridley, 1930).

ACACIA P. Mill.

Acacia acanthophylla (Britt. & Rose) Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18:488. 1937

Lianas climbing into canopy; trunk and branches sulcate, generally glabrous, the ribs (3)4 (to several), pubescent, armed with prickles, the prickles numerous, 3–5 mm long, broad-based, recurved. Leaves bipinnate with 4–9 pairs of pinnae; rachis and petiole glabrous to puberulent, usually armed and sometimes with many slender stalked glands ca 0.5 mm long, the glands sometimes at nodes on rachis; leaflets in 8–25 pairs per pinna, oblong-elliptic, oblique, acute to ± rounded and apiculate at apex, truncate at base and attached at a corner, 8–14 mm long, 1.5–4 mm wide, the margins entire or sparsely ciliate. Flowers in short, paniculate spikes; calyx and corolla glabrous. Legumes tan, 15–20 cm long, ca 3.5 cm wide, flat. *Croat 15568.*

Collected once in the old forest above the escarpment. Seasonal behavior unknown. Immature fruits have been seen in December.

The flower and fruit description given here is taken from the *Flora of Guatemala* (Standley & Steyermark, 1946). BCI vegetative material differs from the descriptions of other authors by having larger leaflets (to 14 mm long and 4 mm wide, compared to 10 mm long and 2 mm wide).

Mexico, Guatemala, Honduras, Costa Rica, and Panama. In Panama, known only from tropical moist forest on BCI.

Acacia glomerosa Benth., Hooker's J. Bot. Kew Gard. Misc. 1:521. 1842

Moderate to large tree, often buttressed, unarmed or armed with recurved prickles on stems and rachises; branchlets becoming glabrous in age. Leaves bipinnate with 6–8 pairs of pinnae; petioles ca 4–5 cm long, glandular near the base; leaflets many (ca 30 pairs per pinna), oblong to subfalcate, apiculate at apex, truncate at base, 8–12 mm long, ca 2 mm wide, puberulent, the underside paler; midvein submarginal. Flowers cream or white, fragrant, in terminal panicles, the heads small, dense, globose, to 12 mm diam, bearing 12–20 flowers; calyx ca 1 mm long, strigillose; corolla ca 2 mm long, deeply 5-lobed; stamens numerous, showy, white, to 7 mm long. Legumes narrowly oblong, flattened, 10–20 cm long, ca 3 cm wide, becoming glabrous; seeds few. *Aviles 10b.*

Collected once; not seen in recent years. Flowers mostly from September to January, especially from September to November. The fruits mature mostly from January to May.

The species is perhaps conspecific with *A. polyphylla* DC., which ranges from Colombia to Brazil. *Aviles 10b* differs from most material of *A. glomerosa* in that both surfaces of the leaflets are more densely pubescent with appressed trichomes. The inflorescence is also somewhat more diffuse than the typical *A. glomerosa*, and the pedicels are more slender.

Mexico to southern Brazil. In Panama, collected only from tropical moist forest on BCI, but reported by Holdridge et al. (1971) from moist and wet areas at low elevations.

Acacia hayesii Benth., Trans. Linn. Soc. London 30:524. 1875

Large canopy liana; trunk to 12 cm diam near the ground, with prominent raised horizontal lenticels; all but the smallest woody parts glabrous, ± 5-sided, the angles with prominent retrorse prickles. Leaves 30–60 cm long, bipinnate with 9–14 pairs of pinnae, each pinna 6–24 cm

KEY TO THE SPECIES OF ACACIA

Plants armed with large, paired, stipular spines resembling bull horns; flowers yellow; fruits subterete ..... *A. melanoceras* Beurl.
Plants armed with recurved prickles or unarmed; flowers usually white; fruits flat:
  Plants large buttressed trees ..... *A. glomerosa* Benth.
  Plants lianas or small, vinelike or arching shrubs:
    Leaflets 3–7 mm long (usually 4–5 mm), glabrous or with the lower edge nearest the rachis conspicuously pubescent; fruits less than 15 cm long and less than 2.5 cm wide, conspicuously rufous-pubescent; flowers in globular heads ..... *A. riparia* H.B.K.
    Leaflets 6–14 mm long (usually 8–12 mm), glabrous or pubescent, but the trichomes never restricted to lower inner edge; fruits more than 15 cm long and more than 2.5 cm wide, tan, inconspicuously pubescent; flowers in short, oblong spikes:
      Branches predominantly quadrangular, sulcate; petioles usually displaying more than 2 large sessile glands; rachis usually armed with recurved prickles; interfoliar glands on rachis usually present ..... *A. acanthophylla* (Britt. & Rose) Standl.
      Branches predominantly 5-angled to several-angled; petioles with 1(2) conspicuous sessile glands; rachis usually not armed; interfoliar glands on rachis usually lacking ..... *A. hayesii* Benth.

long; petiole and rachis puberulent; petioles bearing 1 or 2 round or oblong, sessile glands; rachis canaliculate above, often aculeate below, with glands at the nodes; leaflets in 20–30 pairs per pinna, oblong, blunt at apex, truncate and very inequilateral at base, mostly 9–14 mm long, ca 2.5 mm wide, glabrate to pubescent especially below, the trichomes appressed or erect. Inflorescences large terminal panicles of pedunculate spikes; peduncles 1–2 cm long, puberulent; spikes 10–12 mm long, dense; flowers glabrous, subsessile, greenish; calyx cupulate, ca 2 mm long, as broad as long; corolla cylindric-campanulate, ca 4 mm long; stamens numerous, 7–8 mm long. Legumes thin, linear to oblong, 15–24 cm long, 2.5–3.5 cm wide, softly puberulent, acute or acuminate apically, rounded at base, the margins markedly raised, the surface broadly undulate; seeds ± disk-shaped, 7–8 mm diam, dark, displayed against the light inner valve surface, borne on a slender funiculus to 13 mm long. *Croat 6202.*

Common within the forest, generally in the canopy, but the leafy branches may occasionally be seen at lower levels where the vine has fallen. Elsewhere this species becomes a tree (*fide Flora of Panama*), but on BCI its habit is always decidedly vinelike. Flowers in late October and November. The fruits develop to more or less mature size by late January and are dispersed throughout the rest of the dry season and early rainy season (to early May). Plants lose their leaves during the dry season.

The flowering description is based on the *Flora of Panama* (Woodson & Schery, 1950).

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

Acacia melanoceras Beurl., Kongl. Svenska Vetenskapsakad. Handl. 1854:123. 1856

Shrub or small tree, to 6 m tall; branchlets and rachis puberulent, otherwise glabrous; branchlets armed with large spines, the spines 3–4.5 cm long, hornlike, paired, hollow, black, stipular. Leaves bipinnate with 15–26 pairs of pinnae; petioles 1–3 cm long, with several raised glands on upper side near base; rachis 12–25 cm long, usually with a single raised gland between pairs of pinnae; leaflets in 15–30 pairs per pinna, oblong, rounded to obtuse at apex, truncate and inequilateral at base, to 7 mm long, 1–2 mm wide. Inflorescences terminal, raceme-like groupings of pedunculate heads; peduncles short, subtended by a 3- or 4-parted involucre; heads globular, densely flowered; floral bracts peltate, ± equaling flowers; flowers minute, yellow; calyx cupulate, ca 1 mm long, obscurely lobed; corolla funnelform, somewhat longer than calyx, puberulent apically; stamens numerous, 2–3 mm long. Legumes linear-oblong, to 11 cm long and 1.5 cm wide, ± compressed-subterete, short-beaked, longitudinally striate, glabrous, tardily dehiscent. *Croat 6667.*

Occasional, in the forest, especially on the west side of the island. Seasonal behavior uncertain. Probably flowering in February and March. Mature fruits have been seen in May.

Stipular spines often house ants that bite fiercely and remove any vegetation contacting the plant. The plant rewards the ants with sugars from the petiolar glands and with protein from the small beltian bodies along the margins of the leaflets (Janzen, 1967a). According to D. Janzen (pers. comm.), seeds merely spill out of the pods at maturity but may be dispersed further from the ground. Unless later regurgitated, seeds would probably not survive the passage through a bird.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone and from tropical wet forest in Colón (Portobelo).

Acacia riparia H.B.K., Nov. Gen. & Sp. 6:276. 1824

Vine or scandent shrub, to 5 m tall; branchlets ± angulate, the angles of the branchlets and sometimes the rachis armed with recurved prickles; petiole and rachis above puberulent and leaf margins ciliate, otherwise glabrous. Leaves bipinnate with 8–15 pairs of pinnae, each pinna 2.5–4(5) cm long; petioles 1–3 cm long, with 2 oblong glands on upper side; rachis 5–8 cm long, with an oblong gland at base of each pinna mostly in upper portions; leaflets in 20–40 pairs per pinna, oblong, rounded at apex, rounded to truncate at base, 4–7 mm long, ca 1 mm wide, glabrous but ciliate and sometimes with tufts in inside axil at base of leaf; midrib subcentral. Inflorescences terminal or upper-axillary; peduncles 1–2 cm long; flowers ± glabrous, sessile, clustered in white globular heads to ca 2 cm wide; rachis less than 5 mm long; calyx 1–2 mm long, acutely lobed; corolla tubular, 3–4 mm long, acutely lobed. Legumes flat, thin, mostly 10–15 cm long, 2–2.5 cm wide, tomentulose, stipitate, with a sharp beak 5 mm long at apex of fruit; seeds disk-shaped, ca 6 mm long, borne on a slender funiculus, the funiculus attached laterally to the seed, with a sharp bend near its middle. *Croat 8000, Foster 1392.*

Uncommon, on the shore on the eastern and southern sides of the island. Flowers in the rainy season. The fruits are of mature size by January and February, but probably are not dispersed until late in the dry season (April).

Panama to Ecuador, Bolivia, and southern Brazil. In Panama, known from tropical moist forest on BCI and from tropical dry forest in Panamá (Taboga Island).

See Fig. 257.

ADENOPODIA Presl

Adenopodia polystachya (L.) J. Dixon, comb. nov.
Mimosa polystachya L., Sp. Pl. 520. 1753; *Entada polystachya* (L.) DC., Prodr. 2:425. 1825; Mém. Leg. 422, 434, t. 61, 62. 1826

Liana; trunk to 15 cm dbh; stems striate; pinnular rachises and inflorescences puberulent, otherwise ± glabrous. Leaves bipinnate with 2–5 (mostly 3 or 4) pairs of pinnae; petiole and rachis lacking glands; leaflets in 5–7 pairs per pinna, oblong, rounded at both ends, oblique at base, 1.5–4 cm long, 0.5–1.8 cm wide. Inflorescences terminal racemes to 25 cm long, of many slender spikes to 10 cm

Fig. 257. *Acacia riparia*

Fig. 258. *Albizia guachapele*

Fig. 259. *Entada monostachya*

Fig. 260. *Enterolobium cyclocarpum*

long; flowers small, sessile or short-pedicellate, mostly white, but reportedly also reddish, with a foul odor; calyx cupulate, shallowly lobed to subentire, ca 1 mm long; corolla of 5 petals, the petals ± free, 2.5–3 cm long, acute; stamens 10, somewhat exserted, ca 4 mm long. Legumes oblong, 15–30(40) cm long, 5–7.5 cm wide, flat, thin, curved; exocarp thin, peeling away at maturity, the valves then breaking into narrow, wind-dispersed, transverse segments, each carrying a small seed; seeds ellipsoid, 1–1.4 cm long, shiny, brown. *Foster 731, Starry 318.*

Occasional, in the canopy of the forest; seldom seen, except for its fallen rectangular fruit segments. Flowers from July to September. Mature fruits were seen in December.

The transfer of *Entada polystachya* (L.) DC. to *Adenopodia* was convincingly argued by John Dixon (unpublished Ph.D. dissertation, University of Southern Illinois, Carbondale, 1965). *Adenopodia* and *Entada* as represented on BCI are two very different taxa both morphologically and ecologically.

Mexico to central South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá and from tropical dry forest in Herrera (Pesé).

ALBIZIA Durazz.

Albizia guachapele (Kunth) Dug., Phytologia 13:389. 1966

Albizia longepedata (Pitt.) Britt. & Rose

Deciduous tree, to 15 m tall, tomentose to sparsely tomentose all over. Leaves bipinnate with 3–5 pairs of pinnae; petioles 3–6 cm long with a round sessile gland near the middle of upper surface; stipules acicular, caducous; rachis 7–15 cm long, usually with a sessile gland at insertion of each pair of pinnae; pinnular rachis 8–12 cm long, with similar glands at insertion of each pair of leaflets; leaflets in 3–7 pairs per pinna, variable, ovate to obovate, asymmetrical, rounded or emarginate at apex, obtuse and inequilateral at base, 1.5–3(4) cm long, 1–2(2.5) cm wide. Inflorescences 1–3, subterminal in axils; peduncles 3–7(9) cm long; pedicels 8–20 mm long; bracts linear, caducous, small; flowers in dense umbels, dimorphic, the central flower large and sessile; calyx 5–7 mm long (10 mm long in central flower), the lobes acute, ca 1 mm long; corolla green, 8–11 mm long (20 mm long in central flower), the lobes acute, ca 2 mm long, glabrous inside; stamens long-exserted, ca 2 cm long, white, the staminal tube included. Legumes oblong-linear, flat, 15–20 cm long, 2–3.5 cm wide, markedly short-pubescent, with a narrow marginal rib, tardily dehiscent. *Croat 8707.*

Apparently rare, known only from the cove between Slothia Island and Colorado Point. Flowers from December to March, in the early dry season. The fruits mature from January to May. Leaves are lost in the early dry season.

Guatemala to northern South America. In Panama, known from low elevations in moist, monsoon areas (Holdridge, 1970).

See Fig. 258.

ENTADA Adans.

Entada monostachya DC., Prodr. 2:425. 1825

E. gigas (L.) Fawc. & Rendle

Tendriled liana; trunk to 40 cm diam near the ground; larger stems with densely and minutely fissured, rusty-brown outer bark; smaller stems green, shiny, almost glabrous. Leaves bipinnate with usually 2 pairs of pinnae, the pinnae opposite, each 6–10 cm long; rachis 6–12 cm long, ending with a simple tendril to 15 cm long; petiolules short, with prominent basal pulvinus; leaflets in (3)5(6) pairs per pinna, asymmetrically oblong, blunt to emarginate at apex, unequal at base, mostly 2.5–5(7) cm long, 1.2–3 cm wide, glossy above, dull below; midrib puberulent. Inflorescences densely flowered, slender, spikelike racemes inserted shortly above leaf axils, to 25 cm long; flowers green, with a strong and sweet but disagreeable odor, maturing from base of rachis upward; pedicels short; calyx cupulate, about 1 mm long, the lobes minute; petals elliptic, ca 3 mm long and 1 mm wide, the margins sometimes scarious; stamens 10, ca 6 mm long; filaments white, the connective bearing a minute, stalked, papillate food body at apex. Legumes very large, 30–120 cm long, 10–13 cm wide, forming a broad spiral, the margins raised; seeds button-shaped, 5–6 cm diam, to 2 cm thick, dark and shiny at maturity. *Croat 4957, 7869.*

Occasional, in the canopy of the forest and pendent from the trees on the lakeshore. Seasonal behavior uncertain. Flowers from November to May. The fruits reach mature size by the late rainy season, but it is not known when they are dispersed, perhaps during the dry season.

Recognized by the huge fruits, which require about a year to mature. Seeds either are removed from the stout valves by animals, which tear holes in the valves, or fall from the weathered valves. The species is common in riparian situations, and water is known to play an important role in seed dispersal. Seeds are apparently carried great distances by rivers and may often be found in great abundance on ocean beaches.

Central America and tropical South America; West Indies; West Africa. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

See Fig. 259.

ENTEROLOBIUM Mart.

Enterolobium cyclocarpum (Jacq.) Griseb., Fl. Brit. W. Ind. 226. 1860

Coratú, Corotú, Curutú, Ear tree, Genisero, Guanacaste, Jarina

Tree, to 30 m tall and 1.5(3) m dbh, branched from near the ground, the crown widely spreading; outer bark with

KEY TO THE SPECIES OF ENTEROLOBIUM

Leaves with 4–15 pairs of pinnae and 15–30 pairs of leaflets per pinna; stems, petioles, and rachises usually glabrate, not ferruginous ..... *E. cyclocarpum* (Jacq.) Griseb.
Leaves usually with more than 15 pairs of pinnae and more than 60 pair of leaflets per pinna; young stems, petioles, and rachises ferruginous-tomentulose ..... *E. schomburgkii* Benth.

rough fissures; wood reddish-brown; branchlets usually glabrous in age. Leaves sometimes several at a node, bipinnate with 4–15 pairs of opposite pinnae, puberulent; petioles 4–8 cm long, with a round gland near middle of upper surface; rachis and pinnular rachis with glands at insertions near apex; leaflets in 15–30 pairs per pinna, ± oblong, decidedly inequilateral, acute at apex, rounded at base, 8–15 mm long, 2–4 mm wide, sometimes glabrate. Inflorescences axillary in groups of 1–3, white, puberulent to glabrate throughout, 2–4 (6) cm long; heads globular, ca 2 cm wide; bracts minute; flowers sessile, green; calyx 2–3 mm long, the lobes to 0.5 mm long, subacute; corolla 5–6 mm long, the lobes to 1.5 mm long, subacute; stamens to 12 mm long; filaments united in basal half; anthers white; style ± equaling stamens. Legumes reniform, flat, glabrous, 4–6 cm wide, curved into a nearly complete or overlapping circle to 11 cm diam; seeds ovoid-compressed, 1.5–2 cm long, to 1 cm wide, smooth, brown, bearing a lighter submarginal ring on either flattened surface. *Croat 7365, 8708.*

Uncommon, persisting as large trees in areas of previous cultivation. Flowers principally in the dry season (January to May). The fruits mature one year later in the dry season. The tree is leafless for a short time before flowering and produces new leaves at about the same time as the flowers. Neal Smith (pers. comm.) reports that an individual of *E. cyclocarpum* flowered in January in three consecutive years.

Tropical Mexico to northern South America; introduced into the West Indies and West Africa. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Darién; reported also from premontane moist forest in Panamá (Tosi, 1971).

See Fig. 260.

Enterolobium schomburgkii Benth., Trans. Linn. Soc. London 30:599. 1875
Mimosa wilsonii Standl.
Jarina

Tree, to 25 m tall; trunk weakly buttressed, to 45 cm dbh; outer bark unfissured, rough, hard, thin; inner bark reddish-brown, granular; young branches, petioles, rachises, and pinnular rachises rufous-tomentose; sap with an indistinct odor. Leaves bipinnate with 10–25 pairs of opposite pinnae; petioles 1.5–3 cm long, swollen basally, bearing a small, sessile gland ca 0.5 mm wide just above the pulvinus; stipules minute, caducous; rachis to 25 cm long, ridged along the center of the upper surface, with a similar gland at each node; pinnular rachis 4–10 cm long with 1 to several glands at terminal nodes; leaflets in 50–70 pairs per pinna, linear-oblong, less than 5 mm long and 0.8 mm wide, glabrous above, rufous-puberulent below, the midrib eccentric. Inflorescences rufous-tomentulose, axillary, in groups of 3–8; peduncles 1–4 cm long; heads short-spicate, appearing globular with the axis ca 2.5 mm long; bracts miniscule; flowers sessile to subsessile, green with white anthers; calyx turbinate, ca 2.5 mm long, the teeth 5, obtuse to acute, ca 1 mm long; corolla 2.5–5 mm long, the 5 segments acute, densely sericeous outside, glabrous inside; stamens 10, to 10 mm long, united at base into a short tube (if the tube extends nearly the entire length of the stamens, the stamens reduced to staminodia). Legumes reniform, 2–2.5 cm wide, curved into an overlapping circle to 5 cm diam, flat, reddish-brown, glabrous; seeds ellipsoid- to triangular-compressed, 6–8 mm long, smooth, brown, ringed on the largest circumference with a lighter area. *Croat 14986, Wilson 130, Woodworth & Vestal 688.*

Rare; a large tree grows at Miller Trail 875. Flowers in the dry season (February to April). The fruits mature from April to May (or later).

Mexico and Guatemala to Brazil. In Panama, scattered and possibly cultivated; known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Panamá.

INGA Scop.

Small to medium-sized trees. Leaves alternate, paripinnate; stipules usually minute; rachis with interfoliar glands, the glands filiform, conic, or patelliform; leaflets opposite, often asymmetrical, the basal leaflets reduced in size. Inflorescences axillary or terminal, racemose or spicate, with a peduncular and floriferous part; flowers

KEY TO THE SPECIES OF INGA

Rachis not winged:
Bracts large, obscuring calyces; terminal leaflets more than 20 cm long ... *I. spectabilis* (Vahl) Willd.
Bracts not obscuring calyces; terminal leaflets less than 20 cm long:
Inflorescences capituliform or umbelliform (rachis of inflorescence very short); flowers on pedicels 3–8 mm long; legumes short, curved, about half as thick as broad, densely ferruginous; leaflets in 3 or 4 pairs ..... *I. quaternata* Poepp.
Inflorescences spicate or racemose; flowers sessile or on pedicels less than 1 mm long:

All leaves with fewer than 4 pairs of leaflets:
Leaflets obovate; calyx less than 2 mm long; legumes with rounded sides at maturity .... *I. fagifolia* (L.) Benth.
Leaflets elliptic to lanceolate; calyx more than 2 mm long; legumes flat at maturity ..... *I. punctata* Willd.
Most leaves with more than 3 pairs of leaflets:
Calyx usually less than 2 mm long; leaves with fewer than 6 pairs of leaflets; young stems glabrous or puberulent ..... *I. pezizifera* Benth.
Calyx more than 3 mm long; usually some leaves with more than 5 pairs of leaflets; young stems mostly ferruginous-pubescent:
Upper leaflets usually narrowly long-obovate; corollas less than 9 mm long ..... *I. ruiziana* G. Don
Upper leaflets usually elliptic or lanceolate; corollas more than 10 mm long:
Calyx more than 7 mm long; leaflets in 7–10(13) pairs ..... *I. multijuga* Benth.
Calyx less than 7 mm long; leaflets in 4–8 pairs:
Lower leaflets usually asymmetrical; legumes flat; leaf rachis often with a linear appendage ca 4 mm long at apex; corollas often more than 15 mm long ..... *I. thibaudiana* DC.
Lower leaflets ± symmetrical; legumes subterete; leaf rachis without appendage at apex; corollas less than 15 mm long ..... *I. cocleensis* Pitt.

Rachis winged:
Calyx at anthesis less than 6 mm long:
Leaflets densely pubescent below; legumes subterete ..... *I. minutula* (Schery) Elias
Leaflets glabrous or sparsely pubescent below; legumes flat:
Inflorescences umbelliform; flowers and fruits on long slender pedicels ..... *I. umbellifera* (Vahl) Steud.
Inflorescences racemose; flowers and fruits almost sessile:
Most leaves with more than 3 pairs of leaflets; floral rachis shorter than peduncle, less than 3 cm long; legumes at least 2.5 cm wide at maturity ..... *I. pezizifera* Benth.
Most leaves with 2 pairs of leaflets; floral rachis longer than peduncle, more than 4 cm long; legumes less than 2 cm wide at maturity:
Leaflets obovate, in 2 or 3 pairs ..... *I. fagifolia* (L.) Benth.
Leaflets elliptic, in 2 pairs ..... *I. marginata* Willd.
Calyx at anthesis more than 6 mm long:
Stems bearing dense reddish-brown pubescence (in age); terminal leaflets more than 7 cm wide; legumes usually 20 cm or more long, bearing dense reddish-brown pubescence:
Corollas slender, less than 5 mm wide, sparsely sericeous; leaflets lacking a gland on midrib ..... *I. mucuna* Walp. & Duch.
Corollas thick, more than 8 mm wide, densely sericeous; leaflets with a gland on midrib within 2 cm of base (sometimes obscured by pubescence) ..... *I. goldmanii* Pitt.
Stems not bearing dense reddish-brown pubescence, at least not in age:
Bracts large, obscuring calyx; terminal leaflets more than 9 cm wide ..... *I. spectabilis* (Vahl) Willd.
Bracts small, the calyx visible; terminal leaflets frequently less than 9 cm wide:
Corollas more than 20 mm long; petioles usually more than 20 mm long; legumes tetragonal, ± glabrous (at least in age) ..... *I. sapindoides* Willd.
Corollas less than 20 mm long; petioles usually less than 20 mm long; legumes flat or terete, usually densely pubescent:
Some leaves with more than 4 pairs of leaflets; legumes terete ..... *I. vera* Willd. subsp. *spuria* (Willd.) J. León
All leaves with fewer than 5 pairs of leaflets (rarely 5 in *I. hayesii*); legumes terete or flat:
Calyx sparsely pilose to glabrate, not bearing dense reddish-brown pubescence; marginal ridge of legume narrow, the fruit remaining ± flat until nearly fully mature; trichomes of fruit sparse enough to be individually distinguished without difficulty ..... *I. hayesii* Benth.
Calyx densely pubescent, the young branches, petioles, and rachises bearing dense reddish-brown pubescence; marginal rib of legume broad and rounded, giving the fruit an overall terete appearance; trichomes of fruit so dense and short as to be not easily distinguished individually ..... *I. pauciflora* Walp. & Duch.

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usually many, with sweet aroma, subtended by bracts; calyx usually tubular, 5-toothed, usually somewhat irregularly lobed, sometimes splitting; corolla gamopetalous, tubular to tubular-funnelform, usually greenish, pubescent outside, glabrous inside; stamens numerous, fused into a tube at the base, the tube length variable relative to length of free filaments, even between flowers on same branch; filaments white at anthesis; style slender,

± equaling anthers; stigma discoid. Legumes linear; seeds surrounded by a sweet, pulpy, white mesocarp.

Inga flowers are visited by *Eulaema* bees in Ecuador (Dodson & Frymire, 1961). In Panama members of the genus are commonly called Guava or Ice cream beans.

Inga cocleensis Pitt., Contr. U.S. Natl. Herb. 18:211. 1916
Nacaspiro, Cuje

Tree, to 13 m tall, ± tomentose throughout, the trichomes sparser on upper leaflet surface, the pubescence reddish-brown except for surfaces of leaflet and corolla. Rachis terete; petiolules 1–2 mm long; leaflets in 4–8 pairs per pinna, ± elliptic, sometimes inequilateral, acute at apex, obtuse to rounded at base, the terminal pair 7–11 cm long and 2–4 cm wide. Spikes solitary or in groups of 2 or 3; peduncles mostly 2–3 cm long; rachis mostly 2–4 cm long; bracts nearly obsolete, less than 1 mm long; flowers sessile; calyx tubular, 4–6 mm long, the lobes acute, ca 1 mm long; corolla 10–15 mm long, the lobes acute, ca 2 mm long; stamens and style ca 2.5 cm long. Legumes subterete, to 35 cm long and 2.5 cm diam. *Croat 7941.*

Infrequent or rare, along the shore and in the forest. Flowers in the dry season, with the fruits maturing in several months.

Guatemala to Panama. In Panama, known from tropical moist forest in the Canal Zone and Coclé and from premontane wet forest in Panamá.

Inga fagifolia (L.) Willd. ex Benth., Trans. Linn. Soc. London 30:607. 1875
I. laurina (Sw.) Willd.
Guavo, Sweet pea, Guama

Tree, to 8(23) m; calyx and axis of inflorescences puberulent, otherwise ± glabrous. Leaves with (1)2 or 3 pairs of leaflets; petioles terete to margined; rachis terete to narrowly winged; leaflets obovate to elliptic, retuse to obtuse or bluntly short-acuminate, acute and slightly inequilateral at base, the terminal pair 6–14 cm long, 3–6 cm wide. Spikes usually 1–5 in axils of terminal leaves; peduncles mostly 1–3 cm long; rachis mostly 4–9 cm long; bracts nearly obsolete, less than 1 mm long; flowers sessile; calyx tubular, 1–2 mm long, the teeth shallow, acute; corolla funnelform, 3–6 mm long, the lobes acute, ca 1 mm long, somewhat pubescent at apex; staminal tube included to long-exserted; stamens and style to ca 12 mm long. Legumes flat and ribbed to bulged in the middle with raised margins at maturity, mostly 7–15 cm long, 1.5–2.5 cm wide. *Croat 5537, 6119.*

Common at least on the shore and in the young forest. Flowers mostly from January to May. The fruits mature mainly from August to November.

Mexico to Bolivia, Brazil, and Paraguay; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from tropical dry forest in Coclé (Penonomé), and from premontane wet forest in Panamá (Cerro Azul).

Inga goldmanii Pitt., Contr. U.S. Natl. Herb. 18:198. 1916
Guavo de mono

Tree, to 20 m tall, densely ferruginous-hirsute all over to sparsely so or glabrate on leaflet surface and sericeous on corolla. Rachis conspicuously winged; interfoliar glands stalked, to ± 3 mm tall; leaflets in 3–5 pairs, ovate to elliptic, acute to caudate-acuminate, rounded to slightly cordate and asymmetrical at base, sometimes ± bullate between veins, the terminal pair 11–24 cm long, 6–13 cm wide, usually with a gland on midrib above within 2 cm of base (sometimes obscured by pubescence); juvenile leaves less densely pubescent and to 80 cm long with the terminal leaflets to 42 cm long and 19 cm wide. Spikes axillary, usually solitary; peduncles 3–9 cm long, stout; rachis 10–20 cm long; bracts to 6 mm long; flowers sessile; calyx campanulate, 12–20 mm long, the lobes acute, 3–7 mm long; corolla campanulate, sericeous, 20–28 mm long, more than 8 mm wide; stamens and style to ca 50 mm; style sometimes persistent on growing legume. Legumes flat or twisted, 10–25 cm long, 4–6 cm wide, to 1.5 cm thick, densely ferruginous-hirsute; valves splitting open (usually from bottom) at maturity to expose seeds; seeds oblong, to 1.8 cm long, not colorful. *Croat 8300, 13107.*

Occasional, in the forest. Flowers mostly from November to February. The fruits probably mature in the rainy season.

Similar to *I. mucuna,* but distinguished by the short corolla, more reddish-brown fruits, and the gland on the midrib of the leaflet above.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Veraguas, Los Santos, and Panamá.

See Fig. 261.

Inga hayesii Benth., Trans. Linn. Soc. London 30:617. 1875
Guavo, Guamo

Tree, to 15 m tall; branchlets ferruginous-pilose when young, glabrate in age. Leaves sparsely pilose on axis and veins; petioles 5–40 mm long; rachis conspicuously winged; leaflets in 2–4(5) pairs, ovate-elliptic to obovate, acuminate to broadly acute, acute to rounded at base, usually asymmetrical, the terminal pair 7–14 cm long, 3–6 cm wide. Spikes 1 to several per axil; peduncles very short or to 1.5 cm long, strigose; rachis strigose, 1.5–2.5 cm long; flowers sessile; bracts ca 3 mm long; calyx 7–10 mm long, puberulent but with pilose base, longitudinally striate, the lobes acute to subacute, 1–2 mm long; corolla 10–19 mm long, densely white-sericeous, the lobes narrow, to ca 5 mm long; stamens and style to ca 45 mm long. Legumes flat until nearly fully mature, 4–15 cm long, 1.5–2.5 cm wide, strigose, usually with low, thin, transverse wrinkles. *Zetek 3497.*

Probably at one time more abundant than at present; the species was collected several times by Zetek when there were more disturbed areas on the island. Juvenile

plants have been seen in the forest, and the species is fairly common in the Canal Zone along roadsides. Seasonal behavior uncertain. Flowers principally from May to July, infrequently as early as January, with the fruits probably maturing in the rainy season.

Easily confused with *I. pauciflora,* except in fruit, and sometimes with *I. vera.*

Known only from Panama, from tropical moist forest on the Pacific slope in the Canal Zone, Panamá, and Darién and from premontane wet forest in Panamá (Cerro Azul).

Inga marginata Willd., Sp. Pl. 4:1015. 1806
Guavo de mono, Sweetwood

Tree, to 20 m tall; leaflet midribs above and axes and calyces of inflorescences puberulent, otherwise glabrous. Rachis and petiole winged, sometimes narrowly so; leaflets in 2 pairs, ± elliptic, asymmetrical in lower half, acuminate, ± acute at base, the terminal pair 4.5–12 cm long, 2–4.5 cm wide. Spikes axillary, in groups of 1–4; peduncles usually less than 1 cm long; rachis 4–11 cm long; bracts linear, ca 2 mm long; flowers usually sessile; calyx ca 1 mm long, shallowly lobed; corolla 2–4 mm long, the lobes acute, ca 1 mm long; stamens and style to ca 10 mm long. Legumes flat, the seminiferous areas bulged, 8–14 cm long, 1–2 cm wide. *Croat 8185.*

Occasional, in the forest, perhaps more abundant along the shore. Apparently flowers twice a year, principally in February and March, but also in September and October. The fruits appear to develop quickly, probably maturing 1 to 3 months after flowering.

Similar to *I. fagifolia* and *I. pezizifera,* but separated by always having four leaflets and a winged rachis.

Costa Rica to Bolivia and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, and Darién and from premontane wet forest in Coclé (El Valle).

Inga minutula (Schery) Elias, Phytologia 14:211–12. 1967
I. edulis Mart.; *I. oerstediana* Benth.
Guavo, Guava, Ice cream bean

Tree, 4–20 m tall, densely tomentose on most parts, sparsely so on upper surface of leaflets; stems with prominent ribs extending below petioles. Petioles terete, to 7.5 cm long; rachis winged, the interfoliar glands unusually large for the genus, 3–5 mm wide; leaflets in 3–6 pairs, oblong to lanceolate-elliptic, acuminate, rounded at base, the terminal pair 8–25 cm long, 3–11 cm wide. Spikes axillary in groups of 1–7; peduncle, floral rachis, and calyx cinereous-tomentose; rachis flattened, angulate; bracts ca 4 mm long and ca 2 mm wide; flowers sessile; calyx 3–5 mm long, irregularly lobed, the sinuses 1–4 mm deep; corolla 7–11 mm long, sericeous, the lobes 1–4 mm long; stamens and style to ca 30 mm long. Legumes ± terete, many-ribbed, 15–40(120) cm long, 1.5–2.5 cm diam. *Croat 11721, 11966.*

Occasional, in the forest, perhaps more abundant on the shore. Flowers from July to November, principally in August and September. Fruit maturity time not determined. Mature fruits in September in Costa Rica (Frankie, Baker, & Opler, 1974).

Mexico to South America; West Indies. In Panama, known from most areas of tropical moist forest and from tropical wet forest in Coclé. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 262.

Inga mucuna Walp. & Duch. in Walp., Ann. Bot. Syst. 2:456. 1851–52

Tree, to 10(20) m tall; branchlets densely ferruginous-velutinous. Leaves densely rufous to golden-tomentose on axis and veins, sparsely so on leaf surface; rachis widely winged; petioles terete; leaflets in 3 or 4 pairs, ovate to broadly elliptic, acute to acuminate, obtuse to rounded and asymmetrical at base, the terminal pair 13–21 cm long, 6–12 cm wide. Spikes axillary, usually solitary or paired, the axis densely brownish-tomentose; bracts to ca 8 mm long; flowers sessile; calyx 15–21 mm long, glabrous except on tips of teeth, conspicuously longitudinally striate, the lobes to ca 2 mm long, blunt, bearing conspicuous tuft of trichomes at apex; corolla 35–55 mm long, white-sericeous, the lobes to ca 6 mm long; stamens and style to ca 80 mm long. Legumes flat, densely ferruginous-hirsute, 25–45 cm long, 4–6 cm wide, often twisted, the margins raised, rounded. *Croat 6858, 12959.*

Uncommon, in the young forest and along the shore. Flowers from August to February. The fruits are most common in the dry season.

Similar to *I. goldmanii,* but having a long slender corolla, fruit of a lighter reddish-brown color, and no gland near the base of midrib on upper leaflet surface.

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

See Fig. 263.

Inga multijuga Benth., Trans. Linn. Soc. London 30:615. 1875

Tree, to 20 m tall and 40 cm dbh; inner bark reddish, granular; branchlets densely ferruginous-tomentose when young, glabrate in age; lenticels prominent. Petiole and rachis terete, tomentose; leaflets in (5)7–10(13) pairs, narrowly ovate to oblong-elliptic or oblong, acute to acuminate, obtuse to rounded at base, glabrous above except on midrib, tomentose below on veins, sparsely so on surface, the terminal pair 7–18 cm long, 2–4.3 cm wide. Spikes terminal or axillary, usually solitary or paired, the axis and calyx densely ferruginous-tomentose; bracts subulate, ± 1 mm long; flowers sessile; calyx 7–10 mm long, densely villous, the lobes to ca 1 mm long; corolla 2–3 cm long, sericeous, the lobes narrow, to ca 4 mm long; stamens and style to ca 40 mm long. Legumes flat, 20–30 cm long, to 4.5 cm broad, tomentose when young, glabrate in age, remaining flat, often markedly curved, the margins stout, raised. *Croat 8282, Foster 1418.*

Infrequent, along the shore. Flowers from September

Fig. 262. *Inga minutula*

Fig. 261. *Inga goldmanii*

Fig. 263. *Inga mucuna*

to April, principally at the beginning of the dry season. The fruits mature in the early to middle rainy season.

Distinguished from *I. thibaudiana* by normally having nine or ten pairs of leaflets on some leaves and by having larger fruits, which are glabrate in age.

Honduras to Panama. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Chiriquí, Veraguas, Panamá, and Darién, from premontane wet forest in the Canal Zone and Panamá, from tropical wet forest in Veraguas, and from premontane rain forest in Panamá (summit of Cerro Jefe).

Inga pauciflora Walp. & Duch., Linnaea 23:746. 1850

Tree, to 10 m tall; branchlets densely ferruginous-tomentose when young, glabrate in age. Leaves velutinous especially on axes and veins, sparsely so on upper surface; petioles very short, terete; rachis cuneate-winged; leaflets in 3 or 4 pairs, ovate to elliptic, acute to short-acuminate, obtuse to rounded at base, asymmetrical, the terminal pair 7–16 cm long, 3–7 cm wide, the basal pair often much reduced. Spikes axillary or terminal, solitary or in pairs; peduncle, rachis, and calyx densely ferruginous-tomentose; peduncles 1.5–2.5 em long; rachis 1.5–3.5 cm long; bracts to 3 mm long; flowers sessile; calyx 8–15 mm long, the lobes to ca 3 mm long; corolla 13–18 mm long, sericeous, the lobes ca 3 mm long; stamens and style to ca 50 mm long. Legumes subterete, with broad ribs, densely ferruginous-pubescent, mostly 4–20 cm long, 1–2 cm diam, often curled, yellowish-brown at maturity. *Croat 6105, 13967.*

Common along the shore. Flowers from March to July. The fruits probably mature from July to October.

Easily confused with *I. hayesii* and *I. vera.* It may be distinguished from *I. hayesii* by its more or less terete fruit and more densely pubescent calyx, and from *I. vera* by having fewer than five pairs of leaflets.

Known only from Panama, from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién and from premontane wet forest in Panamá (Cerro Campana).

See Fig. 264.

Inga pezizifera Benth. in Hook., London J. Bot. 4:587. 1845

Tree, to 27 m tall and 40 cm dbh, glabrous to puberulent throughout; trunk ± involuted with many prominent horizontal wrinkles; outer bark thin; inner bark reddish; young stems very prominently lenticellate. Petioles margined; rachis margined to narrowly winged; leaflets in 2–5 (usually 4) pairs, narrowly ovate to lanceolate-elliptic or oblanceolate, acuminate, rounded to acute at base, slightly asymmetrical, the terminal pair 8–22 cm long, 2.5–8 cm wide. Spikes axillary in groups of 1–6; peduncles 1.5–3.5 cm long; rachis shorter than peduncle, very densely flowered, 0.5–3 cm long; bracts ca 5 mm long; flowers sessile; calyx 1–2(3) mm long, the lobes ca 0.5 mm long, blunt; corolla 4–8 mm long, the lobes blunt to acute, ca 1 mm long; stamens and style ca 1 cm long. Legumes flat, 10–22 cm long, (2)2.5–3 cm wide, ± glabrous, ± straight, the marginal ribs prominent, the seminiferous areas individually raised, the axes of the inflorescences persisting with warty bases of fallen fruits. *Croat 14881.*

Common in the forest, especially the young forest. Flowers most commonly in May and June, beginning as early as December. The fruits mature in the rainy season.

Separated from *I. ruiziana* by the lanceolate-elliptic leaflets, which are always in less than six pairs, and by the shorter calyx, usually less than 2 mm long.

Panama to Brazil. In Panama, known from tropical moist forest in the Canal Zone and from premontane wet forest in Panamá (Cerro Jefe).

Inga punctata Willd., Sp. Pl. 4:1016. 1806

I. leptoloba Schlecht.

Guavita cansa-boca, Bribri, Guava, Guava del mono

Tree, to 15 m tall; branchlets sparsely strigose when young, glabrate in age, minutely lenticellate, minutely ribbed below petioles (at least when dried). Leaves strigose throughout, especially on axis and midrib of leaflets; petiole and rachis terete to narrowly margined; leaflets in 2 or 3 pairs, lanceolate to elliptic, long-acuminate, acute to rounded at base, the terminal pair 9–18 cm long, 3.5–7.5 cm wide. Spikes axillary, in groups of 1–7; peduncle and rachis strigose; peduncles 2–4 cm long; rachis much shorter, 1–2.5 cm long; bracts subulate, to ± 2 mm long; calyx puberulent, 3–5 mm long, the lobes ± 1 mm long; corolla moderately sericeous, 5–9 mm long, the lobes to 2 mm long; stamens and style to ca 2 cm long. Legumes flat, to 16 cm long and 2 cm wide, minutely puberulent, the margins raised. *Croat 7418.*

Common in the forest. Flowers throughout the rainy season (May to December, rarely to January). One individual on BCI flowered for a week in early June in two consecutive years. Mature fruits seen in late dry season.

Fruits are similar to those of *I. pezizifera,* but that species lacks persistent warty fruit bases.

Mexico to Peru; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Panamá, and Darién, from premontane wet forest in Colon, Chiriquí, Coclé, and Panamá, from tropical wet forest in Panamá and Darién and from lower montane wet forest in Chiriquí. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

Inga quaternata Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3:79. 1845

I. roussoviana Pitt.

Guavito, Cansa boca, Bribri

Tree, to 15 m tall; branchlets densely ferruginous-tomentose to glabrous-lenticellate. Petiole and rachis ± terete, tomentose; leaflets in 3 or 4 pairs, oblanceolate to oblong-obovate, acuminate to obtuse at apex, acute to obtuse at base, puberulent especially on veins, the terminal pair 7–19 cm long, 3–7.5 cm wide. Racemes axillary, solitary (2 to 3 elsewhere); peduncle and floral rachis densely ferruginous-tomentose; peduncles 0.5–2.5(3.5) cm long; rachis very short, to 5 mm long, giving the inflorescence a capituliform appearance; bracts ca 1 mm

Fig. 264. *Inga pauciflora*

Fig. 265. *Inga ruiziana*

Fig. 266. *Inga umbellifera*

long; pedicel and calyx villous; pedicel 3–8 mm long; calyx 3–6 mm long, the lobes to 1 mm long; corolla sericeous, 6–11 mm long, the lobes to 1.5 mm long; stamens and style to 15 mm long. Legumes flat, 3–9(18) cm long, 1.5–3 cm wide, 1–1.5 cm thick, curved, ferruginous-tomentose when young to glabrate in age, ribbed on margins. *Croat 7699, Foster 1013.*

Common, at least on the shore. The flowers often appear on denuded branchlets or on branchlets with new leaves. Flowers possibly throughout the year, mostly in the late rainy and early dry seasons. Mature-size fruits have been seen from June to September.

According to the label on *Foster 1013,* the white pulp of the green fruits is eaten by the white-faced monkeys.

Mexico to Panama and possibly Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and San Blas, from tropical dry forest in Coclé (Penonomé), and from premontane wet forest in Chiriquí (San Félix). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

Inga ruiziana G. Don, Gen. Hist. Dichl. Pl. 2:391. 1832

I. confusa Britt. & Rose

Bribri

Tree, to 9(25) m tall; branchlets lenticellate, minutely ferruginous-pubescent, sometimes ribbed below petioles. Petiole and rachis unwinged, minutely margined, minutely pubescent; leaflets in (4)6–7(8) pairs, obovate-oblong to obovate, short-acuminate, obtuse to rounded at base, glabrate but with puberulent veins, the terminal pair 15–25(34) cm long, 4.5–8(12) cm wide. Spikes axillary (appearing paniculate on new growth) in groups of 1–4; peduncle and rachis tomentose; peduncles 1–2.5(4.5) cm long; rachis 1–1.5 cm long; flowers dense, very short-pedicellate; bracts ca 1 mm long; pedicel and calyx sparsely pubescent; calyx 3–5 mm long, the lobes ca 0.5 mm long; corolla minutely, sparsely pubescent, 7–9 mm long, the lobes ca 1.5 mm long; stamens and style to 4 cm long. Legumes flat, minutely puberulent, curved slightly, to 16 cm long and 4 cm wide, the marginal ribs prominent. *Croat 8436.*

Infrequent or rare; collected along the shore of Gigante Bay and the shore of Bat Cove. Seasonal behavior uncertain. Flowers from August to April, possibly with individuals flowering twice a year. Fruit maturity period not determined.

Nicaragua to Peru and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién.

See Fig. 265.

Inga sapindoides Willd., Sp. Pl. 4:1012. 1806

I. panamensis Seem.; *I. pittieri* Micheli

Bribri, Guavo

Tree, to 15 m tall; branchlets ferruginous-puberulent when young, glabrate and prominently lenticellate in age. Petioles ribbed, 2–7 cm long; rachis winged; petiole and rachis sparsely ferruginous-pubescent; leaflets in 2–5 pairs, obovate to elliptic, acute to acuminate, obtuse to rounded at base, densely tomentose to puberulent especially on midrib and veins below, the terminal pair 11–26 cm long, 4.5–12 cm wide. Spikes usually axillary in groups of 1–3; peduncles usually sparsely tomentose, 1–5(6) cm long; floral rachis much shorter, 0.5–2(3) cm long; bracts to 12 mm long; calyx and corolla sparsely sericeous; calyx 6–13(17) mm long, the lobes to 2 mm long; corolla 18–30 mm long, the lobes to 3 mm long; stamens and styles 4–5.5 cm long. Legumes tetragonal with prominently ribbed corners, 11–30 cm long, 1.5–3.5 cm wide, ca 1.5 cm thick, glabrate to densely pubescent. *Croat 5025, 7345.*

Common, at least along the shore. Seasonal behavior uncertain. Flowers from August to May, especially from November to February. Most fruits mature in the rainy season.

An extremely variable species. Often planted for shade in coffee plantations.

Mexico to Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Coclé, Panamá, and Darién and from premontane wet forest in Chiriquí (San Félix).

Inga spectabilis (Vahl) Willd., Sp. Pl. 4:1017. 1806

Bribri, Guavo, Monkey tambrin, Guava de castilla, Guava real

Tree, to 22 m tall and 34 cm dbh; outer bark smooth, light brown; inner bark pale reddish-brown or tan; branchlets 4-angled, ± lenticellate, glabrate in age. Leaves glabrate in age above except on veins, sparsely short-pilose below, more densely on veins; petiole and rachis narrowly winged to only margined; leaflets in 2 pairs (rarely 3), sessile, broadly elliptic to obovate, rounded to acute or mucronate at apex, obtuse to subcordate and inequilateral at base, the terminal pair 17–28 cm long, 9–17 cm wide, the basal pair much reduced. Flowers in capituliform spikes, the spikes axillary or terminal, in groups of 1–6, with dense bracts; peduncles tomentose, 3–8 cm long; rachis 1–3 cm long; bracts large, to 14 mm long and 11 mm wide, obscuring calyx, tomentose, ovate, deciduous as flowers open; calyx tomentose, 7–9 mm long, the lobes 2.5 mm long; corolla short-sericeous, 15–22 cm long, the lobes to 3 mm long; stamens and style to ca 25 mm long. Legumes flat, 30–70 cm long, 5–8 cm wide, 1.5–3 cm thick, glabrous, the margins not elevated. *Croat 10480, Shattuck 925.*

Uncommon, possibly restricted to the older forest. Flowers from March to August with a peak in June and July. The fruits probably mature from February to May of the following year.

Mexico and Costa Rica to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Los Santos (Pocrí), from premontane wet forest in Chiriquí (Tolé), and from tropical wet forest in Colón.

Inga thibaudiana DC., Mém. Leg. 12:439. 1826

Tree, to 8 m tall; branchlets, petioles, rachises, leaflets, below, and midribs above densely short-pubescent; lenti-

cels ± prominent, small. Petiole and rachis not winged; leaflets in 4–8 pairs, variable in shape, asymmetrical, mostly narrowly ovate to elliptic, acute to long-acuminate, obtuse to rounded at base, puberulent above except on midrib, the terminal pair 7–10(15) cm long, 2.5–4(6) cm wide. Spikes axillary or terminal, in groups of 1–4; peduncles 3–4 cm long, densely tomentose; bracts 1 mm long; calyx 3–5 mm long, the lobes acute, ca 0.5 mm long, tomentose; corolla 14–20 mm long, sericeous-villous, the lobes to 1.5 mm long. Legumes flat, 6–20 cm long, 1.5–2.5 cm wide, bearing dense short, ferruginous-tomentose pubescence, the marginal ribs prominent. *Foster 703, Shattuck 1122.*

Rare; collected along the shore of Gigante Bay and Burrunga Point. Seasonal behavior uncertain. Flowers from January to May. The fruits were mature in the rainy season.

Confused with *I. multijuga,* which often has nine or ten pairs of leaflets.

Belize to Panama; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Darién and from tropical wet forest in Colón (Salúd) and Darién.

Inga umbellifera (Vahl) Steud., Bot. Nom. Phan. 431. 1821

I. gracilipes Standl.

Tree, to 10 m tall; young branches and inflorescences puberulent, otherwise glabrous. Petioles unwinged or winged near apex; rachis winged; leaflets in 2 or 3 pairs, elliptic to oblong-elliptic, acuminate, obtuse to rounded at base, the terminal pair 11–17 cm long, 4–6.5 cm wide. Racemes umbelliform, axillary and solitary (appearing paniculate on new growth); peduncles 2–4(5) cm long; rachis very short, 3–4 mm long; bracts subulate, ca 4 mm long; flowers long-pedicellate; pedicels slender, 8–12(15) mm long; calyx 3–5 mm long, the lobes acute, ca 0.5 mm long; corolla 9–14(17) mm long, the lobes acute, to ca 2 mm long; stamens and style to ca 20 mm long. Legumes flat, 6–18 cm long, 1.5–3.5 cm wide, straight or curved, glabrate in age, the marginal ribs prominent. *Croat 7877, 11889.*

Common, at least on the shore. Flowers from August to May, possibly twice a year. Fruit maturity period uncertain; mature fruits have been seen in the early rainy season.

Inga quaternata, the only other species in the genus with long-pedicellate flowers, is distinguished by its unwinged rachis.

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

See Fig. 266.

Inga vera Willd. subsp. **spuria** (Willd.) J. León, Ann. Missouri Bot. Gard. 53:339. 1966

Guava, Coralillo

Tree, to 12(20) m tall, ca 30 cm dbh; branchlets sometimes ribbed below petioles, tomentose when young, glabrate in age, lenticellate. Petiole and rachis tomentose; petioles winged or not, 8–40 mm long; rachis winged; leaflets in 4–8 pairs (rarely 9 or 10), oblong-elliptic to lanceolate, acuminate, obtuse to rounded at base, tomentose to sparsely pubescent, more densely on veins, the terminal pair 4.5–12(17) cm long, 2.5–5.5 cm wide. Spikes axillary or terminal, in groups of 1 to many; peduncles 3–5(7) cm long, tomentose; rachis 1–3(5) cm long, tomentose; bracts ca 3 mm long; calyx densely villous, 11–19 mm long, sometimes striate or minutely ribbed, the lobes acute, ca 3 mm long; corolla lanate, 15–20 mm long, the lobes acute, ca 4 mm long; stamens and style to 80 mm long. Legumes terete, densely tomentose, usually less than 15 cm long (to 30 cm), to 2 cm wide, usually curved, the base blunt, the apex pointed, the margins prominently raised, the lateral margins rounded and narrowly ribbed, the intervening area of the valve minutely transversely ribbed. *Zetek 3464.*

Though several old collections were made by Zetek, the species has been collected only once in recent years, along the shore of Gigante Bay. Flowers throughout the dry season (January to June), rarely in the rainy season; an individual plant may flower twice a year. Synchronous bursts of flowering have been observed in April. The fruits may be of mature size by June, with seed dispersal in the rainy season.

Mexico to northern South America; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Los Santos, Herrera, Coclé, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in Los Santos, and from premontane wet forest in Chiriquí (Boquete).

LEUCAENA Benth.

Leucaena multicapitula Schery, Ann. Missouri Bot. Gard. 37:302. 1950

Tree, to 20 m tall; branchlets glabrate and lenticellate in age. Leaves bipinnate with 2–4 pairs of opposite pinnae, with minute appressed pubescence above and below; petioles 3–5 cm long with a small, sessile, conical gland near apex; rachis 5–9 cm long, usually eglandular; pinnular rachis to 9 cm long with a gland at the apex; leaflets in 3–5 pairs per pinna, ovate to elliptic, acute at apex, acute to rounded at base, 1.5–5.5 cm long, 1–2.5 cm wide. Inflorescences terminal and upper-axillary, compounded 3 times, the heads orbicular, ca 1 cm wide, in simple or compound fascicles, the branches 1–5 per axil, to 20 cm long; peduncles ca 1 cm long, tomentose; flowers green, sessile, each subtended by a peltate bract as long as calyx; calyx ca 1.1 mm long; petals to 3.3 mm long, linear-oblong, weakly adnate to calyx; stamens 10, free, exserted ca 3 mm; style 1–2 mm longer than stamens. Legumes linear, flat, 7–14 cm long, 2.5–4.5 cm wide, thin, glabrous; seeds ovate, flat, ca 8 mm long, dark brown with prominent margins. *Croat 11735.*

Uncommon; collected on the shore of Miller Peninsula south of Orchid Island and at Gross Point. Flowers from June to August (sometimes as early as May) in central Panama. The fruits mature from July to October.

Albizia adinocephala (Donn. Sm.) Britt. & Rose, as reported by Standley (1933), is clearly this species. *Bailey*

281 has no more than ten stamens per flower, and the upper sides of the leaflets are not conspicuously reticulate-veined, as is *A. adinocephala.*

The species has been confused with *L. trichodes* (Jacq.) Benth., a closely related South American species, and is distinguished from it by having its inflorescence more highly branched.

The dark-colored seeds may either be displayed against the opened light-colored interior of the valves or fall free as the valves open.

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

See Fig. 267.

MIMOSA L.

Mimosa casta L., Sp. Pl. 518. 1753

Vine, rarely to 5.5 m long, ± glabrous but sometimes with puberulent lower surface of leaflets, armed throughout with stout, recurved thorns. Leaves bipinnate with 1 pair of pinnae; petioles to 10 cm long, eglandular; stipules lanceolate, paired, to ca 5 mm long, striate; leaflets in 3–6 pairs per pinna, inequilateral, elliptic to lanceolate-oblong, acute at apex, oblique and rounded at base, 1–3 cm long, 7–10 mm wide, setose-ciliate on margins and sometimes on surface below; venation at base palmate. Flowers minute, in globular, white, pedunculate, axillary clusters ca 1–1.5 cm diam, the outermost in each head staminate; floral bracteoles linear-lanceolate, 1–2 mm long, pectinate-ciliate at base; calyx obsolete; corolla greenish, 4-lobed, ca 2.5 mm long; stamens (4)5, 5–8 mm long; style ± equaling stamens. Legumes usually 10–20 in a dense, usually globular cluster, flat, 3–4.5 cm long, ca 1 cm wide, usually 3–6-seeded, each segment distinct, the margins ± sinuate with laterally directed setae. *Croat 12821, 13157.*

Rare; seen only on the shore at the edge of Rear #8 Lighthouse Clearing. Locally abundant in the Canal Zone along roadsides, especially near water. Flowers and fruits from December to January.

Panama and the northern coast of South America to Brazil; Jamaica and Lesser Antilles. In Panama, known only from tropical moist forest in the Canal Zone.

See Fig. 268.

Mimosa pigra L., Cent. Pl. 1:13. 1755

Bashful plant, Zarza, Dormilón

Usually an erect shrub, less than 2 m tall; branchlets setose-hispid and armed with stout, recurved thorns. Leaves bipinnate with 8–15 pairs of pinnae; stipules ovate, to 8 mm long, appressed-pubescent, subpersistent; petiole and rachis hispid with trichomes ca 2 mm long, eglandular, armed, the spines stout to slender, straight or recurved, to 4 mm long; petioles less than 1 cm long; rachis 10–20 cm long; pinnae opposite, 3–6 cm long, hispid; leaflets in 20–30 pairs per pinna, oblong, acute at apex, rounded to truncate at base, ca 8 mm long and 1 mm wide, appressed-pubescent especially below, the margins setose-ciliate; veins few, longitudinal. Flowers in dense, globular, white, pedunculate heads in terminal axils; peduncles hispid, 3–5 cm long; floral bracteoles linear, 2–3 mm long, pectinate above middle; calyx 1–2 mm long, cleft ca two-thirds its length, the lobes setaceous, glabrous; corolla 2–4 mm long, glabrous except short-hispid near apex, 4-lobed for nearly half its length; stamens 8, 4–5 mm long; style about as long as stamens. Legumes in dense clusters of 10–15, linear, 4–8 cm long, 1–1.5 cm wide, densely setose-hispid, flat, stipitate, with 7–20 segments, the margins persistent, the rectangular, 1-seeded segments 2.5–4 mm wide, falling free individually. *Croat 6868.*

Common in clearings at the margin of the lake, apparently preferring moist habitats. Flowers and fruits throughout the year, especially from May to August.

Pantropical. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Veraguas, Coclé, Panamá, and Darién, from tropical dry and premontane moist forests in Los Santos, from premontane wet forest in Chiriquí, and from tropical wet forest in Colón and Darién.

Mimosa pudica L., Sp. Pl. 518. 1753

Sensitive plant, Dormidera, Ciérrate, Cierra tus puertas, Shameface, Shameweed

Prostrate herb, usually less than 1 m tall, but occasionally to 2 m or more when undisturbed; stems weakly ribbed, sparsely setose and armed with sharp spines. Leaves bipinnate with (1)2 closely spaced pairs of pinnae, the pinnae mostly 3.5–6.5 cm long; leaflets in 10–20 pairs per pinna, sensitive, folding upon disturbance, oblong, 3–12 mm long, 1–2 mm wide, glabrous, ciliate. Flowers dense, globular, pink clusters (congested racemes) on peduncles 1–2.5 cm long; floral bracteoles linear-lanceolate or linear-oblanceolate, setose; rachis elongating in fruit; calyx nearly obsolete; corolla funnelform, 1–2 mm long; stamens 4, ca 7 mm long; style sharp at apex, ± equaling stamens. Legumes brown, oblong, mostly 3- or 4-seeded, equally notched on both sides, glabrous but with multidirectional setae on lateral margins. *Croat 12712, 12813.*

Very abundant in the Laboratory Clearing; rare else-

KEY TO THE SPECIES OF MIMOSA

One pair of pinnae per leaf; leaflets usually more than 15 mm long; 3–6 pairs of leaflets per pinna ..... *M. casta* L.

Two or more pairs of pinnae per leaf; leaflets less than 15 mm long; more than 10 pairs of leaflets per pinna:

Pinnae per leaf in 2 pairs; flowers pinkish; legumes setose-aculeate only on margin .... *M. pudica* L.

Pinnae per leaf in 8–15 pairs; flowers white; legumes densely setose-hispid throughout .. *M. pigra* L.

Fig. 268. *Mimosa casta*

Fig. 267. *Leucaena multicapitula*

Fig. 269. *Pithecellobium barbourianum*

Fig. 270. *Pithecellobium hymeneaefolium*

where in clearings. Flowers and fruits principally from November to April.

Pantropical; native to northern South America. Throughout Panama in all life zones where disturbed habitats exist.

PITHECELLOBIUM Mart.

Pithecellobium barbourianum Standl., Contr. Arnold Arbor. 5:74, pl. 11. 1933

Unarmed tree, to 12 m tall and 25 cm dbh; outer bark thin, coarse, cracked; inner bark tan, finely granular; branchlets, leaf axes, and lower surface of leaves densely villous with reddish-brown trichomes; sap with weak, pungent odor. Leaves bipinnate, to 20 cm long, with 7–11 pairs of pinnae; petioles with a gland near apex; rachis and pinnular rachis with glands at nodes; leaflets in 9–16 pairs per pinna, oblong, oblique, ca 10 mm long, 4–5 mm wide, thick, glabrous above except on midrib, pubescent below, the margins revolute. Flowers minute, sessile, in globular, long-pedunculate, axillary heads; peduncles ca 6 cm long; flowering rachis ca 4 mm long; calyx funnelform, ca 3 mm long, golden-brown, hirsutulous, shallowly 5- or 6-dentate; corolla funnelform, ca 4 mm long, the outside bearing dense, golden-brown, hirsute pubescence; stamens ca 13, the filaments united basally. Legumes prominently coiled and somewhat constricted between each seed, to ca 11 cm long and 1.4 cm wide, brown, densely short-villous, twisting open irregularly at maturity to expose black seeds on the red-orange inner surface of the valves. *Shattuck 237.*

Represented from the island only by the type collection made at Zetek Trail 2400. Flowers in October. Some fruits known from August to December.

Known only from Panama, from tropical moist forest in the Canal Zone (BCI and adjacent areas around Gatun Lake).

See Fig. 269.

Pithecellobium dinizii Ducke, Arch. Jard. Bot. Rio de Janeiro 3:66. 1922

P. umbriflorum Ducke

Tree, to 8 m tall; young stems, leaf axes, and inflorescence branches tomentose. Leaves bipinnate with 2 or 3 pairs of opposite pinnae; petioles 4–6 cm long with a small gland near the base; stipules paired, oblong, acute, to 1 cm long, persistent; rachis slightly longer with a similar gland at each node; pinnular rachis 10–15 cm long with a gland at all but the lowermost nodes; leaflets in 4–8(9) pairs per pinna, opposite, sessile, asymmetrical, oblong to elliptic, acuminate often ending in a slender dark cusp, acute to rounded at base, 2–9 cm long, 1–3 cm wide (to 6 cm long and 2 cm wide in South America), gradually reduced in size toward base, sparsely to densely pubescent on midrib. Flowers dense on densely clustered, axillary spikes to 2 cm long, usually at defoliated nodes; peduncles short; floral rachis swollen beneath flower, forming a small shelf; bracts ca 1.5 mm long; calyx to 4 mm long, irregularly lobed, usually deeply divided on one side, sparsely pubescent and ciliate; corolla white, to 5 mm long, sparsely pubescent, ± regularly 5-lobed; staminal tube exserted; anthers and apex of filaments red-violet; anthers broader than long, attached basally, the thecae directed upward. Legumes ca 8 cm long and 1 cm wide, bearing dense, golden-brown, tomentose pubescence, flattened with a narrow marginal ridge. *Croat 17024, 17027, Foster 1676.*

Known only from the shore along Chapman Cove. Flowers in the dry season. The fruits mature in the early rainy season.

Mature specimens on BCI differ from mature South American specimens by having larger leaflets, with the lower edge often obtuse to acute, compared to the somewhat auriculate edge in the South American material.

Panama, Colombia (*Cuatrecasas 16075,* Valle on the Pacific coast), Peru (Loreto), and Brazil (*Krukoff 1302,* "Amazonas, Calama on Río Madeira"). In Panama, known only from BCI.

Pithecellobium hymeneaefolium (H. & B.) Benth. in Hook., London J. Bot. 3:198. 1844

P. panamense Walp. & Duch.

Liana or climbing shrub, to 7 m long, minutely puberulent throughout but with the leaves and older stems glabrous to glabrate; stems minutely lenticellate, armed, the thorns paired, recurved, to 1 cm long at most nodes, persisting on older stems. Leaves bipinnate with 1 pair of pinnae; petiole and pinnular rachis each with a sessile cupular gland at apex; petioles 2–4 cm long, canaliculate; pinnae bifoliolate; pinnular rachis 1–2 cm long; leaflets very asymmetrical, ovate to ± elliptic, bluntly acute to rounded at apex, oblique at base with one side rounded, 4.5–12 cm long, 3–6 cm wide, sometimes barbate on

KEY TO THE SPECIES OF PITHECELLOBIUM

Leaves pinnate ..... *P. rufescens* (Benth.) Pitt.
Leaves bipinnate:
  Leaflets in 1 pair per pinna ..... *P. hymeneaefolium* (H. & B.) Benth.
  Leaflets in 4 or more pairs per pinna:
    Leaflets less than 1 cm wide; leaves with more than 6 pairs of pinnae .... *P. barbourianum* Standl.
    Leaflets more than 1 cm wide; leaves with less than 6 pairs of pinnae:
      Peduncles more than 5 cm long; petioles bearing large cupular gland at apex; legumes curled; pinnae in 3–5 pairs per leaf ..... *P. macradenium* Pitt.
      Peduncles less than 5 cm long; petioles bearing small gland at apex; legumes flat; pinnae in 2 or 3 pairs per leaf ..... *P. dinizii* Ducke

narrow side (*fide Flora of Panama,* Woodson & Schery, 1950). Flowers showy in long-pedunculate, axillary or terminal spikes, greenish with anthers white; peduncles to 4.5(6) cm long; rachis ca 7 cm long; calyx cupular, ca 2.5 mm long; corolla funnelform, ca 10 mm long, the lobes acute, ca 2 mm long; stamens 25–40, united at base, the staminal tube long-exserted, 2–4 cm long. Legumes 5–10 cm long, 1.5–2 cm wide, curved, densely tomentose, becoming bright red and twisting open at maturity; inner valve surface bright orange-red; seeds ovoid, black, ca 1.5 cm long and 1.2 cm wide, somewhat compressed, shiny, dangling from a very irregular pale red-orange funiculus and enveloped on most of one side by a finely dissected aril of the same color. *Croat 8176, Foster 1030.*

Occasional, along the shore on north side of the island and on Orchid Island. Flowers throughout the year, especially during the early rainy season (May to August). The fruits mature mostly from June to September.

Panama to Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién, from tropical dry forest in Los Santos and Panamá (Taboga Island), and from premontane wet forest in Panamá.

See Fig. 270.

Pithecellobium macradenium Pitt., Contr. U.S. Natl. Herb. 20:465. 1922

Tree, to 30(40) m tall, to 1 m dbh; young branchlets with brownish short pubescence, becoming glabrous and sometimes lenticellate in age. Leaves bipinnate with 3–5 pairs of pinnae, the axes minutely pubescent; petioles 4–7 cm long; stipules acicular, caducous; rachis 8–16 cm long, bearing a large cupular gland to 1 cm long between pairs of basal pinnae and a smaller gland at node of successive pair; pinnular rachis to 15 cm long, with small glands at nodes; leaflets in 7–12 pairs per pinna, asymmetrical, ovate to oblong, obtuse to rounded at apex, usually obtuse at base, 2–5 cm long, 1–2 cm wide, minutely appressed-puberulent with longer trichomes on midrib. Flowers in condensed umbels or short spikes; peduncles 5–12 cm long, ferruginous-tomentose; floral rachis ca 5 mm long; pedicels 1–2.5 mm long; flowers pale green, 9–12 mm long excluding stamens, with minute, brown, appressed trichomes outside; calyx 5–6 mm long, the lobes irregular, ca 2 mm long, sometimes ± cleft on one side; corolla usually 5(6)-lobed ca one-third its length, fused to the staminal tube near base; stamens many, ca 3 cm long, the staminal tube nearly as long as corolla. Legumes linear, short-stipitate, curved into a nearly complete circle ca 6 cm diam, to 12 cm long and 2–2.5 cm wide, very thick at seminiferous areas, the valves splitting apart and twisting to display seeds; seeds flattened, ovoid, ca 8 mm long, on alternate segments of the valve. *Croat 5205.*

Uncommon; known only from a few places along the north shore and in the forest on the north side of the island. Flowers principally from February to May, with the fruits maturing from April to September, chiefly in the rainy season.

Costa Rica and Panama. In Panama, reported by Holdridge (1970) from wet regions at low elevations; collected only from tropical moist forest on the Atlantic slope in the Canal Zone. Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Figs. 271 and 272.

Pithecellobium rufescens (Benth.) Pitt., Contr. U.S. Natl. Herb. 18:181. 1916

Coralillo, Flor de indio, Harino, Jarino

Shrub or tree, to 7(12) m tall; branchlets, leaf axes, and inflorescences ferruginous-tomentulose; branchlets lenticellate. Leaves pinnate, usually with 3–5 pairs of pinnae; petioles very short; stipules acicular, caducous; rachis to 15 cm long with small gland at each node; leaflets variable, oblong to broadly elliptic, rounded to short-acuminate, rounded to obtuse at base, 5–13 cm long, 3.5–10 cm wide, weakly pubescent to glabrous above except on midrib, sparsely pubescent below, more densely on midrib. Flowers white, sessile, in globular, pedunculate, subterminal heads ca 2 cm wide; peduncles 1–2 cm long, ferruginous-tomentose; floral bracts linear, to 4 mm long, giving the head a burrlike appearance before anthesis; calyx 1–2 mm long, shallowly lobed, pubescent at apex of lobes; corolla 6–8 mm long, the lobes ca 1 mm long, pubescent at apex. Legumes linear-moniliform, curled, to 15 cm long, reddish, splitting and twisting at maturity to expose black, ellipsoid or orbicular seeds ca 7–10 mm long. *Croat 5355, 5925.*

Common along the shore on the north side of the island. Seedlings have been seen in the forest at Wheeler Trail 1900. Flowers mostly in the dry season (January to June). The fruits mature mostly in August and September (less often as early as February or as late as December).

Costa Rica, Panama, and Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Los Santos, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone, from premontane wet forest in Colón, Coclé, and Darién, and from premontane rain forest in Panamá (summit of Cerro Jefe).

See Fig. 273.

63B. CAESALPINIOIDEAE

Leaves simple or pinnate; stipels lacking. Flowers zygomorphic, in racemes or panicles, ebracteate; calyx sometimes 4-parted by union of 2 lobes, the lobes usually imbricate; petals 5 with 4 petals imbricate and the adaxial petal (upper) held within the bud, or petal 1 (*Swartzia*) or lacking (*Prioria*); stamens 10, or numerous, sometimes monadelphous.

Members of the subfamily Caesalpinioideae are most easily distinguished by their open, weakly zygomorphic flowers and ten free stamens. Zygomorphy is usually due to having only one petal or to having one petal unlike the others; this petal (the adaxial one) is held within the bud.

Flowers of most species are insect pollinated. Bees are known to be regular visitors of some species of *Cassia* and *Bauhinia,* which have both pollinating and feeding

KEY TO THE TAXA OF CAESALPINIOIDEAE

Leaves simple *or* leaflets 2 and plants vines:
  Leaflets 2 or blades deeply cleft at apex ..... *Bauhinia*
  Leaves simple, the blades not cleft at apex .....
  ..... *Swartzia simplex* (Sw.) Spreng. var. *ochnacea* (A. DC.) Cowan
At least some leaves compound *or* leaflets 2 and plant not a vine:
  Leaves bipinnate:
    Leaves with 12 or more pairs of leaflets per pinna; flowers yellow; plants large forest trees ...
    ..... *Schizolobium parahybum* (Vell.) S. F. Blake
    Leaves with 9–11 pairs of leaflets per pinna; flowers red-orange; plant a cultivated shrub in the Laboratory Clearing ..... *Caesalpinia pulcherrima* (L.) Sw.
  Leaves pinnate:
    Leaves with 2 or 4 leaflets:
      All leaves bifoliolate:
        Inflorescences terminal; petals more than 10 mm long; sides of leaflets not coming together on petiolule at base, the gap 2–7 mm; blades not emarginate .....
        ..... *Hymenaea courbaril* L.
        Inflorescences terminal or axillary; petals less than 5 mm long; fruits less than 5 cm long; sides of leaflets coming together on petiolule; blades sometimes emarginate:
          Leaflets emarginate; dominant axis of inflorescence less than 1 cm long .....
          ..... *Cynometra bauhiniifolia* Benth.
          Leaflets acuminate; dominant axis of inflorescence more than 10 cm long .....
          ..... *Peltogyne purpurea* Pitt.
      Most leaves 4-foliolate:
        Leaves lacking gland between lower pair of leaflets; flowers very small, greenish-white; legumes suborbicular, concave or flat on one side, convex on the other .....
        ..... *Prioria copaifera* Griseb.
        Leaves bearing prominent gland on rachis between lower pair of leaflets; flowers more than 1 cm long, yellow; legumes linear-cylindrical ..... *Cassia* (in part)
    Leaves not with 2 or 4 leaflets:
      Leaves imparipinnate, with 3 or 5 leaflets:
        Leaves 3-foliolate or simple; inflorescences less than 10 cm long, bearing few flowers; legumes subterete, less than 5 cm long .....
        ..... *Swartzia simplex* (Sw.) Spreng. var. *grandiflora* (Raddi) Cowan
        Leaves 3- or 5-foliolate; inflorescences more than 20 cm long, bearing many flowers; legumes broad, flattened, more than 15 cm long ..... *Swartzia panamensis* Benth.
      Leaves paripinnate:
        Leaflets 4 or 6; plants rare or absent from the island ..... *Cassia obtusifolia* L.
        Leaflets more than 8:
          Flowers orange, in large, dense, usually globular clusters; leaflets in 5–7 pairs; legumes densely brownish-tomentose ..... *Brownea macrophylla* Linden
          Flowers yellow, in elongate racemes or spikes; leaflets in 7–14 pairs; legumes not densely brownish-tomentose:
            Plants small trees or shrubs of swampy areas; flowers markedly pedicellate; leaflets in 9–14 pairs; fruits oblong-linear, to 2 cm wide; seeds many .....
            ..... *Cassia reticulata* Willd.
            Plants large forest trees; flowers ± sessile; leaflets in 7–9 pairs; fruits flat, elliptic, more than 3 cm wide; seed 1 ..... *Tachigalia versicolor* Standl. & L. O. Wms.

anthers (Faegri & van der Pijl, 1966). While the bee (usually *Xylocopa* in *Cassia*) "milks" the feeding anthers, it vibrates its wings, raising a cloud of pollen from the pollinating anthers. Some grains land on the insect's back despite the fact that it sits atop the androecium. Some species of *Bauhinia* (not BCI species) and *Hymenaea courbaril* are known to be visited by several species of bat (Heithaus, Fleming & Opler, 1975).

No category of seed dispersal predominates. A number of species are endozoochorous, including *Cassia* spp., *Swartzia simplex*, and possibly also *Peltogyne purpurea*; these are probably taken mostly by birds. Van der Pijl (1968) reported the fruits of *Swartzia prouacensis* (Aubl.) Amsh. to be bat dispersed, but they are more long-dangling than those of *Swartzia simplex*. Fruits of *Cynometra retusa* Britt. & Rose are taken by the bat *Artibeus jamaicensis* in Mexico (Yazquez-Yanes et al., 1975), and *Cassia undulata* is dispersed by bats (Bonaccorso, 1975). Howard Irwin (pers. comm.) has seen the pods of *Cassia fruticosa* and *C. undulata* being worked by mammals and lizards. The fruits of *Cynometra bauhiniifolia* and *Hymenaea courbaril* are taken by mammalian frugivores, but may also be dispersed from the ground by rodents. *Hymenaea* is reported to be dispersed by rodents in Central America and Mexico (J. Langenheim, pers. comm.). *Prioria copaifera* is sometimes eaten by white-faced mon-

Fig. 271. *Pithecellobium macradenium*

Fig. 272. *Pithecellobium macradenium*

Fig. 273. *Pithecellobium rufescens*

Fig. 274. *Bauhinia guianensis*

keys (Hladik & Hladik, 1969) and also by peccaries (Enders, 1935) and agoutis (N. Smythe, pers. comm.) when food is scarce.

Wind-dispersed species include *Schizolobium parahybum* and *Tachigalia versicolor.* Water plays a role in the dispersal of the seeds of *Prioria copaifera* and possibly also of *Swartzia panamensis* and *Cassia reticulata.* Ridley (1930) reported the seeds of *Cynometra bauhiniifolia* and *Hymenaea courbaril* to be buoyant and possibly water dispersed. Pods of *Hymenaea* can survive long periods of time in both fresh and salt water, but quickly decompose when attacked by soil microorganisms (J. Langenheim, pers. comm.).

Bauhinia reflexa and *B. guianensis* have autochorous, disk-shaped seeds, which are thrown long distances by the elastically dehiscent valves.

BAUHINIA L.

Bauhinia guianensis Aubl., Hist. Pl. Guiane Fr. 1:377. 1775

B. excisa (Griseb.) Hemsl.; *B. manca* Standl.

Bejuco de cadena, Bejuco de mono

Tendriled liana; trunk to 20 cm diam near the ground; pubescence when present appressed, 0.3 mm long; older stems flattened and ± regularly folded, winged on both sides, the old stem scars thus borne medially; younger stems terete, appressed-pubescent; tendrils simple, watch-spring-like. Leaves simple; petioles 2.5–3.5 cm long, swollen at both ends; blades ovate, usually cleft about one-third their length at apex on mature plants or to the base on younger plants, cordate at base, 6–10 cm long, 4–10.5 cm wide, glabrous above, densely pubescent below, the pubescence appressed-ferruginous, often not conspicuous. Racemes terminal or axillary, to 15 cm long; pubescence on all parts ± densely appressed-ferruginous; lower flowers opening first, the ovoid flower buds above the flowers conspicuous, longitudinally striate, 4–7 mm long; bracts 1–3, subulate, ca 1 mm long; flowers sweetly aromatic, subsessile; calyx ca 7 mm long and expanding to 13 mm wide in flower, the lobes obtuse, ca 2 mm long; petals 5, white, obovate, 4 of them ca 2 cm long and 1 cm wide, puberulent inside, the fifth petal narrower and shorter, keeled, recurved at apex; stamens 10, of various lengths, some to 8 mm long; anthers held within the keeled petal both above and below the stigma; style stout, its stigma protruding into the keeled petal. Legumes flat, oblong, ca 8 cm long and 2.5 cm wide, glabrous, apiculate at apex on one side; seeds 2–4, disk-shaped, 0.5 cm diam. *Croat 10931, 13810.*

Occasional, in the forest. Flowers February and March (sometimes to April). The fruits apparently mature in the early rainy season, but have been seen only in June. The species loses its leaves in the early dry season.

Because this is an exceedingly variable species, it has been placed under many different names throughout its range.

Southern Mexico to Bolivia and southern Brazil; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Veraguas, Panamá, and Darién and from premontane rain forest in Coclé.

See Fig. 274.

Bauhinia reflexa Schery, Ann. Missouri Bot. Gard. 38:317. 1951

Tendriled liana; pubescence brown-hirsute on most parts, especially branchlets, petioles, pedicels, and veins of leaf below, the trichomes ca 1 mm long; older stems flattened, irregularly twisted and folded, bearing a single wing much thicker than the major axis that bears the old stem scars. Leaves simple; stipules 5–10 mm long, foliaceous, curved, oblique, caducous; petioles 2–4 cm long (to 9 cm on juveniles), swollen at both ends; blades broadly ovate to orbicular, cleft about one-third their length when mature, cordate at base, 4–12 cm long, about as broad as long, glabrous above, bearing an apicule to ca 3 mm long at base of cleft; basal veins 11–13; juvenile leaves to 18 cm long, often cleft to base. Racemes terminal or axillary, to ca 15 cm long; flowers with 1–3 linear bracts ca 1 cm long; pedicels ca 1 cm long; calyx cup-shaped, conspicuously ca 15-ribbed, 6–8 mm long, expanding to ca 10 mm wide, the lobes slender, reflexed to spreading, ca 6 mm long and 1 mm wide; petals 5, obovate and clawed, 2–2.5 cm long, pale lavender to pink, glabrous within except at base, with dense, ± appressed brown trichomes outside ca 1 mm long, 4 of the petals spreading, ca 6 mm wide, the fifth ca 4.5 mm wide and turned sharply inward toward the lower petals, usually reflexed above the middle, the base thickened and curled inward along the margins, partly enclosing the stamens; stamens 10, unequal, the longest to 1 cm, the shortest ± equaling the length of the style; filaments thick; anthers ca 1.3 mm long, dehiscing toward the reduced petal, forming an oblique surface appressed against the reduced petal; style to ca 7 mm long, nearly surrounded by the anthers; stigma oblique; ovary elongate, coarsely pubescent. Legumes linear-oblong, flat, 8–12 cm long, 2.8–3.5 cm wide, glabrous or sparsely long-pubescent, apiculate at apex on one side, explosively dehiscent; seeds usually 5 or 6 or fewer by abortion, disk-shaped, dark brown, shiny, 0.5–2 cm diam. *Croat 6152, 8126.*

Occasional, along the edge of the lake; no doubt in the canopy of the forest as well. Flowers from May to September. Mature fruits have been seen from June to November and also in February.

KEY TO THE SPECIES OF BAUHINIA

Young stems, petioles, and rachises of inflorescences hirsute, the trichomes ca 1 mm long . . . . . *B. reflexa* Schery

Parts glabrous or pubescent, the trichomes appressed, ca 0.3 mm long . . . . . *B. guianensis* Aubl.

Panama and northwestern Colombia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, and Darién.

BROWNEA Jacq.

Brownea macrophylla Linden, Cat. no. 18:11. 1863
Cuchillito, Ariza, Palo de la cruz, Rosa del monte, Cacique negro

Small tree, to 7(10) m tall; young branchlets, petioles, rachises, and petiolules tomentulose. Leaves pinnate; petioles swollen, ca 1 cm long (to 10 cm long on nonflowering stems); petiolules swollen, to 5 mm long; leaflets in 5–7 pairs, narrowly elliptic to elliptic-lanceolate or elliptic-oblanceolate, 10–25 cm long, 2.5–6 cm wide, long-acuminate, asymmetrical at base and acute to subcordate, scattered-puberulent below, glaucescent, bearing a single globose gland ca 1 mm diam on the underside of leaflet at base. Inflorescences axillary or nearly terminal, densely flowered, capitate to short-racemose; peduncles, pedicels, and the outside of the bracteolar sheaths tomentose; pedicels ca 5 mm long; bracteolar sheaths bilobed, 3–4 cm long, ± enclosing calyx; sepals usually 4, somewhat petaloid, obovoid, ca 3 cm long and 0.6–3 cm wide; petals orange, 5, obovate and clawed, 3–3.5 cm long and 1–1.5 cm wide, rounded, oblique at base, the narrow claw ca 1 cm long; stamens 10–15(20), 8 cm long, united at base into a tube 2.5 cm long, the tube open on the upper side, wrapping only three-fourths of the way around the pistil; pistil narrow, 10 cm long; ovary tomentose. Legumes flat, slightly turgid, oblong, peaked, to 20 cm long and 4.5 cm wide, brownish-tomentulose when immature, with heavy ridges along both edges; seeds flat, rectangular, 3.5 cm long, 2.5 cm wide, black. *Croat 7200, 14660.*

Rare; known only from one area along the shore of Bat Cove, and possibly a remnant from cultivation. Flowers from November to May, principally in the late dry season. The fruits mature mostly in the early rainy season.

Panama and northern South America. In Panama, known only from tropical moist forest in the Canal Zone, Panamá, and Darién.

CAESALPINIA L.

Caesalpinia pulcherrima (L.) Sw., Obs. Bot. 166. 1791
Gallito, Barbados pride, Bird of paradise flower, Flower bence

Glabrous shrub or small tree; older stems bearing sharp prickles to 1 cm long. Leaves bipinnate, with 7–9 pairs of opposite pinnae; petioles to 5(8) cm long; rachis and pinnular rachis bearing minute, acicular, glandlike structure at each node; petiolules ca 5 mm long; leaflets usually in 9–11 pairs per pinna, opposite or subopposite, oblong or obovate, rounded or emarginate at apex, obtuse to rounded at base, slightly inequilateral, ca 1.5 cm long and 7 mm wide (to 2.3 cm long and 10 mm wide). Racemes subcorymbose, terminal or subterminal; bracts caducous, subulate, to 3 mm long; pedicels 2–6 cm long; calyx tube 3–4 mm long, 5-lobed, the lobes obovate, to 1.5 cm long; petals bright orange, 5, obovate, clawed, spreading, ca 2 cm long, 1 reduced, ca 5 mm wide; stamens 10, ca 4 cm long, unequal, the filaments orange, villous at the base; style orange, extended about 2 cm beyond stamens. Legumes flat, 9–12 cm long, broader above the middle, beaked at apex, obliquely acute at both ends, pendent, elastically dehiscent; seeds about 6, ovate, ca 8 mm long, brown. *Croat 4856.*

Cultivated at the Laboratory Clearing. Probably flowers and fruits throughout the year, especially in the late dry season to the middle of the rainy season.

Pantropical in cultivation; probably native to tropical Asia. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from tropical dry forest in Los Santos and Panamá.

CASSIA L.

Cassia fruticosa P. Mill., Gard. Dict. ed. 8, no. 10. 1768

Shrub or small tree, mostly to 5 m tall (occasionally to 10 m), puberulent all over, especially on lower leaflet surface. Leaves paripinnate; stipules linear, caducous; petioles 2–4 cm long; rachis 1–4 cm long, bearing stipulelike, subconic gland between pairs of leaflets, the terminal gland often missing; petiolules to 6 mm long, stout; leaflets 4, elliptic, sometimes inequilateral, acuminate, obtuse to rounded at base, 6–24 cm long, 2–9 cm wide; juvenile blades often pruinose beneath. Inflorescences terminal or subterminal, paniculate to racemose; bracts brown, subulate, ca 3 mm long, caducous; pedicels to 4 cm long; calyx with a disklike base, the sepals rounded, imbricate, ca 12 mm long; petals 5, mostly obovate-suborbicular, 2.5–3 cm long, with a slender claw at base ca 1 mm long, yellow to orange-yellow, spreading at anthesis; stamens 10, the 3 uppermost aborted, minute, the 4 fertile stamens curved, the 3 fertile stamens nearest the style curved to sigmoid, often with the pores reduced to 1 at apex; anthers ca 7 mm long, with 2 apical pores; style densely pubescent, emerging from one side of flower and broadly curved;

KEY TO THE SPECIES OF CASSIA

Leaves sometimes with more than 4 leaflets:
- Leaflets 4 or 6 ..... *C. obtusifolia* L.
- Leaflets 18–28 ..... *C. reticulata* Willd.

Leaves all with 4 leaflets:
- Petals less than 2 cm long; floral bracts and stipules persistent; leaflets mostly less than 3.5 cm wide; glands on rachis between both pairs of leaflets ..... *C. undulata* Benth.
- Petals more than 2 cm long; floral bracts and stipules caducous; leaflets mostly more than 3.5 cm wide; gland on rachis between apical pair of leaflets usually missing ..... *C. fruticosa* P. Mill.

Fig. 275. *Cassia reticulata*

Fig. 276. *Cassia undulata*

stigma deeply cupular, held above the anthers. Legumes linear-cylindrical, straight or slightly curved, 20–30 cm long, ca 1 cm diam at maturity, splitting dorsally; seeds 60–80, transverse, black. *Croat 6012, Hladik 234.*

Sparse in the forest, along the lakeshore, and at the edges of clearings; elsewhere often common. Flowers and fruits apparently throughout the year, especially in the dry season and in the middle of the rainy season, from August to September, with little flowering activity at the beginning of the rainy season. Fruit maturity time not determined. Leaves are replaced in the dry season.

The variety *gatunensis* (Britt.) Schery intergrades with the typical variety and probably does not merit recognition. Both forms can be seen on BCI.

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

Cassia obtusifolia L., Sp. Pl. 377. 1753
Senna, Dormidera

Slender erect herb or suffrutex, to 1.2 m tall. Leaves paripinnate; stipules linear, to 1.5 cm long; rachis bearing a gland between the leaflets of basal pair; leaflets in 2 or 3 pairs, obovate, inequilateral, obtuse and mucronate at apex, rounded to cuneate at base, 1.5–2 cm long, 1–1.5 cm wide, ciliolate, glabrous above, pubescent and glaucescent below. Flowers solitary or paired at the nodes, oblique on pedicels; pedicels ca 11 mm long; sepals ovate to oblong, to 8 mm long, ciliate; petals 5, yellow, obovate, to 11 mm long and 5 mm wide; fertile stamens 7, of unequal sizes, dehiscent by a single terminal pore; anthers 2–4 mm long; filaments 1–2.5 mm long; ovary pubescent. Legumes linear, arcuate, to 17 cm long, ca 4 mm wide, subglabrous, somewhat quadrangular; seeds rhomboid, ca 4 mm long and 2.2 mm wide, dark brown, shiny.

No specimens have been seen, but to be expected in clearings. Flowers and fruits mostly in the dry season (November to April). The fruits persist until about May.

Reported by Standley for BCI as *C. tora* L., an Old World species.

Cosmopolitan in the tropics and subtropics; native to India. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Herrera, Panamá, and Darién.

Cassia reticulata Willd., Enum. Pl. 1:443. 1809
Laureño, Wild senna

Tree, usually 2–4(6) m tall; branchlets puberulent, pithy. Leaves paripinnate, mostly 20–50 cm long; petioles with prominent basal pulvinus; leaflets in 9–14 pairs, oblong, acute and downturned at apex, obtuse-rounded at base, 4–13 cm long, 1.5–5.5 cm wide, usually densely pubescent on both surfaces, especially below. Racemes terminal and upper-axillary; flowers subtended in bud by a yellow, ovate, caducous bract ca 2 cm long; pedicels 2–5 mm long; sepals elliptic, to 13 mm long; petals 5, yellow, conspicuously dark-veined, rounded at apex and turning inward at anthesis, obtuse at base, ca 16 mm long, with a slender claw ca 1 mm long; stamens 10, the outer 2 large, fertile, with the anthers prominently curved, ca 11 mm long, with 2 apical pores and lateral slits (sometimes not opening), each loculus almost filled with a juicy matrix, the 4 medial stamens much smaller, 4 stamens aborted; pistil puberulent, held between the 2 large stamens; style slender, recurved, the stigmatic surface sunken. Legumes flattened, to 15 cm long and 2 cm wide, marginally ribbed, breaking into many, 1-seeded, linear parts at maturity. *Wetmore & Abbe 166.*

Occasional in marshy areas near Frijoles and elsewhere in the isthmus, but not seen recently on BCI. On the basis of old collections, it was once common on the island, but apparently prefers more disturbed, swampy areas than now exist. Flowers mostly in the dry season; Allen (1956) reported the species to flower from late August to February. The fruits persist for a long time. Time of dehiscence is not known.

Mexico to Bolivia and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Los Santos, Herrera, Panamá, and Darién and from tropical wet forest in Coclé.

See Fig. 275.

Cassia undulata Benth. in Hook., J. Bot. (Hooker) 2:76. 1840

Slender arching shrub or liana, 2–5 m high; older stems glabrous, terete or angulate, lenticellate; younger stems and petioles sparsely to densely pubescent with spreading trichomes. Leaves paripinnate, set on a prominent woody base, mostly less than 15 cm long; stipules conspicuously falcate, subpersistent; petiole and rachis ribbed above; rachis bearing a raised gland between leaflets of each pair; petiolules short; leaflets 4, laneeolate-subfalcate, acuminate, unequal at base, to 11 cm long and 4 cm wide, ± glabrous above, dull and with appressed trichomes below, ciliate. Inflorescences racemose-paniculate, terminal or subterminal, puberulent; bracts ovate-lanceolate, ca 8 mm long, mucronate, persistent; pedicels ca 20 mm long; sepals elliptic to obovate, 7–8 mm long; petals 5, yellow, rounded, cuneate at base, to 15 mm long; anthers conspicuous, 4 large (ca 7 mm long) and 3 small (ca 4 mm long), blunt, with usually 2 terminal pores; style long, pubescent, emerging from one side of flower, recurved over anthers; stigma deeply cup-shaped, the outer margin minutely fringed. Legumes linear, irregularly cylindrical, 10–20 cm long, ca 1 cm thick, usually splitting open on one side; seeds many, smooth, brown, ± elliptical, flattened, to 5 mm long, stuck together laterally by a sweet, sticky, reddish-black, tarlike substance. *Croat 4827.*

Abundant along the shore. Flowers from November to April, mostly during the dry season. The fruits mature from April to June, possibly later also.

Standley confused this species, which he named *C. hayesiana* (Britt. & Rose) Standl., with *Cassia maxonii* (Britt. & Rose) Schery.

The flower unfolds to some extent well in advance of being functional, the petals remaining erect, the anthers closed, and the style recurved with its apex between the stamens. Later (sequence unknown) the anthers become functional, the style uncurls somewhat (the stigma still protruding downward), and the stigmatic cup begins to secrete nectar. Pollen is apparently deposited on the stigma by insects seeking the nectar.

Southern Mexico to northern South America; Trinidad. In Panama, known from tropical moist forest in the Canal Zone and Veraguas and from premontane wet forest in the Canal Zone and Panamá.

See Fig. 276.

CYNOMETRA L.

Cynometra bauhiniifolia Benth. in Hook., J. Bot. (Hooker) 2:99. 1840

Tree, to 15 m tall, ca 40 cm dbh; outer bark thin, sandpapery, unfissured, dark brown; inner bark thick, hard, reddish-brown with irregular, white, radial lines, the sap sweet, not aromatic; stems conspicuously lenticellate. Leaves bifoliolate, stiff; petioles to 5 mm long; leaflets very inequilateral, emarginate at apex, acute at base, 3–6 cm long, 1–2.8 cm wide, glabrous or sparsely pubescent on midrib. Fascicles short-pedunculate, 5–15 mm long, 1 to several in leaf axils, conspicuous and conelike in bud; bracts prominently veined, 1–2.3 mm long; pedicels crisp-villous, 4–8 mm long; sepals 4, ca 3 mm long, membranaceous, deciduous; petals 5, white, to 3.6 mm long, unequal, inserted on a disklike receptacle; stamens exserted. Legumes oblong to subrotund, 3.5–4.5 cm diam, minutely and densely tomentose, with a hard exocarp to 2 mm thick; seed 1. *Foster 1663.*

Known only from the shore of Chapman Cove. Seasonal behavior uncertain. Flowers have been seen in April and July, and fruits in July and September.

Guatemala to Argentina. In Panama, known only from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Colón.

HYMENAEA L.

Hymenaea courbaril L., Sp. Pl. 1192. 1753

West Indian locust, Algarrobo, Courbaril, Cuapinol, Quapinol

Tree, mostly to 20(30) m tall and 50(200) cm dbh; outer bark brown, closely lenticellate, bitter tasting, pale orange beneath surface, glabrous; wood reddish-brown, hard. Leaves bifoliolate; petioles 1–2 cm long, rugose when dry; leaflets narrowly oblong to elliptic-lanceolate, asymmetrical, short-acuminate, unequally rounded at base, 4–10 cm long, 2–5 cm wide, coriaceous, punctate, the midrib conspicuous below. Inflorescences terminal, subcorymbose, to ca 8(12) cm long, the branches puberulent, the parts jointed and articulate; flowers white or purplish, soon falling, probably opening at night; bracts caducous; pedicels thick, ca 7 mm long; calyx tube ca 8 mm long, 4-lobed, the lobes ovate to oblong, expanding to ca 15 mm long, coriaceous, densely tomentose inside, easily caducous; petals 5, white, sometimes tinged with purple, rounded, 1.5–2 cm long, ca 9 mm wide, clawed below, the claw ca 1.5 mm long; stamens 10, alternately short and long, the long ones to 2 cm long; style attached laterally at apex of ovary, directed somewhat to one side of the flower; stigma held above the lower anthers and at some distance from the divergent longer set. Legumes oblong, flattened, to 17 cm long and 6.5 cm wide, turgid, hard, reddish-brown; seeds (2)4–6, embedded in sticky pulp. *Croat 10209.*

Rare, in the young forest. Flowers during the dry season and the early rainy season (December to May). The fruits mature chiefly during the rainy season, especially late in the rainy season.

The flowers are believed to be bat pollinated.

Mexico to Peru, Paraguay, and Brazil; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Veraguas, Herrera, Panamá, and Darién, from premontane dry forest in Herrera, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí, Coclé, and Darién. Tosi (1971) listed this species as characteristic of tropical dry, premontane moist, and tropical moist forests in Panama. Reported also from tropical wet forest in Costa Rica (Holdridge et al., 1971).

PELTOGYNE J. Vogel

Peltogyne purpurea Pitt., J. Wash. Acad. Sci. 5:471. 1915

Nazareno, Morado, Purple heart

Tall tree, to 50 m tall and 1 m dbh; wood dark purple, hard; branchlets slender. Leaves bifoliolate; petioles to 2 cm long; petiolules 3–4 mm long; leaflets lanceolate-elliptic, subfalcate, long-acuminate, obliquely rounded or obtuse at base, 5–7 cm long, 2–3 cm wide, the veins reticulate. Inflorescences racemose, terminal or subterminal, bearing few to many flowers; branches of the inflorescence 5–7 cm long, the branches, pedicels, and calyces tomentose; pedicels to 2 mm long, nodose in middle; sepals ca 2.5 mm long, obtuse; petals 5, ca 3 mm long, obovate; stamens ca 3 mm long; ovary tomentose; style slender, maroon, ca 2 mm long. Legumes broadly obovate, flattened, ca 3 cm long and 1.6 cm wide, glabrous, mucronulate at apex, somewhat arcuate above, rounded below, on pedicels to 8 mm long; seminiferous area indistinct; seed 1, ca 2 cm long, obliquely ovate, depressed, persistent on the dehisced fruit, hanging by the funicle.

Reported by Standley for the island, but no collection was cited and none has been seen. The only material of this species from the Canal Zone that I have seen was growing at Summit Garden. It is possible that the species is not native to central Panama.

Allen (1956) reported that in Costa Rica individuals flower several times from August to December at two-week intervals, with flowers lasting about three days and the fruits maturing in February. The leaves of these plants were briefly deciduous in the early dry season.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone and reported to be common in Darién in tropical moist and tropical wet forests (Duke, 1968; Allen, unpubl.; Lamb, 1953). Tosi (1971) listed the species as characteristic of premontane wet forest in Panama. Holdridge (1970) reported it from tropical moist and tropical wet forests on well-drained soils.

PRIORIA Griseb.

Prioria copaifera Griseb., Fl. Brit. W. Ind. 215. 1860
Amansa mujer, Cativo, Cantivo

Tree, to 40 m tall; trunk to 75(150) cm dbh, unfissured, coarse, roughly lenticellate; inner bark light brown becoming darker in time, the sap usually black, sweet, with faint aroma; stems lenticellate, puberulent. Leaves compound, glabrous; petiole and rachis lenticellate; petioles 1–3 cm long; rachis longer, to 4 cm; petiolules callous-rugose, 5–10 mm long; leaflets (2)4, ± elliptic, acuminate, rounded at base, 4–16 cm long, 2.5–8 cm wide, inequilateral. Inflorescences to ca 30 cm long, branched, the spikes to 10 cm long, unbranched, bearing many flowers; flowers greenish-white, sessile, ca 4 mm diam, subtended by 2 bracts, forming a cuplike structure ca 1 mm deep; sepals petaloid, spreading, rounded, concave, ca 2.5 mm long, obscurely pellucid-punctate, ciliate; petals lacking; stamens 10, ca 5 mm long, exserted and weakly spreading; filaments villous below the middle; pistil to ca 3 mm long; ovary villous, gradually tapered to a simple style. Legumes suborbicular, to 10 cm long and 7 cm wide, concave or flattened on one side, convex on the other. *Croat 6860.*

Common along the shore on the southern side of the island (e.g., on the shore of Gigante Bay) and in the old forest along Armour Trail; apparently rare or absent elsewhere. Elsewhere in Panama the species usually occurs along the margins of rivers and swamps. Seasonal behavior is uncertain. Flowering is possibly bimodal, with a major period of flowering in September and October (possibly in response to the slight decrease in rainfall in September) and another period of flowering in the dry and earliest rainy season (December to May). The fruits mature in about 6 months.

White-faced monkeys eat the fruits in April and May (Hladik & Hladik, 1969), and Standley (1928) found peccaries to be fond of them. Seeds are very buoyant and are often found floating in the water at the edge of the lake. According to Chapman (1938), seeds are not eaten by animals.

Nicaragua to Colombia; Jamaica. In Panama, common in tropical moist forest on the Atlantic slope in the Canal Zone, Bocas del Toro, San Blas, and Darién, but also common in tropical wet forest in Darién, where it forms nearly pure stands in flooded areas (Holdridge & Budowski, 1956; Holdridge, 1970; Lamb, 1953). Tosi (1971) listed the species as characteristic of tropical wet forest in Panama, but also common in tropical moist forest.

See Figs. 277 and 278.

SCHIZOLOBIUM J. Vogel

Schizolobium parahybum (Vell.) S. F. Blake, Contr. U.S. Natl. Herb. 20:240. 1919
Indio, Tinecú

Tree, 25–30(40) m tall, 30(100) cm dbh, with narrow, low buttresses; outer bark hard, planar, with minute fissures and fine lenticels; inner bark thin, granular, whitish, the sap sweet-tasting; branches glabrous to sparsely puberulent; juvenile plants often with very resinous stems. Leaves bipinnate, very large, to 130 cm long, with ca 8 pairs of opposite pinnae; petioles ca 30 cm long; rachis flattened or sulcate above; petiolules ca 1 mm long; leaflets mostly in 12–22 pairs per pinna, ± oblong, rounded to emarginate at apex, often with a minute apiculum, rounded at base, ± equilateral, 1.3–3 cm long, ca 0.9 cm wide, appressed-pubescent especially below, the lateral veins obscure. Inflorescences axillary or terminal racemes or panicles of several racemes; bracts lanceolate, ca 2 mm long; pedicels to 1 cm long; calyx deeply lobed, ferruginous-tomentose, the tube turbinate, 2–3 mm long, the lobes ovate-elliptic, 3–7 mm long; petals 5, yellow, obovate-spatulate, to 2 cm long, 4–6 mm wide; stamens 10, ± equaling petals; ovary subfalcate, hispid-tomentose. Legumes oblanceolate, somewhat asymmetrical, to 12 cm long, 3–5 cm wide, the venation conspicuously reticulate; seed 1, round, flat, ca 8 mm diam, shiny, brown, borne in a thin endocarp, the endocarp shaped like the fruit with a one-sided wing. *Croat 12968, Zetek 6018.*

Rare, in the forest near the Laboratory Clearing. Flowers in the early dry season (December to February); the principal flowering period may be followed by a smaller one. The fruits mature from the middle of the dry to the early rainy seasons and require about a year to develop. Plants lose their leaves just prior to flowering and replace them after flowering.

Juvenile plants can be recognized by their large leaves and very viscid stems.

Caribbean coast of southern Mexico to southern Brazil. In Panama, collected from tropical moist forest on the Atlantic slope of the Canal Zone and in Panamá and Darién; reported also from tropical wet forest in Costa Rica (Holdridge et al., 1971). Holdridge (1970) reported the species to be common in secondary growth in moist and wet areas in Panama.

SWARTZIA Schreb.

Swartzia panamensis Benth. in Mart., Fl. Brasil. 15(2):38. 1870
Cutarro, Malvecino

Tree, 4–30 m tall; wood hard, dark brown. Leaves imparipinnate; petioles 4–7 cm long; petiolules 4–6 mm long; leaflets 3 or 5, ovate-lanceolate to elliptic-lanceolate, acuminate, rounded to acute at base, 7.5–17(22) cm long, 4–7(8.5) cm wide, glabrous above, shortly patulous-pubescent on veins below, the surface often with short, appressed trichomes, the lowermost blades smaller and

Fig. 277. *Prioria copaifera*

Fig. 278. *Prioria copaifera*

KEY TO THE TAXA OF SWARTZIA

Leaves simple ..... *S. simplex* (Sw.) Spreng. var. *ochnacea* (A. DC.) Cowan
Leaves with 3 or 5 leaflets:
  Most leaves 3-foliolate (never 5-foliolate); inflorescences less than 10 cm long, bearing few flowers; legumes subterete, less than 5 cm long ..... *S. simplex* (Sw.) Spreng. var. *grandiflora* (Raddi) Cowan
  Leaves 3- or 5-foliolate; inflorescences more than 20 cm long, bearing many flowers; legumes broad, flattened, more than 15 cm long ..... *S. panamensis* Benth.

± ovate. Inflorescences axillary, from leaf scars on old branches, pendent, 40–60 cm long, racemose, minutely strigillose on most exterior parts; bracts minute; pedicels 12–20(30) mm long; buds many, globose, to nearly 1 cm diam, bearing a leathery covering at anthesis, splitting into (3)4 or 5(6) irregular parts; petal 1, pale yellow, clawed, the claw 5–8 mm long, the blade ± rounded, 2–3 cm long; stamens unequal, the larger (7)10–12 with filaments 8–12 mm long and anthers ca 4 mm long, the smaller ones numerous, their anthers ca 2 mm long; ovary glabrous. Legumes oblong, flat, 19–26 cm long excluding the persistent style to 2 cm long, 8–10 cm wide, minutely white-lenticellate; seeds few (usually less than 4), ± rounded in outline, flattened, to ca 6 cm diam, ± fleshy. *Croat 8202.*

Rare; seen along the shore of Burrunga Peninsula as small but mature individuals. Seasonal behavior uncertain. In Panama the species is believed to flower from December to July, especially in February and April. The fruits require about a year to develop and are commonly mature or nearly so at the time of the next season's flowering. Plants may have both flowers and mature fruits simultaneously. Allen (1956) reported that the species apparently flowers and fruits at irregular intervals throughout the year on the Osa Peninsula in Costa Rica and that it produces a new flush of leaves in December.

Easily distinguished by its long pendulous raceme of flowers, each with one yellow petal, and by its large oblong fruits.

Honduras (Lancetilla Valley) to Panama. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, and Darién.

See Fig. 279.

Swartzia simplex (Sw.) Spreng. var. **grandiflora** (Raddi) Cowan, Flora Neotropica 1:172. 1968
Naranjita

Tree, to 15 m tall, ca 25 cm dbh; outer bark thin, light brown; inner bark thin, ± granular, the sap with ± strong, pungent odor. Differing from var. *ochnacea* by having most of the leaves trifoliolate, the lateral pair smaller than the terminal leaflet; juvenile leaves often with 5 leaflets, the rachis narrowly winged. *Croat 14965.*

Occasional, apparently more common within the forest than on the shore, generally on slopes or in ravines; much less abundant than var. *ochnacea.* Flowers abundantly from June to September, possibly year-round. Mature fruits have been seen from July to March.

Ranges throughout most of the areas where var. *ochnacea* is found, but known also from northwestern Venezuela, western Peru, and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién and from premontane wet forest in Panamá.

Swartzia simplex (Sw.) Spreng. var. **ochnacea** (A. DC.) Cowan, Flora Neotropica 1:178. 1968
Naranjita

Tree, usually to 15 m, glabrous or minutely strigillose and glabrate all over. Leaves simple; stipules minute, subpersistent; petioles ca 5(35) mm long, with a produced wing at the apex on the upper surface; blades elliptic to oblong-elliptic, bluntly acuminate, acute to rounded at base, quite variable in size, (4)8–18(24) cm long, (2.5)3–7.5(8) cm wide, the midrib often arched, the sides folded somewhat upward along the midrib. Racemes short, upper-axillary or terminal, mostly 4–10 cm long; pedicels ca 4 mm long, elongating to 10 mm; buds few, round or ellipsoid to obovoid (looking like small fruits), 7–12 mm diam, bearing a leathery covering splitting at anthesis into 3–6 irregular sepals, the sepals recurving and soon deciduous; petal 1, ± rounded-cordate, broader than long, palmately veined and clawed at base, to 3.5 cm long and 4.5 cm wide, pale yellow; stamens many, of 2 sizes, the smaller more numerous, to 1.5 cm long, the larger 5–15, to 2 cm long; filaments and gynoecium both curved toward the petal; ovary and style to 3 cm long, the ovary glabrous. Legumes orange, 2.5–5 cm long, ovoid to oblong, borne on a prominent stipe, apiculate at apex, the valves curling inward along their margins at maturity to expel seeds; seeds 1 or 2 (sometimes 4), irregular in shape, smooth, black, shiny, borne on a long funiculus, enveloped at base by prominent, white, bitter-tasting aril. *Croat 4097, 10847.*

Frequent in the forest; locally and sporadically abundant along the shore. Flowers along the shore during much of the year, especially during the dry season and most abundantly by May; flowering begins in the forest usually in June. Most fruits seem to mature in January and February (sometimes to May).

Western Mexico (Nayarit) to western Guatemala and on both coasts of Honduras, Costa Rica, and Panama, south to both coasts of Colombia and to eastern lowlands of Peru and Ecuador; known also from the east-central coast of Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí (Burica Peninsula), Panamá, and Darién and from premontane wet forest in Panamá.

See Fig. 280.

Fig. 279. *Swartzia panamensis*

Fig. 280. *Swartzia simplex* var. *ochnacea*

Fig. 281. *Tachigalia versicolor*

TACHIGALIA Aubl.

Tachigalia versicolor Standl. & L. O. Wms., Ceiba 3:27. 1952

Tree, to 30 m tall, ca 75 cm dbh, often buttressed to 10 m; branches widely spreading, the crown nearly as broad as the tree is tall; outer bark thin, reddish-brown (especially on buttresses), minutely fissured, bearing irregular small lenticels; inner bark thin, granular, reddish-brown, the sap sweet-tasting, with a faint pleasant aroma. Leaves pinnate; petioles solid, angled, 5–9 cm long (much longer on juvenile plants); petiolules pulvinate, ca 4 mm long; leaflets in 7–9 pairs, oblong, short-acuminate, obliquely rounded to obtuse at base, the 1 or 2 pairs nearest the stem somewhat shorter than the rest, the longest 9–14 cm long, 3–4.5 cm wide, minutely puberulent below, subcoriaceous, the primary lateral veins in 13–15 pairs. Inflorescences terminal panicles of spikes, rufous-pubescent, the spikes ca 12 cm long; flowers pink in bud, pale yellow when open, each flower subtended by a subulate, caducous bract ca 3 mm long; calyx tube oblique, ca 5 mm long, the lobes 5, ca 5 mm long; petals 5, spatulate, ca 6 mm long, lanate-pubescent; stamens 10, curved, 7–12 mm long, orange, lanate in basal fourth, particularly on the inner side; pistil ca 6 mm long, very densely orange-lanate. Legumes flat, forming a single, elliptic, fibrous wing, 11–15 cm long, 4–5 cm wide, cordate to rounded at point of attachment; seed 1, flat, rectangular, ca 2 cm long and 1.3 cm wide, olive-brown. *Croat 9575, 12568.*

Common in the forest. Flowers from March to July, sometimes from January. The fruits may develop to mature size by August, but they remain green until the following dry season. Most trees drop old leaves and produce new ones in August and September, sometimes briefly remaining leafless. The few trees that flower drop their leaves at the start of the dry season. The large flat green fruits give the tree a leafy appearance well into the dry season before the exocarp peels off and the seeds are dispersed by the wind. All plants that were observed to flower on BCI and elsewhere have died following flowering, i.e., after fruiting no new leaves emerged. Studies by R. Foster (pers. comm.) both on BCI and elsewhere have conclusively proved that the species is monocarpic.

Costa Rica to northern Colombia. In Panama, known from tropical moist forest in the Canal Zone and Panamá, from premontane wet forest in the northeast part of the Canal Zone, Colón, and Darién, and from tropical wet forest in Colón.

See Fig. 281.

63C. PAPILIONOIDEAE

Leaves usually trifoliolate or pinnate, rarely unifoliolate (simple in *Crotalaria retusa, Dalbergia brownei*); stipules and stipels usually present. Flowers zygomorphic, in racemes or panicles, ebracteate; calyx 5-parted, the carinal tooth (posterior tooth) usually longest, anterior teeth often united; petals imbricate; stamens 10, monadelphous (all stamens united) or more frequently diadelphous (all but one stamen united).

Members of the subfamily Papilionoideae are most easily distinguished by their very zygomorphic flowers with the adaxial petal (banner) held outside the bud and by their usually united stamens.

Flowers of the subfamily are typically bee pollinated, but some, such as those of *Erythrina costaricensis* var. *panamensis,* are hummingbird pollinated. *Mucuna* species

KEY TO THE TAXA OF PAPILIONOIDEAE

- Leaves all trifoliolate:
  - Plants trees or shrubs (soft-wooded in *Cajanus*), not at all scandent:
    - Plants trees in the forest or along the shore; flowers bright red to pale orange, ca 5 cm long or more; leaflets mostly more than 5 cm wide ..... *Erythrina*
    - Plants shrubs or trees in clearings, soft-wooded, often cultivated; flowers yellowish at least in part, less than 3 cm long; leaflets less than 3.5 cm wide:
      - Flowers completely yellow; fruits terete, ca 2 cm long, lacking purple stripes; leaves lacking glands below ..... *Crotalaria vitellina* J. Ker
      - Flowers yellow, often marked with red, purple, or brown; fruits flattened, more than 5 cm long, with dark stripes; leaves with microscopic globular glands below ..... *Cajanus bicolor* DC.
  - Plants herbs, vines, or lianas (stems suffruticose in *Desmodium canum* and *D. cajanifolium*):
    - ◆ Plants lianas, at least the older parts definitely woody:
      - Calyx 5–20 mm long; flowers purplish to pink:
        - Free stamen entirely free; upper lobe of calyx minutely bifid; plants semiherbaceous ..... *Cymbosema roseum* Benth.
        - Free stamen united apically to staminal column at anthesis; upper lobe of calyx not minutely bifid; plants woody ..... *Dioclea*
      - Calyx at anthesis less than 5 mm long *or* more than 2 cm long; flowers pink, white, or greenish-yellow:
        - Calyx less than 5 mm long; corolla greenish-yellow, less than 6 mm long; legumes less than 3 cm long, constricted between seeds, the seeds usually 2; younger parts with globular orange glands ..... *Rhynchosia pyramidalis* (Lam.) Urban

Calyx more than 20 mm long; corolla more than 4 cm long; legumes more than 7 cm long, the seeds several to many; plant parts lacking glands:
Flowers yellowish on long pendent racemes; legumes bearing stiff, irritating trichomes ..... *Mucuna rostrata* Benth.
Flowers pinkish, the racemes not pendent; legumes softly brown-villous ..... *Clitoria javitensis* H.B.K.

◆ Plants herbs or herbaceous vines, rarely woody at base:
Corolla more than 1.5 cm long:
Stems and petioles bearing conspicuous, spreading, brownish trichomes 1.5–2 mm long (in *Clitoria rubiginosa*, the trichomes 1 mm long, the keel white with violet medial lines):
Calyx more than 1.5 cm long; standard white with violet medial lines, often more than 3 cm long, the keel petals straight; legumes glabrescent, with submarginal ridges; apex of terminal leaflet often rounded or blunt, bearing short apiculum or tuft of trichomes ..... *Clitoria rubiginosa* Adr. Juss.
Calyx less than 1.5 cm long; standard white to bluish becoming yellow during the day, usually less than 3 cm long, the keel petals twisted; legumes conspicuously hirsute, not ridged; apex of terminal leaflet usually sharply acute ..... *Vigna vexillata* (L.) A. Rich.
Stems and petioles lacking long, brown, spreading trichomes 1.5–2 mm long:
Flowers flesh-colored or yellowish; calyx very densely pubescent, the trichomes totally obscuring surface, of 2 sizes (the longer often sparse); legumes densely covered with irritating trichomes; inflorescences pendent, the peduncles usually more than 15 cm long (sometimes less than 15 cm long in *M. rostrata*) ..... *Mucuna*
Flowers reddish to blue; calyx glabrous or not as densely pubescent as above; legumes not densely covered with irritating trichomes; inflorescences erect, the peduncles usually less than 15 cm long:
Flowers marked with blue; legumes less than 8 mm wide, with both lateral margins raised; flowers subtended by conspicuous, ovate, striate bracts ..... *Centrosema pubescens* Benth.
Flowers pinkish to reddish; legumes more than 15 mm wide, not with *both* lateral margins raised; flowers subtended by inconspicuous bracts:
Flowers red (lavender when dry), to 3.5 cm long; calyx pubescent becoming glabrous, with both long-appressed and short erect trichomes; legumes less than 5 cm long, densely pubescent with appressed acicular trichomes, lacking submarginal ridges ..... *Cymbosema roseum* Benth.
Flowers lavender, to 2.5 cm long; calyx ± glabrous; legumes more than 10 cm long, ± glabrous, the submarginal ridges prominent .. *Canavalia dictyota* Piper
Corolla less than 1.5 cm long:
Stems, petioles, peduncles, and legumes conspicuously long-pilose, the trichomes more than 1.5 mm long:
Flowers yellow; calyx shallowly lobed; stipules oblong, with a long basal lobe ..... *Phaseolus trichocarpus* C. Wright
Flowers blue; calyx narrowly lobed to two-thirds its length; stipules acute, lacking a basal appendage ..... *Calopogonium mucunioides* Desv.
Stems, petioles, peduncles, and legumes not conspicuously long-pilose or the trichomes less than 1.5 mm long:
Corolla less than 7 mm long, bluish or tinged with blue:
Flowers in terminal inflorescences or, if axillary, in elongate racemes ..... *Desmodium* (in part)
Flowers in small axillary clusters or much-reduced axillary racemes:
Leaflets less than 1 cm long, obovate, emarginate or truncate at apex ..... *Desmodium triflorum* (L.) DC.
Leaflets more than 1 cm long, ± lanceolate, acute to rounded at apex ..... *Teramnus*
Corolla more than 8 mm long, white, yellow, or blue (*Calopogonium*):
Flowers blue; keel petals not coiled; legumes usually more than 4 cm long and 6 mm wide; secondary lateral veins of leaflets prominulous, perpendicular to and often extending between the pairs of primary lateral veins ..... *Calopogonium caeruleum* (Benth.) Sauv.
Flowers white to yellowish (sometimes lavender); keel petals coiled or not; legumes usually less than 4 cm long *or* less than 4 mm wide; secondary lateral veins of leaflets reticulate:
Plants erect herbs or suffrutices; terminal leaflets acute at base ..... *Crotalaria vitellina* J. Ker
Plants vines; terminal leaflets rounded to truncate at base ..... *Phaseolus*

- Leaves mostly not trifoliolate:
  - Plants herbaceous or essentially so:
    - Leaflets mostly less than 5 mm wide ..... *Aeschynomene*
    - Leaflets or leaves more than 5 mm wide:
      - Leaves simple; calyx more than 10 mm long; flowers yellow ..... *Crotalaria retusa* L.
      - Leaves imparipinnate, the leaflets 5 or 7; calyx less than 5 mm long; flowers red ..... *Indigofera mucronata* DC.
  - Plants woody:
    - Leaves simple; flowers white, ca 1 cm long; legumes flat, ± oblong, the seeds 1 or 2 ..... *Dalbergia brownei* (Jacq.) Urban
    - Leaves compound:
      - Plants lianas or climbing shrubs:
        - Fruits flattened, orbicular, ca 4 cm long; flowers white; leaflets 1–5, abruptly acuminate, the acumen to 1.8 cm long; plants growing along the shore .... *Dalbergia monetaria* L.f.
        - Fruits samaroid, with a conspicuous, usually curved wing; flowers white to purple; leaves not as above; plants growing in the canopy of the forest or along the shore ..... *Machaerium*
      - Plants trees, never scandent:
        - Leaves opposite; flowers golden-orange, precocious; fruits oblong-elliptic, 1-seeded, with a broad marginal wing ..... *Platymiscium pinnatum* (Jacq.) Dug.
        - Leaves alternate:
          - Rachises of leaves conspicuously winged; flowers ± red-violet; fruits large, 1-seeded, oblong drupes ..... *Dipteryx panamensis* (Pitt.) Rec. & Mell.
          - Rachises of leaves not winged:
            - Leaflets rounded to emarginate at apex; fruits samaroid, the seminiferous area distal; leaflets mostly more than 4 cm long; plants usually more than 10 m tall ..... *Platypodium elegans* J. Vogel
            - Leaflets acute to acuminate at apex (sometimes slightly emarginate in *Dalbergia retusa*):
              - Fruit drupaceous, 1-seeded, green, ± globose, 3–5 cm long; stipels usually persistent at bases of leaflets; flowers purple, ca 1 cm long ..... *Andira inermis* (W. Wright) H.B.K.
              - Fruits not drupaceous, flattened, often winged (except *Ormosia*):
                - Fruits not winged *or* the wing lateral and the seminiferous area at apex:
                  - Fruits prominently winged, indehiscent, the seminiferous area at apex; flowers whitish or yellowish; petals to ca 1 cm long; major lateral veins of leaflets mostly less than 5 mm apart, scarcely more prominent than reticulate veins ..... *Myroxylon balsamum* (L.) Harms var. *pereirae* (Royle) Harms
                  - Fruits not winged, flattened, dehiscent with colored seeds; flowers purple; petals more than 1 cm long; major lateral veins of leaflets usually more than 5 mm apart, much more prominent than reticulate veins ..... *Ormosia*
                - Fruits winged, the wing surrounding the seminiferous area:
                  - Fruits about as long as broad:
                    - Fruits thin, indehiscent, with wing more than 1 cm broad; flowers pale orange-yellow or violet-purple; sap red ..... *Pterocarpus*
                    - Fruits thick except at margin, dehiscent, with wing very narrow, the seeds 1–4, red; flowers lilac; sap not colored ..... *Ormosia panamensis* Seem.
                  - Fruits much longer than broad:
                    - Fruits samaroid, the wing tissue all apical ..... *Vatairea erythrocarpa* Ducke
                    - Fruits not samaroid, the wing tissue surrounding the seminiferous area:
                      - Fruits glabrous, conspicuously stipitate, the stipe ca 1 cm long; flowers white ..... *Dalbergia retusa* Hemsl.
                      - Fruits pubescent to glabrate, not conspicuously stipitate; flowers purple or greenish to cream-colored ..... *Lonchocarpus*

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are bird or bat pollinated (Faegri & van der Pijl, 1966; Baker, 1970; Proctor & Yeo, 1973); *Mucuna mutisiana* is reported to be bat pollinated (Vogel, 1958). In the typical papilionoid flower the banner acts as the chief attractive part of the flower. The keel petals generally enclose and protect the stamens and pistil. These parts sometimes project from the keel, but are generally hidden until the pollinator (typically a bee) enters the flower. Bees usually alight on the keel of wing petals and probe the flower for nectar. The style is often equipped with antrorse trichomes (e.g., *Vigna*) and, acting like a piston, pushes out a load of pollen with each successive visit. Pollen is deposited on the lower side of the insect.

In *Centrosema, Canavalia,* and *Clitoria,* the flower is turned upside down (Faegri & van der Pijl, 1966). The bee alights on the banner but, while probing for nectar

in the same manner, receives pollen on its back. In *Phaseolus,* which has an erect flower, the keel, pistil, and stamens are spirally wound. In some cases, notably species of *Desmodium,* the filaments are held under tension until released by a visitor, at which time all their pollen is shed at once in an explosive manner. *Mucuna* also has an explosive mechanism for the release of pollen (Baker, 1970; Proctor & Yeo, 1973).

Papilionoid fruits show a different seed development than do the Mimosoideae and Caesalpinioideae, with more extended dormancy and greater development of the pericarp, which assists in dispersal (van der Pijl, 1968).

Species with small colored seeds well suited for bird dispersal include *Erythrina costaricensis* var. *panamensis, Rhynchosia pyramidalis,* and all species of *Ormosia.* These are mimetic, looking like arillate seeds and no doubt dispersed by forest-dwelling birds. Other species that occur in clearings also have fruits suited for bird dispersal; these usually have dark, shiny seeds displayed against the generally paler inner valve surface. Moderately large seeds or those borne in pods too short to twist at dehiscence are usually displayed on untwisted (or only slightly twisted) valves, for example, *Calopogonium caeruleum, C. mucunioides,* and *Dioclea guianensis.* Other species with smaller seeds have the valves of the legume markedly twisted in such a way as to display a single seed within each twist of the valve; this modification is an adaptation that makes the seeds more conspicuous by exposing alternately the usually dark outer surface and the light-colored inner surface bearing the seed. Among such probably bird-dispersed species with twisted valves are *Phaseolus peduncularis, Teramnus uncinatus, T. volubilis, Vigna vexillata,* and *Centrosema pubescens.*

Other endozoochorous Papilionoideae include *Dipteryx panamensis,* the pod of which is eaten by most frugivores (including bats), as well as most species of *Dioclea* and *Andira inermis.* Kinkajous reportedly eat fruits of *Dipteryx* at night (Chapman, 1931), and several animals eat them by day including agoutis, peccaries, coatis, and monkeys (Carpenter, 1934; Hladik & Hladik, 1969; Kaufmann, 1962; Enders, 1935; Bonaccorso, 1975). Partially eaten fruits or seeds are dropped to the ground by monkeys. Both *Andira* and *Mucuna* have been suggested as genera with bat-dispersed fruits. The bat *Artibeus jamaicensis* (Phyllostomidae) takes fruits of *Andira inermis* in Trinidad (Goodwin & Greenhall, 1961). D. Janzen (pers. comm.) suggests that forest-floor rodents move seeds of *Mucuna.*

Species of *Desmodium* are epizoochorous with flattened fruits, which break up into segments covered with hooked trichomes. *Aeschynomene americana* and *A. ciliata* are at least partly epizoochorous.

Autochorous species include *Clitoria javitensis* and *Canavalia dictyota,* the pods of which have thick, woody, elastically dehiscent valves, and apparently *Indigofera mucronata,* whose thin valves become twisted from the apex to the base. With each turn of the spiral valve a few of the tiny seeds are pushed out; they are small enough to be windblown a short distance.

Other species with wind dispersed seeds include *Dalbergia retusa, Myroxylon balsamum, Platymiscium pinnatum, Platypodium elegans,* and all species of *Pterocarpus, Machaerium,* and *Lonchocarpus,* but none of these are exceptionally good fliers.

Species that have buoyant seeds and are at least in part hydrochorous include *Mucuna mutisiana, Dalbergia brownei, D. monetaria, Dioclea reflexa* (and no doubt others of this genus), *Canavalia dictyota,* and *Erythrina fusca.* Seeds of both *Dioclea* and *Andira inermis* are reported to be river dispersed (Ridley, 1930). The flat seeds of *Dalbergia brownei* float nicely, owing to surface tension, but once sunk they will not resurface; they are probably wind dispersed to a lesser extent. *Aeschynomene ciliata* and especially *A. sensitiva* are also hydrochorous. Seeds of *Vigna* float (Ridley, 1930). Guppy (1912) reported *Dioclea reflexa* to be sea dispersed. Rain wash may be important in the dispersal of *Desmodium triflorum* and *Crotalaria* (Ridley, 1930).

The inflated pod of *Crotalaria* is not adapted for wind or water dispersal, since it dehisces before breaking free from the plant, and seeds often fall free from the funiculus even before dehiscence. Probably the pod snaps open rapidly and throws the seeds.

AESCHYNOMENE L.

Aeschynomene americana L. var. **glandulosa** (Poir.) Rudd, Contr. U.S. Natl. Herb. 32:26. 1955

Pega-pega

Erect or somewhat reclining herb, 1–3 m tall; stems and inflorescences sparsely hirsute. Leaves pinnate, 2.5–6.5 cm long, short-petiolate; stipules narrowly lanceolate, to ca 12 mm long, with a narrowly lanceolate appendage ca 8 mm long at base pointing antrorsely; leaflets folding together top to top upon dessication, in mostly 12–30 pairs, oblong, obliquely apiculate, oblique at base, 6–9 mm long and less than 2 mm wide, ± scarious, the costae 3, parallel, conspicuous below. Inflorescences axillary, racemose, to 5 cm long; bracts conspicuous, foliaceous,

KEY TO THE SPECIES OF AESCHYNOMENE

Leaflets with 2 to several costae ..... *A. americana* L. var. *glandulosa* (Poir.) Rudd
Leaflets with 1 costa:
  Plants with stems, petioles, and rachises conspicuously hispid, sometimes glandular, the trichomes to 4 mm long ..... *A. ciliata* J. Vogel
  Plants strigose to glabrous, any trichomes much shorter than 3 mm ..... *A. sensitiva* Sw.

broadly lanceolate, to 3 mm long and 1.5 mm wide, the veins 5–15, conspicuous, parallel, the margins setaceous; pedicels to 10 mm long; flowers few, oblique on pedicels, to 9 mm long; calyx bilobed, hispid, to 5.5 mm long, subtended by 2 bracts nearly equaling calyx lobes; standard 8 mm long, rounded, pale orange with a yellow spot near its base, often marked with dark red as well, held erect at anthesis; wings slightly shorter than standard, the keel fused only on outer edge, loosely holding stamens and style; stamens in 2 clusters of 5 each, equaling length of style, shedding pollen before opening. Loments stipitate, 3–9-lobed, to 26 mm long and 2.5 mm wide, densely pubescent, the lobes ca 3 mm diam, the upper margin of loment ± entire, the lower margin deeply constricted between each seed; seeds 2–3 mm long, 1.5–2 mm wide. *Croat 13154.*

Occasional, in the Lighthouse Clearing. Flowers and fruits mostly from December to February.

The plants are often more or less reclining in age, perhaps dispersing fruits by lateral displacement. The plant has been seen visited briefly by small black bees (possibly *Trigona*) in rapid succession. The fruits do not stick to clothing (at least before maturity), although they have many trichomes.

Florida and southern Mexico to Argentina; West Indies; introduced into West Africa. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, and Panamá, from premontane dry forest in Herrera, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí.

Aeschynomene ciliata J. Vogel, Linnaea 12:84. 1838
A. hispida sensu Standl. non Sw.

Herb, 1–2.5 m tall; stems and rachises hispid, the trichomes yellow, glandular, 2–4 mm long. Leaves pinnate, 10–15 cm long; stipules 1–2 cm long, acute; petioles 8–10 mm long; leaflets in 15–20 pairs, short-petiolulate, oblong, rounded to retuse at apex, subcordate and slightly asymmetrical at base, 10–15(30) mm long, 3–5(8) mm wide, glabrous, lighter below, the midvein central. Cymes terminal, to ca 4 cm long; bracts foliaceous, ovate, subacuminate, ca 4 mm long and 2 mm wide, setaceous on margins; flowers few, yellow; calyx bilabiate, the upper lip trifid, the lower lip bifid, ca 6 mm long, subtended by 2 bracts; corolla reflexed, the standard 8–10 mm long, the claw 2 mm long, the blade orbicular, 5–8 mm diam, noticeably serrulate-ciliate; stamens ca 8 mm long. Loments mostly 8–10-articulate on stipes 5–10 mm long, smooth, hispid, the margins entire; articles ca 4 mm long and 6 mm wide; seeds 3–4 mm long and ca 2 mm wide. *Foster 1403.*

Rare; collected once at the margin of the lake near the dock. Apparently flowers and fruits principally from November to January.

Southern Mexico to Ecuador and Amazonian Brazil; Jamaica. In Panama, known only from tropical moist forest in the Canal Zone and the immediate vicinity, usually near water.

Aeschynomene sensitiva Sw., Prodr. Veg. Ind. Occ. 107. 1788

Erect, slender-stemmed herb, to 2(4) m tall, glabrous to densely hispidulous appearing glabrous, drying slightly dark. Leaves pinnate; stipules narrowly subulate, 5–20 mm long, caducous; petiole and rachis hispidulous; rachis to ca 5 cm long; leaflets in 5–20 pairs, oblong, rounded and mucronate at apex, obliquely rounded to subcordate at base, 4–6 mm long, 1–2 mm wide, glabrous, the midvein central, obscure. Panicles generally upper-axillary; peduncles and pedicels hispidulous; flowers few, yellow; bracts ovate, 1–2 mm long, ciliolate; calyx ca 4 mm long, the lips at most obscurely dentate; petals ca 7 mm long, obscurely ciliate; stamens ca 6 mm long. Loments drying dark, mostly 7- or 8-articulate, ca 5 cm long, on stipes ca 4 mm long, only slightly notched between articles, sparingly pubescent, appearing glabrous, ± smooth, the upper margin essentially entire, the lower margin crenate; articles ca 5 mm long and wide; seeds obliquely reniform, ca 3 mm long and 2 mm wide, black. *Croat 4199, 13232.*

Growing in water at the shore near the dock. Probably flowers and fruits year-round.

Southern Mexico to central South America as far as Paraguay and Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Coclé, Panamá, and Darién; known also from tropical dry forest in Coclé and premontane wet and tropical wet forests in Colón.

ANDIRA Adr. Juss.

Andira inermis (W. Wright) H.B.K., Nov. Gen. & Sp. 6:385. 1824
Geoffroea inermis W. Wright
Cabbage bark, Cocú, Arenillo, Pilon, Quira, Almendro del río

Tree, to 10(15) m tall, 30–40 cm dbh; bark with disagreeable odor; stems glabrous. Leaves alternate, imparipinnate; stipules prominent especially on juvenile plants, persistent, slender, to 1 cm long; leaflets in (5)7–15 pairs, opposite to subopposite along the rachis, oblong, acuminate, rounded at base, mostly 4–9.5(13) cm long, 1.5–4.5(5) cm wide, glabrate to minutely puberulent on midrib. Panicles terminal, 15–30 cm long; branches, pedicels, and calyces brown-puberulent; flowers red-violet, subsessile, ca 1 cm long, with sweet aroma; calyx campanulate, the teeth short, ± equal, ca 3 mm long; standard darker inside in a broad submarginal band, white at center below; wings slightly exceeding length of keel, the keel petals held together loosely by overlapping on outer edge; stamens diadelphous, the staminal sheath open, glabrous; filaments alternating long and short, curved inward somewhat; style sharply curved inward, glabrous; stigma small, brushlike, longer than the anthers. Drupes ligneous, oval, to ca 5 cm long, the exocarp green, woody, thick; seed 1, oval, slightly shorter than drupe. *Croat 5342, 12272.*

Common along the margin of the lake and occasional in the young forest. Flowers and fruits may be seen throughout the year. Flowers mostly in the middle to late dry and early rainy seasons (February to May), with most fruits maturing in the middle to late rainy season, especially in September and October. A second flush of flowering may occur in October, with the fruits maturing in January and February.

The fruit and bark of this species are poisonous (Allen, 1956; Blohm, 1962). The species is an obligate outcrosser, since it is self-incompatible (Bawa, 1974).

Southern Florida and Mexico south to Bolivia and the Amazon basin; West Indies; introduced to West Africa. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Panamá, and Darién; known also from premontane moist forest in the Canal Zone and from premontane wet forest in Chiriquí, Coclé, and Darién. Characteristic of tropical dry, tropical moist, and premontane moist forests in Panama (Tosi, 1971).

CAJANUS DC.

Cajanus bicolor DC., Cat. Hort. Bot. Monsp. 85. 1813
Pigeon pea, Guandú, Frijol de palo

Shrub, woody at base, to 3 m tall; stems minutely sericeous, 3-ridged from the nodes. Leaves trifoliolate; stipules lanceolate, 2.5–3 mm long; petioles 1–4 cm long; rachis 5–15 mm long; leaflets narrowly elliptic, acute or slightly acuminate at apex, cuneate at base, softly puberulent and grayish-green above, glandular-dotted, tomentose, and pale below, the terminal leaflet 5–10 cm long, 2–3.5 cm wide, the veins at base 3. Racemes terminal or upper-axillary, 2–6 cm long, the flowers often paired at the nodes; pedicels 5–10 mm long; calyx bilabiate, to 8 mm long, lobed half its length, the lobes acute to acuminate, the upper 2 ± united along their common side; petals to 2 cm long, yellow, the standard often red to maroon outside. Legumes oblong, 5–10 cm long, 1–1.5 cm wide, puberulent, strongly beaked, yellowish-green with brown-striped mottling, with oblique constrictions between the seeds on the side of the legume, the calyx persisting at base; seeds 2–5, flattened, ca 7 mm diam, gray, the hilum prominent. *Croat 7238.*

Cultivated in the Laboratory Clearing. Flowers and fruits primarily from January to March, but sometimes flowering much earlier, even in the late rainy season. The fruits develop in about 1 month.

Probably native to the East Indies; introduced sporadically in the New World tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Coclé, Panamá, and Darién.

CALOPOGONIUM Desv.

Calopogonium caeruleum (Benth.) Sauv., Ann. Acad. Havana 5:337. 1869

Vine, to 5 m long, softly orange-tomentose all over. Leaves trifoliolate; stipules inconspicuous, caducous; petioles 3–10 cm long; rachis lacking or to 1.5 cm long; petiolules slightly pulvinate, articulate, ca 5 mm long; leaflets rhombic-ovate, rounded to acuminate at apex, obtuse to slightly subcordate at base, 5–11 cm long, 4–8 cm wide, the veins at base 3, the secondary lateral veins prominulous, perpendicular to primary lateral veins and often extending between pairs of primary laterals. Racemes axillary, 2–40 cm long; flowers in fascicles arising from tubercles 2–8 mm long; bracts subulate, ca 2 mm long; pedicels 1–2 mm long; calyx ca 4 mm long, densely hispid, bilabiate, lobed ca half its length, the upper lip shallowly bifid, the lower lip with 3 linear teeth; petals blue, to 10.5 mm long; standard emarginate at apex, flat and erect, marked at center with green; wings and keel slightly shorter than standard, the wings adhering weakly to sides of keel, the keel fused apically, not enclosing style or stamens; stamens diadelphous, ca 4 mm long; filaments free above from about the middle; style straight, antrorsely hispidulous, almost equaling standard, much longer than anthers; neetar copious, storing in calyx. Legumes narrowly oblong, flattened, acuminate, 3.5–6 cm long, 6–8 mm wide; seeds 4–8, ovoid, ca 5 mm long, reddish-brown. *Hladik 136.*

Rare; collected only once. Occurring commonly along roadsides and at the edges of clearings in other areas of the Canal Zone. Flowers mostly in January and February (sometimes to March), with the fruits maturing in March and April.

Southern Mexico to northern South America; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Herrera, Panamá, and Darién; known also from premontane moist forest in Herrera and premontane wet forest in Chiriquí.

Calopogonium mucunioides Desv., Ann. Sci. Nat. Bot., sér. 1, 9:423. 1826

Twining vine, to 2 m long, densely hispid, the trichomes to 2 mm long, many, especially on fruit and stem, pustular at base. Leaves trifoliolate; stipules acute, to 5 mm long,

KEY TO THE SPECIES OF CALOPOGONIUM

Stems, petioles, calyces, and fruits densely reddish-brown-tomentose, the trichomes not individually visible; inflorescences usually more than 20 cm long; fruits usually more than 3.5 cm long ..... *C. caeruleum* (Benth.) Sauv.

Stems, petioles, calyces, and fruits sparsely long-hispid, the trichomes to ca 2 mm long; inflorescences less than 15 cm long; fruits usually less than 3.5 cm long ..... *C. mucunioides* Desv.

striate; petioles 3–10 cm long; petiolules of terminal leaflet ca 1 cm long, of lateral leaflets ca 2 mm long; terminal leaflet ± ovate, acute to rounded at apex, rounded at base, 4.5–13 cm long, 3–9 cm wide, the lateral leaflets inequilateral, the veins at base 3. Racemes axillary, to 15 cm long; pedicels to 3 mm long; bracts linear, to 5 mm long, striate; flowers blue, inconspicuous, 8–10 mm long, clustered; calyx slender, densely hirsute, ca 6 mm long, lobed ca two-thirds its length, the lobes subequal, subulate; standard 6–8 mm long, ± spatulate, emarginate; wings white, slender, ± equaling standard, weakly fused to the shorter and inconspicuous keel, the keel petals ± free; stamens diadelphous, loosely held, ca 4 mm long, straight; filaments united in basal third, shedding pollen in bud; style equaling anthers, straight; stigma globular, somewhat eccentric, sticky. Legumes narrowly oblong, flattened, briefly acuminate, 2.5–3.5 cm long, ca 5 mm wide, densely brown-hispid, often occurring in dense clusters; seeds 5–9, ovoid, ca 5 mm long, light brown. *Croat 6925, 13169a.*

Occasional, in clearings. Flowers mostly in December and January. The fruits mature from December to March.

Southern Mexico to northern South America; West Indies; introduced into the Old World tropics. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, Herrera, and Panamá; known also from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé.

CANAVALIA DC.

Canavalia dictyota Piper, Contr. U.S. Natl. Herb. 20:574. 1925

Twining herbaceous vine. Leaves trifoliolate; petioles 3–9 cm long, densely pubescent; rachis 1.5–4.5 cm long; leaflets lanceolate-elliptic, rounded to acute at apex, obtuse at base, 9–19 cm long, 4–12 cm wide, glabrous above, sparsely strigillose below. Flowers lavender, in axillary racemes; peduncles ca 10 cm long; rachises to 20 cm long; pedicels to 2 mm long, elongating to 1 cm and thickening greatly in fruit; calyx bilabiate, glabrous, to 13 mm long and 7 mm wide, with the 2 superior teeth ± rounded and to 5 mm long, the lower 3 teeth acute and to 2 mm long; standard pale lavender, to 2.5 cm long, the margins revolute, strengthening petal; wings and keel white with lavender tips, somewhat shorter than standard, the keel petals fused only briefly below their summit; stamens diadelphous, to 2 cm long, arching into keel petals; filaments united about four-fifths of their length; style ± equaling the stamens, apparently receptive when pollen is shed; nectaries 2, on either side of the ovary. Legumes to 20 cm long, to 3.5 cm wide, glabrous, brown, the upper margin broad with prominent submarginal ridges and an apical beak; valves at maturity twisting open violently and throwing the seeds; seeds 6–9, vertically oriented, to 2 cm long, 1.5 cm wide, and 1.2 cm thick, brown with dark brown and black markings, buoyant. *Croat 4794.*

Occasional, in open areas, especially along the shore near the dock. Flowers from November to February (rarely later). The fruits ripen mostly from February to June, with most mature perhaps by April.

May be confused with *C. brasiliensis* Mart. ex Benth., which differs chiefly in having the leaves more broadly ovate and the seeds not buoyant.

The nectaries of the flower can be approached by the pollinator only at the open side of the staminal cluster. Bees land on the standard, which is strengthened by its revolute margin and supported beneath by the two large calyx lobes. In forcing its way in, the bee pushes the keel upward and rubs the stationary stigma and anthers with its back.

Panama to the northern Amazon basin and eastern Brazil; West Indies. In Panama, known only from tropical moist forest in the Canal Zone, San Blas, and Panamá.

CENTROSEMA (DC.) Benth.

Centrosema pubescens Benth., Comm. Leg. Gen. 55. 1837

Campanilla, Caracucha

Slender vine. Leaves trifoliolate; stipules ovate, ca 2 mm long; petioles 1.5–4 cm long; petiolules to 15 mm long on terminal leaflet, ca 2 mm long on lateral leaflets; leaflets lanceolate to oblong, acute to acuminate, rounded at base, villous above, velutinous below, the terminal leaflet 5–13 cm long, 2.5–5.5 cm wide, the lateral leaflets somewhat reduced, the veins prominent on both surfaces. Racemes axillary; peduncles 8–11 cm long; rachises to 2 cm long; bracts ovate, acute, striate, to 8 mm long, caducous; calyx bifid, shallowly lobed, ca 10 mm long, pubescent, becoming glabrate in age except for carinal lobe, the carinal lobe arcuate, slender, ca 5 mm long; standard ± rounded to emarginate, to 3.5 cm long and 4 cm wide, sparsely pubescent and usually white outside, blue to orchid or violet-purple inside, prominently marked with purple and white along median line, often yellow at base, clawed at base; keel and wings white or tipped with violet, ca 3 cm long, the keel at first weakly sealed on both sides except at base; stamens 10, diadelphous, enclosed within keel, the staminal column forming an arched open tube below, fan-shaped at apex; style to ca 3.5 cm long, held within the open staminal tube, flat, truncate and puberulent at apex, longer than anthers, the outer margin bristled. Legumes 10–14 cm long, ca 7 mm wide, long-acuminate at apex, sparsely appressed-pubescent, the lateral margins raised; seeds as many as 25, black, round, flattened, ca 3 mm diam. *Croat 4398, 6986.*

An occasional weed in clearings. Flowers and fruits throughout most of the year, especially in the dry season, but principally in December and January.

The style extends from the keel beyond the anthers and presses against the wing and keel petals. Both of its flat surfaces are covered with a thick, pasty layer of pollen.

Standley (1933) also reported *Centrosema virginianum* (L.) Benth., but that species does not appear to be distinct from *C. pubescens* Benth. in Panama. It is reported to

range from Mexico to Panama, but possibly does not come as far south as Panama.

Mexico to tropical South America; West Indies; introduced in the Old World tropics. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién; known also from premontane dry forest in Herrera, from tropical dry forest in Coclé and Panamá, from premontane wet forest in the Canal Zone, Coclé, and Panamá, and from tropical wet forest in Darién.

CLITORIA L.

Clitoria javitensis H.B.K., J. Linn. Soc., Bot. 2:42. 1858
C. portobellensis Beurl.; *C. arborescens* sensu auct. non H.B.K.
Peronil

Liana, becoming shrubby elsewhere in open areas, lacking tendrils; younger stems reddish-brown, to 12 mm diam. Leaves trifoliolate; stipules lanceolate, ca 7 mm long, pubescent, persistent; petioles 1–15 cm long, reddish-villous; rachis of terminal leaflet to 30 mm long; petiolules of lateral leaflets ca 4 mm long, pulvinate and articulate at apex; leaflets elliptic to obovate, abruptly short-acuminate, rounded at base, 6–22 cm long and 3.5–11 cm wide, dark above, paler below, glabrous above, ± pubescent below at least on the midrib. Racemes axillary, to 30 cm long; bracts and bracteoles ovate, acute, ca 7 mm long, striate; pedicels to 4 mm long; calyx to 3.5 cm long and 1 cm wide, the lobes sharply and abruptly acuminate, the carinal tooth to 8 mm long, the others somewhat shorter; standard white with divergent red lines at center, often infused throughout with pink, rounded at apex, the sides folded over other petals, to ca 8 cm long; wings white, fused to keel above, the keel white, the 2 sides free except at ± twisted apex, enclosing style and stamens, the wings and keel each to ca 6.5 cm long; stamens of 2 lengths, the free stamen and alternate stamens of the staminal tube short, the others slightly longer, the longest to ca 5.5 cm long, considerably exceeded by the densely pubescent style. Legumes on stipes 3 cm long, linear, flattened, sometimes broader toward the apex, to 27 cm long and 2.5 cm wide, abruptly long-acuminate (the acumen to 4 cm long), softly brown-villous; valves twisting when dry at maturity and capable of straightening or twisting repeatedly with changes in humidity; seeds 7–11, ca 12 mm long, 10 mm wide, and 5 mm thick, black. *Croat 4853, 8497.*

Common in the forest, growing to the top of the canopy, and at the edges of clearings. Flowers from October to May, mostly early in the dry season, in January and February. The fruits mature from January to May, mostly in April and May.

Pollen is shed in the bud. The style and anthers are released violently by the pollinator.

This species has been confused with *C. arborescens* Ait. from the Lesser Antilles and the Guianas and also with *C. glaberrima* Pitt., which generally occurs in drier regions of Panama than does *C. javitensis.* It is possibly conspecific with *C. leptostachya* Benth.

Panama to the Guianas, northern Brazil, Peru, and Ecuador. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Chiriquí, Veraguas, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island) and from premontane wet forest in Chiriquí.

Clitoria rubiginosa Adr. Juss. in Pers., Synops. Pl. 2:303. 1807

Vine; stems, peduncles, calyces, and underside of leaves moderately brown-pilose. Leaves trifoliolate; stipules ovate, acute, ca 4 mm long; petioles 1.5–4.5 cm long; rachis of terminal leaflet subtending the stipels 1–2 cm long; petiolules pulvinate and articulate; leaflets lance-elliptic to oblong, rounded at base, 2.5–7.5 cm long, 1.5–4 cm wide, glabrous above, villous and paler below, the terminal leaflet rounded-acute to retuse at apex, often bearing short apiculum or tuft of trichomes. Panicles axillary, bearing few flowers; peduncles to 15 cm long; rachises 2–3 cm long; calyx 2–3 cm long, acutely lobed ca one-third its length, the lobes subequal; standard white, drying yellow, tinged with violet along median line below apex, to 4 cm long, enclosing other petals and surpassing them by ca 2 cm; keel straight; stamens ca 2.5 cm long, arcuate. Legumes stipitate, somewhat flattened, linear-oblong, 3–5.5 cm long, with 2 ribs ca 4 mm below the upper edge, glabrous; seeds to ca 10, globose, ca 3 mm diam. *Woodworth & Vestal 693.*

This species occurs sporadically in the Canal Zone, but has not been seen or collected in recent years on the island. The plant could be expected to occur in the Lighthouse Clearing. Flowers at least from September to March. The fruits develop quickly and are usually present at the same time as the flowers.

Southern Mexico to tropical South America; West Indies; introduced in West Africa. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Coclé, and Panamá, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí.

KEY TO THE SPECIES OF CLITORIA

Plants lianas, common in the forest; flowers pinkish, more than 5 cm long ..... *C. javitensis* H.B.K.
Plants vines, in clearings, rare or absent; flowers mostly white, less than 5 cm long .....
..... *C. rubiginosa* Adr. Juss.

KEY TO THE SPECIES OF CROTALARIA

Leaves simple ..... *C. retusa* L.
Leaves trifoliolate ..... *C. vitellina* J. Ker

CROTALARIA L.

Crotalaria retusa L., Sp. Pl. 715. 1753
Gallito, Frijolillo

Erect herb, usually less than 1 m tall; stems ribbed, appressed-pubescent. Leaves simple, nearly sessile; blades obovate, rounded to emarginate at apex, tapered gradually to base, 3–10 cm long, 1.5–2.5 cm wide, glabrous above, appressed-pubescent below, generally bluish-green and lighter below. Racemes terminal, ca 20 cm long; pedicels ca 1 cm long, spreading to reflexed; calyx strigillose, ca 1.5 cm long, lobed ca two-thirds its length, the lobes subequal, acute, those subtending the standard broader; standard ca 2.5 cm long and 3 cm wide, yellow with dark nectar guidelines near base inside and with a broad maroon to brown spot outside; wings ca 2 cm long, ca 1.2 cm wide, covering keel at apex, the keel deeply saccate, the common margins fused but the free portion folded near apex to form a funnel, the lower margins of the keel densely pubescent; stamens 10, fused in basal half into an open-sided tube with alternating long and short anthers, the longer anthers ca 3 mm long, borne on the shorter filaments, shedding pollen in bud, the shorter anthers probably sterile; style strongly bent at about the height of the sterile anthers, the stigma flat-tipped, ciliolate, the trichomes distal, antrorse; pollen about the consistency of cake frosting, squeezed out by stigma and trichomes. Pods oblong, inflated, glabrate, ca 3.5 cm long, brown to black; seeds ca 10, reniform, flat, ca 2 mm diam, becoming black at maturity. *Croat 8659.*

Rare, in clearings; collected once in recent years in the Laboratory Clearing, where it had possibly been planted. The species was once abundant on the island. With the reduction in the number of clearings, it has probably disappeared, though it might easily reoccur in one of the two large clearings. Flowers and fruits throughout the year.

A cosmopolitan tropical weed. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Coclé, Panamá, and Darién, from premontane dry forest in Los Santos, and from premontane wet and tropical wet forests in Colón.

Crotalaria vitellina J. Ker in Lindl., Edward's Bot. Reg. 6, pl. 447. 1820
Zapatito del Obispo

Erect herb or suffrutex, 1–1.5 m tall; stems sericeous. Leaves trifoliolate; stipules linear-lanceolate, to ca 4 mm long, caducous; petioles to 5 cm long, sericeous; leaflets lanceolate-elliptic, apiculate, cuneate at base, 5–7.5 cm long and 1.8–2.5 cm wide, glabrous above, hirtellous and glaucous below, the secondary veins reticulate, the terminal leaflet acute at base. Racemes terminal or axillary, to 16 cm long, the flowers bracteate, oblique on pedicels; bracts subulate, ca 3 mm long; pedicels 5(6) mm long; calyx ca 7 mm long, lobed three-fourths of its length, hirtellous, the lobes slenderly lanceolate, to 5 mm long; petals yellow, tinged with purple, with thin longitudinal ribs; standard to 1 cm long; wings to 8 mm long with a claw ca 2 mm long, the keel united along upper common margins, to 12 mm long; style linear, strigose, curving into sac formed by keel, then following bottom surface of keel forward. Legumes terete, ca 2 cm long and 7 mm wide, the curved remnant of the style often still attached, ca 8 mm long, the trichomes less than 0.2 mm long; seeds ca 10. *Aviles 13.*

Not seen on the island in recent years. Flowers from July to January. The fruits develop within about 1 month.

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Herrera, and Panamá, from premontane dry forest in Herrera (Chitré), from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Chiriquí and Coclé.

CYMBOSEMA Benth.

Cymbosema roseum Benth. in Hook., J. Bot. (Hooker) 2:61. 1840

Semiherbaceous liana climbing to the top of trees, soft-villous all over, generally with tendrils. Leaves trifoliolate; stipules acuminate, ca 2 mm long; petioles 3–7(12) cm long; leaflets broadly lanceolate to elliptic, broadly rounded to acute and sometimes retuse at apex, rounded-truncate at base, 6–12 cm long, 3–6 cm wide, darker above than below, the veins finely reticulate. Racemes terminal; peduncles to 25 cm long; rachises to ca 10 cm long; flowers bright red turning lavender on drying; pedicels ca 2 mm long; calyx ca 1 cm long, lobed ca one-fourth its length, bilabiate, the upper lip with 2 minute teeth, the lower with 3 acute teeth, gibbous at base; petals subequal, to ca 3.5 cm long; standard oblong-ovate, ca 1 cm wide; wings ca 5 mm wide, the keel flaring open; stamens 10, diadelphous, barely exceeding the petals. Legumes oblong-elliptic, 4.5 cm long and 2 cm wide, beaked, densely appressed-pubescent, the trichomes acicular, the beak attenuate, to 2 cm long; seeds 3–6. *Croat 8304.*

Apparently rare, seen only along the shore. Some flowers have been seen in October and February, and mature fruits in February and July.

May be confused with *Dioclea guianensis,* but *Cymbo-*

sema is distinguished by having a free stamen associated with the banner, long petals, and fruits with a falcate stigma even at maturity.

Mexico (Chiapas), Costa Rica, Panama, Colombia, and Peru. In Panama, known only from tropical moist forest in the Canal Zone and Panamá.

DALBERGIA L.f.

Dalbergia brownei (Jacq.) Urban, Symb. Ant. 4:295. 1905

Bejuco frijolillo, Sisa guidup

Shrub, small tree, or small liana, to 5 m tall; young stems and petioles rufous-pubescent. Leaves simple; petioles to 1.5 cm long, pulvinate and often articulate at both ends, less often basally; blades ovate, obtuse to acute at apex, rounded to subcordate at base, 5–8 cm long, 3–5 cm wide, inconspicuously strigillose when young, possibly glabrous in age, shiny above, pale below. Panicles short, axillary or subterminal; flowers fragrant, white; pedicels 2–5 mm long, pubescent; calyx ca 4–5 mm long, bilabiate, lobed about half its length, the upper lobe shallowly bifid, the lowermost tooth elongated and subulate, the calyx subtended by bracts, the bracts 2, opposite, obtuse, ca 1 mm long; petals ca 10 mm long, obovate, the keel petals united; stamens 10, diadelphous, ca 5 mm long, the staminal column open basally. Legumes usually 1 per inflorescence, 1- or 2-seeded, oblong, mostly 1.5–2 cm long (to 3 cm long if 2-seeded), 1 cm wide, and ca 3 mm thick, glabrous, speckled; seeds flattened, brown, to ca 7 mm diam. *Croat 7903, Foster 955.*

Occasional, along the shore, usually partly in water. Flowers mostly from February to May. The fruits mature from April to August.

Florida and southern Mexico to Colombia and Venezuela; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién, from tropical dry forest in Panamá, and from premontane moist forest in the Canal Zone and Los Santos.

Dalbergia monetaria L.f., Suppl. 317. 1781

Liana or climbing shrub, to 13 m tall, forming dense masses along shore; stems minutely fissured and bearing prominent round lenticels. Leaves compound; stipules caducous; petioles 1–2 cm long; rachis puberulent when young, 2–6 cm long, often zigzag with the leaflets alternate; leaflets (1)2–5, ovate to elliptic, abruptly long-acuminate (the acumen to 1.8 cm long), rounded or obtuse at base, 5.5–12 cm long, 3–6 cm wide, glabrous and shiny above except for pubescent midrib, glabrous and pale below, the reticulate veins prominulous but not raised. Racemes axillary; rachises to ca 2 cm long, ± strigose; pedicels slender, 2–3 mm long; calyx inflated, campanulate, to 2 mm long and wide, ± irregularly lobed ca one-third its length, the teeth acute and subequal; petals 5–7 mm long, white, clawed ca half their length, the wings truncate to subcordate and oblique at base; stamens diadelphous, 4–5 mm long, the column split into 2 fascicles; ovary stipitate, the stipe slender, about as long as ovary; style bent sharply forward. Legumes ± orbicular, flattened, becoming bowl-shaped in age, 3.5–4.5 cm long, 2–3 mm thick, glabrous, borne on stipes 5–7 mm long, one margin sometimes raised, the surface often with raised reticulations; seeds brown, discoid, ca 1.5 cm diam, the margin thin. *Croat 13960, Foster 1349.*

Distribution unknown, but locally abundant along the northern shore of Gigante Bay. Flowers in the late rainy season and early dry season, especially in early dry season. The fruits mature in the late dry season and early rainy season (to July).

Mexico along the Atlantic slope of Central America to northern South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone and probably in Bocas del Toro; known also from premontane and tropical wet forests in Colón.

Dalbergia retusa Hemsl., Diag. Pl. Mex. 8. 1878, non Baillon 1884

Cocobola, Rosewood

Tree, to 20 m tall, ca 30 cm dbh; outer bark coarse, becoming fissured and loosened in age; wood dark, hard, heavy. Leaves alternate, pinnate; stipules caducous, ovate-elliptic, to 2 cm long, persistent on juvenile plants; petioles to 6 cm long, puberulent; rachis 10–20 cm long; leaflets 7–15, alternate on rachis, oblong to ovate-oblong, obtuse and often slightly emarginate at apex, obtuse to rounded at base, 6–10 cm long, 2.5–3.5 cm wide, appressed-pubescent below when young, becoming glabrate in age. Panicles axillary or terminal, appearing just before or at same time as new leaves; branches, pedicels, and calyces sparsely to densely pubescent, the trichomes short, brown, appressed; pedicels 3–4 mm long; calyx 5–7 mm long, lobed to one-third its length, weakly bilabiate, the teeth acute; petals white, 1–1.4(2) cm long; standard emarginate, clawed; keel petals fused at apex; stamens fused into a single tube with an open slit apically, markedly curved at apex, exceeded by the style. Legumes ± oblong, flat, 6–8 cm long, ca 2 cm wide, borne on stipes ca 1 cm long, glaucous, glabrous, mostly 1-seeded (if 2-seeded, the fruit to 13 cm long), the winged area of

KEY TO THE SPECIES OF DALBERGIA

Leaves simple; plants usually growing in water around edge of lake ..... *D. brownei* (Jacq.) Urban
Leaves with 2–15 leaflets; plants usually not growing in water:
  Plants trees; leaflets 7–15, ± oblong; fruits oblong ..... *D. retusa* Hemsl.
  Plants lianas or climbing shrubs; leaflets 2–5, ovate to elliptic; fruits orbicular .... *D. monetaria* L.f.

equal thickness throughout; seeds discoid, to ca 1 cm diam, medial on fruit body. *Croat 5320.*

A single tree, which undoubtedly was planted, grows near the laboratory. Herbarium collections from central Panama have shown flowers throughout much of the year, but the tree on BCI loses its leaves in the dry season and then flowers as the new leaves are emerging from February to July, usually in March and April. The species may flower only every other year (Frankie, Baker, & Opler, 1974). The fruits develop to full size within 2 months, but persist until the following dry season.

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

See Fig. 282.

DESMODIUM Desv.

The genus consists of herbs or suffruticose shrubs with alternate, stipulate, trifoliolate leaves. The flowers are racemosely arranged in pairs. The style is longer than the stamens and is enclosed with the stamens within the keel under tension. The stamens and style are held in position until triggered by a flower visitor, when they spring forward and throw pollen.

The genus is distinguished by the flattened loment of one-seeded, indehiscent sections, usually bearing uncinate trichomes.

Desmodium adscendens (Sw.) DC., Prodr. 2:332. 1825
Beggarlice, Pega-pega

Perennial, often rooting at the nodes, to 50 cm long; stems slender, white-pilose, the trichomes rubbing off easily. Leaves trifoliolate; stipules long-attenuate, ca 7 mm long; petioles to ca 12 mm long; stipels subulate, to 4 mm long; petiolule of terminal leaflet ca 5 mm long, the petiolules of lateral leaflets ca 2 mm long; leaflets ± elliptic, ± rounded at both ends, often emarginate at apex, 1.5–4 cm long, 1–2 cm wide, ± glabrous above, appressed-pilose and pale below. Racemes terminal, slender, 5–20 cm long; peduncles 2–3.5 cm long; pedicels ascending, 7–10 mm long; flowers 2 or 3 per node of inflorescence, blue to pinkish-blue; calyx 2–4 mm long, bilabiate, lobed three-fourths of its length, the teeth slender, subequal; corolla 4–5 mm long, inconspicuous, withering quickly. Loments

KEY TO THE SPECIES OF DESMODIUM

Leaflets often emarginate at apex:
- All leaflets less than 1 cm long, rarely rounded at apex; upper margin of fruits nearly entire .... *D. triflorum* (L.) DC.
- Most leaflets more than 1 cm long, often rounded at apex; upper margin of fruits nearly entire or as deeply incised as lower:
  - Segments of fruit less than 2 times longer than broad .... *D. adscendens* (Sw.) DC.
  - Segments of fruit ca 3 times longer than broad .... *D. scorpiurus* (Sw.) Desv.

Leaflets not emarginate at apex:
- Fruits with 1 or 2 segments; leaves acute to acuminate at apex:
  - Fruits on stipes 1–2 mm long; flowers borne singly .... *D. wydlerianum* Urban
  - Fruits on stipes more than 4 mm long; flowers on paired pedicels:
    - Stems and petioles conspicuously villous, the trichomes 0.5–1 mm long .... *D. axillare* (Sw.) DC. var. *acutifolium* (O. Kuntze) Urban
    - Stems and petioles minutely puberulent, the trichomes usually 0.1 mm long .... *D. axillare* (Sw.) DC. var. *stoloniferum* (Poir.) Schub.
- Fruits with mostly 3 to many segments; leaves rounded to acute at apex:
  - Fruits deeply lobed on both margins; most terminal leaflets at least 4 cm long; flowers usually not single at nodes of inflorescence:
    - Segments of fruit 5–6 mm long; most petioles below inflorescence less than 1.5 cm long .... *D. cajanifolium* (H.B.K.) DC.
    - Segments of fruit 2.5–5 mm long; most petioles below inflorescence more than 1.5 cm long:
      - Pedicels mostly 1–1.6 cm long; fruiting nodes on rachis (6)10–30 mm apart; segments of fruit 3–3.5(4) mm long, 2.6–3.5 mm wide .... *D. tortuosum* (Sw.) DC.
      - Pedicels usually less than 1 cm long; fruiting nodes on rachis (4)6–10 mm apart; segments of fruit smaller, 1.5–2.5 mm long, 1.5–2 mm wide .... *D. distortum* (Aubl.) J. F. Macbr.
  - Fruits deeply lobed only on lower margin; leaflets less than 4 cm long *or* flowers borne singly at nodes of inflorescence:
    - Flowers usually borne singly at nodes of inflorescence; terminal leaflets acute at apex, at least 3 times as long as petioles; plants often shrublike .... *D. canum* (J. F. Gmel.) Schinz & Thell.
    - Flowers (not fruits) in 2s or 3s at nodes of inflorescence; terminal leaflets obtuse to rounded at apex, less than 3 times as long as petioles; plants usually sprawling or prostrate .... *D. adscendens* (Sw.) DC.

to 20 mm long and ca 3 mm wide, densely uncinate-puberulent, the upper margin entire, the lower margin lobed to about the middle between seeds; articles 2–4(5), 4–5 mm long. *Croat 11846.*

Common in clearings. Flowers and fruits all year, perhaps mainly from May to September.

Mexico to South America; West Indies; tropical Africa. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Los Santos, and Darién, from tropical wet forest in Colón, Panamá, and Darién, from premontane wet forest in Coclé, and from premontane rain forest in Chiriquí and Coclé.

Desmodium axillare (Sw.) DC., Prodr. 2:333. 1825

Repent perennial; stems creeping over ground, usually rooting at nodes. Leaves trifoliolate; stipules 5–10 mm long, connate about one-third their length; petioles 4–7 cm long, puberulent, the pulvinus at base terete; rachis of terminal leaflet 4–10 mm long; leaflets ovate, ± inequilateral, 4–8 cm long, 3–6 cm wide, glabrous above, white-pilose below, the reticulate veins often conspicuously raised and sometimes close together below. Racemes axillary, erect, elongate; peduncles 15–20 cm long; axis elongating to ca 20 cm; bracts ovate, acuminate, ca 4 mm long, strigillose, concave at base; pedicels paired, ca 5 mm long (to 15 mm in fruit); flowers pink to lavender, spring-loaded, ca 5 mm long, often paired; calyx 1.5–2 mm long, acutely lobed to half the length, the lobes 4, ± equal, deltoid, puberulent to hispid, purplish; corolla ca 4.5 mm long, pink to rose or reddish-violet; standard emarginate at apex; stamens ca 4 mm long, ± equal, the staminal column open basally, spring-loaded, forcibly emerging from closed keel on disturbance. Loments at right angles on stipes 5–6 mm long, each with the upper margin entire, the lower margin deeply lobed; segments usually 2, more or less reniform, 8–13 mm long.

Desmodium axillare (Sw.) DC. var. **acutifolium** (O. Kuntze) Urban, Symb. Ant. 4:292. 1905

Stems conspicuously villous, the trichomes 0.5–1 mm long. Leaflets strigillose above, thickly pilose below. Loments 10–15 mm long, densely white-tomentose; segments 2. *Croat 7063.*

Occasional, in clearings. Probably flowers and fruits year-round.

Belize to South America; Jamaica. In Panama, known only from tropical moist forest in the Canal Zone, Colón, Panamá, and Darién.

Desmodium axillare (Sw.) DC. var. **stoloniferum** (L. C. Rich. ex Poir.) Schub., J. Arnold Arbor. 44:289. 1963

Stems minutely puberulent, the trichomes ca 0.1 mm long. Leaflets glabrous above, densely pilose below. Loments 20–25 mm long, yellowish-hispid-uncinate, on stipes ca 7 mm long; segments 2. *Croat 6630.*

Frequent along trails in the forest. Possibly flowers and fruits year-round, but more abundantly in the early to middle rainy season.

Central America; Greater Antilles. In Panama, known only from tropical moist forest in the Canal Zone.

Desmodium cajanifolium (H.B.K.) DC., Prodr. 2:331. 1825

Pega-pega

Stout erect suffrutex, usually 1–3 m tall; stems finely pubescent to pilose, to 2 cm thick at base. Leaves trifoliolate; stipules 3–7 mm long, often persistent; petioles 5–10(30) mm long, sericeous; rachis of terminal leaflet 3–10 mm long; leaflets lanceolate to ovate, acute to rounded at apex, obtuse to rounded and inequilateral at base, 4.5–7 cm long, 2–3 cm wide, puberulent above, densely soft-pilose and paler below, the reticulate veins conspicuously raised below. Inflorescences terminal, racemose-paniculate, some lower racemes axillary, to ca 40 cm long and 25(30) cm wide; floral bracts deciduous, subulate, ca 1 mm long; pedicels ca 3 mm long (to 5 mm in fruit); calyx 2.5–3 mm long, bilabiate, acutely 4-lobed to middle, hispidulous; corolla 4–6 mm long; standard violet (turning blue), marked inside on either side and above the base of the medial groove with a greenish spot; wings the same color as the standard on their upper margin (nearest stamens), the keel usually white; stamens diadelphous, 5–6 mm long, shedding pollen in bud, only loosely held by keel. Loments subsessile, lobed from both margins but more deeply so from below, the isthmus between joints very narrow, sparsely puberulent; segments 4–6, each 5–6 mm long, chartaceous, the veins reticulate. *Shattuck 561.*

Possibly no longer occurring on the island, though abundant at Frijoles and to be expected in clearings. In central Panama, flowers and fruits from November to April (sometimes as early as October). Since fruits are probably wind dispersed, most probably mature during the dry season.

Southern Mexico to South America. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá.

Desmodium canum (J. F. Gmel.) Schinz & Thell., Mem. Soc. Neuchat. Sci. Nat. 5:371. 1914

D. frutescens (Jacq.) Schindl.

Pega-pega, Pegadera

Perennial suffrutex, becoming over 1 m tall, puberulent, the trichomes sparse on upper leaflet surface, often uncinate especially on inflorescence. Leaves trifoliolate; stipules ovate, attenuate, often connate, persistent, 6–10 mm long, ciliate, becoming brown and striate; petioles 5–15 mm long; stipels acicular, paired, 3–4 mm long, subpersistent; leaflets ovate to elliptic, acute to obtuse at apex, rounded to slightly subcordate at base, 2–7 cm long, 1–4 cm wide. Racemes terminal or subterminal; pedicels 5–8 mm long; flowers pale blue, ca 4 mm long, borne singly at nodes of inflorescence; calyx ca 4 mm long, somewhat reddish, the vexillar lobes joined to near the apex; standard rounded, ca 3 mm wide, with 2 green

spots near base; wings shorter than keel, the keel petals at first joined near apex; stamens 3–4 mm long, bent toward standard at apex, of 2 lengths, the free stamen and alternate stamens of tube shorter; style longer than the stamens, enclosed under tension with stamens within keel, released by pollinator, springing forward toward standard and throwing pollen; ovary densely villous, the hairs minute. Loments narrow, sparsely pubescent, the upper margin entire, the lower margin deeply lobed; segments usually 3–7. *Croat 6928.*

Occasional in clearings and rare in disturbed areas on the shore. Flowers and fruits throughout the year.

The pubescence on the fruit apparently does not attach to passing mammals as in the other species of *Desmodium.* The fruits are probably wind dispersed, the height of the plant allowing the seeds to be borne for some distance by the wind.

Throughout the New World tropics; tropical Africa. 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 premontane dry forest in Herrera and Coclé, from premontane wet forest in the Canal Zone, Colón, Coclé, and Panamá, and from tropical wet forest in Darién.

Desmodium distortum (Aubl.) J. F. Macbr., Publ. Field Columbian Mus., Bot. Ser. 8:101. 1930
D. asperum (Poir.) Desv.

Erect perennial to 2 m tall; stems uncinate-hirtellous. Leaves trifoliolate; stipules 10–15 mm long, clasping; petioles 2–5 cm long; stipels noticeable; leaflets ± elliptic-ovate, rounded at apex and base, hispidulous or hirsute-puberulent on both surfaces, the terminal leaflet 4–8 cm long and 1–3.5 cm wide, the lateral leaflets smaller, the reticulate veins prominulous below. Panicles of racemes large, terminal, the lower racemes axillary; bracts inconspicuous, subulate, ca 3 mm long; pedicels ca 7 mm long (to 12 mm in fruit); flowers small, purplish; calyx 4-lobed, ca 3 mm long; standard ca 5 mm long. Loments briefly stipitate, lobed equally from both margins, uncinate-puberulent; segments 5 or 6, orbicular, ca 2.5 mm diam. *Starry 307.*

Collected only once at the edge of the Laboratory Clearing; not seen in recent years. Apparently flowers and fruits throughout the year.

Mexico to South America; West Indies. In Panama, ecologically variable, known from tropical moist forest in the Canal Zone and Darién, from tropical dry forest in Herrera and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí and Coclé, and from tropical wet forest in Darién.

Desmodium scorpiurus (Sw.) Desv., J. Bot. Agric. 1:122. 1813

Sprawling, weak-stemmed herb, often from a stout woody root; stems and leaves villous to hispidulous. Leaves trifoliolate; stipules often cordate at lower edge, ca 4 mm long; petioles 1–5 cm long; leaflets rounded, elliptic or oblong, usually emarginate to rounded at apex, obtuse to rounded at base, sparsely strigose above, more densely so below, the terminal leaflet 0.8–3.5 cm long, 0.8–2.5 cm wide, the lateral leaflets slightly smaller. Racemes terminal, slender; pedicels 5–10 mm long; flowers few, bluish or whitish, 3–4 mm long; calyx deeply divided, ca 3 mm long; stamens didynamous, shorter than style; filaments fused to near apex; style sharply turned inward. Loments turgid, mostly 2.5–3 cm long and 1.5 mm wide, lobed along both margins, densely uncinate-puberulent, very sticky; segments 5–7, separating easily, oblong, ca 5 mm long. *Croat 6923, 15580.*

Occasional in open areas of the Laboratory Clearing. Flowers and fruits mainly from January to March (sometimes from December to April).

This is a variable species in terms of vegetative characters. Though superficially similar to *D. adscendens,* it may be distinguished by its generally uncinate pubescence, its broad, ovate-cordate stipules, and (when the fruit is mature) its very distinctive, oblong articles.

Mexico to Venezuela, the Guianas, Brazil, and Bolivia; West Indies; naturalized in parts of tropical East Indies and West Africa. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá, from tropical dry forest in Los Santos, and from premontane wet forest in Chiriquí.

Desmodium tortuosum (Sw.) DC., Prodr. 2:332. 1825
D. purpureum (P. Mill.) Fawc. & Rendle

Erect or straggling herb, to 2 m high; stems, petioles, and inflorescences puberulent, the trichomes dense, uncinate, glandular. Leaves trifoliolate; stipules striate, attenuate, to 1(1.4) cm long; petioles 1–2(5) cm long; leaflets lanceolate to ovate, obtuse to acute at apex, cuneate to obtuse at base, uncinate-puberulent and pilose on both surfaces, the terminal leaflet 3–6.5(11) cm long, 1.5–2.5(4.5) cm wide, the lateral leaflets somewhat smaller, the reticulate venation prominent. Racemes or panicles terminal or subterminal; pedicels 5–16 mm long, ascending; calyx 2–3 mm long, lobed to three-fourths of its length, the lobes linear, attenuate; corolla white or pink, fading light blue or mauve, 3–4 mm long; stamens didynamous, 4–5 mm long, the staminal column arched downward, the free stamen arched upward; style slender, to 2 mm long, exceeding the stamens, upon maturation of the fruit acquiring a contortion at the base and thus held ± persistently and obliquely on fruit. Fruiting rachis with nodes (6)10–30 mm apart; loments stipitate, lobed equally on each side; segments (2)3–6(7), each 3–4 mm long, 2.5–3.5 mm wide, uncinate-pubescent. *Standley 40950.*

Seen only once on the island, possibly no longer occurring there. A plant of weedy open areas. Apparently flowers and fruits all year.

Distinguished from other species by the prominently reticulate venation, the large persistent stipules, and the long, ascending pedicels.

Throughout American tropics and subtropics; introduced in most other tropical areas of the world. In Pan-

Fig. 282. *Dalbergia retusa*

Fig. 283. *Dioclea reflexa*

Fig. 284. *Dioclea wilsonii*

ama, known primarily from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Darién; known also from tropical dry forest in Panamá (Taboga Island) and from premontane moist forest in the Canal Zone (Balboa).

Desmodium triflorum (L.) DC., Prodr. 2:334. 1825
Pega-pega

Prostrate, rooting, often matting herb; stems slender, usually pilose, to 30 cm long. Leaves trifoliolate; stipules ovate, ca 2.5 mm long; petioles ca 4 mm long; leaflets broadly obovate, emarginate or truncate at apex, obtuse at base, glabrous above, moderately to densely sericeous below, the terminal leaflet 7–10 mm long, 6–10 mm wide, the lateral leaflets smaller. Flowers bright lavender, small, in axillary clusters of 1–3; pedicels 4–7 mm long; calyx deeply dentate, 4–5 mm long, pilose; corolla little longer than the calyx. Loments not stipitate, curved upward, entire along upper margin, undulate on lower margin, uncinate-puberulent, the trichomes retrorse, reticulate; segments 4–6, ca 3 mm long. *Hladik 89.*

Collected once in the Laboratory Clearing. Flowers and fruits probably only in the dry season (December to April).

Pantropical. In Panama, known from tropical moist forest in the Canal Zone (Atlantic slope), Bocas del Toro, and Colón and from tropical dry forest in Panamá (Taboga Island).

Desmodium wydlerianum Urban, Symb. Ant. 2:302. 1900

Prostrate or ascending perennial herb, rooting at nodes; stems uncinate-puberulent. Leaves trifoliolate; stipules to 7 mm long, caducous; petioles 3–6 cm long; leaflets ovate to ovate-deltoid, acute or gradually acuminate at apex, ± truncate at base, sparsely strigillose on both surfaces, thinly and palely pubescent below, the terminal leaflet 5–8 cm long, the lateral leaflets smaller. Racemes axillary, elongate; pedicels solitary, slender, ca 1.5 cm long; calyx ca 3.5 mm long; corolla blue or pink, ca 4.5 mm long. Loments briefly stipitate, downcurved, entire on upper margin, cleft from the lower margin, uncinate-pubescent; segments 2, each 8–10 mm long. *Croat 14958.*

Rare, in the forest along trails. Flowers at least in May and June.

Guatemala to northwestern South America. In Panama, known only from tropical moist forest on BCI and in Darién.

DIOCLEA Kunth

Dioclea guianensis Benth., Comm. Leg. Gen. 70. 1837
Haba de monte

Liana; stems short-pilose. Leaves trifoliolate; stipules subulate, to 1.5 cm long, subpersistent; petioles usually 3–5 cm long (to 12 cm on juvenile leaves), the pulvinus terete, basal; rachis usually ca 2 cm long (to 4.5 cm on juvenile leaves); stipels acicular, 5–15 mm long; petiolules 5–10 mm long, swollen; leaflets broadly elliptic, acuminate, rounded to somewhat cordate at base, 7–11 cm long, 4–7 cm wide, sparsely appressed-pilose all over or glabrate above except on midrib (young leaves sericeous above). Racemes long-stalked, to 50 cm long; rachises studded with tuberculate knobs on which the flowers develop; pedicels 2–4 mm long at anthesis, enlarging in fruit; calyx 10–12 mm long, lobed, the lobes 4, acuminate, spreading; standard, wings, and tip of keel violet; standard rounded, 16–20 mm wide, emarginate, reflexed, with a small yellow guide spot at base in center; wings ca 17 mm long, erect, joined to keel near base, the keel weakly fused apically; stamens and style curved upward near apex, equal in length, the free stamen and alternate stamens of the staminal tube somewhat shorter than the others; anthers and style fully exposed to a pollinator approaching the nectary from the base of the standard; pollen tacky, adhering to anther after dehiscing; nectary prominently raised. Legumes densely pubescent (less so at maturity), 7–10 cm long, ca 14 mm wide, the upper margin with sharp lateral ribs; segments 8–10. *Croat 4841.*

Infrequent, along the shore and in clearings, especially the Lighthouse Clearing. Probably more abundant in earlier years, since it grows in weedier areas in other parts of the Canal Zone. Flowers mostly throughout the dry season (December to April). The fruits mature mostly in

KEY TO THE SPECIES OF DIOCLEA

Stipules basifixed, lacking a produced lobe; fruits less than 1.5 cm wide; stamens with the anthers uniform, all fertile; plants of secondary areas, usually at the edges of clearings ..... *D. guianensis* Benth.

Stipules not appearing basifixed, with a produced basal lobe; fruits more than 1.5 cm wide; stamens with 5 fertile and 5 sterile anthers; plants usually in the canopy of the forest:

Legumes indehiscent, the lower edge (the narrowest edge not associated with the beak at the distal end) knifelike or at least not deeply sulcate along its length; inflorescence bracts and young fruits dark ferruginous-pubescent (at least on drying), the bracts linear, erect ..... *D. wilsonii* Standl.

Legumes dehiscent, the lower edge not knife-edged, deeply sulcate along its length; inflorescence bracts and young fruits yellowish-brown-pubescent, the bracts linear to linear-lanceolate, usually reflexed ..... *D. reflexa* Hook.f.

the late dry and early rainy seasons (March to May).

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

Dioclea reflexa Hook.f. in Hook., Nig. Fl. 306. 1849

Twining liana; stems to 5 cm diam; vegetative branchlets strigillose. Leaves trifoliolate; stipules subulate, to 2 cm long, with a produced basal lobe; petioles 4–7 cm long; leaflets elliptic-obovate, briefly acuminate, rounded-truncate at base, 6–14 cm long, 4–9 cm wide, glabrous above, sparsely strigillose below, thinly coriaceous, shiny. Racemes to 30 cm long, rufous-tomentose; pedicels at anthesis 5–7 mm long, enlarging in fruit; calyx densely pubescent, the trichomes appressed, brown, the subtending bracts linear to narrowly lanceolate, usually reflexed, the carinal tooth curved inward; standard violet to purple, to 1.5 cm long, recurved, rounded and emarginate, broader than long, the upper margin violet to orchid, lobed and clawed at base; stamens diadelphous, weakly connate to form a tube, the tube curved forward, the free stamen and 4 additional alternate stamens of the tube sterile, the 5 fertile stamens longer; style recurved near apex in bud, then straightening; stigma round, at height of sterile anthers, later at height of fertile anthers as the style lengthens. Legumes oblong, somewhat turgid, 12–18 cm long, 5–6 cm wide, at most only slightly concave along the upper margin, constricted somewhat in thickness between the seeds, sulcate along the lower margin, rufous-tomentose when young, the upper suture with a broad costa on either side; seeds 2 or 3, orbicular, ca 3 cm diam, dark brown. *Croat 5017, 8390.*

Occasional, along the shore and in the canopy of the forest. Flowers from September to April, mostly from December to March. The fruits are full size from January to May, but their time of maturity is not known, possibly in the rainy season.

The stigma is at first recurved near the apex in bud, at which time the five fertile anthers are undehisced. Before the petals open, the stigma straightens and is disposed among the sterile anthers below the fertile anthers, which then shed their pollen.

Pantropical. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Coclé, Panamá, and Darién.

See Fig. 283.

Dioclea wilsonii Standl., Publ. Field Columbian Mus., Bot. Ser. 4:310. 1929

D. violacea sensu auct. non Mart. ex Benth.

Liana; young branchlets and petioles long-pilose. Leaves trifoliolate; stipules with a produced basal lobe; petioles 4–9 cm long; leaflets elliptic, rounded or sometimes very abruptly acuminate at apex, rounded, truncate, or subcordate at base, 7–15 cm long, 4–13 cm wide, becoming glabrous above, strigillose below. Racemes to 45 cm long; inflorescences and bracts dark ferruginous-pubescent; rachises studded with tuberculate knobs on which the flowers develop; bracts linear, erect; pedicels 4–6 mm long at anthesis; flowers purple; calyx to 1.2 cm long; standard to 3 cm long, longer than wide; stamens with 5 anthers fertile, 5 sterile. Legumes completely indehiscent, 10–14 cm long, to 5.5 cm wide and 1–1.7 cm thick, purplish-pilose (dark ferruginous-pubescent when young), only slightly concave along the upper margin, not at all constricted between the seeds, obliquely sulcate, not sulcate along the lower margin; seeds plump, 3 or 4, ca 3 cm diam, brown with black mottling. *Croat 6726.*

Occasional, along the shore; probably less common than *D. reflexa.* Flowers mostly in the rainy season, especially in October. The fruits are nearly full size by November or December and seem to ripen by May.

Seeds of this species cannot easily be distinguished from those of *D. reflexa.* The species has been confused with *D. violacea* Mart. ex Benth., which R. Maxwell considers to be equal to *D. paraguariensis* Hassl. (pers. comm.).

Belize to Panama, the Guianas, and Brazil; Trinidad and Granada. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Panamá (Perlas Islands), and Darién.

See Fig. 284.

DIPTERYX Willd.

Dipteryx panamensis (Pitt.) Rec. & Mell, Timbers Trop. Am. 303. 1924

Oleiocarpon panamense (Pitt.) Dwyer

Almendro, Almendro corozo, Ebo, Tonka bean

Tree, to 40 m tall; trunk more than 1 m dbh, usually weakly buttressed; outer bark light brown, thick, hard, the surface granular and loose; inner bark tan (becoming brown in time), the cells isodiametric. Leaves alternate, paripinnate; stipules conspicuous, linear, to ca 15 cm long, 1 cm wide, caducous; petioles flat, canaliculate at base, 6–15 cm long; petiole and rachis revolute-winged; rachis 15–30 cm long, continuing past the terminal pair of leaflets into a conspicuous flange 2–7 cm long; petiolules pulvinate, 4–6 mm long, subtended by acute stipels ca 4 mm long; leaflets 10–16, alternate on rachis or opposite, elliptic to oblong, acute to retuse at apex, ± inequilaterally obtuse at base, 7–22 cm long, 2.5–7.5 cm wide. Panicles terminal, to 40 cm long; pedicels 3–5 mm long, expanded at apex; flowers conspicuous, red-violet, ca 2 cm long; calyx with 2 lobes, these much expanded, obliquely oblong, spreading laterally, to 1.7(2) cm long, the carinal and lateral teeth very reduced; calyx orchid-colored, sparsely punctate and puberulent; standard to 1.5 cm long and 1.3 cm wide, emarginate, green at base medially, surrounded by a dark band of red-violet, the claw short and strongly recurved; stamens to 1.4 cm long, subequal; filaments fused in basal two-thirds, directed upward near apex; style a little longer than stamens, directed sharply upward; ovary glabrous. Drupes borne on thick stipes ca 8 mm long, plump, oblong, ca 6 cm long and 3 cm wide, at first gray-green-pubescent, be-

coming brown-pubescent, at maturity filled with an oily, fragrant liquid, the liquid crystalizing when the fruit dries; seed 1, flattened, ca 5 cm long and 1.5 cm wide. *Croat 6084, Foster 1326, Hladik 441.*

Common to locally abundant in most areas of the forest. Flowers from May to August, generally in July. The fruits develop to mature size by the late rainy season, with most maturing from January to April. Leaves are deciduous during part of the dry season.

Recognized by the light granular bark.

Bees are very active visitors when the tree is in full flower. The fruits are taken by white-faced, spider, and howler monkeys as early as November (Hladik & Hladik, 1969). White-faced monkeys eat the fruits mostly from January to April (Oppenheimer, 1968), removing a part of the mesocarp surrounding the seed before discarding the remainder. Fruits are also taken by bats, rodents, and coatis (R. Foster, pers. comm.).

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién. The species is a characteristic tree in tropical moist forest in Panama (Holdridge & Budowski, 1956).

ERYTHRINA L.

Erythrina costaricensis Micheli var. **panamensis** (Standl.), comb. nov.

E. panamensis Standl., J. Wash. Acad. Sci. 17:10. 1927. Holotype: *Pittier 2656* (*US*)

Palo santo, Pito, Collins machete

Shrub or small tree, usually 3–7 m tall; trunk and branches armed with short, stout, corky prickles; branches few, stout. Leaves trifoliolate; stipules linear-lanceolate, ca 1 cm long, caducous; petioles 17–34 cm long, often with prickles; petiolules 6–12 mm long, articulate at base; leaflets broadly ovate, acuminate, rounded or truncate at base, thin, ± glabrous above, closely matted with long appressed trichomes below, the terminal leaflet to 28 cm long and 19 cm broad, the lateral leaflets somewhat smaller, inequilateral at base. Racemes congested at ends of leafless branches, soon falling; pedicels 2–3 mm long; flowers red; calyx bilobed, ca 2.5 cm long; standard to 9 cm long, ca 1 cm wide, conduplicate, shaped like the blade of a machete; other petals much reduced, shorter than calyx; stamens 10, 9 united more than halfway; anthers held at 5 levels in a 1-2-4-2-1 arrangement, the lowermost being on the free filament; style densely pubescent except near apex, at first shorter than most anthers, longer than anthers by the time the flower falls. Legumes reddish, densely pubescent, 15–25 cm long, long-pointed at apex, deeply constricted between seeds with the isthmus 2–20 mm long, splitting open and twisting slightly at maturity to expose seeds; seeds several, bright red, ca 8 mm long. *Croat 6560, 12710.*

Common in the forest, especially the old forest. Flowers appear before the leaves from September to December (especially in September and October), rarely later. The fruits mature mostly during November and December and have usually shed all their seeds by March. The leaves fall around September, growing out again during the early dry season.

The banner of the flower is weakly sealed along its outer margins. When the flower first opens, the style is held below all but the lowermost anther. At this time even the shorter anthers are shedding pollen. The stigmatic surface of the style is somewhat cupular and is filled with a jellylike plug that collects much pollen. The anthers continue shedding pollen until the style has grown beyond the longest stamen. At this time, when the flower falls, the stigma is flattened, without the jellylike substance. It has been presumed that hummingbirds pollinate the plant, but it is difficult to see how the plant prevents self-pollination—possibly the jellylike substance prevents self-pollination.

Although Krukoff (1939) originally distinguished both *E. costaricensis* and *E. panamensis* Standl., he has in recent years clumped them. Though admitting extreme variability in the taxa, I feel that many of the Panamanian materials of this species, including BCI plants, are at least subspecifically distinct. The BCI plants have larger, thinner leaves and fruits that are usually so constricted between the seeds that the seed-filled segments are broader than long and scarcely more than 1 cm apart. Flowers are bright red and appear while the plant is leafless; Costa Rican specimens are often reported as orange-flowered and flower when the plant has leaves. They also have smaller, thicker leaves and fruits that are not nearly so constricted between the seeds, so that the seed-filled segments are usually as long as to much longer than broad. Costa Rican plants are often reported to be large trees, whereas the BCI plants are never more than 7 m tall.

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

See Figs. 285 and 286.

KEY TO THE SPECIES OF ERYTHRINA

Plants small trees in the forest; corolla bright red, the standard narrowly tubular, more than 6 cm long, the other petals much reduced; legumes deeply constricted between seeds; trunk bearing small, conical spines ..... *E. costaricensis* Micheli var. *panamensis* (Standl.) Croat

Plants large trees on the shore; corolla pale orange, the standard reflexed, not tubular, ca 5 cm long; legumes only slightly constricted between seeds; trunk bearing broad corky spines ..... *E. fusca* Lour.

Fig. 286. *Erythrina costaricensis* var. *panamensis*

Fig. 285. *Erythrina costaricensis* var. *panamensis*

Fig. 287. *Erythrina fusca*

Erythrina fusca Lour., Fl. Cochinch. 427. 1790
E. glauca Willd.
Palo santo, Gallito, Bois immortelle, Palo bobo, Pito, Immortal

Tree, mostly 10–20 m tall; trunk ca 1 m dbh; outer bark grayish, coarse, sparsely covered with broad corky prickles; wood white to yellowish, moderately soft; branches glabrous, sparsely armed with short prickles; petiolar bases persistent, prominent; on juveniles, the prickles larger and extending onto petioles, rachises, and midribs. Leaves trifoliolate; stipules caducous; petioles 8–18 cm long; rachis 4–8 cm long; both petiole and rachis with 2 glands at their apices; leaflets ± ovate, ± rounded at both ends or acute at apex, glabrous above, with a dense mat of white appressed trichomes below, the terminal leaflet 8–14 cm long and 7–12 cm wide, the lateral leaflets smaller. Flowers thick, mostly 3 per node, in large, terminal, somewhat pendent racemes; pedicels stout, turned away from apex, ca 2 cm long; flowers showy, pale orange; calyx spathelike; standard spatulate, ca 5 cm long, reflexed; keel open at apex, ca 2.5 cm long, the wings somewhat shorter, greenish below, bright orange above; stamens diadelphous, green, gradually arched, about halfway exserted; filaments of 3 lengths in 5-4-1 arrangement, the free stamen one of the shorter 5; anthers held in an open pattern over the entrance to the nectaries through the open end of the keel; style bent sharply away from anthers just below apex; stigma usually between the shorter 2 sets of anthers in length; nectar copious. Legumes ca 19 cm long and 2 cm wide, densely brown-tomentose, pointed at apex, weakly ribbed on margins; seeds several, ellipsoid, dark brown, ca 12 mm long, possibly expelled forcibly. *Croat 8203.*

Rare, on the shore. Elsewhere in the Canal Zone common to locally abundant, generally near bodies of water. The leaves are deciduous shortly after flowering. Flowers from November to March, usually in February. The fruits mature from February to May, mostly in May.

The plant is probably hummingbird pollinated. The curare-like alkaloids erthraline, erythramine, and erythratine have been obtained from this species (Blohm, 1962).

Guatemala throughout the Amazon basin; West Indies; widespread in the Old World tropics. In Panama, known only from tropical moist forest in the Canal Zone, Bocas del Toro, Coclé, Panamá, and Darién. The species sometimes forms pure stands in freshwater marshes (Holdridge, 1970).

See Fig. 287.

INDIGOFERA L.

Indigofera mucronata Spreng. ex DC., Prodr. 2:227. 1825
Añil

Perennial herb, erect or usually decumbent, sometimes greatly elongate and ± scandent, most parts densely to sparsely strigose; stems slender, branched, angulate, to ca 1 m long or sometimes much longer. Leaves imparipinnate; stipules subulate, ca 3 mm long; petioles 1.5–2 cm long; rachis 1.5–4 cm long; leaflets 5–7, ovate to elliptic, ± rounded at both ends, apiculate at apex, 1.5–2.5(4) cm long, 0.8–1.5(2.5) cm wide, paler below. Racemes axillary, lax, often greatly elongate in fruit, to 20 cm long, mostly longer than the leaves; pedicels to 2 mm long, reflexed in fruit; bracteoles subulate, ca 1 mm long; calyx 2–3 mm long, weakly bilobed, deeply toothed, the teeth attenuate; corolla 5–6 mm long, shades of red; stamens diadelphous; style longer than stamens. Legumes linear, 2.5–3.5(4) cm long, ca 1.5 mm wide, with a persistent cusp at apex ca 2 mm long, reflexed; seeds 10–15, ca 2 mm long and 0.8 mm wide, dark brown or maroon. *Shattuck 562.*

Collected once on the island, but possibly no longer there. It could be expected, however, in the larger clearings and along the shore. Elsewhere the species may be found in flower throughout most of the year, but most flowering and fruiting occurs during the dry season (December to March).

Mexico to Argentina. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Herrera, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí and Panamá.

LONCHOCARPUS Kunth

Lonchocarpus pentaphyllus (Poir.) DC., Prodr. 2:259. 1825
Gallito

Tree, to 30 m tall; trunk to 50 cm dbh; outer bark roughened in age; inner bark granular, often with fine radial reddish lines, the outer margin wavy, the sap with a weakly pungent odor; stems minutely rufous-strigillose, becoming prominently lenticellate in age. Leaves alternate, imparipinnate, to 35 cm long; stipules inconspicuous, caducous; petioles 5–15 cm long; petiolules 5–7 mm

KEY TO THE SPECIES OF LONCHOCARPUS

Pedicels golden-sericeous; calyx drying golden-brown; veins on underside of leaflets not prominulous, the trichomes scarcely longer than height of veinlets; fruits glabrous to touch ..... *L. pentaphyllus* (Poir.) DC.

Pedicels white-villous; calyx drying blackish; veins on underside of leaflets prominulous, the trichomes usually several times longer than height of veinlets; fruits conspicuously pubescent to touch ..... *L. velutinus* Seem.

long; leaflets 5–9(13), ovate to ± elliptic-oblong or oblong-lanceolate, acute or abruptly acuminate at apex, rounded to obtuse at base, 6–14(24) cm long, mostly 4–7 cm wide, ± glabrous above, densely but minutely strigillose below, the trichomes short, appressed. Racemes mostly 8–14 cm long, solitary in axils or several on short, leafless, lateral branches; peduncles and all exposed parts of flower densely but minutely golden-pubescent; flowers usually purple, rarely tan or cream-colored, 7–9 mm long, often paired on short, secondary peduncles; calyx cupular, drying golden; standard somewhat spreading at anthesis, with a green center inside; wings and keel erect; stamens monadelphous, the tube straight, the anterior stamen free at base, the tube flared to either side providing an opening to the nectary; pistil pubescent; style curved sharply inward; stigma remote from anthers; nectar copious. Legumes flattened, elliptic, 5–8 cm long, 1.5–2.5 cm wide, acute to rounded at both ends, apiculate, glabrate, tan, the margin ca 1 mm wide; seeds 1 or 2, central. *Croat 4804, 5227.*

Occasional along the shore; rare in the forest. Flowers in March and April or later in the rainy season. The fruits mature mostly from May to October.

The stems are generally hollow and infested with ants.

Central and South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Colón, Veraguas, and Panamá and from tropical wet forest in Colón.

Lonchocarpus velutinus Benth. ex Seem., Bot. Voy. Herald 111. 1853

Gallote

Tree, to 18 m tall; trunk to 25(30) cm dbh; branchlets strigillose. Leaves alternate, imparipinnate, to 30 cm long; stipules inconspicuous, caducous; petioles 2.5–10 cm long; petiolules ca 6 mm long; leaflets 5–9, ± elliptic-obovate, mostly rounded-acuminate at apex, obtuse at base, 6–13 cm long, 3–7 cm wide, minutely puberulent appearing glabrous above, velutinous below, the trichomes not appressed, pilelike, the veins on the lower surface very conspicuous, anastomosing. Panicles of racemes axillary or terminal, 6–12 cm long; peduncles and all exposed parts of the flower densely pubescent, the trichomes short, appressed, whitish; flowers reddish-purple, ca 6 mm long, solitary or on secondary peduncles of 2 or 3 flowers; calyx flattened-cupular, drying black; petals conspicuously pubescent; standard somewhat spreading at anthesis; wings and keel erect. Legumes flattened, elliptic, at least 5–6 cm long, 1.5–2 cm wide, mostly rounded at apex, acute at base, apiculate, tan, the margins generally ca 1 mm wide, the pubescence dense, minute, golden, strigillose, soft to the touch and with a slight sheen; seed 1, central. *Croat 5121, 7772.*

Occasional, along the shore and in the forest. Flowers in February and March. The fruits mature from March through May. Most of the leaves fall around January, and the new leaves are immature or generally absent when flowering begins.

The stems are generally not hollow.

Central America to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Veraguas, and Panamá and from premontane moist forest in the Canal Zone.

See Fig. 288.

MACHAERIUM Pers.

The genus is easily distinguished by its stout, recurved, modified stipules, which carry the shrublike lianas into the canopy. The fruits are one-seeded samaras.

KEY TO THE SPECIES OF MACHAERIUM

Blades of leaflets rounded, obtuse, or rarely acute at apex, never acuminate, mostly less than 1 cm wide:
- Leaflets mostly more than 30, the blades mostly less than 12 mm long ..... *M. microphyllum* (E. Meyer) Standl.
- Leaflets usually fewer than 30, the blades mostly more than 15 mm long:
  - Plants rare; secondary veins conspicuously straight and parallel, usually 16–24 per cm; fruits ± glabrous in age ..... *M. riparium* Brandegee
  - Plants common; secondary veins not conspicuously straight and parallel, usually 8–12 per cm; fruits pubescent ..... *M. milleflorum* Pitt.

Blades of most leaflets acuminate, mostly more than 1 cm wide:
- Largest blades mostly less than 2.5 cm wide, often rufous-pilose on petiole and underside of midrib ..... *M. seemannii* Seem.
- Largest blades mostly more than 3 cm wide, glabrous or pubescent on petiole and underside of midrib but not rufous-pilose:
  - Leaflets 5–7; midrib glabrous, the stems lacking long, stiff setae .... *M. arboreum* (Jacq.) J. Vogel
  - Leaflets 9–17; midrib pubescent or the stems bearing conspicuous, stiff setae:
    - Leaflets 11–17, the underside glabrous, the major lateral veins scarcely more prominent than the reticulate veins; stems bearing conspicuous slender setae and thick, recurving, stipular spines; flowers to 1.5 cm long ..... *M. kegelii* Meisn.
    - Leaflets 9–11, the underside strigillose, the major lateral veins much more prominent than the reticulate veins; stems lacking slender setae but sometimes bearing thick stipular spines; flowers less than 10 mm long ..... *M. floribundum* Benth.

Machaerium arboreum (Jacq.) J. Vogel, Linnaea 11:182. 1837

Liana or erect to climbing shrub, to 8 m tall, glabrous except on inflorescences; spinescent stipules lacking. Leaves compound; rachis 4–14 cm long; petiolules 2–6 mm long, wrinkled; leaflets 5–7, alternate on rachis, ovate to elliptic, gradually to abruptly acuminate, often long-acuminate, usually obtuse to rounded at base, less frequently acute or slightly cordate at base, 2.5–11 cm long, 1.5–6 cm wide, drying dark brown, often arched along the midrib, the sides folded ± upward, the veins prominulous on lower surface; juvenile leaves much larger, more abruptly and conspicuously long-acuminate than adult leaves, to 17 cm long and 8 cm wide. Panicles 3–9 cm long, several per axil in upper axils, the branches densely ferruginous-tomentose; bracteoles broadly reniform, prominently striate, ciliate, glabrous to inconspicuously pubescent; flowers white, sessile; calyx ca 4.5 mm long, prominently striate, glabrate to inconspicuously pubescent, more so on the lobes, the lobes subequal, the lateral lobe ± deltoid, the carinal tooth much narrower; standard to 9 mm long and 13 mm wide; keel and wings only slightly shorter, the outer surface of all petals conspicuously and densely golden-brown sericeous. Fruits samaroid, 6–8 cm long, 1.5–2 cm wide, becoming glabrous in age, borne on narrow stipes ca 7 mm long, the upper margin thick, ± straight, the lower margin thin, curved; seminiferous area brown, the wing yellow-brown with prominent, dark, reticulate veins. *Croat 7951, Foster 1301.*

Frequent along the shore and in the canopy; juvenile plants have been found in the forest. Probably the most common *Machaerium* in the canopy. Flowers mostly in the late rainy season and the earliest part of the dry season, especially from October to December. The fruits are fully developed by February and are dispersed in the dry season. Leaves are replaced at the end of the dry season.

The species has been confused with *M. darienense* Pitt., which is now considered to be synonymous with *M. striatum* J. R. Johnston and does not occur on BCI.

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

Machaerium floribundum Benth., J. Proc. Linn. Soc., Bot. 4, Suppl. 68. 1860
M. woodworthii Standl.

Liana; branches with coarse, short, spinescent stipules; branchlets ± glabrous, bearing thick, spinescent stipules 5–10 mm long; outer bark smooth and flaking. Leaves compound; petiole and rachis usually inconspicuously pubescent; petiolules wrinkled, 2–6 mm long; leaflets 9–11, alternate or opposite on rachis, ovate, oblong, or obovate, obtuse to abruptly acuminate, obtuse to rounded at base, 3–10 cm long, 1.5–4.5 cm wide (juveniles to 19 cm long and 8.5 cm wide), glabrous on upper surface, minutely appressed-pubescent on lower surface, the major lateral veins 10–14, much more conspicuous than secondary veins and merging imperceptibly with the enlarged, discolored leaflet margin. Panicles axillary, 4–7 cm long, the branches densely golden-puberulent; bracteoles ca 1.3 mm long; flowers mostly sessile, white with a purple throat; calyx urceolate, 3–4 mm long, the lobes very short, obtuse; standard glabrous, ca 6.5 mm long, abruptly flexed near the middle; keel and wings to ca 5 mm long; stamens monadelphous, the filaments about half the length of the sheath; ovary pubescent, the trichomes dense, brown, appressed. Fruits unknown. *Croat 10093, 17033, Woodworth & Vestal 422* (type of *M. woodworthii* Standl.).

Infrequent, in the forest and along the shore. Seasonal behavior uncertain. Flowers at least in February. The fruits probably mature in the same dry season.

Mexico to Venezuela and Peru. In Panama, known only from tropical moist forest on BCI.

Machaerium kegelii Meisn., Linnaea 11:194. 1837
M. pachyphyllum Pitt.

Liana or arching and scandent tree, to ca 15 m tall; trunk to ca 12 cm diam, the upper part straight, rarely branched, usually arching or pendent from trees; old stems armed with recurved, spiny, woody stipules and conspicuous, stiff, long setae. Leaves compound, clustered near stem apex; stipules triangular, to 2 cm long and 1 cm wide, pubescent, paired, becoming woody in age; petioles to 8 cm long, the pulvinus conspicuous, terete, sparsely pubescent; petiolules stout, ca 5 mm long; leaflets 11–17, mostly oblong, long-acuminate, rounded to truncate or obtuse at base, 4–17 cm long, 2–6 cm wide, usually glabrous or reddish-villous on midrib below, coriaceous, the reticulate veins prominulous, about as conspicuous as the major lateral veins, the margins conspicuously enlarged and discolored. Panicles axillary or terminal, to 90 cm long, usually less than 50 cm long, on short, lateral, usually leafy branches on the terminal 3–4 m of the stem; rachises, peduncles, pedicels, and calyces bearing dense velvety-brown pubescence; flowers to 1.5 cm long; calyx subtended by 2 ovate bracts appressed to the anterior lobes, the carinal tooth acute, exceeding lateral lobes; standard spreading, rufous-pubescent outside, glabrous and lavender inside at least near apex, the center greenish, fringed with violet-purple; wings and keel usually white, weakly held together, the keel petals fused along their outer margin; free stamen united to the staminal tube, all stamens ± equal, the apical fourth free, strongly turned inward, the free part alternating with short erect appendages; style exceeding the anthers; pistil densely appressed-pilose. Samaras oblong, ca 8 cm long and 2 cm wide, distally winged; seminiferous area narrower, ca 2 cm long, rufous-villous, the trichomes interspersed with much stouter trichomes that have dark swollen bases. *Croat 5346, 13984.*

Occasional, in the forest and along the shore. Flowering infrequently, usually in the early dry season (February and March). Immature fruits have been seen in early April; fruits probably mature in April and May. Leaves are deciduous just before flowering.

Easily distinguished by its larger inflorescences and flowers and by the conspicuous setae on the stems. This

Fig. 288. *Lonchocarpus velutinus*

Fig. 290. *Machaerium kegelii*

Fig. 289. *Machaerium kegelii*

species was reported by Standley (1933) and by Johnston (1949) as *M. marginatum* Standl. Although the paratype of that species is referable to *M. kegelii,* the holotype of *M. marginatum* is referable to *M. microphyllum.*

The pollinator is apparently a strong bee, since the flower is strong and the keel is not easily moved.

Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone (both slopes) and Panamá (San José Island), from tropical dry forest in Coclé (Penonomé), and premontane moist forest in Panamá (Panamá City).

See Figs. 289 and 290.

Machaerium microphyllum (E. Meyer) Standl., J. Wash. Acad. Sci. 15:459. 1925

M. isadelphum (E. Meyer) Amsh.; *M. marginatum* Standl.

Slender liana (elsewhere sometimes a tree), armed at the nodes with pairs of stout recurved spines; outer bark usually smooth. Leaves compound, 8–15 cm long; stipules sharply triangular, becoming brown in age; rachis ferruginous-pubescent; leaflets 40–60, subsessile, oblong, rounded on both ends, 6–12(23) mm long, 2–6 mm wide, glabrous or pubescent, folding tightly under water stress. Panicles terminal, rarely axillary, 10–30 cm long with 1–3 short, densely rufous-pubescent racemes at each node, each raceme subtended by a recurved spine; flowers purple or light purple, usually less than 10 mm long; calyx maroon, 4–5 mm long, tubular, subtended by 2 rounded bracts; standard usually whitish outside, lavender inside, recurved, rounded and emarginate; wings and keel recurved, the keel petals fused only in apical third; ovary pubescent. Samaras borne on slender stipes, 5 cm long and 1 cm wide, strongly curved above the flat seminiferous area. *Croat 12704, 13969.*

Common on the shore and in the canopy of the forest. Flowers from October to January. The fruits mature from December to April.

The leafless stems can be recognized on the forest floor by the pairs of large, straight or slightly recurved spines, which are stout, sharp, and 1–2 cm long.

Panama to northern South America. In Panama, known from premontane dry forest in the Canal Zone and Panamá, from tropical dry forest in Herrera, and from tropical moist forest in the Canal Zone, Colón, San Blas, Chiriquí, Veraguas, Panamá, and Darién.

Machaerium milleflorum Pitt., Contr. U.S. Natl. Herb. 20:119. 1918

M. purpurascens Pitt.

Vine or liana in the canopy; trunk to 16 cm diam, unarmed but often with prominent horizontal ridges (old spine bases), the slash with a fairly strong foul odor, ultimately producing sparse red sap; small spiny branches extended over the forest floor for great distances, then climbing into the canopy by means of stipules, the stipules stout, paired, recurved, spinescent, to 6 mm long; at least the younger stems pubescent. Leaves compound, usually 3–19 cm long; petioles 1–2 cm long, densely golden-pilose marginally; leaflets 10–70, oblong, rounded to acute at apex, rounded at base, 0.7–2.5(4) cm long, (3)5–10(20) mm wide, bicolorous, ± glabrous or sparsely pubescent above, soft- and often appressed-pubescent at least on midrib below; juvenile leaves similar to adult leaves in shape but to 9.5 cm long and 3 cm wide, sparsely to densely pubescent. Panicles densely floriferous, 20–70 cm long, the branches densely ferruginous-tomentose; calyx violet-purple, ca 3.3 mm long, glabrous, the teeth mostly acute; corolla violet-purple; standard 4–5 mm long, densely appressed-pubescent outside, emarginate at apex, strongly reflexed at anthesis; wings shorter than standard, held erect, the keel petals fused in the distal half; stamens fused in 2 groups of 5 each, turned inward in apical third, slightly shorter than the style; style similarly bent. Samaras reddish, in dense purplish clusters, stipitate for ca 4 mm, 3.5–5.5 cm long, ca 1 cm wide, narrowed above the seminiferous area; seminiferous area ca 1 cm long, more densely golden-villous than the wing. *Croat 8371, 13813.*

Common along the shore, but probably flowering in the forest also since juvenile plants have been seen there. Flowering generally during February, rarely as late as March or April. Fruits are dispersed from March to May.

Johnston (1949) reported that the species has its active period of vegetative growth in the early dry season just before flowering.

Costa Rica to Colombia. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Colón, Panamá, and Darién; known also from tropical dry forest in Coclé and Panamá and from premontane moist forest in the Canal Zone and Panamá.

Machaerium riparium Brandegee, Univ. Calif. Publ. Bot. 6:500. 1919

Suberect shrub or usually a liana, to ca 12 m long; branchlets densely ferruginous to glabrate; stipular spines retrorsely curved, 5–7 mm long, the bases to 3 mm wide. Leaves compound, 10–20 cm long; petioles ca 1 cm long; leaflets in 10–15(20) pairs, ± oblong, rounded to rarely retuse at apex, mucronate, rounded at base, 1–4 cm long, 0.8–2 cm wide, strigose to glabrous, paler below than above, the secondary veins many, fine, parallel. Panicles terminal, densely flowered; bracts acute, to 6 mm long; pedicels ca 2 mm long; calyx cup-shaped, 3–4 mm long, puberulent on and near the shallow lobes, drying dark; corolla purple to pale violet, the standard 7–8 mm long; exposed parts of petals sericeous. Legumes stipitate for ca 3 mm, samaroid, 3.5–4.5(5.8) cm long and 0.8–1.4(1.8) cm wide, glabrous in age, rounded at apex; seminiferous area 1.6–2 cm long, the wing venation conspicuously reticulate. *Montgomery 128, Woodworth & Vestal 327.*

Apparently rare on the island; known from two collections. Seasonal behavior unknown.

The species is similar to *M. milleflorum,* but may be distinguished by the fine, parallel, secondary veins of the leaflets.

Mexico, Belize, and Panama. In Panama, known only from BCI.

Fig. 291. *Mucuna mutisiana*

Fig. 292. *Mucuna mutisiana,* fruits only (the leaves are of *Tetracera* sp., 88. Dilleniaceae)

Fig. 293. *Ormosia coccinea* var. *subsimplex*

Machaerium seemannii Benth. ex Seem., Bot. Voy. Herald 110. 1853

Liana or less often a climbing shrub, to 4 m or more long; mature branchlets glabrous, lacking spinescent stipules; younger plants with some branches leafless and with well-developed spinescent stipules. Leaves compound; rachis 5–9 (18) cm long; rachis, petiolule, and underside of blade sparsely ferruginous-pilose; petiolules 1–3 mm long; leaflets 6–13, oblong-lanceolate, ovate or narrowly elliptic, gradually acuminate and often falcate at apex, obtuse to rounded at base (rarely acute), 1.5–7.5 cm long, 0.7–2.7 cm wide, thinly coriaceous. Panicles 1–5 cm long, congested in the upper axils; branches densely ferruginous-tomentose; bracteoles reniform, densely appressed-pubescent; flowers purple, sessile; calyx 3–4 mm long, densely appressed-pubescent, the lobes inconspicuous; standard to 8 mm long; keel and wings only slightly shorter, the outer parts of all petals golden-brown-sericeous. Samaras borne on narrow stipes (to 7 mm long), 6–9.5 cm long, 1.8–2.5 cm wide, very densely golden-puberulent all over, the carinal margin conspicuously thickened to 1.5 mm thick, straight to curved. *Croat 6049, 7983.*

Frequent along the shore and in the forest to the top of the canopy; juvenile plants have been seen along trails. Flowering mostly during September and October but sometimes much later and in the early dry season. The fruits mature by January or February and are dispersed in the dry season (to April).

Guatemala to Colombia. In Panama, known principally from tropical moist forest in the Canal Zone (principally on the Pacific slope) and in Colón, Chiriquí (Puerto Armuelles), Panamá, and Darién; known also from premontane wet forest in Chiriquí (Boquete) and Coclé and from tropical wet forest in Colón (Salúd).

MUCUNA Adans.

Mucuna mutisiana (H.B.K.) DC., Prodr. 2:406. 1825
Ojo de venado

Large herbaceous vine, climbing to 15 m high in trees, somewhat twining. Leaves trifoliolate, usually drying black; stipules linear-lanceolate, to 5 mm long; petioles 4–9 cm long; petiolules dark, slightly pulvinate, articulate, subtended by stipels at base; leaflets ovate to elliptic, acuminate, oblique at base, 7–16 cm long, 4–7 cm wide, often drying dark, the veins at base 3 or 4. Inflorescences densely tomentose, in many, umbellate clusters of usually 3 flowers each at the end of pendent peduncles to 2 (5) m long, each umbel subtended by deciduous ovate bracts, their nodose bases persisting on the peduncle; pedicels spreading, to 5 cm long, curved down at apex, the flowers pendent; calyx cup-shaped, 11–13 mm long, dark-ferruginous, the trichomes numerous, slender, irritating, ca 2 mm long, the lobes inconspicuous except for the carinal tooth; petals inconspicuously colored, violet to flesh-colored; standard rounded, emarginate at apex, to 4 cm long; keel greenish, the wings ca 5 cm long and 1.5 cm wide, twisted, clawed and markedly auriculate at base; stamens 10, 9 fused into a tube except near apex, the free stamen and 4 alternate stamens of the staminal tube bearing shorter anthers, these anthers perpendicular to filament, cordate at base, attached medially, with one end bearing a conspicuous loose tuft of brown trichomes, the other anthers erect, glabrous; anthers shedding pollen in bud; style longer than anthers in bud, pushing through point of keel before keel is fully opened. Legumes oblong, to 13 cm long and 6 cm wide, constricted between seeds, densely covered with sharp, reddish-brown trichomes and numerous, narrow, transverse ridges to 1.5 cm high; seeds usually 1 or 2, round, flattened, 2.5–4 cm wide, dark brown, with a conspicuous flat scar three-fourths of the way around their circumference. *Croat 7426, 12611.*

Uncommon, hanging over the edge of the lake along the shore, perhaps also in the forest. More abundant in the Canal Zone along roads. Flowers from October to January, especially in November. The fruits mature from January to April, but seeds may hang on the pods until June. Plants have been seen putting on new leaves in August.

The nectary is functional prior to the opening of the flower. Bats, as pollinators (R. Foster, pers. comm.), probably gain entrance by pushing the banner back and forcing open the auricles of the wings. The wing petals are fused to the keel petals at the base and consequently are pulled apart from the base to the apex. The style and staminal tube then spring forward and strike the pollinator's abdomen.

Specimens of this species (*Wetmore & Abbe 53* and *Shattuck 53*) were misidentified as *M. bracteata* Dwyer, which may not be a distinct species. *M mutisiana* has also been confused with *M. urens* (L.) Medic., which also may not be specifically distinct.

Panama to Venezuela. In Panama, known principally from tropical moist forest in the Canal Zone, San Blas, Panamá (San José Island), and Darién; known also from premontane moist forest in the Canal Zone.

See Figs. 291 and 292.

Mucuna rostrata Benth. in Mart., Fl. Brasil. 15 (1):171, pl. 47. 1859
Pica-pica

Liana; branchlets glabrous, drying dark. Leaves trifoliolate; petioles 5–10 cm long, pulvinate about 1 cm at base;

KEY TO THE SPECIES OF MUCUNA

Flowers flesh-colored, less than 5 cm long; peduncles to 2 m or more long; legumes with conspicuous, raised, transverse lamellae ..... *M. mutisiana* (H.B.K.) DC.
Flowers yellowish, usually more than 5 cm long; peduncles less than 1 m long; legumes lacking ridges ..... *M. rostrata* Benth.

leaflets rhombic-ovate, abruptly acuminate, broadly rounded at base, 10–14 cm long, 6–9 cm wide, the veins at base 3–5, sparsely strigose below. Racemes pendent; peduncles 8–18 cm long; flowers yellow; calyx 5-lobed ca half its length, 2–2.5 cm long, densely pubescent, often also with many, appressed, slender, irritating trichomes; corolla 6–8(9) cm long; standard orbicular, 4–5 cm long, coriaceous, glabrous, the claw 5–7 mm long; wings 7–8(9) cm long, ca 16 mm wide, basally auriculate, the keel as long as the wings; stamens diadelphous. Legumes oblong, at least 7 cm long and 2–3.5 cm wide, curved, beaked, bearing erect stinging trichomes, lacking ridges or crests; seeds several, orbicular, ca 2–5 cm diam, somewhat compressed, black. *Shattuck 489.*

Collected once by Shattuck, but not seen in recent years and possibly no longer present on the island. Flowers in the early dry season, usually in December but as late as March. The fruits probably mature late in the dry season.

Belize to the Amazon basin. In Panama, known only from tropical moist forest on BCI and in Darién.

MYROXYLON L.f.

Myroxylon balsamum (L.) Harms var. **pereirae** (Royle) Harms, Notizbl. Königl. Bot. Gart. Berlin 5:95. 1908

Balsam, Balsam of Peru

Tree, to 35(40) m tall and ca 1 m dbh; trunk straight; branches ascending; outer bark smooth, bearing abundant lenticels; heartwood reddish-brown; sapwood pale, the freshly cut bark emitting a pungent, obnoxious odor. Leaves alternate, generally imparipinnate, fragrant when crushed; petioles 1–4 cm long; rachis and petiolules pubescent, terete; rachis 5–15 cm long; leaflets 5–10, alternate on rachis, lanceolate to elliptic, acute to acuminate, obtuse at base, 3–11 cm long, 1.8–4 cm wide. Racemes axillary, to 20 cm long, closely cinereous-tomentose; pedicels 1–1.5 cm long; flowers oblique on pedicel; calyx campanulate, 3.5–4.5(6) mm long, with obvious, fine ribs, the lobes ca 1.5 mm long; standard orbicular, ca 9 mm diam, cordate basally, the claw ca 1 mm long; wings elliptic to narrowly spatulate, ca 1 cm long, ca 4 mm wide, their claws 2 mm long, the keel subelliptic, ca 8.5 mm long and 3 mm wide, its claw ca 1.5 mm long; ovary sparsely villous, borne on stipe 2 mm long; style subulate. Samaras narrowly obovate, to 11 cm long, glabrous, on stipes to 1 cm long; wing to 8 cm long, 1–2 cm wide, the seminiferous area turgid, at the apex of the fruit, obliquely oblong, 2–3 cm wide, ca 1 cm thick, extending as a low, longitudinal ridge into the pedicel; appearance of fruit much like that of *Platypodium elegans. Ebinger 215.*

Apparently rare; collected once on the island. Flowers from January to June. Fruits from September to March.

Southern Mexico to the Amazon basin of Brazil and Peru; planted as a street tree in Ceylon and in tropical botanical gardens. In Panama, known only from tropical moist forest in the Canal Zone, Panamá, and Darién. Characteristic of tropical moist forest in Panama (Tosi, 1971). Holdridge (1970) reported it for low and medium elevations in moist and wet areas with a dry season.

ORMOSIA G. Jackson

Ormosia coccinea (Aubl.) G. Jackson var. **subsimplex** (Spruce ex Benth.) Rudd, Contr. U.S. Natl. Herb. 32:328–29. 1955

Alcornoque, Pernillo de monte

Tree, to at least 25 m; trunk commonly 60(100) cm dbh; outer bark thin, hard, with a ± reticulate pattern of very shallow fissures, flaking easily; inner bark granular, its outer surface reddish with large whitish spots; stems weakly flexuous, with ribs extending downward below each petiole; stems, petioles, and midribs densely pubescent, the trichomes matted, short, brown. Leaves alternate, imparipinnate, 25–40 cm long; petioles 6–10 cm long, the basal pulvinus prominent; petiolules ca 6 mm long; leaflets usually 9, oblong, abruptly acuminate and downturned at apex, obtuse to slightly cordate at base, 7–18 cm long, 4–7.5 cm wide, coriaceous, glabrous above, sparsely appressed-pubescent and somewhat viscid below, more densely so on veins, the margins turned somewhat upward and wavy in age; secondary veins in 10–16 pairs, prominently raised on lower surface. Inflorescences cymose-paniculate, terminal, to 30 cm long; flowers purple; calyx tomentulose, 7–9 mm long, 5-lobed to half its length; corolla 1–1.5 cm long, rose-purple. Legumes flattened, oblong to obovate, 3.5–5 cm long, 2–2.5 cm wide, glabrous, abruptly narrowed at apex, the valves reddish-brown at maturity, opening to expose seeds; seed 1 (rarely 2), red and black, somewhat flattened, ca 1 cm long. *Croat 5120.*

Occasional, in the forest and along the shore. Flowers from June to August. The fruits probably mature in 4–6

KEY TO THE SPECIES OF ORMOSIA

Underside of leaflet midribs conspicuously brown-tomentose; leaf bases rounded to slightly cordate; seeds bicolorous, red and black; pods obliquely obovate to elliptic, lacking an alate margin ..... *O. coccinea* (Aubl.) G. Jackson var. *subsimplex* (Benth.) Rudd

Underside of leaflet midribs glabrous or essentially so, yellow-green:

Leaflets acuminate, very inconspicuously golden-pubescent below; mature legumes suborbicular, light brown, ± winged along margins ..... *O. panamensis* Seem.

Leaflets very abruptly acuminate to rounded at apex, glabrous on both surfaces; mature legumes much longer than wide, dark, with a thick marginal suture and a submarginal ridge ..... *O. macrocalyx* Ducke

weeks, but may persist with the colorful seeds exposed until about flowering time of the next year. Plants are deciduous before flowering.

Panama to Brazil. In Panama, known only from tropical moist forest on BCI.

See Fig. 293.

Ormosia macrocalyx Ducke, Arch. Jard. Bot. Rio de Janeiro 3:137. 1922

Tree, to 30(40) m tall, ca 50 cm dbh; outer bark planar, ca 1 cm thick, minutely fissured, the intervening areas with thin, smooth, brown strips; inner bark granular, tan; branchlets minutely strigillose. Leaves alternate, imparipinnate, 15–40 cm long; petioles 4.5–9 cm long, conspicuously swollen at base, glabrous to minutely pubescent; petiolules pulvinate, 5–8 mm long; leaflets usually 9, elliptic-oblong to ovate or obovate, abruptly acuminate to rounded at apex, acute at base, 5.5–15 cm long, 3.5–10 cm wide, ± glabrous; secondary veins in 4 or 5 pairs. Inflorescences terminal, paniculate, to 30 cm long; flowers purplish; calyx 8–15 mm long, grayish-pubescent, 5-lobed; petals ca 2 cm long; standard minutely biappendiculate at base. Legumes ± circular to oblong, flattened, to ca 10 cm long and ca 3 cm wide, the lateral margins straight or weakly constricted between the seeds, the free margin with a submarginal ridge, the surface glabrous, dull, depressed between seeds; seeds 1–4, solid red, ± ovoid, ca 1 cm long. *Croat 13217.*

Apparently rare; known only from the old forest south of Armour Trail above the escarpment and from near the tower at Barbour Trail 700. Probably flowers in the middle of the rainy season. The fruits persist most of the year.

Southern Mexico to Brazil; at elevations under 100 m. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Veraguas and from premontane wet forest in Chiriquí (Progreso).

Ormosia panamensis Benth. ex Seem., Bot. Voy. Herald 111. 1853

Alcornoque, Sur espino

Tree, to 8(30) m tall; young stems golden-sericeous. Leaves alternate, compound, 9–17 cm long; petioles 5–8 cm long, pulvinate at base; petiolules pulvinate, ca 5 mm long, golden-sericeous; leaflets 5–9, oblong-lanceolate, gradually long-acuminate at apex, obtuse at base, 10–14 cm long, 3–4.5 cm wide, inconspicuously golden-puberulent below, the secondary veins in 10–16 pairs, ± straight, 5–20 mm apart. Flowers lilac; calyx densely fulvous-sericeous, 8–11 mm long, 5-lobed; corolla nearly 2 cm long. Legumes suborbicular when mature, flattened, ca 4 cm diam, not constricted between seeds, the valves thick with an alate margin 5–15 mm wide; seeds 1–4, separated by septa, ca 1.5 cm long, dark red. *Foster 1128.*

Collected only once along the shore of a cove by Peña Blanca Point; seen also south of Armour Trail 1200 by R. Foster. Seasonal behavior uncertain. Some flowers have been seen from March to June, with the fruits maturing from August to December. Trees have been seen in July with both full-sized fruits and very juvenile fruits, indicating that individuals may flower more than once per year.

Guatemala, Costa Rica, and Panama. In Panama, known from tropical moist forest on BCI and in Bocas del Toro and Chiriquí and from Cerro Pajita in Coclé, which is possibly tropical wet forest.

PHASEOLUS L.

Phaseolus peduncularis H.B.K., Nov. Gen . & Sp. 6:447. 1824

Slender, herbaceous vine; stems twining or prostrate, and puberulent, pilose, or glabrate. Leaves trifoliolate; stipules lanceolate, to 6 mm long; petioles 2–7 cm long; rachis 5–10 mm long; leaflets ovate-deltoid, acuminate or acute, truncate at base, thin, sparsely strigillose, the terminal leaflet 2.5–8.5 cm long, 2–6 cm wide, the lateral leaflets smaller, the basal veins 3. Inflorescences fasciculate-racemose, often erowded at apex of peduncle; peduncles equaling or surpassing leaves; rachises 2–5 cm long; pedicels to 2 mm long; flowers pale violet, green in bud; bracteoles shorter than calyx; calyx ca 3 mm long, closely subtended by acute bracts to one-third the length of the calyx; petals white to pale blue on outer margins; standard 1–1.5 cm long, about as broad as long; keel ciliate, closely enveloping style and stamens, turning sideways after anthesis and spreading the outer margins of the standard apart; stamens diadelphous; filaments slender, free in apical half; style bearing sharp erect trichomes near apex. Legumes 4–5 cm long, to 3 mm wide, acuminate at apex, strigose, with a minute marginal rib on both sides of each valve, the valves twisting at maturity; seeds subcylindrical, greenish-white with purple mottling, to 3 mm long, leaning out from the dehisced valves. *Croat 5256, 7032.*

Common in clearings, usually growing among other weedy plants. Flowering and fruiting year-round with a peak of flowering during the middle of the rainy season (August to October). The fruits develop quickly.

Normal movements of the flower parts do not appear to force much pollen from the open end of the carinal tube.

Guatemala to northern South America; West Indies.

KEY TO THE SPECIES OF PHASEOLUS

Stipules with prominent basal lobe; bracteoles longer than calyx; petals yellow; legumes 6–7 mm wide, pilose ..... *P. trichocarpus* C. Wright

Stipules lacking basal lobe; bracteoles shorter than calyx; petals white or pale lavender; legumes ca 3 mm wide, strigose ..... *P. peduncularis* H.B.K.

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

Phaseolus trichocarpus C. Wright in Sauv., Anales Acad. Ci. Méd. Habana 5:337. 1868

Slender, twining, herbaceous vine; younger stems orange-pilose, the trichomes often retrorse. Leaves trifoliolate; stipules persistent, lanceolate, to 9 mm long, appendaged at base, the appendage to 4 mm long, usually oblong and blunt, sometimes divided and narrowly acute; petioles 2–5 cm long, orange-pilose; rachis 5–10 mm long; leaflets oblong-lanceolate, acute at apex, rounded-truncate at base, 3.5–12 cm long, 0.8–3 cm wide, ciliate, essentially glabrous above but the veins strigose, strigose below. Racemes bearing 1–3 pairs of opposite pedicels per inflorescence, each raceme subtended by a peduncle 8–14 cm long; pedicels becoming spiraled, to 5 mm long; base of the flowering rachis (just above the lowermost pair of flowers) with conspicuous glandular area to 3 mm long; flowers few, subtended by 2 narrow bracts to 5 mm long, these longer than calyx; calyx ca 2.5 mm long, lobed, the lobes 5, shallow, subequal; corolla yellow, to 1 cm long and wide; standard cordate, strongly cucullate, 6 mm long and 10 mm wide; wings broadly obovate, 7 mm long and 6 mm wide, the keel spiraled; stamens diadelphous; anthers 3.2 mm long, 1.5 mm wide, wider at base; ovary pubescent; style 8 mm long; stigma recurved, ca 7.5 mm long, pubescent along one edge. Legumes oblong, 2.8–3.2 cm long, 6–7 mm wide, only slightly inflated, short-beaked, turning black at maturity, long-yellow-pilose; seeds 7–9, ovoid, to 3 mm long and 2 mm wide, black with a prominent white hilum. *Croat 5717, 8250.*

Known from the shoreline on the south and west sides of the island. Probably flowers and fruits throughout the year, chiefly from May to December. The fruits apparently develop quickly.

This species has been mistaken for *Vigna unguiculata* (L.) Walp., which also has appendaged stipules. The *Vigna* is distinguished by having leaves at most lanceolate, not oblong, and pods 10 cm or more long, not pilose, with lighter seeds and a dark hilum.

Aviles 909, identified by Standley as *Vigna repens* (L.) O. Kuntze (= *V. luteola* (Jacq.) Benth.), is an aberrant specimen of this species. It differs only in having the produced part of the stipule bilobed and acute.

Panama to the Guianas; Greater Antilles. In Panama, known only from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién.

PLATYMISCIUM J. Vogel

Platymiscium pinnatum (Jacq.) Dug., Contr. Hist. Nat. Colomb. 1:11. 1938

P. polystachyum Benth. ex Seem.

Quirá, Swamp kaway, Sangrillo, Panama redwood

Tree, to 30 m tall and 40 cm dbh; outer bark light brown, fissured, ± flaky, soft, ringed (like *Tabebuia guayacan,* 25. Bignoniaceae); wood reddish-brown, hard. Leaves opposite, imparipinnate; stipules interpetiolar, lanceolate, to 1.2 cm long, deciduous, leaving distinct scars; leaflets in 4–7 pairs, opposite on the rachis, ovate to elliptic, acuminate, obtuse to rounded at base, 5–11(22) cm long, 2.5–4.5(15) cm wide, glabrous, entire and sometimes undulate. Racemes or panicles 9–17 cm long, terminal, subtending new leaves or in lower leafless axils; pedicels 3–6 mm long, glabrous; bracteoles ovate; flowers 1–1.5 cm long, often paired at nodes, yellow-orange tinged with purplish-brown toward center, especially on standard; calyx narrowly campanulate, glabrous to warty-puberulent, with short, acute teeth, the lateral and carinal teeth somewhat shorter than the vexillar teeth; standard orbicular, emarginate at apex; keel petals fused at apex and on outer edge, ciliate below point of fusion; stamens ca 1 cm long, in 2 fascicles of 5 each, loosely fused to form an open tube; anthers reniform, about as broad as long; ovary and style glabrous, the style bent sharply inward, much longer than anthers. Fruits samaroid, oblong-elliptic, obtuse to rounded at apex, acute at base, flat, 5–11 cm long, to 3.5 cm wide, thin, on stipes ca 1 cm long, the winged portion of same thickness throughout; seminiferous area medial, to 3.5 cm long, 1 cm wide; seed 1. *Croat 5218, 5652, Standley 40945.*

Occasional, in the forest. Leaves fall shortly before the flowers appear, and new leaves are produced with the flowers from March to May (rarely earlier). The species may flower only every other year. The fruits are dispersed one year later in the dry season (R. Foster, pers. comm.).

From a distance the flowers and new leaves appear somewhat brown.

Guatemala to Panama on the Pacific slope and along the Atlantic slope from Colombia to Trinidad. In Panama, known from tropical moist forest on both slopes in the Canal Zone and on the Pacific slope in Chiriquí and from the Azuero Peninsula to Darién. Characteristic in Panama of tropical dry forest (Holdridge & Budowski, 1956) and tropical moist forest (Tosi, 1971). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

PLATYPODIUM J. Vogel

Platypodium elegans J. Vogel, Linnaea 11:420. 1837

P. maxonianum Pitt.

Carcuera, Costilla, Tigre, Canalua

Tree, to 30 m or more, usually 75–100 cm dbh; trunk with conspicuous, deep, irregular, longitudinal invaginations in age; bark soft, minutely fissured, the sap becoming reddish-brown in time, with a foul odor at least in younger parts. Leaves alternate, imparipinnate, to 25 cm long; petiole, rachis, petiolule, and underside of blade puberulent; leaflets 10–20, oblong, rounded to emarginate at apex, obtuse to rounded at base, 2.5–7.5 cm long, 1–3 cm wide, glabrous above. Inflorescences lax racemes from upper axils; pedicels 8–12 mm long, bracteate near apex; bracts oblong, ca 2 mm long, persistent; calyx ca 4 mm long, turbinate, sparsely appressed-pubescent, the carinal tooth acute, equaling lateral teeth, the vexillar teeth ±

united; corolla yellow-orange; petals clawed; standard reniform, ca 1.8 cm long; keel petals fused only near apex; stamens ca 1 cm long, 2 stamens free, the others in clusters of 4 each; stigma about as long as anthers. Samaras obliquely oblong, to 13 cm long and 3 cm wide, on stipes ca 2 cm long; seminiferous area distal. *Croat 5411.*

Common. Flowers synchronously every two years from April to June (sometimes as early as March), apparently initiated by the beginning of the rainy season. The fruits may be full size by June but mature over a long period, ripening by December or January. Leaves are replaced in the dry season before the time of flowering. A few individuals are out of phase (R. Foster, pers. comm.).

Panama to Venezuela, and in southeastern Brazil and Paraguay. In Panama, known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién.

PTEROCARPUS Jacq.

Pterocarpus officinalis Jacq., Select. Stirp. Am. 283, f. 92. 1763

Bloodwood, Dragon blood tree, Sangre de drago, Chuella, Suela

Tree, to 20(30) m tall; trunk to 30(90) cm dbh, often widely buttressed; wood yellow or whitish, the sap copious, red; trichomes on younger parts and inflorescence axes minute, appressed-ferruginous, otherwise glabrous. Leaves alternate; petioles 2.5–11 cm long; petiolules 4–6 mm long; leaflets 5–9, oblong to ovate-oblong, acuminate, rounded to truncate at base, 3.5–17 cm long, 2.5–7.5 cm wide, the terminal leaflet largest. Panicles terminal or upper-axillary, to ca 25 cm long; calyces and pedicels reddish-brown; pedicels to 4 mm long; calyx ca 6 mm long, markedly toothed, glabrous except on the upper margin; standard obovate, ca 1 cm long, rounded at apex, yellow-orange, with a red, inverted V-shaped area in the middle, the lateral margins folding back along these lines; wings shorter than the standard, exceeding keel, the keel petals weakly connate on outer upper margins; stamens weakly connate, often free above the middle; ovary glabrous or bearing a few trichomes on one edge. Fruits indehiscent, stipitate for ca 3 mm, suborbicular, ± flattened; wing asymmetrical, not quite oblong on 1-seeded fruits, to ca 5 cm long on 2-seeded ones, dark brown or black when mature, glabrous; seminiferous area ca 1 cm thick, the margins thick and hard, distinctly veined, corky; seeds 1 or 2, to ca 3 cm long. *Knight 1043.*

Rare. Flowers in central Panama from April to October, but mostly in June and July. The fruits mature from August to October (sometimes to December). Leaves fall in the early dry season.

Although the Knight collection cited here is sterile, it is almost certainly this species. Knight reported it as common, but most of the specimens he had were *P. rohrii. Bangham 502,* reported as this species in the *Flora of Panama,* is really *P. rohrii* also. R. Foster (pers. comm.) has seen fruits of *P. officinalis* along the shore. The description given here is based on material from nearby areas of the Canal Zone.

On the Atlantic slope from Belize to the mouth of the Amazon and on the Pacific slope from Panama to Ecuador; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Colón. Typical of tropical moist forest in Panama (Tosi, 1971) and occasionally forming pure stands next to mangroves (Holdridge & Budowski, 1956).

Pterocarpus rohrii Vahl, Symb. Bot. 2:79. 1791

P. hayesii Hemsl.

Bloodwood, Sangre de gallo

Tree, to 50 m tall; trunk 30–100 cm dbh, buttressed; outer bark whitish, thin, often loose; inner bark moderately thick, with numerous red streaks exuding minute sap droplets, the streaks forming concentric rings especially near wood, the sap copious, red; branchlets glabrous to densely pubescent. Leaves alternate; stipules caducous, linear to ± falcate, 3–10 mm long; petioles 2.5–4.5 cm long, pulvinate at base; rachis glabrous to densely ferruginous-pubescent, 3–12(20) cm long; petiolules 3–6(9) mm long; leaflets (3)5–9(12), ovate to elliptic, bluntly acuminate, acute to rounded or rarely slightly cordate at base, 3.5–10(13) cm long, 2–4(5.5) cm wide, glabrous above, usually with short, appressed pubescence below, the midrib sometimes arched with the sides folded somewhat upward. Racemes usually axillary, to 12 cm long, shorter than leaves; calyces and pedicels densely pubescent, the trichomes short, golden-brown, appressed; pedicels 5–7(10) mm long; flowers pinkish-orange, ca 1.5 cm long; calyx to 7(11) mm long, oblique, narrowly campanulate, the teeth blunt, 1–2 mm long, the vexillar teeth larger; standard ca 1.5 cm long, emarginate, violet-purple at the center, clawed, the claw ca 4.5 mm long; keel and wings slightly shorter than standard, both marked with violet-purple, the keel petals weakly connate on their outer edge; stamens diadelphous, those of the tube weakly connate; pollen golden; ovary appressed-pilose, uniformly oblong; style longer than stamens. Fruits round to oval,

KEY TO THE SPECIES OF PTEROCARPUS

Inflorescences paniculate, branched many times; fruits stipitate, much thickened medially, the wing narrow; underside of leaves glabrous at least in age; leaves and branchlets usually drying blackened ..... *P. officinalis* Jacq.

Inflorescences racemose or, rarely, branched only at base; fruits ± sessile, scarcely thickened medially, the wing broad; underside of leaves bearing sparse, ± appressed, short, inconspicuous, brownish trichomes; leaves and branchlets drying green ..... *P. rohrii* Vahl

flat and thin, mostly 5.5–7 cm long and 5–6 cm wide, usually unequal at the base, minutely pubescent, yellowish- to rusty-brown, indehiscent; seminiferous area central, ca 3 cm long, slightly raised, the margins very thin, reticulate, often minutely wrinkled; seed 1. *Croat 14866, 16623, 16627.*

Frequent in the forest, possibly less abundant on the western side of the island. Flowers every other year (R. Foster, pers. comm), usually in May and June, less frequently earlier in the dry season. The fruits mature from August to November.

Southern Mexico to the upper reaches of the Amazon, as far south as Bolivia, and in the lowlands along the Atlantic as far south as southern Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién.

RHYNCHOSIA Lour.

Rhynchosia pyramidalis (Lam.) Urban, Feddes Repert. 15:318. 1918

R. phaseoloides DC.

Liana; older stems flattened and several cm broad, the larger with 3 ribs below each petiole, the lateral ribs becoming prominent and corky in age, the smaller stems puberulent; most vegetative parts bearing raised, orange glands. Leaves trifoliolate, to 15 cm long; petioles 2.5–5 cm long, swollen at base, hispidulous; rachis with a raised margin above; leaflets ovate to rhombic-ovate, acuminate at apex, obtuse to rounded at base, mostly 4–16 cm long, 3.5–11.5 cm wide, glabrous to sparsely pubescent especially on veins below, the lateral leaflets inequilateral, the veins at base palmate. Racemes apical, to ca 15 cm long; flowers dense, yellowish-green, short-pedicellate; calyx to 2 mm long, puberulent and glandular-dotted; standard obovate, clawed, ca 6 mm long, purple-striate, puberulent and glandular-dotted outside; wings narrow, puberulent outside near apex, fused to keel near base, the keel petals fused in apical half, weakly enclosing stamens; stamens diadelphous; style bearing antrorse trichomes near apex; stigma borne among the anthers. Legumes ca 1.5 cm long and 1 cm wide, constricted between the seeds, puberulent; seeds 2, black and red. *Croat 13817.*

Occasional, in all parts of the forest; possibly extending into the canopy. Though some flowers have been seen along the edge of the lake, they are rarely seen in the forest. Flowers from January to March. The fruits develop soon, but seeds may persist throughout the rainy season.

Baja California, Sonora, and southern Mexico south to Peru, and the Guianas to eastern Brazil and Argentina; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Coclé, and Darién.

TERAMNUS P. Browne

Teramnus uncinatus (L.) Sw., Prodr. Veg. Ind. Occ. 105. 1788

Glycine uncinata (L.) J. F. Macbr.

Vine; most parts sericeous. Leaves trifoliolate; stipules ovate, ca 3 mm long; petioles 3–6 cm long; petiolules pulvinate, articulate; leaflets ovate to oblong-lanceolate, 5–8 cm long, acute to obtuse at apex, rounded or slightly subcordate at base, green and densely strigose above, pale and densely sericeous below. Racemes axillary, slender, bearing few flowers; calyx pilose, 5–6 mm long, the 5 lobes narrow; corolla purplish or whitish, only slightly exceeding the calyx. Legumes flattened, 4–7 cm long, 3–4 mm wide, densely long-villous, beaked; seeds numerous, oblong, ca 3 mm long, shiny, brown. *Croat 13151.*

Collected at the edge of the forest, in shade near the Animal House in the Laboratory Clearing. Flowers and fruits in the early dry season, from December to February.

Southern Mexico to South America; West Indies; introduced into tropical Africa. In Panama, known from tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién, from premontane wet forest in Chiriquí, and from premontane rain forest in Los Santos.

Teramnus volubilis Sw., Prodr. Veg. Ind. Occ. 105. 1788

Slender twining vine; stems pubescent to glabrate. Leaves trifoliolate; stipules ovate, ca 2 mm long; petioles 2–4 cm long; petiolules minutely pulvinate; leaflets lanceolate to oblong-elliptic, narrowly rounded at apex, rounded at base, glabrous above, sparsely strigose below, the terminal leaflet 2–6 cm long, 1.5–2 cm wide, the lateral leaflets smaller. Flowers solitary to few, axillary or racemose; calyx 3.5–4 mm long, 4-lobed by fusion of the 2 upper lobes; corolla ca 5 mm long; standard ± spatulate, emarginate and recurved near apex at anthesis, white or tinged with violet; wings pale violet, held erect, attached to keel near apex, the keel white, much shorter than wings, fused only near apex; stamens monadelphous, alternate; anthers small. Legumes 2–3(7) cm long, ca 2 mm wide, somewhat flattened, with an obliquely descending beak, appressed-pubescent; seeds oblong, ca 2 mm long, olive-green. *Croat 13222.*

Apparently rare; collected once in the Laboratory

KEY TO THE SPECIES OF TERAMNUS

Leaflets densely sericeous below; calyx 5-lobed, about as long as corolla; fruits densely long-villous ..... *T. uncinatus* (L.) Sw.

Leaflets sparsely strigose below; calyx 4-lobed, much shorter than corolla; fruits appressed-pubescent ..... *T. volubilis* Sw.

Clearing. Apparently flowers and fruits mostly in the dry season.

Costa Rica to northern South America; Trinidad and Jamaica. In Panama, known only from tropical moist forest on BCI and in Darién.

VATAIREA Aubl.

Vatairea erythrocarpa Ducke, Arch. Jard. Bot. Rio de Janeiro 5:139, 192, pl. 12, f. 25. 1930

Tree, to ca 27 m tall, ca 30 cm dbh; outer bark with many shallow fissures; inner bark smooth, light-colored, the sap with a faint, sweet aroma; young stems puberulent, soon almost glabrous, lenticellate. Leaves alternate, imparipinnate, 25–40 cm long; stipules narrowly deltoid, ca 1.5 mm long; petioles 5–11 cm long; petioles, rachises, and petiolules puberulent; petiolules 4–5 mm long; leaflets 11–15, alternate to opposite, narrowly ovate to oblong-elliptic, bluntly acuminate at apex and downturned, rounded to truncate at base, (3)5.5–11 cm long, (2.5)3–5.5 cm wide, glabrous or weakly appressed-pubescent on midrib of lower surface, drying subcoriaceous, the margins somewhat thickened and turned down; major veins in 6–10 pairs, anastomosing and somewhat loop-connected 5–10 mm from the margin, the reticulate veins prominulous on dried specimens. Inflorescences terminal; flowers not seen. Fruits samaroid, ca 8.5 cm long, 1-seeded, yellowish-green, glabrous except sparsely appressed-pubescent on ventral margin of seminiferous area, the seminiferous area ca 3 cm long, oval, bearing a conspicuous, almost medial ridge, this ridge continuous with the dorsal margin of the wing; wing obovate, mucronate at apex, thin, ca 5.5 cm long, the dorsal margin thickened. *Croat 16624, Folsom 3509, Foster s.n.*

Apparently rare; known only from the beginning of Snyder-Molino Trail and at the junction of Armour and Conrad trails. R. Foster collected fruits in the late dry season.

The leaves and twigs of this species are indistinguishable from those of *Pterocarpus officinalis,* making sterile determination impossible.

Sterile collections by Folsom and Croat are presumably leaves of this species, which represents a new genus for the island's flora. The determination is doubtful, because the species has been known only from Brazil. Because determination is in doubt, it is not considered in the section of the introduction on geographical affinities.

VIGNA Savi

Vigna vexillata (L.) A. Rich. in Sagra, Hist. Cuba 10:191. 1845

Twining herbaceous vine; stems and petioles conspicuously brownish-pilose. Leaves trifoliolate; stipules narrowly lanceolate, 4–7 mm long, sagittate at base, the lobes to 1 mm long; petioles 1.5–4 cm long; rachis 5–15 mm long; leaflets generally oblong-lanceolate, usually narrowly acute at apex, obtuse to truncate at base, 2.5–11 cm long, 1.5–5 cm wide, ± strigillose above and below, the lateral leaflets oblique. Racemes bearing few flowers; peduncles 5–18 cm long, with stout, brown, retrorse trichomes near apex; pedicels opposite, in 1 or 2 pairs; calyx to 12 mm long, the lobes ± equal, the lowermost lobe longest; petals white to blue when opening in the morning with yellow spots on either side of the standard at base, becoming pale yellow through the course of the day, then falling; standard to 2.5 cm long and 3.7 cm wide, emarginate at apex; wings free, ca 1.5 cm wide, the keel petals free to about the middle, enveloping the stamens and very much twisted to one side; style protruding from the tube formed by the outer part of the keel petals, ca 8 mm longer than stamens, the trichomes fine, retrorse, villous, near the apex. Legumes linear, narrowly acute at apex, 7–10 cm long, ca 5 mm wide, dark brown, pilose; seeds many, oblong, to 5 mm long, dark brown, with a white hilum. *Croat 5625.*

Infrequent, in small clearings and along the shore. Apparently flowers throughout the year, more abundantly during the rainy season. Though flowers are produced every day, few fruits are set—those seen were mature in the early dry season.

Standley (1933) reported *Vigna repens* (L.) O. Kuntze on the basis of a misidentified collection of *Phaseolus trichocarpus.*

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

See Fig. 294.

64. OXALIDACEAE

Trees. Leaves alternate, imparipinnate, petiolate; leaflets entire; venation pinnate; stipules lacking. Flowers bisexual, actinomorphic, in axillary, cymose panicles; calyx deeply 5-lobed, imbricate; petals 5; stamens 10, in 2 series, 5 fertile, 5 sterile; anthers 2-celled, versatile, dehiscing longitudinally; ovary superior, 5-locular, 5-carpellate; placentation axile; ovules many, anatropous; styles 5; stigmas capitate. Fruits fragrant, deeply ridged berries; seeds many, with little fleshy endosperm.

The family is represented on BCI by a single cultivated species. Corner (1964) reported that *Averrhoa* is possibly bat dispersed.

Seven genera and about 950 species; subtropics and tropics.

AVERRHOA L.

Averrhoa carambola L., Sp. Pl. 428. 1753
Carambola

Tree, to 10 m tall; twigs reddish and generally tomentose. Leaves imparipinnate; rachis 10–16 cm long, ferruginous-tomentose; petiolules ca 2 mm long, swollen, tomentose;

Fig. 294. *Vigna vexillata*

Fig. 295. *Erythroxylum panamense*

leaflets 7–11 (15), opposite or alternate, the lowermost leaflets smallest, the terminal leaflets largest, ovate, 6–9 cm long, 3–4 cm wide, acuminate, rounded at base, mostly glabrous but strigillose on and near veins below and near margins, dark green above, light green below and near veins above. Inflorescences reddish, axillary, at first growing near ends of branches, later overtopped by new leaf growth and occurring on older wood behind leaves; flowers 5-parted, on articulate pedicels; calyx ca 3 mm long, deeply 5-lobed, reddish, on a tube ca 0.5 mm long; corolla ca 5 mm long, rotate, the petals ± obovate, maroon, paler on margins, puberulent inside, weakly connate just above base; stamens 10, in 2 series, the outer 5 fertile, short, alternating with even shorter staminodia, the longer set of 5 sterile; filaments pubescent; anthers held horizontally, the pollen shed in bud; style simple, short, deeply encircled by sterile stamens. Berries ovoid or ellipsoid, 8–14 cm long, usually with 5 deep ribs, yellow; mesocarp sour tasting. *Croat 4558, 7036.*

Cultivated at the laboratory. Flowers from December to January. The fruits mature in April. It may flower and fruit at other times as well.

Native to Malaya, but incidentally cultivated throughout the tropics and presumably naturalized in Central America.

65. HUMIRIACEAE

Large trees; wood reddish, hard. Leaves alternate, simple, petiolate, usually more or less coriaceous; blades entire; venation pinnate; stipules small, deciduous. Inflorescences paniculate; pedicels short, articulate; bracts and bracteoles deciduous, small; flowers with sepals more or less united into a cupular calyx; petals free, thick; stamens many, in 3 or 4 rows, connate basally in a tube surrounding ovary; anthers ovate-lanceolate, the thecae 2, bilocular, attached at the lower side, the connective thick; disk cupular; ovary superior, sessile, 5-locular; ovules 2 per cell, anatropous; integuments 2; style 1, as long as or longer than stamens; stigma somewhat thickened, 5-lobed. Fruits drupes, the surface smooth; endocarp woody, with 5 linear-oblong valves extending most of the length of the fruit; seeds 1 or 2, oblong.

Humiriaceae in Panama can be recognized by being large trees with unbranched trunks, rather smooth bark, reddish wood, and a dense rounded crown with dark green, coriaceous leaves and by having drupaceous fruits with woody, usually very hard endocarps, 1 or 2 seeds, and many resin-filled cavities.

Eight genera and 50 species; American tropics and western Africa.

VANTANEA Aubl.

Vantanea occidentalis Cuatr., Trop. Woods 96:40. 1950

Tree, to 40 m; branchlets glabrous. Leaves alternate, coriaceous; petioles 1–10 mm long, flattened toward apex, canaliculate and thickened at base; blades elliptic to obovate-elliptic, obtuse to bluntly acuminate at apex, the tip downturned and emarginate, cuneate at base, 6–16 cm long, 3–8.5 cm broad. Panicles terminal; branchlets dichotomously articulate, subcoriaceous, puberulent; bracts caducous; flowers (*fide* Cuatrecasas, 1961) many; pedicels thick, puberulent, 1–2.5 mm long; sepals orbicular, glabrous or nearly so, 6–7 mm long, bearing a single gland outside; petals oblong, obtuse at apex, ca 9 mm long and 3 mm wide, glabrous, greenish-white outside, white inside; stamens many (ca 80); filaments unequal, ca 8 mm long, linear, white, glabrous, united at base; anthers small, ovate-lanceolate, the connective thick at base, acute at apex; disk cupular, 1 mm high, minutely denticulate; ovary 3–4 mm high, hirsute; style 5 mm long. Drupes ovoid-ellipsoid, narrowed at both ends, ca 3.5 cm long and 1.2–1.7 cm thick; endocarp woody, 2.2–3.3 cm long, 1.2–1.7 cm thick, ellipsoid-ovoid, acute at apex, tapering to a rounded base, the surface moderately smooth, with 5 broad ribs, the ribs alternating with 5 oblong valves, the valves 1.8–2.1 cm long, 3–4 mm wide (only 1 of them removable); seed 1, oblong, ca 2 cm long. *Garwood & Foster 400.*

Apparently rare; discovered recently between Wheeler Trail 2400 and 2500. Seasonality uncertain. Flowering has occurred in August. Mature-sized fruits have been collected in February, and the old endocarps may be seen on the ground year-round.

Central Panama to western Colombia. In Panama, most common in premontane wet forest and tropical wet forest (Gentry, 1975); known from premontane wet forest in the Canal Zone (Pipeline Road) and Veraguas (Cerro Tute). The BCI collection is the first report from tropical moist forest.

66. ERYTHROXYLACEAE

Trees or shrubs. Leaves alternate, petiolate, simple, entire, glabrous or nearly so; venation pinnate; stipules present and sometimes greatly expanded. Flowers bisexual, actinomorphic, terminal or axillary, solitary or in fascicles or clusters; calyx campanulate, 5-lobed; petals 5, free, appendaged at base; stamens 10, in 2 series, united at base; anthers 2-celled, basifixed, dehiscing longitudinally; ovary superior, 3-locular (only 1 fertile); placentation axile; ovule 1, anatropous, pendulous; styles 3; stigmas capitate. Fruits drupaceous, prominently sulcate on drying; seed with fleshy endosperm.

The family is represented in the New World only by *Erythroxylum,* which can be distinguished by having ten stamens in two unequal series, appendages at the base of the petals, and clavate or capitate stigmas. Members of the family often have prominent stipules, a discolored band along the lower midrib, and an ellipsoid fruit that dries markedly sulcate and usually has the old stamens persisting around the base. Bawa and Opler (1975) reported *Erythroxylum lucidum* var. *costaricense* O. E. Schultz to be dioecious. Dioecy should be looked for in other species as well.

Four genera and about 250 species; primarily in the neotropics, but also in Africa, chiefly Madagascar.

KEY TO THE SPECIES OF ERYTHROXYLUM

Petioles more than 1 cm long; blades more than 12 cm long; stipules more than 10 mm long; bracts subtending inflorescences equaling or exceeding length of pedicels ..... *E. multiflorum* Lund.
Petioles less than 7 mm long; blades less than 11 cm long; stipules less than 3 mm long; bracts subtending inflorescences much shorter than pedicels ..... *E. panamense* Turcz.

ERYTHROXYLUM P. Browne

Erythroxylum multiflorum Lund., Amer. Midl. Naturalist 29:474. 1943

Glabrous shrub or tree, to 6 m tall; stems marked with scars of deciduous stipules. Stipules lanceolate, 1–6 cm long, brown, overlapping at apex, subpersistent; petioles 1–2 cm long, canaliculate; blades oblong-elliptic, acute or short-acuminate and downturned at apex, acute at base and often decurrent, 10–24 cm long, 3.5–10 cm wide (to 34 cm long and 15 cm wide on seedlings), ± leathery, bicolorous, glossy above, lighter and dull beneath, the margins revolute especially near base; reticulate veins distinct. Flowers white, in dense axillary or terminal clusters, interspersed with brown striate bracts 5–8 mm long; pedicels 5–10 mm long, 5-angulate, the edges winged; calyx lobed, persisting in fruit, the lobes 5, ovate, ca 5–7 mm long; petals 5, ovate, smaller than calyx lobes, bearing a petaloid ligule on the inner surface; stamens 10, united basally into a tube with 10 small teeth at apex; styles 3, persistent, slightly exserted; ovary 3-celled. Drupes ± ovoid-ellipsoid, ca 1 cm long, fleshy, the thick, corky pedicels persisting among bracts after fruits have fallen. *Croat 8265, Foster 1331.*

Occasional, in the forest; seen also along the shore. Seasonal behavior uncertain. Some flowers have been seen from May to September and again in February and March. The fruits are probably mature in about 1 month.

Recognized by the large, brown, persistent stipules. This species was considered *Erythroxylum amplum* Benth. by Standley (1933), but *E. amplum* occurs only in South America. *E. multiflorum* belongs to a difficult species complex, of which *E. macrocalyx* Cav. is the earliest name. All of these species are characterized by having conspicuous clusters of stipules associated usually with the younger branches.

Known only from lowland central Panama, from tropical moist forest in the Canal Zone, and from tropical wet forest in Colón.

Erythroxylum panamense Turcz., Bull. Soc. Imp. Naturalistes Moscou 36(1):581. 1863

Tree or shrub, to 3 m; young stems lenticellate, reddish-brown. Leaves very sparsely pubescent throughout; stipules deltoid, ca 3 mm long; petioles 3–7 mm long, drying brown, canaliculate; blades ± elliptic, acute at apex and base, 4.5–11 cm long, 2–4 cm wide, with discolored area ca 5 mm wide on both sides of midrib below. Flowers solitary or fasciculate on stems, 5-parted; pedicels 1–2 mm long, with well-marked, rounded angles; calyx deeply lobed, the lobes valvate, acute, ca 1.3 mm long; petals greenish, 4 mm long, rounded at apex, keeled medially, with a white, bifid, petaloid ligule inside to 2.7 mm long (the petals appearing to be borne on the ligule); stamens 10, to 4 mm long, fused into a tube 1.3 mm long at base, 5 borne on rim of tube, 5 from somewhat within tube near apex (free part of filaments ± irregular); ovary oblong, glabrous; styles 3, united to about middle, then curved outward; stigmas capitate; nectar apparently stored above appendages on petals. Drupes ellipsoid, red, 7–10 mm long; exocarp thin; mesocarp fleshy; seed white, drying ribbed. *Croat 8662, 11127.*

Frequent in the forest. Some flowers have been seen from February to May and also in September and October. The fruits mature within 1 month.

Endemic to Panama; known from lower elevations in tropical moist forest on the Atlantic slope of the Canal Zone and in Colón, San Blas, Los Santos, Panamá, and Darién, from premontane wet forest in Los Santos (Loma Prieta), and from tropical wet forest in Colón (Río Guanche) and Darién (Cerro Pirre).

See Fig. 295.

67. RUTACEAE

Trees, usually armed; leaves, flowers, and fruits usually punctate-glandular, the glands with aromatic oils. Leaves alternate, simple (*Citrus*) or pinnate (*Zanthoxylum*), petiolate; petioles often winged (in *Citrus*, the wing representing reduced leaflets of a compound leaf); blades pellucid-punctate, occasionally stellate-pubescent; venation pinnate; stipules lacking. Flowers fragrant, bisexual and few or solitary in axils (*Citrus*) or dioecious and paniculate (*Zanthoxylum*); sepals 4 or 5, imbricate, basally connate; petals 4 or 5, imbricate, free; stamens as many as petals and in one whorl (*Zanthoxylum*) or 2 to several times as many as petals (*Citrus*); filaments weakly fused; anthers 2-celled, introrse, dehiscing longitudinally; disk present; ovary superior, 4- or 5-locular (8–15 in *Citrus*), 4- or 5-carpellate, often lobed; placentation axile; ovules 1 to several per locule; styles 1 (*Citrus*) or 1 per carpel (*Zanthoxylum*), connate. Fruits berries with a leathery rind (the hesperidium; *Citrus*) or of several follicles (*Zanthoxylum*); seeds with or without endosperm.

Members of the family are distinguished by the frequent spines, the translucent pellucid dots on the leaves, the lobed ovary elevated on the disk, and the frequently aromatic sap.

The flowers of *Zanthoxylum* are open. Their pollination system is unknown, but they are probably insect pollinated. I have seen flowers of *Citrus* visited by small bees and hummingbirds.

KEY TO THE GENERA OF RUTACEAE

Flowers more than 10 mm long; stamens numerous; fruits large, fleshy, with many seeds; leaves appearing simple; plants cultivated trees in the Laboratory Clearing ..... *Citrus*
Flowers less than 5 mm long; stamens 4 or 5; fruits of 1–5 follicles each dehiscing on one side with a single shiny seed; leaves pinnately compound; plants large forest trees ..... *Zanthoxylum*

Seeds of most *Zanthoxylum* are well suited for bird dispersal, but those of *Z. procerum* are apparently autochorous, being released by the hydroscopic contractions of the inner wall of the follicle. The same inner wall is used in other species to project the shiny black seed out of the follicle, where it may be displayed on the pendent funicle. Other animals, such as monkeys, may also play an important role in dispersal of *Zanthoxylum.* Howler and white-faced monkeys are reported to take the seeds (Oppenheimer, 1968; Hladik & Hladik, 1969). *Citrus* species are eaten by spider monkeys (Hladik & Hladik, 1969) and no doubt by other mammals as well.

About 150 genera and over 1,500 species; widely distributed in warm regions, most numerous in South Africa and Australia.

CITRUS L.

Citrus aurantifolia (Christman) Swingle, J. Wash. Acad. Sci. 3:465. 1913
Lime, Limón, Limón verde

Shrub or tree, 2–8 m tall, glabrous, usually with numerous axillary spines 5–17 mm long. Leaves simple; petioles oblanceolate-winged, 5–28 mm long, 2–9 mm wide, articulated at apex; blades ovate to ± elliptic, acute to bluntly acuminate at apex (the acumen sometimes emarginate), obtuse to rounded at base, 4–13 cm long, 2–6 cm wide, crenate. Flowers solitary to few, in short corymbose cymes, (4) 5-parted; pedicels 3–5 mm long; calyx shallowly 4- or 5-lobed; petals white, oblong-lanceolate, 11–14 mm long, 3–5 mm wide; stamens 20–25; filaments 4–6 mm long, connate into small clusters; anthers 2–3 mm long; disk ca 1 mm high; ovary obovoid, 2–3 mm long; style 2–3 mm long, soon deciduous; stigma subglobose. Fruits ellipsoid at maturity, 3.5–6 cm diam, mammillate at apex, green to yellow, sour, the core solid. *Croat 9190, 14945.*

Cultivated at the Laboratory Clearing; reported by Standley (1933) to be naturalized at some places on the island. Flowers mostly during the dry season. The fruits mature mainly in the rainy season.

Native apparently to East Pakistan, Assam, Burma, Thailand, and Malaysia; now widely cultivated in the tropics and subtropics and throughout Panama.

Citrus aurantium L., Sp. Pl. 782. 1753
Sour orange, Seville orange

Tree, 3–6 m tall, unarmed or the few axillary spines to 5 mm long. Leaves simple, glabrous; petioles broadly winged at apex, 14–27 mm long, usually 10–15 mm wide, narrowed to an almost wingless base, articulated at apex; blades broadly elliptic to obovate, bluntly acuminate and ± emarginate at apex, cuneate at base, 5–12 cm long, 3–7.5 cm wide, crenate. Flowers 5-parted, solitary in axils; pedicels puberulent, 9–11 mm long in fruit; calyx puberulent, the lobes ca 2 mm long; petals white. Fruits globose, 4–6 cm diam, depressed or flattened at apex, orange, sour, the core hollow. *Croat 9184, 14944.*

Cultivated at the laboratory but uncommon. Flowers in the dry season. The fruits mature in the rainy season.

KEY TO THE SPECIES OF CITRUS

Petioles broadly winged, the wings oblanceolate to apically broadened, 2–15 mm wide:
  Fruits 10 cm or more diam; petioles and lower surface of blades sparsely pubescent (at least on veins) ..... *C. grandis* (L.) Osbeck
  Fruits less than 8 cm diam; petioles and lower surface of blades glabrous:
    Petiole wings oblanceolate, 2–9 mm wide; branchlets usually with numerous axillary spines 5–17 mm long; mature fruits ellipsoid, mammillate apically, green to yellow, the core solid ..... *C. aurantifolia* (Christman) Swingle
    Petiole wings apically broadened, mostly 10–15 mm wide; branchlets usually spineless, or the few spines 5 mm long or less; mature fruits globose, depressed or flattened apically, orange to red, the core hollow ..... *C. aurantium* L.
Petioles narrowly winged or narrowly margined, the wings usually 2 mm wide or less (rarely wider in *C. sinensis*):
  Branchlets usually spineless; mature fruits depressed-globose, green to orange or reddish-orange, the peel easily separating from the segments ..... *C. reticulata* Blanco
  Branchlets usually with at least a few axillary spines; mature fruits globose or ovoid, the peel not easily separating from the segments:
    Petioles winged; axillary spines few, 5 mm long or less; mature fruits globose, flattened or depressed apically, yellow-green to orange, sweet ..... *C. sinensis* (L.) Osbeck
    Petioles margined; axillary spines usually many, to 27 mm long; mature fruits ovoid, mammillate apically, light yellow, sour ..... *C. limon* (L.) Burm.f.

Native apparently to East Pakistan, Assam, Burma, and adjacent southwestern China; now widely cultivated in the tropics and subtropics and throughout Panama.

Citrus grandis (L.) Osbeck, Dagbok Ofwer Ostin. Resa 98. 1757
Shaddock, Pummelo

Tree, 3–10 m tall, unarmed or bearing axillary spines; twigs pubescent. Leaves simple; petioles broadly obcordate-winged, articulate at apex; blades oval to broadly ovate, rounded to retuse at apex (bluntly pointed on young shoots), 8–20 cm long, 6–15 cm wide, sparsely pubescent at least on veins below. Flowers 5-parted, solitary or usually clustered in axils, 2–2.5 cm long, very fragrant; petals white, broad; stamens 20–25; ovary globose; style columnar; stigma large, capitate. Fruits globose or depressed-globose, 10–15 cm diam, smooth, pale yellow, sour; segments ca 12. *Croat 4210.*

Cultivated in the Laboratory Clearing between the dock and the boathouse, now engulfed in secondary vegetation. Seasonal behavior unknown.

Native to southeastern Asia and India; now widely cultivated in the tropics.

Citrus limon (L.) Burm.f., Fl. Ind. 173. 1768
Lemon

Tree, to 6 m tall, glabrous, heavily armed with axillary spines 5–27 mm long. Leaves simple; petioles narrowly margined, 5–7 mm long, ca 2 mm wide, articulate at apex; blades elliptic to oval, rounded to bluntly acuminate at apex, widely cuneate at base, 4–11 cm long, 1.5–6 cm wide, crenate. Flowers 5-parted, solitary or clustered in axils, 8–17 mm long; petals pinkish outside, white inside; stamens 20 or more; ovary tapered at apex. Fruits oblong to ovoid, 5–10 cm long, mammillate at apex, light yellow, somewhat roughened, sour; segments 8–10. *Croat 10767.*

Occasional; cultivated at the Laboratory Clearing. Seasonal behavior not determined.

Apparently native to northeastern India, Bangladesh, northern Burma, and southern China; now widely cultivated in the tropics and subtropics and throughout Panama.

Citrus reticulata Blanco, Fl. Filip. 610. 1837
Tangerine, Mandarin orange

Tree, to 8 m tall, glabrous, unarmed; stems prominently ribbed below petioles. Leaves simple; petioles narrowly winged near apex, 6–14 mm long, ca 2 mm wide, articulate at apex; blades ovate to elliptic, blunt to retuse at apex, obtuse to acute at base, 3–8.5 cm long, 1.5–4.5 cm wide, densely punctate, ± stiff, bicolorous, subentire to crenate. Flowers strongly aromatic, 5-parted, solitary (or paired) in axils; calyx short, thick, lobed to about middle, with prominent submarginal bumps, the margin thin, often minutely ciliolate; petals oblong-obovate, acute to rounded at apex, white, spreading at anthesis, 11–14 mm long, ca 3 mm wide, with sparse, large, glandular dots; stamens ca 20, ± unequal, 8–10 mm long, the filaments weakly fused laterally; anthers oblong, the connective prolonged into a greenish knob; pollen yellow-golden, tacky, adhering in large clusters; ovary depressed-globose, glabrous; disk prominent; style shorter than stamens; stigma globose. Fruits depressed-globose, 3–3.5 cm diam, orange at maturity, sweet, the rind easily separating. *Croat 14579.*

Common; cultivated in the Laboratory Clearing. Flowers throughout the dry season and the early rainy season. The fruits mature in the late dry season and in the rainy season.

Flowers are visited by hummingbirds.

Apparently native to Indochina; now widely cultivated in the tropics and subtropics and throughout Panama.

Citrus sinensis (L.) Osbeck, Reise Ostind. China 250. 1765
Sweet orange, Orange, Naranja

Shrub or tree, to 8 m tall; axillary spines few, 2–5 mm long. Leaves simple; petioles usually with a narrow, oblanceolate wing 6–18 mm long and 1–2(5) mm wide, articulate at apex; blades ± elliptic, acute or obtuse and retuse at apex, cuneate at base, 3.5–9 cm long, 1.5–4.5 cm wide, crenulate. Flowers solitary in axils, 5-parted; pedicels 7–12 mm long in fruit; calyx to 6 mm diam, the lobes acute, ciliate, to 2 mm long; petals white. Fruits globose, 4–12 cm diam, yellow-green to orange, sweet, the rind not separating easily from segments. *Croat 10765.*

Occasional; cultivated in the Laboratory Clearing. Flowers in the dry season. The fruits mature in the rainy season.

Apparently native to Bangladesh, northern Burma, southeastern China, and Indochina; now widely cultivated in the tropics and subtropics and throughout Panama.

ZANTHOXYLUM L.

Zanthoxylum belizense Lund., Contr. Univ. Michigan Herb. 6:35. 1941
Arcabú, Tachuelo

Dioecious tree, 13–30 m tall, to almost 1 m dbh; trunk of younger trees armed, the prickles large, corky, horizontally flattened, to ca 5 cm wide and 1 cm thick (somewhat rounded and numerous on juvenile plants), generally deciduous on older trees, the scar often visible; branches and branchlets with ribs extending downward from petioles and with occasional small conical prickles; outer bark thin, brown, sparsely stellate-pubescent. Leaves pinnate, generally imparipinnate or the terminal pair bearing the scar of an aborted terminal leaflet (occasionally with 1 leaflet merely appearing terminal), 16–67 cm long; petioles mostly 5–10 cm long, sparsely stellate-pubescent; leaflets 8–20(26), subopposite to alternate, oblong-elliptic to oblong, abruptly acuminate, acute to obtuse at base, 4.5–16(21) cm long, 1.5–5.5(7) cm wide, sessile or obscurely petiolulate, pellucid-punctate, ± entire and revolute on margin, dark green, shiny and sparsely stellate-pubescent above, duller and densely pubescent below, the trichomes stellate, mostly sessile; juvenile leaves as much as 1.5 m long, the leaflets 22 cm long and 7.5 cm wide. Panicles terminal and upper-

KEY TO THE SPECIES OF ZANTHOXYLUM

Leaves densely pubescent on lower surface:
- Trichomes stellate; corky prickles on trunk flattened, horizontally oriented ..... *Z. belizense* Lund.
- Trichomes unbranched; corky prickles on trunk rounded in outline, somewhat vertically oriented ..... *Z. setulosum* P. Wils.

Leaves glabrous or minutely pubescent on lower surface:
- Petals 3; follicle 1, the valves deciduous; leaflets equilateral and ± decurrent at base, markedly pellucid-punctate on margin, otherwise opaque, both surfaces densely lepidote, the underside glabrous, lacking prickles ..... *Z. procerum* Donn. Sm.
- Petals 5; follicles 3 or 4 (rarely 2), the valves persistent; leaflets inequilateral at base, not decurrent, pellucid-punctate all over, lacking lepidote scales, the underside often minutely puberulent, often bearing 1 or 2 long prickles ..... *Z. panamense* P. Wils.

axillary, 15–33 cm long, widely branched, the branches and pedicels sparsely stellate-pubescent; branchlets scaly, the scales deltoid, ciliate; pedicels to 1.5 mm long; calyx triangular, ciliate; flowers unisexual, greenish-white, 5-lobed, to 3.7 mm wide; petals ± elliptic, acute, imbricate, 1.4–3.3 mm long; stamens 5, alternate, broadly exserted, to 4 mm long in staminate flowers, shorter and sterile in pistillate flowers; ovary 5-lobed, pubescent; style short; stigma simple. Fruits of 1 or 2 globose follicles, 3.5–5 mm long, punctate-verrucose; seeds dark brown, shiny, somewhat shorter than follicle. *Croat 12497.*

Occasional in the forest, though sometimes locally abundant in older forest. Flowers from August to October; individual plants may flower for at least a month. The fruits mature from January to March. Leaves fall off in the dry season, but the new ones all grow out before flowering begins.

Southern Mexico to Panama and possibly Colombia. In Panama, known from tropical moist forest in the Canal Zone, Colón, and San Blas, from premontane wet forest in Colón (Santa Rita Ridge), and from tropical wet forest in Colón (Icacal).

See Fig. 296.

Zanthoxylum panamense P. Wils., Contr. U.S. Natl. Herb. 20:479. 1922

Arcabú, Acabú, Alcabú, Prickly holly, Prickly yellow, Lagarto

Medium to large, dioecious tree, to 28 m tall; trunk to 75 cm dbh, buttressed to ca 1.5 m, armed, the prickles conical, corky, the base to 3.5 cm long, the apex somewhat flattened laterally, deciduous from older trunks at base, persistent above and on branches (especially the smaller ones); outer bark thin, not deeply fissured, often very roughened; inner bark thick, tan, granular, flaking upon slash; twigs puberulent, the trichomes appressed or uncinate; sap usually bitter, not noticeably aromatic. Leaves alternate, compound, imparipinnate or rarely paripinnate, mostly 15–60 cm long; petioles minutely puberulent, mostly 3–9 cm long, the basal pulvinus pronounced; rachis often canaliculate above, broadly so below leaflets, glabrous to minutely puberulent, sometimes armed; petiolules 3–5(7) mm long; leaflets 10–20, opposite to subopposite, sometimes alternate especially basally, mostly ± oblong-elliptic, abruptly acuminate (the acumen sharp or blunt), rarely rounded at apex, rounded or cuneate and usually inequilateral at base (except terminal leaflet), 4–19 cm long, 1.5–7 cm wide, entire or obscurely crenulate, glabrous above or inconspicuously puberulent especially on midrib, glabrous or with inconspicuous, short, appressed trichomes below, occasionally bearing 1 or more, long, sharp prickles on midrib beneath, both surfaces shiny, with small and numerous pellucid dots (sometimes obscure before drying), sometimes with a few much larger, plate-shaped glands on both surfaces. Panicles terminal, 20–30 cm long (shorter on pistillate plants), highly branched, the branches densely hispidulous; pedicels ca 1 mm long; flowers unisexual, white or greenish, 5-parted; calyx puberulent, the lobes short, acute to rounded; petals ± elliptic, acute at apex, 1.5–3 mm long, to 1 mm wide; staminate flowers with stamens 5, exserted, the filaments ca 3 mm long, alternating with lobes of pistillode, the anthers oblong, the pistillode minutely pubescent; pistillate flowers lacking stamens, the ovary broadly obovoid, 3- or 4-lobed, to 1.5 mm long, glabrous and glandular-dotted, the styles (2)3, the stigmas broadly discoid, nearly sessile, round or obtusely 3-sided, more than three-fourths as broad as ovary. Fruits of usually 3 or 4 brown follicles, each 6–8 mm long, puberulent, dehiscing from an apical, medial suture, the valves persistent; seeds 1 per follicle, shiny, black or dark brown, 3–5 mm long, suspended from capsule on a tough fiber. *Croat 6249* and *12574* (large-leaved form), *14885* and *16589a* (small-leaved form).

Occasional, especially in the young forest. Flowers from April to October, mostly from June to September; plants may flower only once every two years. The fruits mature mostly from June to December. Plants have been seen replacing their leaves over a short span of time in the late dry season.

Probably the most variable *Zanthoxylum* on the island, especially in terms of leaf shape. Some BCI plants have consistently much smaller leaflets than others, and additional morphological and phenological study may show them to be distinct species. Plants of the small-leaved form generally flower and fruit ahead of those with larger leaves, although the seasons overlap. This is further evidence that two taxa may be involved in what is being called *Z. panamense.* The small-leaved plant corresponds with the type.

This species and *Z. setulosum* are different from *Z. procerum* in their manner of dehiscence. The fruits of

Fig. 296. *Zanthoxylum belizense*

Fig. 297. *Zanthoxylum panamense*

Fig. 298. *Zanthoxylum procerum*

Fig. 299. *Zanthoxylum setulosum*

Z. procerum expel their seeds from the follicle by the elastic movements of the inner wall of the carpel, whereas *Z. panamense* is thought to be bird dispersed because of the shiny black seeds displayed outside the valves on a slender fiber.

The prickles on the trunk may be hollow and are often inhabited by ants.

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

See Fig. 297.

Zanthoxylum procerum Donn. Sm., Bot. Gaz. (Crawfordsville) 23:4. 1897

Alcabú, Ikor, Lagarto

Dioecious tree, 8–17(20) m tall; trunk to 18 cm dbh, armed, the prickles corky, conical, with the sharp apex usually slightly off-center, the sides with weak vertical grooves; branches sparsely armed with short prickles; outer bark with lenticels arranged in irregular vertical streaks; inner bark tan; twigs soon glabrous. Leaves alternate, imparipinnate or paripinnate, 12–45 cm long (to 60 cm on juveniles), glabrous; petioles 1–10(14) cm long, the pulvinus moderately small to much expanded; rachis canaliculate above, especially beneath insertion of each leaflet; petiolules 3–7 mm long; leaflets (2)4–18, unarmed, mostly opposite, sometimes alternate especially basally, broadest in middle, narrowed gradually to either end, gradually acuminate at apex, cuneate to attenuate with both sides ± equally decurrent at base, 4.5–14.5 cm long, 1.5–5 cm wide (to 25 cm long and 8 cm wide on juveniles), the margins usually minutely crenate and conspicuously pellucid-punctate, the surfaces ± shiny and glabrous, with numerous, minute, lepidote scales on both surfaces, lacking pellucid dots except near margin, often somewhat viscid when dried. Panicles terminal, 10–20 cm long, the branches many, sparsely puberulent, densely lenticellate and punctate, with markedly constricted articulations at the base at maturity; flowers unisexual, with sweet aroma, ca 2 mm long, 3-parted; calyx lobes triangular; petals broadly oblong, rounded at apex; staminate flowers with the stamens 5, well exserted, 2–3 mm long, the pistillode minute, conical, the style short; pistillate flowers unknown. Fruits of 1 brown follicle, 3–3.3 mm diam, globose, densely covered with lenticels and minute glandular projections, on a short stalk ca 7 mm long, the valves 2, persistent, translucent, hydroscopic, dehiscing at maturity, folding together laterally to expel seed; seed 1, rounded, ca 3 mm diam, black with brown reticulations. *Croat 11670, 12189.*

Frequent in the forest. Flowers from February to May (sometimes from January). The fruits mature from June to November, mostly in August and September. Allen (1956) reported this species to flower in August and September in the Golfo Dulce area of Costa Rica, although he was possibly dealing with a different species.

Distinguished by the small, glabrous leaves, which are acute at the base, and the three-parted flower. Cut parts of the plant have a very strong odor similar to that of the citron fruit, and the flowers have a sweet odor. The valves of the fruit are capable of expanding and contracting repeatedly during alternate periods of high and low humidity.

Southern Mexico to Panama. In Panama, known from tropical moist forest in the Canal Zone, Panamá, and Darién and from premontane wet forest in Chiriquí (Progreso) and Panamá (Cerro Campana). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 298.

Zanthoxylum setulosum P. Wils., Contr. U.S. Natl. Herb. 20:480. 1922

Prickly yellow, Arcabú, Acabú, Alcabú, Tachuelo

Dioecious tree, (3)6–12(20) m tall; trunk 10–15(20) cm dbh, armed, the prickles many, large, corky, oval or rounded in basal outline, the apex rounded with a sharp point set somewhat off-center; outer bark ± smooth, light brown, with many raised lenticels; inner bark tan; wood pale yellow, the cambial layer fluted. Leaves alternate, pinnate, 15–50 cm long, conspicuously pubescent (particularly below), the trichomes erect, simple; petioles terete; rachis margined above, sometimes bearing small prickles; leaflets 15–27, subopposite, ± sessile, ovate to oblong or oblong-elliptic, acuminate, acute to rounded at base, usually inequilateral at base, 2.5–10(15) cm long, 1.5–3.5 cm wide, entire or crenulate, obscurely pellucid-punctate, sometimes glabrate in age above, rarely with a few prickles on midrib below. Panicles terminal or upper-axillary, ± congested, to 21 cm long, the branches short, sparsely puberulent; pedicels 2–3.7 mm long, glabrous or crisp-pubescent; flowers unisexual, 5-parted, 2.7 mm long; calyx ca 1 mm long, usually glabrous, rounded at apex; petals elliptic, boat-shaped, spreading, white to greenish-white, the veins prominent, 2–2.3 mm long, rounded at apex, glabrous or inconspicuously pubescent inside; stamens of staminate flowers 5, included or exserted and spreading, 1.7–2.7 mm long, the anthers about as long as or much shorter than filaments, the pistillode small, 1–4-lobed, the styles 1–4; pistillate flowers not seen. Fruits of (2)4(5) follicles, tan or brown, glabrous, the valves persistent, muricate, the inner valve whitish, curling from the base to force seed from follicle; seeds 1 per follicle, ± globose or ovoid, black, shiny, 2.5–3.3 mm long, suspended on a strong slender fiber. *Croat 5430.*

Frequent in the forest. Flowers in the late dry season (March and April). The fruits develop soon but may persist for a long time, maturing from April to October (sometimes to December). Leaves are shed in the dry season, and the trees may be bare for more than a month.

Ants may inhabit old spines and hollow parts of some stems.

Panama and possibly Costa Rica. In Panama, known principally from tropical moist forest on the Pacific slope in the Canal Zone, Panamá, and Darién; known also from tropical dry forest in Los Santos, from premontane moist forest in Coclé (La Pintada), and from premontane wet forest on Coclé (El Copé).

See Fig. 299 and fig. on p. 20.

KEY TO THE SPECIES OF SIMAROUBACEAE

Flowers large (more than 2 cm long), bright pink, bisexual; fruits on a broad, red receptacle, the drupes 3–5, black, ovoid; rachis and petiole conspicuously winged ..... *Quassia amara* L.
Flowers small (less than 1 cm long), greenish, white, or cream, unisexual; fruits not as above; rachis and petiole not winged:
Leaflets mostly more than 7; inflorescences usually branched, open ..... *Simarouba amara* Aubl. var. *typica* Cronq.
Leaflets 5–7; inflorescences unbranched ..... *Picramnia latifolia* Tul.

68. SIMAROUBACEAE

Trees or shrubs, with bitter sap. Leaves alternate, pinnate, petiolate; leaflets entire; venation pinnate; stipules lacking. Flowers actinomorphic, in leaf-opposed racemes or spikes (*Picramnia, Quassia*) or in terminal panicles (*Simarouba*), bisexual (*Quassia*) or unisexual (dioecious in *Simarouba* and *Picramnia*); calyx 4- or 5-lobed or 4- or 5-parted, imbricate; petals 5, imbricate; stamens 5, opposite the petals, or 10 (*Quassia, Simarouba*), inserted on a toral disk; anthers 2-celled, dehiscing longitudinally; ovary superior, mostly 5-locular and 5-carpellate (2- or 3-carpellate in *Picramnia*, the carpels weakly united in *Quassia* and *Simarouba*); placentation axile; ovules 2 per locule (1 in *Picramnia*); styles 2, or solitary and 2- or 5-lobed. Fruits berries (*Picramnia*) or several drupes (*Quassia, Simarouba*); seeds lacking endosperm.

The family is related to the Rutaceae (67), but lacks the pellucid dots on the leaves. The BCI species have little in common and are all individually unique and easily distinguished.

The flowers of *Quassia amara* are principally hummingbird pollinated. *Simarouba* and *Picramnia* are probably best suited for insect pollination.

The fruits of all species are mostly bird dispersed, but no doubt attract some attention from climbing frugivores as well. The bright red receptacles are taken by white-faced monkeys (Oppenheimer, 1968), and fruits of *Simarouba amara* are eaten by howler monkeys (Hladik & Hladik, 1969). Fruits of *Quassia amara* are taken by birds (Duke, 1968).

About 30 genera and 200 species; mostly in the tropics.

PICRAMNIA Sw.

Picramnia latifolia Tul., Ann. Sci. Nat. Bot., sér. 3, 7:258. 1847
Canjura

Dioecious shrub or small tree, to 7(10) m tall; bark and wood with bitter sap. Leaves imparipinnate; petiolules ca 5 mm long, swollen throughout; leaflets mostly 5 or 7, alternate, elliptic to elliptic-ovate, acuminate, acute to rounded at base, 6–15 cm long, 3.5–6.5 cm wide, glabrous. Spikes opposite leaves, the staminate ones densely flowered, to 5 cm long, the pistillate ones long, pendent, to 46 cm long, usually on leafless stems; rachis and calyx scabridulous; calyx bowl-shaped, (4)5-lobed to about middle; staminate flowers with calyx ca 1.5 mm long; petals (4)5, white, cream, or greenish-white, linear-lanceolate, ca 2.5 mm long, glabrous; stamens (4)5, long-exserted; anthers orange. Pistillate flowers numerous; calyx lobes and petals ovate, 1.5–2 mm long; ovary densely appressed-pubescent; style short; stigmas 2, stout, recurled, persisting in fruit. Fruits broadly oblong, to 1 cm long, orange-red; seeds 1 or 2, red outside. *Croat 5263.*

Frequent in some areas of both young and old forests and along the shore in shady areas. Flowers in the early dry season (January to March), with the fruits maturing in the late dry or early rainy seasons (April to June).

Costa Rica to Colombia. In Panama, a typical component of tropical dry forest (Holdridge & Budowski, 1956); known also from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, and Darién.

QUASSIA L.

Quassia amara L., Sp. Pl. ed. 2, 553. 1763
Cruceta, Guavito, Guavito amargo, Guavo amargo, Hombre grande, Puesilde, Quassia, Bitterwood

Shrub or small tree, to 4(8) m tall, glabrous; sap bitter. Leaves imparipinnate; rachis and petiole winged; leaflets 3 or 5, elliptic to oblanceolate, abruptly acuminate, gradually tapered to base, 5–16 cm long, 3–6.5 cm wide, sessile, bicolorous. Flowers 5-parted, in elongate, terminal racemes (rarely paniculate basally); branches of inflorescences and pedicels pinkish; pedicels 1–4 cm long; sepals minute, free; corolla 2.5–4.5 cm long at anthesis, the slender petals glabrous, bright pink outside, white inside, soon falling; stamens 10, exserted at anthesis; filaments curiously hooked, flattened and bearded near base; anthers yellow, longitudinally dehiscent; styles connate, equal to or longer than stamens; stigma 1, simple or slightly lobed. Drupes 4 or 5 (rarely 2 or 3), black, ovoid, 1–1.5 cm long, on a broad red receptacle; seed suspended from apex. *Croat 4038, 4754.*

Common in the forest, especially in some areas. Flowers principally in the late rainy and early dry seasons (August to March). The fruits mature within about 2 months, mostly from December to February.

Distinguished by the distinctive leaf and quinine-like sap in all parts of the plant. Prior to the opening of the flower, a small hole 2–3 mm diam may be produced near the base of the corolla. The organism that makes the hole is not known, but hummingbirds have been seen using the holes to remove nectar.

The fruits are eaten by white-faced monkeys (Hladik & Hladik, 1969).

Southern Mexico to northern South America. In Panama, known principally from tropical moist forest in the

Canal Zone, Bocas del Toro, Colón, Chiriquí, Veraguas, Coclé, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island) and from tropical wet forest in Panamá and Darién.

SIMAROUBA Aubl.

Simarouba amara Aubl. var. **typica** Cronq., Bull. Torrey Bot. Club 71:229. 1944
Aceituno

Dioecious tree, 5–35 m tall, to 70 cm dbh, glabrous except for inflorescence; outer bark hard, with many minute lenticels and small, ± vertical cracks; inner bark and wood with bitter sap; older stems minutely fissured. Leaves pinnate; petioles 4–8 cm long; leaflets (5)9–13(21), oblong-elliptic, rounded or abruptly short-acuminate, acute to obtuse at base, 4–12(15) cm long, 2–4(6) cm wide, dark green and shiny above, lighter green below; lateral veins inconspicuous. Flowers unisexual, campanulate, green, in terminal panicles ca 30 cm long; peduncles and pedicels often minutely puberulent; pedicels 5–15 mm long; calyx shallowly bowl-shaped, 5-lobed, the lobes acute, minutely ciliate; petals 5, ovate to elliptic, beaked inside at apex; staminate flowers 4–5 mm long; stamens 10, equaling lobes, in 2 whorls, the inner whorl to ca 4 mm long, the outer whorl slightly shorter; filaments subulate, the appendages densely tomentose; gynoecium rudimentary, cushion-shaped, weakly 5-lobed, the trichomes tufted, forming a ring around outer edge; pistillate flowers 3–3.5 mm long; pistil ± oblong, deeply 5-lobed, 5-locular; style ca 1 mm long, stout; stigmas 5, slender; carpels 5, soon becoming free (usually not more than 3 surviving until maturity); staminodia much shorter than pistil, the filaments villous near the middle. Fruits of 3–5 drupes to 17 mm long, with a medial ridge, green becoming red-orange or black at maturity; seeds ellipsoid, to ca 14 mm long. *Croat 8441, 9508.*

Occasional, in the forest; locally common, at least in the vicinity of Zetek Trail 250. Flowers in the late dry season (March and April). The fruits mature within 2 months.

The fruits are taken by many birds, including flycatchers, motmots, thrushes, and chachalacas (Duke, 1968).

Guatemala to Panama and south to Brazil; Lesser Antilles. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Panamá (Cerro Campana). Reported from tropical wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

See Figs. 300 and 301.

69. BURSERACEAE

Trees, often with aromatic sap. Leaves alternate, pinnate, petiolate; leaflets entire; venation pinnate; stipules lacking. Flowers usually functionally unisexual (dioecious) but similar in appearance, actinomorphic, minute, in axillary or rarely terminal, cymose panicles or racemes; calyx cupulate, 3–5-lobed; petals 3–5, free or rarely connate into a lobed tube; disk present; stamens usually 2 times the number of corolla lobes, in 2 whorls; anthers 2-celled, introrse, dehiscing longitudinally; ovary superior, 2–5-locular, 2–5-carpellate; placentation axile; ovules 2 per locule, anatropous; style 1; stigma 1, simple or in some cases 2–5-lobed. Fruits drupaceous, each a tardily dehiscent capsule or a drupe with 1–5 pyrenes (*Trattin-*

KEY TO THE SPECIES OF BURSERACEAE

Petals united to form a tube at base:
- Leaves conspicuously asperous, scabridulous on both surfaces; flowers 3-parted, reddish; fruits ovoid, ca 1 cm diam, indehiscent, the seeds (1)2 ..... *Trattinnickia aspera* (Standl.) Swart
- Leaves not asperous, sparingly pubescent; flowers 4- or 5-parted, greenish-yellow; fruits broadly turbinate to depressed-globose, more than 2.5 cm diam, the valves deciduous, the seeds usually 3 or more ..... *Tetragastris panamensis* (Engler) O. Kuntze

Petals free:
- Leaves deciduous, the flowers appearing with new leaves; fruits ± 3-sided, the seed 1, white, 3-sided, indurate, remaining attached at base after valves fall; bark on trunk and larger branches papery, reddish-brown, often peeling ..... *Bursera simaruba* (L.) Sarg.
- Leaves not deciduous, the flowers concurrent with mature leaves; fruits or seeds not 3-sided, the seeds covered with a fleshy white aril, falling from fruit at maturity; bark on trunk and branches not papery, reddish-brown, not peeling:
  - Leaves and inflorescences glabrous; fruits glabrous; mature fruits usually obtuse to acute at both ends ..... *Protium panamense* (Rose) I. M. Johnston
  - Leaves and inflorescences pubescent (at least inflorescence branches; leaves glabrescent in *P. tenuifolium* subsp. *sessiliflorum*); fruits pubescent (often scantily so at maturity); mature fruits obtuse to rounded at base:
    - Flowers 4-parted, pedicellate; petioles, rachises, and petiolules densely brownish-hirtellous, the leaf blades (at least below) sparsely hirtellous; fruits ± ovoid, mostly obtuse at base and at apex, the seed 1 ..... *Protium costaricense* (Rose) Engler
    - Flowers 5-parted, sessile or nearly so; petioles, rachises, and petiolules not densely brownish-hirtellous, the leaf blades glabrous except for minute papillae; fruits usually rounded at both ends, 2–5-lobed, the seeds frequently 2–5 ..... *Protium tenuifolium* Engler subsp. *sessiliflorum* (Rose) Porter

Fig. 300. *Simarouba amara* var. *typica*

Fig. 301. *Simarouba amara* var. *typica*

nickia); seeds 1 (rarely 2) per pyrene, lacking endosperm.

Members of the family may be confused with Anacardiaceae (76) and Meliaceae (70), both of which have alternate, similarly compound leaves with leaflets frequently inequilateral at the base. The BCI species of Burseraceae can be distinguished from these other families by the presence of resin ducts in the bark, by the free stamens and single short style, and by the absence of pellucid dots. The sap of most species is resinous and has a characteristic aroma that is faintly turpentine-like but pleasant.

The pollination system is unknown, but the flowers are best suited to insect pollination.

The fruits are probably chiefly bird dispersed. Those of *Protium* and *Tetragastris* have white arillate seeds, which are displayed against the often bright-red inner carpel wall after one of the valves falls free. Seeds are often pendent, ideally suited to bird dispersal. The pyrenes or pits are very hard and probably pass through the digestive tract unharmed. The fruits are also taken by white-faced and spider monkeys (Oppenheimer, 1968), which eat the fleshy aril. Fruits of *Tetragastris panamensis* are taken by howler monkeys (Carpenter, 1934).

About 20 genera and 600 species; in the tropics.

BURSERA Jacq. ex L.

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

Naked Indian, Almácigo, Carate, Huechichi, Indio desnudo

Dioecious or polygamodioecious tree, 5–25 m tall, to ca 40(100) cm dbh; bark coppery red, shiny, thin, peeling to expose green layer beneath; sap, at least of fruit, very aromatic. Leaves pinnate, deciduous, clustered at apex of branches, densely woolly when young to glabrate except on veins below in age; petioles to 14 cm long; leaflets 5–7(9), ovate-elliptic to lanceolate-elliptic (terminal ones usually obovate), long-acuminate, inequilateral and obtuse to rounded at base, 4.5–14.5 cm long, 2.5–8 cm wide, entire. Flowers 3–5-parted, functionally unisexual, in axillary raceme-like panicles (sometimes appearing terminal before leaves appear), appearing ± with new leaves; calyx bowl-shaped, shallowly 5-lobed, the lobes acute to blunt; petals greenish-white, narrowly ovate, acute, cucullate, 2–3 mm long, spreading at anthesis, later recurved; stamens twice the number of and shorter than petals, those opposite the petals usually ± spreading, the alternate ones erect; pollen golden-yellow, covering all sides of anther at anthesis; pistillode ovoid, white, glabrous, scarcely longer than weakly lobed and undulate disk. Capsules drupaceous, ellipsoid, obtusely 3-sided, maturing reddish-brown, ca 1 cm long, a single valve falling free at maturity to expose the pyrene, followed by both remaining valves falling off as a unit, leaving the pyrene attached at base; pyrene 1(2), 1-seeded, 3-angled, bony, lenticular-ovoid, white, ca 7 mm long. *Croat 5325.*

Occasional, but locally common, especially along the shore on the northwest side of the island and on Orchid Island. Flowers in the late dry and early rainy seasons (March to the middle of June), just before or during the onset of new leaves. Mature fruits may be seen throughout much of the year, but most fruits mature during the late rainy or early dry seasons of the following year, generally after the plant has lost its leaves. Most trees are bare by February, beginning to put on new leaves and flowering by March or April. Allen (1956) reported that the trees are leafless throughout most of the dry season in Costa Rica.

Easily recognized by the reddish-brown, papery bark.

Southern Florida and northeastern Mexico to Colombia, Venezuela, and the Guianas; West Indies. In Panama, a characteristic species in tropical moist forest (Tosi, 1971), known all along the Pacific slope; known also from from premontane dry forest in Coclé, from tropical dry forest in Los Santos, Coclé, and Panamá, and from premontane moist forest in the Canal Zone and Panamá. Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

PROTIUM Burm.f.

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

P. salvozae Standl.

Functionally dioecious tree, to 11(25) m tall, the trunk usually less than 20 cm dbh; outer bark minutely roughened; inner bark reddish, forming minute, cloudy, viscid droplets; sap lacking typical burseraceous aroma; stems, petioles, rachises, inflorescence branches, and veins of leaflet pubescent, the trichomes stiff, erect, brownish, of varying lengths. Leaves pinnate; petioles 4–6.5 cm long, flattened on upper surface; leaflets (3)5–7(9), mostly oblong-elliptic, abruptly acuminate, obtuse to acute at base, slightly inequilateral, 6–17 cm long, 2.5–8 cm wide. Flowers cream, 4-parted, in axillary panicles 1–13.5 cm long, often branched from near base; pedicels 1.5–3 mm long, puberulent; calyx bowl-shaped, broader than long, 1–2 mm long, shallowly lobed, the lobes acute to rounded; petals ca 3 mm long, narrowly ovate, acute and weakly spreading at apex; stamens 8, arising from beneath a prominent disk, the disk weakly lobed, half as high as ovary in pistillate flowers (2 mm tall), as high as ovary in staminate flowers; filaments inflexed; anthers held directly over style; pollen white, tacky; ovary ovoid, appressed-pubescent, much shorter than stamens; style ± sessile; stigma 4-lobed. Capsules drupaceous, ± ovoid, 1.5–2 cm long, violet-purple to brownish, sparsely lenticellate, obtuse at both ends, the valves 2(5), one falling free; pyrene 1, tan, 1-seeded, ca 1 cm long, falling free from funiculus (this ca 5 mm from apex) and suspended on a narrow band of tissue, enveloped in a white, sweet, fleshy aril displayed against the bright red inner valve surface. *Croat 8262, 14926.*

Rare, in the older forest along Zetek and Drayton trails. Apparently flowers twice per season, once in February and early March, with the fruits maturing in March and April, and again in May and June, with the fruits developing mostly in August and September.

Known from Costa Rica and Panama. In Panama, known only from tropical moist and premontane wet forests in the Canal Zone on the Atlantic slope; no doubt occurring on the Atlantic slope of western Panama also.

Fig. 302.
Protium panamense

Fig. 303. *Tetragastris panamensis*

Fig. 304. *Trattinnickia aspera*

Protium panamense (Rose) I. M. Johnston, Contr. Gray Herb. 70:72. 1924
Copá

Functionally unisexual tree, usually less than 12 m tall (to 40 m elsewhere), ± stilt-rooted at base, glabrous; outer bark thin, smooth, the leaf scars on younger trees ca 5 cm broad; inner bark pinkish; sap with sweet strong odor typical of family. Leaves pinnate; petioles 6–13 cm long, flattened on upper surface, swollen at base; petiolules 1–4(8) cm long, swollen at both ends; leaflets 3–7(9), mostly ovate-lanceolate to oblong, bluntly short-acuminate, obtuse to rounded at base, 13–35 cm long, 6–9(16) cm wide, coriaceous. Inflorescences paniculate (rarely racemose), axillary or terminal, sometimes cauliflorous, mostly to 15 cm long; flowers greenish-white to greenish-yellow, 4(5)-parted, with a strong, sweet aroma; pedicels to ca 4 mm long; calyx ± truncate or shallowly lobed, very short; petals 3 mm long, valvate, ± spreading at anthesis, papillose-puberulent on margins, the apex acute; stamens 8(10), 2 mm long; filaments broadened below, recessed somewhat in fleshy yellowish disk; pistil conical, short; stigma simple, almost sessile, persistent in fruit. Capsules drupaceous, red at maturity, often in a large congested cluster, ellipsoid to ovoid, apiculate, shortly stipitate, to 2.8 cm long, the valves 2 or 4, unequal, the smaller falling free at maturity; pyrene 1(4), to ca 1.5 cm long, bearing 1 or 2 seeds, greenish, covered with a thick, white, fleshy, sweet mesocarp ca 3 mm thick, attached to larger valve near apex, becoming pendent, displayed against red inner valve surface. *Croat 4834, 11110.*

Abundant, especially in the younger forest and along the shore; rare in the older forest. Flowers usually twice per year (sometimes three times per year), once in the early dry season (January to February, rarely as late as April), once in the early rainy season (usually July and August), and rarely again in the late rainy season. Fruit maturation is considerably more staggered, and mature fruits have been seen from February to August, often at the same time as flowering.

Though flowers are functionally unisexual, there are few conspicuous differences between staminate and pistillate flowers or inflorescences.

Known only from Panama, probably extending into both Costa Rica and Colombia. In Panama, known only on the Atlantic slope from tropical moist forest in the Canal Zone, Bocas del Toro, and San Blas, from tropical wet forest in Colón and Coclé, and from premontane wet forest in the Canal Zone and Colón.

See Fig. 302.

Protium tenuifolium Engler subsp. **sessiliflorum** (Rose) Porter, Ann. Missouri Bot. Gard. 56:475. 1969
P. sessiliflorum (Rose) Standl.; *P. neglectum* var. *panamense* Swart; *P. neglectum* var. *sessiliflorum* (Rose) Swart
Animé, Chutras, Comida de mono

Functionally unisexual tree, to 18 m tall, to 27 cm dbh; outer bark thin, flaking in firm sheets, lenticellate; inner bark moderately thick, reddish; sap slowly forming viscid, cloudy droplets after slash, with strong, sweet aroma; stems glabrous, prominently brown-lenticellate. Leaves imparipinnate; petioles flattened above with sharp margins; petiolules thickened at both ends; leaflets 5–9(13), mostly oblong to oblong-elliptic, acuminate with blunt acumen, acute to rounded at base, often ± inequilateral, 10–20(27) cm long, 5–9(12) cm wide, glabrous except for minute papillae. Panicles axillary, near stem apex, the branches ferruginous; staminate inflorescences somewhat larger than pistillate (to 24 cm long); flowers 5-parted, sessile, 3.5–5 mm long; calyx to 2 mm long, cupulate, 5-lobed, minutely pubescent, the lobes acute; petals lanceolate, yellow-green, thickened medially on outside, ca 3 mm long, erect to somewhat spreading at anthesis; stamens 10, alternately long and short, the longest to 2 mm long, the shortest to 1.3 mm long, scarcely longer than the prominent, pubescent disk; ovary ovoid, densely pubescent; style short, the ovary and style together ca 2.7 mm long; stigma 5-lobed, persisting in fruit. Capsules drupaceous, bearing 1–5 pyrenes, ovoid to depressed-globose, with 4 or 5 lobes (rarely 2- or 3-lobed), mostly 2–3 cm diam, red at maturity, usually rounded at both ends, the carpels 4 or 5, each dehiscing by a single valve, the valve falling free to expose the white mesocarp surrounding pyrene; pyrenes black, 1 per carpel, 1-seeded, ovoid in face view, irregular in side view. *Croat 11109, 14822.*

Common along the shore; occasional in the forest. Flowers chiefly in April and May. The fruits mature chiefly in the middle of the rainy season (August to October).

Small bees, possibly *Trigona,* have been seen visiting the flowers. The fruits are edible.

Costa Rica and Panama. In Panama, known only from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién. Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

TETRAGASTRIS Gaertn.

Tetragastris panamensis (Engler) O. Kuntze, Rev. Gen. Pl. 1:107. 1891
Animé

Dioecious tree, to 35 m tall and 60 cm dbh, scarcely buttressed; outer bark rough, unfissured, flaky. Leaves imparipinnate; petioles flattened on upper surface, nearly glabrous; leaflets 7–9(11), ± oblong-elliptic, acuminate, acute to nearly rounded at base (lateral leaflets often inequilateral), 5–20 cm long, 2–7 cm wide, nearly glabrous, stiff, the midrib arched. Panicles axillary (or terminal by abortion of stem apex), loosely branched, 2–15 cm long, with most exposed parts ± appressed-puberulent; flowers (4)5-parted; pedicels ca 1 mm long; calyx cup-shaped, shallowly lobed, to 1.5 mm long; corolla yellowish-green, 3–5 mm long, lobed ca one-third its length, the lobes acute, thick, erect; stamens (8)10, included, abortive in pistillate flowers; disk annular, (8)10-lobed; ovary ovoid, (4)5-lobed and (4)5-locular, sparsely pubescent; style short, pyramidal; stigma 5-lobed. Capsules drupaceous, purplish or reddish to brown, broadly turbinate to depressed-globose, round in cross

section, to 2.5 cm long and 3.5 cm wide, usually with all 5 carpels developing, rarely 3 or 4, the thick wedge-shaped valves red within, falling free at maturity; mesocarp spongy, sweet; pyrenes 1 per carpel, 1-seeded, ca 1.5 cm long (including aril), attached subapically and situated between slender, red, platelike partitions of the main body, covered with a fleshy, sweet, white aril ca 2 mm thick. *Croat 6823, 11195.*

Common in the forest. Flowers chiefly in June and July (rarely as late as August and September); individuals of the species may flower every two years. The fruits mature mainly from March to the middle of May (rarely to July).

On BCI, fruits are generally found on the ground, though usually only the star-shaped main axis and loose valves remain. The seeds are quickly taken by large birds and mammals.

Belize to Peru and Brazil. In Panama, ecologically variable; characteristic of tropical moist forest (Tosi, 1971), known in the Canal Zone, San Blas, Veraguas, Panamá, and Darién; known also from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Panamá and Darién, and from tropical wet forest in Colón. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 303.

TRATTINNICKIA Willd.

Trattinnickia aspera (Standl.) Swart, Recueil Trav. Bot. Néerl. 39:426. 1942

Protium asperum Standl.

Caraño

Functionally dioecious tree, 25–50 m tall, to ca 75 cm dbh, weakly buttressed, the base becoming very roughened and warty; outer bark hard, dark brown; inner bark granular, tan; sap with faint, pleasant aroma (not characteristically burseraceous). Leaves deciduous, imparipinnate; petioles flat above, with a raised marginal rib; rachis triangulate on upper surface, rounded below; petiole and rachis shortly pubescent; leaflets 7–11 (to 19 on juveniles), oblong-ovate to oblong-elliptic, acuminate, cuneate to cordate at base (sometimes inequilateral on lateral leaflets), 10–20(30) cm long, 4–6(12) cm wide, asperous and scabridulous on both surfaces, sparsely hispidulous below especially on veins, stiff, the margins entire and ± undulate; lateral veins prominent below. Flowers 3-parted, functionally unisexual, in terminal panicles to 29 cm long, usually in dense glomerules, the branches sharply angulate, densely floriferous, hispidulous; pedicels to 4 mm long at anthesis, broadened apically, flattened; calyx sericeous inside, ca 2.7 mm long, caducous; corolla ± urceolate, ca 5 mm long, dull red (tinged with green in pistillate flowers), trilobate, the lobes acute, divided ca halfway to base in staminate flowers and one-fourth to three-fourths the way to base in pistillate flowers; stamens 6 (rarely 10), almost sessile (abortive in pistillate flowers); filaments strap-shaped; anthers oblong, ca 2 mm long, introrse; ovary ± ovoid, glabrous, 2–2.7 mm long at anthesis (reduced in staminate flowers); styles 2, short and thick. Fruits drupaceous, ovoid, ca 1 cm long, blunt or rounded at apex, smooth (drying ± wrinkled and acute at apex), indehiscent, violet-purple at maturity; pyrenes (1)2, each 1-seeded. *Croat 11667, 11881, 13932.*

Frequent in the old forest. Flowers in late July and August. The fruits mature during the dry season from January to April. Trees lose all their leaves during the early rainy season, but are renewed soon.

Easily distinguished from all other species by its sandpapery, compound leaves with the petiole flattened on the upper surface. Because of the differences in stamen size and condition of the ovary, the sex of any tree can be determined in the field by fallen flowers. Staminate flowers usually fall soon after the pollen has been shed, in most cases with the corolla still attached.

Fruits are probably consumed whole by large birds and mammals, since there is relatively little mesocarp.

Known only from Panama; characteristic of tropical wet forest, principally on the Atlantic slope (Tosi, 1971); known also from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá and from premontane wet forest in the Canal Zone (Pipeline Road).

See Fig. 304.

70. MELIACEAE

Functionally dioecious or monoecious (*Cedrela*) trees, the wood often scented. Leaves alternate, petiolate, pinnately compound; leaflets entire; venation pinnate; stipules lacking. Flowers appearing bisexual (see discussion below), actinomorphic, in terminal or axillary, cymose panicles bearing few to many flowers; perianth mostly 5-parted; calyx variously lobed; petals free or attached to the staminal tube; disk present; stamens as many or twice as many as the petals; filaments variously united into a tube; anthers 2-celled, longitudinally dehiscent; ovary superior, 2–5-locular and 2–5-carpellate; placentation axile; ovules 1, 2, or many per locule, pendulous, anatropous; style 1; stigma capitate or discoid. Fruits loculicidally or septicidally dehiscent capsules, with 1, 2, or many (*Cedrela*) seeds per cell; seeds often winged, often arillate, with or without fleshy endosperm.

Members of the family may be confused with Burseraceae (69) and Anacardiaceae (76). They can be distinguished by having the stamens united into a tube or adnate to the gynophore and by having discoid or capitate stigmas. In addition, leaves are sometimes paripinnate (*Guarea*), and the petioles are usually markedly flattened on the upper side.

Styles (1972) believed *Guarea, Cedrela,* and *Trichilia* to be functionally dioecious. Flowers of the two sexes are only slightly modified, with the stamens and pistil reduced in the respective unisexual flowers. I have called dioecious only those species that I am confident are dioecious, on the basis of field observations on BCI. Some species certainly appear to have bisexual flowers. For example, all trees of *Trichilia cipo* observed set fruit after flowering. For most species not enough observations were made to be certain of their breeding behavior.

KEY TO THE SPECIES OF MELIACEAE

Leaflets mostly in more than 6 pairs (10–22 leaflets):
- Leaflets equilateral at base; leaves to 2 m long; flowers ca 1 cm long; fruits ± globose, to 3.5 cm diam; seeds with a red aril ..... *Guarea multiflora* Adr. Juss.
- Leaflets inequilateral at base:
  - Flowers ca 3 mm long; capsules subglobose, 3-valved, ca 1 cm long; seeds arillate; leaflets thin, usually less than 4.5 cm wide, lacking axillary domatia; bark not coarsely fissured ..... *Trichilia hirta* L.
  - Flowers 6–10 mm long; capsules oblong-ellipsoid, 5-valved, to 4.5 cm long; seeds winged; leaflets thick, often more than 4.5 cm wide, bearing pocketlike axillary domatia; bark coarsely fissured ..... *Cedrela odorata* L.

Leaflets in 6 or fewer pairs:
- Flowers 6–10 mm long; anthers borne on inner surface of staminal tube; disk columnar or obsolete; fruits 4- or 5-valved, not warty, usually conspicuously covered with raised lenticels ..... *Guarea glabra* Vahl
- Flowers less than 4 mm long; anthers borne at apex of staminal tube; disk ring-shaped; fruits mostly 3-valved, somewhat to markedly warty, lacking lenticels:
  - Filaments united only in basal half; terminal leaflet larger than lateral leaflets, 20–32 cm long, 6.5–16 cm wide; inflorescences axillary, usually less than 8 cm long ..... *Trichilia montana* H.B.K.
  - Filaments united to form a staminal tube; terminal leaflet usually ± equaling lateral leaflets, less than 20 cm long and 8 cm wide; inflorescences subterminal, often more than 8 cm long:
    - Leaflets heteromorphic, 3–5 full-sized and 1 or 2 pairs abortive; midrib flat; staminal tube pubescent; fruits round, green, only slightly bumpy ..... *Trichilia verrucosa* C. DC.
    - Leaflets regular, 5–9, all full-sized; midrib sharply raised; staminal tube glabrous; fruits ellipsoid to oblong, orange, conspicuously warty ..... *Trichilia cipo* (Adr. Juss.) C. DC.

Flowers are somewhat specialized and nectar is usually present. The anthers provide little pollen, and the pollination system is unknown.

Seeds of *Cedrela odorata* are wind dispersed. *Guarea* and *Trichilia* are probably for the most part bird dispersed, but fruits of *Trichilia cipo* are taken by white-faced, spider, and howler monkeys (Oppenheimer, 1968; Hladik & Hladik, 1969).

Fifty genera and about 1,000–1,400 species; mostly in the tropics.

CEDRELA Scop.

Cedrela odorata L., Syst. Nat. ed. 10, 940. 1759
Cedro, Spanish cedar, Cigar-box cedar

Monoecious tree, to 40 m tall; trunk reddish-brown especially near base, grayish above, deeply fissured, sometimes buttressed to 2 m; outer bark hard, persistent; sweet odor of cedar from slash. Leaves alternate, glabrous, to 60 cm long; leaflets in 5–11 pairs, opposite or subopposite, ovate-elliptic, acuminate, asymmetrical and acute to rounded at base, 6–17 cm long, 3–5.5 cm wide, the axils of major veins with pocketlike domatia on lower surface. Panicles pyramidal, open, terminal; branchlets generally at right angles to axis; bracts caducous; inflorescence branches and pedicels glabrous to minutely puberulent; pedicels to 2 mm long (to 5 mm and thickened in fruit); flowers functionally unisexual; calyx cupulate, 1.5–3 mm long, usually split on one side, ± irregularly 5-dentate, usually glabrous; petals 5, oblong-elliptic, 6–9 mm long, fused to gynophore medially, puberulent outside, white; stamens 5, slightly shorter than petals; filaments free above, ± fleshy, uniform; anthers introrse, ca 1 mm long; style slightly longer than stamens; stigma green, thick, capitate, almost as long as petals. Capsules oblong-ellipsoid, to 4.5 cm long, green with light brown scurfy patches, becoming brown, dehiscing from apex, 5-valved, the valves thin; seeds many, samaroid, ca 3 cm long, with membranaceous wing, suspended from the seminiferous apex on the central column, the column thick, corky, 5-ribbed. *Croat 10332.*

Rare; known from only a few places in the forest—one tree is at Barbour Trail 1400. Flowers usually in the early rainy season. The fruits mature in the dry season. Trees are deciduous in the early dry season.

Northern Mexico south to Peru, Bolivia, and Brazil; West Indies; introduced into the Old World. In Panama, known from tropical moist forest on BCI and in Bocas del Toro and Darién and from premontane wet forest in Chiriquí; known also from tropical dry forest in Panamá (Tosi, 1971). The closely related *C. angustifolia* Sessé and Moc. is more widespread in tropical moist and tropical dry forests along the Pacific slope.

See Fig. 305.

GUAREA Allem. ex L.

Guarea glabra Vahl, Eclog. Amer. 3:8. 1807
Cedro macho

Dioecious tree, 3–15 m tall, the trunk to 16 cm dbh; outer bark soft, flaky, easily scraped off; stems roughened with fine lenticels; young petioles and leaves ± sericeous,

Fig. 305. *Cedrela odorata*

Fig. 306. *Guarea multiflora*

Fig. 307. *Guarea multiflora*

KEY TO THE SPECIES OF GUAREA

Leaflets in usually fewer than 6 pairs, less than 7 cm wide ..... *G. glabra* Vahl
Leaflets in usually more than 6 pairs, frequently more than 7 cm wide ..... *G. multiflora* Adr. Juss.

becoming glabrate. Leaves paripinnate, to 54 cm long; petioles flat and margined above, swollen at base; petiolules 5–10 mm long, swollen; leaflets 6–12, ovate-elliptic to oblong, acuminate and downturned at apex, acute to obtuse at base, 7–25 cm long, 4–7 cm wide, glabrous above, glabrate below. Inflorescences racemose, axillary or on older leafless branches, to 23 cm long; flowers with sweet aroma, functionally unisexual, well spaced, ca 1 cm long, solitary along rachis or clustered on very short branches; calyx cupular, 2–4 mm long, irregularly lobed, the lobes often fewer than petals, puberulent outside; petals white, 4 or 5(6), to ca 10 mm long, usually puberulent outside, spreading or recurved near middle at anthesis; staminal tube cylindrical, white, 6–8 mm long; anthers 8 or 10(12), borne inside near rim; ovary ± glabrous to sericeous, borne on a gynophore broadened just below ovary; style exserted above staminal tube; stigma capitate. Capsules subglobose to pyriform, to 2.5 cm diam, usually borne on a short stipe, reddish, variously mottled with lenticels in age, dehiscent by 4 or 5 woody valves; seeds 1 or 2 per carpel, covered with a red aril, irregular. *Croat 8493, 8814.*

Frequent in the forest. Seasonal behavior uncertain. Flowers at least from December to July, especially from March to June. The fruits probably mature mostly from April to September, especially in the rainy season.

A variable species, it has been identified by C. E. Smith under three other names as well, including *G. guidonia* (L.) Sleumer, *G. kunthiana* Adr. Juss., and *G. tonduzii* C. DC. It can be reported with certainty that *G. tonduzii* does not occur on BCI and furthermore that there is but a single species in this complex thus far collected on the island. The pubescence of the ovary, used in distinguishing *G. glabra* and *G. guidonia,* is at best a poor character.

A large caterpillar with stinging hairs has been seen eating the leaves.

Mexico to Colombia, Venezuela, and Ecuador; West Indies. 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 Chiriquí; probably occurring in most areas of tropical moist and tropical wet forests.

Guarea multiflora Adr. Juss., Mém. Mus. Hist. Nat. 19:284. 1830

Dioecious tree, 5–40 m tall; bark flaking. Leaves paripinnate, mostly 30–200 cm long; petioles flattened above; rachis and petiole puberulent to tomentose; petiolules 3–7 mm long, ± glabrous above, glabrous to minutely scabrid below, becoming glabrous in age; leaflets 8–34, elliptic to oblong-elliptic, acute to acuminate or sometimes rounded at apex, acute to rounded at base, 7–30 cm long, 4.5–12 cm wide. Flowers in slender, sparsely branched, axillary panicles to 35 cm long; all exposed parts tomentose; pedicels short; calyx cupular, to 3 mm long, glabrous inside, the lobes blunt to acute, mostly 4 or 5(6); petals 4 or 5(6), oblong, blunt at apex, spreading at anthesis, ca 1 cm long, staminal tube slightly shorter than petals, ± glabrous; anthers 8 or 10(12), mounted within tube below rim, ca 1.3 mm long; ovary usually 5-sulcate, mounted on a stout gynophore, the ovary and style sericeous; stigma discoid, to 1.5 mm broad, held just above apex of staminal tube. Capsules ± pyriform, 3–3.5 cm diam, reddish to reddish-brown, scurfy with numerous lenticels and persistent short pubescence, dehiscing by 4–6 woody valves to expose seeds; seeds 1(2) per carpel, ellipsoid, to 2 cm or more long, covered with a thin red aril. *Croat 8443, 11300.*

Rare, in the forest. Flowers from June to October. The fruits mature mostly from February to June.

Woodworth & Vestal 747, cited by Standley as *G. guarea* P. Wils. (= *G. guidonia* (L.) Sleumer), is *G. multiflora,* since he said it has 8–20 leaflets. C. E. Smith (1965) reported the specimen in the *Flora of Panama* as *G. guidonia,* but said the species has no more than 14 leaflets.

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

See Figs. 306 and 307.

TRICHILIA P. Browne

KEY TO THE SPECIES OF TRICHILIA

Capsules very densely and conspicuously pubescent; staminal tube entire or the anthers merely alternating with apicula:
Leaflets more than 9, the uppermost less than 15 cm long and 4.5 cm wide ..... *T. hirta* L.
Leaflets fewer than 7, the uppermost more than 15 cm long and 6.5 cm wide ... *T. montana* H.B.K.

Trichilia cipo (Adr. Juss.) C. DC. in Mart., Fl. Brasil. 11(1):214. 1878

Trichilia tuberculata C. DC.

Alfaje, Alfajeo colorado, Camfine, Fosforito

Tree, to 30 m tall and 40 cm dbh (often much shorter along the shore); outer bark hard, closely fissured; inner bark red; younger stems, leaf rachises, and axes of inflorescences densely strigose and puberulent (in Panama) or sparsely strigose, sparsely puberulent, or nearly glabrous (often in South America). Leaves alternate, imparipinnate, mostly 15–30 cm long; petioles flat on upper surface with marginal ribs; leaflets apparently never

Capsules glabrous or only sparsely and inconspicuously pubescent; staminal tube divided for at least one-third its length:
Capsules ± globose, green, only slightly bumpy, not conspicuously warty; staminal tube pubescent; leaflets usually 5 or fewer, usually with 1 or 2 pairs of abortive leaflets at base, the midrib not raised ..... *T. verrucosa* C. DC.
Capsules oblong or ellipsoid, orange, conspicuously warty; staminal tube glabrous; leaflets usually more than 5, lacking abortive leaflets, the midrib prominently raised ..... *T. cipo* (Adr. Juss.) C. DC.

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dimorphic, usually 5–9 (rarely 3 or 10), usually alternate, ± elliptic, acuminate, obtuse-attenuate at base, 4–21 cm long, 1.5–8 cm wide, usually glabrous or minutely puberulent and/or strigose on midrib on both surfaces, rarely strigose below; midrib sharply raised. Panicles axillary (often appearing terminal), mostly 8–20 cm long; flowers white or greenish-yellow, 4–6-parted, as wide as long, globular in bud, the trichomes (at least on calyx) erect or appressed; calyx saucer-shaped, the lobes acute or blunt; petals valvate, ovate, to ca 2 mm long, glabrous or sparsely appressed-pubescent outside, glabrous inside, the margins papillose-puberulent; staminal tube two-thirds to three-fourths as long as petals, broader than long, glabrous outside and in but sometimes pubescent inside near apex, the lobes narrowly acute; anthers twice as many as petals, very narrowly ovoid, ca 0.5 mm long, alternating with and usually longer than lobes of staminal tube; ovary broadly ovoid, densely appressed-pubescent with white trichomes all over; style usually glabrous. Capsules ellipsoid, 11–18 mm long, orange at maturity, prominently tuberculate, the 3(4) valves folding back to expose shiny red aril; seeds 1 or 2, smooth, ellipsoid, ca 1 cm long. *Croat 12271, 12500.*

Abundant as seedlings; common as adults in the forest, especially in the old forest. Flowering is bimodal, but principally from April to June, especially in June; a second but much smaller flowering period may occur from September to November. It is not known whether the second flowering occurs each year or only sporadically. The fruits from the first flowering mature mostly during September and October, especially in October; mature fruits from the second flowering have been seen in June.

Guatemala to the Guianas and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, principally on the Atlantic slope, and in Bocas del Toro, Colón, San Blas, Chiriquí (Progreso), Panamá, and Darién; known also from tropical wet forest in Colón (Salúd).

Trichilia hirta L., Syst. Nat. ed. 10, 2:1020. 1759
Conejo colorado, Huesito, Souca

Tree, to 10 m tall; young stems, petioles, rachises, veins of blades below, and inflorescence branches sparsely hirsute. Leaves pinnate, imparipinnate or paripinnate, to 30(45) cm long; petioles 3–5(9) cm long, pulvinate at base, the pulvinus ± flat above; leaflets (9)13–21, opposite or subopposite near apex, sometimes becoming alternate toward base, ± elliptic, long-acuminate, acute to rounded and slightly inequilateral at base, 5–9(14) cm long, 1.5–3(4.4) cm wide, sparsely ciliate. Panicles 3–15(18) cm long, solitary or paired (when paired, 1 usually very short) in upper axils; lateral branches short; peduncles and basal part of axis often ± flattened; pedicels to 1 mm long, with minute narrowly acute bracts at base; flowers 5-parted, 2–3 mm long; calyx saucer-shaped, the lobes short, acute; petals oblong, acute at apex, white, densely papillate (especially on margins); stamens 10, free except near base, to 2.3 mm long, included; filaments flattened, contiguous, forming a loose staminal tube, stiff-villous on margins and within above middle, the lateral margins weakly prolonged at apex; anthers ca 0.7 mm long, narrowly ovoid, introrsely dehiscent, sparsely villous all over; ovary orange, depressed, ca 1.2 mm wide, about half as high, glabrous to densely pubescent; style thick, ca 2.3 mm long, swollen slightly below apex, villous, especially near base; stigma simple, depressed; nectar stored within stamens at base of ovary. Capsules subglobose, obtuse and apiculate at apex, ca 1 cm long, brown to violet-purple at maturity, densely and minutely papillate-puberulent and sparsely hirtellous at least when young, 3-valved, the open capsule bowl-shaped with a prominent narrow midrib inside; seeds (2)3(4), ovoid, ca 6 mm long, covered with a fleshy orange aril. *Croat 15099.*

Apparently rare; collected on the west edge of Bat Cove. Flowers mostly from May to July. The fruits mature during the dry season of the following year, at least in some cases while the trees are bare.

Smith (1965) in the *Flora of Panama* stated that the inflorescences are racemose. He uses this character in the key to separate this species from *T. tomentosa* H.B.K. However, most of the Panamanian materials I have seen have paniculate inflorescences. Reported to be dioecious (Bawa & Opler, 1975).

Mexico to Brazil; West Indies. In Panama, reported by Smith (1965) to be a species of fence rows, forest margins, and forests; known from tropical moist forest in the Canal Zone, Chiriquí, Panamá, and Darién.

Trichilia montana H.B.K., Nov. Gen. & Sp. 7:226. 1825

Tree, to 10(25) m tall, slender; outer bark light brown, very smooth, with minute whitish lenticels; inner bark and wood whitish, the sap with sweet aroma; branches low-arching; most parts glabrous but with leaf axes, young stems, and inflorescences puberulent. Leaves imparipinnate, to 45 cm long; petioles mostly 4–8 cm long; leaflets (3)5(7), ± elliptic, acuminate, acute to obtuse at base, the terminal leaflet 20–32 cm long, 6.5–16 cm wide, the lower leaflets reduced in size. Flowers 3–4 mm long, ± sessile, white, cream or greenish, 4–6-parted,

in axillary panicles to 8 cm long (usually to 4 cm long, sometimes reduced to appear fasciculate); calyx ca 1 mm long, the lobes acute; petals ± oblong; stamens 8–12, to 3.5 mm long; filaments united into a tube in basal half, the tube orange, fleshy within, the free part villous, broader than anther; anthers villous; ovary bearing straight erect trichomes; style short. Capsules obovate, ca 1 cm long, yellowish or reddish, densely velutinous, sometimes transversely striate or bearing dense, flat, sharp protuberances ca 1 mm long, the valves 3 or 4; seeds 1 or 2, ca 6 mm long, black, partly covered by a red-orange aril. *Croat 14847, Foster 1123.*

Rare; seen in the vicinity of the large *Ceiba pentandra* trees (86. Bombacaceae) between Armour Trail 700 and Zetek Trail 400. Flowers from April to August (sometimes from March), with the fruits maturing from June to September (sometimes from April). Plants from the Osa Peninsula in Costa Rica flowered in October, with the fruits maturing in January and February.

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Darién and from tropical wet forest in Darién. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

Trichilia verrucosa C. DC., Monogr. Phan. 1:695. 1878

Tree, 5–20 m tall; outer bark minutely fissured, thin (bearing short, raised, horizontal lines on inner surface); inner bark reddish-brown on the outer edge, bearing impressed short horizontal lines, the sap with sweet, distinctive aroma; young twigs, rachises, axes of inflorescences and of leaves moderately short-appressed-pubescent, glabrous in age. Leaves alternate, pinnate, mostly 8–25 cm long, essentially glabrous; petioles flat on upper surface with marginal ribs; leaflets usually alternate, often dimorphic, those of full size usually 3–5, often with 1 or 2 pairs of minute, aborted leaflets at base, rarely with 7 full-sized leaflets, the blades ± elliptic, acuminate, acute to obtuse at base, 6–16 cm long, 2.5–6(7) cm wide; major lateral veins mostly 8–12, scarcely raised below, joining before the margin, the midrib usually flat above. Panicles solitary in upper axils, 5–17 cm long; flowers greenish, mostly 5-parted; calyx bowl-shaped, shallowly lobed, 1–2 mm long, glabrate; petals ovate, 2–3 mm long, usually glabrous but with minute papillae on margin; staminal tube one-half to two-thirds as long as petals, much broader than long, moderately to sparsely pubescent outside at least toward base (often glabrous outside in South America), sparsely to densely pubescent inside; anthers twice the number of petals, slender, slightly tapered toward apex, ca 1 mm long, dehiscing along lateral margins, alternating with and ± equaling acicular lobes of staminal tube; ovary broadly ovoid, 1–2 mm wide, with 2 or 3(4) locules, the trichomes dense, appressed, white on basal half; style ± equaling ovary at anthesis; stigma capitate, inconspicuously lobed, held about at height of anthers. Fruits ± globose, green at maturity, weakly verrucose, 2–3 cm diam, ± glabrous, dehiscing by 3 valves; seeds 1 or 2, covered with a shiny red aril. *Croat 5354, 6035.*

Rare; collected only along the shore between Bat Cove and the dock. Flowers from March to May. The fruits mature from August to September.

The species was considered synonymous with *T. cipo* by Smith (1965) in the *Flora of Panama,* but has been shown to be distinct from that species (Croat, 1975a).

Panama to the Guianas, Brazil, Bolivia, and Peru; Trinidad. In Panama, known from tropical moist forest on both slopes in the Canal Zone, Colón, Los Santos, Panamá, and Darién.

71. MALPIGHIACEAE

Trees, shrubs, or scandent lianas (may be only slightly woody in *Stigmaphyllon*). Leaves opposite, petiolate; petioles often glandular; blades simple, entire or irregularly toothed when juvenile; venation pinnate; stipules present; T-shaped trichomes frequently present. Flowers bisexual, actinomorphic or zygomorphic principally by modification of one petal, in axillary panicles, pseudo-

KEY TO THE TAXA OF MALPIGHIACEAE

Plants trees or shrubs, not scandent; fruits drupes, cocci, or capsules (except *Heteropteris*):
- Inflorescences much-branched, usually pyramidal panicles; fruits winged ..... *Heteropteris laurifolia* (L.) Adr. Juss.
- Inflorescences racemose or pseudocorymbose; fruits not winged:
  - Leaves densely and conspicuously soft-tomentose below ..... *Byrsonima crassifolia* (L.) H.B.K.
  - Leaves not tomentose below:
    - Flowers yellow:
      - Leaves glaucous and with appressed, white trichomes below, the younger parts not furfuraceous; flowers mostly 8–16; fruits 1.5–2.5 cm long, orange to red, the pyrenes usually 2 ..... *Bunchosia cornifolia* H.B.K.
      - Leaves not glaucous, ± glabrous in age, the younger parts densely furfuraceous; flowers many, usually more than 16; fruits ca 1 cm diam, green to yellow-orange, the pyrenes 3 ..... *Byrsonima spicata* (Cav.) H.B.K.
    - Flowers pink, red, or whitish:
      - Inflorescences pendent, to 20 cm long, the fertile part more than 5 cm long; fruits cocci of 2 carpels, ca 5 mm long ..... *Spachea membranacea* Cuatr.
      - Inflorescences erect or nearly so, to ca 8 cm long, the fertile part less than 4 cm long; fruits drupelike with 3 pyrenes, to 10 mm long ..... *Malpighia romeroana* Cuatr.

Plants scandent; fruits of 3 winged samaras:
- Wings of fruit lateral, each samara with 2 or 4 wings (sometimes united at apex into a nearly complete circle):
  - Lateral wings of samara deeply 2-lobed, the lobes narrow, elongate (contiguous or separate at the base); inflorescences mostly terminal panicles ..... *Tetrapteris*
  - Lateral wings of samara not lobate, the lobes often as broad as or broader than long; inflorescences various, mostly axillary:
    - Pedicels appearing articulate, with 2 bracteoles at the node or articulation; stipules small, at base of petioles; inflorescences panicles ..... *Mascagnia*
    - Pedicels sessile; stipules usually conspicuous, borne somewhere above base of petiole; inflorescences umbellate ..... *Hiraea*
- Wings of fruit dorsal, each samara with essentially one wing (lateral wings when present much smaller):
  - Inflorescences umbels of few flowers or series of widely separated umbels; stamens with 2 or more reduced and sterile; petioles bearing sessile glands at apex ..... *Stigmaphyllon*
  - Inflorescences panicles of many flowers, not appearing distinctly umbellate or as a series of umbels; stamens all fertile:
    - Inflorescence branches reddish-brown; petioles eglandular; samaras lacking reduced lateral wings or crests ..... *Heteropteris laurifolia* (L.) Adr. Juss.
    - Inflorescence branches not reddish-brown; petioles usually bearing 2 sessile glands near apex; samaras with reduced lateral wings or crests ..... *Banisteriopsis cornifolia* Small

racemes, or umbels of many flowers; sepals 5, free, often with conspicuous glands; petals 5, showy, free, clawed, fringed or toothed, alternate to the sepals; stamens (8)10, equal or unequal, sometimes with 4 reduced to staminodia; anthers 2-celled, introrse, dehiscing longitudinally, often with a thickened connective; ovary superior, mostly 3-locular, 3-carpellate; placentation axile; ovules solitary in each locule, pendulous, semianatropous; styles 3, free (rarely connate or with only 1 developed), sometimes forming a hood over the stamens; stigmas 1 per style or 3 when styles united, entire or minutely lobed. Fruits usually schizocarps of three samaras, sometimes drupes with 1–3 pyrenes (*Bunchosia, Byrsonima, Malpighia*), or sometimes berries of 2 separable cocci (*Spachea*).

Distinguished by the usually T-shaped (medicentric) trichomes, glandular calyx, and fringed petals. Most species are lianas.

Many species are markedly zygomorphic. Flowers are insect pollinated, and I have seen them visited by small bees. Vogel (1958) reported the family to be pollinated by anthophorid bees, usually *Centris*.

Fruits are mostly wind dispersed. A few species, including *Spachea membranacea, Bunchosia cornifolia, Malpighia romeroana,* and species of *Byrsonima,* are endozoochorous. *Malpighia romeroana* might be bat dispersed, since a similar species, *M. glabra* L., is eaten by bats in Trinidad (Goodwin & Greenhall, 1961).

About 60 genera and 850 species; mostly in the American tropics.

BANISTERIOPSIS C. B. Robinson ex Small

Banisteriopsis cornifolia (H.B.K.) C. B. Robinson ex Small, N. Amer. Fl. 25:132. 1910

B. cornifolia (H.B.K.) Spreng.

Liana; young stems, petioles, and blades below densely to sparsely pubescent, the trichomes appressed, T-shaped. Petioles 5–10 mm long, bearing 1 or 2 sessile glands along each side near apex; blades ovate to elliptic, acuminate (the acumen often downturned), rounded at base, 9–16(18) cm long, 4.5–7 cm wide, glabrous and somewhat shiny and rugulose above. Panicles axillary or terminal, solitary or several per axil, 4–15 cm long, branched many times; peduncles, pedicels, and sepals densely pubescent, the trichomes short, appressed; peduncles to 3.5 cm long; pedicels sessile, to 1 cm long (to 1.5 cm long in fruit); sepals ovate, 2–3 mm long, bearing large exterior glands; petals clawed, 4–7 mm long, yellow, glabrous, caducous; stamens and styles glabrous; stamens unequal; anthers ± oblong, glandular; styles 3, distinct, ± equaling stamens. Fruits of 1–3 samaras, each samara with a single dorsal wing thickened along the inner side; seminiferous area ca 8 mm long, densely pubescent, raised, with a small wing or ridge on both sides; dorsal wing 2.5–3.5 cm long, ca 1 cm wide, bearing short appressed pubescence especially near seed and a small protrusion on inner margin just above seed. *Foster 1478.*

Rare, in the forest, usually growing in the canopy. Probably flowers in late rainy and early dry seasons, with the fruits maturing in the dry season.

Southern Mexico to Peru. In Panama, known from tropical moist forest on BCI and from premontane wet forest in Panamá (Cerro Campana).

BUNCHOSIA L. C. Rich. ex Adr. Juss.

Bunchosia cornifolia H.B.K., Nov. Gen. & Sp. 5:154. 1822

Shrub or tree, to 6 m tall, pubescent especially on the younger and lower parts and on the leaf blades below, the trichomes appressed, T-shaped; stems becoming glabrous in age, the outer bark very thin, grayish, the lenticels and outer bark easily scraped off. Petioles to 1 cm long; blades ± elliptic to oblong-elliptic, acuminate, obtuse to acute at base and decurrent-revolute onto petiole, 6–15(35) cm long, 3–6(14) cm wide, the upper surface soon glabrous, the lower surface persistently pubescent and also glaucous, with scattered glands especially

near base, the margin often somewhat undulate; dried leaves making a characteristic oily deposit on drying papers. Pseudoracemes axillary, 5–8 cm long; flowers mostly 8–16, 1–1.5 cm broad, 5-parted; sepals oblong-elliptic, rounded at apex, each lobe inflexed, bearing 2 conspicuous, large glands; petals yellow, clawed, rounded to oblong, spreading, the margin irregular, 1 or more petals markedly concave, 1 petal somewhat erect, its margin entire; stamens 8, subequal, in a staggered whorl, 5 held in close proximity to style, the longest ca 2.7 mm long; filaments thickened at base, weakly fused; anthers dehiscing inward, the connective somewhat thickened apically; styles 3, to 1.5 mm long; stigmas 3, short, fleshy, held just above anthers; ovary weakly pubescent. Drupes ovoid, orange turning red at maturity, 1.5–2.5 cm long, the style bases persistent; exocarp thin; mesocarp pasty, eventually sweet and tasty, ca 2–3 mm thick; pyrenes 2(3), ovoid-hemispheroid, to 17 mm long, with a thin reticulate covering. *Croat 11107.*

Known from a few areas along the northern shore. Elsewhere in the Canal Zone the plant is common. Flowers from December to July, principally from April to July. The fruits mature from June to January, sometimes on flowering plants.

Fruits are probably dispersed chiefly by birds and other arboreal frugivores.

Southern Mexico to Colombia and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from tropical wet forest in Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

BYRSONIMA L. C. Rich. ex Adr. Juss.

Byrsonima crassifolia (L.) H.B.K., Nov. Gen. & Sp. 5:149. 1822

Nance, Nance blanco, Nance colorado

Tree, 4–13 m tall, to 30 cm dbh; bark fissured and lenticellate; wood dull reddish-brown, hard, heavy; younger parts densely downy-tomentose (sparsely on upper leaf surface and becoming glabrate); stems bearing prominent leaf scars. Petioles ca 1 cm long, stout; blades obovate to elliptic or ovate, acuminate, narrowed to an acute or obtuse base, 7–14 cm long, 3–8 cm wide, densely pubescent below becoming glabrate except on midrib in age; midrib ± arched. Pseudoracemes terminal, usually solitary, to 20 cm long; pedicels to 1.5 cm long; flowers many, yellow, becoming red-orange in age; sepals each bearing 2 conspicuous glands, blunt, recurved, glabrous inside; petals clawed, 10–13 mm long, the blade orbicular, often concave, ± equaling length of claw, the margin irregular, 1 petal often smaller and held somewhat erect, the others spreading to reflexed; stamens 10, 4–5 mm long, interspersed with long straight trichomes; anthers introrse, equaling length of styles, the thecae prominently raised, shedding pollen in bud, the connective thickened; ovary usually pubescent; styles 3, distinct, slender, longer than stamens, persisting on young fruits. Drupes ± globose, 1–1.5 cm diam, green turning yellow to reddish; pyrenes 1–3. *Croat 6068, 8702.*

Locally common along the shore; infrequent in the forest, usually near old settlement sites. Flowers from November to July, principally from March to June. Each tree flowers for about 6 weeks. The fruits mature principally in August and September. Leaves turn old and reddish, falling in the dry season and gradually growing out again in March just before the greatest flush of flowering. Allen (1956) reported that the species had fruits during April and May in Costa Rica, but the fruits were probably not ripe.

Byrsonima crassifolia may be confused with *B. cumingiana* Adr. Juss., which ranges from Nicaragua to Colombia. *B. cumingiana* is distinguished by having a glabrous ovary and leaves that are more thickly coriaceous and rugose above.

The fruits are probably dispersed by large birds and by mammals.

Veracruz, Mexico, south to Brazil and Paraguay; West Indies. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Coclé, Panamá, and Darién, from premontane dry forest in Coclé, from tropical dry forest in Los Santos and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, and from tropical wet forest in Colón. Tosi (1971) listed this species as characteristic of tropical dry and tropical moist forests in Panama.

Byrsonima spicata (Cav.) H.B.K., Nov. Gen. & Sp. 5:147. 1822

B. coriacea (Sw.) Kunth

Nance, Nancillo

Tree, to 22 m tall, the trunk to 40 cm dbh; outer bark thin, light brown, with many minute fissures; inner bark brownish-red, moderately thick, the sap lacking odor; young parts ferruginous, appressed-pubescent. Stipules narrowly triangular, ca 3 mm long; petioles to 8 mm long; blades oblong-elliptic, acuminate, acute and decurrent at base, 5–10(14) cm long, 1.5–3(4.5) cm wide, glabrate or sparsely pubescent below and on midrib above in age. Pseudoracemes terminal, 6–10 cm long; pedicels 4–8 mm long; flowers many, ca 1.5 cm diam, yellow; sepals to 2 mm long, lobed, glandular, the glands 10, oblong-obovate, yellow, the lobes curved outward at apex; petals subequal, ± orbicular, concave, clawed, 4–6 mm diam, subentire, 1 petal flat and somewhat more erect than the others; stamens 10, in 2 series, nearly erect, 3–3.5 mm long; filaments pubescent, nearly as long as anthers; anthers introrse, the connective swollen, somewhat prolonged at apex; styles 3, narrowly pointed, distinct, slightly longer

KEY TO THE SPECIES OF BYRSONIMA

Leaves softly and conspicuously tomentose below ..... *B. crassifolia* (L.) H.B.K.
Leaves glabrate to sparsely pubescent below ..... *B. spicata* (Cav.) H.B.K.

than stamens, persisting in fruit. Drupes ± globose, ca 10 mm diam, glabrous, green to yellow or yellow-orange at maturity; pyrenes 3. *Croat 11133.*

Infrequent; known from the younger forest on Colorado Peninsula. Flowers from June to August, with the fruits maturing from August to October.

The fruits are probably dispersed by birds or other arboreal frugivores.

Costa Rica to Colombia and Venezuela; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Darién and from tropical wet forest in Colón (Salúd) and Darién.

HETEROPTERIS Kunth

Heteropteris laurifolia (L.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13:276. 1840

Liana or climbing shrub (rarely elsewhere a small tree or shrub), 1–8 m tall; young stems and petioles pubescent, the trichomes dense, short, appressed. Petioles to 1.2 cm long; blades oblong-elliptic, acuminate, acute to obtuse at base, 10–17 cm long, 3.5–6(7.5) cm wide, glabrate, sometimes bearing small glands near margin at base. Panicles solitary, terminal or upper-axillary, to 12 cm long; inflorescence branches, pedicels, and sepals bearing dense, ferruginous, T-shaped trichomes; sepals lanceolate to oblong, recurved at apex, 2.5–4 mm long, eglandular or bearing glands covering the basal half; petals yellow, clawed, 4–5 mm long, glabrous; stamens 10, 3–4 mm long, ± equal, enlarged and fused at base; anthers ca 1 mm long; styles 3, distinct, truncate at apex, ± equaling stamens; stigmas ± equal. Schizocarps of 3 samaras, each samara with a well-developed dorsal wing, ferruginous-tomentose especially on the seminiferous area; wings 2–3 cm long, with a small protrusion on the apical end near the seed. *Croat 5122, 9550.*

Known only from several areas along the shore. Flowers from January to May, with the fruits maturing from March to June.

Mexico to Peru, Brazil, and the Guianas; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone and Panamá from tropical wet forest in Colón (Santa Rita Ridge); collected in 1839 in what was probably tropical wet forest on the Pacific slope of Veraguas.

HIRAEA Jacq.

Hiraea faginea (Sw.) Niedenzu, Gen. Hiraea 16. 1906

Liana; younger stems, axes of inflorescences, sepals, and lower leaf surfaces densely pubescent, the trichomes appressed, T-shaped, those of the stem very short, those of the lower leaf surface light brown. Petioles 4–6 mm long; stipules paired, subulate, to ca 4 mm long, borne near apex on upper surface of petiole; blades ± oblong-elliptic, acuminate, narrowly rounded to subcordate at base, 9–16 cm long, 3.5–6 cm wide, glabrous above, the trichomes of the lower surface contiguous. Umbels small, axillary; peduncles short, appearing solitary, branched, mostly shorter than pedicels; pedicels to 1 cm long; sepals ovate, all but 1 usually bearing conspicuous glands; petals clawed, yellow, orbicular, ca 6 mm wide, their margins lacerate, the claw to 3.3 mm long, the petal opposite the eglandular sepal somewhat erect, smaller than the other petals (to ca 4.5 mm wide), its margin with glandular teeth; stamens 10, ± equal, glabrous; styles 3, pubescent at base, 1 erect, the 2 opposite the erect petal arched-spreading. Schizocarps of 3 samaras (sometimes 1 or 2 by abortion), each samara with 2 large lateral wings; seminiferous area ± globular, ca 5 mm long, densely appressed-pubescent; wings shaped like butterfly wings, ca 2.5 cm wide and 3 cm long, thin, moderately appressed-pubescent especially near seed. *Foster 1105.*

Rare, along the shore. Some flowers were seen in January, June, and July, and mature fruits in August.

Nicaragua to Panama, Venezuela, probably also Colombia. In Panama, known from tropical moist forest on BCI and in Darién. Standley (1928) in the *Flora of the Canal Zone* says the species is frequent on the Atlantic slope.

Hiraea grandifolia* Standl. & L. O. Wms., Ceiba 3:116. 1952

Large, woody canopy vine, the trunk 10 cm or more broad near base; bark brown, densely lenticellate; all but the older stems very densely ferruginous-tomentose. Petioles densely furfuraceous, 1.5–3 cm long; stipules paired, prominent, subulate, at about the middle of peti-

*José Cuatrecasas finds *H. grandifolia* from Costa Rica to be distinct; the Panamanian species will be published as *H. croatii* Cuatr. in the *Flora of Panama.*

KEY TO THE SPECIES OF HIRAEA

Lower leaf surface not very densely and conspicuously pubescent except on midrib or when very young; leaves usually acute or rounded at apex and less than 20 cm long ..... *H. reclinata* Jacq.
Lower leaf surface densely and conspicuously pubescent; leaves acuminate at apex or more than 20 cm long:
  Umbels markedly pedunculate, the peduncle more than 1.5 cm long ... *H. quapara* (Aubl.) Sprague
  Umbels sessile or the peduncle less than 1 cm long:
    Leaves rounded to cuspidate or very short-acuminate at apex, the larger ones mostly more than 10 cm wide, pubescent on veins above; stems very densely and conspicuously ferruginous-pubescent ..... *H. grandifolia* Standl. & L. O. Wms.
    Leaves ± narrowly acuminate, the larger ones mostly less than 7 cm wide, glabrous above; stems not as above ..... *H. faginea* (Sw.) Niedenzu

ole; blades obovate, rounded and cuspidate to short-acuminate at apex, tapered to a narrow, cuneate, rounded or subcordate base, 12–30(67) cm long, 6–14(28) cm wide, glabrous except on veins above, densely pubescent below with branched trichomes; major lateral veins in 9–14 pairs, impressed above, raised below. Umbels axillary; peduncles short or to 8 mm long, 2–4 per axil; peduncles, pedicels, and calyces densely tomentose; pedicels 1–2 cm long; flowers 5-parted; sepals blunt, to 3 mm long, 4 of these bearing 2 red-orange, shiny, ovate glands to 1.5 mm long; petals yellow, clawed, the margins fimbriate, the petal opposite the eglandular sepal somewhat erect and marked with orange, its margins fimbriate, gland-tipped; stamens 10, of 2 lengths, shorter than styles and curling after anthers have fallen; styles 3, interspersed with dense straight trichomes, 2 twisted to either side of the erect petal; stigmas subterminal. Schizocarps of 3 samaras; wings lateral, ± reniform to semicircular, thin, 1–3 cm long, 2–5.5 cm wide, sparsely to moderately pubescent, the body densely pubescent with stiff straight trichomes. *Croat 12697.*

Frequent in the forest. Flowers from November to February. The fruits mature from February to April.

Seedlings often consist only of a long leafless stem.

Costa Rica and Panama. In Panama, known from tropical moist forest on BCI and in Colón.

See Fig. 308.

Hiraea quapara (Aubl.) Spraque, J. Bot. 62:22. 1924

H. smilacina Standl.

Liana; outer bark of older stems thin, reddish-brown, becoming fissured; most parts except upper leaf surface densely pubescent with T-shaped trichomes, those of the stems, petioles, peduncles, pedicels, and calyces appressed-pubescent. Petioles 1–2 cm long, with 2 sessile glands at apex; stipules 2, subulate, to 2 mm long, borne at about the middle of petiole; blades sublanceolate-elliptic to elliptic, gradually long-acuminate, ovate to subcordate at base, mostly 15–25 cm long, 6–11 cm wide, glabrous above except on midrib, softly pubescent all over the underside with stalked T-shaped trichomes. Umbels solitary, axillary, with small bracteoles at apex of peduncles; peduncles 2.5–4 cm long; pedicels 13–20 mm long; flowers (6)35–60 per peduncle, 10–12 mm diam; sepals triangular-ovate, 4 of these sometimes bearing 2 large glands; petals yellow, ovate-suborbicular, subcordate at base, 4–5 mm diam, the margin sinuate, fimbriate on all but the inner small petal; stamens 10, ± equal; ovary hirsute; styles 3, 1 erect, 2 curved, the apices narrowly spatulate-truncate with the outer angle acute or shortly apiculate. Schizocarps of 3 samaras, softly hirsute especially on seed; wings lateral, ± reniform, 0.5–2 cm long, 2–3 cm wide, thin. *Croat 6842, 11931.*

Occasional, in the canopy of the forest. Flowers in July and August. The fruits mature in October and November.

Costa Rica (possibly Belize) to Colombia and the Guianas. In Panama, known only from tropical moist forest on BCI.

Hiraea reclinata Jacq., Select. Stirp. Am. 137, t. 174, f. 42. 1763

H. obovata (H.B.K.) Niedenzu

Liana, ranging widely in forest over low vegetation or ± pendent from larger trees; younger parts, including peduncles, pedicels, and calyces, densely pubescent with T-shaped trichomes. Petioles usually ca 5 mm long, bearing paired sessile glands near apex; stipules subulate, borne about midway on petiole, slender, 3–5 mm long; blades elliptic to obovate, acute or rounded at apex (sometimes acuminate especially when young), tapered to a subcordate base, 5–15(22) cm long, 2.5–8.5 cm wide, glabrate to sparsely pubescent below; veins below densely appressed-pubescent. Umbels small; peduncles nearly obsolete or to 1.5 cm long; pedicels 9–25 mm long; sepals triangular to ovate, 4 usually glandular, the glands prominent, ± stalked, greenish-yellow, round to ellipsoid, ca 1.5 mm long; petals yellow, often marked with orange near base, to ca 7 mm long, clawed, the blade orbicular, the petal opposite the eglandular sepal with a fimbriate margin; stamens 10, of irregular sizes, some directed inward beneath styles; ovary lobed, the lobes densely pubescent; styles 3, ± flattened, curved, to 4.5 mm long; stigmas green, minute, lateral, directed inward. Schizocarps of 3 samaras; seminiferous area sparsely setaceous; wings lateral, orbicular to reniform, 1.2–1.6 cm long, 2–3 cm wide, thin, with sparse, appressed, T-shaped trichomes and prominent reticulate veins. *Croat 5614, 14028.*

Common in the forest. Found at all levels to over 30 m, but rarely flowering at the lower levels. Flowers from January to May. The fruits mature from February to June.

Mexico, Guatemala (probably throughout Central America), and Panama to Venezuela and Brazil. In Panama, known from tropical moist forest on BCI and in Colón, Panamá, and Darién.

MALPIGHIA L.

Malpighia romeroana Cuatr., Webbia 13:561. 1958

Shrub, to 2.5 m tall; stems and leaves glabrate. Petioles 2–4 mm long; blades elliptic, long-acuminate, acute at base, 10–16 cm long, 3.5–6 cm wide, sometimes bearing 4 glands at base ca midway between margin and midrib. Pseudocorymbs solitary in leaf axils, 3–8 cm long, bearing many flowers; inflorescence branches, pedicels, and calyces with sparse T-shaped trichomes; peduncles 1.5–3 cm long, bracteate about midway and at nodes; pedicels 5–8 mm long; sepals 5, ovate-elliptic, bearing 6 large, oblong-elliptic glands; petals pinkish outside, white inside, clawed, glabrous, to 5 mm long; stamens 10, unequal; styles 3, free, 1 reduced. Fruits drupaceous, ovoid, to 1 cm long and wide, red, with 3 crestlike appendages, drying ± 6-ridged; pyrenes 3. *Croat 6716, Foster 1590.*

Occasional. Flowers principally from August to October (sometimes to February). Time of fruit maturity is not known.

Fig. 309. *Mascagnia nervosa*

Fig. 308. *Hiraea grandifolia*

Fig. 310. *Stigmaphyllon ellipticum*

KEY TO THE SPECIES OF MASCAGNIA

Petioles bearing 2 large glands at apex; flowers yellow to orange ..... *M. hippocrateoides* (Tr. & Planch.) Niedenzu
Petioles eglandular (pair of glands at base of blade); flowers pinkish ..... *M. nervosa* Niedenzu

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

MASCAGNIA Bertero

Mascagnia hippocrateoides (Tr. & Planch.) Niedenzu, Arb. Bot. Inst. Lyc. Braunsberg 3:24. 1908
Hiraea hippocrateoides Tr. & Planch.

Liana, growing into canopy to ca 30 m; stems glabrate to glabrous in age. Petioles 7–15 mm long, canaliculate, biglandular near apex, the glands 2–3 mm broad; blades ovate to ovate-elliptic, acuminate, rounded at base, 5.5–20 cm long, 3–10 cm wide, glabrous. Panicles axillary, to 25 cm long, branched many times; flowering peduncles 5–12 mm long, bearing 2 small bracteoles and a large sessile gland at apex; bracteoles paired at nodes of inflorescence, 2–12 mm long, the larger ones near the base often toothed, 1 of each pair bearing a large gland; inflorescence branches and pedicels moderately pubescent with short T-shaped trichomes (somewhat ferruginous); pedicels pedunculate (appearing articulate just below flower), 2–4 mm long, enlarged at apex; sepals five, 1.5–3 mm long, oblique on pedicel, glabrous, curved inward against stamens, the lateral margins turned outward, the glands 9, mostly 2 per sepal, ± irregular, greenish, to 1.5 mm long; petals 5, clawed, obovate, 4 of these yellow, rounded at apex, undulate and rounded to truncate at base, 8–10 mm long, entire, the fifth petal orange (at least on margin), minutely undulate and fimbriate on margin, 11–13 mm long, to 7 mm wide, usually somewhat erect and held above the entire petals; stamens 10, spreading, unequal, 3 directed toward the orange petal between 2 of the styles, the longest to 4 mm long; anthers nearly as broad as long; ovary 3-parted, each part with 3 ribs, densely pubescent; styles 3, somewhat spreading, to ca 4 mm long, the upper edge prolonged into a point on the outer edge opposite the stigmatic surface. Schizocarps of 3 samaras, sparsely appressed-pubescent with short T-shaped trichomes; dorsal wings small, to ca 5 mm long, subglabrous, the lateral wings fan-shaped, 1.8–2.5 cm long, 1.7–3.3 cm wide, subglabrous. *Croat 14867, Foster 880, 2321.*

Occasional, in the forest. Flowers in May and June. The fruits probably develop to full size in a month.

Panama, Colombia, and Ecuador. In Panama, known only from tropical moist forest on BCI.

Mascagnia nervosa Niedenzu, Arb. Bot. Inst. Lyc. Braunsberg 3:12. 1908

Liana or scandent shrub, to 3 m or more long; stems bearing sparse T-shaped trichomes when young, glabrate in age. Petioles 8–15 mm long, sparsely pubescent, eglandular; blades ovate-elliptic, acuminate, obtuse to rounded at base, 7–16 cm long, 4.5–9 cm wide, glabrous above, glabrous below or moderately to densely pubescent on veins, especially midrib, the trichomes T-shaped, the glands 2, sessile, at base beside midrib below. Panicles axillary, divaricately branched, bracteolate at nodes; inflorescence branches, pedicels, and sepals short-pubescent; branches ending in a corymb of 4–12 flowers; peduncles ca 2 mm long, thicker than pedicel, minutely bracteolate at apex; pedicels pedunculate, 8–18 mm long; calyx bearing usually 8 large, green glands; sepals 5, ovate-oblong, 1.5–2 mm long, glabrous to sparsely pubescent; petals pink, clawed, ± equal, 4–4.5 mm long, keeled, entire; stamens 10, unequal (2 much larger than the others), ca 2 mm long; anthers oblong, introrse, yellowish, the connective conspicuously swollen on the outer side; ovary densely whitish-hirsute; styles 3, exceeding stamens, with a narrow lateral arm at apex. Schizocarps of 3 samaras; seminiferous area moderately appressed-pubescent; dorsal wings reduced, the lateral wings thin, ± semicircular, ca 3 cm long and 1.5 cm wide, often not divided at apex. *Croat 11681.*

Rare; growing in the canopy and along the shore. Flowers sporadically, mostly in the rainy season (March to October), with the fruits maturing from April to October.

Panama, Colombia, and Venezuela; Trinidad. In Panama, known from tropical moist forest on BCI and in adjacent areas of the Canal Zone and Panamá.

See Fig. 309.

SPACHEA Adr. Juss.

Spachea membranacea Cuatr., Webbia 13:548–49. 1958

Slender tree, to 10 m tall; trunk sap often somewhat milky; young stems, petioles, midribs of leaves, and inflorescence branches strigose, the trichomes ferruginous, T-shaped. Petioles 6–9 mm long; stipules minute, ovate, axillary; blades ovate-elliptic to oblanceolate, long-acuminate, rounded at base, 4–18 cm long, 1.5–6 cm broad, glabrate except on midrib above and below, bearing several round glands, usually 1 on each side of midrib below and others sometimes scattered on both surfaces, the margin entire, revolute in age. Racemes long, pendent, axillary, 10–20 cm long, the axis and peduncles sparsely ferruginous-pubescent with ± appressed, T-shaped trichomes; peduncles to ca 5 mm long, bearing 1 flower, 2 small bracteoles midway, and 5 inconspicuous glandular appendages at apex; pedicels appearing articulate, 5–10 mm long, pink; flower to 9 mm diam; sepals acute to rounded and reflexed at apex, ciliate, biglandular, the glands prominent, white, to 3 mm long, narrowed and curved outward at apex; petals magenta, obovate, ca 4 mm long, ciliate, spreading; stamens 10, ca 2 mm long,

shorter than sepals, ± equal; pistil bipartite, each part with a slender style; styles longer than ovary; stigmas ± divergent, held at about the level of anthers, persisting in fruit. Cocci fleshy, with a thin fleshy red covering at maturity; the carpels 2, separable, indehiscent, ovoid, 3.5–5 mm long and ca 2 mm wide; seeds 1 per carpel, hemispheroid, tan, smooth, ca 4 mm long. *Croat 6397, Foster 873.*

Frequent in the young forest. Flowers in the early rainy season (April to June). The fruits mature from June to August, though old fruits have been seen until February or March.

Fruits are probably dispersed chiefly by birds.

The species has been confused with *S. elegans* (G. Meyer) Adr. Juss., a species from the Lesser Antilles, the Guianas, and the Amazon basin, and it closely resembles *S. herbert-smithii* (Rusby) Cuatr. from Colombia. Both those species, however, have a prominent stalked gland on each one-flowered peduncle.

Colombia and Panama. In Panama, known only from tropical moist forest on BCI and in Darién.

STIGMAPHYLLON Adr. Juss.

Stigmaphyllon ellipticum (H.B.K.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13:290. 1840

Liana, essentially glabrous except for appressed T-shaped trichomes on some younger parts; stems reddish-brown. Petioles 1–3 cm long, bearing a pair of apical glands; blades ovate-elliptic to oblong-ovate, usually abruptly acuminate and often downturned at apex, obtuse to rounded at base, mostly 6–13 cm long, 2.5–6.5 cm wide, glaucous below. Pseudoumbels axillary, bearing few flowers; peduncles sparsely pubescent, 1.5–3.5 cm long, sometimes with sparsely pubescent bracteoles at apex; pedicels mostly 1–1.5 (2) cm long, glabrate; flowers to 2.5 cm wide; sepals rounded at apex, all but 1 bearing 2 conspicuous glands; petals 12–14 mm long, yellow, rounded, clawed at base, the margins fimbriate, the petals on either side of eglandular sepal somewhat to markedly cupular and usually fitted together after anthesis (cupped over the fertile parts); stamens 10, unequal, 6 long and equaling style, 3 of these situated beneath or adjacent to stigmas, producing much pollen, 3 long stamens sterile or producing little pollen, 2 short fertile stamens on either side of eglandular sepal, the other 2 short stamens on the opposite side of the flower sterile; anthers whitish, globular, fleshy, the connective produced above; pollen tan, sticking together loosely; styles 3, the stigmas green, the 1 opposite the eglandular sepal spatulate with an active gland near apex, the other 2 stigmas adjacent, broadly expanded, with a slit on the inner side, this oozing pollen from the anther below. Fruits usually of 3 samaras fused at base, reddish at maturity, especially the outer margin and apex, pubescent especially on seeds; dorsal wing 2–3 cm long, ca 1 cm wide, with a small crest or lobe on inner margin above seed, the lateral wings reduced, variously lobed or sometimes divided into 2–4 narrow appendages. *Croat 6438, 7901.*

Common in the forest, along the shore, and in clearings, growing over vegetation or along the ground. Flowers and fruits throughout the year.

Veracruz, Mexico, to Colombia and Ecuador; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Herrera, Panamá, and Darién, from tropical dry forest in Panamá, from premontane wet forest in Panamá and Chiriquí, and from tropical wet forest in Colón.

See Fig. 310.

Stigmaphyllon hypargyreum Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 18:318. 1862

Vine; branches, lower leaf surfaces, peduncles, pedicels, and sepals densely sericeous. Petioles 1–7 cm long, bearing 2 sessile, lateral glands at apex; blades broadly ovate, acuminate, rounded to truncate or subcordate at base, 8–13 (15) cm long, 5–9 (10) cm wide, glabrous above except on midrib, densely sericeous below, mostly eglandular, entire or irregularly crenate. Pseudoumbels terminal and axillary, simple or branched, pedunculate, of 10–16 flowers; peduncles 2–4 mm long; pedicels 5–8 mm long; sepals turned inward above, 4 bearing basal glands 2 mm long, 1 eglandular; petals rounded, clawed, at least the outer margin fimbriate, the 2 petals on either side of the eglandular sepal larger (to 9 mm diam), concave, yellow or with orange on center basally, the other 3 petals

KEY TO THE SPECIES OF STIGMAPHYLLON

Lower blade surface densely whitish-sericeous, the trichomes contiguous, the surface not visible ..... *S. hypargyreum* Tr. & Planch.

Lower blade surface not densely sericeous:

Lower leaf surface glaucous, the veins of adult leaves glabrous to sparsely pubescent; blades mostly ending abruptly at petiole; petals mostly more than 10 mm wide ..... *S. ellipticum* (H.B.K.) Adr. Juss.

Lower leaf surface not glaucous, the veins of adult leaves densely pubescent; blades mostly ending gradually at petiole; petals mostly less than 8 mm wide:

Larger leaf blades broadly ovate, palmately veined at base, the trichomes of lower blade surface short (less than 1 mm long); petals yellow or tinged with orange on one petal; samaras constricted at base, broader at apex ..... *S. lindenianum* Adr. Juss.

Larger leaf blades ± elliptic, not palmately veined at base, the trichomes of lower blade surface ca 2 mm long; petals yellow with violet-purple tips; samaras broad at base, tapering to apex ..... *S. puberum* (L. C. Rich.) Adr. Juss.

reduced, orange to red, the middle one often held higher, ± erect, its claw thicker; stamens 10, 6 long, fertile; anthers of long stamens covered (at least in part) by flaplike apices of styles, the connective enlarged, introrsely dehiscent; pollen tacky; styles 3, the stigmas expanded, the stigma of the style opposite the eglandular sepal concave. Schizocarps of 3 samaras; samaras 2–4 cm long, pubescent on seed and along thickened inner margin of wing; wing dorsal, 3–5 mm wide at base, enlarged to 1 cm wide at apex; seeds ± tuberculate. *Croat 7726, 13476.*

Infrequent, along the shore. Flowers in January and February. The fruits mature from February to April.

Trigona tataira bees visit the flowers (pers. obs.).

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

Stigmaphyllon lindenianum Adr. Juss., Arch. Mus. Hist. Nat. 3:362. 1843

Liana, moderately pubescent all over, the trichomes small, ± appressed, T-shaped, sparse between veins on upper leaf surfaces. Petioles 1–5 cm long, bearing 2 sessile, lateral glands at apex; blades ovate, obtuse to broadly acuminate, cordate or truncate to abruptly acute at base, 5–16 cm long, 4–11 cm wide, entire to variably and irregularly toothed (deeply lobed when juvenile), bicolorous, palmately veined at base, drying dark. Pseudoumbels several, often 1 sessile at each inflorescence node and 2 pedunculate at ultimate branches; peduncles 2–5 mm long, bearing 2 small bracteoles at apex; pedicels appearing articulate, very short or to 6 mm long; sepals 5, acute to acuminate, appressed-pubescent, held inward at apex, 4 bearing 2 thick glands ca 2 mm long; petals 5, yellow, caducous, rounded at apex, narrowed to a claw at base, ca 8 mm long, the margin ± revolute and irregularly toothed, the petal opposite the eglandular sepal with a thickened claw, the blade sometimes marked with orange at base, ± erect, the petals on either side of eglandular sepal with the lower margin upturned and cupulate; stamens 10, 2 or 3 elongating into hoods of styles, 4 reduced and sterile; anthers dehiscing inward, the connective much thickened; styles 3, to 4 mm long; stigmas broadened and hooded, ± divergent. Fruits of 3 samaras, often becoming reddish, appressed-pubescent especially on seeds; wing dorsal, 3–4 cm long, ca 5 mm wide at base, broadened to ca 9 mm near apex. *Croat 14083.*

Occasional, at the margin of clearings and in the canopy to a height of more than 30 m. Flowers and fruits throughout the year.

Mexico to Venezuela. In Panama, known from premontane moist forest in the Canal Zone, from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Panamá, and Darién, from premontane wet forest in the Canal Zone and Panamá, and from tropical wet forest in Colón, Chiriquí, and Darién.

See Fig. 311.

Stigmaphyllon puberum (L. C. Rich.) Adr. Juss., Ann. Sci. Nat. Bot., sér. 2, 13:289. 1840

Vine, moderately to densely appressed-pubescent with T-shaped trichomes on most parts. Petioles 1–4 cm long, bearing 2 sessile, lateral glands at apex; blades ovate to elliptic, long-acuminate, obtuse to rounded at base, 8–17 cm long, 3–10 cm wide, glabrous above except on midrib, moderately pubescent all over the underside. Pseudoumbels axillary, serial, to 12 cm long, divaricately branched, usually 1 sessile at each node; peduncles 2–4 mm long, minutely bracteolate at apex; pedicels appearing articulate, 2–5 mm long; inflorescence branches, peduncles, pedicels, and calyces densely pubescent; sepals to 4 mm long, ovate-oblong, rounded at apex, held against stamens, 4 bearing 2 broadly oblong glands 2–2.3 mm long, the fifth sepal sometimes with much-reduced glands, the glands with a thin, sticky covering; petals yellow, ± rounded, clawed, to 9 mm broad, the margins fimbriate, the 3 opposite the eglandular sepal spreading, usually tinged with purple-violet, the 2 petals on either side of the eglandular sepal ± erect, strongly concave, yellow or purple-violet at center outside; stamens 10, unequal, 4 reduced and sterile; styles 3; stigmas thin and broadly spreading, 1 bilateral. Schizocarps of 3 samaras; samaras pubescent especially on seed, dorsally winged; wing wider at base, 2–3 cm long, to 1.2 cm wide at base, ca 5 mm wide near apex. *Croat 11303.*

Rare; seen on the shore of Burrunga Point. The flowers were seen in June and July.

Guatemala to Peru, Brazil, and the Guianas; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Darién.

TETRAPTERIS Cav.

Tetrapteris discolor (G. Meyer) DC., Prodr. 1:587. 1824

Liana or scandent shrub; young branches densely whitish-sericeous with appressed, T-shaped trichomes, glabrous in age. Petioles 3–15 mm long, canaliculate, eglandular; blades ovate-lanceolate to ovate, acuminate, cuneate to obtuse at base, 6–16 cm long, 2.5–7 cm wide, ± thin, glabrous or nearly so at least in age. Panicles terminal and upper-axillary, with numerous pairs of reduced, ± rounded, leaflike bracts, the branches sericeous; flowers 9–12 mm diam, in umbels; floral bracts oval or elliptic, 5–30 mm long, glabrate or sparsely appressed-pubescent especially along midrib; peduncles 2–5 mm long; pedicels slender, 2–5 mm long; sepals ± ovate, obtuse, glabrous but sparsely ciliate, the glands oval, 2.5–3 mm long; petals yellow, ± elliptic, rounded at apex, sagittate at base, 4–5.5 mm long, entire; stamens 10; anthers 1.2 mm long; styles 3, ca 2 mm long. Samaras 3, sparsely pubescent, the trichomes white, appressed, more dense on seminiferous area; wings moderately thin, the superior wings obovate-oblong to oblong, 1.2–2 cm long, 6–10 mm wide, the inferior wings ovate, 6–8 mm long, 4–5 mm wide, the dorsal crest 2–3 mm high, the appendages between the dorsal crest and the wings 1–5, irregularly linear or ovate, longer or shorter than dorsal crest. *Wetmore & Abbe 186, Wilson 149.*

Known only from several old collections made from along the shore on the east side of the island. Although these were made at a time when that area was much more

Fig. 311. *Stigmaphyllon lindenianum*

Fig. 312. *Tetrapteris macrocarpa*

KEY TO THE SPECIES OF TETRAPTERIS

Fruits bearing several appendages between the lateral wings and the dorsal crest, the largest wing less than 2 cm long; flowers less than 12 mm wide; inflorescence bracts glabrate or sparsely pubescent:
- Samaras with several appendages on the seminiferous area between the dorsal and lateral wings (these distinct from the base and spreading); leaf blades gradually long-acuminate, 2.5–3 times longer than broad; stems densely pubescent, the pubescence persisting in age ..... *T. discolor* (G. Meyer) DC.
- Samaras lacking appendages between the dorsal and lateral wings; leaf blades acute to shortly acuminate, usually 2–2.5 times longer than broad; stems sparsely pubescent when young, the pubescence usually not persisting ..... *T. seemannii* Tr. & Planch.

Fruits lacking appendages between the lateral wings and the dorsal crest, the largest wing more than 3 cm long; flowers more than 13 mm wide; inflorescence bracts densely sericeous ..... *T. macrocarpa* I. M. Johnston

disturbed, the species probably still occurs on the island. Flowers and fruits in the early dry season.

Mexico to Bolivia; the Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, and Panamá and from premontane wet forest in Coclé (El Valle).

Tetrapteris macrocarpa I. M. Johnston, Sargentia 8:172. 1949

Liana, climbing into canopy; stems and axes of inflorescences densely pubescent, the trichomes whitish, appressed or stalked, T-shaped. Petioles canaliculate, 5–20 mm long; blades ± ovate to ovate-elliptic, acute to short-acuminate, rounded to subcordate at base, 4–15 cm long, 2.3–10 cm long, moderately thick, pubescent when young, glabrate in age, the trichomes dense, ± appressed. Panicles terminal or upper-axillary, with numerous, ± rounded, leaflike bracts; flowers 13–17 mm broad, in umbels; floral bracts pinkish, ovate to rounded, densely pubescent all over, 10–15 mm long; peduncles 2–4 mm long; pedicels 2–5 mm long; sepals ovate, blunt at apex, sericeous, the glands 2.5–4 mm long; petals yellow, prominently clawed, the blade ca 7 mm wide, ± rounded but weakly sagittate at base, the margin irregular; stamens 10; anthers ca 1.5 mm long; styles 3, ca 2 mm long. Samaras 3, persistently sericeous, the trichomes moderately dense all over; wings moderately thick, the superior wings ± oblong, rounded to ± truncate on the end, 3–5.5 cm long, 10–14 mm wide, not at all confluent with the inferior wing, the inferior wings spatulate, 6–15 mm long, 3–6 mm wide, the dorsal crest 2–3 mm high. *Croat 12703, Foster 1913.*

Occasional, along the shore and in the canopy of the forest. Flowers from July to September in the early rainy season. The fruits mature to full size from October to December and are dispersed in the late rainy and early dry seasons.

Standley and Steyermark erroneously called this taxon *T. acapulcensis* in the *Flora of Guatemala* (1946b). According to Cuatrecasas (1958) that species was erroneously reported as being described from Mexico; the species was actually described from Colombia.

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

See Fig. 312.

Tetrapteris seemannii Tr. & Planch., Prodr. Ann. Sci. Nat., sér. 4, 18:335. 1862

T. alloicarpha Rusby; *Banisteria ferruginea* Seem.

Liana or scandent shrub; stems slender, sparsely pubescent with T-shaped trichomes when young, soon glabrous, bearing interpetiolar ridges at least when young. Leaves thin; petioles 5–11 mm long, glabrous; blades elliptie to oblong-elliptic or ovate-elliptic, short-acuminate to acute at apex (the acumen downturned), mostly acute to obtuse but sometimes rounded at base, 5.5–13(16) cm long, 2–7 cm wide, glabrous above, glabrous below except the midrib at least sometimes sericeous when young, both surfaces with scattered glands less than 0.5 mm diam; major lateral veins 4–7 per side. Panicles terminal or upper-axillary, usually exceeding the leaves; branches, peduncles, and pedicels sericeous, soon glabrate; bracts inconspicuous, oval to elliptic, appressed-pubescent especially near base, 5–20 mm long; peduncles 2–5 mm long; pedicels slender, 2–5 mm long; sepals narrowly ovate, obtuse, 2.5–3 mm long, glabrous but ciliate; calycine glands thick, shiny, 2–2.5 mm long; petals clawed, yellow, probably turning orange in age, glabrous, the blade obovate to oblong-elliptic, sagittate at base, 4–5.5 mm long, 2.6–4 mm wide, the margin entire, the medial vein thickened toward the base, the claw thick, 1.5–2 mm long; anthers elliptic, glabrous, 1–1.2 mm long; styles held ca 1.5 mm above the sepals, slightly longer than stamens. Samaras stramineous to brown, glabrous, the wings thin but rigid, the veins often conspicuous, the superior wing narrowly spatulate, 15–30 mm long, 6–10 mm wide, the inferior wing ovate to obovate or rarely spatulate-oblong, 6–9 mm long, 4–6 mm wide, the adjacent margins of the superior and inferior wings confluent at base, the dorsal wing semiorbicular, rigid, 2–4 mm high; appendages between dorsal and lateral wings usually lacking; seed glabrous, ca 6 mm diam. *Aviles 17b.*

Collected once by Aviles; not seen in recent years, but the species could easily be overlooked. Flowers in Sep-

tember and October (rarely as late as November). The fruits develop to mature size by late November and are dispersed in the dry season beginning in December and are usually lost by late March.

Tetrapteris seemannii is easily confused with *T. discolor,* especially in flower. *T. discolor* tends to be more densely pubescent, with more pubescence persisting on the stem in age. Its leaves tend to be gradually long-acuminate and 2.5–3 times longer than wide. *T. seemannii,* on the other hand, has blades merely acute to short-acuminate at apex and usually 2–2.5 times longer than wide. Its stems bear less pubescence on the younger parts and are soon glabrate.

Panama and Colombia. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Chiriquí, Los Santos, Panamá, and Darién and from premontane moist forest in Panamá.

72. TRIGONIACEAE

Lianas. Leaves opposite, petiolate; blades simple, entire; venation pinnate; stipules present, interpetiolar. Panicles terminal, thyrsoid; flowers bisexual, zygomorphic; sepals 3 or 4, basally connate, unequal; petals 5, free, white, very unequal, the posterior one largest and spurred; stamens 10, with 4 usually sterile, the filaments basally united into a tube, the tube cleft opposite the spurred petal; anthers 2-locular, introrse, longitudinally dehiscent; glandular disk present; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules several per locule; style 1; stigma truncate. Fruits 3-valved, septicidal capsules; seeds several per locule, woolly, with endosperm.

The family is represented on BCI only by *Trigonia.* This liana can be recognized by its zygomorphic flowers with the stamens only partly fertile and united into a cleft tube.

Flowers are zygomorphic and seem well suited to pollination by small bees.

Seeds are wind dispersed.

About 4 genera and 40 species; tropical South America, Madagascar, and Malaya.

TRIGONIA Aubl.

Trigonia floribunda Oerst., Vidensk. Meddel. 38. 1856

Liana, growing into canopy, the ultimate branches usually pendent; young stems and inflorescence branches densely grayish-tomentose to glabrate in age; stems angulate to terete in age. Leaves moderately pubescent to glabrate; petioles 1–1.5(2) cm long; stipules interpetiolar, caducous, leaving conspicuous scar; blades obovate-oblong to oblong-elliptic, acute to short-acuminate, obtuse to rounded at base, 9–15 cm long, 4.5–7.5 cm wide. Panicles terminal, thyrsoid, to 23 cm long; pedicels to 2 mm long; flowers ca 7 mm diam; sepals 3, irregular, 2.5–4 mm long, recurved, acute to blunt, variously imbricate, glabrous inside, densely tomentose outside, one or both margins woolly; petals 5, white, unequal, 3–4 mm long, rounded at apex, the lateral petals narrower, obovate-spatulate, ± erect, the anterior petals folded medially and concave inside, weakly enclosing the cluster of anthers, the posterior petal spreading, ± rounded at apex, yellow to brown medially, the base produced into a ± globose spur, densely bearded at its apex inside, enclosing a glandular-crenate projection of the disk (appearing to be continuous with staminal tube); fertile stamens 6; filaments 10, unequal, connate more than half their length, forming an open tube around style; ovary and style together ca 3 mm long; ovary ovoid, densely white-villous; style slightly longer than stamens; stigma ± oblique. Capsules ca 2 cm long, 1.5 cm broad, bifid at apex, dark, rugose, glabrous, the valves coriaceous; seeds oval, 6–9 in each locule, pubescent, the trichomes long, yellowish, silky. *Croat 16581.*

Rare; known only from a few locations in the younger forest, though doubtlessly more abundant. Because of its growth habit high in the canopy and its inconspicuous white flowers it is seldom seen. Flowers in the middle of the rainy season. The fruits are probably mature in the late rainy and early dry seasons.

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

73. VOCHYSIACEAE

Trees. Leaves opposite, petiolate; blades simple, subentire; venation pinnate; stipules present. Thyrses terminal, axillary; flowers bisexual, zygomorphic; calyx 5-lobed, 1 of the lobes spurred; petals 3, free, unequal, showy; fertile stamen 1; anther 2-celled, introrse, dehiscing longitudinally; staminodia 2; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules 2 per locule, anatropous; style 1; stigma lateral. Fruits 3-valved, loculicidal capsules; seeds 3, winged, exalbuminous.

The family is represented in Panama only by *Vochysia.* It is distinguished by having opposite leaves and many brownish-orange, zygomorphic flowers with five sepals (one spurred) and three petals.

The flowers are visited by bees and butterflies (R. Dressler, pers. comm.).

Seeds are wind dispersed. Plants tend to be very underdispersed, with most of the plants in large clumps, indicating that the seeds are not carried very far and/or have few predators.

Six genera and about 200 species; tropical America and West Africa.

VOCHYSIA Aubl. mut. Poir.

Vochysia ferruginea Mart. in Mart. & Zucc., Nov. Gen. Sp. Pl. 1:151, t. 92. 1824

Yemeri mayo, Yemeri macho, Yemeri wood, Flor de mayo, Pegle, Mocri, Mecri, Palo malin

Tree, 6–25 m tall (taller elsewhere); trunk usually to 30 cm dbh; bark smooth; branches widely spreading, the crown somewhat flattened; branchlets, rachises, and lower leaf surfaces softly ferruginous-tomentulose. Leaves

short-petiolate; stipules minute; blades elliptic-oblong, long-acuminate, acute to obtuse at base, glabrous and shiny above except on midrib, 6–13 cm long, 2–4.5 cm wide, the margin revolute. Cincinni terminal and axillary, cylindrical, ca 15 cm long; flowers 1–5, zygomorphic, yellow-orange; calyx lobes 5, unequal, 1 equaling petals and spurred at base, the spur recurved; petals 3, oblong-spatulate, to 1 cm long; stamen 1, opposite the anterior petal, slightly shorter than petals; anther boat-shaped; staminodia 2; style equaling anther, sunken in face of anther in bud; stigma lateral. Capsules 3-angular, ± oblong-obovoid, 3-celled, obtuse to subretuse at apex, 1.7–2.5 cm long, 5–8 mm wide, slightly verrucose, gray-green; seeds to 2.3 cm long, with a unilateral wing, the limb tomentose. *Croat 5428, Foster 1112.*

Occasional; locally abundant in young areas of the forest, especially north of Barbour Trail, on Gross Peninsula, and on Orchid Island. Flowers from late March to early July, mostly from April to June, with individual trees flowering for as long as 2 months. A second, much smaller flowering may occur in September and October. The fruits mature from August to October.

Nicaragua to Peru and Brazil. In Panama, known from tropical moist forest in the Canal Zone and Panamá and from premontane wet forest in Colón and Panamá. Reported from tropical wet and premontane rain forests in Costa Rica (Holdridge et al., 1971).

74. POLYGALACEAE

Scandent shrubs, short lianas, or annual herbs. Leaves alternate, petiolate; blades simple, entire or undulate; venation pinnate (vein 1 in *Polygala*); stipules lacking. Racemes terminal or axillary; flowers bisexual, zygomorphic, subtended by 1 bract and 2 bracteoles; sepals 5, 2 enlarged; petals 3, the lower one keel-shaped; stamens 8, monadelphous; anthers 1-celled, dehiscing by terminal pores; ovary superior, 2-locular (1-locular by abortion in *Securidaca*), 2-carpellate; placentation axile; ovules 1 per locule, pendulous, anatropous; style 1; stigmas 2 or bilobed. Fruits samaras (*Securidaca*) or 2-valved, loculicidally dehiscent capsules; seeds arillate in *Polygala,* with soft endosperm.

Though the flower parts are not analogous, the flowers resemble those of Leguminosae (63). Members of the family may be distinguished by having simple leaves (relatively few Leguminosae have simple leaves) and a bilocular ovary.

Flowers are well suited for bee pollination, possibly by very small bees in the case of *Polygala paniculata.*

Seeds of *Securidaca* are wind dispersed. Those of *Polygala paniculata* are possibly just spilled locally, but Ridley (1930) reported the presence of elaiosomes on the seeds of *Polygala* and thus suggested ant dispersal.

Twelve genera and about 800 species; widely distributed.

POLYGALA L.

Polygala paniculata L., Syst. Nat. ed. 10, 1154. 1759

Annual herb, to 50 cm tall, usually branched many times; stems densely and minutely stalked-glandular. Leaves short-petiolate; blades mostly linear-lanceolate, acute, to 3.2 cm long and 3.5 mm wide; vein 1. Racemes long, slender, terminal or upper-axillary, 3–7 mm long; flowers red-violet, pedicellate, 2–2.5 mm long; sepals 5, the outer 3 minute, green or tinged with white or red-violet, the inner 2 equaling petals, red-violet, oblong, rounded at apex; petals 3, the upper 2 white, ± connate laterally and enfolding the lower petal, the lower petal keel-shaped, crested, enclosing stamens and style, the crest 6–10-lobed, the lobes often tinged with red-violet; stamens 8, arranged in a fan-shaped pattern within the lower petal; filaments connate nearly to apex; ovary obovoid to orbicular, 0.6–0.8 mm long; style curved, flattened, recessed among stamens; stigmas 2, widely spaced, on either end of the staminal cluster. Capsules ± oblong, 1.8–2.6 mm long, 2-valved; seeds oblong, to 1.8 mm long, black, densely erect-pubescent, arillate at base, the aril slender, bilobed, more than one-third as long as seed. *Croat 11988.*

Seasonally frequent in clearings. Flowers and fruits principally in the rainy season.

Pantropic weed. Throughout Panama in weedy situations in tropical dry, tropical moist, tropical wet, and premontane wet forests; known from the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Herrera, Coclé, Panamá, and Darién.

See Fig. 313.

SECURIDACA L.

Securidaca diversifolia (L.) S. F. Blake in Standl., Contr. U.S. Natl. Herb. 23:594. 1923

Bejuco amarrar, Bejuco mulato, Elsota

Scandent shrub or liana, usually to 4 m but sometimes also in canopy; strigose all over but the upper leaf surface glabrate; stems bearing raised round glands at the

KEY TO THE SPECIES OF POLYGALACEAE

Plants herbs less than 50 cm tall; leaves less than 5 mm wide ..... *Polygala paniculata* L.
Plants lianas or scandent shrubs; leaves more than 10 mm wide:
- Leaves and stems usually strigose or glabrate, usually drying green; petals less than 7 mm long; samaras with a small triangular lobe or tooth above seed partly free from wing; flowering principally from February to April ..... *Securidaca diversifolia* (L.) S. F. Blake
- Leaves and stems softly and densely pilose; petals more than 8 mm long; samaras with a small stipitate gland above on margin of wing; flowering principally in May and June ..... *Securidaca tenuifolia* Chodat

Fig. 313. *Polygala paniculata*

Fig. 314. *Securidaca diversifolia*

base of each petiole. Petioles 5–10 mm long; blades ovate-elliptic, bluntly acuminate at apex, rounded to obtuse at base, 6–11 cm long, 3–4.5 cm wide (much reduced and oval on flowering branches). Racemes terminal or axillary, to 11 cm long; pedicels ca 5 mm long; flowers 1.5–2 cm broad; enlarged sepals 2, petaloid, lavender, ± rounded and clawed, the other 3 ovate, to ca 3 mm long; petals 3, red-violet, the upper petals subspatulate, 5–7 mm long, the lower 1 keeled, 7.5–10 mm long, enclosing sexual parts, the apex with a folded, fimbriate crest; stamens 8, united basally into a thick sheath, the apical one-third free, tapered, the inside pubescent; anthers much shorter than stigma; style curved inward; stigmas bilobed. Samaras 4–6 cm long; wing ± oblanceolate, 3–5 cm long, 1–1.5 cm wide; seed apical, 5–8 mm long, margined above, the margin extended above into a small triangular lobe partly free from rest of wing. *Croat 8660.*

Occasional, along the edge of the lake, in older clearings, or at the edges of clearings; rarely high in the forest. Flowers in the dry season, usually from February to April (rarely in May in the early rainy season). Most fruits are mature in the late dry season.

Stems sometimes twine in a manner characteristic of the Hippocrateaceae (78).

Mexico to Peru; Lesser Antilles. In Panama, known from tropical dry forest in Coclé and Panamá, from premontane moist forest in Los Santos and Panamá, from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, and from premontane wet forest in Coclé and Panamá.

See Fig. 314.

Securidaca tenuifolia Chodat, Bull. Herb. Boissier 3:545. 1895

Scandent shrub or liana; stems bearing raised, round, stipular glands at the junction of each petiole; most parts softly short-pilose. Petioles 2–4 mm long; blades oblong-ovate to ovate, obtuse to rounded and sometimes emarginate at apex, rounded to truncate at base, 3.5–9.5 cm long, 2–3.5(4) cm wide, sparsely pilose or glabrate above, densely velvety-pilose below. Racemes terminal, 3–3.5 cm long; pedicels 5–8 mm long; flowers magenta, to 1 cm long; outer sepals 2, enlarged, 3.5–5 mm long, the other 3 oval, 2.5–4 mm long; petals 3, the upper 2 obovate or obovate-spatulate, 8–11 mm long, the lower 1 keeled, enclosing sexual parts, folded, with a minute fimbriate crest at apex less than 1 mm long; stamens 8, united at base into a sheath, pubescent at base; anthers much shorter than stigma; style 7.5–11 mm long; stigma bilobed. Samaras 4.5–7 cm long, densely short-pilose at least on seminiferous part; wing obovate-oblong, 4–6 cm long, 1–2 cm wide, with a small stipitate gland on margin near seed; seed apical, 5–8 mm long. *Woodworth & Vestal 505.*

Not seen in recent years; rare or no longer present on the island. The species apparently flowers more than once per year, mostly in May and June (rarely early July), with the fruits maturing in July and August, and again in September, with the fruits maturing in January.

Woodworth & Vestal 505 was collected in flower in February. It is intermediate in several ways between *S. tenuifolia* and *S. diversifolia* and may represent only an aberrant collection of the latter species.

Panama; Trinidad. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién and from premontane wet forest in Colón (Santa Rita Ridge).

75. EUPHORBIACEAE

Trees, shrubs, lianas, vines, or annual or perennial, erect or repent herbs, with or without spines, often with milky sap. Leaves alternate or less commonly opposite, petiolate; blades simple or palmately compound or lobed, entire to serrate, often stellate-pubescent; venation pinnate or occasionally palmate at base; stipules present (may be reduced). Flowers unisexual (monoecious or dioecious), actinomorphic, the inflorescences various, usually axillary, often specialized into condensed partial inflorescences (cyathia); calyx 2–11-lobed or lacking; petals 4–13 and free or commonly lacking; stamens 1 to many, in 1 or 2 series, often united by their filaments; anthers 2-celled, dehiscing longitudinally; intrastaminal disk often present; ovary superior, (2)3-locular, 2- or 3-carpellate (4-locular and 4-carpellate in *Phyllanthus,* 4- or 5- in *Margaritaria,* 10- in *Hura*); placentation axile; ovules 1(2) per locule, anatropous; styles 2–5, free or connate, simple or lobed; stigmas discoid (sometimes compound). Fruits usually explosive, septicidally dehiscent capsules or schizocarps, often with mericarps attached apically to columella, or fruits drupaceous (*Drypetes, Hyeronima*) or pyrenes; seeds 1 or 2 per locule or 1 per fruit by abortion; endosperm usually copious, rarely lacking.

Together with the Flacourtiaceae (96), one of the most morphologically diverse families. Euphorbiaceae are most easily recognized by their unisexual flowers and generally three-valved woody capsules with elastically dehiscent cocci separating from a persistent columella.

Most species are probably insect pollinated, although a few species are adapted for wind pollination (*Acalypha* and perhaps also *Adelia triloba*). Most flowers are unisexual but otherwise not very specialized. The tacky

KEY TO THE TAXA OF EUPHORBIACEAE

- Leaves conspicuously lobed or compound:
  - Plants vines ..... *Dalechampia* (in part)
  - Plants erect herbs, shrubs, or trees:
    - Leaves deeply lobed, glaucous beneath; capsules ribbed ..... *Manihot esculenta* Crantz
    - Leaves shallowly lobed, not glaucous beneath; capsules not ribbed ..... *Jatropha curcas* L.

- Leaves simple and not lobed:
  - Plants herbs:
    - Leaves all less than 1.5 cm long:
      - Leaves opposite; plants repent, forming mats; stipules toothed or conspicuously ciliolate; capsules ca 1 mm diam ..... *Chamaesyce thymifolia* (L.) Millsp.
      - Leaves alternate; plants erect or ascending; stipules entire; capsules ca 2 mm diam ..... *Phyllanthus* (in part)
    - Leaves sometimes more than 1.5 cm long:
      - Leaves opposite:
        - Leaves more than 5 cm long ..... *Poinsettia heterophylla* (L.) Klotzsch & Garcke
        - Leaves less than 3.5 cm long ..... *Chamaesyce* (in part)
      - Leaves alternate:
        - Leaves palmately veined at base; stems and petioles conspicuously pubescent:
          - Petioles bearing stalked glands at apex; stems with acicular, stiffly spreading, stellate trichomes with one branch larger and 2 mm or more long ..... *Croton hirtus* L'Hér.
          - Petioles lacking glands; stems with simple trichomes ..... *Acalypha arvensis* Poepp.
        - Leaves not palmately veined at base; stems and petioles not conspicuously pubescent; petioles eglandular:
          - Leaves less than 4.5 cm long; inflorescences axillary; capsules on slender pedicels more than 1 cm long:
            - Leaves linear to oblong-ovate, obtuse to mucronate at apex, 2–6(9) mm wide; capsules with pedicels less than 5 mm long ..... *Phyllanthus urinaria* L.
            - Leaves ovate to elliptic, acuminate at apex, 10–25 mm wide; capsules with pedicels 5–12 mm long ..... *Phyllanthus acuminatus* Vahl
          - Leaves more than 5 cm long; inflorescences terminal; capsules nearly sessile ..... *Poinsettia heterophylla* (L.) Klotzsch & Garcke
  - Plants vines, shrubs, or trees:
    - Leaves pinnately veined at base:
      - Petioles bearing conspicuous stalked glands at apex ..... *Sapium*
      - Petioles lacking glands at apex:
        - Flowers borne in fascicles or short racemes less than 1 cm long:
          - Inflorescences terminal (becoming overtopped by branches in fruit); pedicels more than 1 cm long; fruits 3-valved capsules more than 3 cm wide ... *Garcia nutans* Vahl
          - Inflorescences axillary; pedicels less than 5 mm long; fruits drupes ca 1.5 cm wide or capsules ca 1 cm wide with 5 or 6 cocci:
            - Ovary densely pubescent, the stigmas discoid to weakly lobed; fruits broadly ovoid, indehiscent; stipules lacking; leaf acumen thickened at apex, hyaline or discolored ..... *Drypetes standleyi* Webster
            - Ovary glabrous, the stigmas free, on frequently bifid to tripartite styles; fruits depressed-globose, irregularly dehiscent; stipules subpersistent; leaf acumen not thickened ..... *Margaritaria nobilis* L.f.
        - Flowers borne in panicles or racemes more than 5 cm long:
          - Plant densely covered with lepidote scales; leaf blades more than 5 cm wide; plants dioecious, the pistillate inflorescences producing many fruits; fruits ca 3 mm diam, fleshy ..... *Hyeronima laxiflora* (Tul.) Müll. Arg.
          - Plants glabrous, not bearing lepidote scales; leaf blades less than 5 cm wide; plants monoecious, each inflorescence producing few fruits; fruits more than 1 cm diam (*Codiaeum* on BCI not setting fruit):
            - Leaves strap-shaped, often variegated; plants cultivated shrubs in the Laboratory Clearing ..... *Codiaeum variegatum* (L.) Blume
            - Leaves oblong, not variegated; plants common in the forest ..... *Mabea occidentalis* Benth.
    - Leaves conspicuously palmately veined at base:
      - ◆ Petioles bearing conspicuous, usually stalked glands at apex:
        - Plants vines or lianas:
          - Plants herbaceous vines; glands at apex of petiole stalked, at least in part acicular; flowers borne in conspicuous, foliaceous bracts; fruits capsules less than 1.5 cm diam ..... *Dalechampia dioscoreifolia* Poepp.
          - Plants lianas; glands at apex of petiole sessile, disk-shaped; flowers not borne in foliaceous bracts; fruits fleshy, more than 6 cm diam ..... *Omphalea diandra* L.
        - Plants trees:
          - Plants large trees with spiny trunks; leaf blades glabrous or bearing simple trichomes on lower surface, usually conspicuously toothed ..... *Hura crepitans* L.
          - Plants small to medium-sized trees, unarmed; leaf blades stellate-pubescent, ± entire ..... *Croton* (in part)

◆Petioles lacking glands:
Leaves ovate-cordate:
Plants cultivated shrubs in Laboratory Clearing; leaves usually reddish; plants ± glabrous ..... *Acalypha wilkesiana* Müll. Arg.
Plants trees in forest; leaves not reddish; plants conspicuously and densely pubescent ..... *Acalypha macrostachya* Jacq.
Leaves not ovate-cordate, mostly ± elliptic and at most subcordate at base:
Leaves with glands at base of blade on lower surface; trichomes stellate (may be branched from near base); capsules 2-valved, with 2 persistent, simple styles usually 7–20 mm long ..... *Alchornea*
Leaves eglandular; trichomes simple or lacking; capsules trilobate, lacking a conspicuous style:
Plants dioecious; flowers clustered in axils; capsules more than 7 mm diam, borne on a pedicel more than 1.5 cm long; stipules inconspicuous ..... *Adelia triloba* (Müll. Arg.) Hemsl.
Plants monoecious; flowers in dense catkinlike spikes; capsules ca 3 mm diam, sessile, borne at base of spike; stipules lanceolate, persistent, 4–8 mm long ..... *Acalypha diversifolia* Jacq.

pollen of *Hura crepitans* oozes forth in great abundance, but the pollination system is unknown. The extrafloral nectaries of *Chamaesyce* and *Poinsettia* provide their only attractants for insects and birds. G. Webster (pers. comm.) reports that most Euphorbiaceae are pollinated by *Diptera* (midges) and that *Dalechampia* is pollinated by carpenter bees.

Seeds of most species are mechanically dispersed by the elastically dehiscent cocci that break free from the persistent columella. This is a very effective means of dispersal. *Hura crepitans* has been known to throw seeds 14 m (van der Pijl, 1968). A few taxa have fruits that are variously colored and mostly bird dispersed. They may be indehiscent (*Hyeronima*) or dehiscent with a colorful seed (*Sapium, Alchornea*). *Margaritaria nobilis* has mimetic fruits, not fleshy, but brightly colored, apparently functioning to deceive fruit-eating birds (van der Pijl, 1968). *Drypetes* and possibly also *Omphalea* are mammal dispersed. Fruits of *Sapium* are taken by white-faced monkeys (Oppenheimer, 1968). Both white-faced and howler monkeys take fruits of *Hyeronima* (Oppenheimer, 1968; Carpenter, 1934). *Acalypha* have beetle-like seeds which may be taken by carnivorous ants. Fruits of *Mabea occidentalis,* while basically mechanically dispersed, are colored and are also taken by white-faced monkeys (Oppenheimer, 1968) before the pericarp becomes fully woody. It is not known if the seeds are viable after passing through the monkeys. Hydrochory may be important in *Omphalea diandra* (Ridley, 1930). Seeds of *Croton* and *Euphorbia* (*Chamaesyce*) are harvested by ants in the southeastern United States (Wheeler, 1910). This is possibly also true of *Chamaesyce* in the tropics.

More than 300 genera and 7,000 species; widely distributed, but mainly in the tropics.

ACALYPHA L.

Acalypha arvensis Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3:21. 1841

Monoecious herb, 20–50 cm tall; stems and petioles moderately to densely pubescent, at least the smaller trichomes conspicuously recurved. Leaves alternate, simple; stipules lanceolate, to ca 1 cm long; petioles mostly 1–2.5 cm long; blades ovate, acute at apex, cuneate at base, mostly 3–6 cm long and 1.5–3 cm wide, strigose-hirsute above, glabrous below except on veins, the margins crenate-serrate; veins palmate at base. Spikes axillary; bisexual spikes ellipsoid to short-cylindrical, the peduncles 6–12 mm long, the pistillate part to 2 cm long and 1.5 cm wide, the staminate part usually a terminal projection 4–7 mm long, bearing 5–10 nodes of flowers and sometimes a bractless pistillate flower. Pistillate flowers solitary, sessile; floral bracts 4–8 mm long, with usually 5 lobes, the medial lobes mostly 2.5–5 mm long; ovary apically 3-keeled, hispidulous, eglandular; styles 1.7–4 mm long, with 3–5 distal branches. Staminate spikes uninterrupted, ca 5–20 mm long, the peduncles 3–25 mm long. Capsules sharply keeled, hispid to hispidulous; seeds 1–3, ellipsoid, to 1.3 mm long, grayish. *Croat 17748.*

KEY TO THE SPECIES OF ACALYPHA

Plants herbs, less than 50 cm tall ..... *A. arvensis* Poepp.
Plants shrubs or trees, more than 1 m tall:
Stems and petioles conspicuously pilose ..... *A. macrostachya* Jacq.
Stems and petioles ± glabrous:
Leaves ovate-cordate, usually reddish; plants cultivated shrubs in the Laboratory Clearing ..... *A. wilkesiana* Müll. Arg.
Leaves ± elliptic, not reddish; plants abundant in the forest ..... *A. diversifolia* Jacq.

Fig. 315. *Acalypha diversifolia*

Fig. 316. *Acalypha macrostachya*

Fig. 317. *Adelia triloba*

Collected once in the clearing north of the dock. Flowers and fruits principally in the rainy season.

Throughout the New World tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Panamá, and Darién, from premontane wet forest in Bocas del Toro, Chiriquí, and Coclé, and from lower montane rain forest in Chiriquí (Cerro Horqueta).

Acalphya diversifolia Jacq., Hort. Schoenbr. 2:63, t. 244. 1797

Monoecious shrub or small tree, to 6 m tall; stems sparsely pubescent. Leaves alternate, simple; stipules lanceolate, 4–8 mm long, persistent; petioles 1.5–3 cm long; blades ± elliptic, long-acuminate, narrowed and obtuse or subcordate at base, 5–15(22) cm long, 1.5–8(10) cm wide, sparsely pubescent (more densely on veins), serrate. Spikes densely flowered, axillary, 3–8 cm long; flowers minute, greenish-white, chiefly staminate; petals and disk lacking; pistillate flowers, when present, few in number and restricted to base of spike, sessile, 2 or 3 per bract; bracts ovate, to 4.5 mm broad, toothed, larger in fruit; staminate calyx 4-lobed, somewhat raised on pedicel at anthesis; ovary and capsule hispidulous and muricate; styles 3, free, pubescent, divided at apex into many branches, persisting in fruit. Capsules trilobate, to 3 mm diam, sparsely pubescent, explosively dehiscent; seeds 3, 1 per carpel, ± ovoid, 1–1.2 mm long, black, densely punctate. *Croat 8544.*

Abundant in the old forest. On BCI, flowers mostly from March to May (sometimes from February). The fruits are seen from May to July. Elsewhere, such as in the drier areas of the Azuero Peninsula and in Chiriquí, flowering collections have been made in August and September.

This species, perhaps more than any other, is subject to attacks by gall-forming insects. Galls of three distinctly different forms have been found. One form often looks so similar to a fruit that it was at first considered to be one. Specimens bearing all three types of galls are deposited at the Missouri Botanical Garden.

Southern Mexico to Peru, Bolivia, and Brazil. Throughout Panama; occurring on both slopes in tropical moist forest at mostly lower elevations, though known also from premontane wet forest in Bocas del Toro, Coclé, and Panamá and from tropical wet forest in Coclé and Panamá.

See Fig. 315.

Acalypha macrostachya Jacq., Hort. Schoenbr. 2:63, t. 245. 1797

Monoecious or dioecious shrub or small tree, 3–5(8) m tall; stems often clustered, densely pubescent. Leaves alternate, simple; stipules paired, lanceolate, long-acuminate, pilose, caducous leaving a scar; petioles 12–25 cm long, pilose; blades ± ovate, long-acuminate, truncate to cordate at base, 10–21 cm long, 7–15 cm wide, pilose especially on veins, crenate-serrate. Spikes axillary, usually unisexual, usually a few pistillate spikes alternating with many staminate ones on apical part of stem, the staminate spikes usually 14–20 cm long, the pistillate spikes to 22 cm long in flower (to ca 30 cm long in fruit); petals and disk lacking; staminate flowers 4-lobed, ca 1 mm or less wide; filaments fleshy, the thecae divergent; pollen ± tacky; pistillate flowers solitary, subtended by foliaceous bracts, the bracts 2.5–5 mm long (to 8 mm in fruit), their margins deeply toothed; styles 3, ca 1 cm long, red, slender, branched many times. Capsules trilobate, to 4.3 mm diam, hispid, explosively dehiscent; seeds 3, 1 per carpel, ellipsoid, ca 2 mm long. *Croat 8602.*

Occasional, in the forest, generally in areas of disturbance along trails. Flowers principally from February to May, less frequently elsewhere in Panama during August and September. The fruits develop within about 6 weeks, the majority being dispersed during the late dry and early rainy seasons.

Although the stigmas are ideally suited to catching wind-dispersed pollen, the pollen is tacky and does not appear to be blown from the staminate flowers. However, the entire staminate flower is light and easily loosened and may be wind borne. Though capsules are explosively dispersed, the large bracts may act as receptacles for the dispersed seeds and thus serve as a wind ballast.

Southern Mexico to Peru, Bolivia, and Brazil. In Panama, ranging about the same as *A. diversifolia,* but less abundant and preferring weedier habitats.

See Fig. 316.

Acalypha wilkesiana Müll. Arg. in DC., Prodr. 15(2):817. 1866

Copperleaf, Jacob's coat

Monoecious shrub, to 2.5 m tall; stems sparsely pubescent in age, the young parts densely pubescent. Leaves alternate, simple; petioles to 7 cm long, with a broad band of trichomes above near apex; blades ovate-cordate, abruptly acuminate, 10–25 cm long, 8–15 cm wide, dentate with gland-tipped teeth, maroon beneath, sparsely pubescent on veins; veins at base 5, palmate. Spikes axillary, 6–20 cm long, 3–8 mm wide, reddish, the pistillate bracts 5–6 mm long, divided almost to base, purple-violet; pistil to 1 mm long, 1.2 mm wide; styles 3, free, purple-violet, to 5 mm long, each with numerous filiform segments. Fruits not seen. *Croat 8658.*

Cultivated in the Laboratory Clearing. Flowers in the dry season.

BCI plants would be best considered var. *macageana* W. Miller.

Native to the Pacific Islands (Standley, 1928); cultivated throughout the world.

ADELIA L.

Adelia triloba (Müll. Arg.) Hemsl., Biol. Centr.-Amer. Bot. 3:130. 1883

Dioecious shrub or small tree, usually to 5(15) m tall; trunk slender, to 20 cm dbh; outer bark peeling; branchlets with thin, grayish periderm, sparsely puberulent, rarely short and tapered to a sharp spine at apex. Leaves

alternate, simple; stipules inconspicuous, lanceolate, less than 1 mm long; petioles 4–9 mm long; blades elliptic to obovate, cuspidate-acuminate, tapering to base and usually subcordate, 6–12 cm long, 2–6 cm wide, glabrous but with axillary tufts below and puberulence on major veins. Inflorescences glomerulate; flowers small, cream to white, apetalous, the disk fleshy; staminate flowers pedicellate, the pedicels 4–7 mm long, puberulent; calyx lobes 4 or 5, elliptic, reflexed, ca 2.5 mm long; stamens mostly 13–16 but to more than 20, forming a ± globular mass; filaments connate into a short column terminated by a pistillode; pistillate flowers on glabrate pedicels 2–7 cm long in fruit; calyx lobes 6, ± lanceolate, 3–6.5 mm long; ovary densely pubescent; styles free or connate basally, spreading, fimbriate-lacerate. Capsules prominently trilobate, 7–11 mm diam, about two-thirds as long as broad, pubescent, the valves woody, dehiscing explosively into 6 parts, leaving a persistent columella; seeds 3, globose, smooth, black and shiny, glaucous. *Croat 9347, 13160.*

Frequent along the shore and in the young forest. Flowers from December to February. Fruits from late January to early April.

Known only from Costa Rica and Panama. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién. Reported from premontane wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 317.

ALCHORNEA Sw.

Alchornea costaricensis Pax & Hoffm., Pflanzenr. IV. 147. VII (Heft 63):235. 1914

Dioecious tree, 5–15 m tall, usually less than 30 cm dbh; trunk often forming sucker shoots near base. Leaves alternate, simple; stipules inconspicuous, less than 0.5 mm long; petioles 1.5–3.5(9) cm long, short-pubescent; blades elliptic or ovate-elliptic, long-acuminate, obtuse at base, 8–18 cm long, 3–6.5 cm wide, pinnately veined, 3-veined at base, minutely and sparsely stellate-pubescent below and on veins above, becoming glabrate, remotely crenate-dentate, with 2 foliar glands at base of blade. Spikes stellate-pubescent, the staminate axes unbranched, mostly 2–18 cm long, the pistillate spikes 2–8(10) cm long; staminate flowers apetalous, subsessile, to 1.5 mm diam, clustered with 3 or 4 per bract; calyx lobes 3 or 4; stamens 7 or 8, in 2 series; filaments ± equaling anthers, confluent with disk; pistillate flowers apetalous, solitary, densely pubescent; calyx 4-lobed to about midway; ovary ellipsoid, ca 1.5 mm long, densely pubescent; styles 2, more than twice length of ovary, usually persisting in fruit, simple, ± divergent, 7–10 mm long; stigmatic surface glabrous. Capsules subglobose, green to brown, 2-valved, 5–7 mm long, 6.5–8.5 mm wide, the valves falling free at maturity to expose bright red seeds; seeds 2, 1 per carpel, ellipsoid, 4–6 mm long, displayed on the central columella, flattened on 1 side, the testa brown, irregularly tuberculate, covered with a bright red, thin, pulpy layer. *Croat 10914, 14546, 14619.*

Frequent in the forest. Flowers from March to June, with the fruits maturing mainly from May to July. According to R. Foster (pers. comm.), individuals may flower twice in quick succession following the start of the rainy season. Flowers of the second wave are produced at the time the first fruits ripen.

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

See Fig. 318.

Alchornea latifolia Sw., Prodr. Veg. Ind. Occ. 98. 1788

Dioecious tree, to 15(22) m tall, ca 45 cm dbh; stems and leaves glabrate. Leaves alternate, simple; stipules minute, caducous; petioles 2.5–5 cm long; blades ovate to elliptic, acuminate, obtuse to rounded at base, 8–18 cm long and 4–8.5 cm wide (larger on juveniles), the trichomes tufted, stellate, branched from base in vein axils below, the glands 2–4 at base in vein axils and scattered on both surfaces, the margins entire or toothed, the teeth minute, remote, gland-tipped; venation pinnate, 3-veined at base. Spikes axillary, stellate-pubescent, the flowers apetalous, the staminate axes 5–15(30) cm long, branched many times, the lateral branches 1–3 cm long, the pistillate spikes simple or branched few times near the base, 5–20 cm long; staminate flowers subsessile; calyx lobes 2–4, to 1.5 mm long; stamens 8; pistillate flowers on stout pedicels 1–1.5 mm long; ovary stellate-pubescent; styles 2, simple, 1–2 cm long. Capsules to 11 mm long and wide, bilocular, dark purplish-brown; seeds 2, tuberculate, red, ca 6 mm long and nearly as wide. *Croat 4871, 5024.*

Rare, in the forest; apparently more abundant elsewhere in Panama on the Atlantic slope. Seasonal behavior uncertain. Flowers mainly in April and May. The fruits mature mostly from April to June. In Puerto Rico it is reported to flower all year (Little & Wadsworth, 1964).

Mexico to Panama, introduced into southern Florida; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro, from pre-

KEY TO THE SPECIES OF ALCHORNEA

Staminate spikes unbranched; leaf axils not tufted on underside; leaves usually drying green . . . . . *A. costaricensis* Pax & Hoffm.

Staminate spikes compound; leaf axils conspicuously tufted on underside; leaves usually drying brown . . . . . *A. latifolia* Sw.

Fig. 318. *Alchornea costaricensis*

Fig. 319. *Chamaesyce hirta*

Fig. 320. *Chamaesyce hyssopifolia*

montane wet forest in Panamá (Cerro Campana) and Colón (Santa Rita Ridge), and from premontane rain forest in Panamá (summit of Cerro Jefe).

CHAMAESYCE S. F. Gray

Chamaesyce hirta (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 2:303. 1909
Euphorbia hirta L.
Hierba de pollo, Saca teta, Golondrina

Monoecious annual herb, erect or decumbent at base, pubescent, some trichomes short and ± uncinate, some longer and straight. Leaves opposite, simple; stipules minute, paired, acicular; petioles 2–4 mm long; blades ± elliptic, asymmetrical, obtuse to acute at apex, slightly cordate and oblique at base, 2–3(5.5) cm long, 10–15(25) mm wide, serrate. Flowers naked, in cyathia, the glomerules terminal and axillary, leafless, strigose (often reddish), to ca 1 cm wide; disk bearing 4 glands and minute, white, petaloid appendages; staminate flowers with a single red anther; pistillate flowers solitary, medial in the cyathia; styles 3, deeply bifid. Capsules ovoid, to 1.7 mm long and wide, strigose, held to one side of the cyathia toward maturity by bending of the pedicel, explosively dehiscent, the seeds being thrown several meters; seeds 3, 1 per carpel, ovoid, less than 1 mm long, angulate, reddish-brown. *Croat 8508.*

Abundant in clearings. Flowers and fruits throughout the year. The most abundant species of *Chamaesyce* on the island.

Pantropic weed. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Herrera, Panamá, and Darién, 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 Bocas del Toro, and from tropical wet forest in Colón.

See Fig. 319.

Chamaesyce hypericifolia (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 2:302. 1909
Euphorbia hypericifolia L.
Hierba de pollo

Monoecious, glabrous herb, usually erect, to 60 cm tall; stems somewhat woody at base, ca 3 mm diam, reddish. Leaves opposite, simple; petioles 2–4 mm long; stipules interpetiolar, subpersistent, triangular or sometimes forked especially at apex of plant; blades ovate-elliptic to obovate-elliptic, obtuse to acute at apex, rounded and inequilateral at base, 1.5–3(3.5) cm long, 7–15 mm wide, serrate. Flowers naked, the cyathia glabrous, the glomerules loose, short-stalked, axillary or terminal, leafless or bearing a few inconspicuous reduced leaves; disk with glands suborbicular, their appendages white or pink; stamen 1; styles 3, bifid. Capsules subspherical, to 1.6 mm diam (1.2 mm when dry); seeds reddish-brown, less than 1 mm long, obtusely 3-angulate. *Croat 9201.*

Occasional in clearings, less abundant than *C. hirta* or *C. hyssopifolia;* perhaps preferring taller-grass areas than *C. hyssopifolia.* Found fertile throughout the year.

Throughout the New World tropics and subtropics. 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 moist forest in Panamá, from premontane wet forest in Panamá, and from tropical wet forest in Colón.

Chamaesyce hyssopifolia (L.) Small, J. New York Bot. Gard. 3:429. 1905
Euphorbia brasiliensis Lam.
Golondrina

Monoecious herb, to 50(70) cm tall, essentially glabrous all over; stems straw-colored, reddish, or brown. Leaves opposite, simple; stipules minute, interpetiolar; petioles 1–2 mm long; blades variable, obovate to ovate, obtuse at apex, rounded to slightly cordate and oblique at base, 1–3 cm long, 6–10 mm wide, serrate. Flowers naked, the cyathia glabrous, the glomerules loose, short-stalked, terminal or axillary, usually noticeably leafed; disk with glands elliptic or suborbicular, their appendages white or pink; stamen 1; styles 3, bifid. Capsules oblong-ovoid, glabrous, to 1.8 mm long, 1.7–2 mm wide, sometimes broader than long; seeds ovoid, ca 1 mm long, reddish-brown, angulate. *Croat 16526.*

Common in the Laboratory Clearing. Flowers and fruits throughout the year.

Standley (1933) erroneously reported this as *Euphorbia brasiliensis* L.

Throughout tropical America; adventive in the Old World. In Panama, ecologically variable; known from tropical moist forest throughout Panama and from premontane dry forest in Los Santos, from tropical dry

KEY TO THE SPECIES OF CHAMAESYCE

Capsules and stems pubescent, at least when young:
- Leaves less than 5 mm wide; flowers borne on leafy lateral branches, the clusters less than 4 mm wide; plants usually growing prostrate ..... *C. thymifolia* (L.) Millsp.
- Leaves more than 5 mm wide; flowers borne in leafless glomerules much more than 4 mm wide; plants growing erect ..... *C. hirta* (L.) Millsp.

Capsules and stems glabrous:
- Flowers in almost leafless glomerules; capsules subspherical, less than 1.6 mm wide ..... *C. hypericifolia* (L.) Millsp.
- Flowers in leafy dichasia; capsules oblong-ovoid, more than 1.7 mm wide ..... *C. hyssopifolia* (L.) Small

forest in Coclé and Panamá, from premontane moist forest in Panamá, from premontane wet forest in Bocas del Toro, Colón, Chiriquí, and Panamá, and from tropical wet forest in Colón.

See Fig. 320.

Chamaesyce thymifolia (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 2:412. 1916

Monoecious annual herb, commonly with a thick prostrate root, usually forming dense mats; stems usually villous above and glabrous below, often reddish-brown; sap ± milky. Leaves opposite, simple; stipules distinct, linear, toothed; blades oblong-elliptic, rounded to acute at apex, rounded to subcordate and inequilateral at base, 4–10 mm long, 2–5 mm wide, glabrous above, glabrous to sparsely pubescent below, inconspicuously serrate. Flowers naked, the cyathia 1 to several in axils of lateral branches, the glomerules less than 4 mm wide; disk with glands broadly elliptic to rounded, reddish; stamen 1; styles 3, bifid. Capsules long-ovoid, appressed-pubescent, to 1.3 mm long, not fully exserted but splitting cyathium at maturity; seeds conical-ovoid, to 1 mm long, 4-angled, tan. *Croat 16527.*

Collected once on the mossy sides of a concrete drainage ditch near the laboratory. Flowers and fruits throughout the year, especially during the rainy season.

Throughout the tropics of the New World. In Panama, known throughout from tropical moist forest, as well as from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone, and from tropical wet forest in Colón.

CODIAEUM Adr. Juss.

Codiaeum variegatum (L.) Blume, Bijdr. Ned. Ind. 606. 1826
Croton

Monoecious, small, glabrous tree, to 5 m tall. Leaves alternate, simple; petioles 1–2 cm long; stipules ca 2 cm long, linear; blades strap-shaped, acute or apiculate at apex, acute and decurrent at base, 25–30 cm long, ca 1 cm wide (to ca 5 cm wide elsewhere), reddish or mottled with various shades of green, the margins entire and revolute. Racemes upper-axillary, 15–20 cm long, solitary, subtended by a broad leaflike bract ca 2.5 cm long; staminate flowers clustered under the bracts; sepals 5 (rarely 3 or 6), oblong-elliptic, ca 3 mm long; petals 5 or 6; stamens 15–30 or more, inserted on receptacle, the filaments free; pistillate flowers white, solitary, on articulated pedicels 1–2 cm long; petals lacking; calyx 5-lobed; disk of 5–15 glands; ovary 3-celled, each cell with a single ovule; styles 3, distinct. Capsules globose, dehiscing into 2-valved cocci; seeds 2 per coccus (*fide* Bailey, 1949). *Croat 7037.*

Cultivated in the Laboratory Clearing. It has been reported in flower from January to August. No fruits are set on BCI.

Native to the Pacific Islands (Standley, 1928); widely cultivated. In Panama, known only from tropical dry forest on BCI and in Panamá (Taboga Island).

CROTON L.

Croton billbergianus Müll. Arg., Linnaea 34:98. 1865
Sangrillo, Baquero

Monoecious shrub or tree, 3–10 m tall, densely stellate-pubescent all over except on upper leaf surface; sap copious, ± sticky, yellowish, fragrant. Leaves alternate, simple; stipules subulate-lanceolate, 5–7 mm long; petioles to 6 cm long, with 2 or more sessile, round, yellow glands at apex on lower side; blades usually ovate, acuminate, usually cordate at base, 7–25 cm long, 5–18 cm wide, entire; basal veins 6–9, the cauline veins in 6–10 pairs. Racemes terminal (paniculate by aggregation), 6–15(20) cm long, bisexual or staminate; pedicels 3–5 mm long; calyx cupulate, 4–5 mm long, greenish-white at anthesis, glabrous inside, lobed to ca middle, the lobes 5, broadly acute and somewhat spreading; receptacles villous; staminate flowers terminal on (or full length of) racemes; petals 5, ± elliptic, ca 3.5 mm long, villous; stamens 14–16, well exserted, erect or spreading, to 4.5 mm long; filaments villous; pistillate flowers 1–6 on basal part of raceme, developing before staminate flowers; calyx 5-lobed; petals lacking; ovary broader than high, subtended by a 5-parted, ringlike disk; styles 3, connate into a short column, each style bifid 2 or 3 times, the ends exserted as much as 4 mm and spreading, white, persisting in fruit, the ovary and basal parts of style densely stellate. Capsules obovoid to depressed-globose, to 1 cm diam, stellate-tomentose, green, the columella 4–4.5 mm long; seeds 3, obovoid, 4–5 mm long, 3–4 mm broad. *Croat 14848, 16546.*

Frequent in the forest, mostly the older forest; also along the shore. Flowers from April to August, especially in April and May. The fruits mature from June to October, especially in August and September.

Known only from Panama, from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién and from tropical wet forest in Colón and Panamá.

KEY TO THE SPECIES OF CROTON

Leaves sometimes opposite; plants herbaceous ..... *C. hirtus* L'Hér.
Leaves alternate; plants arborescent:
  Glands at apex of petiole sessile, only on lower surface; inflorescences mostly less than 15 cm long ..... *C. billbergianus* Müll. Arg.
  Glands at apex of petiole stalked, on upper and lower surfaces; inflorescences mostly more than 20 cm long ..... *C. panamensis* (Klotzsch) Müll. Arg.

Croton hirtus L'Hér., Stirp. Nov. 17, t. 9. 1785

Monoecious herb, to 40 cm tall; stems retrorsely stellate-hispid. Leaves alternate, sometimes opposite at branch nodes, simple; stipules subulate, 5–8 mm long; petioles to 3.5 cm long, bearing 2 stalked glands at apex, densely stellate-pubescent; blades ovate to elliptic, acute to obtuse at apex, broadly cuneate at base, 2–6 cm long, 1.5- 4 cm wide, one side sometimes shorter, sparsely stellate-pubescent all over, irregularly crenate, basal veins 5, the cauline veins in 3–6 pairs. Inflorescences terminal, bisexual, ± sessile, to 2.5 cm long, subtended by reduced leaves; staminate flowers white, terminal, 5-parted, ca 3 mm wide; calyx lobed to about middle; petals oblong, equaling calyx lobes; stamens 10 or 11, exserted, in 2 whorls of 5 each plus a central stamen; filaments glabrous; pistillate flowers subsessile; calyx lobes usually 4, slender, unequal; disk 5-angled; petals 5, ellipsoid, to 0.3 mm long; styles 3, free to connate at base, bipartite to bifid. Capsules explosive, subglobose, ca 3.7 mm diam, stellate-hispidulous; seeds compressed, dark brown, smooth, ca 3 mm long, 2 mm wide. *Croat 5855.*

Infrequent in the Laboratory Clearing. Flowers and fruits throughout the year, especially in the early rainy season.

Widespread in disturbed areas of tropical America; West Africa; Malaya. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Herrera, Coclé, and Panamá; known also from premontane dry forest in Los Santos, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí.

Croton panamensis (Klotzsch) Müll. Arg. in DC., Prodr. 15(2):546. 1866

Sangaree, Sangrillo

Monoecious tree, to 20 m tall (rarely to 30 m); most parts densely stellate-pubescent; sap becoming red in time. Leaves alternate, simple; stipules linear, to 2 cm long; petioles 8–20 cm long, with a row of stalked orange glands at apex; blades ovate, long-acuminate, cordate at base, 12–25(30) cm long, 10–23 cm wide, softly whitish-pubescent below, entire to denticulate; basal veins 5–7, the cauline veins in 6–10 pairs. Racemes terminal, ± pendent, (15)20–40 cm long; flowers pedicellate, 5-parted; staminate flowers usually distal, to 7 mm diam; sepals acute; petals obovate, both petals and receptacle densely villous; stamens 13–20, exserted and broadly spreading, to ca 4.5 mm long; anthers dehiscing along lateral margins; pollen tacky; pistillate flowers extending to ca one-third of the raceme; calyx deeply lobed, the lobes acute, persistent; petals usually filiform, inconspicuous; styles 3, bifid or bipartite. Capsules subglobose, ca 6.5 mm diam; seeds 3–4 mm long, 2.6–2.8 mm wide, brown, obscurely costate-roughened. *Croat 16529a.*

Though abundant in other parts of the Canal Zone, the plant is now rare on BCI, having been collected only three times along the shore. Flowers to some extent throughout the year, but the principal flowering season is the early rainy season (June to August, especially July), with the fruits maturing usually by September. A second burst of flowering occurs in the late wet and early dry seasons (October to January), with the fruits developing from April to July. Individual plants may flower twice, since plants in flower in July have had mature fruits also. Allen (1956) reported that the species flowers only from September to November in Costa Rica, so perhaps there are different phenological races of the species.

Allen (1956) reported that the species may form small, almost pure stands along forest margins.

Pollination system is unknown: the pollen does not seem to be wind borne; staminate flowers do not appear to have nectaries, though a faint aroma is present; and, since the pollen is not very copious, it would not appear to be visited by pollen collectors.

Mexico to Colombia. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Herrera, Panamá, and Darién; known also from premontane wet forest in Chiriquí, Coclé, and Panamá and from lower montane rain forest in Chiriquí.

DALECHAMPIA L.

Dalechampia cissifolia Poepp. subsp. **panamensis** (Pax & Hoffm.) Webster, Ann. Missouri Bot. Gard. 54:193. 1967

D. panamensis Pax & Hoffm.

Monoecious vine, sparsely short-pubescent all over, more densely on petioles and pedicels. Leaves alternate, compound; stipules paired, linear, 5–10 mm long, persistent; petioles 1.5–6 cm long, with 2 small acicular stipels at apex; leaflets 3, ± narrowly elliptic, acute to acuminate, acute to rounded at base, 4–12 cm long, 1–3 cm wide, the lateral leaflets markedly asymmetrical, all margins with minute, apiculate teeth. Inflorescences bisexual, axillary; peduncles 1–2(2.5) cm long; flowers subtended by a pair of involucral bracts, the bracts trilobate, greenish, ca 1.5–2.5 cm long, pubescent on veins and margins; staminate flowers 8 or 9, in a nearly sessile cymule; pedicels articulate, 2–3 mm long; calyx lobes 4 or 5; disk and

KEY TO THE SPECIES OF DALECHAMPIA

Leaves simple and unlobed ..... *D. dioscoreifolia* Poepp.
Leaves trifoliolate or trilobate:
  Leaves trifoliolate; involucral bracts green at anthesis .....
  ..... *D. cissifolia* Poepp. subsp. *panamensis* (Pax & Hoffm.) Webster
  Leaves trilobate; involucral bracts cream-colored at anthesis ..... *D. tiliifolia* Lam.

petals lacking; stamens ca 25, the staminal column minute; pistillate flowers 3, subtended by 2 bractlets ca 3 mm long; calyx lobes 3–11, unequal; disk and petals lacking; ovary densely hispidulous; styles 3, connate, 5–6 mm long; stigma 1, compound, concave, 0.5–1 mm wide. Capsules 6.5–8.5 mm diam, with 3 coeci 5–7 mm long; seeds nearly globose, ca 3–3.5 mm diam, mottled. *Croat 7449.*

Known only from the Laboratory Clearing in the shade at the edge of the forest. Apparently flowering and fruiting throughout the year, possibly flowering twice.

Guatemala to Peru. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Panamá and from premontane wet forest in Panamá (Cerro Campana).

Dalechampia dioscoreifolia Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3:20. 1841

Monoecious vine; stems, petioles, and blades pubescent (sparsely so on blade above between veins), the trichomes fine, short, white. Leaves alternate, simple; stipules linear-lanceolate, to 6 mm long, paired, persistent; petioles 2–11 cm long, with 2–4 glands at apex, 2 of them to 3 mm long, acicular; blades ovate, short-acuminate, cordate at base, 4–15 cm long, often as broad as or broader than long, subentire to obscurely glandular-toothed; basal veins 5, the cauline veins in 1–3 pairs. Inflorescences bisexual, axillary, short-pedunculate; flowers subtended by a pair of involucral bracts, the bracts ovate-cordate, caudate-acuminate, reddish particularly on veins, the margins lacerate-toothed; staminate flowers with 4 calyx lobes; disk and petals lacking; stamens 20–30; pistillate flowers with the sepals 6–11, deeply pectinate-lobed; disk and petals lacking; ovary densely hispidulous; styles 3, connate, 3–5.5 mm long; stigma 1, disk-shaped, 2–3.5 mm wide. Capsules deeply trilobate, ca 12 mm diam; seeds 3, ca 5 mm long, ± cube-shaped, dark-mottled. *Croat 14456.*

Uncommon or rare, seen infrequently in lower levels of the canopy; two old collections are from Wheeler Trail. Probably more abundant than would appear, owing to its inconspicuous manner of growth. Flowering mostly throughout the rainy season, but often as early as April. The fruits mature mostly in the dry season and early rainy season.

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

Dalechampia tiliifolia Lam., Encycl. Méth. Bot. 2:257. 1786

Monoecious vine; all parts densely short-pubescent. Leaves alternate, simple; stipules 3–5 mm long, caducous; petioles 2.5–14 cm long; blades variable, entire or trilobate to about middle, mostly 10–16 cm long, usually broader than long, the margins serrulate to entire. Inflorescences borne within large involucral bracts on short axillary shoots; involucral bracts ovate, exceeding inflorescence, prominently veined, 3-dentate at apex, white at anthesis, becoming green; both the staminate and pistillate cymules contained within same inflorescence, the old staminate cymule persisting; staminate flowers with (3)4–6 calyx lobes; disk and petals lacking; stamens 30–45; pistillate flowers with 9–12 fimbriate calyx lobes; ovary densely hispidulous; styles 3, connate, ca 1 cm long; stigma 1, compound, peltate, concave, 1.5–2.5 mm wide. Capsules 3 per cymule, ca 1 cm diam, densely hispid, the trichomes irritating; seeds ca 4 mm long, mottled. *Wetmore & Abbe 156.*

An abundant plant in disturbed areas in the vicinity of the Canal Zone, but it has not been seen recently on the island. Flowers from October to February. The fruits mature mostly from February to April (sometimes to July).

Honduras to Brazil. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Los Santos, Herrera, Coclé, Panamá, and Darién; known also 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 and Panamá.

DRYPETES Vahl

Drypetes standleyi Webster, Madroño 24:65. 1977

Dioecious tree, ca 30 m tall and 45 cm dbh, glabrous all over; outer bark thin, unfissured, prominently lenticellate, the lenticels round to flattened horizontally; inner bark tan; sap at first with a faint, sweet aroma. Leaves alternate, simple, estipulate; petioles less than 1 cm long; blades variable, usually oblong-elliptic to elliptic, acuminate, obtuse and decurrent at base, 8–12 cm long, 4–6 cm wide, the acumen thickened, hyaline or discolored. Flowers green, sessile, apetalous, in axillary fascicles; pedicels and sepals minutely puberulent; sepals 4, obovate, concave, rounded at apex, 2.5–4 mm long, glabrous or appressed-pubescent inside, ciliate; staminate flowers numerous; pedicels slender, to 1 cm long; stamens 8, in 2, ± spreading series, 2.5–3 mm long, arising from margin of a flat cross-shaped pistillode; anthers oblong, to 1.5 cm long, dehiscing laterally; pistillate flowers 1–5 per axil; pedicel thick, to 4 mm long; ovary ovoid, densely gray-sericeous, borne on a flat pubescent disk; stigmas discoid, sessile, green, ca 1.5 mm broad, persisting in fruit. Drupes broadly ovoid, to 2 cm long and 1.5 cm wide, densely pubescent, the trichomes ± appressed; seed 1. *Croat 14849, 16516.*

Rare; known only from three individuals above the escarpment in the old forest. Seasonal behavior uncertain. Flowers at least in May and June. The fruits probably mature in July and August. Elsewhere the fruits have been observed to be cream-colored or yellowish at maturity (G. Webster, pers. comm.).

Panama and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, from tropical wet forest in Colón (Santa Rita Ridge), and from lower montane wet forest in Veraguas (Cerro Tute).

See Fig. 321.

Fig. 321. *Drypetes standleyi*

Fig. 322. *Hyeronima laxiflora*

Fig. 323. *Hyeronima laxiflora*

GARCIA Vahl

Garcia nutans Vahl in Rohr, Skr. Naturhist-Selsk. 2:217, t. 9. 1792

Monoecious shrub or tree, to 15 m; latex scanty; twigs tomentose, soon glabrous. Leaves alternate, simple, moderately thick, estipulate; petioles variable, 1–9 cm long, pulvinate at apex; blades ± elliptic, abruptly acuminate to obtuse at apex, obtuse to rounded at base, 8–19(25) cm long, 2.5–8 cm wide, glabrous above, pilose to glabrous below, stellate-tomentose on midrib when young; basal pair of lateral veins arising from midrib below the pulvinus. Flowers unisexual, the cymes terminal, pedunculate, reduced, of 1 or 2 pistillate and several staminate flowers; pedicels 1–3.5 cm long, pubescent; calyx rupturing into 2 or 3, valvate segments; petals 6–13, slender, 10–17 mm long, sericeous, longer than calyx, pinkish to dark red; staminate flowers with calyx persistent; disk with numerous segments; stamens numerous (60–150); filaments free; anthers apiculate; pistillate flowers with calyx deciduous; disk lobed; ovary densely sericeous; styles 3, thick, 1.5–2 mm long, reflexed, bifid. Capsules trilobate, 2–2.5 cm long, 3–4 cm diam, sericeous; seeds 3, globose, to 17 mm diam. *Knight 1090.*

Rare; collected only once. The plant was sterile but there is no doubt of its determination. Seasonal behavior uncertain. The fruits apparently mature in the dry season. Costa Rican collections show flowers mostly in the late dry season and early rainy season.

Mexico to Colombia; Greater Antilles. Apparently rare in Panama, perhaps only from drier parts of tropical moist forest in the Canal Zone and Los Santos.

HURA L.

Hura crepitans L., Sp. Pl. 1008. 1753

Sandbox, Javillo, Coquillo macho, Nuno, Nune, Tronador, White cedar

Large monoecious tree, to 25 m tall; trunk to 1(2) m dbh, bearing hard conical spines; branches glabrous; second-year growth with a thin, smooth, brown periderm. Leaves alternate, simple, deciduous; petioles to 20 cm long, with 2 glands at apex; blades ovate, abruptly acuminate, cordate at base, 11–25 cm long, 7–15 cm wide, glabrous above, sparsely long-pubescent to glabrous below, crenate, the teeth often gland-tipped. Receptacle fleshy, conical, 2–4.5 cm long; flowers lacking petals and disk; staminate peduncles to 10 cm long, the flowers red, emerging from the ruptured tissue of a large, conical, fleshy receptacle, to 4 mm high and 3 mm diam, maturing acropetally (toward apex), numbering well over 100, as many as 80 functional at one time; calyx cupulate; pollen yellow, oozing simultaneously from many pores around circumference; pistillate flowers solitary in upper axils; pedicels 2–5 cm long, woody in fruit; calyx cupulate, 3–5 mm long, truncate or shallowly 5-lobed; styles 3, connate into a slender column 2–5 cm long, terminated by a fleshy disk to 1 cm diam with radiating tips to 1 cm long; ovary with ca 15 carpels, each with 1 ovule. Capsules oblate, 5–8(10) cm diam, 2.5–5 cm long, woody, dehiscing explosively into many concentric cocci; seeds many, disk-shaped, 1.5–2 cm diam. *Croat 4907, 5791.*

Common in both the young and old forests. Flowers from April to December. The fruits mature during the late rainy season and in the dry season. Leaves are lost and replaced during the dry season.

Sap and seeds are poisonous to humans and irritating to the skin (Blohm, 1962). Fruits dehisce with a loud report. They are eaten by macaws and monkeys (Allen, 1956).

Costa Rica to Peru and Brazil; West Indies; introduced into California, Florida, the Bahamas, and the Old World tropics (Allen, 1956). In Panama, known principally from and a characteristic component of tropical moist forest (Tosi, 1971) in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Los Santos, from premontane moist forest in Panamá, and from premontane wet forest in Chiriquí.

HYERONIMA Allem.

Hyeronima laxiflora (Tul.) Müll. Arg., Linnaea 34:67. 1865

Bully tree, Palo chancho, Pilon, Zapatero, Platano, Pantano

Dioecious tree, to 40 m tall; trunk usually less than 1 m dbh, buttressed, the buttresses sometimes continuous with exposed lateral roots extending over ground surface as much as 30 m from tree; bark reddish-brown and often weathered (appearing chewed up) at base; all younger parts densely lepidote. Leaves alternate, simple; stipules lanceolate, to 1.5 cm long, deciduous; petioles 3–10 cm long; blades broadly elliptic, abruptly acuminate, obtuse to rounded at base, 7–23(30) cm long, 4–12(19) cm wide; juvenile blades 30 cm long and 16 cm wide, ovate-cordate, inflated and rounded at base, usually inhabited by ants, the stipules enlarged. Panicles upper-axillary, the branches densely lepidote, the staminate panicles to 17 cm long, the pistillate ones to 10 cm long and 15 cm broad; main axis with bracts 5–15 mm long, the lateral axis with minute bracts; flowers apetalous, greenish-white; staminate flowers on minute pedicels; calyx cupuliform, shallowly 3- or 4-lobed, less than 1 mm high; disk nearly equaling calyx; stamens 4; filaments to 1 mm long, free; anthers with an enlarged connective with 2 anther sacs pendent and divergent at anthesis; pistillate flowers on stout pedicels 1–2 mm long; calyx cupuliform, shallowly 3- or 4-lobed, to 0.8 mm high; disk smaller than calyx; ovary ovoid, to 1 mm high; styles 3, obsolete; stigmas minute, bifid. Drupes green turning red then purple-black at maturity, subglobose, ca 3 mm diam, sweet; seed 1, ellipsoid, ca 2 mm long, brown. *Croat 8403, 14964.*

Common in the forest, especially the old forest. Flowers mostly from March to June, also sporadically in the late rainy season. The fruits mature mainly from March to July, also sporadically in the late rainy season.

The fruits are eaten by white-faced monkeys.

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

See Figs. 322 and 323.

JATROPHA L.

Jatropha curcas L., Sp. Pl. 1006. 1753
Coquillo, Physic nut, Piñon, Arbol santo

Monoecious shrub or small tree, usually 2–5(6) m tall, glabrous but with puberulence on young leaves and inflorescence branches; stems thick, the leaf scars close and pronounced; sap red in time. Leaves alternate, simple; stipules minute, acicular, caducous; petioles 7–15 cm long; blades ovate, unlobed or with 5–7 shallow lobes, acuminate, cordate, 10–25 cm long, 9–15 cm wide; veins palmate at base. Flowers green, 5-parted, in short terminal dichasia becoming 10–25 cm long; staminate flowers ca 7 mm diam; pedicels 1–5 mm long, puberulous; calyx deeply lobed, the lobes rounded at apex and recurved; petals obovate to oblong, rounded and recurved at apex, to 6 mm long, densely villous inside, weakly imbricate and united below middle; disk segments free, ellipsoid, white, ca 1 mm long; nectar copious, enclosed by petals; stamens 8–10, to 6 mm long, in a close erect cluster; anthers oblong, to 1.7 mm long, extrorse; pollen pale yellow; pistillate flowers on pedicels 5–9 mm long (to 13 mm in fruit); calyx lobes ± oblong-lanceolate, 7–9 mm long; petals as in staminate flowers; ovary glabrous; styles 3, slender, 1.5 mm long, connate in basal half, dilated into massive stigmas. Capsules ± globose, smooth, turning yellow, 2.5–3 cm long, at first fleshy but eventually drying and dehiscent; seeds 3, 1.5–2.2 cm long, black, broadly oblong. *Croat 10223, 12606.*

Cultivated in the Laboratory Clearing. The plant loses leaves for a short time during the dry season, then flowers shortly after the new leaves grow out at the beginning of the rainy season (April to August). These fruits mature mostly from June to September. The plant rarely flowers again at the beginning of the dry season, with the fruits maturing in the late dry season.

Seeds are purgative and may cause death if eaten in quantity (Standley, 1928; Blohm, 1962).

Probably native to northern Central America, but widely cultivated throughout the tropics. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, but also known frequently from premontane dry forest in Los Santos and Herrera and from tropical dry forest in Los Santos, Coclé, and Panamá.

MABEA Aubl.

Mabea occidentalis Benth., Hooker's J. Bot. Kew Gard. Misc. 6:364. 1854

Monoecious shrub or small tree, usually 4–6(10) m tall, glabrous all over except on inflorescences; sap whitish, not copious. Leaves alternate, simple; stipules paired, linear, ca 5 mm long, caducous; petioles to 8 mm long; blades oblong, long-acuminate at apex, obtuse to rounded at base, 6–13 cm long, 2.5–4.5 cm wide, the margins subentire to crenulate and often undulate. Inflorescences pendent from leaf axils, ± granular-puberulent on axes and pedicels, to 12 cm long; staminate flowers in groups of 3, the peduncles stout, short, bearing a conspicuous biglandular bract at base; pedicels slender, articulate above base, ca 1 cm long; flowers globular, maroon, 1.5–2 mm wide; calyx of 3–5 ovate lobes; petals and disk lacking; anthers many; pistillate flowers solitary at basal nodes, 3–7 per inflorescence; pedicels 1–1.5 cm long, subtended by a mostly eglandular bract; sepals 6, maroon, bifid at apex, subequal; petals and disk lacking; ovary 3-carpellate, each carpel with 1 ovule; styles 3, connate into a slender column more than 1 cm long, free and simple near apex, densely whitish-pubescent. Capsules subglobose, ca 1.5 cm diam, 3-valved, explosively dehiscent, the valves in turn splitting into 2 parts; seeds 1 per carpel, ca 8 mm long, suspended by a fleshy funicle at apex. *Croat 7026, 7303.*

Frequent in the forest, especially the young forest. Flowers sporadically throughout the year, mostly from October to April. Most fruits mature during the dry season. Individuals are often found in the dry season with new flowering inflorescences that produce fruits in the rainy season.

Mexico to Brazil. In Panama, known from tropical moist forest in the Canal Zone, Colón, Veraguas, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in Panamá, from premontane wet forest in Colón, and from premontane rain forest in Panamá (summit of Cerro Jefe).

MANIHOT P. Mill.

Manihot esculenta Crantz, Inst. Rei Herb. 1:167. 1766
Yuca, Cassava

Glabrous, monoecious shrub, 1–3 m tall; stems with milky sap. Leaves alternate, simple; stipules lanceolate, acuminate, 7–8 mm long, deciduous; petioles to 12(17) cm long; blades deeply lobed, acuminate, 8–12(17) cm long, 1–3.5(5) cm wide, glaucous below, the lobes 3–5(7), narrowly elliptic. Panicles axillary and terminal, to 10 cm long in flower, longer in fruit; staminate flowers racemose along main axis; pedicels 4–6 mm long; calyx campanulate, 3–7 mm long, yellowish-green, 5-lobed, puberulent on outside; petals lacking; disk ca 2 mm wide; stamens 10; filaments to 12 mm long, unequal; anthers ca 2 mm long; pistillode lacking; pistillate flowers several along basal branches; pedicels slender and 7–12 mm in flower, stout and to 17 mm in fruit; calyx 5-lobed to near middle, to 10 mm long; petals lacking; disk ca 3 mm wide; ovary 6-winged or 6-ribbed; styles three, ca 2 mm long, dilated and divided into capitate tips. Capsules subglobose, 1.5–2 cm long, 6-ribbed; seeds 3, compressed, ca 9 mm long and 6 mm wide, smooth, with a darker beak at apex. *Croat 7248.*

Cultivated in the Laboratory Clearing. Seasonal behavior uncertain. Flowers at least from October to Jan-

uary, with mature fruits known from January and July.

Plant tissues contain hydrocyanic acid (Blohm, 1962).

Apparently native to South America (Brazil), but widely cultivated in the tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién.

MARGARITARIA L.f.

Margaritaria nobilis L.f., Suppl. Pl. Syst. Veg. 428. 1781

Phyllanthus nobilis (L.f.) Müll. Arg.

Dioecious shrub or tree, to 15 m tall, to 20 cm dbh; outer bark thin, flaky; inner bark thin, rose-colored, with faint longitudinal grains; sap at first with a sweet aroma; stems glabrous; branchlets conspicuously warty-lenticellate. Leaves alternate, simple, glabrous or sometimes bearing short trichomes on petioles and on veins below; stipules paired, triangular, 1–2 mm long, subpersistent; petioles 3–5 mm long; blades ovate-elliptic to elliptic, acuminate, obtuse to rounded and decurrent at base, 7–12(19) cm long, 3–7.5 cm wide, moderately thin; smaller reticulate veins clearly visible. Inflorescences axillary, bearing few flowers; flowers unisexual, green, 4-parted, apetalous; disk round to minutely 4-lobed, annular, 2.5–3 mm wide, the lobes opposite calyx lobes; staminate flowers green, 5–6 mm wide; pedicels 2.5–5 mm long; calyx lobes somewhat unequal, ovate to suborbicular, spreading, 1–2 mm long; stamens 4 and opposite the calyx lobes; filaments to 2 mm long; anthers minute, slightly longer than broad, extrorse; pistillate flowers solitary or clustered or in short racemes; pedicels stout, ca 3 mm long, becoming 5–14 mm long in fruit; calyx lobes 1–2 mm long, about as broad as long, rounded at apex; disk thin, round or minutely 4-lobed; ovary (3)4- or 5-carpellate, ovoid, weakly angled, glabrous or minutely puberulent, together with style ca 2.5 mm long; styles 1 per carpel, entire or bifid or tripartite. Capsules with 4–6 cocci, depressed-globose, ca 1 cm diam, dehiscing irregularly; seeds paired in each coccus. *Croat 6104, 14634, 14656, 14915.*

Occasional in the forest, especially the young forest. Flowers mostly from May to July, rarely later in the rainy season. The fruits mature mostly from July to October. Leaves fall late in the dry season, growing out again at the time of flowering.

Mexico to Peru and Brazil; West Indies. In Panama, 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 Chiriquí and Panamá, and from tropical wet forest in Colón.

OMPHALEA L.

Omphalea diandra L., Syst. Nat. ed. 10, 2:1264. 1759

Monoecious liana, to more than 30 m high in canopy, sparsely pubescent to glabrate all over except on inflorescence; trunk to 7 cm dbh; outer bark unfissured; inner bark tan with raised white areas on outer surface, the sap violet-purple, often forming droplets between inner bark and wood. Leaves alternate, simple; stipules minute; petioles to 11 cm long, with 2 large round glands at apex; blades ovate to broadly elliptic, bluntly mucronate at apex (rarely abruptly acuminate), rounded to truncate or slightly cordate at base, 8–21 cm long, 5–15 cm wide, entire; veins at base 3–5, the major lateral veins in 2 or 3 pairs. Panicles 10–50 cm long, terminal or upper-axillary, bracteate; bracts biglandular, the basal 2–3 mm long, the apical 2–3.5 cm long and very narrow; branches and bracts densely pubescent; flowers apetalous, green or yellowish, clustered in cymules in 3 possible arrangements: with all staminate flowers, with a central pistillate flower and several staminate flowers, or with a solitary pistillate flower at apex of branches; staminate flowers globular; pedicels ca 2 mm long; calyx lobes 4, biseriate, 1.5–2.5 mm long and wide, glabrate and ciliate; stamens 2 (rarely 3); anthers ca 0.7 mm long; pistillate flowers on pedicels 1–2 mm long; calyx lobes 4, ovate, ca 2 mm long and wide, pubescent to glabrate; styles 3, connate, the column stout, densely pubescent, 2–2.5 mm long. Fruits ± round, 8–12 cm diam, fleshy but ultimately dehiscent into 3 woody cocci (*fide Flora of Panama*); seeds 1 per coccus, compressed-globose, 4–4.5 cm diam, brown or black, slightly rugose. *Croat 5236.*

Uncommonly encountered in the forest and at the margin of the lake. Since the plant is a high-canopy vine with inconspicuous flowers, it might be more common than collections and observations indicate. Flowers mostly throughout the dry season and in the early rainy season. Nearly mature-sized fruits are seen late in the dry season, probably dehiscing in the early rainy season. Leaves fall for at least a short time in the middle of the dry season.

The fruits are reported to be capsular, but I have never seen them open. They are possibly mammal dispersed or, as some have suggested, in part water dispersed, since the plant perhaps grows more frequently near water. Larvae of the moth *Urena fulgens* (Urenidae) are leaf-miners apparently restricted to this species (Neal Smith, pers. comm.).

Honduras to Peru and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién and from tropical wet forest in Chiriquí.

See Fig. 324.

PHYLLANTHUS L.

Phyllanthus acuminatus Vahl, Symb. Bot. 2:95. 1791

P. conami Sw.

Jobitillo

Glabrous, soft-wooded, monoecious herb or shrub, usually less than 3(8) m tall, sparsely branched, the branches usually bipinnatiform (the earliest simply pinnate), the primary axis to 65 cm long, margined below branchlets, the ultimate branches 8–20, each 5–25 cm long, with 7–20 leaves. Leaves alternate, simple; stipules triangular, ca 1 mm long, blunt; petioles 1.5–3 mm long; blades ovate to elliptic, gradually acuminate, acute to obtuse at base, 2–4.5 cm long, 1–2.5 cm wide. Flowers apetalous,

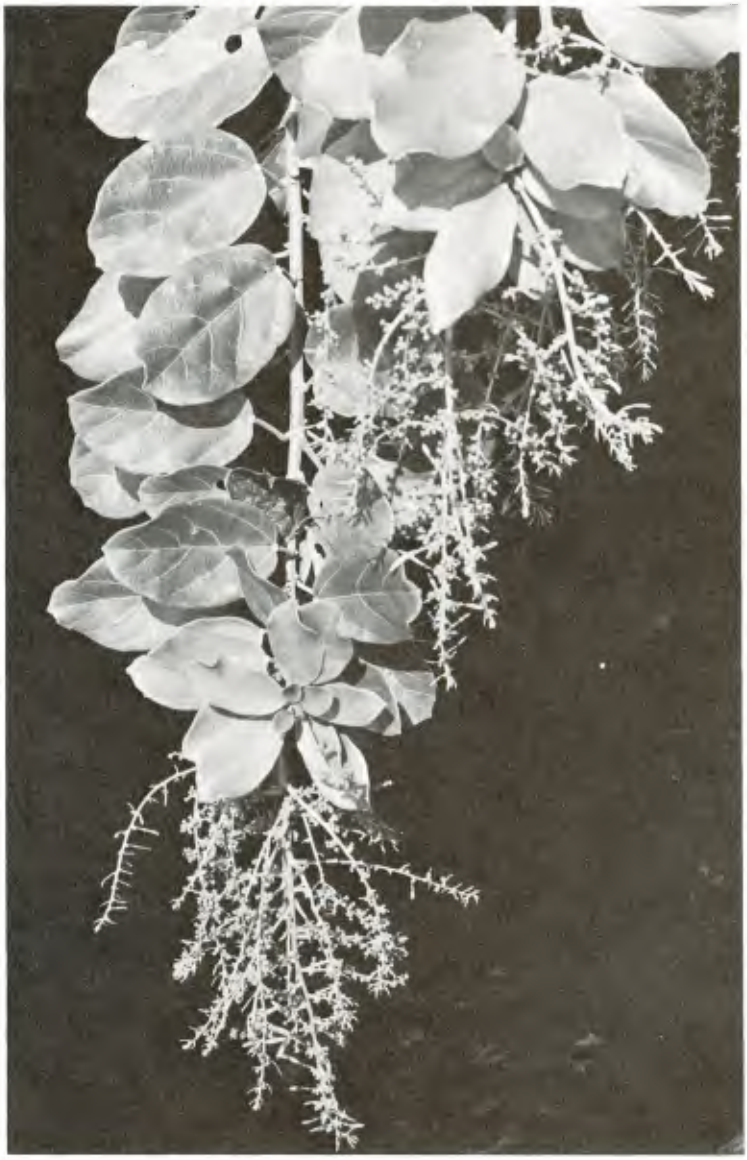

Fig. 324. *Omphalea diandra*

Fig. 325. *Sapium caudatum*

KEY TO THE SPECIES OF PHYLLANTHUS

Leaves more than 1.5 cm long, gradually acuminate ..... *P. acuminatus* Vahl
Leaves less than 1.5 cm long, rounded or mucronate at apex:
  Leaves rounded at apex, glabrous; seeds not transversely ribbed, not pitted ... *P. amarus* H. Schum.
  Leaves mucronate at apex, bearing very short trichomes near margins below; seeds transversely ribbed, often pitted on sides ..... *P. urinaria* L.

small, in bisexual cymules in axils of ultimate branches; staminate flowers 5–20 per cymule; pedicels to 5 mm long; calyx lobes 6, in 2 unequal series, the inner rounded, to 1.2 mm long; disk prominent, trilobate; stamens 3; filaments connate into a short column; anthers fused at base, forming a 3-sided structure, dehiscing laterally; pistillate flowers 1 per cymule; pedicels 5–12 mm long; calyx lobes 6, in 2 series, the inner broadly ovate, to 1.7 mm long; disk cup-shaped, trilobate; ovary trilobate; styles 3, flattened, spreading, bifid at apex. Capsules 4.5–5 mm diam, prominently trilobate, explosively dehiscent; seeds plano-convex, ca 2.5 mm long, smooth, reddish-brown. *Croat 10240.*

Occasional, usually in tree falls or clearings; sometimes locally common along the shore. Flowers throughout the year, but principally from February to August. The fruits are mature mostly from July to September. Plants may have mature fruits while still in flower.

Mexico to northern Argentina; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón.

Phyllanthus amarus H. Schum., Beskr. Guiana Pl. 421. 1827

P. niruri L. var. *amarus* (H. Schum. & Thonn.) Leandri

Monoecious herb, 10–50 cm tall, glabrous; branchlets deciduous, 4–10 cm long, very slender. Leaves alternate, simple, thin; stipules lanceolate, ca 1 mm long; petioles to 0.5 mm long; blades elliptic-oblong, ± rounded at both ends, 5–11 mm long, 3–6 mm wide. Flowers minute, apetalous, greenish, 5-parted, usually 2 in each axil, the lowermost axils with staminate flowers, the others with 1 staminate and 1 pistillate flower; staminate flowers on pedicels 0.5–1.3 mm long; calyx lobes ± ovate, ca 0.5 mm long; stamens (2)3; filaments connate into a column ca 0.3 mm long; pistillate flowers on pedicels to 1–2 mm long in fruit; calyx lobes obovate-oblong, to 1 mm long; disk flat, 5-lobed; ovary 3-carpellate, 2 ovules per locule; styles 3, free, ca 0.2 mm long, bifid at apex. Capsules globular, with 3 cocci, ca 2 mm diam, dehiscent, leaving persistent columella; seeds 2 per locule, trigonous, ca 1 mm long. *Shattuck 398.*

Collected once by Shattuck, but not seen in recent years on the island; to be expected as a weed in clearings. Seasonal behavior not determined. The few specimens seen had flowers and fruits in the dry season.

Throughout the tropics. In Panama, known from tropical moist forest in the Canal Zone (both slopes), Chiriquí, and Panamá.

Phyllanthus urinaria L., Sp. Pl. 982. 1753

Monoecious herb, to 80 cm tall; branchlets deciduous, 5–10 cm long; stems and petioles glabrous. Leaves alternate, simple; stipules lanceolate, to 1.5 mm long, paired, the pairs unequal; petioles 1 mm or less long; blades linear to oblong-obovate, obtuse to mucronate at apex, rounded at base, 8–25 mm long, 2–6(9) mm wide, glabrous but with hispidulous margins below, entire. Flowers minute, axillary, greenish-white, apetalous; staminate flowers 5–7, in cymules in upper axils of branchlets; calyx lobes 6, ca 0.5 mm long; stamens 3; filaments connate their entire length; pistillate flowers solitary in lower branchlet axils; pedicels ca 0.5 mm long; calyx lobes 6, less than 1 mm long; ovary papillate; styles 3, connate into a column, bifid at apex. Capsules globular, ca 2 mm diam, green, often reddish-tinged, nearly sessile, dehiscing into 3 cocci, leaving a persistent columella; seeds 1 per coccus, ca 1 mm long, transversely ribbed, often pitted on sides. *Croat 16528.*

Common in clearings. Flowers and fruits at various times throughout the year.

Native to tropical Asia; introduced throughout tropical America. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, San Blas, Chiriquí, and Panamá, from premontane moist forest in the Canal Zone, from premontane wet forest in Coclé and Panamá, and from tropical wet forest in Colón and Coclé.

POINSETTIA R. Grah.

Poinsettia heterophylla (L.) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859:253. 1859

Euphorbia heterophylla L.

Monoecious herb, to 120 cm tall, with milky latex; stems ± glabrous. Leaves alternate at base of plant, opposite above, petiolate; stipules lacking or minute; blades mostly elliptic, 5–11 cm long, 2–5 cm wide, glabrous or sparsely pubescent. Floral bracts leaflike, green or sometimes purple-spotted; cyathia glabrous, terminal, usually bearing 1 stipitate, tubelike gland, several staminate flowers, and 1 pedicellate pistillate flower, this developing well in advance of the staminate

flowers; flowers naked; staminate flowers with 1 stamen; pistillate flowers with the styles 3, joined at base, each bifid most of its length. Capsules dehiscent, 3-celled, to 2.5 mm long; seeds 1 per cell, ovoid, sculptured. *Croat 4070, 5952.*

Occasional in clearings, seasonally abundant. Flowers and fruits principally in the rainy season.

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

SAPIUM P. Browne

Sapium aucuparium Jacq., Enum. Syst. Pl. Ins. Carib. 31. 1760

S. jamaicense Sw.

Wild fig, Olivo, Nipa

Glabrous, monoecious tree, to 20 m tall; bark minutely, shallowly fissured. Leaves alternate, simple, membranaceous; stipules obsolete; petioles 2–4 cm long, with 2 stipitate glands at apex; blades elliptic to obovate, acuminate (the acumen sometimes cucullate), obtuse to rounded at base, 9–12 cm long, 3–5 cm wide, subentire to finely serrate. Spikes in clusters of 3–5 (rarely fewer), to 10 cm long, bisexual; flowers with corolla and disk lacking; staminate flowers in groups of 2 or 3(5), the subtending bracts deltoid, to 3 mm long, bearing 2 large glands at base, the apical part caducous; calyx to ca 1 mm long, 2-lipped; stamens 2; pistillate flowers 8–15, solitary at basal nodes of spike, the basal bracts like staminate bracts but with smaller glands; calyx cupular, bilobed, the lobes unequal, free almost to base; ovary orbicular; styles 3, simple, caducous, to 2 mm long, connate for about half their length, the apical half uncinate. Capsules ovoid, to 8 mm long; seeds usually 3, flattened-ovoid, the outer seed coat red. *Kenoyer 661.*

Collected once on the island, and possibly still occurs there. Seasonal behavior not certain. Flowers mostly in March, but sometimes also in the rainy season during September and October. The fruits mature probably mostly from May to July, but full-sized fruits have also been seen in October.

Mexico to northern South America; Cuba, Jamaica. In Panama, known principally from tropical moist forest along the Atlantic slopes in the Canal Zone, Bocas del Toro, and San Blas; known also from tropical moist forest in Los Santos and from premontane wet forest in Chiriquí.

Sapium caudatum Pitt., Contr. U.S. Natl. Herb. 20:127. 1918

Monoecious tree, to 30 m tall and 90 cm dbh, glabrous all over. Trunk weakly buttressed; younger trunks and branches bearing short, stout, branched spines; outer bark thin, hard, in ± rectangular patches, easily peeling, with horizontal scars 6–20 cm long staggered on trunk; inner bark very granular; sap copious, milky, especially in branches. Leaves alternate, simple, somewhat coriaceous; stipules ca 1 mm long, triangular, subpersistent; petioles 2–5.5 cm long, with 2 stipitate glands near apex; blades oblong-elliptic to obovate, with a hooded acumen, obtuse at base, (9)13–18(27) cm long, 3–5(8) cm wide, the margins revolute, irregularly and minutely toothed; juvenile leaves thinner, the teeth much longer and gland-tipped. Spikes solitary, terminal or in uppermost axils, bisexual, to 25 cm long; corolla and disk lacking; staminate flowers globular to pyriform, to 1.3 mm long, in groups of 7–14, inserted on axis above a minute bract, the bract bearing a pair of flattened glands ca 3 mm long, the flowers and glands violet-purple; calyx 4-lobed, ca 0.5 mm long, the pairs of lobes unequal; stamens 2, included; anthers extrorse; pollen orange, tacky; pistillate flowers 5–10, solitary at basal nodes, the bract as in staminate flowers but usually larger; calyx (2)3–5-lobed, sometimes obscurely so; ovary orbicular; styles 3, simple, ca 2 mm long, united only at base, in part deciduous. Capsules ovoid, to 1 cm long, short-stipitate, with 6 longitudinal grooves, splitting into 3 segments; seeds 1 per segment, compressed-ovoid, ca 6 mm long, minutely warty, covered most of its length at maturity with a bright red, thin, pulpy layer. *Croat 14998, Foster 1787.*

Occasional in the forest. Flowers from late May to July. The fruits mature from July to September. Leaves fall in the early dry season, usually in February, and grow back toward the end of the dry season or in the early rainy season.

Range uncertain, possibly restricted to Panama where it is known principally from tropical moist forest in the Canal Zone, Veraguas, Panamá, and Darién and also from lower montane wet forest in Chiriquí (near Cerro Punta).

See Fig. 325.

KEY TO THE SPECIES OF SAPIUM

Spikes in clusters of 3–5 (rarely fewer); staminate flowers 2–5 per node ..... *S. aucuparium* Jacq.
Spikes solitary; staminate flowers 7–14 per node ..... *S. caudatum* Pitt.

76. ANACARDIACEAE

Trees. Leaves alternate, petiolate, simple (*Anacardium* and *Mangifera*) or pinnately compound; blades entire or undulate, glabrous or pubescent; venation pinnate; stipules lacking. Plants dioecious or polygamodioecious (*Astronium, Spondias*); flowers bisexual or unisexual,

KEY TO THE SPECIES OF ANACARDIACEAE

Leaves simple:
- Blades acute or acuminate at apex ..... *Mangifera indica* L.
- Blades mostly rounded or emarginate at apex:
  - Mature leaves mostly more than 15 cm long; trees more than 20 m tall; stamens 10, 4 longer than the rest ..... *Anacardium excelsum* (Bertero & Balb.) Skeels
  - Mature leaves mostly less than 15 cm long; trees less than 10 m tall; stamens 10, 1 much longer than the rest ..... *Anacardium occidentale* L.

Leaves compound:
- Stamens 10; fruits more than 2.5 cm long and 1.5 cm wide; leaves usually sharply acuminate:
  - Pubescent parts minutely puberulent (trichomes short and straight); pedicels and calyces usually pubescent; bark coarsely fissured; fruits orange at maturity; endocarp ovoid ..... *Spondias mombin* L.
  - Pubescent parts short-villous (trichomes seldom straight, if so not very short); pedicels and calyces usually glabrous; bark not coarsely fissured (with paper-thin strips of periderm); fruits green at maturity; endocarp oblong ..... *Spondias radlkoferi* Donn. Sm.
- Stamens 5; fruits less than 1.5 cm long and 0.6 cm wide; leaves not acuminate or bluntly acuminate:
  - Flowers pedicellate, unisexual; styles 3, separate to ovary; pistillode lacking in staminate flowers; fruits greenish, with winglike, accrescent sepals ..... *Astronium graveolens* Jacq.
  - Flowers sessile, bisexual; styles tripartite only at apex; pistil present in staminate flowers; fruits reddish, lacking accrescent sepals ..... *Mosquitoxylum jamaicense* Krug & Urban

actinomorphic, numerous, in terminal panicles; sepals 5, free, imbricate in bud; petals 5, free, imbricate or subvalvate in bud; intrastaminal disk present or absent (*Anacardium*); stamens 5, or (8)10 with 4 or 1 longer fertile stamens; filaments united basally; anthers 2-celled, introrse, basifixed, dehiscing longitudinally; ovary superior, 1-locular (sometimes 3-); placentation basal; ovule 1, anatropous; styles 3 (3–5 in *Spondias*), or style 1 and tripartite. Fruits drupes or nutlike seeds (*Anacardium*) with little or no endosperm.

Confused with Burseraceae (69) and Meliaceae (70), and distinguished from these families by the combination of an intrastaminal disk and a drupaceous or nutlike fruit.

Flowers are more or less open with easily accessible nectaries. They are probably pollinated by a wide variety of small bees and other small insects. Though bats have been found bearing pollen of *Anacardium* and *Mangifera indica*, it is presumed that they collected it accidentally while visiting the fruits (Heithaus, Fleming & Opler, 1975).

Diaspores are carried chiefly by mammals and, to a lesser extent, by birds, though rodents play an important role in the dispersal of *Spondias* (Smythe, 1970; Croat, 1974c). Bats are known to disperse fruits of *Anacardium excelsum* and *Spondias* (Heithaus, Fleming & Opler, 1975; Bonaccorso, 1975; Yazquez-Yanes et al., 1975). Fruits of *Mangifera* are eaten by white-faced and spider monkeys (Hladik & Hladik, 1969) and by coatis (Kaufmann, 1962). *Anacardium excelsum* is taken by coatis (Kaufmann, 1962) and also by white-faced and howler monkeys, which eat only the fleshy receptacle and discard the seeds. All of the larger monkeys and the coati eat the mesocarp of *Spondias mombin* (Hladik & Hladik, 1969). *Astronium graveolens* is wind dispersed by the winged calyx.

About 60–70 genera and 600 species; mainly in the subtropics or tropics, but widely distributed.

ANACARDIUM L.

Anacardium excelsum (Bertero & Balb.) Skeels, U.S.D.A. Bur. Pl. Industr. Bull. 242:36. 1912
Espavé, Wild cashew

Tree, 15–37 m tall; trunk often to 160 cm dbh, somewhat buttressed at base; outer bark coarse, deeply fissured, sometimes flaking loose in large patches, even younger bark (on trees 60 cm diam) with many narrow vertical fissures; inner bark pale pinkish-orange, forming minute close droplets of rust-colored sap soon after slash. Leaves simple, alternate, glabrous; petioles 1–2 cm long, pulvinate at base; blades long-obovate, rounded and sometimes emarginate at apex, tapering, obtuse and decurrent at base, 15–31 cm long, 6.5–10.5 cm wide, broadly undulate; veins lighter than surface. Panicles terminal, sparsely to densely pubescent all over, 15–35 cm long; pedicels 1–6 mm long; flowers bisexual, 5-parted, with strong, sweet, clovelike aroma; calyx lobes ovate, ± fleshy, densely ferruginous-pubescent; petals oblong-linear, ca 6 mm long, ± adnate to staminal tube, recurved at anthesis, cream-colored or green, ferruginous-pubescent; stamens usually 10, 4 much longer, exserted to 4 mm; filaments villous nearly full length; ovary minute; style 1, narrow, simple, equaling length of ovary. Nuts reniform, 3–4 cm long, glabrous, green at maturity, borne on a twisted or recurled green hypocarp ca 3 cm long and 5 mm wide. *Croat 7757, 8518.*

Abundant in the forest and along the lakeshore. Flowers for 6–8 weeks from February to April (sometimes to May). The fruits mature mostly from March

Fig. 326. *Anacardium excelsum*

Fig. 327. *Anacardium excelsum*

to May. Leaves fall in the early dry season and grow in again within 2 or 3 days or sometimes even before the old ones fall.

Nuts contain anacardic acid and a caustic oil called cardol. They are poisonous before they are roasted (Blohm, 1962). Fruits are eaten by white-faced and howler monkeys (Hladik & Hladik, 1969) and by the bat *Micronycteris hirsuta* (Wilson, 1971).

Costa Rica to Ecuador and Venezuela. In Panama, a characteristic tree species in tropical moist forest (Tosi, 1971; Holdridge & Budowski, 1956); known also from tropical dry forest in Coclé and from premontane moist forest in Veraguas and Panamá (Panamá City). Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Figs. 326 and 327.

Anacardium occidentale L., Sp. Pl. 383. 1753
Cashew, Marañón

Small cultivated tree, usually to 8 m tall and 25–30 cm dbh; branches roughened somewhat with prominent lenticels. Leaves simple, alternate; petioles 1–1.5 cm long; blades obovate, rounded to emarginate at apex, mostly acute at base, 6–16 cm long, 4.5–8 cm wide, glabrous; midrib and major lateral veins impressed and paler above, raised and paler below, the reticulate veins obscure. Panicles terminal; flowers bisexual, pedicellate, 5-parted, fragrant, puberulent on exposed parts outside; calyx lobes sharp; petals reflexed at about middle, sharply lobed, 1–2 mm wide, white to reddish near middle at anthesis, otherwise greenish; stamens 10, 1 much longer, exserted, the shorter ones held about midway in tube formed by recurved petals, often of different lengths, sometimes sterile; anthers occasionally with one theca held higher than the other; filaments fused near base; style 1, minute; nectar collecting both within ring of petals and between petals and sepals. Nuts reniform, 2–3.5 cm long, violet-purple to brown, borne at apex of an obovate, bright red, edible, fleshy hypocarp (the accrescent pedicel); mesocarp thin; seed 1. *Croat 6917.*

Cultivated at the Laboratory Clearing. Flowers from November to May (sometimes from October). The fruits mature from April to July (sometimes from December).

Native to the American tropics, but cultivated throughout the tropics. In Panama, known principally from tropical moist forest in the Canal Zone (both slopes), Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién; known also from tropical dry forest in Panamá (Taboga Island), from premontane wet forest in Colón, Chiriquí, and Panamá, and from premontane moist forest in Panamá.

ASTRONIUM Jacq.

Astronium graveolens Jacq., Enum. Syst. Pl. Ins. Carib. 33. 1760
Gonzolo alves, Zorro, Tigrillo

Dioecious tree, to 35 m tall and 80(100) cm dbh; outer bark lenticellate, peeling off in small, ± round patches leaving irregular shallow depressions; inner bark yellowish, granular, thick. Leaves imparipinnate, alternate; rachis and petiole 20–35 cm long; leaflets (2)9–15, mostly opposite; petiolules to 6 mm long; blades lanceolate-oblong to elliptic, bluntly acuminate, acute to rounded and sometimes inequilateral at base, 4–14 cm long, 2–7 cm wide, glabrous or pubescent especially on veins below. Panicles terminal, to 25 cm long; pedicels 1–3 mm long (much longer in fruit), articulate; flowers unisexual, ca 2 mm long, 5-parted, yellowish-green; sepals ovate to elliptic, minute, enlarging to 1.5 cm and persisting as fruit matures; petals to 3 mm long, ± elliptic; staminate flowers with 5 stamens to 3 mm long; pistillode lacking; pistillate flowers with the styles 3, ca 1 mm long, persistent or deciduous; stigmas small, disciform; ovary ovoid-oblong, with a single subapical ovule; staminodia reduced. Drupes narrowly oblong, 1–1.5 cm long, subterete. *Croat 13492.*

A few individuals are known in the old forest; seedlings, however, are rather common. Plants lose their leaves for a short time just before flowering, and new leaves appear with the flowers in the late dry season. The fruits develop quickly and are dispersed in the late dry and early rainy seasons. In Mexico, the fruits mature from April to June (Pennington & Sarukhan, 1968).

Southern Mexico to Bolivia. In Panama, a typical component of tropical dry and tropical moist forests (Tosi, 1971); known also from premontane moist forest in Panamá and from premontane wet forest in Chiriquí.

MANGIFERA L.

Mangifera indica L., Sp. Pl. 200.1753
Mango

Tree to 40 m tall, to 1 m dbh; sap milky; stems and leaves glabrous. Leaves simple, alternate, dense at apex of branchlets, more widely spaced below; petioles 1–6 cm long; blades mostly oblong, acute to long-acuminate, cuneate at base, 9–35 cm long, 2–7 cm wide, often undulate. Panicles terminal, 20–50 cm long; flowers bisexual, 5-parted; sepals ovate, to 3 mm long; petals greenish-white, ± oblong, to 5 mm long; stamens 5, 1 large and fertile, the other 4 reduced to staminodia; ovary obliquely subglobose or the style eccentric, slender, about equal to fertile stamen. Drupes oblong or semireniform, 10–20(30) cm long, greenish-yellow or orange at maturity; mesocarp thick, juicy, yellow or orange; seed oval, flattened. *Croat 5435, 7107.*

Cultivated at the Laboratory Clearing and persisting in several places in the younger forest and at the margin of the lake. Flowers in the dry season. The fruits are mature from April to July.

Touching these plants, especially the fruit, causes some people to be poisoned in the same manner in which they are from poison ivy (Blohm, 1962).

Native to Asia; cultivated throughout the tropics and throughout Panama. In Panama, known from tropical moist forest in the Canal Zone, from tropical dry forest in Panamá (Taboga Island), from premontane moist

Fig. 328. *Mosquitoxylum jamaicense*

Fig. 330. *Spondias mombin*

Fig. 329. *Spondias mombin*

forest in Los Santos, and from premontane wet forest in Chiriquí.

MOSQUITOXYLUM Krug & Urban

Mosquitoxylum jamaicense Krug & Urban, Notizbl. Königl. Bot. Gart. Berlin 1:79. 1895

Mosquito wood, Jobillo, Carbonero

Tree to 30 m high; trunk to 60 cm dbh, weakly buttressed; outer bark weakly fissured; inner bark thin, reddish, forming white sap droplets when cut; wood white. Leaves imparipinnate, alternate, 10–30 cm long, clustered toward apex of branches; leaflets 5–17, usually opposite, short-petiolulate; blades mostly oblong, variable and emarginate to acuminate at apex, cuneate and unequal at base, 2.5–10 cm long, 1.5–3.5 cm wide, usually pubescent on both surfaces especially on midrib. Panicles 7–27 cm long, hirtellous; flowers minute, 5-parted, sessile, bisexual, each subtended by 3, persistent, deltoid bracts ca 1 mm long; sepals ovate, ca 1 mm long, ciliate; petals ca 1 mm long; stamens 5, ca 1 mm long, inserted at margin of disk; disk cupular, 5-lobed, each lobe secondarily lobed; style 1, persistent, tripartite at apex. Drupes 6–9 mm long, red, shiny, glabrous, laterally oblique and somewhat flattened; mesocarp thin, bitter but edible; seed 1, its funiculus subbasal. *Croat 12565.*

Uncommon, in the forest. Seasonal behavior uncertain. Flowers from June to August, but probably later in the rainy season as well. The fruits mature from July to January, but mostly from August to December. The January fruiting record is from higher elevations in Panama in tropical wet forest.

The tree may be infested with moderately large, biting ants when in fruit. The fruits are probably dispersed by birds.

Mexico to Panama; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Darién, from premontane wet forest in the Canal Zone, Colón, and Panamá, and from tropical wet forest in Coclé.

See Fig. 328.

SPONDIAS L.

Spondias mombin L., Sp. Pl. 371. 1753

Hog plum, Jobo, Wild plum

Tree, mostly 10–30 m tall, to 60 cm dbh; outer bark gray, deeply and coarsely fissured, the raised segments hard, rough, the inner margin irregular; inner bark variously colored, usually with triangular patches of red or tangerine alternating with white; wood soft, white; sap clear, at least never forming viscid droplets; at least the youngest branches puberulent. Leaves imparipinnate, alternate, to 60 cm long (to 70 cm on juveniles); petiole and rachis usually finely puberulent; leaflets mostly (3)9–17, opposite or subopposite; petiolules 6–9(14) mm long; blades oblong to ovate, usually acuminate, acute to rounded and asymmetrical at base, 3–20 cm long and 1.5–7 cm wide, usually ± glabrous but with puberulence on midribs and major veins above and below, minutely revolute with a prominent submarginal vein; midrib of larger leaflets arched, the reticulate veins prominulous. Panicles terminal, to 60 cm long; branches, peduncles, pedicels, and calyces usually puberulent; pedicels 1–5 mm long, usually articulate near base; flowers 5–7 mm wide, 5-parted, bisexual or rarely pistillate, globular to obovoid in bud; calyx shallow, the lobes short, triangular, sharply acute, usually minutely puberulent, ciliate; petals white, acute and inflexed-apiculate at apex, somewhat reflexed at anthesis; stamens 10, exserted, 1.5–3 mm long, alternating with fleshy, undulate segments of disk; disk fleshy, undulate-lobed, to ca 1 mm wide, the width of one side less than width of clump of styles; styles usually 4 or 5 (rarely 3), much shorter than stamens at anthesis; stigmas linear, on dorsal surface of style near apex. Fruits oblong to obovoid, 2.5–3 cm long, yellow to orange at maturity; mesocarp to 6 mm thick, fleshy, sweet and tasty; endocarps obovoid, 2–2.5 cm long, hard, covered by a tough, coarse, fibrous matrix. *Croat 10751, 14090.*

Frequent in the forest. Flowering principally from March to June (rarely earlier), but most abundantly in April and May. The fruits are mature from July to October, mostly in August and September. Leaves fall during the early part of the dry season, beginning in December and January, and grow in again before flowering commences.

The species is reportedly dioecious in Mexico (Pennington & Sarukhan, 1968) and monoecious in Costa Rica (Bawa & Opler, 1975). In Panama, flowers are apparently mostly bisexual with some pistillate flowers also.

Throughout tropical America; introduced in tropical Africa and East Indies. In Panama, a typical component of tropical moist forest (Tosi, 1971), known principally from the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién; known also from tropical dry forest in Coclé, from premontane moist forest in Panamá (Farfan Beach), and from premontane wet forest in Chiriquí (Progreso).

See Figs. 329 and 330.

Spondias radlkoferi Donn. Sm., Bot. Gaz. (Crawfordsville) 16: 194. 1891

Tree, to 30 m tall and to 75 cm dbh; outer bark not deeply fissured, the surface with thin, narrow strips of periderm; inner bark similar to *S. mombin* except producing whitish, viscid droplets within a short time after being cut; younger branches glabrate to sparsely crisp-villous to densely villous becoming glabrate. Leaves imparipinnate, alternate, to 54 cm long, usually sparsely crisp-villous on petiole, rachis, upper midrib, and underside of leaflets, especially on younger leaves; leaflets mostly 7–19; blades ovate to oblong-elliptic or oblong, abruptly long-acuminate, acute to subcordate and markedly inequilateral at base, 2.5–16 cm long and 1.8–6 cm wide, ± revolute, usually ciliate, submarginal vein usually lacking. Panicles terminal and upper-axillary, to 55 cm long; axes and rarely pedicels sparsely to densely crisp-villous; pedicels glabrous or less often pubescent,

articulate usually 0.5–2.5 mm below calyx (the articulation sometimes obscured by bracteoles); flowers 5-parted, usually bisexual, rarely pistillate, the first open ones usually appearing with new leaves, the buds usually ± pyriform; calyx cupulate, the lobes thick, prominent, rounded to blunt-triangular, ca 1 mm long, usually glabrous all over; petals ± oblong-elliptic, acute and inflexed-apiculate at apex, 2.3–4.3 mm long, white or greenish-white, recurved at anthesis, the veins 3 (including marginal vein); stamens 10, 1.7–2 mm long, in 2 series, exserted at anthesis; disk to 2.3 mm wide, fleshy, undulate-lobed, the width of one side more than width of clump of styles; ovary subglobose, pubescent; styles usually 3 or 4 (rarely 5), usually free and shorter than stamens at anthesis in bisexual flowers; stigmatic surfaces linear, on dorsal surface near apex; pistillate flowers rare; styles to ca 2 mm long, ca twice as long as stamens, united below middle; stigmatic surface ovate, turned inward. Fruits 3–3.5 cm long, minutely pubescent when immature, oblong to obovate and green at maturity; mesocarp thin, green, with a ± unripened flavor, faintly sweet to acidic; endocarp oblong, nearly as long as fruit, hard, covered by a tough, coarse, fibrous matrix. *Croat 11682.*

Frequent in the forest. Flowers 4–6 weeks later than *S. mombin* on the island, but since the flowering periods overlap, both species may be seen flowering at the same time. Flowers mostly from April to June, especially in May and June. The fruits mature from September to December, especially in October and November. Leaves fall shortly before flowering, growing in again at the time of flowering.

The species has long been confused with *S. mombin* (Croat, 1974c).

Southern Mexico (Veracruz, Chiapas, Campeche) through Central America into Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá (El Llano), and from premontane wet forest in Chiriquí.

77. CELASTRACEAE

Trees. Leaves alternate, petiolate; blades simple, entire; venation pinnate; stipules present. Flowers polygamous, functionally unisexual, actinomorphic, solitary or in condensed racemes; calyx weakly 5-lobed; petals 4 or 5, imbricate; disk present; stamens 4 or 5, alternate with petals, arising from below the disk; anthers 2-celled, introrse, dehiscing longitudinally; ovary superior, 2–4-locular, 2–4-carpellate, immersed in the disk; placentation axile; ovules 2 per placenta, anatropous; stigma sessile, 2–4-lobed. Fruits loculicidal capsules; seeds usually 2, arillate, with endosperm.

Celastraceae are most easily confused with Hippocrateaceae (78), which are only lianas on BCI. The family is represented on BCI by a single species. It may be recognized by its two-valved capsule with arillate seeds.

About 80 genera and over 1,000 species; widely distributed.

MAYTENUS Mol.

Maytenus schippii Lund., Phytologia 1:305. 1939

Glabrous tree, 7–10 m tall. Stipules ± deltoid, less than 1 mm long, ± entire; petioles 5–10 mm long, narrowly winged; blades elliptic to oblong-elliptic, abruptly acuminate, attenuate and decurrent at base, 6–12 cm long, 3–5.5 cm wide, moderately thick, drying gray-green, the acumen obtuse, the margins entire and weakly revolute. Racemes very short, condensed; pedicels 2–6 mm long, articulate at base; flowers functionally unisexual, solitary, appearing before or with new leaves; calyx ca 3 mm wide, weakly 5-lobed, the lobes irregular; petals 4 or 5, ovate, rounded at apex, ca 2 mm long and 1.6 mm wide, imbricate in bud, spreading at anthesis, cream to yellowish; stamens 4 or 5, inserted below the broad, flattened disk, ca 1.5 mm long; filaments broadest and ± flattened at base; anthers introrse; ovary embedded in disk and confluent with it, 2–4-locular; stigma ± sessile, 2–4-lobed. Capsules usually few, often apparently paired, obovate, ca 1.5 cm long, smooth, orange; valves usually 2, coriaceous, opening broadly to expose seeds; seeds usually 2, arillate, the aril white, about as long as seed. *Croat 6135, Hayden 144.*

Rare, along the shore of Bat Cove and Channel Point. Flowers in the dry and early rainy seasons. The fruits mature from July to September or later.

The pollination system is unknown. The arillate seeds are well suited for bird dispersal.

The *Flora of Panama* treatment by Edwin and Hou (1975) included *Hayden 144* under *M. guyanensis* Klotzsch & Schomb. However, that collection differs in no important way from other BCI material included under *M. schippii,* and I believe it was collected from the same tree as *Croat 6135. Stern et al. 863* from Darién is also *M. schippii.*

Mexico to Panama. In Panama, known from tropical moist forest on BCI and in Darién and from tropical wet forest in Colón (Salúd).

78. HIPPOCRATEACEAE

Lianas, occasionally with colored sap. Leaves opposite, petiolate; blades simple, entire; venation pinnate; stipules when present small, interpetiolar. Cymes terminal or axillary, bracteolate; flowers bisexual, actinomorphic, occasionally aromatic; sepals 5, free, imbricate; petals 5, free, imbricate or subvalvate (*Hippocratea*) or valvate (*Prionostemma*); stamens 3, usually inserted within the disk; anthers 2-celled, dehiscing by a transverse slit; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules 2 to many per cell, anatropous; style 1, simple; stigma 3-sided. Fruits of 3 capsular mericarps with many seeds per mericarp and the seeds winged, or the fruits drupaceous (*Tontelea*); endosperm lacking.

Closely allied to the Celastraceae (77). Members of the family are most easily recognized by being lianas with usually small greenish flowers, by the three, usually

KEY TO THE SPECIES OF HIPPOCRATEACEAE

Fruits drupes, more than 10 cm long with a thick pericarp; seeds wingless, embedded in a fleshy matrix; flowers yellow-orange, 5–7 mm diam; leaves more than 7 cm wide, the petiole more than 1 cm long ..... *Tontelea richardii* (Peyr.) A. C. Smith
Fruits 3 capsular mericarps; seeds winged; flowers greenish, 2–15 mm diam; leaves less than 7 cm wide, or if wider on a petiole less than 1 cm long:
  Mericarps connate, forming a shallow, trilobate bowl; petals narrowly ovate, serrate, ca 4 mm long ..... *Anthodon panamense* A. C. Smith
  Mericarps attached to receptacle separately; petals not as above:
    Mericarps 1 cm or more thick; flowers fragile, ca 2 mm diam; seeds irregularly oblong, less than 5 per mericarp, probably water-dispersed, the wing smaller than the seminiferous part ..... *Hylenaea praecelsa* (Miers) A. C. Smith
    Mericarps ± flat, less than 5 mm thick; flowers not falling so easily, more than 5 mm diam; seeds samaroid, more than 4 per mericarp, wind-dispersed, the wing larger than the seminiferous part:
      Leaves asperous; flowers more than 9 mm diam; mericarps ca 1.5 times longer than broad, somewhat swollen; sap red ..... *Prionostemma aspera* (Lam.) Miers
      Leaves smooth; flowers less than 9 mm diam; mericarps ca 2 times longer than broad, flat; sap clear ..... *Hippocratea volubilis* L.

fused stamens mounted on a conspicuous disk, and by the three-parted fruits with winged seeds. On BCI only *Tontelea* has simple fruits.

The flowers are greenish and mostly open. Pollination systems are unknown. The fruits of *Anthodon panamense, Hippocratea volubilis,* and *Prionostemma aspera* have winged, more or less samaroid, wind-dispersed seeds. Seeds of *Hylenaea,* though also released from a capsular mericarp, are fewer in number, fleshy, and probably mostly water dispersed. Seeds of *Tontelea* are dispersed by agoutis and probably other terrestrial animals as well.

Eighteen genera; tropics of both hemispheres.

ANTHODON R. & P.

Anthodon panamense A. C. Smith, Brittonia 3:422, f. 8(a–f). 1940

Hippocratea malpighiifolia sensu Standl. non Rudge

Bejuco de estrella

Glabrous liana; stems terete (often faintly quadrangular on drying). Petioles 5–8 mm long; stipules lacking or inconspicuous and early deciduous; blades elliptic to oblong-elliptic, obtuse to acuminate at apex, obtuse to acute or rounded at base, 5–13.5 cm long, 2.5–5.7 cm wide. Inflorescences cymose, axillary or terminal, dichotomously branched, to 6 cm long; flowers greenish-yellow to olive-green, 10–12 mm diam, 5-parted; sepals semiorbicular, ca 1 mm long, broader than long; petals ± ovate-lanceolate, 4–5 mm long, blunt at apex, serrate; disk prominent; stamens 3, ca 1.5 mm long, held closely against the 3-sided stigma; filaments flattened, broadened at base; anthers broadly reniform, broader than long, dehiscing by a transverse slit; ovary ovoid; style short, slightly shorter than stamens. Fruits trilobate, shallowly bowl-shaped, to 15 cm wide, pendent at maturity; mericarps 3, conspicuously flattened, rounded to emarginate at apex, connate 3–5 cm at their bases, dehiscing along a median suture to allow seeds to slowly drift out, the margins thin; seeds 10–14 per mericarp, thin-winged, ca 2 cm long and 2.5 cm wide including wings. *Croat 11734, 12622.*

Occasional, in the canopy of the forest. Flowers most abundantly from July through August, but also from December to April. Fruit maturity time uncertain.

Known only from Panama, from tropical moist forest on the Atlantic slope of the Canal Zone and in Bocas del Toro, Colón, and Darién.

See Figs. 331 and 332.

HIPPOCRATEA L.

Hippocratea volubilis L., Sp. Pl. 1191. 1753

Liana; branches usually opposite, the older branches minutely fissured, the younger branches glabrous to puberulent. Leaves opposite; stipules deltoid, ca 2 mm long, widely separated on stem; petioles short, canaliculate; blades usually elliptic to oblong-elliptic, bluntly cuspidate to acuminate and often downturned at apex, rounded to acute at base, mostly 4–11(17) cm long, 2–6(8) cm wide, glabrous, the margins subentire to crenate, continuous with edges of petiole. Inflorescences axillary and terminal, cymose-paniculate with dichotomous branching, mostly 6–15 cm long, most parts minutely tomentulose; flowers greenish-white or yellowish, with a faint sweet aroma, 5-parted, 6–8 mm diam, short-pedicellate, bracteolate; sepals rounded, minute; petals 3–4 mm long, glabrous at base inside, completely pubescent at apex or bearing an inverted Y-shaped fringe of trichomes; disk prominent; stamens 3, erect at anthesis, hiding style, later folding outward to expose style; filaments flattened; style ca 1 mm long. Mericarps 3, flattened, oblong or elliptic, 4–6(8) cm long, mostly to 3 cm broad, rounded or deeply emarginate at apex; seeds samaroid, mostly 3.5–5 cm long; seminiferous area apical, darker, 13–25 mm long. *Croat 5040, 7275.*

Very abundant in the canopy and over the water at the edge of the lake. Flowers most of the year except in the early rainy season. Fruit maturity time uncertain.

Fig. 331. *Anthodon panamense*

Fig. 332. *Anthodon panamense*

Fig. 333. *Hippocratea volubilis*

Southern Florida and Mexico to northern Argentina. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from premontane wet forest in Colón.

See Fig. 333.

HYLENAEA Miers

Hylenaea praecelsa (Miers) A. C. Smith, Brittonia 3:410. 1940

Salacia praecelsa (Miers) Standl.

Colmillo de puerco, Gorotillo

Nearly glabrous liana; outer bark gray, thin, becoming fissured and peeling to expose reddish-brown inner bark; sap sometimes red in older wood. Stipules lacking or minute and early deciduous; petioles short, to 8 mm long; blades ± elliptic, acuminate, rounded or subcordate at base, mostly 6–26(33) cm long, 2–11 cm wide, somewhat coriaceous, the sides ± upturned, broadly undulate. Inflorescences axillary, to 15 cm long, branched many times, fragile; pedicels ca 1.5 mm long, slender; flowers greenish, to 2 mm diam, 5-parted; sepals minute; petals spreading, ca 1 mm long, papillose-puberulent; stamens 3, minute, included. Mericarps 3, divergent, capsular, longer than broad, rounded or emarginate at apex, 7.5–10 cm long, 5–6 cm wide, 1–2 cm thick; exocarp light brown, ± roughened; seeds usually 4 per mericarp, 4–7.5 cm long, 1–1.5 cm wide, fleshy, buoyant, irregularly angulate. *Croat 7677.*

Occasional in the canopy; more common at the edge of the lake. Flowers in the dry season, with the fruits maturing 9–12 months later.

Flowering inflorescences disappear quickly. The fruits are quite distinctive and are probably principally water dispersed.

Known from Panama and Colombia (Chocó). In Panama, known from tropical moist forest on the Atlantic slope of the Canal Zone and in San Blas and Panamá (San José Island).

PRIONOSTEMMA Miers

Prionostemma aspera (Lam.) Miers, Trans. Linn. Soc. London 28:355. 1872

Hippocratea malpighiifolia Rudge

Liana climbing into canopy; stems retrorsely asperous when young, glabrous in age; sap red. Leaves apparently estipulate; petioles 5–10 mm long; blades ovate-oblong to oblong-elliptic or oblong, short-acuminate, rounded to subcordate at base, 4.5–15 cm long, 2–7 cm wide, ± scabrous and asperous above and below. Inflorescences axillary, 3.5–10 cm long; inflorescence branches and petals minutely puberulent; flowers yellowish-green, 9–15 mm diam, pedicellate, 5-parted; sepals ± rounded, fimbriate; petals broadly spatulate, clawed, rounded at apex, the margin minutely toothed; disk prominent, to ca 8 mm broad; stamens 3, to 3.3 mm long; filaments strap-shaped, broadened below, at first erect, later twisting and holding the anther close to disk; style conic, minutely puberulent; stigma simple. Mericarps 3, divergent, capsular, to 7 cm long and 4.5 cm wide, less than 5 mm thick, truncate, obtuse or slightly emarginate at apex, obtuse at base; seeds 4–8 per mericarp, winged; seminiferous area darker, to 14 mm long and 7 mm broad; wing elliptic or obovate, to 6 cm long and 3 cm broad. *Croat 7675.*

Frequent in the canopy of the forest. Flowers in February and March. The fruits possibly mature 1 year later.

Easily recognized by the moderately large green flowers, which fall to the ground. Juvenile plants of this species have two noteworthy features: the stems exude copious red sap when cut; and the smaller branches are very asperous with many, very short, stout-based trichomes, which no doubt assist the plants in climbing. Like most other species of Hippocrateaceae, climbing is assisted at least in later stages of growth by the twining of lateral branches.

Panama to Bolivia. In Panama, known only from tropical moist forest on BCI and in Darién.

See Fig. 334.

TONTELEA Aubl.

Tontelea richardii (Peyr.) A. C. Smith, Brittonia 3:478. 1940

Bejuco de canjura

Glabrous liana climbing into canopy; stems terete. Stipules deltoid, 1–2 mm long, often leaving conspicuous, usually unconnected scars; petioles 12–17 mm long; blades ovate-oblong to elliptic-oblong, abruptly acuminate to mucronate at apex, rounded at base, 12–24 cm long, 7–11 cm wide, coriaceous. Inflorescences terminal or in uppermost axils, 3–12 cm long; flowers 5-parted, sweetly aromatic, 5–7 mm diam; calyx thick, ca 3.3 mm diam, deeply lobed, the lobes ± orbicular, imbricate; petals spreading, obovate, to 2.7 mm long, rounded at apex, thick, yellow-orange becoming burnt-orange in age; disk fleshy, bowl-shaped; stamens 3, arising from between disk and ovary, erect, to ca 1 mm long; filaments flattened, broader toward base; anthers obcordate, about as broad as long, extrorse; ovary 3-sided; styles 3, very short, united into equilateral triangle. Fruits heavy drupes to 17 cm long and 12 cm broad; exocarp brown and scurfy outside, 1–1.5 mm thick; locules 3; seeds 2 per locule, large, irregular, to 6 cm wide, with abundant white endosperm, covered with a thick scurfy layer of tissue. *Croat 7932, 15069.*

Common in the forest, usually high in the canopy; occasional along the shore and at lower levels. Flowers from December to June. The fruits mature about 1 year later.

The large cannonball-like fruits often fall to the ground and break open or are opened by rodents. Some fruits are buried by agoutis, which dig them up late in the rainy season when food is scarce. Some germinate where they are buried.

Panama and the Guianas. In Panama, reported only from tropical moist forest on BCI.

See Fig. 335.

Fig. 334. *Prionostemma aspera*

Fig. 335. *Tontelea richardii*

Fig. 336. *Turpinia occidentalis* subsp. *breviflora*

79. STAPHYLEACEAE

Trees or shrubs. Leaves opposite, petiolate, pinnately compound; leaflets serrate; venation pinnate; stipules present. Panicles terminal; flowers bisexual and actinomorphic; sepals 5, free; petals 5, free; stamens 5, arising from between the lobes of the conspicuous disk, alternate with the petals; anthers 2-celled, dehiscing longitudinally; ovary superior, 3-locular, 3-carpellate; placentation axile; ovules few, anatropous; styles 3. Fruits berries; seeds with fleshy endosperm.

Sometimes confused with Caprifoliaceae but with no other family on BCI. Distinguished by the opposite, pinnately compound leaves with serrate-margined leaflets and by the small white flowers with pistils of three free carpels.

Pollination system is unknown.

Fruits are endozoochorous, apparently by arboreal frugivores. Many are found on the ground as well and are probably further dispersed by other animals. *Turpinia pinnata* Schlechter, with a very similar fruit, is taken by bats in Mexico (Yazquez-Yanes et al., 1975).

Five to seven genera and about 60 species; mostly from North America.

TURPINIA Vent.

Turpinia occidentalis G. Don subsp. **breviflora** Croat, Ann. Missouri Bot. Gard. 63:397. 1976

T. paniculata sensu auct. non Vent.

Tree, to 18 m tall and 30 cm dbh, ± glabrous all over; outer bark with many, small, closely spaced, vertical fissures; inner bark brown with white markings; sap without odor. Leaves opposite; petioles 4–6(11) cm long; petiolules less than 1 cm long on lateral leaflets, longer on terminal leaflet; leaflets 3–9, elliptic or ovate-elliptic, acuminate, obtuse to rounded at base, 6–13 cm long, 2.5–5 cm wide, sharply to obscurely serrate. Panicles terminal, branched many times, to 30 cm long; pedicels to 1.5 mm long; flowers 5-parted, fragrant; sepals ± irregular, concave, at least 1 somewhat longer than others, to 2.7 mm long, rounded at apex, persisting in fruit; petals white, obovate, rounded above, 2.3–2.7 mm long; stamens 5, as long as and alternating with petals from between the lobes of the fluted disk; anthers ovate, attached at center, the thecae directed upward; pistil of 3 free carpels; styles connate at anthesis, later becoming free; stigmas united, at about the level of anthers. Berries yellow, subglobose to obovate, 3-locular, to 2 cm diam, with 3 radial grooves at apex; seeds several per locule, irregularly ovate, 4–5 mm long, smooth, orange-brown. *Croat 15048, 17048.*

Occasional, in the forest. Flowers principally from April to June. The fruits mature from July to September.

The subspecies *occidentalis* occurs in Panama also but usually at elevations above 1,000 m. It is distinguished by having flowers more than 3.5 mm long.

Southern Mexico to Colombia; West Indies; most abundant in lower middle America and Panama, from sea level to 850 m. In Panama, known from tropical moist forest in the Canal Zone and Darién and from premontane wet forest in Veraguas, Coclé, and Panamá.

See Fig. 336.

80. SAPINDACEAE

Trees or shrubs (*Allophylus, Cupania, Talisia*) or watch-spring-tendriled lianas (*Paullinia, Serjania, Thinouia*), the climbing species generally with milky sap and complex wood structure. Leaves alternate, petiolate, pinnate or compound-pinnate; leaflets sometimes lobed, entire or serrate; venation pinnate (palmately veined at base in *Thinouia*); stipules present only in climbing species. Cymose inflorescences or thyrses terminal or axillary, bracteate, sometimes racemose; flowers unisexual or

KEY TO THE TAXA OF SAPINDACEAE

- Leaves more than pinnate, at least on basal pair of pinnae:
  - Leaves with only the basal pair of pinnae ternate, the remainder pinnate ..... *Paullinia glomerulosa* Radlk.
  - Leaves strictly biternate (3 sets of 3 leaflets) *or* leaves with more than 3 sets of 3 leaflets *or* leaves more than bipinnate:
    - Leaves more than bipinnate *or* with more than 3 sets of 3 leaflets:
      - Leaflets less than 2 cm wide, glabrate; petioles unwinged ..... *Serjania trachygona* Radlk.
      - Leaflets more than 2 cm wide, minutely hispid with the vein axils densely tomentose; petioles and rachises conspicuously winged ..... *Serjania mexicana* (L.) Willd.
    - Leaves strictly biternate (3 sets of 3 leaflets):
      - Lower blade surface bearing tufts of trichomes in vein axils, otherwise glabrate:
        - Rachis winged; young stems prominently lenticellate; flowers in congested, unbranched, ± cylindrical inflorescences, the flowers ± contiguous; fruits suborbicular, 3-angled, red, woody capsules ..... *Paullinia fuscescens* H.B.K. var. *glabrata* Croat
        - Rachis not winged; young stems not lenticellate; flowers diffuse, often in branched terminal racemose panicles; fruits ovate-cordate or ovate-elliptic, 3-winged schizocarps:
          - Cells of fruit and ovaries glabrous; stems with simple wood ..... *Serjania pluvialiflorens* Croat
          - Cells of fruit and ovary puberulent; stems with composite wood, the large central core surrounded by 10 regular peripheral bundles ..... *Serjania decapleuria* Croat
      - Lower blade surface lacking axillary tufts ..... *Serjania* (in part)

- Leaves all pinnate:
  - Leaflets always 3:
    - Plants shrubs or trees lacking tendrils; cocci 1 or 2, red, obovoid, less than 1 cm long ..... *Allophylus psilospermus* Radlk.
    - Plants tendriled lianas:
      - Leaflets bearing axillary tufts of trichomes on underside; stems not ribbed or striate, lenticellate:
        - Leaflets palmately veined at base; stamens long-exserted; petals less than 1 mm long; fruits schizocarps of 3 samaras, more than 5 cm long ..... *Thinouia myriantha* Tr. & Planch.
        - Leaflets not palmately veined; stamens ± included; petals ca 5 mm long; fruits 3-sided, thick-walled capsules, less than 2.5 cm long ..... *Paullinia turbacensis* H.B.K.
      - Leaflets lacking axillary tufts of trichomes on underside; stems striate or ribbed, not lenticellate ..... *Serjania circumvallata* Radlk.
  - Leaflets usually more than 3:
    - Leaflets 10 or more ..... *Talisia*
    - Leaflets 3–9:
      - Petioles or rachises winged ..... *Paullinia* (in part)
      - Petioles and rachises unwinged:
        - Plants lianas; leaflets opposite, the apical 3 attached at the same point on rachis, the base of terminal leaflet different from base of lateral leaflets:
          - Plants essentially glabrous ..... *Paullinia pterocarpa* Tr. & Planch.
          - Plants conspicuously brownish-hirsute on most parts ..... *Paullinia rugosa* Radlk.
        - Plants shrubs or trees; leaflets alternate or only subopposite, the apical 3 not attached at the same point on rachis, the terminal leaflet as others ..... *Cupania*

sometimes bisexual (polygamous); sepals 4 or 5, free or briefly connate, the lobes imbricate; petals 4 or 5, free, clawed, often with petaloid appendages (scales); extrastaminal nectariferous disk present, sometimes glandular; stamens 8 (sometimes 5, 7, 9, or 10), free (united in *Serjania*); anthers 2-celled, versatile or basifixed, introrse, longitudinally dehiscent; ovary superior, (2)3-locular, (2)3-carpellate; placentation axile; ovules 1 or 2 per locule; style simple or trifid. Fruits samaroid mericarps (*Serjania, Thinouia*) or capsules (*Cupania, Paullinia*), rarely indehiscent cocci (*Allophylus*) or indurate berries (*Talisia*); seeds sometimes arillate (*Cupania, Paullinia*), lacking endosperm.

Sapindaceae are distinguished by the pinnate or compound-pinnate leaves, by the watchspring tendrils on the lianas, by the small, usually polygamodioecious flowers with scale- or gland-appendaged petals, and by the usually schizocarpous and samaroid or capsular, arillate fruits with shiny black seeds.

Flowers are generally pollinated by small bees. *Trigona* are frequently seen visiting flowers of *Serjania* and *Paullinia*. In Costa Rica, *Serjania* is visited by *Augochloropsis* (Halictidae), *Paratetrapedia* (Anthophoridae), *Trigona,* and *Melipona.* Also in Costa Rica, *Allophylus* is visited by *Trigona, Exomalopsis* (Anthophoridae), and *Phthiria* (Bombyliidae). D. Janzen (pers. comm.) reports that in Costa Rica and Mexico, however, *Serjania* and *Paullinia* are pollinated by *Ptiloglossa* very early in the morning, and that the rest of the bee visitors are robbing pollen and nectar. Heithaus (1973) reported small chrysomelid beetles to visit *Allophylus* in Costa Rica.

Serjania and *Thinouia* are wind dispersed. *Paullinia* and *Cupania* are principally bird dispersed, although Oppenheimer (1968) reported a number of species, including *Cupania rufescens, C. sylvatica,* and *Paullinia turbacensis,* to be taken by white-faced monkeys, and seeds of *Cupania rufescens* have been eaten by coatis (Kaufmann, 1962). *Allophylus* is perhaps equally dispersed by birds and other animals such as the white-faced monkey (Oppenheimer, 1968). Many seeds fall to the ground and may be further dispersed. *Talisia* is probably mammal dispersed.

Some 150 genera and about 2,000 species; subtropics and tropics.

ALLOPHYLUS L.

Allophylus psilospermus Radlk., Sitzungsber. Math.-Phys. Cl. Königl. Bayer. Akad. Wiss. München 20:230. 1890

A. panamensis Radlk.

Slender, polygamous tree, usually 5–10(20) m tall; stems terete, glabrous except when young. Leaves trifoliolate; petioles somewhat flattened laterally, 2–5(7) cm long, strigose; leaflets ± elliptic, subsessile, acuminate at apex, acute and sometimes inequilateral at base, 2.5–26 cm long, 1.5–7.5 cm wide, remotely serrate, ± glabrous but with sparsely pubescent veins and sometimes tufts of trichomes in axils of veins below. Thyrses puberulent, simple or paniculate, chiefly axillary; flowers 4-parted, campanulate, cream or greenish-white, ca 2 mm wide, pedicellate; sepals ciliolate, orbicular to obovate; petals obovate, 1–2 mm long, the scales united with petals to near apex, densely villous, each subtended by a yellowish basal gland; staminate flowers with the stamens 8, well exserted, to ca 2.3 mm long, clustered on one side of the flower; filaments villous at least near base; pistillode obscure; pistillate flowers with the stamens less than 1 mm long, included; ovary 2-celled, minutely hispidulous; style borne between 2 cells of ovary, 1.5–2 mm long, persisting in fruit but very oblique, held at base of fruit;

stigmas 2, recurved, densely papillate. Fruits of 2 obovoid cocci (1 often aborting), 6–9 mm long, yellow to orange, finally red and glabrate at maturity with a thin fleshy pericarp covering the seed; seed 2–3 mm diam. *Croat 5862, 10754.*

Frequent in the forest, especially the young forest; possibly most abundant along the shore. Flowers in the dry season (January to May), with the fruits maturing in the early rainy season (May to August).

The species is variable throughout Panama. BCI plants are generally glabrate on the surface of the leaves and sparsely pubescent on the veins, sometimes with axillary tufts of trichomes in the vein axils. The closely related *A. occidentalis* Sw. (not on BCI) is puberulent to villous over the entire leaf surface.

Mexico to Panama; West Indies. In Panama, known principally from tropical moist forest in the Canal Zone, Chiriquí, Veraguas, Los Santos, Panamá, and Darién; known also from tropical dry forest in Los Santos and Coclé, from premontane moist forest in Los Santos (Punta Mala), from premontane wet forest in Chiriquí (Tolé), and from tropical wet forest in Coclé (El Valle). Standley (1928) reported the species to be occasional on the Atlantic slope of the Canal Zone. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

CUPANIA L.

The scale of the petals is usually fused to the margin of the petal in *Cupania* so that the petal and the scale form a small pocket when pulled apart at the apex. All species are polygamous.

Cupania cinerea Poepp. in Poepp. & Endl., Nov. Gen. Sp. Pl. 3:38. 1843

C. costaricensis Radlk.

Gorgojo blanco, Gorgojo, Gorgojero

Tree, to ca 8(10) m tall; stems terete, conspicuously lenticellate, often flexuous, glabrous but with young stems tomentose. Leaves pinnate; petioles 1–6 cm long, tomentose to glabrate; petiolules ca 5 mm long; leaflets 3–7, obovate, rounded to truncate or emarginate at apex, acute at base, 6–17 cm long, 3.5–7 cm wide, densely white-tomentose below, glabrate above, serrate-dentate. Panicles dense, terminal or subterminal, racemose; sepals and petals 5; sepals ovate, tomentose, greenish; petals ± obovate, white, to 2 mm long, villous, the blades fused to the scales laterally (deeply divided in middle); stamens 8, inserted on inner edge of disk; filaments villous below middle; disk fleshy, ca 0.7 mm high, tomentose; staminate flowers with the stamens exserted, 2.5–3 mm long, the ovary abortive, pubescent, lacking style; bisexual flowers with the stamens 1.5–2 mm long, only slightly exserted, the ovary ovoid, obtusely 3-angulate, with a stout style about as long as ovary, the style and ovary together ca 3 mm long; stigmas 3, recurved; ovary, style, and stigmas tomentose. Capsules obovate, ± rounded to bilobed, short-stipitate, ca 1.5 cm long and 1 cm wide, pale greenish-tomentose or brown-tomentose outside, woolly inside; seeds oblong, more than 1 cm long, shiny black, the lower half covered with an orange aril. *Croat 6696, 11767.*

Occasional, on the northern side of the island along the shore. Flowers in the early rainy season (June and July). The fruits mature in September and October.

The species is closest to *C. latifolia.*

Costa Rica to Colombia, Venezuela, Peru, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién and from tropical wet forest in Colón.

See Fig. 337.

Cupania latifolia H.B.K., Nov. Gen. & Sp. 5:126. 1821

C. papillosa Radlk.

Tree, 4–20 m tall; trunk 5–25 cm dbh, often somewhat twisted; outer bark smooth, bearing fine, granular lenticels which wipe off easily; inner bark thin, tan; sap with faint, pleasant aroma; stems densely lenticellate, the younger parts (including petioles and branches of inflorescence) densely brown-tomentose. Leaves pinnate (juvenile plants often with some large simple leaves); petioles to 6 cm long (15 cm long on juvenile leaves);

KEY TO THE SPECIES OF CUPANIA

Leaf blades ± glabrous below or the pubescence inconspicuous and usually sparse (except possibly on veins) (*C. latifolia* is sometimes moderately pubescent but the trichomes are not contiguous or long):

- Leaflets crenate to wavy, obtuse to truncate at apex; inflorescences usually branched many times, often 15 cm or more long; fruits ± round, brown, to 2.5 cm diam (when fresh) ..... *C. latifolia* H.B.K.
- Leaflets entire, acute to acuminate at apex; inflorescence usually unbranched, usually less than 10 cm long; fruits depressed-globose, markedly 3–6-lobed, orange, usually less than 2 cm diam ..... *C. sylvatica* Seem.

Leaf blades conspicuously pubescent below, the trichomes either long or very close:

- Younger stems and branches densely brown-hirsute; blades hirsute below, the trichomes not contiguous; flowers crowded on inflorescence; capsules with narrow wings ..... *C. rufescens* Tr. & Planch.
- Young stems and branches glabrous or very short-pubescent; blades white-tomentose below, the trichomes contiguous; flowers not crowded on inflorescence; capsules not winged ..... *C. cinerea* Poepp.

Fig. 337. *Cupania cinerea*

Fig. 338.
Cupania latifolia

Fig. 339. *Cupania rufescens*

Fig. 340. *Cupania sylvatica*

leaflets 3–11, oblong-elliptic to obovate, obtuse to truncate and sometimes emarginate at apex, obtuse to acute and inequilateral at base, 8–20 cm long and 2–6.5 cm wide (to 35 cm long and 15 cm wide on juveniles), densely short-pubescent to glabrate on veins above, usually papillate and glabrous to sparsely pubescent and with inconspicuous stalked glands below, the margin obscurely crenate to wavy. Inflorescences 15 cm or more long, paniculate, the panicles axillary or subterminal, to ca 2.5 cm long; flowers white, 5-parted, ca 2–2.7 mm long; sepals ovate to oblong, tomentose; petals villous, obovate, rounded or emarginate at apex, the margin fringed, the scales fused to margins of petals, deeply divided in middle; disk thick, bowl-shaped, weakly lobed, densely velutinous except on inner margin; stamens 8, villous below middle; staminate flowers with the stamens to 3.5 mm long, exserted, the pistillode with 3 minute styles; bisexual flowers with the stamens ca 1.5 mm long; ovary ovoid, tomentose, gradually tapered to a stout style; style and stigmas pubescent, together about equaling the ovary; stigmas 3, ca 1.5 mm long, divergent. Capsules subglobose to trilobate, short-stipitate, to ca 2.5 cm diam at maturity, greatly shrinking upon drying and becoming more markedly trilobate; valves thick, woody, densely dark-brown-tomentose outside, woolly inside; seeds black, shiny, ca 1 cm long, enveloped at base with an orange-yellow aril. *Croat 11076, 11981.*

Occasional, in the forest and at least near the lake margin in the vicinity of the laboratory cove and on the northern side of the island. Flowers in June and July. The fruits mature in September and October.

Like most other *Cupania,* this species is variable throughout its range, especially in the type and degree of pubescence. It merges almost imperceptibly at times with a number of other species, including *C. americana* L. (West Indies and northern South America), *C. scrobiculata* L. C. Rich., and *C. oblongifolia* Mart. (Brazil). *C. papillosa* Radlk., segregated by Radlkofer on the basis of the dense papillations and glandular trichomes on the lower surface, is only an extreme form of this species.

On BCI this species is closest to *C. cinerea* and may hybridize with it. *Croat 11981* bears pubescence intermediate between the two species.

Panama to Colombia, Venezuela, Ecuador, Peru, and Amazonian Brazil. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Panamá and from tropical wet forest in Colón (Portobelo).

See Fig. 338.

Cupania rufescens Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 28:374. 1862

C. fulvida Tr. & Planch.

Candelillo

Tree, to 15 m tall; trunk to 25 cm dbh, sulcate at least when young; outer bark with shallow, horizontal and vertical fissures, flaking off to expose reddish inner bark; wood cream-colored, with sweet odor; younger stems densely ferruginous-hirsute, obscurely 5-ribbed. Leaves pinnate; rachis conspicuously hirsute; leaflets 3–7(9), obovate-oblong, mostly rounded at apex (sometimes obtuse or acute), often inequilateral at base, the larger 7–22(33) cm long, 3.5–10 cm wide, glabrous above but with densely pubescent midrib, conspicuously hirsute below especially on veins, the margins entire to usually denticulate (serrate on juvenile plants); all veins prominent, the major laterals impressed above; simple leaves on juvenile plants to 45 cm long and 15 cm wide. Panicles stout, densely floriferous, upper-axillary, ± equaling leaves, densely hirsute; flowers white, 5-parted; calyx densely pubescent, 2.8–3.3 mm long, equaling corolla, regular; petals obovate, pubescent, the scales fused along the margin at base; disk orange, prominent, nearly glabrous; stamens 8, the filaments villous on basal three-fourths; staminate flowers opening before bisexual flowers and mostly deciduous when bisexual flowers open, with the stamens to 3.5 mm long, exserted; anthers ca 1 mm long, attached to filament at middle, the thecae divergent in lower half; ovary and style very densely pubescent, the trichomes stiff, straight, usually exceeding stigmas; ovary narrowly ovoid, strongly 3-angulate; style and stigmas less than 2 mm long; stigmas 3, ± erect; bisexual flowers with the stamens 2–2.5 mm long, not exserted; anthers smaller than in staminate flowers, otherwise similar; ovary ovoid, ca 2 mm high, the pubescence as in staminate flowers but with style and stigmas not exceeded by trichomes; style ± equaling ovary; stigmas 3, recurved. Capsules in dense clusters, burnt-orange to Indian red, sharply 3-sided, 1.5–2 cm broad, nearly as long as broad, densely pubescent outside, less so inside, dehiscing broadly along the angles, each angle narrowly winged; seeds 3, obovoid, ca 1 cm long, black, shiny, partly enveloped by a yellow to greenish aril. *Croat 14627.*

Frequent in the forest, especially the young forest. Seedlings are often abundant; they are more deeply toothed and more densely hirsute and often look quite unlike adult plants. Flowers in the early to middle dry season, usually in February and March. The fruits mature in late dry and early rainy seasons, from late April to June. Dehisced fruit valves hang on the tree all year.

Seeds are probably bird dispersed.

Mexico to Colombia, Venezuela, the Guianas, and Brazil. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Los Santos, Panamá, and Darién, from tropical wet forest in Darién, and from premontane rain forest in Chiriquí and Veraguas.

See Fig. 339.

Cupania sylvatica Seem., Bot. Voy. Herald 93. 1853

C. seemannii Tr. & Planch.; *Talisia svensonii* Standl.

Tree, to 8 m tall; trunk to 16 cm dbh, often in clumps of 2 or more of various sizes, sometimes with sucker shoots at base; bark smooth; younger branches and inflorescences densely rufous-tomentose, otherwise glabrous to inconspicuously puberulent. Leaves pinnate, to 45 cm long; petiolules 3–15 mm long, pulvinate at base; leaflets 3–7, ± elliptic, acuminate, sometimes weakly falcate, acute to obtuse at base (sometimes inequilateral), 4–30 cm long,

1.7–12 cm wide, the axils of veins sometimes weakly tufted below. Inflorescences axillary, 1–3 per axil, to 12 cm long; pedicels very short, subtended by tiny bracts; flowers white, 5-parted, 4–5 mm wide, with a faint sweet aroma, in short clusters of 3 each, most parts villous; calyx cupular, divided to near base, the lobes ovate, erect; petals obovate to rhombic, rounded to acute, to 2.7 mm long, the scales nearly as long as or longer than petal, ± emarginate, fused to petal along both margins and forming a pocket; ovary ± rounded; stigmas 3 in bisexual flowers, lacking in staminate flowers. Capsules few or many in dense globose clusters, 3–6-lobed, broader than long, to 2 cm wide, densely tomentose, bright red-orange to red at maturity at least at apex; valves 3, densely silky-pubescent inside; seeds 2 or 3, ovoid or subglobose, ca 1 cm long, 8–10 cm wide, shiny, black, at least the apex exserted from the open capsules, the aril fleshy, white, ± acidy but tasty. *Croat 5080, 13481.*

Common at least in some areas of the island. Flowers from the late rainy season throughout the dry season (November to May), with the fruits maturing mostly from March through June.

Panama and northern Colombia. In Panama, known from tropical moist forest in the Canal Zone and Darién, from tropical dry forest in Panamá (Taboga Island), and from premontane wet forest in Panamá.

See Fig. 340.

PAULLINIA L.

The genus is easily confused with *Serjania* when sterile or in flower. Usually leaves are once-pinnate and thus easily separable from *Serjania,* which generally has biternate leaves. However, both genera may have trifoliolate leaves or leaves that are more than once-pinnate. In *Paullinia,* generally only the basal part of the blade is more than once-pinnate and the apical part is merely pinnate; in *Serjania,* the blades, if more than once-pinnate, are usually more than once-pinnate farther toward the apex as well.

Inflorescences of *Paullinia* tend to be narrow and spikelike, while those of Serjania are more frequently paniculate. Flowers are like those of *Serjania* (see the discussion following that genus). Fruits are definitive for separation of the two genera. In *Paullinia* the fruit is generally an unwinged (or obscurely winged), often woody capsule. In *Serjania,* the fruit is tricoccal, with each coccus samaroid. In *Paullinia,* seeds are arillate and animal dispersed. In *Serjania,* each individual samara of the three-winged schizocarp is wind dispersed.

All *Paullinia* species are apparently polygamous.

Paullinia baileyi Standl., Contr. Arnold Arbor. 5:95, pl. 14. 1933

Woody liana; stems 6-ribbed or grooved, long-hispid, with milky sap; tendrils axillary, forked, bracteate at fork, the arms watchspring-like; pubescence brown-pilose all over but with upper leaf surface between veins glabrous. Leaves pinnate; stipules paired, lanceolate, to 3 cm long, ciliate; petioles 1–12 cm long; rachis winged; leaflets 5, ± elliptic or elliptic-oblong, acuminate, acute at base (lower pair often rounded or subcordate), 2.5–22 cm long, 1.5–11 cm wide, remotely dentate. Thyrses short, glomerulate, in leaf axils or borne on tendrils; flowers white, ca 5 mm long; sepals 5, oblong, glabrous; petals 4, oblong to obovate, acute, the scales ca three-fourths as long as petals, their crests yellow, slender, pointed, the scales of the anterior petals held together by villous trichomes, the glands of the anterior petals slender, erect, flattened; stamens 8; filaments ± glabrous, fused into a tube at base; ovary 3-angled, glabrous; styles 3, longer than

KEY TO THE SPECIES OF PAULLINIA

Leaves more than pinnate:
- Leaves with basal pair of pinnae ternate, otherwise pinnate, the leaflets usually 11 ..... *P. glomerulosa* Radlk.
- Leaves strictly biternate (3 sets of 3 leaflets) ..... *P. fuscescens* H.B.K. var. *glabrata* Croat

Leaves pinnate:
- Leaflets 3 ..... *P. turbacensis* H.B.K.
- Leaflets usually more than 3:
  - Petiole and rachis not winged:
    - Plants essentially glabrous ..... *P. pterocarpa* Tr. & Planch.
    - Plants conspicuously brownish-hirsute on most parts ..... *P. rugosa* Radlk.
  - Petiole or rachis winged:
    - Petioles not winged, densely long-hispid; leaflets and stems densely hirsute ..... *P. baileyi* Standl.
    - Petioles winged, not densely long-hispid; leaflets glabrous but possibly with tufted axils:
      - Stems terete; petioles glabrous or minutely and obscurely puberulent; leaflets usually entire; pubescence of capsules dense, short, rufous, tomentose ..... *P. fibrigera* Radlk.
      - Stems ribbed or striate; petioles not puberulent; leaflets usually toothed; pubescence of capsules not dense, short, rufous, tomentose:
        - Leaflets lacking tufted axils below; stipules often persistent, more than 2 cm long; capsules ellipsoid, more than 1.5 cm wide ..... *P. bracteosa* Radlk.
        - Leaflets tufted in axils below; stipules less than 2 cm long; capsules pyriform, less than 1 cm wide ..... *P. pinnata* L.

staminal tube. Capsules reddish, suborbicular, 1–1.5 cm long, 3-celled, 3-winged, glabrous; seeds 1 or 2, oblong-obovate, dark, shiny, covered at base with a white aril. *Croat 4000a, 8723.*

Occasional, in the forest. Flowers mostly in the late dry season (March and April). Most fruits mature in the late rainy season, some in the early dry season.

The flowers and fruits usually occur on leafless stems near the ground.

Known only from Panama. In Panama, known from tropical moist forest in the Canal Zone and Bocas del Toro and from premontane rain forest in Colón and Panamá (Cerro Jefe).

Paullinia bracteosa Radlk., Bull. Herb. Boissier, sér. 2, 5:321. 1905

Liana; young stems 5-sulcate, the older stems winged, the wings 3, broad, corky; sap milky; stems, petioles, and rachises bearing sparse long pubescence. Leaves pinnate; stipules paired, lanceolate, 2–4 cm long, to 1.5 cm broad, minutely pubescent, often persistent, ciliate; petioles, rachises, and blades ciliate; petioles to 22 cm long, winged; rachis winged; leaflets 5, ± elliptic, acuminate, acute at base, 8–30 cm long, 4–12 cm wide, glabrous above but with pubescent midrib and principal veins, glabrate to hispidulous all over below, crenate above the middle. Thyrses dense, arranged ± densely on strong, slender, densely rufous, bracteate, axillary inflorescences; flowers white, 4–7 mm long; sepals 5, unequal, suborbicular, concave, tomentulose, ciliolate (the largest to 5.3 mm long); petals 4, equaling or exceeding sepals, glabrous, the scales two-thirds to three-fourths as long as petals (± enclosed within concavity of petal), the margin and reflexed appendage markedly bearded, the crest prominent, orange, the glands of the anterior petals whitish, erect, flattened laterally, broader than high, pubescent especially at base; stamens 7 or 8; filaments densely villous, to 3 mm long, held closely together around pistil; anthers dehiscing laterally; ovary bearded at base of staminate styles; styles 3, in staminate flowers short and reduced (held well below the anthers), in bisexual flowers 3-branched to below the middle, to 2.3 mm long, held well above the anthers, the unbranched part pubescent. Capsules ellipsoid to turbinate, 3–5 cm long, rounded to subcordate and apiculate at apex, tapered to base, terete to broadly 3-sided, striate, puberulent to glabrous; seed solitary, to 2 cm long. *Croat 4814, 5363.*

Occasional, on the shore and in the forest; seedlings common. Flowers from the early dry to early rainy seasons (December to August), with the fruits maturing mostly from February to August.

The fruits are perhaps tardily dehiscent—an opened capsule is rarely seen.

Costa Rica (Atlantic slope and the Osa Peninsula) south to Venezuela and the western and south-central parts of the Amazon basin from the Río Madeira in Brazil to Peru and Bolivia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Los Santos, Panamá, and Darién.

See Fig. 341.

Paullinia fibrigera Radlk., Smithsonian Misc. Collect. 61(24):2. 1914

Liana; stems terete except when very young, minutely puberulent and lenticellate; sap milky, forming droplets near periphery of stems. Leaves pinnate, glabrous but with puberulent petioles, rachises, and midribs on upper sides; stipules ovate, small; petioles to 10 cm long; petiole and rachis winged; leaflets 5, oblong-elliptic, obtuse to acuminate at apex, obtuse at base, 7–23 cm long, 3–9 cm wide, punctate on both surfaces (especially below), bearing axillary tufts below, entire, sometimes with a single tooth on each side. Inflorescences slender, usually unbranched, upper-axillary, usually to 12 cm long (to 25 cm long in fruit); flowers white, to ca 3 mm long, solitary or in few-flowered thyrses; sepals 5, tomentulose, unequal (2 reduced), 1 concave and partially enclosing the anterior petals; petals 4, glabrous, the scales shorter, their reflexed appendages villous, their crests yellow, bilobed, the lobes slender, the anterior petals subtended by glands, the glands large, orange, erect, flattened, puberulent outside, glabrous inside; stamens 8, shorter than petals; filaments villous, weakly fused at base; ovary ovoid, terete, densely tomentose; styles short, stout. Capsules globose to broadly clavate, beaked at apex, gradually narrowed to stipitate base, densely rufous-tomentose, to 2 cm long and 1.5 cm wide; valves thin; seed 1, ellipsoid, laterally compressed, ca 1.2 cm long. *Croat 6731, 12841.*

Common along the shore and in the canopy of the forest. Flowers in the late rainy season through the early dry season (October to February). The fruits mature in the dry season.

Probably the most common *Paullinia* in the canopy. The species is most easily confused with *P. pinnata*, but can be distinguished by having a terete stem and a densely rufous-tomentose fruit. Vegetation dries dark grayish in contrast to the green of *P. pinnata.*

Known only from Panama, from tropical moist forest in the Canal Zone, Chiriquí, and Darién and from tropical wet forest in Panamá (Cerro Jefe).

See Fig. 342.

Paullinia fuscescens H.B.K. var. **glabrata** Croat, Ann. Missouri Bot. Gard. 63:480. 1976

Hierba de alacran

Tendriled liana; stems terete, inconspicuously pubescent and bearing many small lenticels; tendrils borne on a short branch, usually bifid. Leaves biternate, to 12 cm long; petioles with a raised pubescent margin on upper surface; rachis narrowly winged, the wing sometimes widest in apical half; blades ± elliptic or oblanceolate, bluntly acute to acuminate (rarely rounded to emarginate) at apex, attenuate to base, sparsely crenate, glabrous above except on sharply raised midrib, glabrate below but with tufts of trichomes in axils, the terminal leaflets 3–9 cm long, 3.3(5) cm wide. Inflorescences terminal or axillary, borne often on the same short branches as the tendrils, to 10 cm long and 1 cm wide; pedicels short, 1.5–2.5 mm long at anthesis, puberulent, articulate about middle or above; flowers with a faint, very sweet aroma,

Fig. 341. *Paullinia bracteosa*

Fig. 342. *Paullinia fibrigera*

Fig. 343. *Paullinia glomerulosa*

ca 2.5–3.5 mm long; sepals sparsely to moderately appressed-pubescent, boat-shaped, rounded at apex; petals white, the glands of all 4 petals ovoid, yellow to orange, the scales of the anterior petals to 1.5 mm long, about as broad as long, the reflexed appendage densely bearded, the scale crest slender, 0.7 mm long, often as long as reflexed appendage; stamens 8, the staminate flowers with the short stamens to 1.5 mm long, the longer stamens to 2.5 mm long, the pistillate flowers with the stamens ca 1.5 mm long, about as long as ovary; anthers narrowly ellipsoid; pollen golden-brown, tacky; pistil small, well concealed by the densely pubescent filaments; stigmas 3, short, 0.7 mm long. Capsules suborbicular to broadly obovate, to 2 cm long, red, sharply 3-angled, glabrate to sparsely pubescent, short-stipitate, ± beaked at apex, the medial crest sharply raised, the wings 7–8 mm wide; seeds 1–3, oblong, shiny, black, the lower half enclosed in a white aril. *Croat 13235, 13809.*

Occasional, in the canopy and at the margin of the lake. Flowers throughout the dry season. The fruits develop within about 1 month.

It is difficult to distinguish flowering or sterile collections from *Paullinia costaricensis* Radlk., which occurs elsewhere in Panama and Central America.

Mexico to Panama along the Atlantic slope. In Panama, known from tropical moist forest in the Canal Zone, from tropical wet forest in Veraguas, and from an undetermined life zone in Chiriquí (Cerro Vaca).

Paullinia glomerulosa Radlk., Monogr. Paull. 257. 1895

Liana; stems terete, glabrous; tendrils forked. Leaves subbipinnate (lower set of pinnae biternate), pubescent on upper sides of petioles, rachises, and midribs and on lower midrib and major veins, otherwise glabrous; stipules linear-lanceolate, to 1 cm long; petioles 1–2.5 cm long; petiole and rachis narrowly winged, wider at apex; leaflets usually 11, lanceolate, acuminate, acute at base, subsessile, 1.5–10 cm long, 1–3 cm wide, both surfaces often bearing granular punctations, ciliate, serrate-dentate in apical half to entire; foliage of young plants gray-green. Thyrses in leaf axils or on leafless stems often near the ground, aggregated, glomerulate; flowers ca 3 mm long, white; pedicels ca 4 mm long; sepals 5, glabrous, orbicular to obovate and petaloid, to 3 mm long, spreading; petals 4, narrowly obovate, sparsely granular-puberulent, the scales broader than petals, ca half as long, glabrous but with villous margin, the scales of the anterior petals with simple orange crests, the reflexed appendage densely pubescent on margin only, the anterior glands glabrous, ca 1 mm long, ca twice as long as broad; stamens 8, the 3 anterior ones only slightly reduced; filaments glabrous, somewhat flattened; styles 3, short. Capsules suborbicular, sessile, glabrate, 1–1.5 cm long, reddish, with 3 narrow wings to 4 mm wide; valves splitting between the wings; seed solitary, black, shiny, ca 7 mm long, sparsely and softly pubescent with short trichomes, subtended by a white, fleshy aril. *Croat 7997.*

Occasional, in the forest; juveniles often seen as an erect, shrublike plant. Flowers in the middle of the rainy season (June to October). The fruits mature in the dry season.

Mexico, Panama, and Venezuela; West Indies. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Bocas del Toro, Panamá, and Darién, and from premontane moist forest in the Canal Zone (Farfan Beach), and from premontane wet forest in Panamá (Cerro Campana).

See Fig. 343.

Paullinia pinnata L., Sp. Pl. 366. 1753
Barbasco

Liana; older stems 3-ribbed, the younger ones mostly 6-ribbed, glabrous to puberulent; tendrils forked. Leaves pinnate, strigillose on upper sides of petioles, rachises, and midribs; stipules lanceolate-sericeous, 18 mm long, deciduous; petioles to 8 cm long; petiole and rachis winged, ciliate; leaflets 5, ± elliptic, short-acuminate, obtuse at base, 5–11 cm long, 2.5–4.5 cm wide, bearing granular punctations on both surfaces and tufted axils below, remotely crenate. Thyrses solitary, 5–25 cm long, axillary or borne at fork of tendrils, spikelike; flowers white or yellowish, ca 3 mm wide, wider than long; sepals 5, ± equal, tomentulose; petals 4, each fused with the scales to form single, broadly clavate structures, these structures densely villous, ca 1.5 mm long with a pocket at the apex, regular, alternating with sepals; stamens 8, exserted, ca 2.5 mm long; filaments flattened, villous below middle; pistil short; staminate flowers with the styles not obvious. Capsules broadly clavate, 2–4 cm long, rounded to truncate and abruptly acuminate at apex, gradually tapered to long-stipitate base, red, round to bluntly 3-sided in cross section; seeds 1–3, ellipsoid, 1.5–3 cm long, black, shiny, partly enclosed by a white aril. *Croat 11111, 12845.*

Uncommon; seldom seen now, though many older collections exist. Flowers principally in the middle of the rainy season (June to August). The fruits mature in the early dry season (December to February). Rarely flowers in the dry season, with the fruits maturing in the middle of the rainy season.

The species seems to intergrade with *P. clavigera* Schlechter in Central America.

Seeds are reportedly poisonous (Blohm, 1962; Standley, 1928).

Throughout tropical America and in tropical central Africa. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Panamá, and Darién and from premontane wet forest in Panamá (Cerro Azul).

See Fig. 344.

Paullinia pterocarpa Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 18:356. 1862

Glabrous liana; stems terete or 3-ribbed. Leaves pinnate; stipules lanceolate-linear; petioles unwinged, ribbed above, 5–9 cm long; rachis unwinged; leaflets 5, opposite, ovate to elliptic, long-acuminate, 6–22 cm long, 3.5–8 cm wide, entire to remotely coarse-crenate, the terminal

Fig. 345. *Paullinia rugosa*

Fig. 344. *Paullinia pinnata*

Fig. 346. *Paullinia turbacensis*

leaflet attenuate at base, the lateral leaflets obtuse at base. Thyrses densely clustered, glomerulate, axillary (rarely solitary); flowers white, ca 4.5 mm long; sepals 5, glabrous, irregular, ciliate; petals 4, obovate, often asymmetrical, about twice as long as their scales, the anterior scales ciliolate, about as broad as long, their inner margins extending laterally and overlapping, the reflexed appendage as broad as long, ciliolate, the glands on anterior petals ovoid, hispidulous, on lateral petals lacking; stamens 8; filaments flattened, glabrous; ovary pubescent near apex; staminate flowers with 3 sessile stigmas; bisexual flowers with the style 3-branched at middle. Fruits broadly 3-winged, red, 3-celled (only 1 functional), ca 2 cm long, glabrous; valves striate on outside, tomentose inside; seed solitary, ca 9 mm long, ovoid, black, the lower half white-arillate. *Aviles 46, Croat 14850.*

Rare; collected once in flower by Aviles and once sterile recently. Elsewhere the fruits mature in the middle of the rainy season (August to October).

Distinguished by being glabrous and having five leaflets, with the rachises and petioles unwinged.

Costa Rica to Peru. In Panama, known from tropical moist forest on BCI and in Bocas del Toro, Chiriquí, Coclé, Panamá, and Darién, from premontane wet forest in Panamá (Cerro Campana), and from tropical wet forest in Colón, Coclé, and Panamá.

Paullinia rugosa Benth. ex Radlk., Monogr. Serj. 75. 1875

P. fimbriata Radlk.

Liana; stems 5-ribbed, obscurely so in age, ca 2–2.5 cm diam, with milky sap; stems, tendrils, petioles, and rachises bearing dense, reddish-brown, hirsute pubescence; tendrils stout, forked. Leaves pinnate; stipules semiorbicular, sericeous, to 1 cm diam, the margins fimbriate; petioles 5–18 cm long, terete; leaflets 5, opposite, broadly elliptic, acuminate, attenuate to rounded and sometimes inequilateral at base, 12–35 cm long, 7–17 cm wide, hirtellous above on veins, hirsute below especially on veins, bearing apiculate teeth at ends of lateral veins. Thyrses short, closely congested on slender bracteate spikelike inflorescences, simple and borne in axils or on tendrils or compound and terminal; flowers white, ca 3.5 mm long; sepals 5, unequal, tomentulose, orbicular or ovate and acute; petals 4, obovate, the scales with the lateral margin and the distal edge of appendage bearded, the crest orange, weakly lobed, the glands about as broad as long, sparsely pubescent, weakly concave on outside; stamens 8; filaments densely pubeseent; ovary and outer surface of styles densely pubescent. Capsules bright red-orange, suborbicular, to 1.5 cm diam, ± round in cross section, densely tomentose; seed solitary, subglobular, ca 1 cm diam, black, covered by a thin white aril. *Croat 6036, 11783.*

Adult plants frequent in the forest; seedlings common and recognizable by the large orbicular fimbriate stipules. Flowers in the late rainy season (August to November). The fruits mature within 1 month.

Costa Rica to Peru and Brazil. In Panama, known from tropical moist forest in the Canal Zone and Colón and from premontane wet forest in the Canal Zone (Pipeline Road), Veraguas, and Panamá (Cerro Jefe).

See Fig. 345.

Paullinia turbacensis H.B.K., Nov. Gen. & Sp. 5:114. 1821

P. wetmorei Standl.

Tendriled liana; stems terete, ± glabrous, bearing conspicuous brown lenticels; sap at periphery milky, not copious. Leaves trifoliolate; petioles to 14 cm long, with marginal ribs above, glabrate; leaflets broadly elliptic, acuminate or acute at apex, attenuate to rounded at base, 5–15 cm long, 3–12 cm wide (to 23 cm long and 11 cm wide as juveniles), glabrate but with axillary tufts below, subentire to remotely crenate-dentate. Thyrses small, helicoid, to 7 cm long, solitary or clustered at nodes, often on leafless stems near the ground but occurring to 5 m high; flowers white, ca 5 mm long; petals with the scales ca two-thirds as long as petals, yellow-crested, the anterior scales bilobed, their appendages pubescent, the glands white, acute, densely pubescent; staminal cluster equaling petals; filaments densely pubescent; nectar abundant, stored near the large glands; ovary glabrous; styles pubescent. Capsules elliptic to obovate, 2 cm long, red, short-pubescent, the 3 boat-shaped valves broadly spreading to expose seeds; seeds 1–3, black, shiny, less than 1 cm long, covered on the lower half by a fleshy white aril, dangling on a thin funiculus when fully displayed. *Croat 7213, 7817.*

Frequent in the forest. Flowers in the early dry season (November to February). The fruits mature from February to April.

Mexico, Guatemala, Panama, and Colombia. In Panama, known from tropical moist forest on both slopes of the Canal Zone and in Colón, San Blas, Chiriquí, Panamá, and Darién and from premontane wet forest in Panamá (Cerro Jefe) and Darién.

See Fig. 346.

SERJANIA C. J. Schum.

Serjania is easily confused with *Paullinia.* (See the discussion of that genus for distinguishing features of vegetation and fruits.) Flowers of both genera have five

KEY TO THE SPECIES OF SERJANIA

Leaves trifoliolate (ternate) or bipinnately compound:
- Leaves trifoliolate; stems and leaves glabrous ..... *S. circumvallata* Radlk.
- Leaves bipinnately compound:
  - Leaves at most 3-pinnate; leaflets more than 3 cm wide ..... *S. mexicana* (L.) Willd.
  - Leaves often 4- or 5-pinnate; leaflets less than 2 cm wide ..... *S. trachygona* Radlk.

Leaves biternate (3 sets of 3 each):
- Rachis winged:
  - Seminiferous area (cell) of fruit glabrous; larger stems armed with short spines; wood simple ..... *S. mexicana* (L.) Willd.
  - Seminiferous area of fruit conspicuously pubescent; stems unarmed; wood simple or composite:
    - Lower surface of leaflets conspicuously pubescent above, densely hirtellous to short-pilose below; leaflets, flowers, and fruits lacking dark lines ..... *S. rhombea* Radlk.
    - Lower surface of leaflets glabrous; leaflets, flowers, and fruits sometimes with conspicuous dark lines:
      - Cells of fruit whitish-hirtellous; lower leaflet surface, flowers, and fruits with conspicuous dark black lines; peripheral vascular bundles usually flattened, irregular, often more than 1 mm wide ..... *S. atrolineata* Sauv. & Wright
      - Cells of fruit brown-hispid; lower leaflet surface, flowers, and fruits lacking conspicuous black lines; peripheral vascular bundles usually terete, regular, usually less than 1 mm wide ..... *S. paucidentata* DC.
- Rachis unwinged:
  - Cells of fruit and ovaries glabrous or essentially so ..... *S. pluvialiflorens* Croat
  - Cells of fruit or ovaries conspicuously pubescent:
    - Lower leaflet surface densely and conspicuously pubescent, the trichomes usually reddish-brown; flowers ca 7 mm long; fruits subrectangular-oblong, the cells conspicuously brown-hispid, the trichomes ca 2 mm long, each cell bearing a sharp horn ..... *S. cornigera* Turcz.
    - Lower leaflet surface glabrous or only very sparsely pubescent, any trichomes not reddish-brown; flowers less than 5 mm long; fruits ovate-cordate, the cells not brown-hispid, not at all horned:
      - Apical leaflet rachis conspicuously margined; lower leaflet surface with conspicuous blackish lines visible to naked eye; stems with 3 flattened vascular bundles; fruits constricted below the cell ..... *S. atrolineata* Sauv. & Wright
      - Apical leaflet rachis not conspicuously margined; lower leaflet surface lacking conspicuous blackish lines visible to the naked eye; stems usually with 10 weak ribs and 10 vascular bundles; fruits not at all constricted below the cell ..... *S. decapleuria* Croat

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unequal sepals and four petals. Each petal bears a petaloid appendage (called a scale) on its inner surface, usually one-half to three-fourths as long as the petal. The scales of the anterior petals are larger than those of the lateral petals and are usually held closely together. They are provided with reflexed appendages, which are generally densely villous at least on their common margin. The appendages of the scales are usually coherent by means of their intertwining trichomes. The upper part of the scale, referred to as the crest, is usually colored yellow and is variously shaped. At least the anterior petals are borne on or subtended by conspicuous, white or yellow disk glands, which apparently function as nectaries. Stamens are arranged in a tight whorl surrounding the pistil, and the entire structure is set to one side of the flower opposite the anterior petals. The three stamens adjacent to the pair of anterior petals are usually much shorter than the other five. The pistil of the staminate flowers is much reduced and has three obscure style branches; the pistil of the bisexual flowers is much larger and has three prominent styles.

Plants in the genus are usually polygamous, but possibly dioecious in *S. cornigera.*

Serjania atrolineata Suav. & Wright, Fl. Cubana 24. 1873

Tendriled liana, glabrate in age (juveniles with pubescent midribs); stems ribbed; tendrils bifid. Leaves biternate; stipules minute, ovate; petioles, rachises, and petiolules ribbed to narrowly winged; leaflets ± elliptic to lanceolate, obtuse to acuminate, acute at base, 4–8.5 cm long, 1.5–3 cm wide, usually dentate above middle, ciliate when juvenile, with distinct, irregular black lines on lower surface (sometimes inconspicuous when fresh). Thyrses small, either racemose and solitary in leaf axils and on tendrils or paniculate, open, and terminal; flowers white, ca 3 mm long; sepals densely tomentose outside; petals each subtended by a broad green gland, the scales of the anterior petals yellow, bilobed at apex, held in front of and slightly below the cluster of stamens; stamens 7–9; filaments pubescent; ovary tomentose. Fruits ovate-cordate, ca 2.5 cm long, constricted below the cell, the cells blackened and whitish-hirtellous on inner margin, conspicuously marked with irregular black lines. *Croat 4673, 7685.*

Frequent along the shore and no doubt in the canopy of the forest as well. Flowers throughout the dry season. The fruits mature within about 1 month.

Mexico to northern South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone and San Blas and all along the Pacific slope, from tropical dry forest in Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Colón.

Serjania circumvallata Radlk., Monogr. Serj. 345. 1875

Glabrous, tendriled liana; younger stems striate, the older stems grooved, flattened to 3-angled. Leaves trifoliolate and pinnate; petioles 2–7 cm long, with marginal ribs

above; petiolules very short or to 13 mm long; leaflets lanceolate-elliptic, ovate or ± elliptic, acuminate, attenuate to rounded at base, entire to obtusely crenate above the middle, the teeth usually glandular, the terminal leaflet usually 10–14 cm long, 6–8 cm wide, the lateral leaflets somewhat smaller. Thyrses solitary in leaf axils or in terminal paniculate racemes, the ultimate branches densely bracteate and cincinnal; branches, pedicels, and calyces minutely tomentose; flowers white, ca 3 mm long; sepals 5, unequal, oblong to obovate, the 2 opposite the staminal cluster enlarged, obovate, petaloid; petals 4, obovate, glabrous but with villous margins, glandular inside near middle, to 1.7 mm long, all borne atop large glands, the anterior petals with an obscure, densely villous appendage medially and with a yellow crest, lobed to about midway and extending above the petals, the scales of the lateral petals lacking an obvious appendage; stamens 8; filaments villous to near the apex, the longest to 2.3 mm long, exserted; all anthers facing anterior petals; ovary minute, glabrous, 3-sided, glandular; styles 3, equaling ovary. Fruits ovate, subcordate, 4.5–5 cm long, less than 3.5 cm wide, glabrous, the cells ca 7 mm long, rugose, the veins of the wings prominulous. *Croat 12668, Wetmore & Abbe 195, Woodworth & Vestal 638.*

Rare; collected near Fuertes House and near the Redwood House at the end of Armour Trail and on Drayton Trail. Flowers and fruits in the dry season.

Distinguished by the glabrous, trifoliolate leaves with blunt, gland-tipped teeth.

At present known from Costa Rica to Colombia, but possibly more widespread in South America where a number of other similarly trifoliolate species occur. In Panama, known only from tropical moist forest on BCI and in Bocas del Toro.

Serjania cornigera Turcz., Bull. Soc. Imp. Naturalistes Moscou 32:267. 1859

Tendriled liana, densely rufous-pubescent except sparsely so on upper surface of leaflets; stems 5-ribbed. Leaves biternate; petioles mostly 3–6.5 cm long, ribbed above; rachis margined, unwinged; leaflets ± elliptic, blunt to acuminate, abruptly tapered to base (especially lateral leaflets), remotely serrate-dentate, the terminal leaflet mostly 7–13 cm long, 3.5–5.5 cm wide, the lateral leaflets gradually smaller. Thyrses paniculate, terminal or upper axillary, the branches to 15 cm long; pedicels to 1 cm long; flowers white, ca 7 mm long, unisexual; sepals 5, tomentulose; petals 4, oblong-obovate, ciliolate, the 2 anterior petals subtended by a rounded gland, minutely pubescent on lower margins, depressed on outer face, white in staminate flowers, purple at apex in bisexual flowers, the scales of the anterior petals to two-thirds the length of the petals, the crest yellow, thin, emarginate, the appendage villous, slender, pendent to just above glands (scales of lateral petals lacking appendages); staminate flowers with the 5 longer stamens to 6.5 mm long, the shorter ones to 4 mm long; filaments sparsely villous; style nonfunctional; pistillate flowers with the stamens 8, nonfunctional, to 3.5 mm long; ovary pubescent; style 3–4 mm long; stigmas 3, ca 1 mm long. Fruits subrectangular-oblong, ca 4 cm long, the cells rufous-pubescent, subapical, hirtellous and setose with a hornlike projection, the wings hirtellous. *Croat 7823, 12714, 12715.*

Occasional. Flowers in the earliest part of the dry season, with the fruits maturing in the middle to late dry season.

This species is possibly dioecious and is unusual for its large flowers.

Honduras to Panama. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Darién.

See Fig. 347.

Serjania decapleuria Croat, Ann. Missouri Bot. Gard. 63:515. 1976

Tendriled liana; stems weakly 10-costate; branchlets bearing short crisp pubescence, the branchlets, petioles, rachises, and petiolules minutely appressed-puberulent; tendrils forked near apex. Leaves biternate; petioles 2–10 cm long; rachis unwinged; leaflets sessile to short-petiolulate (juveniles often on longer petiolules), oblong-ovate to elliptic, acute to acuminate at apex, acute to attenuate at base, entire to dentate with irregular black lines (at least on drying), glabrous but with strigillose midrib and main veins above, the basal axils sometimes bearing very slight tufts of trichomes below, the terminal leaflet 6–12 cm long, 2.5–5 cm wide. Thyrses in solitary and axillary racemes or in terminal paniculate racemes; flowers white, ca 4 mm long; sepals tomentulose; petals obovate, the scales of the anterior petals three-fourths as long as petals, the crest as broad as or broader than high, the upper margin thin, the appendages about as wide as long, bearded, fused laterally, the anterior glands broader than high, the lateral glands about half as broad as anterior glands; stamens 8; filaments ± flattened, villous; ovary and style pubescent; style 3-branched; stigmas apical. Fruits ovate, subglabrous, 3.5–4 cm long, the cells puberulent, the wings sometimes reddish, subglabrate. *Croat 7704.*

Occasional, along the shore. Flowers and fruits throughout the dry season.

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

Serjania mexicana (L.) Willd., Sp. Pl. 2:465. 1799

S. nesites I. M. Johnston

Barbasco

Tendriled liana; trunk to 7 cm diam, involuted, twisted, warty, lacking milky sap (at least sometimes); stems with milky sap, glabrous to villous especially when young, (3)5-ribbed (the ribs on larger stems in turn 2-ribbed), often sparsely armed with short prickles, especially larger stems; tendrils bifid, axillary. Leaves biternate to bipinnate or tripinnate, 10–40 cm long, often much reduced on inflorescence; stipules linear, paired, ca 1 cm long (on juveniles); petioles with marginal ribs above; rachis winged; leaflets 9–26, ovate to elliptic, acute to bluntly acuminate, rounded to attenuate at base, 2–8 cm long,

Fig. 347. *Serjania cornigera*

Fig. 348. *Serjania mexicana,* juvenile stem and leaves

Fig. 349. *Serjania paucidentata*

1.5–5 cm wide, ± glabrous to sparsely pubescent especially on veins, the margins sinuate-dentate near apex (conspicuously dentate on juveniles). Thyrses in solitary and axillary racemes or on tendrils or in terminal or axillary racemose panicles; flowers white, sweetly aromatic, ca 4 mm long; pedicel and calyx densely pubescent; sepals elliptic, ca 2.5 mm long, reflexed or spreading at anthesis; petals spatulate to obovate, 2.3–3.5 mm long, the glands large, ovoid, orange, glabrous, subtending petals, the scales of the anterior petals orbicular, nearly three-fourths as long as petals, their appendages slender, attached laterally to appendage of neighboring scale by villous pubescence, pendent nearly to base of scale, the crest yellow, hammer-shaped, the lateral petals borne on large glands; stamens 8; filaments flattened, sparsely villous; ovary 3-sided, glabrous. Fruits ovate-cordate, 1.7–2.7 cm long, glabrous, the cells with raised veins, the wing sometimes not constricted above seed. *Croat 13959, 14611.*

Common both as an adult plant and as a seedling in the forest. Flowers from February to April (sometimes from January). The fruits mature from March to May.

This is vegetatively the most variable species of *Serjania* on the island.

Mexico to Colombia and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Veraguas, Los Santos, Herrera, Panamá, and Darién, from premontane wet forest in Chiriquí (Boquete) and Veraguas, and from tropical wet forest in Coclé and Panamá.

See Fig. 348.

Serjania paucidentata DC., Prodr. 1:603. 1824
Paullinia protracta Steud.

Liana; stems glabrous, 6-ribbed but with 3 more prominent, sulcate when young, glabrous; wood composite, the vascular bundles usually 3, small, terete, peripheral. Leaves biternate, glabrous, 8–15(26) cm long; petioles 1.5–4(8) cm long, canaliculate on upper surface; rachis narrowly winged; leaflets narrowly elliptic to oblanceolate, acute to acuminate and often deeply incised on both sides beneath acumen, attenuate at base, 3–13 cm long, 1.8–5 cm wide, thick, mostly entire except for a few crenate, often glandular teeth near apex, the acumen blunt with a gland-tipped apiculum. Inflorescences terminal or usually axillary and borne on tendrils, slender, to ca 20 cm long; pedicels densely tomentose, to ca 1.5 mm long; rachis weakly tomentose; flowers white, to 4.5 mm long; sepals ovate to obovate, densely tomentose outside, glabrous inside, to 2 mm long; petals narrowly obovate, glabrous, to 4.3 mm long, the anterior scales ca three-fourths as long as petals, stiffly pubescent on margins, the appendage deflexed, slender, extending down to about the middle of the scale, densely stiff-pubescent throughout, the crest slightly bilobed, orange, equaling the length of appendage; disk glands 2 or 4, semicircular, nearly glabrous; stamens villous, flattened; staminate flowers with the stamens to 4 mm long, the pistil minute, 3-sided, hispid at apex; bisexual flowers not seen. Fruits narrowly ovate-cordate, weakly constricted above the cells, 2.3–2.8 cm long, sparsely hispidulous on wing, densely brown-hispid on cell. *Croat 7887.*

Infrequent; collected several times along the shore on the east side of the island. Flowers from February to April. The fruits are distributed mostly in the dry season, but may persist until as late as June.

Serjania paucidentata is closest to *S. mexicana*, but can be distinguished by having larger flowers, hispid fruits, unarmed stems, and composite wood.

Mexico to the Guianas, Brazil and Peru; Trinidad. In Panama, known only from tropical moist forest on BCI.

See Fig. 349.

Serjania pluvialiflorens Croat, Ann. Missouri Bot. Gard. 63:522. 1976

Tendriled liana; stems terete, glabrate to sparsely puberulent. Leaves biternate; petiole and rachis ± angled and slightly ribbed, usually pubescent at least on upper side; petioles to 6 cm long; leaflets elliptic to ovate, ± sessile, obtuse to acuminate, acute at base, 3–9 cm long, 2–4 cm broad, crenate above middle (the teeth usually glandular), the surface pellucid-punctate, glabrous but sometimes with short-pubescent veins and usually with axillary tufts on lower surface. Thyrses on solitary racemes borne on tendrils and in leaf axils or densely congested in terminal paniculate racemes; pedicels to 1.5 mm long; flowers white, to ca 4.5 mm long; sepals orbicular to obovate, glabrate to tomentulose outside, pubescent or glabrous inside; petals obovate, the scales of the anterior petals two-thirds the length of petals, subtended by a triangular to oblong, ± glabrous gland, the crest yellow, glabrous, the appendage villous, the lateral petals with or without subtending glands, their scales lacking crest; stamens 8; filaments flattened, villous; ovary glabrous or villous near apex and on dorsal side of stigmas. Fruits ovate-cordate, glabrous, the cells deeply rugose, 2–3 cm long, the wing reddish. *Croat 12421.*

Rare. Flowers and fruits in the middle to late rainy season (September to November).

Known only from Panama, from tropical moist forest in the Canal Zone and Bocas del Toro.

Serjania rhombea Radlk., Monogr. Serj. 324. 1875

Tendriled liana; stems 6-ribbed, brown-hirtellous especially on ribs. Leaves biternate, mostly to 15 cm long; rachis narrowly winged; leaflets ovate to rhomboid, obtuse to acuminate at apex, attenuate at base, coarsely and obtusely toothed above middle, softly pubescent (especially below and on raised midrib above), the terminal leaflet mostly 5–9.5 cm long, 2.5–6 cm broad, the lateral leaflets smaller. Thyrses in racemes 5–15 cm long and borne in axils and on tendrils, or in terminal racemose panicles; inflorescence branches softly short-pubescent; flowers white, ca 3 mm long; sepals ovate, short-tomentose; petals narrowly obovate, borne atop large greenish glands, spreading broadly at anthesis, the scales of the anterior petals with the margin villous and turned

inward, the appendage short, villous, the crest broader than long, bifid, recurved toward outside; staminal cluster spreading, leaning away from axis, otherwise typical; filaments sparsely villous, all ± recurved at apex; ovary glabrous. Fruits cordate-ovate, 1.7–2.2 cm long, the cells sparsely to densely (when young) villous, the wing ± glabrous or subvillous, often reddish at maturity. *Wetmore & Woodworth 83.*

Perhaps the most abundant species in central Panama, particularly in disturbed areas, and to be expected on BCI. A sterile collection is the only record of the species from the island (*Wetmore & Woodworth 83*). In the Canal Zone, flowers in the late rainy and dry seasons (October to April), with the fruits maturing throughout the dry season into the early rainy season (January to May).

The flower is unlike any other of the genus. Being spread open with the colored crown held to the outside, it presents a different type of pollinating unit.

Mexico to Colombia, Venezuela, and Ecuador. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Panamá, Los Santos, and Darién, from tropical dry forest in Coclé, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé and Panamá.

Serjania trachygona Radlk., Monogr. Serj. 327. 1875
S. deltoidea Radlk.

Tendriled liana; younger stems merely striate or obscurely 3–6-lobed, the older stems prominently 3-ribbed, each rib consisting of 2 small strands loosely attached to a much larger central core; sap milky; tendrils forked; stems, petioles, and rachises puberulent to hirsute. Leaves 2- or 3(5)-pinnate in 4–6 sets; petioles ribbed; rachis narrowly winged; leaflets small, acute to acuminate, acute to attenuate at base, 1–3 cm long, 0.7–2 cm wide, the terminal leaflet rhomboid, often trilobate, the lateral leaflets ovate-elliptic, crenate, sessile, glabrate to hirsute (especially on midrib); juvenile leaves usually with more leaflets than adults. Thyrses racemose and axillary or in terminal racemose panicles; flowers white, 2–3 mm long, short-pedicellate; petals ca 1.7 mm long, obovate, the anterior petals borne on the outer face of large glands, their scales with yellow, prominently bilobed crests, the appendages densely villous all over, united as a single unit, pendent to apex of glands, the lateral petals borne atop glands, their crests slender, entire, usually white; staminal cluster leaning away from the axis; filaments villous; ovary glabrous. Fruits ovate-cordate, 1.5–2 cm long, as broad as or broader than long, weakly viscid (at least on the cell when dried), the cells sparsely hirsute with raised veins, the wing glabrous or sparsely hirsute on inner margin, reddish at maturity. *Croat 7867, 13123.*

Occasional, in the forest. Flowers in the early dry season (December to February). The fruits mature in the late dry season (February to April).

The species is variable throughout its range in size of flowers, leaflet shape, and degree of compounding of the leaves.

Panama, Peru, and Bolivia, and probably more widespread in South America. In Panama, known only from tropical moist forest in the Canal Zone, Colón, and Panamá.

See Fig. 350.

TALISIA Aubl.

Talisia nervosa Radlk., Smithsonian Misc. Collect. 61(24):4. 1914
Mamón de monte

Polygamous shrub or small tree, usually less than 5 m tall; trunk to 6 cm dbh, unbranched (unless previously damaged). Leaves pinnately compound, clustered near apex, often 1 m or more long, lacking reduced leaflets at apex; petioles ca 25 cm long, terete; petiolules swollen, 5–10 mm long; leaflets usually in 5–8 pairs, oblong-elliptic, acute at apex and base, 20–45 cm long, 6.5–13 cm wide, glabrous above, glabrous to puberulent below. Thyrses small, arranged in panicles to 70 cm long, widely branched, the major branches ribbed; branches, pedicels, and calyces puberulent to tomentulose; pedicels short, to 2 mm long, articulate below calyx; calyx bowl-shaped, to ca 2 mm long, 5-lobed to about middle, the lobes indurate, acute, ciliate; petals 5, oblong, white, 3–5 mm long, acute to blunt at apex, spreading above calyx, glabrous, the scale ± exceeding petal, sericeous, tufted and slightly spreading at apex; disk raised, 5-angulate, the points alternating with petals; stamens 5 or 8, equaling scales, 3 often reduced or aborted; filaments weakly pubescent, shorter than anthers; anthers oblong, 1–4 mm long, the connective beaked at apex; staminate flowers with the ovary densely pubescent, less than 1 mm long; style lacking; stigmas 3, minute, hidden by the pubescence of ovary; bisexual flowers with the ovary ovoid; style nearly glabrous, about as long as ovary; stigmas capitate, held at about the level of anthers. Fruits ± ellipsoid to globose, brown, sharply apiculate at apex, sparsely pubescent, minutely lenticellate, usually 2–3.5 cm long, with a thick (2–3 mm) woody pericarp; seeds ellipsoid, flat on side if more than 1, 1.5–2.5 cm long, embedded in a firm or jellylike, whitish to orange mesocarp. *Croat 8236, 14921.*

Occasional in both the young and old forests; abundant along Snyder-Molino Trail 400–700. Flowers in the dry season (December to April), with the fruits maturing in

KEY TO THE SPECIES OF TALISIA

Calyx less than 3 mm long; leaflets in fewer than 9 pairs, more than 7 cm wide; reduced leaves lacking; filaments villous ..... *T. nervosa* Radlk.
Calyx more than 3 mm long; leaflets in more than 9 pairs, the largest less than 7 cm wide; reduced leaves often present at apex of stem; filaments glabrous ..... *T. princeps* Oliv.

Fig. 350. *Serjania trachygona*

Fig. 351. *Talisia princeps*

Fig. 352. *Talisia princeps*

the middle to late rainy season, chiefly from July to October.

The genus *Talisia* is said to be polygamodioecious, i.e., functionally dioecious but with a few bisexual flowers or flowers of the opposite sex. However, at least some specimens of this species are polygamous, i.e., with large numbers of both bisexual and staminate flowers.

Costa Rica to Colombia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas (Coiba Island), Panamá, and Darién and from tropical wet forest in Colón (Santa Rita Ridge) and Darién.

Talisia princeps Oliv., Hooker's Icon. Pl. 18, t. 1769. 1888

Polygamous tree to 6 m tall; trunk slender, to ca 3 cm dbh, prominently ribbed. Leaves pinnately compound, to 1 m long or more, sparsely to densely puberulous except on blade surface; petiolules pulvinate; leaflets in 6–14 pairs, opposite or alternate, oblong to oblong-obovate, abruptly acuminate, obtuse to acute at base, slightly inequilateral at base, 7–28 cm long, 2.5–6 cm wide, ± entire; apical leaves (called Kataphylls by Uittien, 1937) often reduced or aborted, 20–30 cm long, the petiole and rachis flattened, acicular, the leaflets narrowly oblong to linear, brown, dry, achlorophyllous, less than 2 cm long, with fascicles of still further reduced leaves in their axils like adult leaves. Thyrses arranged in large terminal panicles to 70 cm long, the lower branches to ca 40 cm long, the branches ribbed; bracts linear-lanceolate, 8–10 mm long; branches, bracts, pedicels, and calyces puberulent; calyx coriaceous, ca 4 mm long, deeply 5-lobed, the lobes ovate, ciliate, their margins thin; petals 5, white, regular, narrowly obovate, ca 7 mm long, rounded at apex, spreading and concave in upper half, sericeous near base outside, glabrous inside, the scales fused to lower third of petal inside, the free part erect, very densely white-velutinous, ± equaling petals; stamens 8; filaments glabrous, longer than anthers; anthers ca 1.5 mm long, the connective beaked at apex; disk prominently 5-lobed, the lobes densely villous at apex; staminate flowers with the stamens ca 5 mm long, the 5 outer ones each subtending a large pubescent lobe of the disk, alternating with the petals, the 3 inner ones surrounding the pistil; ovary minute, less than 1 mm long, densely sericeous, the trichomes obscuring the 3 triangular stigmatic lobes; bisexual flowers with the stamens ca 3 mm long; ovary, style, and stigmas together to 6 mm long; ovary ovoid, 2.5–3 mm long, gradually tapered into style; style stout, thick, ca 1.5 mm long; stigmas 3, short, triangular, usually obscured by pubescence of style. Fruits (*fide* Radlkofer) to 2.5 cm long and 1.5 cm diam, acuminate, tomentulose, 1-celled, 1-seeded. *Croat 8820, 12494, Zetek 3570.*

Occasional, in the forest. Flowers in October and November. Time of fruit maturation not known.

Some plants observed in flower on BCI did not set any fruit. Possibly the plants are functionally dioecious rather than polygamous, as is the general rule in the family.

Except for the pubescence of the leaves and petals, the species is very close to *T. megaphylla* Sagot from the Guianas and Amazonian Brazil. The species has other seemingly close relatives in South America, including *T. stricta* (Tr. & Planch.) Radlk. (Ecuador), *T. cupularis* Radlk. (Brazil), *T. hemidasya* Radlk. (Surinam), and *T. tiricensis* Steyerm. & Maguire (Venezuela).

Panama and Venezuela. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Darién, from premontane wet forest in Darién, and from tropical wet forest in Panamá (Serrania de Majé).

See Figs. 351 and 352.

THINOUIA Tr. & Planch.

Thinouia myriantha Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 369. 1862

T. tomocarpa Standl.

Polygamous, tendriled canopy liana; trunks to 12 cm diam, involuted; younger stems terete, pubescent, lenticellate, the trichomes minute, appressed, ferruginous; tendrils watchspring-like. Leaves trifoliolate; petioles 2–4 cm long; terminal petiolule mostly 2–2.5 cm long, the lateral ones ca half as long; leaflets mostly ovate to ovate-elliptic, acute to acuminate, obtuse to rounded (or rarely subcordate) at base, 6–12 (15) cm long, 2.5–9 cm wide, sparsely pubescent when young, ± glabrous in age except on midrib above and in vein axils below, the midrib arched, the sides folded somewhat upward along midrib, the margins undulate, entire, or crenate near apex, the teeth blunt, usually glandular; veins at base 3. Cincinni in umbellate clusters 3–4 cm diam, borne on short axillary or terminal branches, the branches to 7 cm long, often bearing tendrils; branches, peduncles, pedicels, and calyces appressed-puberulous; pedicels mostly 2.5–3.5 mm long; flowers ± actinomorphic, minute, greenish; calyx bowl-shaped, lobed, the lobes 5, uniform, acute, 0.7–1 mm long; petals 5, uniform, obovate, ca 0.4 mm long, each bearing from inside the base a deeply bifid, pubescent scale ca 1 mm long; disk prominent, ca 1.7 mm broad, glabrous; stamens 8, actinomorphic, in a tight cluster around pistil at center of flower, 3 erect and held closely together, 5 somewhat divergent; filaments villous in basal half, attached to anthers midway; anthers about as broad as long, the thecae usually separate below middle; pollen tacky; staminate flowers with the stamens ca 2.7 mm long; pistil minute; styles lacking; bisexual flowers with the stamens less than 2 mm long; pistil stipitate, to 3 mm long, 3-angled, weakly to densely appressed-pubescent; style short; stigmas 3, ca 1 mm long, pubescent, recurved. Fruits narrowly ovate-cordate, to 6.5 cm long, brown, glabrous, borne on a slender stalk 5 mm long, the samaras 3, to 1.9 mm wide, the cells lunate, submarginal, ca 1.5 cm long, the veins prominulous. *Croat 13803.*

Rare; known from several places on Armour and Zetek trails. Flowers and fruits in the dry season. On BCI, plants that flowered in late February had mature fruits during April and early May.

The species is variable throughout its range in pubes-

cence, leaf shape, petal size, and particularly the shape and degree of pubescence of the flower petal scales. Herbarium specimens with the name *T. marginata* Tr. & Planch. are also this species, but the name was apparently never published. Some Peruvian specimens identified as *T. repens* Radlk. are also this species. The type (from Paraguay) was not seen.

Probably along the entire Atlantic slope of Central America from Belize and Guatemala to Colombia, Venezuela, the Guianas, and Peru; in Central America known presently only from Belize and Panama. In Panama, known from tropical moist forest in the Canal Zone and Darién and from tropical wet forest in Darién.

81. RHAMNACEAE

Trees or tendriled lianas. Leaves alternate or subopposite, petiolate; blades simple, entire to serrulate; venation pinnate, somewhat palmate at base; stipules present, minute. Racemes terminal or axillary, cymose (may be glomerate); flowers bisexual, actinomorphic, many; calyx cupular, (4)5-lobed, the lobes valvate; petals (4)5, free, alternate with calyx lobes; stamens (4)5, opposite the petals, arising between the lobes of the disk; disk prominent, sometimes nectariferous; anthers 2-celled, longitudinally dehiscent; ovary inferior (*Gouania*) or semi-inferior (*Colubrina*), 3-locular, 3-carpellate; placentation basal; ovules 1 per locule; style trilobate. Fruits schizocarps of 3, 2-winged mesocarps (*Gouania*) or explosively dehiscent 3-valved capsules (*Colubrina*), with little or no endosperm.

Rhamnaceae may be recognized by their open, bowl-shaped flowers with stamens borne opposite the usually prominently concave petals.

Pollination system is unknown.

Seeds are wind dispersed (*Gouania*) or autochorous by means of explosively dehiscent capsules (*Colubrina*). Seeds of *Colubrina* are buoyant because of an air space between the cotyledons (Ridley, 1930) and may be further dispersed by water currents.

About 58 genera and 900 species; widespread but mostly in the tropics and warmer temperate regions.

COLUBRINA L. C. Rich. ex Brongn.

Colubrina glandulosa Perk., Bot. Jahrb. Syst. 45:465. 1911

C. rufa (Vell.) Reiss. var. *glandulosa* (Perk.) M. C. Johnston

Spanish elm

Tree, (3)6–20(40) m tall, to ca 50 cm dbh, ± glabrous but with ferruginous, ± antrorse puberulence on younger parts including peduncles, pedicels, and cupules; bark moderately coarse in age. Leaves opposite or nearly so; stipules subulate, 3–10 mm long, caducous; petioles 0.5–18 cm long; blades ± ovate-elliptic, acute to short-acuminate at apex, rounded to very shallowly cordate at base, 7–15(25) cm long, 2.5–10 cm wide, the lower surface dull, often inconspicuously pubescent on veins and with some moderately large submarginal glands, the upper surface shiny, the margin weakly revolute, markedly so near petiole. Thyrses axillary, 1–5 cm long; peduncles 1–7 mm long; pedicels 1–4 mm long, 3–12 mm long in fruit; flowers 10–50, 5-parted; petals, sepals, and stamens borne on apex of floral cup, the cup 2.5–3 mm wide; sepals yellowish, ± triangular, ca 1 mm long, with a prominent medial ridge inside; petals ± oblong, ca 1 mm long; stamens opposite and slightly longer than petals; anthers less than 0.5 mm long; disk prominent, filling floral cup at anthesis and hiding the 3-celled ovary; style much shorter than stamens, tripartite one-fourth to two-thirds its length. Capsules explosively dehiscent, ± globose, 6–8 mm long, dark brown or black, glabrous, enveloped only slightly at base by the cup and disk at maturity; endocarp hard, separating into 3 dry endocarpids; seeds 1–3, ± obovate, 4–5 mm long, dark brown, shiny. *Croat 7349, Wetmore & Abbe 165.*

Apparently rare, collected only along the shore but no doubt growing in the forest as well. Flowers in the earliest part of the dry season, from December to January. The fruits mature from February to April.

Panama to Colombia, Venezuela, the Guianas, Brazil, and Peru. In Panama, known only from tropical moist forest in the Canal Zone, Los Santos (south of Macaracas), and Panamá.

GOUANIA Jacq.

Gouania adenophora Pilg., Notizblatt 6:314. 1915

Liana, climbing into canopy of forest; younger stems densely puberulent, the older stems glabrous; outer bark grayish. Petioles 1–3 cm long, canaliculate, weakly pubescent to glabrous; blades ovate to ovate-elliptic, abruptly acuminate and downturned, rounded to subcordate at base, 4–14 cm long, 2.5–9 cm wide, glabrous above, sparsely and inconspicuously pubescent below especially on the major veins; major lateral veins in 4–6 pairs, arcuate-ascending, the 2 basal pairs arising at the base of leaf, the tertiary veins more or less conspicuous, extending almost straight between primary lateral veins. Cymes umbelloid, less than 1 cm long, arranged in terminal racemes 15–25 cm long; peduncles bracteate, the bracts deltoid, acute, pubescent; flowers bisexual, densely aggregated, numerous; pedicels ca 1 mm long, densely

KEY TO THE SPECIES OF RHAMNACEAE

Plants trees, lacking tendrils; leaves subopposite; fruits not winged, of thick-walled, explosively dehiscent capsules ..... *Colubrina glandulosa* Perk.

Plants tendriled lianas; leaves alternate; fruits winged:

Wings of fruit 11–12 mm high and 7 mm wide ..... *Gouania adenophora* Pilg.

Wings of fruit 5–6 mm high and 5 mm wide ..... *Gouania lupuloides* (L.) Urban

villous; calyx bowl-shaped, densely villous especially toward base, the lobes deltoid, ca 1 mm long; petals obovate, cupulate, with the margins partially enclosing the subtending stamen, rounded at apex, somewhat clawed at base; stamens 5, borne on the margin of the disk with the petals, ca 1 mm long; disk 5-sided, the inner margin adjacent to the ovary with 3 erect lobes opposite the stigmas; pistil ca 0.3 mm long, depressed in disk; stigmas 3, about as long as style. Schizocarps of 3, 2-winged mericarps, each 8–11 mm wide, glabrous except near apex, the body 7–9 mm long; wings reniform, 8–12 mm long; seeds narrowly ellipsoid, flattened, 4 mm long. *Foster s.n.*

Apparently rare, though reported by R. Foster (pers. comm.) to drop fruits in the old forest near Armour Trail 700 and Drayton Trail 100. Flowering in July and August. Fruiting in September and October.

Determination of the species is doubtful, because the plant most closely matches a Peruvian plant. Perhaps it is a new species, but because of the polymorphic nature of *Gouania* I am reluctant to describe it as new.

Peru and Panama. In Panama, known from tropical moist forest in the Canal Zone (BCI), from premontane wet forest in the Canal Zone (Pipeline Road) and Panamá (El Llano–Cartí Road), and from tropical wet forest in Colón (Río Guanche) and Panamá (El Llano–Cartí Road).

Gouania lupuloides (L.) Urban, Symb. Ant. 4:378. 1910
G. polygama (Jacq.) Urban
Jaboncillo

Tendriled liana; stems striate, densely pubescent; tendrils watchspring-like, terminating short branches, becoming woody in age. Leaves alternate, short-petiolate; blades ± ovate, acuminate to acute or cuspidate at apex, obtuse to subcordate at base, 5–11 cm long, 2–6.5 cm wide, sparsely to densely pubescent, the pubescence variable; veins at base 3. Racemes terminal or upper-axillary, spikelike, 5–15 cm long; flowers mostly bisexual, sometimes pistillate or staminate by reduction, sessile or subsessile, ca 3 mm wide, in few-flowered glomerules, opening 1 to few at a time in each glomerule; calyx cupular, white or greenish, acutely 4- or 5-lobed, pubescent on outer surface, the lobes ca 1 mm long; petals minute, equaling calyx lobes, partially enclosing stamens; stamens (4)5, mounted on rim and alternate with lobes of the disk; disk prominent, cupular; anthers emerging above petals; styles 3, short at anthesis, later elongating and exceeding height of disk lobes, the tips becoming recurved. Schizocarps of 3, 2-winged mericarps, the central part sparsely to densely pubescent, 3–4 mm long; wings rounded, 5–6 mm high and ca 5 mm broad, glabrous to densely reddish-brown-pubescent, splitting medially at maturity; mericarps 3, consisting of one-third of the central axis and one-half of each of 2 wings. *Croat 5744, 7075.*

Abundant at the edges of clearings and occasional in the forest canopy. Flowers from November to March, principally in the early dry season; flowering is rare in March and even more rare during the rainy season. The fruits develop to mature size as early as January, but are dispersed from February to May (rarely June or later), especially in March and April.

The cuplike disk may become partly filled with a sweet watery nectar, especially while the anthers are shedding pollen. The nectar appears to be absent when the style is receptive.

The species is represented on BCI by two distinct races. The less common of the two is characterized by dense reddish-brown pubescence all over but especially on the stems, the lower leaf surfaces, and the seminiferous areas of the fruit. Examples of the more pubescent form include *Croat 7274, 7984, 12699, 12739, 13482, Shattuck 290, 444, 523,* and *Woodworth & Vestal 326.* Although the difference between the two races is striking on BCI, variation of *G. lupuloides* throughout Panama is so great that they cannot be recognized at any higher taxonomic level. Apparently identical collections made in Mexico and Brazil have been identified as *G. tomentosa* Jacq. and *G. mollis* (L.) Urban. Further monographic work with *Gouania* may well prove that these two BCI variants should be considered distinct at the varietal or even the specific level.

Mexico to northern South America; West Indies. In Panama, ecologically wide-ranging, probably occurring in all areas of tropical moist forest; known also from tropical dry forest in Coclé (near Antón), Herrera, and Los Santos, from premontane wet forest in Chiriquí (Boquete), and from premontane rain forest (south of Volcán) in Chiriquí.

82. VITACEAE

Lianas and vines, with leaf-opposed tendrils and often with swollen nodes. Leaves alternate (lower ones sometimes opposite), petiolate; blades simple and trilobate or trifoliolate, serrate; venation palmate at least at base; stipules interpetiolar. Inflorescences cymose, appearing corymbose, umbellate or paniculate; flowers primarily bisexual (bisexual and staminate in *Vitis*), actinomorphic, 4-parted (*Cissus*) or 5-parted (*Vitis*); calyx shallowly toothed or lobed; petals valvate, free (apically fused in *Vitis*); stamens inserted at base of disk, of the same number as petals and opposite them; anthers 2-celled, introrse, longitudinally dehiscent; ovary superior, 2-locular, 2-carpellate; placentation axile; ovules 2, anatropous; style 1; stigma discoid (may be slightly bilobed). Fruits berries; seeds 1 or 2, with copious endosperm.

Members of the family are recognized by their climbing habit, the apparently terminal buds developing into lateral tendrils, the leaf-opposed, branched, cymose inflorescences, and the valvate petals opposite the stamens.

The small open flowers are probably insect pollinated. In Costa Rica, *Cissus* is visited by the vespid wasps *Polistes* and *Stelopolybia* (Heithaus, 1973).

The fruits are well suited for bird dispersal and those of *Cissus sicyoides* are much sought by birds (Duke, 1968).

Twelve genera and 700 species; primarily in the tropics but extending to temperate regions.

KEY TO THE SPECIES OF VITACEAE

Leaves simple:
- Flowers 5-parted, in panicles; petals fused at apex; blades on lower surface ± densely floccose-tomentose ..... *Vitis tiliifolia* R. & S.
- Flowers 4-parted, in cymes branched many times; petals free; blades glabrous or velutinous only on veins below:
  - Plants glabrous or the trichomes villous and simple; pedicels always glabrous; blades ovate-oblong, drying green, the larger truncate to only slightly cordate (not ovate-cordate) ..... *Cissus sicyoides* L.
  - Plants pubescent at least on veins of lower leaf surface and on inflorescences with minute, close, puberulent trichomes and also usually with appressed T-shaped trichomes; pedicels pubescent; blades ± ovate, drying blackened, the larger broadly ovate-cordate ..... *Cissus pseudosicyoides* Croat

Leaves trifoliolate:
- Plants densely pubescent, some trichomes gland-tipped; terminal leaflets ± rhombic; flowers pale yellow to yellowish-green ..... *Cissus rhombifolia* Vahl
- Plants glabrous or sparsely pubescent on surface with simple trichomes; terminal leaflets ± elliptic; flowers red to orange:
  - Mature peduncles less than 2.5 cm long; leaves often velutinous only on veins below, with tufted axils; stems not winged; fruits obovoid, more than 6 mm long ..... *Cissus microcarpa* Vahl
  - Mature peduncles more than 5 cm long; leaves glabrous or sparsely pilose below, lacking tufted axils; stems often winged; fruits orbicular, less than 6 mm diam ..... *Cissus erosa* L. C. Rich.

CISSUS L.

Cissus erosa L. C. Rich., Actes Soc. Hist. Nat. Paris 1:106. 1792

C. salutaris Kunth ex H.B.K.

Vine with simple tendrils, glabrous or with scattered pilose pubescence throughout; stems angled or winged on margins, usually maroon at nodes and speckled with maroon all over (not obvious on dried specimens), the older stems woody. Leaves trifoliolate; stipules ovate, subpersistent, minute (to 5 mm long); petioles 2–6 cm long, maroon at base and apex, angled and often winged on margins; leaflets crenate-serrate, the terminal one ± elliptic, obtuse to bluntly acuminate at apex, cuneate at base, 4.5–16 cm long, 1.5–8 cm wide, on a short petiolule, the lateral leaflets smaller than terminal leaflet, inequilateral, ovate to ovate-elliptic, acute to obtuse at apex, rounded to subcuneate at base, 3.5–12 cm long, 2–6 cm wide. Cymes corymbiform, opposing leaves, congested in pseudoumbels; peduncles tetragonal, 5–12 cm long; flowers 4-parted, red; pedicels 2–5 mm long, villous; calyx cupular, the lobes short or obscure; petals valvate, acute at apex, cucullate within, often falling free at anthesis; stamens 4, set between notches in the thick disk, erect at anthesis, later recurved, somewhat reflexed; anthers open in bud; filaments and connective red; style short; stigma simple. Fruits orbicular, to 6 mm diam, purple-black at maturity; seeds usually 2. *Croat 12943.*

Occasional, on the shore and at the edge of clearings; possibly also in the forest canopy. One of the most common species of *Cissus* on the island. Flowers throughout the year, especially in the early rainy season. The fruits develop rapidly.

Mexico to Colombia, Venezuela, the Guianas, Peru, and Bolivia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Veraguas, Herrera, and Panamá, from premontane moist forest in the Canal Zone and Los Santos, from premontane wet forest in Colón, Coclé, and Panamá, and from tropical wet forest in Colón.

Cissus microcarpa Vahl, Eclog. Amer. 1:16. 1796

Tendriled climbing vine, becoming woody; stems to 7 cm diam, usually angulate, sometimes bearing 2-sided, narrow, peltate scales. Leaves trifoliolate; stipules (on youngest stems) broadly ovate, to 4 mm long; petioles 2–4.5(6) cm long; leaflets velutinous especially on veins below with appressed, long, flattened, T-shaped trichomes on veins, the major veins crisped-villous at least near tufted axils, the margins obscurely mucronate-serrate, the terminal leaflet broadly elliptic to ovate-elliptic, acuminate, cuneate at base, 4–10 cm long, 1.5–5.5 cm wide, the lateral leaflets somewhat smaller and inequilateral. Cymes corymbiform, umbellate, 3–8 cm long; peduncles 6–18 mm long; inflorescence branches reddish, moderately pubescent, the pedicels and branches of the inflorescence with long, flattened, T-shaped trichomes; pedicels to 4 mm long; flowers 4-parted, red; calyx cupular, nearly truncate, minute; corolla ca 1.5 mm long, the lobes ovate, valvate; stamens 4; pistil 1–1.5 mm long. Fruits obovoid, 7–9 mm long, green to orange at maturity; seed usually 1, pyriform, to 7 mm long. *Croat 6396, 11890.*

Frequent along the margin of the lake; found also in trees in the forest to 10 m high. Flowers and fruits throughout the rainy season.

Mexico to Brazil; Greater Antilles. In Panama, known from tropical moist forest all along the Atlantic slope and

Fig. 353. *Cissus microcarpa*

Fig. 354. *Cissus pseudosicyoides*

in the Canal Zone, Veraguas, Herrera, and Panamá and from premontane wet forest in the Canal Zone, Coclé, and Panamá.

See Fig. 353.

Cissus pseudosicyoides Croat, Ann. Missouri Bot. Gard. 60:564. 1973

Tendriled herbaceous vine, probably ultimately arising from a woody stem; at least smaller stems, petioles, and veins of leaf blades (especially below) densely and inconspicuously puberulent; the same parts but also the axes of the inflorescences, pedicels, and leaf surfaces often sparsely pubescent with flattened, ± appressed, T-shaped trichomes; stems of juvenile parts often white-speckled. Leaves simple, thin, usually drying dark, dimorphic; larger leaves borne below the inflorescences, on petioles mostly 7–11 cm long, ovate-cordate, as broad or nearly as broad as long, 9–15 cm long and 9–12 cm wide, the lateral veins above sinus in 3–6 pairs, extending into apiculate teeth along margins of blade, a single strong trunk vein extending into each basal lobe, the sinus about as deep as broad; smaller leaves higher on stem and opposite inflorescences, on petioles mostly 2–8 cm long, usually narrowly ovate, truncate to obtuse or acute at base (rarely cordate), mostly 3–10 cm long and 2–8 cm wide, otherwise like larger leaves. Cymes terminal or opposite upper leaves, small, congested, branched, umbelliform, 1–4 cm long, about as broad as long; peduncles mostly 2–10 mm long at anthesis (somewhat longer in fruit), densely appressed-pubescent with T-shaped trichomes, densely bracteate at apex, the bracts minute with margins glabrous or very inconspicuously ciliate; pedicels terete, 1.5–3.5 mm long, sparsely pubescent, the trichomes as on peduncles but usually smaller; calyx spreading, ± bowl-shaped, inconspicuously 4-lobed, narrower than buds, nearly glabrous; buds ovoid, 1.5–2 mm long, drying with ridges along margins of petals; petals 4, free, broadly oblong, obtuse and cucullate at apex inside, usually white or cream (rarely red); stamens opposite petals; filaments to ca 1 mm long, equaling or longer than anthers; anthers nearly as broad as long, dehiscing laterally; stigma simple, to ca 1.5 mm long. Fruits ± globose, to 6 mm diam, apparently green at maturity; exocarp and mesocarp thin; seed 1, round, only slightly smaller than dimensions of fruit. *Croat 7017* (type).

Occasional, along the shore and at the edge of the Laboratory Clearing. Flowers at the beginning of the dry season in December and January on BCI (rarely elsewhere as late as March) or in the rainy season (late July to October); individual plants may flower for 1 month or more. The fruits develop promptly, are usually present with flowers, and are usually gone by March.

The fruits are probably dispersed by small to medium-sized birds. It is not known whether the fruits become brightly colored. Observations on BCI indicate that the fruits are probably removed before turning color. *Cissus pseudosicyoides* has been confused with *C. sicyoides* (Croat, 1973), but can be distinguished most easily by its pubescent pedicels, dimorphic leaves, and T-shaped trichomes on the midrib of the blade.

Costa Rica (Guanacaste Province) to northern Colombia. In Panama, widespread in lowland areas; known principally from the Pacific slope in drier areas of tropical moist forest, but also from premontane dry forest in Panamá (Juan Díáz) and from premontane wet forest in Panamá (Chimán).

See Fig. 354.

Cissus rhombifolia Vahl, Eclog. Amer. 1:11. 1796
Batilla

Vine, the older parts woody; most parts conspicuously pubescent with both short gland-tipped trichomes and longer eglandular trichomes, the longer ones often red on those surfaces of stems and petioles, upper veins, and margins of leaves exposed to the sun; stems 4- or 5-angulate to terete, swollen at nodes; tendrils simple, sometimes reddish. Leaves trifoliolate; stipules narrowly lanceolate to ovate, 3–12 mm long, subpersistent; petioles 3–8 cm long, ± angulate; leaflets serrate, the terminal leaflet rhombic, acuminate, cuneate at base, 7–13 cm long, 3–6.5 cm wide, the lateral leaflets inequilateral, acute to acuminate, rounded on one side, acute on the other at base; veins impressed above, raised below. Cymes corymbiform, congested in pseudoumbels; peduncles 1–3 cm long; pedicels 3–8 mm long; flowers 4-parted; calyx bowl-shaped, broadest at base, pubescent, to 1.3 mm long, the teeth obscure; petals pale yellow to greenish-yellow, ± oblong-ovate, acute, to 2.3 mm long, spreading to recurved at anthesis, caducous; stamens 4, erect, ca 1.8 mm long, weakly adnate to base of petal; disk prominently 4-lobed; style to 2.7 mm long, simple. Fruits obovoid, 6–10 mm long, black at maturity; seeds 1 or 2.

Occasional, in disturbed areas in other parts of the Canal Zone and to be expected on BCI, but no recent collections have been made there. The species was reported by Standley (1933) but some older collections identified as this species have proved to be *C. microcarpa*, including *Shattuck 252* cited in the *Flora of Panama* (Elias, 1968). Flowers and fruits throughout the rainy season.

Mexico to Colombia, Venezuela, Peru, and Bolivia; West Indies. In Panama, ecologically variable; known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, Chiriquí, Veraguas, Los Santos, Panamá, and Darién, from tropical dry forest in Herrera and Coclé, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Bocas del Toro, Chiriquí, Coclé, and Panamá.

Cissus sicyoides L., Syst. Nat. ed. 10, 897. 1759
Rockrope, Bejuco loco, Uru cimarrona

Tendriled vine, the herbaceous stems terete, usually arising ultimately from a woody stem; most parts except pedicels and calyces villous; tendrils usually simple. Leaves simple; petioles mostly 1.5–5.5 cm long; blades all ± of same shape, narrowly ovate to oblong-ovate,

Fig. 355. *Vitis tiliifolia*

Fig. 356. *Vitis tiliifolia*

acuminate to acute at apex, mostly obtuse to truncate at base, sometimes subcordate to rarely cordate, the lower surface usually villous especially on veins, rarely nearly glabrous (frequently glabrous elsewhere), the upper surface usually glabrous except on veins; veins arising from base usually few to several, the lateral veins in 4 or 5 pairs above the basal ones, entering the apiculate teeth on margins of blade. Cymes terminal or opposite upper leaves, branched, umbelliform, as broad as or broader than long; peduncles 1–5 cm long at anthesis, to 6.5 cm long in fruit; bracts of inflorescence usually ciliate; pedicels glabrous, 2–3 mm long; flowers 2–3 mm long, greenish-white to white or pale yellow (often red elsewhere in bright exposed areas); calyx spreading, usually with 4 small lobes, glabrous, usually wider than the unopened corolla; petals 4, oblong, free, falling soon after opening; stamens 4, shorter than and opposite petals, arising from between the lobes of the disk; disk prominent, 4-lobed, persisting in fruit; style to 1 mm long. Fruits obovoid, to 6 mm long, green becoming red then black at maturity; seed usually 1. *Croat 4581a.*

Occasional, in and around the edge of the Laboratory Clearing. Flowers principally in the dry season, but some flowers may be seen all year. Individuals probably flower several times per year; certainly they flower more than once, since flowering plants frequently bear juvenile or mature fruit from an earlier flowering. The fruits probably mature within 1 or 2 months.

Southern United States throughout Central America and much of South America; West Indies. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Chiriquí, Los Santos, Herrera, Panamá, and Darién; known also from tropical dry forest in Los Santos, Herrera, Coclé, and Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Panamá.

VITIS L.

Vitis tiliifolia H. & B. ex R. & S., Syst. Veg. 5:320. 1819
Grape, Uva, Bejuco de agua

Polygamous, tendriled liana, the youngest parts herbaceous; stems angulate to terete; stems, peduncles, petioles, and lower leaf surfaces, and veins above densely floccose-tomentose at least when young; tendrils forked. Leaves simple; petioles 2–8 cm long; blades ovate-cordate, acuminate, 8–14 cm long, 6.5–12 cm wide, shallowly trilobate, serrate. Panicles leaf-opposed, to 20 cm long; peduncles 4–10(15) cm long; flowers bisexual or functionally staminate, greenish, ca 2 mm long; calyx bowl-shaped, the margin undulate; corolla to 1.7 mm long, the petals 5, ± oblong, fused at their apex and caducous as a unit; stamens 5, soon spreading, those of bisexual flowers somewhat shorter than those of staminate flowers; disk prominent, more than half as high as calyx; ovary weakly 5-lobed at base, ovoid; style short. Fruits ± globose, to 8 mm diam, becoming brown and sour but tasty at maturity; seeds 2. *Croat 10238, 11138.*

Frequent in the canopy, at the edges of clearings, and along the margin of the lake. Flowers and fruits throughout the year, principally during the dry and early rainy seasons.

Mexico to Colombia; West Indies. In Panama, known from tropical moist forest in the Canal Zone, all along the Atlantic slope, and in Panamá and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí, Coclé, and Darién.

See Figs. 355 and 356.

83. ELAEOCARPACEAE

Trees or shrubs (*Muntingia*) frequently with pubescent stems. Leaves alternate (or subopposite), petiolate, simple, undulate to serrate, pubescent; venation pinnate throughout or palmate at base; stipules present. Cymes axillary, compound; flowers bisexual, actinomorphic, solitary, few or many; sepals 4–6, united into a flat plate below the receptacle; petals 5, free (*Muntingia*) or lacking (*Sloanea*); stamens many, free, arising from a disk; anthers 2-celled, dehiscing by terminal pores; ovary superior, 4- or 5-locular, 4- or 5-carpellate; placentation axile; ovules 2 per locule, anatropous, pendulous; style 1, simple, 4-angled, or stigmas radiate. Fruits loculicidal, 4-valved capsules with 1 or 2 arillate seeds or berries with many seeds (*Muntingia*); endosperm abundant.

Elaeocarpaceae are separated from the Tiliaceae (84) chiefly on the basis of the mucilaginous canals and ducts.

Muntingia and *Sloanea* seemingly have little in common in superficial appearance of flower and fruit structure. The flowers of both are open and seemingly unspecialized.

Both the bright-red, and many-seeded berries of *Muntingia* and the capsular fruits of *Sloanea* with one or two arillate seeds are probably chiefly bird dispersed. *Muntingia calabura* is known to be bat dispersed also (Heithaus, Fleming & Opler, 1975; Yazquez-Yanes et al.,

KEY TO THE SPECIES OF ELAEOCARPACEAE

Blades inequilateral, palmately veined at base, densely stellate-pubescent between veins below; flowers with white petals; fruit baccate, naked ..... *Muntingia calabura* L.
Blades equilateral, pinnately veined throughout, glabrescent between veins below; flowers apetalous, not white; fruit capsular, densely covered with spines or trichomes:
Blades more than 15 cm long; fruits with spines more than 2 cm long ..... *Sloanea zuliinsis* Pitt.
Blades less than 15 cm long; fruits covered with clinging trichomes at most 4 mm long .....
..... *Sloanea terniflora* (DC.) Standl.

1975). White-faced monkeys may eat the pulp around the seed (Oppenheimer, 1968).

Twelve genera and 350 species; tropics and subtropics.

MUNTINGIA L.

Muntingia calabura L., Sp. Pl. 509. 1753
Majaguillo, Pacito, Periquito

Shrub or small tree, rarely to 10 m tall and ca 15 cm dbh; stems hirsute; bark black. Leaves alternate; stipules linear, 3–5 mm long, hirsute, sometimes paired on one side of petiole; petioles ca 5 mm long, densely hirsute; blades inequilateral, ± elliptical, acute to gradually acuminate, strongly inequilateral at base, obtuse on one side, ± cordate on the other, 4–10(11) cm long, 2–3.5 cm wide, with sparse, sessile, stellate pubescence on upper surface and dense, soft, whitish, stellate pubescence on lower surface, serrate; palmate veins at base 3–5. Inflorescences supra-axillary, usually 1-flowered; pedicels 1–2 cm long; flowers 5-parted, with a disagreeable odor, 1.5–2 cm diam; sepals lanceolate, very long-acuminate, to 7 mm long, pubescent on both surfaces, softly so inside; petals fugacious, white to creamy white, rounded at apex, 7–9 mm long, the outer margin undulate; stamens numerous, plainly visible, 4–5 mm long, erect to spreading, borne on outer margin of the disk; disk narrow, the rim velutinous; ovary ovoid, glabrous; style short, thick; stigma radiate, 5-lobed. Berries ovate, baccate, bright red, sweet, rugose when dried, subtended by the receptacle trichomes and the filaments; seeds many, ovoid, ca 0.5 mm long. *C. L. Wilson 152.*

Probably once widespread on the island when there were more clearings, but possibly no longer existing there. Flowering and fruiting throughout the year elsewhere.

Widely distributed in tropical America in secondary areas; introduced elsewhere in the world. In Panama, known chiefly from tropical moist forest in the Canal Zone (Pacific slope), Colón, Chiriquí, Los Santos, Herrera, Panamá, and Darién; known also from premontane moist forest in Panamá.

SLOANEA L.

Sloanea terniflora (Moc. & Sessé ex DC.) Standl., Trop. Woods 79:10. 1944
Terciopelo

Tree, to 30 m tall; trunk buttressed; bark smooth, black; branchlets grayish, but generally hidden by a dense golden puberulence when young. Leaves alternate to subopposite; petioles 5–15 mm long, densely golden-puberulent when young; blades elliptical to obovate, rounded to obtuse at apex, ± cuneate-obtuse and equilateral at base, 6–8(15) cm long, 3–5(7.5) cm wide, entire to sinuate, becoming glabrous above, lighter and glabrous below except on veins; midrib and major lateral veins prominent. Inflorescence 3–7 cm long, umbellately 1–3 flowered, axillary or terminal; peduncles 1.5–5 cm long; pedicels to 1.5 cm long. Peduncles and pedicels reddish, glabrate in age; flowers apetalous, maroon; sepals 4, valvate, ovate, ca 7 mm long, the margins densely puberulent; stamens many, ca 4 mm long, pale yellow; filaments scarcely 1 mm long; anthers opening by an apical pore, the connective produced into a fugacious awn ca 1 mm long; ovary 2–2.5 cm long, tufted-puberulent; style glabrous above, 4-lobed; stigmas 1 per lobe. Capsules ellipsoid, to 2.5 cm long; valves 4, 3–4 mm thick, densely pubescent, the trichomes easily detached, reddish, antrorsely barbed, ca 3 mm long; seeds 1 or 2, ellipsoid, ca 1 cm long and 5 mm wide, nearly enveloped in an aril, the aril firmly attached in basal fourth of the seed. *Croat 9778.*

Frequent in the old forest as canopy trees. Flowers in the dry season (February to April). The fruits mature by the late dry season, though old valves may persist long after the seeds are removed, even until the time of the next flowering. K. Bawa (pers. comm.) reports that the species flowers for only 8–10 days in Costa Rica.

Trichomes of the fruit, which are irritating and cling to the skin, are no doubt beneficial in preventing the fruits from being eaten before maturity. At maturity the arillate seeds are displayed on the open inner valve surface and are probably removed by birds.

Central Mexico to Peru, Bolivia, and Brazil. In Panama, known from tropical moist forest in the Canal Zone (from BCI to the Pacific coast), Chiriquí, Veraguas, Los Santos, Herrera, Coclé, and Panamá.

Sloanea zuliinsis Pitt., Bol. Com. Ind. Venezuela 4(34):31. 1923
S. microcephala Standl.

Tree, usually 5–18 m tall; trunk with narrow buttresses; bark minutely lenticellate, with many horizontal wrinkles; twigs minutely brown-puberulent. Leaves alternate; stipules lanceolate, 12–30 mm long; petioles 5–12(21) cm long, subpuberulent; blades mostly elliptical, ± acute at apex, subacute to rounded at base, 20–40(60) cm long, 8–15(25) cm wide, subcoriaceous, becoming glabrate except on veins below, sinuate; midrib and veins prominently raised below. Cymes compound, the parts minutely puberulent; peduncles 12–26 cm long; pedicels 5–12 mm long; peduncles and pedicels subtended by bracts; flowers apetalous, yellowish, 2–3 mm long; sepals united into a flat, 4–6-lobed plate, beneath the receptacle; stamens many, to 2 mm long, congested to form a tight, subglobose mass to 4 mm across; ovary to 1.5 mm long; style to 1.5 cm long, tapered from base, sometimes 4-angled, glabrous above, the apex obtuse, entire. Capsules ellipsoid, 1.5–2.5 cm long; valves 4, 2–4 mm thick, densely covered with spines, the spines very slender, 2–3 cm long, tapered, yellow-green to reddish, minutely and antrorsely puberulent, not easily removed; seeds 1 or 2, ca 1.5 cm long and 7 mm wide, almost completely covered by aril, the aril unequally 6-lobed, firmly attached to basal third of seed, the three large lobes irregularly laciniate. *Foster 1316.*

Occasional, in the forest, most commonly seen on

Drayton Trail. Flowers principally in September and October. The fruits are mature from October to December.

Sterile collections from Chiriquí, possibly this species, occur at altitudes to 1,900 m. These trees may be 27 m tall.

Pacific coast of Costa Rica to Venezuela (southwest side of Lake Maracaibo). In Panama, known from tropical moist forest in the Canal Zone and Darién.

84. TILIACEAE

Trees or shrubs (sometimes suffrutescent in *Corchorus*), usually with stellate pubescence. Leaves alternate, petiolate; blades simple, sometimes lobed, the margins variously serrate; veins palmate at base; stipules present. Cymes or panicles terminal, axillary or leaf-opposed; flowers bisexual or unisexual (monoecious in *Trichospermum;* gynodioecious in *Heliocarpus*), sometimes apetalous (*Triumfetta*), actinomorphic, solitary; sepals 4 or 5, free, valvate; petals 4 or 5, free, imbricate, showy, sometimes reduced or lacking; stamens 5 (*Triumfetta*) to many (in bisexual flowers), free or rarely connate into a short tube; anthers 2-celled, introrse or extrorse, basifixed or versatile, dehiscing longitudinally; pistil 1; ovary superior, sometimes on a gynophore, 2- or 5-locular and 2- or 5-carpellate; placentation axile; ovules many per locule, anatropous; style 1; stigma capitate to bilobed. Fruits 2- or 5-valved loculicidal capsules, often spiny; seeds albuminate, winged or unwinged.

Members of the family are most easily confused with the Malvaceae (85) and the Sterculiaceae (87), principally because the leaves are palmately veined at base. They are distinguished by the nearly distinct stamens, the two-celled anthers, and the typically cymose inflorescences.

Flowers of all species are probably insect pollinated. Because of the usual abundance of generally exserted stamens and exserted style, it is suspected that the flowers may be pollinated by indiscriminate pollen collectors. In Costa Rica, the bee *Eulaema polychroma* "buzzes" pollen from the anthers of *Apeiba. Luehea* in Costa Rica is nocturnally pollinated by beetles and perhaps by moths (Heithaus, 1973).

Diaspores are diverse. Seeds of *Triumfetta lappula* are epizoochorous. *Apeiba membranacea* and *A. tibourbou* are endozoochorous, at least those of *A. membranacea* being dispersed chiefly by monkeys but also by coatis (Kaufmann, 1962) and parrots (Chapman, 1931) (see that species for discussion). Enders (1935) reported that peccaries also eat the fruits in times of food scarcity. Several species, including *Trichospermum mexicanum, Heliocarpus popayanensis,* and species of *Luehea,* are wind dispersed. *Corchorus siliquosus* has small seeds that are probably shaken slowly from the linear capsule and blown away by the wind.

KEY TO THE SPECIES OF TILIACEAE

Plants shrubs less than 3 m tall; flowers small, less than 6 mm long, yellow; fruits small burrs less than 1 cm diam *or* linear capsules to 6 cm long:
- Petals lacking; fruits small burrs less than 1 cm diam; leaf blades broadly ovate, usually 3–5-lobed; plants common ..... *Triumfetta lappula* L.
- Petals 5; fruits unarmed cylindrical capsules to 6 cm long and 2 mm wide; leaf blades ± elliptic, not lobed; plants probably no longer occurring on the island ..... *Corchorus siliquosus* L.

Plants trees more than 5 m tall; flowers more than 1 cm long *or* not yellow; fruits variable:
- Petals magenta; fruits flattened, obovate, cordate and apiculate at apex, densely pubescent; leaves oblong-lanceolate, very long-acuminate, sometimes with white tufts of trichomes in axils of basal veins on lower surface of blade ..... *Trichospermum mexicanum* (DC.) Baill.
- Petals white or yellow; fruits and leaves not as above:
  - Flowers 4-parted, greenish-white, less than 5 mm long; inflorescences often more than 12 cm long; capsules minute, less than 5 mm long, prominently bristled on margin; leaves broadly ovate, often shallowly trilobate ..... *Heliocarpus popayanensis* H.B.K.
  - Flowers usually 5-parted, yellow or white, more than 1 cm long; inflorescences usually less than 12 cm long (except *Luehea seemannii* longer); capsules more than 2 cm long:
    - Bracteoles 9, conspicuous, valvate, immediately subtending flowers; petals glandular-thickened at base inside; fruits distinctly capsular, longer than broad, unarmed:
      - Flowers ca 1.5 cm long; capsules deeply 5-sulcate, to 2.5 cm long ..... *Luehea seemannii* Tr. & Planch.
      - Flowers ca 3 cm long; capsules 5-angled, not sulcate, more than 2.5 cm long ..... *Luehea speciosa* Willd.
    - Bracteoles few, imbricated and distant from base of calyx; petals eglandular; fruits indehiscent or only tardily so, broader than long, armed:
      - Leaves with tufts of brown trichomes in vein axils below, subentire; stems, petioles, and inflorescence branches not pilose; capsules like sea urchins, bearing short, stiff, conic spines ..... *Apeiba membranacea* Benth.
      - Leaves lacking tufts in vein axils, serrate; stems, petioles, and inflorescence branches conspicuously pilose; capsules bearing long, flexible, stout spines ..... *Apeiba tibourbou* Aubl.

Fig. 357. *Apeiba membranacea*

Fig. 358. *Heliocarpus popayanensis*

About 50 genera and about 600 species; mainly in the tropics.

APEIBA Aubl.

Apeiba membranacea Spruce ex Benth., J. Proc. Linn. Soc., Bot. 5:61, Suppl. 2. 1861

A. aspera Aubl.

Peinecillo, Monkey comb, Cortezo

Tree, 10–30 m tall; trunk to 75 cm dbh, often weakly buttressed and ribbed above buttresses; outer bark thin, flaky, often minutely fissured with small lenticels in vertical rows; inner bark with narrow, radial, V-shaped wedges, these with large pores exuding clear, viscid droplets, the sap with sweet aroma; wood white, soft; stems bearing ± ferruginous, stellate pubescence when young, glabrous in age. Stipules ovate, to 5 mm long, deciduous; petioles slightly swollen at apex, 1.5–3 cm long, minutely stellate-pubescent; blades oblong-elliptic to obovate-elliptic, acute to acuminate, rounded to subcordate at base, 8–25 cm long, 3–10.5 cm wide, sparsely and minutely fimbrillate-lepidote below with tufts of brown trichomes in vein axils, ± entire; palmate veins at base 3. Panicles open, to 8 cm long, opposite leaves; pubescence of inflorescence branches, pedicels, and calyces short, rufous, stellate, tomentose; pedicels 1–2 cm long; flowers few, 5-parted; sepals lanceolate, 1–2.5 cm long, 3–6 mm wide; petals yellow, spatulate or obovate, 1.5–2 cm long, 7–13 mm wide, glabrous; stamens numerous, 3.5–5.5 mm long, long-pilose at base; style ca 12 mm long; stigma shortly denticulate. Fruits shaped like flattened sea urchins, to 6 cm diam and 1.5 cm thick, densely covered with sharp conic spines; seeds numerous, light brown, irregular, to 4 mm long. *Croat 5213, 7281.*

Abundant in some areas of the forest and common all over the island. Flowers mainly in the rainy season (May to December) with flower buds appearing as early as March. The fruits develop in about 9 months and are seen from November to May. White-faced monkeys eat the larvae infesting the fruits from January to May (Oppenheimer, 1968). Leaves fall in the dry season and grow in again soon.

The fruits are perhaps tardily dehiscent, but probably all fruits with viable seeds are opened by monkeys. One surface is removed and the fruits are picked out. Oppenheimer (1968) reported seeing the monkeys pick out grubs that frequently infect part of the seeds while discarding the viable, uninfected seeds. Macaws have been seen eating the fruits on BCI, and Chapman (1929) reported that the fruits are eaten by the Amazona parrot.

Mexico, Costa Rica, Panama, and western South America to Bolivia. In Panama, a characteristic component of tropical dry forest (Holdridge & Budowski, 1956) and tropical moist forest (Tosi, 1971); known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, from premontane wet forest in Colón and Coclé, and from tropical wet forest in Colón and Darién. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 357.

Apeiba tibourbou Aubl., Hist. Pl. Guiane Fr. 1:538, t. 213. 1775

Monkey comb, Cortezo, Cortés, Peinecillo (Chiriquí), Peine de mico, Fruto de piojo

Tree, 6–20(30) m tall, ca 25 cm dbh; outer bark thin, weakly fissured; inner bark white to tan with granular areas interspersed with round pockets containing thick sap; pubescence ferruginous, both long simple trichomes and shorter stellate trichomes on stems, petioles, lower midribs, axes of inflorescences, and calyces. Stipules triangular, to 2 cm long, subpersistent; petioles 1–3 cm long, long-hispid; blades ± oblong-elliptic, acuminate, subcordate at base, 10–30(33) cm long, 6–12(15) cm wide, sparsely stellate-puberulent above with long simple trichomes on midrib, densely stellate-arachnoid below, serrate; palmate veins at base 3–7. Panicles to 11 cm long, opposite leaves; pedicels to 1.8 cm long; flowers few, 4- or 5-parted; sepals ± lanceolate, 1.5–2.2 cm long, spreading at anthesis, thick, densely long-pubescent outside, glabrous inside; petals glabrous, spatulate to narrowly obovate, to 1.6 cm long, yellow or less commonly white, spreading at anthesis; stamens numerous, yellow, ca 7 mm long, the outermost irregularly united into a tube, sometimes sterile; anthers to ca 4 mm long, usually sparsely pilose; ovary globose, densely pubescent; style 8–12 mm long, ± equaling petals; stigma shortly denticulate. Capsules depressed-globose to globose, to 8 cm diam (including bristles), densely covered with bristles, the bristles long, flexible, stout, to 1.5 cm long; seeds numerous, depressed-globose, ca 2.5 mm diam. *Croat 4003a, 8170.*

Frequent in the forest. Flowers mainly in the rainy season (May to December), although a few flowers are seen all year. The fruits probably develop in 6–9 months and are most abundant in the dry season. Leaves fall in the dry season and new leaves are seen in the early rainy season.

Throughout tropical America. In Panama, common in secondary growth and typical of tropical moist forest (Tosi, 1971); known from tropical moist forest in the Canal Zone, Colón, San Blas, Veraguas, Herrera, Chiriquí, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone, Veraguas, and Panamá, from premontane wet forest in Chiriquí, Panamá, and Darién, and from tropical wet forest in Colón and Darién.

CORCHORUS L.

Corchorus siliquosus L., Sp. Pl. 529. 1753

C. orinocensis sensu Standl.

Broomweed, Escobilla

Small shrub, usually less than 1(2) m tall; stems with 1 or 2 vertical bands of short, simple, erect trichomes. Reduced leaves in axils often 1 to several; stipules paired, persistent, bristle-like, to 2.5 mm long; petioles 5–25 mm long, short-pubescent on upper side; blades ovate to elliptic, acute to acuminate, rounded to subcordate at base, 2–7 cm long, 1–3.5 cm wide, nearly glabrous, crenate-serrate; palmate veins at base 3. Pedicels 4–8

mm long; flowers 1–3, in axils or opposite leaves, 5-parted; sepals linear-lanceolate, ca 8 mm long, glabrous; petals obovate, ca 6 mm long, glabrous, yellow; stamens numerous, free, ca 5 mm long; style ca 2.5 mm long; stigma subbilobed, densely papillate. Capsules linear, erect, 4–6 cm long, ca 2 mm diam, minutely puberulent; seeds numerous, ca 1 mm long. *Aviles 12.*

Probably once abundant when the island was weedier; not seen in recent years, but to be expected in the larger clearings. Seasonal behavior uncertain. Elsewhere in Panama flowering most abundantly in the rainy season, with the fruits seen during the dry season.

Native to East Asia; now common as a weed throughout the American tropics. In Panama, known from tropical moist forest all along the Atlantic slope and in the Canal Zone, 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 Colón, Coclé, and Panamá.

HELIOCARPUS L.

Heliocarpus popayanensis H.B.K., Nov. Gen. & Sp. 5:341. 1823

Majaguillo, Majagua

Gynomonoecious tree (with pistillate and bisexual flowers on the same plant), 6–10(30) m tall; branches bearing dense, ferruginous, stellate pubescence when young, glabrous in age. Stipules lanceolate, paired, to 1 cm long, caducous; petioles stellate-pubescent, 4–8 cm long; blades broadly ovate, acuminate (often with 3 shallow acuminate lobes), truncate to cordate at base, 8–25 cm long, 4–20 cm wide, finely serrate, the pubescence sparse, simple, stellate above, densely stellate below; palmate veins at base 5–7. Cymes small, along panicles to 25 cm long, usually terminal, bearing both pistillate and bisexual flowers (the bisexual ones possibly functionally staminate); flowers several, 4-parted, pedicellate (those of the bisexual flowers somewhat longer); sepals narrowly lanceolate, acute, tomentulose outside, glabrous inside; bisexual flowers with petals 4, narrowly spatulate, white, shorter than sepals; stamens many, 3–4 mm long; anthers dehiscing upward; pollen ± tacky; ovary minute; style bifid; pistillate flowers with petals reduced or lacking; staminodia numerous, minute; style to 2 mm long, bifid about one-third its length; stigma lobes usually obscurely 2- or 3-lobed. Capsules ellipsoid, flattened, 2-valved, ca 4 mm long, the pubescence short, stellate, the bristles long, plumose, in 2 rows along the margin; seeds usually 2, mostly compressed-ovoid, 1.7–2.5 mm long. *Croat 14051.*

Common at the margin of the forest around the Laboratory Clearing. Flowers in the dry season (December to March). The fruits mature quickly, mostly from March to June, with flowers and fruits often on the same tree.

Capsules probably dehisce on the tree, but instead of releasing the seeds, each valve may be carried away separately with the seed still attached.

Southern Mexico to northern Argentina. In Panama, common in secondary growth; known from tropical moist forest in the Canal Zone, Colón, and Darién, from premontane wet forest in Coclé, from tropical wet forest in Chiriquí and Darién, and from premontane rain, lower montane wet, and lower montane rain forests in Chiriquí.

See Fig. 358.

LUEHEA Willd.

Luehea seemannii Tr. & Planch., Ann. Sci. Nat. Bot., sér. 4, 17:348. 1862

Guácimo, Guácimo molenillo

Tree, usually 15–30 m tall; trunk to 125 cm dbh, the buttresses 1–3 m high, to 4 m wide at base, usually continuous with ribs on trunk; outer bark thin, peeling easily, with prominent, round, evenly distributed lenticels; inner bark with lighter streaks oozing thick, clear, sometimes sweet sap; stems somewhat flexuous, especially near apex; branchlets, petioles, and inflorescence branches bearing dense, ferruginous, stellate, tomentose pubescence. Petioles ca 1 cm long, thick; blades mostly oblong-elliptic, somewhat asymmetrical (especially at base), acuminate at apex, rounded to subcordate at base, 5–40 cm long, 2–15 cm wide, densely brown-arachnoid below, very sparsely so and shiny above, the margins irregularly serrate especially above middle. Thyrses terminal or upper-axillary, 2–8(16) cm long; flowers 5-parted, enclosed by bracteoles in bud, to 2.5 cm wide when open, the bracteoles 9, densely pubescent, deciduous; sepals free, spreading, ca 12 mm long, oblong-lanceolate, densely pubescent outside; petals spatulate, white or yellow, ± equaling sepals, pubescent near base; stamens many, ca 9 mm long, in 5 clusters each united at the base, slightly shorter than style; style thick, capitate, ca 5 mm long; stigma obscurely 5-lobed. Capsules ± elliptic to obovoid, deeply 5-grooved, to 2.5 cm long, densely brown-tomentulose; seeds many, 6–10 mm long, winged. *Croat 7327, 7996.*

Common in the young forest. Flowers in the late rainy and early dry seasons. The fruits mature late in the dry season and early in the rainy season (March to July). Leaves are gradually lost in the dry season and are renewed sometime from April to July.

Central America to Panama; reported by Jimenez S. (1970) from Colombia (Magdalena River Valley). In Panama, a characteristic tree species in tropical moist forest (Holdridge & Budowski, 1956; Tosi, 1971); known from tropical moist forest throughout Panama, from premontane moist forest in the Canal Zone and Panamá, and from premontane rain forest in Panamá (summit of Cerro Jefe). Reported from tropical dry, premontane wet, and tropical wet forests in Costa Rica (Holdridge et al., 1971).

Luehea speciosa Willd., Ges. Naturf. Freunde Berlin Neue Schriften 3:410, t. 5. 1801

Guácimo, Guácimo molenillo

Tree, 5–20(25) m tall, to 70 cm dbh, the pubescence stellate, ferruginous, dense except on upper leaf surface, the older stems ± glabrous. Leaves deciduous; stipules

ovate-lanceolate, 10–20 mm long, subpersistent; petioles 8–12 mm long; blades broadly elliptic to ovate, abruptly acuminate at apex, truncate, rounded or subcordate and sometimes inequilateral at base, 8–24 cm long, 6–12 cm wide, serrate. Panicles open, terminal or upper-axillary, to 12 cm long; pedicels 1–3.5 cm long; bracteoles 9 or 10, deciduous, lanceolate-linear, to 2 cm long and 4 mm wide, stellate-pubescent on both sides; flowers 5-parted; sepals lanceolate-oblong, 3–4 cm long, to 9 mm wide, glabrous inside; petals light yellow, obovate, to 3.5 cm long and 1.5 cm wide, glabrous but with villous base inside, the margin irregular; stamens many, in 5 or 10 clusters, densely white-hirsute at base, 1–2 cm long; style 1.5–2.5 cm long; stigma capitate. Capsules oblong-obovate, to 4.5 cm long and 1.5 cm wide, obtusely 5-angled, rounded at apex, woody, ferruginous-tomentose; seeds very numerous, winged, flattened, oblique, ca 10 mm long and 4 mm wide, overlapping in 2 rows in each of 5 carpels, the valves opening slightly at maturity. *Croat 4222, 7871.*

Occasional in the young forest; more common elsewhere in the Canal Zone in disturbed areas and along roads. The species flowers in the early dry season while old leaves are still on the tree. The fruits mature in the late dry season, but the valves persist on the tree long after the seeds have been shed. Leaves probably fall late in the dry season and grow in again in the early rainy season.

Mexico to Colombia and Brazil (as far south as Saõ Paulo *fide* Rizzini, 1971); Cuba. In Panama, known from tropical moist forest in the Canal Zone, Colón, San Blas, Herrera, 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 Coclé and Panamá, and from tropical wet forest in Panamá and Darién.

See Fig. 359.

TRICHOSPERMUM Blume

Trichospermum mexicanum (DC.) Baill., Hist. Pl. 4:179. 1872

Belotia panamensis Pitt.

Monoecious tree, to 15(22) m tall; young branches, petioles, and pedicels densely stellate-pubescent. Stipules ca 5 mm long, lanceolate, caducous; petioles 1.5–2.5 cm long; blades oblong-lanceolate to oblong-elliptic, long-acuminate, obtuse to rounded at base, 12–22 cm long, 3.5–9 cm wide, sparsely puberulent above with simple forked trichomes, moderately stellate-pubescent below, sometimes with tufts of trichomes in basal vein axils, entire or serrulate; palmate veins at base 3. Panicles axillary or terminal, bearing flowers of a single sex or of both sexes; pedicels ca 6 mm long with small, caducous bracteoles about 3 mm below base of sepals; flowers many, (4)5-parted; sepals pink, to 1.5 cm long, acute and hooded, densely stellate-tomentose outside; petals magenta, blunt at apex, shorter and narrower than sepals, pubescent outside, ± glabrous inside except around basal gland; stamens numerous; staminate flowers with stamens ca 1 cm long; filaments united into a broad, undulate, pubescent ring below base; style lacking; stigma obscurely lobed; pistillate flowers opening before staminate flowers; stamens apparently nonfunctional, to 3.3 mm long; style 1–4.3 mm long; stigma bilobed, the lobes divided many times. Capsules depressed-obovate, emarginate and apiculate at apex, to 2 cm long and 2.5 cm wide, densely stellate-pubescent; seeds many, broadly ellipsoid, to 2.5 mm long, long-ciliate on margins. *Croat 12844.*

Common in the forest. Flowers from November to January (sometimes to March). The fruits mature mostly from February to April.

Staminate flowers appear to greatly outnumber pistillate flowers on any tree, but pistillate flowers are more abundant on some branches than others. Staminate flowers continue to open after most or all of the pistillate flowers of an inflorescence have been fertilized and after some have developed mature-sized fruits.

Southern Mexico to Ecuador along the Pacific slope. In Panama, common in secondary growth; known from tropical moist forest in the Canal Zone, San Blas, Panamá, and Darién, from premontane moist forest in Veraguas and Panamá, from premontane wet forest in Chiriquí, Coclé, and Panamá, and from tropical wet forest in Colón and Darién.

See Fig. 360.

TRIUMFETTA L.

Triumfetta lappula L., Sp. Pl. 444. 1753

Cadillo, Cepa de caballo, Abrojo

Shrub, usually 1–2.5 m tall; most parts ± densely stellate-pubescent. Petioles mostly 2–8 cm long; blades ovate, 3–5-lobed, acuminate at apex, obtuse to rounded or subcordate at base, 5–12 cm long, 4–10 cm wide, irregularly serrate, the serrations often glandular; palmate veins at base 3–5. Cymes condensed, upper-axillary; sepals reddish-brown, narrowly oblong, about 5 mm long, pubescent outside, with a short apiculum near apex, recurved after anthesis; petals lacking; stamens 5 or 15, (rarely 10), yellow, ca 3 mm long, alternately long and short, the longer ones about the height of the style; anthers not shedding pollen in bud; style shorter than stamens in bud; stigmas 2(3), slender, open, later elongating to height of tallest stamens, mostly or completely closed when anthers shed pollen; ovary with uncinate trichomes. Capsules ellipsoid, to 1 cm long (including spines), covered with long, uncinate spines; seeds 2 per cell, pyriform, ca 2 mm long. *Croat 7476, 7778.*

Common in the Rear #8 Lighthouse Clearing. Flowers early in the dry season (December to February). The fruits mature mostly from February to April.

Throughout tropical America. In Panama, widespread and ecologically variable; known from tropical moist forest throughout the country, as well as from tropical dry forest in Panamá and Coclé, from premontane moist forest in the Canal Zone, Los Santos, and Panamá, from premontane wet forest in Colón, Coclé, and Panamá, and from tropical wet forest in Darién.

See Fig. 361.

Fig. 359.
Luehea speciosa

Fig. 360. *Trichospermum mexicanum*

Fig. 361. *Triumfetta lappula*

85. MALVACEAE

Trees, shrubs, or erect or sprawling herbs, often with mucilaginous sap, usually stellate-pubescent. Leaves alternate, petiolate; blades simple, usually palmately lobed, entire or serrate; venation palmate; stipules present. Flowers bisexual (dioecious in *Hampea*), solitary and axillary or few and corymbose, usually subtended by a crown of conspicuous epicalyx bracts; calyx 5-lobed; petals 5, free, showy; stamens many, in 1 or 2 whorls, united by their filaments into a column; anthers 1-celled, reniform, dehiscing longitudinally; ovary superior, the locules 2 to many, the carpels the same number as locules; placentation axile; ovules 1 to many per locule; style 1, branched, the branches equal to or twice as many as carpels; stigmas capitate to discoid. Fruits loculicidally dehiscent capsules or mericarps; seeds 1 or 2 per locule or many per locule (*Abelmoschus* and *Hibiscus*), sometimes arillate (*Hampea*), with oily endosperm.

Malvaceae are distinguished by their flowers, with a prominent staminal column and epicalyx bracts, and by their usually capsular fruits.

The flowers are generally open. They produce copious pollen and at least some species produce nectar. *Hibiscus rosa-sinensis* at the Laboratory Clearing is visited by hummingbirds, and male *Euplusia surinamensis* bees have been observed collecting nectar. Papilionid butterflies are its normal pollinators in Asia (H. Baker, pers. comm.). Most species of Malvaceae are probably pollinated by pollen-feeding insects. Flowers of *Sida rhombifolia* are reportedly self-pollinated in Java (van der Pijl, 1930), but they are also visited by the cotton-stainer beetle *Dysdercus cingularis* (van der Pijl, 1930) and by numerous bees (Doctors van Leewen, 1938).

Some 75–85 genera and 1,500 species; all temperate and tropical regions.

ABELMOSCHUS Medic.

Abelmoschus moschatus Medic., Malv.-Fam. 46. 1787
Musk okra, Wild okra

Herb or suffrutex, to 3(4) m tall, sparsely to densely hirsute, the trichomes of stem retrorse and spreading. Stipules linear, to 8 mm long; petioles to 15 cm long; blades nearly circular in outline, palmately lobed, 10–20 cm long, 12–24 cm wide, cordate or subsagittate at base, the lobes 3–5, acuminate, narrow, deep, irregularly serrate-dentate. Flowers solitary in upper axils; pedicels 3–6 cm long in flower, to 10 cm in fruit; epicalyx with 8–10 linear bracteoles to 17 mm long, ca 2 mm wide, persistent; calyx spathaceous, 2–4 cm long, 5-dentate, splitting laterally at anthesis; petals 5, obovate, to 8 cm long, yellow with a dark purple spot at base, asymmetrical; staminal tube ca one-third as long as corolla; style slightly longer than staminal tube. Capsules ovoid, 5–7 cm diam, acuminate, densely pubescent; seeds many, globose-reniform, ca 3.5 mm long, prominently brown-striate. *Croat 6376.*

KEY TO THE SPECIES OF MALVACEAE

Leaves deeply cordate at base, broadly ovate to ± circular in outline:
  Leaves mostly palmately lobed to beyond middle:
    Flowers yellow with a purple spot at base; stems and petioles with long trichomes ..... *Abelmoschus moschatus* Medic.
    Flowers red to magenta; stems and petioles with short, pustular-based prickles ..... *Hibiscus bifurcatus* Cav.
  Leaves shallowly lobed or not lobed:
    Epicalyx bracteoles broadened at apex into ± reniform blade, shorter than calyx ..... *Hibiscus sororius* L.f.
    Epicalyx bracteoles lance-linear, acuminate at apex, exceeding calyx ..... *Pavonia dasypetala* Turcz.
Leaves not cordate or very shallowly so:
  Epicalyx bracteoles exceeding calyx:
    Leaves obovate; petals white; herbs usually less than 30 cm tall ..... *Pavonia rosea* Schlechter
    Leaves ovate; petals yellow; herbs more than 1 m tall ..... *Pavonia paniculata* Cav.
  Epicalyx bracteoles shorter than calyx or lacking:
    Plants trees, usually more than 10 m high; blades entire, broadly ovate ..... *Hampea appendiculata* (Donn. Sm.) Standl. var. *longicalyx* Fryx.
    Plants herbs or shrubs, less than 4 m tall; blades toothed:
      Flowers red; staminal tube long-exserted; epicalyx bracts lance-linear; plants usually more than 2 m tall, cultivated ..... *Hibiscus rosa-sinensis* L.
      Flowers white to yellow-orange; staminal tube not exserted; epicalyx bracts lacking; plants usually less than 2 m tall:
        Leaves ± ovate-elliptic, moderately stellate-pubescent below, the trichomes not obscuring surface; stipules linear, usually to 15 mm long; pedicels to 12 mm long ..... *Sida acuta* Burm.f.
        Leaves ± rhomboid, densely stellate-pubescent below, the trichomes obscuring surface; stipules subulate, usually less than 5 mm long; pedicels to 3.5 cm long ..... *Sida rhombifolia* L.

Fig. 362. *Hampea appendiculata* var. *longicalyx*

Fig. 363. *Hibiscus bifurcatus*

Collected once in Rear #8 Lighthouse Clearing. Flowers and fruits elsewhere throughout much of the year, especially during the rainy season.

Native to southeast Asia; cultivated in the tropics throughout the world. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Chiriquí, Herrera, Panamá, and Darién; known also from premontane wet forest in Colón.

HAMPEA Schlechter

Hampea appendiculata (Donn. Sm.) Standl. var. **longicalyx** Fryx., Brittonia 21:391–92. 1969

Dioecious tree, 10–17 m tall, to 40 cm dbh, ± densely stellate-tomentose (sparsely so on upper leaf surface); bark smooth, the wood creamy gray, very soft; stems and petioles reddish-brown. Stipules caducous, less than 2 mm long; petioles 3–7(11) cm long, one-half to one-third length of blade; blades broadly ovate to elliptic, acuminate to long-acuminate at apex, subcordate or obtuse at base, 9–21 cm long, 6–16 cm wide, often with minute, round, erect auricles over petiole at base, entire; palmate veins at base 5 (rarely 7), all veins prominently raised below, with conspicuous glands below especially at lower axils. Involucral bracteoles 3, subulate, 1–3 mm long, inserted at base of calyx, deciduous; flowers unisexual, axillary, in groups of 1–10, ca 2.5 cm diam; pedicels 1–3(5) cm long; epicalyx bracteoles lanceolate, ca 1–5 mm long; calyx truncate or irregularly 3- or 4-lobed to near middle, 8–15 mm long, glabrous inside; petals 5, oblong-elliptic to obovate, fused at base to the staminal tube, white to yellow, 15–25 mm long, glabrous inside, spreading at anthesis; stamens numerous, connate into staminal tube; staminate flowers with the stamens of irregular lengths, 5–11 mm long within a cluster; anthers oblong, 1–1.5 mm long; pistil lacking; pistillate flowers with the stamens much reduced, nonfunctional; style filiform, ca 1 cm long. Capsules obovate to elliptic, rounded at apex, densely stellate-tomentose, 2–3 cm long, the valves 3, spreading widely at maturity to expose seeds; seeds 1 or 2 per locule, ± ovoid, ca 1 cm long, black and shiny, covered on one side by a fleshy, white aril. *Croat 12495.*

Uncommon, in the older forest. Flowers in the rainy season (July to November, especially in September and October). The fruits are mature in the dry season, principally in February and March.

The capsule is reportedly explosively dehiscent, but it is doubtful that this serves to disperse the seeds completely since they are well adapted to bird dispersal. The typical variety of *H. appendiculata* differs in having longer stipules (3–9 mm long), smaller flowers (less than 1.5 cm diam), and a shorter calyx (5–6 mm long).

The species is known from Honduras, Costa Rica, and Panama. The variety *longicalyx* is known only from Panama, where it is ecologically variable, occurring in tropical moist forest on BCI but also in premontane moist, tropical wet, and premontane rain forests in Coclé, Panamá, and Darién.

See Fig. 362.

HIBISCUS L.

Hibiscus bifurcatus Cav., Mon. Cl. Diss. Dec. 146, t. 51(1). 1787

Algodoncito

Sprawling suffrutex or shrub, to 4 m tall; stems and petioles sparsely stellate-pubescent (often in lines); stems, petioles, pedicels, and major veins with retrorse pustular-based prickles. Stipules linear-subulate; petioles 2–10.5 cm long; blades ovate in outline, lobed mostly to beyond middle, deeply cordate at base, 9–16 cm long, sparsely pubescent with both simple and stellate trichomes, the lobes 3–5, mostly narrowly ovate, acuminate, the margins dentate-serrate. Flowers solitary in upper axils; pedicels 2–7 cm long; epicalyx bracteoles 9–13, linear, unequally bifurcate at apex, 1.5–2.5 cm long, pubescent; calyx 1–2 cm long, lobed to about middle, pubescent, accrescent in fruit, the lobes acuminate, 3-veined, the midvein glandular, the gland about midway, secreting sweet nectar; petals 5, obovate, 5–7(9) cm long, rounded at apex, magenta or rose; staminal tube dark violet, sparsely covered with anthers throughout, half to fully as long as corolla; style branches 5, held above staminal tube; stigmas hirtellous. Capsules ca 2 cm long, slightly shorter than accrescent calyx, broadly ovoid, mucronulate, sericeous; seeds many, irregular, 3–4 mm long, minutely papillate. *Croat 4254.*

Rare; possibly restricted to marshes or wet areas at the edge of the lake. Apparently flowers principally in the dry season, especially in the early dry season, with most fruits maturing late in the dry season and in the early rainy season.

Mexico to the Guianas and Brazil; West Indies. In Panama, known from tropical moist forest in the Canal Zone and Panamá and perhaps more abundantly from tropical wet forest in Colón.

See Fig. 363.

Hibiscus rosa-sinensis L., Sp. Pl. 694. 1753

Chinese hibiscus, Papo, Tapo, Papo de la reina

Shrub, to 3(7) m tall; young leaves and stems with dense, simple or branched trichomes, glabrate in age. Stipules lanceolate-linear, 6–8 mm long, paired; petioles 1.5–4 cm long; blades ovate, acuminate, obtuse to cuneate at base, 8–15 cm long, 5–9 cm wide, coarsely serrate. Flowers solitary in axils; pedicel, epicalyx, and calyx sparsely to densely stellate-pubescent; epicalyx bracteoles 5–7, narrow, to 1 cm long; calyx tubular-campanulate, 2–3 cm long, lobed ca one-fourth its length; petals 5, red, obovate, 7–9 cm long; staminal tube long-exserted, to 12 cm long, 5-lobed at apex; filaments to 1 cm long, attached in upper third of tube; style exceeding staminal tube ca 1 cm, the branches pubescent. Fruits not seen. *Croat 5467.*

Cultivated at the laboratory and also present in the Tower Clearing. Flowers throughout the year.

Probably native to tropical Asia; cultivated throughout the tropics of the world. In Panama, known from disturbed areas in tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Panamá and from premontane moist forest in Panamá.

Fig. 364. *Hibiscus sororius*

Fig. 365. *Sida acuta*

Hibiscus sororius L.f., Suppl. Pl. Syst. Veg. 311. 1781
H. sororius L.f. forma *albiflorus* Standl.

Herb or suffrutex, to 2 m tall, densely stellate-pubescent but sparsely on upper blade surface. Stipules minute; petioles 3–9(11) cm long; blades ovate (to irregularly angular), obtuse at apex, deeply cordate at base, 5–16 cm long, 5–13 cm wide, irregularly crenate; palmate veins at base 5–7. Flowers solitary in upper axils, long-pedicellate; epicalyx bracteoles markedly broadened at apex into a ± reniform blade; calyx 5-lobed to middle or beyond, 2–3 cm long, 5–7-veined, persisting in fruit; petals 5, obovate, 5–7.5 cm long, usually white, often magenta in bud; staminal tube antheriferous throughout, about half as long as corolla; pollen sticky, clinging together in chainlike masses; styles 5, occasionally splitting staminal tube, recurving and coming into direct contact with anthers; stigmas minutely fimbrillate, slightly exceeding staminal tube; nectar accumulating between calyx and petals. Capsules oblong-elliptic, ca 2.5 cm long, contained within larger, accrescent calyx, densely hispid, the valves 5, opening at maturity; seeds subglobose-reniform, less than 2 mm long, with glandular droplets, buoyant. *Croat 13231.*

Common in marshy areas on the south side of the island. Usually a component of the floating masses of vegetation (i.e., *Annona-Acrostichum* formations). Flowers and fruits throughout the year.

Throughout the tropics of Central and South America; Cuba. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, usually in swamps.

See Fig. 364 and fig. on p. 12.

PAVONIA Cav.

Pavonia dasypetala Turcz., Bull. Soc. Imp. Naturalistes Moscou 31(1):189. 1858

Shrub or small tree, to 5 m tall; pubescence dense, stellate, often ± viscid especially on inflorescences. Stipules narrowly ovate, to 20 mm long, 2–4 mm wide; petioles 5–15 cm long; blades broadly ovate, acuminate, cordate at base, 12–23 cm long, 10–20 cm wide, sometimes shallowly trilobate, irregularly serrate-dentate. Flowers solitary in axils or paniculate and terminal; pedicels 1–2.5 cm long, articulate near apex; epicalyx bracteoles 12–16, lanceolate-linear, 1.5–2.5 cm long; calyx cupular, hidden by epicalyx, 2–4 mm long; petals 5, rose, narrowly obovate, 3–5 cm long; staminal tube shorter than corolla, lobed, antheriferous on upper part; filaments ca 6 mm long; style exceeding staminal tube, the branches 10, to 7 mm long. Mericarps 5, obovoid, to 6 mm long and 3 mm wide, ± 3-sided, black; seeds ca 4.5 mm long, black, surrounded by a whitish aril. *Croat 4330, Foster 1455.*

Rare, collected twice in recent years on Zetek Trail; probably more abundant in previous years. Elsewhere in the Canal Zone the species usually occurs along roadsides or in open areas. Flowers in the early dry season. The fruits mature principally from January to March.

Costa Rica to Colombia and Venezuela. In Panama, common in premontane wet forest in the Canal Zone and Panamá; known also from tropical moist forest in the Canal Zone and Panamá and from tropical wet forest in Panamá (Cerro Jefe).

Pavonia paniculata Cav., Mon. Cl. Diss. Dec. 135, t. 46(2). 1787
Pape

Herb or shrub, to 3 m tall; trichomes of stems, petioles, and inflorescence branches both long and short, mostly simple, sometimes gland-tipped. Stipules lanceolate, 1–1.5 cm long, persistent, paired; petioles 3–10 cm long; blades ovate to shallowly trilobate, acute to acuminate at apex, truncate to shallowly cordate at base, 5–12 cm long, 4–10 cm wide, crenate-serrate, sparsely pubescent above, moderately stellate-pubescent below; palmate veins 7–9. Flowers solitary in axils, becoming paniculiform or subcorymbose at ends of branches by reduction of leaves; pedicels very short or to 3 cm long; epicalyx hirsute, with 6–12 linear bracteoles 1–2 cm long; calyx cupular, ca 5 mm long, 5-lobed to near middle, long-ciliate; petals 5, yellow, obovate, 1–1.5 cm long, spreading at anthesis, glabrous except inside at base; staminal tube ca half as long as petals, antheriferous throughout; filaments ca 5 mm long; style exceeding staminal tube, the branches 10. Mericarps 5, obovoid, ± 3-sided, 3–4 mm long, minutely tuberculate and appressed-puberulent; seeds trigonous-reniform, ca 2.5 mm long. *Shattuck 731.*

Apparently rare or absent, collected twice in earlier years but not seen recently. The species generally grows in weedy areas along roadsides in the Canal Zone. Flowers from November to March, especially in December and January. Most fruits are mature in February and March.

Mexico to Argentina; Greater Antilles. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, and Panamá, from premontane moist forest in the Canal Zone and Panamá (Saboga Island), and from premontane wet forest in Chiriquí (Boquete), Coclé (El Valle), and Panamá.

Pavonia rosea Schlechter, Linnaea 11:355. 1837

Suffruticose herb, usually less than 30 cm tall; stem usually unbranched; most parts with stellate or less frequently hirsute pubescence but the upper blade surface often glabrous. Stipules paired, linear, 6–8 mm long, persistent; petioles 5–15 mm long; blades obovate, acute to acuminate at apex, tapered to a slightly cordate base, 9–18 cm long, 3–8 cm wide, irregularly dentate. Inflorescences usually terminal, short; flowers few, to ca 1.3 cm diam; epicalyx bracteoles 7–11, linear, united at base, to ca 1 cm long; calyx 3–5 mm long, shorter than epicalyx, lobed to middle, the lobes triangular; petals white, ± obovate, 7–10 mm long, stellate-puberulent outside, spreading at anthesis; staminal tube bearing anthers just below apex; style branches 10, slightly longer than staminal tube, pinkish; stigmas capitate. Fruits to 8 mm long; mericarps 5, prominently 3-ribbed, spiny, the spines

5–7 mm long, 3 per mericarp, retrorsely barbed; seeds trigonous, 4–5 mm long, glabrous. *Croat 9254, 10942.*

Common along trails in the older forest, often forming continuous stands below the escarpment on Zetek Trail; common to rare elsewhere. Flowers from March to November, especially in the early rainy season. The fruits develop rather quickly, and mature fruits may share the same inflorescence with flowers.

Mexico to Colombia and Brazil; Greater Antilles. In Panama, known principally from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién; known also from tropical dry forest in Coclé (Penonomé), from premontane wet forest in Bocas del Toro (Río Guarumo) and Coclé (El Valle), and from premontane and lower montane rain forests in Chiriquí.

SIDA L.

Sida acuta Burm.f., Fl. Ind. 147. 1768
Escobilla

Suffrutex, to 1(1.8) m tall, sparsely pubescent with simple and stellate trichomes. Leaves distichous; stipules lanceolate-linear, 1–1.5 cm long, ca 1 mm wide, persistent; petioles less than 1 cm long; blades narrowly ovate, acute at apex, obtuse to rounded at base, 4.5–10 cm long, 2–3.5 cm wide, serrate-dentate; palmate veins 3. Flowers 5-parted, solitary or in small pseudoumbels, axillary, 18–25 mm broad; pedicels to 12 mm long; calyx campanulate, to 1 cm long, foliaceous, lobed to near middle, moderately accrescent; petals obovate, to 1 cm long and 8 mm broad, yellow or white, oblique; staminal tube ca 4 mm long; filaments ca 2 mm long, with gland-tipped trichomes; style 4–5.5 mm long. Mericarps 5, 7, or 9 (rarely to 12), 3-sided, with 2 ± parallel beaks, 2.5–4 mm long, often densely stellate-pubescent; seeds trigonous, ca 2 mm long. *Croat 10249.*

Locally common in clearings. Flowers and fruits throughout the year, but apparently with the heaviest concentration of flowering in the rainy season with the fruits maturing mostly in the dry season.

Flowers of *S. acuta* reportedly open between 8 A.M. and 1 P.M. (van der Pijl, 1930).

Though beaks of the mericarps are not recurved to assist in epizoochorous dispersal as in *S. rhombifolia,* the closely parallel, usually densely stellate pubescence of the beaks serves nicely to attach the mericarps to passing animals.

Throughout the tropics of Western and Eastern hemispheres. In Panama, abundant and widespread in tropical moist forest; known also from premontane moist forest in Darién (Punta Patiño), from premontane wet forest in Coclé, Panamá, and Darién, and from tropical wet forest in Colón.

See Fig. 365.

Sida rhombifolia L., Sp. Pl. 684. 1753
Escobilla, Hierba de puerco

Herb or suffrutex, to 1.5 m tall; stems usually branched many times, minutely stellate-pubescent. Leaves minutely stellate-pubescent, especially below; stipules subulate, to 5 mm long; petioles 3–5 mm long; blades variable in shape and size, usually ± rhombic, acute to obtuse at apex, obtuse to cuneate at base, 1.5–7.5(8.5) cm long, 0.8–2.5(3.5) cm wide, serrate; palmate veins 3(5). Flowers 5-parted, ca 1 cm wide, solitary in axils, becoming corymbose at apex of stem; pedicels to 3.5 cm long, articulate usually above middle; calyx campanulate, 5-angulate, ca 6 mm long, the lobes deltoid, acuminate; petals ovate, oblique, clawed, emarginate at apex, mostly 7–9 mm long, yellow-orange; staminal tube ca 3.5(6) mm long; styles 4(8), connate to half their length. Mericarps usually 8–12, 3-sided, with a single beak, to 5.5 mm long (including beak); seeds bluntly 3-sided, ca 2 mm long. *Croat 6926.*

Locally common in clearings. Flowers and fruits throughout the year.

The single beak of the mericarp is often recurved and sparsely stellate-pubescent, both adaptations for epizoochorous dispersal.

Throughout tropics and subtropics of the world. In Panama, ecologically widespread, occurring in all provinces and in life zones ranging from tropical moist forest through tropical wet forest.

86. BOMBACACEAE

Trees, stellate-pubescent on some parts and sometimes armed. Leaves alternate, petiolate; blades simple or palmately compound, sometimes lobed, the margins entire; venation pinnate or palmate; stipules present. Flowers bisexual, actinomorphic, bracteolate, solitary or cymose, terminal or axillary; calyx cupular or campanulate, truncate or lobed; petals 5, imbricate, showy; stamens 5 (*Ceiba*) to many, the filaments united into a tube or the entire stamens forming a column (*Ochroma, Quararibea*); anthers 1–3 per stamen, 1- or 2-celled, often horseshoe-shaped, straightening at anthesis, dehiscing longitudinally; ovary superior (subinferior in *Quararibea*), 5-locular (2-locular in *Quararibea*), 2–5-carpellate; placentation axile; ovules 2 to many per locule, anatropous; style with the stigma usually 5-lobed. Fruits usually loculicidal capsules opening by 3–5 valves, the seeds with little or no endosperm and enveloped by woolly mass of trichomes; less frequently fruits pulpy and indehiscent (*Quararibea*) or capsular, the seeds large, not enveloped in a woolly mass of trichomes (*Cavanillesia, Pachira*).

Most members of the family are recognized by their powder-puff-like stamens and large capsular fruits with kapok enveloping the seeds. The genus *Quararibea* is atypical in both respects.

The flowers with large powder-puff-like clusters of stamens (*Bombacopsis, Pachira, Pseudobombax*) are pollinated most effectively by birds and bats. *Bombacopsis quinata, Pseudobombax septenatum, Ceiba pentandra, Ochroma pyramidale,* and *Quararibea asterolepis* are known to be pollinated by bats (Baker & Harris, 1959; Heithaus, Opler & Baker, 1974; Heithaus, Fleming & Opler, 1975; Vogel, 1958; Bonaccorso, 1975). *Ochroma*

KEY TO THE SPECIES OF BOMBACACEAE

Leaves present and simple:
  Leaves ovate-cordate, usually lobed:
    Flowers solitary, more than 10 cm long, not precocious; capsules not winged, more than 6 times longer than wide; leaves shallowly sublobate ..... *Ochroma pyramidale* (Lam.) Urban
    Flowers not solitary (in terminal cymes), less than 3 cm long, precocious; capsules winged, about as wide as long; leaves deeply lobed (usually on ground at time of flowering) ..... *Cavanillesia platanifolia* (H. & B.) H.B.K.
  Leaves ± elliptic, not cordate or lobed:
    Calyx with 10, narrow, longitudinal wings; fruits ca 4 cm diam; plants usually less than 12 m tall ..... *Quararibea pterocalyx* Hemsl.
    Calyx lacking wings; fruits ca 2 cm wide; plants more than 20 m tall ..... *Quararibea asterolepis* Pitt.
Leaves lacking or palmately compound:
  Leaves always present with flowers; leaf blades acuminate; flowers more than 16 cm long and anthers more than 3 mm long; stamens scarlet toward apex; fruits with relatively few large seeds (more than 2 cm long); trees growing usually only in wet areas ... *Pachira aquatica* Aubl.
  Leaves usually lacking at time of flowering; leaf blades acuminate or not; flowers less than 16 cm long *or* anthers less than 3 mm long; filaments whitish toward apex; fruits with many small seeds in kapok; trees not restricted to wet areas:
    Flowers less than 5 cm long; fruits to more than 4 times longer than broad *or* fruits winged:
      Anthers numerous, the staminal tube with numerous deep divisions; fruits broadly winged; twigs lacking noticeable scars; trunk unarmed, only slightly buttressed, with prominent raised rings every meter or so; leaves simple but lobed ..... *Cavanillesia platanifolia* (H. & B.) H.B.K.
      Anthers 10–15, borne on 5 divisions of staminal tube; fruits wingless; twigs with definite stipule scars; trunk usually armed, markedly buttressed; leaves palmately compound .. *Ceiba pentandra* (L.) Gaertn.
    Flowers more than 6 cm long; fruit wingless, less than 3 times longer than broad:
      Fruits ellipsoid, more than 11 cm long, striped green and purplish-brown; leaflets inarticulate; trunk with green stripes; twigs whitish-pruinose; pedicels usually more than 1.8 cm long ..... *Pseudobombax septenatum* (Jacq.) Dug.
      Fruits oblong, less than 8 cm long, not striped; leaflets articulate; trunk not striped; twigs not whitish-pruinose; pedicels usually less than 1.8 cm long:
        Trunk and branches armed; leaflets ± acuminate at apex ..... *Bombacopsis quinata* (Jacq.) Dug.
        Trunk and branches unarmed; leaflets rounded or emarginate at apex ..... *Bombacopsis sessilis* (Benth.) Pitt.

pyramidale is also visited by white-faced and squirrel monkeys (Oppenheimer, 1968; Enders, 1935) as well as kinkajous, marmosets, opossums, parrots, and oropendulas (Chapman, 1938) (see the discussion under that species). Faegri and van der Pijl (1966) reported that movements of the *Ceiba pentandra* flower in the wind may cause self-pollination. Baker (1973) reported that it is freely visited by hummingbirds in Mexico.

Bombacopsis, Ceiba, Ochroma, and *Pseudobombax* have small seeds that are enveloped within a mass of kapok-like fibers and are wind dispersed, as is the winged seed of *Cavanillesia.* The mass of fibers easily supports the seed in water. *Quararibea* and *Pachira* are mammal or water dispersed. *Quararibea asterolepis* fruits are taken by white-faced monkeys (Oppenheimer, pers. comm.), howler, spider, and night monkeys. Fallen fruits are further dispersed by opossums (Hladik & Hladik, 1969) and possibly also by reptiles. *Quararibea* fruits are taken by the bat *Artibeus jamaicensis* Leach in Mexico (Yazquez-Yanes et al., 1975).

About 25 genera and some 150 species; mostly in the American tropics.

BOMBACOPSIS Pitt.

Bombacopsis quinata (Jacq.) Dug., Contr. Hist. Nat. Colomb. 1:2. 1938
B. fendleri (Seem.) Pitt.
Spiny cedar, Cedro espinoso

Deciduous tree, to 30(40) m tall, to 1 m dbh; trunk armed, often broadly buttressed at base; branches armed; wood reddish-brown, light, soft. Leaves alternate, digitately compound, glabrous; stipules lanceolate, caducous; petioles to 12 cm long, canaliculate above; petiolules very short, to 8 mm long; leaflets 5(7), oblong-obovate, acute to acuminate, acute and tapered at base, decurrent on articulate petiolule, 4–17 cm long, 2–8 cm wide, entire. Cymes growing from younger wood; flowers 1 to few, precocious, 7–11 cm long; pedicels 0.4–0.8 mm long, the bracteoles at apex 3, subtending the generally 5-glandular receptacle; calyx ± campanulate, undulate to flat-topped, to 1 cm high and 1 cm wide; both calyx and pedicel generally reddish-brown (at least when dry) and shortly tufted-puberulent, appearing velvety; petals 5, imbricate,

Fig. 366. *Bombacopsis quinata*

Fig. 367. *Bombacopsis quinata*

Fig. 368.
Bombacopsis sessilis

to 10 cm long and 8 mm wide, lighter than calyx, tan, puberulent and ca 14-veined inside, bicolorous in 2 stripes and appearing stellate-pubescent outside, tan on the side protected by next petal and light reddish-brown on exposed side; stamens ca 150, the free portion ca 6 cm long and united basally into a column ca 2 cm long; anthers horseshoe-shaped, dehiscing by unfolding and becoming ± straight, more than 2 mm long; style less than 10 cm long; stigma 5-lobed. Capsules oblong, ca 8 cm long, the valves 5, cinnamon, mucronulate, opening to expose pale yellowish kapok and seeds; seeds several, small, less than 5 mm long. *Croat 8380, 8705.*

Occasional, in the forest, principally in the younger forest. Flowers in February and March. The fruits mature and fall in March or later. Leaves fall during the dry season, growing in again in April and persisting until December or January.

Nicaragua to Colombia and Venezuela. In Panama, a characteristic component of tropical dry forest (Holdridge & Budowski, 1956) and of tropical and premontane moist forests (Tosi, 1971); known from tropical moist forest in the Canal Zone, Panamá, and Darién, from tropical dry forest in Coclé, from premontane moist forest in Panamá, and from premontane wet forest in Panamá (Chimán).

See Figs. 366 and 367.

Bombacopsis sessilis (Benth.) Pitt., Contr. U.S. Natl. Herb. 18:162. 1916

Ceibo, Yuca de monte, Ceibo nuno

Deciduous tree, 15–30 m tall, mostly 20–65 cm dbh; trunk unarmed, with greenish bark, with narrow plank buttresses to 1.5 m high; outer bark thin, grayish, with many vertical rows of lenticels, flaking; inner bark tan, thick, with irregular dark spots near periphery; branches at ± regular intervals, self-pruning, the lowermost branches deciduous; branchlets roughened with lenticels and old petiolar bases. Leaves palmately compound, glabrous; stipules lanceolate; petioles ± equaling leaflets, enlarged at both ends; blades (4)5–7(9), ± narrowly obovate, emarginate at apex, 4–18 cm long, 1.5–6.5 cm wide. Flowers showy, white to pink, terminal on short lateral branches, solitary or as many as 5 on a branch, appearing before or after leaves fall, 13–24 cm long; pedicels 5–18(32) mm long; calyx tubular, truncate or weakly lobed, about 1 cm long and 1 cm wide; petals 5, stellate outside, imbricate in bud, drying greenish, generally not markedly striped, and darker than *B. quinata;* stamens ca 250, fused into a column ca 8 cm long, the free part of filaments ca 6 cm long; anthers horseshoe-shaped, dehiscing by straightening, less than 2 mm long, shedding some pollen in bud; style bright red; stigma of 5 sharp lobes, pubescent inside. Capsules oblong, somewhat more elongate than *B. quinata,* the valves 5, woody, yellow-brown when fresh, opening to expose pale, often brownish kapok and seeds; seeds numerous, medium-sized, to 1 cm. *Croat 8654, 12976.*

Frequent in the forest, especially in the younger forest. Flowers from December to February. The fruits mature from March, persisting to October. Trees are bare for a short time in the dry season.

Costa Rica and Panama; cultivated in Cuba and Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Veraguas, and Panamá, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone, Veraguas, and Panamá, from premontane wet forest in Chiriquí and Panamá, and from tropical wet forest in Colón.

See Fig. 368.

CAVANILLESIA R. & P.

Cavanillesia platanifolia (H. & B.) H.B.K., Nov. Gen. & Sp. 5:306. 1823

Cuipo, Quipo, Bongo, Hamati

Deciduous tree, to 40 m tall, small-crowned; trunk usually 1–1.5 m diam, pale, often somewhat bulging ca 2 m above base, markedly ringed at intervals of ca 1.5 m, the surface planar but roughened with lenticels in age; inner bark granular. Leaves simple, clustered at apex of branches; stipules ovate, 5 mm long; petioles 10–25 cm long; blades ovate, palmately lobed (young leaves entire), the lobes 3–7, acuminate, cordate at base, to 30 cm long and wide, glabrate above, densely puberulent below. Cymes contracted, axillary; pedicels ca 1 cm long, surmounted by 3 fugacious bracteoles; flowers red, precocious, 2–3 cm long; calyx bell-shaped, irregularly 5-lobed, ca 1.5 cm long; calyx and pedicel shortly ferruginous-tomentulose; petals 5, strap-shaped, to 2.5 cm long and ca 5 mm wide, red, ferruginous-tomentulose toward obtuse apex; stamens many, reddish, to 2 cm long, united into a column about one-third their length; anthers ca 1 mm wide, broader than long, dehiscing upward; ovary 4- or 5-celled, the ovules 2 per cell; style straight, exceeding stamens by 5–10 mm; stigma 5-forked. Capsules hard, narrow, linear, to 12 cm long, with 4 or 5 conspicuous wings; wings semicircular, membranous and markedly veined, each to 15 cm long and 8 cm wide, red and green when mature; seeds 4 or 5. *Croat 8348.*

Occasional, in the forest. Flowers in March and April. The fruits mature in April and May. Leaves fall in December or January and reappear in May and June.

The fruits, despite their large wings, are poor fliers, and most land within a few hundred feet of the parent plant.

Nicaragua to Peru. In Panama, a typical component of tropical moist forest (Tosi, 1971) and described as the most abundant tree in upland Darién (Lamb, 1953); known from tropical moist forest in the Canal Zone, Los Santos, Panamá, and Darién, mostly on limestone soils (R. Foster, pers. comm.).

See Fig. 369.

CEIBA P. Mill.

Ceiba pentandra (L.) Gaertn., Fruct. & Sem. Pl. 2:244, t. 133. 1791

Silkcotton tree, Ceiba, Cotton tree, Bongo

Tree, to 40 m tall; trunk ca 1.5 (2.5) m dbh, armed at least when young, with large, curving plank buttresses

Fig. 369. *Cavanillesia platanifolia*

Fig. 370.
Ochroma pyramidale

to 10 m high and 10 m wide at base; outer bark grayish-brown with horizontal lenticular lines. Leaves clustered at tips of branchlets, palmately compound, glabrous; stipules ovate, to 6 mm long, caducous; petioles 5–23 cm long; leaflets 5–9, oblong-lanceolate, acuminate, narrowed and obtuse to acute at base, 10–21 cm long, 2–4.5 cm wide, ± entire. Flowers precocious, in clusters at tips of branchlets, ca 3 cm long; pedicels ca 2.5 cm long; calyx bell-shaped, ca 1 cm long and wide, with 4 or 5 small lobes, glabrous, drying dark; petals 5, oblong, ca 3 cm long and 1 cm wide, light yellow; stamens 5, united at base into a column; anthers 2 or 3 per stamen, linear, 1-celled, spiraled; style slightly surpassing stamens, surmounted by a capitate stigma. Capsules elongate-elliptic to obovoid, 10–26 cm long, to 4 cm diam, the valves 5, greenish, opening to expose copious grayish kapok and seeds; seeds numerous, round, ca 5 mm long. *Croat 14071.*

Frequent in the forest. Flowering usually from December through February, but individuals never flower 2 years in succession and sometimes only once in 5 years. Mature fruits are seen from January to March. Allen (1956) reported flowers in Costa Rica in February, with the fruits maturing in late March. Leaves fall in the late rainy season to the early dry season. In reproductive years individuals may be leafless much longer than during sterile years (R. Foster, pers. comm.).

In open areas the crown of the tree may be wider than the tree is tall.

Pantropical. In Panama, a typical component of tropical dry and tropical moist forests (Holdridge & Budowski, 1956; Tosi, 1971), but growing in many climates and places (Holdridge, 1970); known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, and Panamá.

See fig. on p. 10.

OCHROMA Sw.

Ochroma pyramidale (Cav. ex Lam.) Urban, Feddes Repert. Beih. 5:123. 1920

O. lagopus Sw.; *O. limonensis* Rowlee

Balsa, Balso, Lana, Cotton tree

Tree, usually less than 12 m tall but to 30 m where persisting in the older forest, 30–180 cm dbh, sometimes buttressed; wood very lightweight; branchlets, pedicels, lower blade surfaces, petioles, and exposed parts of calyces with a dense layer of brown, stellate, tufted trichomes. Leaves simple, clustered at ends of branchlets; stipules ovate, to 1.5 cm long; petioles thick, 3–40 cm long; blades ovate, acuminate, cordate, 9–40 cm long, 8–35 cm wide, entire to shallowly 3–5-lobed, glabrous above in age, pale below; palmate veins at base 7(9). Flowers not precocious, leathery, with a pleasant aroma when young; pedicels to 12.5 cm long and 1.5 cm broad; calyx lobes stiffly coriaceous, unequal in shape, to 5.5 cm long, sericeous-villous inside; petals obovate-spatulate, to 15 cm long and 5 cm wide, whitish; staminal column 10–12 cm long, the antheriferous part 5–6 cm long, enlarged at anthesis; pollen with a foul odor, at least in age, evenly distributed over column surface; anthers sessile, longitudinally dehiscent, the theca 1; style completely enveloped by stamens in bud, about as long as stamens at anthesis; stigma stout, spirally 5-sulcate. Capsules long, narrow, to 25 cm long and 2.5 cm diam, black and glabrous outside, densely lanate inside, the valves 5; seeds many, small, ca 5 mm long. *Croat 4637, 7214.*

Common along the margin of the lake or in disturbed areas, rare in the older forest where it is a large tree. Flowers from August to May, mostly from November to March. The fruits mature from February to August. Leaves fall around June and are replaced in August.

The flowers open at night, sometimes persisting to the following day. At anthesis the anthers, which are somewhat spirally arranged around the style, are unfurled and spread broadly. By the following day they are again closely twisted around the stigma. White-faced monkeys have been seen in the daytime poking their faces into the flower, possibly searching for insects, and their faces become liberally covered with pollen. They probably do not regularly effect pollination because the stigma is then covered, but the flowers may be visited by nocturnal mammals in the same way. Birds often cut holes near the base to obtain nectar. Seeds are principally wind dispersed but probably also water dispersed, made buoyant by the brownish kapok fibers within which they are enveloped.

Native to the New World; pantropical in cultivation. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Veraguas, Los Santos, Panamá, and Darién, from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, from premontane wet forest in Chiriquí, and from tropical wet forest in Veraguas (Atlantic slope).

See Fig. 370.

PACHIRA Aubl.

Pachira aquatica Aubl., Hist. Pl. Guiane Fr. 2:726, t. 291, 292. 1775

Provision tree, Sapote longo

Evergreen tree, to 23 m high and 70 cm dbh, often buttressed; outer bark hard, planar, thin, with weak distant vertical fissures; inner bark thick, reddish, marbled with white. Leaves palmately compound, glabrous; stipules ovate, ca 1 cm long; petioles to 24 cm long, often ribbed, swollen at both ends; leaflets 5–7(9), oblong-obovate to elliptic, caudate-acuminate to apiculate at apex, tapered to an acute base and decurrent on petiolule, 5–29 cm long, 3–15 cm wide, whitish-lepidote especially below. Flowers sweetly aromatic, usually solitary in upper axils; pedicels stout, 1–5.5 cm long; calyx ± tubular, truncate, the lobes obscure; petals 5, valvate, linear, greenish-white to brown, 17–34 cm long, ca 1.5 cm wide, curled outward at anthesis, stellate-puberulent outside, glabrous to villous inside; stamens many, scarlet in apical third, white basally, erect to spreading, slightly shorter than petals, variously united in small clusters basally to middle, the clusters finally uniting with staminal column; anthers

Fig. 372. *Pseudobombax septenatum*

Fig. 373.
Pseudobombax septenatum

Fig. 371. *Pachira aquatica*

horseshoe-shaped, dehiscing by straightening; ovary broadly ovoid, ca 1 cm long; style colored like stamens but several cm longer; stigma of 5 tiny lobes. Capsules reddish-brown, elliptic, oblong-elliptic, or subglobose, shallowly 5-sulcate, mostly to 20(30) cm long and 10(12) cm wide, the valves 5, densely ferruginous outside, appressed-silky-pubescent within; seeds usually 2 or 3 per carpel, irregularly angulate, mostly 3–4.5 cm long at maturity, brown, buoyant, embedded in solid, white, fleshy mesocarp. *Croat 5613.*

Known only from the edge of the lake. Flowers to some extent all year, mostly from February to April (sometimes from December to July). Most fruits mature from March to August. New leaves appear around May.

The buoyant seeds are no doubt dispersed by water currents.

Southern Mexico to northern Peru and Brazil; cultivated in the West Indies. In Panama, a characteristic species in tropical moist and tropical wet forest areas (Tosi, 1971), forming small, pure stands in Darién (Holdridge & Budowski, 1956) and usually growing beside fresh water; known from tropical moist forest in the Canal Zone, Bocas del Toro, Colón, Panamá, and Darién, from premontane wet forest in Panamá, and from tropical wet forest in Colón. Reported from premontane rain forest in Costa Rica (Holdridge et al., 1971).

See Fig. 371.

PSEUDOBOMBAX Dug.

Pseudobombax septenatum (Jacq.) Dug., Caldasia 2:65. 1943

Bombax barrigon (Seem.) Dec.

Barrigon, Ceibo barrigon

Deciduous tree, to 25 m tall; trunk to 140 cm dbh; outer bark thin, unarmed, usually with smooth, green, striped areas interspersed with corky areas; inner bark thick, mottled reddish and white; branchlets whitish-pruinose, generally stout and more than 1 cm diam at apex. Leaves palmately compound, glabrous; stipules broadly ovate, to 12 mm long, caducous; petioles 10–56(68) cm long; leaflets subsessile or on petiolules to 1 cm long, inarticulate, obovate, short-acuminate, narrowed to an acute base and decurrent on petiolule, 7–29 cm long, 4–14 cm wide, sometimes sparsely lepidote below, entire. Inflorescences cymose, toward ends of branchlets; flowers 1–3, precocious or not, 7–10 cm long; pedicels 2–4 cm long; receptacle glandular below; calyx cup-shaped, truncate, 1 cm long and 2–3 cm wide; petals 5, leathery, ± white, ± lincar, 7–9 cm long and ca 2 cm wide, curling below calyx; stamens more than 1,000, whitish, in a dense powder puff atop calyx, to 9 cm wide and 6 cm high, in 5 bifurcate clusters; column about 1 cm high; anthers horseshoe-shaped, dehiscing by straightening; style about as long as or somewhat surpassing stamens. Capsules ± ellipsoid, green, irregularly and longitudinally striped with purplish-brown, to 18 cm long, about half as broad, filled with grayish kapok; seeds numerous, ca 5 mm long. *Croat 8191.*

Common throughout the forest. Flowers mostly from January to March. The fruits mature from February to April. Leaves fall in January or February and grow in again in May.

Nicaragua to Brazil and Peru. In Panama, a typical component of tropical moist forest in the Canal Zone, Panamá, and Darién (Tosi, 1971); known also from tropical dry forest in Panamá (Taboga Island), from premontane moist forest in the Canal Zone and Panamá, and from tropical wet forest in Colón.

See Figs. 372 and 373.

QUARARIBEA Aubl.

Quararibea asterolepis Pitt., Feddes Repert. 13:316. 1914

Molenillo, Garrocho, Panula, Cinco dedos, Guayabillo

Tree, to 30 m tall; trunk to 75 cm dbh, buttressed to 2 m; outer bark very thin, peeling, the sap with characteristic spicy aroma; branches drooping. Leaves simple; stipules lanceolate, 5 mm long, caducous; petioles mostly 1–2 cm long, densely fimbriate-lepidote; blades ± elliptic, obtuse to acuminate, obtuse to rounded at base, 8–15(25) cm long, 2.5–8(10) cm wide, glabrous but with dense layer of stellate scales below, sparser above, entire; venation pinnate. Flowers solitary, opposite leaves, mostly on young branchlets but sometimes nearly cauliflorous, ca 3 cm long; pedicels 1–1.5 cm long, bracteolate; calyx ± conical, to 1.5 cm long and 7 mm wide in flower, the lobes 4, ca 3 mm long, wingless; both calyx and pedicel green, densely fimbriate-lepidote; petals 5, oblong, to 2.5 cm long and 5 mm wide, whitish, with short stellate trichomes; stamens joined into a column for most of their length, the column ca 2 mm long, enlarged at apex, lobed, the lobes 5, ca 2 cm long at apex, not obviously separate; anthers 8 per column lobe, sessile, extrorse, longitudinally dehiscent; style surpassing staminal column by about 1 mm, flaring out slightly at summit, appearing several-lobed due to extension of ribs found on style but actually bilobed. Nuts ca 2 cm diam, ± ovate, buff-colored, subtended by and at least one-third enclosed by enlarged calyx, densely short-lepidote, with prominent mammillate apex 5 mm long; seeds more than 1 cm long, 1 (rarely 2) fertile. *Croat 5934, 6719.*

Common to locally abundant. Flowers in June and July. The fruits mature from August to November. Leaves fall around February.

The aroma of *Quararibea* trees can be detected from some distance. Even herbarium specimens retain the aroma for years.

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

See Figs. 374 and 375.

Quararibea pterocalyx Hemsl., Diag. Pl. Mex. 4. 1878

Wild palm

Tree, usually less than 10 m tall; twigs with a strong spicy odor. Leaves simple; stipules lanceolate, to 5 mm long,

Fig. 374. *Quararibea asterolepis*

Fig. 375. *Quararibea asterolepis*

Fig. 376. *Quararibea pterocalyx*

caducous; petioles densely tomentulose, less so in age, 1.5–2.5 cm long; blades broadly elliptic, rounded to acuminate at apex, rounded at base, 13–30 cm long, 7–13 cm wide, glabrous above or tomentulose on veins, densely tomentulose below with whitish stellate trichomes, entire, venation pinnate. Flowers solitary, mostly opposite leaves on young branchlets, 12 cm long; pedicels 1–1.5 cm long, bracteolate; calyx tubular, to 4 cm long and ca 1 cm wide when in flower, the lobes 3, to 4 mm long; both calyx and pedicel generally yellowish, short-tomentulose, with 10 longitudinal wings at least 1 mm high; petals 5, linear, at least 10 cm long when fully expanded and 1–1.5 cm wide, white, with trichomes in scattered groups; staminal column 8–13 cm long, enlarged at its apex, with numerous anthers; anthers subsessile, extrorse, longitudinally dehiscent; style about as long as staminal column, slightly enlarged at apex. Nuts subglobose, ca 4 cm diam, greenish, subtended by and at least two-thirds enclosed by enlarged calyx, tomentulose, with a prominent mammillate apex, generally 2-celled; seeds 1 per cell, more than 2 cm long. *Croat 6828, Foster 1031.*

Occasional along the shore and in the forest on Pearson Peninsula. Flowers from May through July. The fruits mature in September and October. Leaves may be replaced twice per year (R. Foster, pers. comm.).

Fruits are dispersed chiefly by mammals. They are buoyant and may be dispersed by water as well.

Known only from Panama, from tropical moist forest in the Canal Zone, Bocas del Toro, Panamá, and Darién, from premontane moist forest in Panamá, and from premontane wet forest in Darién.

See Fig. 376.

87. STERCULIACEAE

Trees or shrubs (somewhat herbaceous in *Melochia*, scandent with armed stems in *Byttneria*), usually stellate-pubescent. Leaves alternate, petiolate; blades simple and entire or 3–5-lobed (palmately compound in *Herrania*); venation basally palmate; stipules present. Flowers bisexual (or unisexual and functionally monoecious in *Sterculia*), essentially actinomorphic, in axillary umbels and cymes; calyx mostly 5-lobed (trilobate or sepals 3 in *Guazuma, Herrania*); petals 5, free, showy, sometimes appendaged (lacking in *Sterculia*); stamens 5 or 15, united basally; anthers 2-celled, dehiscing longitudinally; ovary superior, 4- or 5-locular and 4- or 5-carpellate; placentation axile; ovules 2 to several per locule, anatropous; styles 5, or style 1 and simple or 2–5-lobed. Fruits leathery or woody berries, or the carpels separating as dehiscent dry cocci; seeds with copious endosperm.

The herbaceous species are often confused with the Malvaceae (85) because the flowers are similar and the leaves are palmately veined at the base and usually toothed. The Sterculiaceae may be distinguished by the monadelphous stamens of two cells, differing from those of the Malvaceae, which have a single cell. In addition, several genera have conspicuously appendaged petals.

Most species are probably insect pollinated, but *Sterculia apetala* and *Herrania purpurea*, with easily accessible purplish flowers, are possibly fly pollinated. G. Frankie (pers. comm.) says flies are common visitors to *Sterculia apetala* flowers in Guanacaste, Costa Rica, and he has seen staphylinid beetles in flowers of *Herrania purpurea* in La Selva, Costa Rica.

Many species have seeds that are clearly eaten by animals, including *Theobroma cacao, Herrania purpurea, Guazuma ulmifolia,* and *Sterculia apetala.* White-faced monkeys eat *S. apetala,* sometimes swallowing the seed but usually eating off the two outer layers of tissue surrounding the seed (Oppenheimer, 1968). Van der Pijl (1968) reported that rodents disperse the seeds of *Theobroma cacao* by eating only the fleshy sarcotesta pulp around the seed, leaving the seed unharmed. Bats also disperse *Guazuma* fruits (Bonaccorso, 1975).

About 70 genera and 1,000 species; mostly tropical.

KEY TO THE SPECIES OF STERCULIACEAE

Plants coarsely armed, vinelike ..... *Byttneria aculeata* Jacq.
Plants unarmed:
  Leaves digitately compound, the leaflets 5, borne on long petiolules ..... *Herrania purpurea* (Pitt.) R. E. Schult.
  Leaves not digitately compound:
    Leaves deeply 3–5-lobed; flowers large, ca 2 cm wide ..... *Sterculia apetala* (Jacq.) Karst.
    Leaves unlobed:
      Blades more than 15 cm long, the petioles pulvinate at both ends ..... *Theobroma cacao* L.
      Blades less than 15 cm long, the petioles not pulvinate:
        Stems hollow:
          Calyx more than 3 mm long, becoming 8 mm long, hiding the fruit from the side; bracts ca 2 mm long ..... *Melochia lupulina* Sw.
          Calyx less than 3 mm long, inconspicuous behind bracts 4–5 mm long ..... *Melochia melissifolia* Benth.
        Stems not hollow:
          Blades becoming oblique at base; inflorescences loose, essentially all flowers visible ..... *Guazuma ulmifolia* Lam.
          Blades not oblique at base; inflorescences compact, some of the flowers partly hidden ..... *Waltheria glomerata* Presl

BYTTNERIA Loefl.

Byttneria aculeata Jacq., Select. Stirp. Am. 76. 1763
Espino hueco, Zarza, Rabo de iguana, Rangay

Woody vine or scandent shrub; older trunk often breaking into 5 distinct, terete stems; stems 5-angulate and hollow; stems, petioles, and often midribs below with small, sharp, recurved prickles, the stems and petioles sometimes short-pilose on one side. Stipules triangular, 1–2 mm long, caducous; petioles 0.5–2 cm long (to 5 cm on juveniles); blades variable, usually lanceolate to elliptic, acuminate, obtuse to rounded, truncate, or subcordate, usually 4–11 cm long and 1.5–4.5 cm wide (juveniles to 19 cm long), entire to remotely serrate, glabrous or sparsely short-pilose above, often blotched with silver; palmate veins at base 3–5. Umbels axillary; peduncles and pedicels sparsely pubescent, slender; peduncles mostly 5–10 mm long; pedicels variable on a single inflorescence, 1–10 mm long; flowers few, 5-parted, white, yellow or greenish; calyx 5-lobed to near base, to 4 mm long, glabrous; petals linear-spatulate, ca 4 mm long but only 1 mm wide, yellowish; stamens 5, the staminal tube minute; anthers opposite petals; staminodia 5, alternate with petals; pistil minute; style very short; stigma inconspicuously 5-lobed (breaking into 5 cocci). Capsules globular, 1.5–2.5 cm diam (including spines), 5-lobed; seeds 5, reniform, ca 4 mm long, 2 mm wide, falling to display the 5-lobed receptacle. *Croat 6767, Wetmore & Abbe 8.*

Occasional, in the forest. Seedlings, which are recognized by having leaf blades with a light medial discoloration, are often locally abundant in clearings. Flowers mostly in October and November. The fruits mature from December to February.

Mexico to Bolivia; introduced into Polynesia. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Veraguas, Panamá, and Darién, from tropical dry forest in Coclé and Panamá, and from premontane moist forest in the Canal Zone.

See Fig. 377.

GUAZUMA P. Mill.

Guazuma ulmifolia Lam., Encycl. Méth. Bot. 3:52. 1789
Cabeza de negrito, Guácimo, Guácimo de ternero, Bastard cedar, West Indian elm

Tree, generally 6–25 m tall; trunk to 60 cm dbh; stems, petioles, lower leaf surfaces, and axes of inflorescences densely stellate-tomentose. Stipules minute, caducous; petioles 5–20 mm long; blades lanceolate, acuminate, rounded to cordate and oblique at base, 6–16 cm long, 2–6 cm wide, glabrate or more often stellate-puberulent on both surfaces, the margins irregularly and finely toothed; palmate veins at base 3–7. Flowers in short, loose, axillary, thyrsiform clusters; pedicels 3–6 mm long; sepals 3, yellow, unequal, stellate-puberulent outside, recurved at anthesis; petals 5, obovate, ca 2.5 mm high, yellowish-green, hooded and bifid at apex, fused to free part of filament, the claw red with several red lines extending up petals, the appendage of the petal deeply bifid, ca 4 mm long; stamens 15, in 5 groups of 3 each, opposite petals, the staminal tube minute, red; pistil minute; staminodia 5, triangular, alternate with petals. Fruits globose to oval, 2–4 cm long, indehiscent or opening partway along 4 or 5, ± regular, longitudinal fissures, covered with many stout brown tubercles, the tubercles separating at maturity to expose the irregularly porate white surface; seeds numerous, irregularly ovoid, 2.5–3.5 mm long, borne among the fibrous inner parts, apparently falling through the holes in the exocarp, the testa maculate, covered by a membrane, the membrane very thin, mucilaginous and very sticky when wet. *Croat 6780, 8484.*

Uncommon, in the forest and at the edge of the Laboratory Clearing. Flowers mostly from March to May and from September to November. The fruits have been seen from March to May and in September.

Though fruits are never completely dehiscent, some seeds may fall through the fissures in the fruit that often form even while the fruits are still on the tree. The fruit has a sweet pericarp and is dispersed principally by bats (R. Foster, pers. comm.).

Mexico to Paraguay; West Indies; introduced into Asia and western tropical Africa. In Panama, widespread and ecologically variable, common in secondary areas and typical of tropical moist forest in Panama (Tosi, 1971); known from tropical moist forest throughout the country and also from premontane dry forest in Los Santos and Coclé, from tropical dry forest in Coclé and Panamá, from premontane moist forest in the Canal Zone and Panamá, and from premontane wet forest in Coclé and Panamá.

HERRANIA Goudot

Herrania purpurea (Pitt.) R. E. Schult., Caldasia 2:333. 1944
Theobroma purpurea Pitt.
Cacao cimarrón, Chocolatillo, Wild cacao

Shrub or small tree, to 5.5 (10) m tall; young stems and petioles densely stellate-pubescent. Leaves digitately compound, deciduous, to 80 cm long; stipules linear, to 5 cm long, caducous; petioles stout, to 40 cm long; petiolules densely pubescent, 3–5 mm long; leaflets 5, narrowly obovate, acuminate, cuneate at base, stellate-pubescent on veins above and below and sparsely on surface below, entire or obscurely crenate, the terminal leaflet to 53 cm long and 19 cm wide, the lateral leaflets somewhat smaller; lateral veins in 10–15 pairs, usually ending in minute teeth on margins. Flowers borne on trunk, globular in bud, all parts violet-purple to maroon, to 1.5 cm wide; calyx deeply trilobate, densely stellate-pubescent, the lobes broadly ovate, longer than petals or staminodia; petals 5, thick and deeply cucullate, papillate, the apex recurved, bearing a slender appendage ca 1 cm long, the inner surface with stout ridges; stamens (10)15, in 5 groups of (2)3 each, the staminal tube short, subtended by a densely pubescent disk; filaments short and stout, (2)3 held within the cucullate petal; style ca 1.5 mm long, tubular, the upper edge sharply 5-lobed, glabrous; ovary

10-ribbed, densely stellate-pubescent with stinging trichomes; staminodia papillate, obovate, recurved over and obscuring petals (except for the erect appendage). Fruits orange at maturity, to 7.5 cm long and 4 cm wide, the ribs and pubescence of ovary persisting; seeds many, to about 1.5 cm long, each surrounded by a pulpy, white, sweet mesocarp. *Croat 6791, 9281.*

Occasional in both the young and old forests, locally common. Flowers mostly from December to February. The fruits mature mostly in the early rainy season (April to May), but have been seen in August and September.

The flower structure is strange. While the style is sunken between the staminodia, it is quite accessible. The anthers are concealed so well, however, that it would be interesting to see what organism effects pollination.

Costa Rica and Panama. In Panama, a characteristic tree species of tropical moist forest (Holdridge & Budowski, 1956); known from tropical moist forest in the Canal Zone, Bocas del Toro, San Blas, and Darién, from premontane wet forest in Chiriquí, and from tropical wet forest in Colón and Darién.

See Fig. 378.

MELOCHIA L.

Melochia lupulina Sw., Prodr. Veg. Ind. Occ. 97. 1788

Shrub, herbaceous when young, mostly erect, to 2 m high; stems hollow; stems and petioles villous. Leaves simple; stipules lanceolate-linear, to 4 mm long, caducous; petioles slender, 1.5–5 cm long; blades ovate, acuminate, rounded to cordate at base, 3.5–8.5(10) cm long, 2.5–6.5(7) cm wide, softly velutinous especially below, crenate-serrate; palmate veins at base 5–7. Cymes small, dense, axillary; peduncles, pedicels, bracts, and calyces stellate-puberulent; peduncles short, ca 3 mm long; pedicels slender, 2–4 mm long; bracts linear, ca 2 mm long; calyx campanulate, ca 4 mm long, enlarging to ca 8 mm, 5-lobed to near middle, glabrous inside; petals 5, clawed, ca 4.5 cm long, white; stamens 5, opposite petals; staminal tube and style heteromorphous; styles 5, free, 1.7–2.8 mm long; staminodium 1.6–2.5 mm long. Fruits capsules, mostly hidden by enlarged calyx, ca 2 mm long and to 3 mm diam, pale, opening by 5 slits to expose seed; seed 1, ca 1 mm diam. *Croat 7471.*

Uncommon along the shore on exposed banks, occasional in Rear #8 Lighthouse Clearing. Flowers mainly from December to April. The fruits mature mostly from January to April.

Scattered from Mexico to Peru; Jamaica. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Chiriquí, Coclé, Panamá, and Darién, from premontane moist forest in the Canal Zone, and from premontane wet forest in Chiriquí (Boquete) and Coclé.

Melochia melissifolia Benth., J. Bot. (Hooker) 4:129. 1842

Herb or suffrutex, to 1 m tall; stems hollow, with both fine stellate trichomes and simple, red, gland-tipped trichomes. Leaves simple, hispidulous; stipules linear; blades ± lanceolate-ovate, acute, ± rounded at base, to 3(4.5) cm long and 2(2.5) cm wide, serrate-crenate. Glomerules axillary, subsessile; bracts subtending flowers prominent, linear, to 5 mm long; calyx persistent, ca 2 mm long, with 5 acute lobes; petals 5, pinkish; ± obovate, ca 2(3.4) mm long, slender at base; stamens 5, united into tube at base, equaling styles; styles 5, free to the base; ovary sericeous. Capsules subglobose, to 3 mm diam, ca 2 mm high, hispidulous, splitting into 4 or 5 cocci, each coccus eventually splitting into 2 valves; seeds 1 or 2 per coccus, shaped like orange wedges, ca 1.5 mm long, black, the surface weakly ribbed. *Croat 7458.*

Locally abundant in the Rear #8 Lighthouse Clearing along the path. Flowers and fruits during the dry season, especially in December and January.

Fruit dispersal method is uncertain. Seeds are perhaps thrown to some extent when capsules open. They are neither viscid nor armed.

Costa Rica to the Guianas; Cuba; tropical Africa. In Panama, known from tropical moist forest in the Canal Zone, Colón, and Panamá, from tropical dry forest in Coclé, and from premontane moist forest in Panamá.

STERCULIA L.

Sterculia apetala (Jacq.) Karst., Fl. Columb. 2:35, pl. 118. 1861

Panama, Panama wood

Functionally monoecious tree, to 40 m tall, to 1 m dbh; outer bark hard, thin, light brown, sandpapery, the lenticels many, closely spaced, raised; inner bark thick, tan, granular; sap with strong, pungent odor. Leaves deciduous; stipules ovate, 5–8 mm long, axillary, caducous; petioles to 25 cm long, densely to sparsely stellate-pubescent; blades deeply and palmately 3–5-lobed, rounded to acute at apex of lobes, cordate at base, to 35 cm long and 45 cm wide, glabrous above except on veins especially near base, softly stellate-arachnoid below to glabrate in age; basal veins usually 5–7, each lobe with 3–7 pinnate veins. Panicles or racemes axillary or subterminal; flowers bisexual or functionally staminate, predominately staminate, with a strong spicy odor; calyx bowl-shaped, greenish, ca 2 cm broad and 1 cm deep, flexible, coriaceous, densely covered outside with short, violet-purple, stellate trichomes, striate and glabrate inside, the lobes acute, recurved; petals lacking; gynophore of staminate flowers hook-shaped, shorter than rim, sparsely glandular-puberulent, also hispidulous at apex; stamens 15, sessile on a raised disk at apex of gynophore; anthers extrorse, dehiscing in bud; pollen ± tacky; pistil rudimentary, sunken deeply at base of staminal disk, produced above into a slender style, gynophore of pistillate flowers similar and shorter, the staminal disk reduced, the nonfunctional stamens much shorter than the pistil; pistil stellate-tomentulose, 5-carpellate, 5-sulcate, the carpels separating at maturity; style solitary, stout, bent to one side; stigma capitate. Follicles obovoid, to 8 cm long and 5 cm wide, short-tomentose outside, with dense,

Fig. 377. *Byttneria aculeata*

Fig. 378.
Herrania purpurea

Fig. 379. *Sterculia apetala*

erect, orangish, stinging trichomes inside, opening very widely along the ventral suture, the periderm woody, 5–7 mm thick; seeds 2–4, oblong-ellipsoid, ca 2 cm long, 1.2 cm diam, covered with trichomes similar to inside of pod, then with a thin, tough, chestnut-brown layer, and then with a thin white layer. *Croat 13244.*

Frequent in the forest. The plant loses its leaves at the beginning of the dry season. After a short span of leaflessness, new leaves are produced. Flowering occurs usually every 2 years and the flowers appear shortly before or shortly after the onset of new leaves, usually in February. The fruits mature about 1 year later, mostly from January to April. Elsewhere in Panama the species may flower twice a year, in November or December and again in March.

All fruits on an individual tree dehisce within about 1 month. Those observed by J. Derr (pers. comm.) in Guanacaste, Costa Rica, fell to the ground within 1 week. The seeds are heavily parasitized by cotton stainer bugs (*Dysdercus bimaculatus*), and any seeds falling beneath the tree are killed by these bugs. Pods that are removed some distance by monkeys, agoutis, or other animals usually have some uneaten seeds discarded because the frugivore becomes distracted by the irritating trichomes lining the pod (Janzen, 1972). In Guanacaste fruit pods are opened by parrots and orange-chinned parakeets and by magpie jays which take the seeds after the pods have opened (J. Derr, pers. comm.).

Mexico to Peru and Brazil; West Indies. In Panama, a typical component of tropical dry forest (Holdridge & Budowski, 1956) and of tropical moist forest (Tosi, 1971); known from tropical moist forest in the Canal Zone, San Blas, 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. Reported from tropical wet forest in Costa Rica (Holdridge et al., 1971).

See Fig. 379.

THEOBROMA L.

Theobroma cacao L., Sp. Pl. 782. 1753
Cacao

Tree, usually 4–8(12) m tall, usually branched from near base and often widely spreading; trunk and larger branches with the persistent bases of the inflorescences; young branchlets and petioles pubescent. Leaves alternate; stipules subulate, deciduous; petioles variable in length, with 2 pulvini; blades ± oblong, acuminate, rounded or obtuse at base, 15–50 cm long, 4–15 cm wide, sparsely stellate-tomentose above and below when young or on veins above, the lower surface a lighter green than the upper; palmate veins at base 3–5. Cymes minute, borne on small tubercles on branches below leaves and on trunk; peduncles and pedicels pubescent; flowers 5-parted, appearing fasciculate; sepals ± lanceolate, 5–8 mm long in flower, acuminate, variously colored; petals white, 3–4 mm long, hooded, the hood enclosing apex of stamens, with 3 maroon veins inside, the lateral veins stronger, the blade of the petal ± obovate, usually obliquely mucronate, the claw S-shaped; fertile filaments 5, alternating with staminodia, reflexed, to 2 mm long; anthers 2 per filament (thus the thecae 4); styles appearing single (actually 5 coherent), surpassing fertile filaments but not staminodia; staminodia 5, erect, narrow and acute, ca 0.5 mm long, ± maroon. Fruits usually oblong-ellipsoid, 10–25 cm long, yellow to brown at maturity; exocarp thick, fleshy, 10-ribbed, densely stellate-pubescent; seeds 20–40 in a sweet pulp, roundish in cross section, 2–4 cm long and 1.2–2 cm wide, brown. *Croat 8131, 12311.*

Infrequent, in the forest. Some flowers have been seen in February and September. Time of fruit maturity is not known.

Native to the New World tropics; cultivated in the Old World tropics. In Panama, known from tropical moist forest in the Canal Zone, Bocas del Toro, Herrera, Panamá, and Darién and from premontane moist forest in Panamá.

WALTHERIA L.

Waltheria glomerata Presl, Rel. Haenk. 2:152. 1835

Slender shrub, 1.5–2 m high; most parts stellate-pubescent. Leaves alternate; stipules lanceolate, ca 9 mm long; petioles 5–10 mm long; blades ± elliptic, acute at apex, obtuse to subcordate at base, 4–13 cm long, 1.5–8 cm wide, irregularly serrate; reticulate veins obvious. Glomerules dense, axillary, globose; peduncles short; flowers 5-parted, sessile, subtended by several linear-obovate bracts to 6 mm long; calyx tubular, to 6 mm long, the lobes triangular-oval, ca 2 mm long, tomentulose; petals narrowly spatulate, 6 mm long, creamy white to somewhat yellowish; stamens 5, united into a tube for only 1 mm; filaments free for ca 4 mm; anthers at about the same height as calyx and corolla; style ca 3 mm long, simple. Fruits capsules, 2-carpellate, ovate, apiculate, 1-celled, 1 mm long and 0.5 mm wide, densely plumose-papillate (the trichomes to 1 mm long); seeds 2, ca 0.5 mm long, attached to septa at base of ovary. *Croat 13477.*

Rare, known only from the shore on the north edge of Orchid Island, but to be expected in clearings and other disturbed areas. Flowers mostly from December to February. Mature fruits have been seen in March.

Mexico to Panama. In Panama, widespread and ecologically variable; known from tropical moist forest in the Canal Zone (both slopes), Veraguas, Los Santos, Herrera, Panamá, and Darién, from tropical dry forest in Coclé, Herrera, and Panamá, 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 Panamá.

88. DILLENIACEAE

Lianas or rarely scandent shrubs (*Tetracera*) or trees (*Saurauia*); bark usually thin, flaking. Leaves alternate, petiolate; blades simple, entire or serrate, the pubescence stellate (*Saurauia*), simple (*Doliocarpus* and *Davilla*),

KEY TO THE TAXA OF DILLENIACEAE

Plants trees, rare; petals connate at base, falling as a unit with stamens; fruits baccate; seeds many, small, reticulate, lacking an aril ..... *Saurauia laevigata* Tr. & Planch.
Plants lianas; petals free, caducous; fruits dehiscent (fruitlike structure in *Davilla*); seeds few, moderately large, smooth, arillate:
  Leaves markedly asperous, pustular and stellate-pubescent above; flowers unisexual; fruits pyriform follicles, gradually tapered to a beaked apex, the pericarp indurate, not at all fleshy; aril thin, lacerate, split on one side, red (usually drying pale yellow) ..... *Tetracera*
  Leaves smooth to scabridulous, not markedly pustular and stellate-pubescent above; flowers bisexual; fruits berrylike, the apex rounded (often with a slender persistent style), the pericarp fleshy at maturity or fruits indehiscent and enclosed in 2 cuplike sepals; aril fleshy, entire, white and almost or entirely enveloping seed:
    Sepals unequal, 2 enlarging, becoming orange and fitting together like petri dishes to enclose ovule and persisting stamens (and ultimately the fruit); entire fruitlike structure usually less than 6 mm diam ..... *Davilla nitida* (Vahl) Kub.
    Sepals nearly equal, not becoming orange, not enclosing ovule and stamens; fruits more than 6 mm diam ..... *Doliocarpus*

or with both simple and stellate trichomes arising from circular pustules; venation pinnate, the secondary veins nearly parallel; stipules lacking. Panicles or glomerules terminal, axillary, or cauliflorous; flowers bisexual or unisexual (androdioecious in *Tetracera,* i.e., flowers either bisexual or staminate), many, actinomorphic, fragrant; sepals imbricate, usually 5 (2-6 in *Doliocarpus,* usually 4 in *Saurauia*); petals (1)2–5(6), free or connate, imbricate, white, caducous (except in *Saurauia*); stamens numerous, exserted; anthers 2-celled, with parallel or basally divergent thecae, dehiscing lengthwise or by apical pores, the connective expanded; pistils 1–5; ovaries superior, 1-locular, 1-carpellate; placentation parietal or ventral; ovules usually 2 (2–12 in *Tetracera,* indefinite in *Saurauia*); styles as many as pistils. Fruits follicular or baccate (or indehiscent); seeds 1–4 per carpel, arillate (except *Saurauia*), with copious fleshy endosperm.

The flowers are of the brush type with stamens and styles exserted. They are probably pollinated by pollen-feeding insects.

The fruits are best suited for bird dispersal. *Tetracera* and *Doliocarpus* usually have shiny black seeds enveloped in part by a red or white aril. *Doliocarpus* fruits are also eaten by white-faced, howler, and spider monkeys (Hladik & Hladik, 1969). Oppenheimer (1968) reported that the fruits of *D. major* may make up a major portion of the diet of white-faced monkeys during the early part of October. The fruits are eaten whole and may pass through the digestive tract intact. It is very likely that the fruits of *D. olivaceus,* which also matures when fruits are scarce, are taken by monkeys as well. It is interesting to note that both of these species of *Doliocarpus* have larger fruits, no doubt more attractive to larger animals, than do *D. dentatus* or *D. multiflorus,* which fruit principally in the dry season or early rainy season when food is not scarce.

Eleven genera and over 300 species; mostly in the subtropics and tropics.

Most BCI species can be distinguished by being lianas bearing flowers with numerous stamens and fruits with arillate seeds. Many have leaves that are conspicuously asperous.

DAVILLA Vand.

Davilla nitida (Vahl) Kub., Mitt. Bot. Staatssamml. München 7:95. 1971
D. multiflora (DC.) St.-Hil.

Liana; outer bark loose, thin, brown, often peeling. Petioles short, narrowly-winged; blades elliptic to obovate, acute to short-acuminate or rounded at apex with a short downturned apiculum, obtuse to attenuate and decurrent at base, 6–10 cm long, 2.5–6 cm wide, glabrate to minutely scabrid with longer trichomes on midrib above, the surface punctate with persistent bases of scabrid trichomes, glabrous or scabridulous below except sparsely hirsute on veins, the midrib often arched. Panicles terminal or upper-axillary; rachis often extended well beyond floriferous part; flowers many, pedicellate, fragrant; sepals 5, unequal (2 enlarged), ± maroon in bud, orange after anthesis, soon closing (perhaps only after pollination) to enclose persistent stamens and developing ovary; petals usually 5, obovate, ca 5 mm long, spreading to reflexed at anthesis, caducous; stamens numerous, ca 5 mm long, bright yellow, dehiscing in bud; carpel 1, globose; style bent in bud; stigma discoid, minutely papillate, held slightly above anthers soon after anthesis. Fruits small, rounded, black, minutely white-arillate, held within 2 orange dishlike sepals until maturity when the sepals open, indehiscent and dispersed by birds; seed 1. *Croat 14610.*

Abundant on trees on the shore, and frequent in the canopy of the forest within the island. Flowers in the early dry season, mostly from January to March; the flowers last for a very short time. The fruits may appear mature from February to August. Infected fruits may persist most of the year.

Standley mistakenly made BCI reports for both *Davilla rugosa* Poir., which is a distinct species from South America, and *D. kunthii* St.-Hil., which is a synonym of *D. aspera* (Aubl.) Benoist.

Pollen appears to be removed rather quickly from the anthers. Since it is somewhat tacky it is unlikely that

considerable amounts blow away. The flowers are ideally suited to pollen feeders and are possibly pollinated by them. The species has been seen visited by the bee *Trigona cupira.*

The fruits fall or are taken by birds mostly in the early rainy season, beginning usually in May. The fruit crop is often very highly infested by Curculionidae beetles, which eat the seeds and then escape as soon as the sepals open.

Southern Mexico to northern Brazil; the Antilles. In Panama, known principally from tropical moist forest in the Canal Zone, Colón, Veraguas, Coclé, and Panamá, but known also from premontane wet forest in Chiriquí.

DOLIOCARPUS Rol.

Doliocarpus dentatus (Aubl.) Standl., J. Wash. Acad. Sci. 15:286. 1925

Liana; younger parts appressed-pubescent with long slender trichomes especially on stems, petioles, and major veins of leaves, glabrate in age. Petioles 5–15 mm long, narrowly winged; blades ± elliptic to obovate or oblanceolate, acuminate, acute to obtuse at base, 7–20 cm long, 3–7 cm wide. Glomerules dense, at usually leafless axils; pedicels 5–10 mm long in flower, to 25 mm long in fruit; flowers 5–8 mm broad; sepals 3–5, obovate, to 5 mm long, slightly pubescent outside, glabrous to slightly pubescent inside; petals 5, white, 4–5 mm long; stamens numerous, sometimes persisting; ovary 1, glabrous; style to 1.5 mm long; stigma peltate, often persisting. Fruits globose, 6–9 mm diam, glabrous, red, dehiscing regularly along median suture, the valves remaining intact; seeds 2, ca 5 mm long, enveloped except at apex by the fleshy white aril. *Croat 5144, 9516.*

Frequent in the forest and at the edge of the lake; sometimes locally common at the top of the canopy. Flowers throughout the dry season, from December to April, but particularly in February. The fruits mature in central Panama from March to May (possibly later), chiefly in April. At least some individuals may flower more than once per season, with individuals flowering in March or April already bearing fruits from an earlier flowering.

The fruits were reported to be indehiscent by Hunter in the *Flora of Panama* (1965). They are smaller and more numerous than for any other species of *Doliocarpus.*

Mexico to Paraguay; Cuba, Trinidad, Tobago. In Panama, known from tropical moist forest in the Canal Zone, 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 Coclé.

Doliocarpus major J. F. Gmel. in L., Syst. Nat. ed. 13, 2:805. 1791

Liana; bark thin and flaking; older stems often prominently angulate and winged, the younger stems ± flexuous, usually angulate. Leaves coriaceous; blades elliptic to oblong-elliptic, abruptly acuminate and often downturned at apex, obtuse and decurrent at base onto markedly canaliculate petiole, 5–18 cm long, 2–8 cm wide, ± glabrous but with the midrib often pubescent, prominently punctate on drying, entire to sparsely serrate, the midrib often arched; juvenile leaves gradually acuminate, prominently serrate, to 32 cm long and 13 cm wide. Flowers 2–3 cm broad, in axillary glomerules or less frequently in 2-flowered cincinni; pedicels 5–12 mm long (10–20 mm long in fruit); sepals 4 or 5, pubescent, to 7 mm long, inconspicuously sericeous inside, persisting in fruit; petals 2 or 3, white or reddish in age, 1–1.5 cm long; stamens numerous, exserted; ovary 1, pubescent; style 6–8 mm long. Fruits red, subglobose, 10–13 mm diam, densely puberulent, dehiscing regularly along median suture, the style 1, often subapical; seeds 2, ca 8 mm long, shiny, black, surrounded except at apex by a fleshy, white, sweet aril, the aril very astringent before maturity. *Croat 6833, 12954.*

Common along the shore and high in trees in the forest. Flowering mostly during June and July, rarely as late as September or as early as May. The fruits mature in the rainy season, mostly from July to November, perhaps chiefly in October, rarely as late as the early dry season. At least some individuals flower twice per season, and they may bear mature fruits when they flower the second time. Leaves usually fall before flowering occurs, dropping mostly at one time and growing in again soon.

This species was mistakenly reported by Standley as *D. brevipedicellatus* Garcke, a species which occurs in the Canal Zone but not on BCI and which is distinguished from *D. major* by having a glabrous ovary.

Nicaragua to Panama, and in South America from Venezuela to the Guianas, Amazonian Brazil, and Peru.

KEY TO THE SPECIES OF DOLIOCARPUS

Ovary and fruit pubescent; style 4–8 mm long, sometimes exceeding sepals; sepals sericeous inside:
- Leaves punctate; pedicels 5–12 mm long; fruits usually less than 1.5 cm diam, the 2 valves remaining intact and convex after dehiscence ..... *D. major* J. F. Gmel.
- Leaves not punctate; pedicels 2–4 mm long; fruits usually more than 1.5 cm diam, the valves splitting and spreading widely after dehiscence ..... *D. olivaceus* Standl.

Ovary and fruit glabrous to slightly pubescent; style 1–2 mm long, not exceeding sepals; sepals glabrous to slightly pubescent inside:
- Inflorescences glomerulate (flowers all arising from a single area) ..... *D. dentatus* (Aubl.) Standl.
- Inflorescences in fascicles of few-flowered cincinni (at least some flowers arising from a branched axis) ..... *D. multiflorus* Standl.

Fig. 380.
Doliocarpus major

Fig. 381. *Doliocarpus olivaceus*

Fig. 382.
Doliocarpus olivaceus