

THE VASCULAR FLORA OF LA SELVA BIOLOGICAL STATION,
COSTA RICA*
GUTTIFERAE

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Trees, shrubs, lianas or elsewhere herbs, often epiphytic, usually with white or yellow latex or the sap resinous and clear to bright orange. *Leaves* opposite, entire and simple, the lateral venation pinnate and usually parallel, less often reticulate near the margin, petiolate and lacking stipules but in some with axillary ligule-like petiolar structures. *Inflorescences* of terminal or axillary, cymose panicles, racemes, fascicles or solitary flowers, bracteate. *Flowers* actinomorphic, often 4- or 5-merous, the perianth usually differentiated into sepals and petals, flowers often unisexual and the plants strictly dioecious or androdioecious, less often bisexual and the plants

hermaphroditic; *staminate flowers* rarely with a rudimentary ovary; *pistillate flowers* always with an androecium either of stamens or reduced staminodia; stamens few to many, the anthers introrse and dehiscent longitudinally; ovary superior, 1-many locular, 1-many ovules per cell, placentation axile or rarely basal, stigmas 1-20 and often sessile or elevated on styles. *Fruits* either capsules, drupes or berries; seeds often arillate, rarely comose.

The Guttiferae can be recognized vegetatively by their simple, entire, estipulate, opposite, often coriaceous leaves, and often milky or resinous and colored sap with a slightly sweet fragrance. Although the family is very diverse at La Selva few of its members are very conspicuous or abundant; only *Symphonia globulifera*, species of *Tomomitopsis*, and some species of *Clusia* are common in primary forest. Species of *Vismia* are sometimes abundant in open, secondary habitats. All five subfamilies of this primarily pantropical family are represented at La Selva. Approximately 100 species in about 14 genera, *Clusia* being the largest, are native to Central America.

KEY TO THE GENERA BASED ON FLOWERS AND FRUIT

1. Flowers in racemes more than 10 cm long; stamens with linear appendages about 1/2 the length of the anther; ovary with a single style and stigma; fruit a slender dry capsule, the valves often twisting; seeds comose at each end; lower leaf surface with very prominent secondary veins, conspicuously loop-connected near the margin and with numerous perpendicular cross veins. 5. *MARILA*.
1. Flowers in panicles, fascicles or, if racemes, then less than 5 cm long; stamens without appendages; ovary with 3 or more stigmas (except 1 in *Calophyllum*); fruit a berry, drupe or fleshy capsule; seeds not comose; leaves lacking numerous perpendicular cross veins.
 2. Leaves stellate pubescent and pellucid punctate beneath, the trichomes rusty brown; petals woolly pubescent within. 10. *VISMIA*.
 2. Leaves glabrous or minutely puberulent with simple trichomes, usually not pellucid punctate (except *Clusiella*); petals glabrous within.
 3. Plants epiphytic, fruits with 10 or more seeds per locule.
 4. Fruits waxy-white spherical berries less than 1 cm in diameter; leaves acuminate, the narrow tip about 2 cm long; petioles 3 mm long or less. 3. *CLUSIELLA*.
 4. Fruits reddish or green, variously shaped fleshy capsules, usually more than 1 cm in diameter; leaf tips acute to rounded; petioles more than 1 cm long. 2. *CLUSIA*.
 3. Plants terrestrial; fruits with 1-2 seeds per locule.

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5. Flowers in panicles; fruit a fleshy capsule.
 6. Leaves broadly ovate, nearly as wide as long; petiole swollen at base into a thick triangular ligule appressed to the stem; inflorescence borne on leafless nodes beneath the leaves. 4. *DYSTOVOMITA*.
 6. Leaves elliptic to narrowly spatulate, 2–5 times longer than wide; petiole without ligule; inflorescence terminal.
 7. Outer pair of sepals valvate or fused in bud, much different from the petals in color and texture but similar in size, persistent, clasping the base of the fruit; fruit axis and inner fruit wall bright burgundy at maturity. 8. *TOVOMITA*.
 7. Outer pair of sepals imbricate, not fused in bud, petaloid in color and texture but smaller, deciduous in fruit; fruit axis and inner fruit wall white at maturity. 9. *TOVOMITOPSIS*.
5. Flowers in fascicles or racemes; fruit a drupe.
 8. Secondary veins very straight, less than 1 mm apart; sap resinous or whitish; canopy trees 25–35 m tall. 1. *CALOPHYLLUM*.
 8. Secondary veins curving and often reticulate near the margin, 3 mm or more apart; sap yellow; understory trees less than 15 m tall.
 9. Flowers inconspicuous, yellow green, 2–3 mm in diameter; midrib prominent above; secondary veins also slightly prominent above and beneath in fresh material. 6. *RHEEDIA*.
 9. Flowers showy, corolla globose in bud, the petals contorted, later depressed to form a red and white pinwheel about 2 cm in diameter; midrib plane above; secondary veins barely visible in fresh material. 7. *SYMPHONIA*.

KEY TO THE GENERA BASED ON VEGETATIVE CHARACTERS

1. Leaves stellate pubescent with brownish trichomes and pellucid punctate beneath; sap resinous, bright orange; bark peeling in large flakes or strips. 10. *VISMIA*.
1. Leaves glabrous or minutely puberulent, not pellucid punctate (except *Clusiella*); sap milky or clear and resinous; bark not peeling in large flakes.
 2. Secondary veins very prominent beneath, conspicuously loop-connected near the margin, and with numerous, closely parallel, perpendicular cross veins; sap clear. 5. *MARILA*.
 2. Secondary veins obscure or prominent, not at all or merely obscurely loop-connected and without closely parallel, perpendicular cross veins.
 3. Plants epiphytic.
 4. Leaves acute to rounded, never pellucid punctate; petioles more than 1 cm long. 2. *CLUSIA*.
 4. Leaves acuminate, the narrow tip about 2 cm long, obscurely pellucid punctate beneath; petioles 3 mm or less long. 3. *CLUSIELLA*.
 3. Plants terrestrial.
 5. Secondary leaf veins mostly less than 5 mm apart; petioles mostly less than 2 cm long.
 6. Leaves spatulate, the lamina gradually tapering to the base and thus lacking a petiole. 8. *TOVOMITA*.
 6. Leaves oblong to elliptic, petiolate.
 7. Secondary veins about 35 per cm, very straight to the margin; sap clear or becoming white; canopy trees 25–35 m tall. 1. *CALOPHYLLUM*.
 7. Secondary veins 2–6 per cm, curving and often reticulate near the margin; sap yellow; understory trees to 15 m tall.
 8. Midrib prominent above; secondary veins conspicuous, prominulous on both surfaces. 6. *RHEEDIA*.
 8. Midrib flush with the upper surface of the leaf; secondary veins barely visible in fresh material. 7. *SYMPHONIA*.
 5. Secondary veins more than 1 cm apart; petioles often more than 2 cm long.
 9. Petiole basally thickened into a triangular appressed ligule; leaves broadly elliptic to nearly orbicular, 15–18 cm wide; sap clear; trees 15–20 m tall. 4. *DYSTOVOMITA*.
 9. Petiole lacking a ligule; leaves elliptic to oblong, 3.5–10(12.5) cm wide; sap clear or milky; shrubs or small trees to 7 m tall. 9. *TOVOMITOPSIS*.

1. *CALOPHYLLUM* L.

STEVENS, P. F. 1980. A revision of the Old World species of *Calophyllum* (Guttiferae). *J. Arnold Arb.* 61: 117–424.

Dioecious or hermaphroditic trees or rarely shrubs, the bark often with characteristic dia-

mond-shaped fissures, the twigs usually flattened and angled; sap milky, yellow to cream colored. *Leaves* more or less coriaceous, the midrib prominent; lateral veins numerous and closely parallel, alternating with the sometimes equally conspicuous resin canals. *Inflorescences* axillary and sometimes terminal, mostly few-flowered ra-

comes or in some species branched and paniculate. *Flowers* globose in bud, the perianth only rarely differentiated into 2 series; tepals 4–16, mostly decussate but sometimes the inner ones imbricate, pale green to white; stamens numerous, the filaments slender, the anthers ovoid to oblong (in dioecious species, the staminate plants also bearing a reduced ovary); ovary 1-locular with the solitary ovule erect, the style slender, capped by an often peltate stigma. *Fruit* a 1-seeded drupe with a leathery exocarp and fleshy to fibrous mesocarp; seed with a stony layer, lacking an aril.

Calophyllum and *Mammea* L. are the only New World members of Engler's subfamily Calophylloideae. Both genera have more species in the Old World. *Calophyllum* is the largest genus in the subfamily containing approximately 190 species best represented in the Indo-Malesian region. About eight species, ranging from the West Indies and Mexico to Argentina, are endemic to the New World.

The genus *Calophyllum* is readily recognizable by its opposite leaves and straight, closely parallel lateral veins. The diamond-shaped fissures on the trunk are also distinctive. Whereas most Old World species are reportedly hermaphroditic, Central American collections of the genus *Calophyllum* appear to consist of two kinds of individuals, hermaphroditic and staminate.

1. *Calophyllum brasiliense* var. *reko* (Standl.) Standl.

Subcanopy trees, 20–25 m tall; trunk distinctly furrowed with reticulating lines; bark grayish tan externally and bark pinkish internally; sap creamy. *Leaf* blades elliptic, 8–10.5 cm long, 3–4.5 cm wide, apically acute to rounded, basally acute, marginally bordered by a thick vein, soon glabrate; midrib prominent on both surfaces; lateral veins very fine and parallel, usually about 20–35 per cm, arising at an angle of 75–85°; buds densely brownish scurfy; petioles 1–2.5 cm long, glabrous. *Inflorescences* of short axillary racemes, 1–3.5 cm long, mostly 3–7-flowered, the peduncle brownish scurfy. *Flowers* about 7 mm in diameter, the tepals greenish white; *staminate flowers* with a small ovary; *pistillate flowers* with numerous fertile stamens; stigma peltate. *Fruits* globose, apiculate, 1.5 cm in diameter (immature?), green. Flowering in the rainy season (August); fruits falling near the end of October. Mexico south into Costa Rica.

At La Selva restricted to slopes and ridges in the primary forest, well removed from the alluvial forest along the Río Puerto Viejo. *Calophyllum brasiliense* is known from very few, widely separated individuals. It can be distinguished from all other Guttiferae in the area by

the very fine, closely parallel, secondary venation of its leaves. In this respect it closely resembles *Qualea* in the Vochysiaceae, another opposite-leaved tree at La Selva. However, a pair of large glandlike stipules at the base of the petiole distinguish *Qualea*. The reticulate or diamond shaped fissures on the straight gray trunk of *Calophyllum* are distinctive.

2. *CLUSIA* L.

MAGUIRE, B. 1976. Apomixis in the genus *Clusia* (Clusiaceae).—A preliminary report. *Taxon* 25: 241–244.

———. 1977–1978. Notes on the Clusiaceae—chiefly of Panama. I–III. *Phytologia* 36: 391–407; 38: 203–214; 39: 65–77.

———. 1979. On the genus *Clusia* (Clusiaceae) in Mexico. *Taxon* 28: 13–18.

Dioecious or possibly polygamodioecious, often epiphytic trees or shrubs; sap milky white, yellow, or sometimes clear. *Leaves* usually stiff and leathery, the venation often obscure but the lateral veins quite parallel and regularly spaced, glabrous throughout. *Inflorescences* terminal cymose panicles of few to many flowers. *Flowers* variable in form and size, often 4-merous, small greenish and inconspicuous to large and then bright white to reddish and showy; sepals 4 or 5, decussate or imbricate, rotund, sometimes grading into subtending bracts; petals 4–9, decussate or imbricate, rotund, thin and membranaceous to thick and fleshy; *staminate flowers* with few to many stamens, the stamens free or sometimes more or less connate and then covered with resin at anthesis, sometimes elsewhere bearing staminodia, with or without sterile pistillate structures (but none present at La Selva); *pistillate flowers* with staminodia consisting in a whorl of toothlike structures, symmetrically placed stamens very similar to those of the staminate flowers, or a resinous ring around the base of the ovary. *Fruit* a fleshy or leathery, tardily dehiscent capsule capped with 4–20 stigmas, septicidally splitting—often to the base—revealing the bright orange (rarely yellow) mass of arillate seeds.

The genus *Clusia* is restricted to the neotropics and contains about 150 species with about 40 to 50 in Central America. Standley reported 11 species from Costa Rica. The nine species at La Selva, as well as most others examined from Central America, fall into three morphologically distinct groups. The flowers of one of these, the *C. minor* group, have more or less connate stamens and staminodia, which at anthesis produce a resin gathered by euglossine bees. Flowers of the other two groups have free stamens and staminodia, which do not produce resin.

KEY TO THE SPECIES

1. Petioles winged and clasping the stem, about 1 cm long; pistillate flowers lacking staminodia or the staminodia merely small teeth; filaments of staminate flowers longer than the anthers and free; fruits with 5–7 narrow outcurved styles. 7. *C. stenophylla*.
1. Petioles not winged; pistillate flowers with staminodia of apparently normal stamens or a resinous ring; filaments of staminate flowers shorter than the anthers and either free or connate; styles not as above.
 2. Stamens more or less connate into a low stigma-like mound, resinous at anthesis; staminodia forming a resinous ring around the base of the ovary; leaves mostly broadly acute, obtuse or rounded at the tip (sometimes narrow in *C. minor*).
 3. Petioles mostly 2–3 cm long; secondary veins scarcely visible in fresh material; flower buds 1.5–2 cm in diameter, pure white; stigmas 5, sessile; fruit red to pink. 9. *C. valerii*.
 3. Petioles mostly less than 2 cm long; secondary veins usually visible in fresh material; flower buds 2- or 3-colored (white, green and pink); stigmas 8 or more; fruit greenish.
 4. Flower buds 0.5–0.8 cm in diameter; petals 4; fruit with 10–13 sessile or slightly raised stigmas (styles less than 2 mm long). 4. *C. minor*.
 4. Flower buds 1.5–2 cm in diameter; petals 5–6; fruit with 8–10 stigmas, the styles about 5 mm long. 8. *C. uvitana*.
 2. Stamens free, the filaments short but distinct; stamens of the pistillate flowers apparently fertile, few in number and usually clustered in 4 groups around the base of the ovary; leaf apex mostly narrowly acute (but see lead 5 below).
 5. Leaves broadly obovate, apically rounded or even truncate; fruit globose-flattened, wider than long, 5–7 cm in diameter. 2. *C. flava*.
 5. Leaves elliptic, apically acute; fruit ovoid to cylindrical, longer than wide, less than 4 cm in diameter.
 6. Plants liana-like with long, often drooping main stems and short lateral branches; leaves with a submarginal vein about 3 mm from margin; fruit ovoid, about 2.5 cm in diameter with 4–5 sessile stigmas. 5. *C. oedematopidea*.
 6. Plants, shrubs or trees with erect trunks; submarginal vein lacking or running much nearer the margin; fruit cylindrical or, if ovoid, with about 20 stigmas.
 7. Leaves mostly 2–3 cm wide; fruit less than 1 cm in diameter; stigmas sessile. 1. *C. cylindrica*.
 7. Leaves mostly 4–5 cm wide; fruit 2.5–3.5 cm in diameter; stigmas raised on styles 2–3 mm long.
 8. Petioles 2–3 cm long; leaves succulent but not stiffly coriaceous; inflorescence many-flowered; fruit quadrate, about 2 times longer than wide, dark red, not subtended by bracts; stigmas 4. 3. *C. gracilis*.
 8. Petioles 1–1.5 cm long; leaves stiffly coriaceous; inflorescence mostly 1-flowered; fruit ovoid, mostly less than 1.5 times longer than wide, green, subtended by a series of decussate, successively smaller bracts; stigmas about 20. 6. *C. quadrangula*.

1. *Clusia cylindrica* Hammel

Epiphytic shrubs often reaching tree-size, the branches 4–8 m long; milky sap scant. *Leaf* blades mostly narrowly elliptic or rarely obovoid, 7.5–10(12) cm long, 3–4.5 cm wide, apically acute (very rarely obtuse or rounded), basally acuminate and often decurrent; midrib prominent above and beneath, the lateral veins very indistinct, 5–8 per cm, arising at an angle of (30)40–45(50)°, submarginal vein about 1 mm from margin; petiole 0.4–1 cm long. *Staminate inflorescence* a small but open, globose panicle 3–5 cm wide; flowers small, inconspicuous, about 0.5 cm in diameter, the petals thick and rubbery, about 4 mm long, pinkish to yellowish green, subtended by 3–5 pairs of decussate bracts, the upper 2 pairs being sepals with the inner sepals about twice as large as the others; stamens few, 12–20, distinct, often reddish, about 1.5 mm long with the filaments equal to or slightly longer than the anthers, elevated on a square receptacle. *Pistillate inflorescences* fewer-flowered than the sta-

minate, about 1–2 cm wide; flowers same as the staminate but the ovary surrounded by 4–8 apparently normal stamens similar to those of the male flowers; stigmas 4, round, about 1 mm in diameter, slightly elevated and offset from the apex of the fruit. *Fruits* narrowly ovoid, 1.5–2 cm long, 5–7 mm in diameter; sepals and bracts accrescent in fruit. Flowering mostly in the dry season, January to April (August), fruit maturing May to June (September). Nicaragua south into Panama from low to middle elevations.

Widespread and common as a canopy epiphyte in the primary forest but also found growing low on trees in pastures and along roads. Among La Selva species, *Clusia cylindrica* is recognized for its relatively small, narrowly elliptic leaves with very indistinct lateral veins. The small, cylindrical fruits with four valves are characteristic. The thick rubbery decussate petals and the stamens of the pistillate flowers clearly place this species in the *C. flava* group together with *C. gracilis*, *C. oedematopidea* and *C. quadrangula*.

2. *Clusia flava* Jacq.

Large treelike epiphytes (free standing elsewhere) with branches to 10 m long; sap cream colored. *Leaves* thick and stiff, drying gray above, tan beneath, the blades broadly obovate to nearly spatulate, 10–15 cm long, 6–9 cm wide, apically rounded to truncate or occasionally emarginate, basally acute to cuneate; midrib plane above, prominent beneath but becoming thin and indistinct just above the middle, lateral veins indistinct in fresh material but prominent on the lower surface when dry, about 4 per cm, arising at angle of about 45°, marginal vein 2 mm from margin; petiole 0–1.5 cm long. *Staminate inflorescences* deflexed, usually with 3–15 flowers, pedicels about 0.5 cm long, bracteate with 7–9 pairs of gradually smaller, decussate bracts subtending each flower, distally grading into the sepals; petals cream colored, thick, about 0.5 cm long, fleshy to almost rubbery, nearly round, 2 cm in diameter, erect at anthesis; stamens about 1 mm long, nearly sessile on a rectangular receptacle; fragrance strong and sweet. *Pistillate inflorescences* usually of a single flower, the peduncle deflexed, 1–3 cm long; bracts and petals as in staminate flowers; ovary more or less globose subtended by 4 symmetrically arranged clusters of stamens with 3 stamens per cluster, the stigmas sessile, foot-shaped, 15–20 (mostly 17), arranged in a rectangle at the top of the ovary. *Fruit* globose-flattened (oblate), 5–7 cm in diameter, 3–4 cm thick, green at maturity; seeds cylindrical, 0.7–1 cm long, aril bright orange. Flowering mostly during the dry season, January to April, fruiting by the end of the dry season, May to July. Central America; West Indies.

The most conspicuous *Clusia* in the La Selva area, where common in trees along the Río Puer to Viejo and in nearby pastures. It is distinctive for its broadly obovate, often apically truncate leaves, for its large, thick, cream colored petals subtended by a series of green, decussate bracts, and for its large globose-flattened fruits. At La Selva it might be confused vegetatively with *C. uvitana* with which it occasionally grows but *C. flava* has thicker, broader leaves with more widely spreading lateral veins. The flowers, of course, lack the sticky staminal mass and staminodial ring of the *C. minor* complex to which *C. uvitana* belongs.

The La Selva material differs from the typical West Indian form of the species by its larger, globose-flattened fruits with more numerous stigmas. In these respects it is very similar to *Clusia tetratrianthera* Maguire of Chiapas, Mexico.

3. *Clusia gracilis* Standl.

Epiphytic shrubs; milky sap scant. *Leaves* membranaceous, neither stiff nor leathery, drying gray green with dark, translucent spots, glabrous throughout, the blades elliptic, 9–15 cm long, 3–6 cm wide, apically acuminate, basally acute; secondary veins very indistinct in fresh material, mostly 4 per cm, arising at an angle of 40–50°, submarginal vein about 1 mm from the margin; petioles 1–3.5 cm long. *Inflorescences* pendent, 5–15 cm long, open and many-flowered, glabrous throughout. Flowers globose, about 5 mm in diameter, the lobes of the perianth erect at anthesis, thick and rubbery; sepals 6, reddish green, grading into 2 or 4 bracts; petals 4, yellowish red; *staminate flowers* with numerous stamens about 1 mm long, raised on an X-shaped receptacle, anthers and filaments about equal in length; *pistillate flowers* with a quadrate ovary, the 4 stigmas slightly raised on styles 1–2 mm long, the 8 staminodia paired at the corners of the ovary. *Fruit* narrowly ovoid, 4-sided, 2–4 cm long, 1.5–2 cm wide, dark burgundy at maturity. Flowering throughout the year but producing fruit mostly between February and July. Costa Rica and Panama.

Widespread at La Selva where found mostly in primary forest but occasionally on trees in open areas. It is the only *Clusia* at La Selva that typically reaches maturity as an understory epiphyte in the forest, often only 3–4 m above the ground. Only one other species at La Selva, *C. valerii*, has fruits that are red at maturity. All other species have green fruits.

The small inconspicuous flowers of *Clusia gracilis* appear to produce only a very faint, somewhat rubbery fragrance at anthesis. This is in sharp contrast to the related *C. flava*, which has a very strong, sweet fragrance. Preliminary observations indicate that members of the *C. flava* group are visited and perhaps pollinated by small weevils.

4. *Clusia minor* L.

Epiphytic shrubs or elsewhere free standing trees. *Leaf* blades obovate-elliptic, 9–12(14) cm long, 3.5–5.5(7) cm wide, apically acute, basally acute to attenuate; lateral veins (4)5–6 per cm, arising at an angle of 30–35°, prominent on both surfaces even in fresh material; petioles 1–1.5(2.5) cm long. *Inflorescences* similar in both sexes, (3)5–6 cm long, 6–8 cm wide; flower buds and pedicels whitish pink, subtended by a pair of bracts much smaller than the sepals. *Staminate flowers* 2–2.5 cm in diameter; sepals 4, coriaceous, whitish pink, smaller than the petals; petals 4(5, elsewhere),

membranaceous, bright pink; stamens connate into a low, 4-sided, mushroom-shaped androecium, seemingly with the anthers embedded in the cap but with numerous, smaller, marginal anthers, dehiscing by 4 oblong, closely parallel pores, and with few (usually 4) larger central anthers, dehiscing by 2 circular pores immersed in the broad connective; surface of the androecium covered at anthesis in a sticky, glistening resin. *Pistillate flowers* as above but the ovary basally surrounded with a ring of fused, resin-exuding staminodia, the ring usually persistent in fruit as a low, darkened collar; stigmas 10–13, narrowly rectangular, sessile or slightly raised, forming a circle on the top of the ovary. Flowers of both sexes with a strong, sweet vanilla-like fragrance. *Fruit* nearly globose to elongate ovoid, 1–2 cm long, 1–1.5 cm wide. Apparently flowering and fruiting mostly from February through June (September). Central America and northern South America; West Indies.

Common in trees along the river at La Selva where the plants may attain an overall branch spread of 5 to 10 m, but at least at La Selva they do not appear to “strangle” and replace the host plant as do some species of *Ficus*. However, elsewhere in Costa Rica, especially at higher elevations, this form of *Clusia minor* does grow as a terrestrial tree to at least 7 m tall.

This dioecious form of *Clusia minor* is known only from relatively wet areas in southern Nicaragua south into Panama. A hermaphroditic form is common in Central America north of Costa Rica, in northern South America and in the West Indies. An apomictic form occurs on the Pacific slope in Panama. The hermaphroditic and apomictic forms occur in relatively dry areas and are always terrestrial.

The name *Clusia odorata* Seem. has been widely applied to dioecious plants in this complex. The few specimens available from the type locality suggest that *C. odorata* could be narrowly defined as a unique species endemic to Volcán de Chiriquí in western Panama possessing narrower leaves, longer and narrower fruit, and larger flowers than other members of the complex. That decision, however, must await more collections and field observations from throughout the region.

5. *Clusia oedematopoeida* Maguire

Epiphytic often liana-like shrub, the long drooping branches with decussate, short branches; twigs with reddish, exfoliating and curling epidermis; sap clear and resinous, slowly turning milky. *Leaf* blades elliptic, 14–19 cm long, 6–8 cm wide, apically acute to abruptly acuminate

with an acumen about 1 cm long, basally acute; midrib prominent, especially beneath, the lateral veins about 3 per cm, very indistinct in fresh material, arising at an angle of 40–45°, merging with a submarginal vein 3–5 mm from the margin; petiole 0.5–3 cm long. *Staminate inflorescences* more or less conical, about 8 cm long, 6 cm wide, pendent, the peduncle reflexed; flowers usually with 5 spreading, thick, rubbery, cream colored petals 5–8 mm long, subtended by 6–7 pairs of decussate bracts and these distally grading into sepals; stamens sessile, 1–1.5 mm long, somewhat appressed to the receptacle with their tips outward. *Pistillate inflorescences* smaller, usually about 2–3 cm in diameter; flowers as above; ovary with 4–5, sessile stigmas, in bud the ovary subtended by 4–5 evenly distributed stamens with broad triangular filaments and anthers about 1 mm long. *Fruit* ovoid to globose, 2.5–3 cm long, 2–2.5 cm wide, the stigmas placed slightly to the side of the apex. Probably flowering and fruiting throughout the year. Costa Rica and Panama.

Widespread but uncommon at La Selva where found in trees along the river, as well as in the dissected southern part of the property. It is the only species at La Selva with long, drooping liana-like branches. This habit is perhaps more frequent for individuals growing along rivers and streams and near swamps, while a somewhat bushy habit seems to be more common in plants from primary forest canopy.

The thick rubbery petals and the stamens of the pistillate flowers clearly place *Clusia oedematopoeida* in a group of related species including *C. cylindrica*, *C. flava*, *C. gracilis* and *C. quadrangula*. The flowers have a sweet, faint citrus-like fragrance. The distant lateral veins, the submarginal vein well removed from the margin, and the reddish brown exfoliating epidermis of the twigs, distinguish this species even vegetatively from all others at La Selva. The few Panamanian collections of *C. oedematopoeida* are from eastern Panama and most of those from Darién. It also occurs on the Osa Peninsula in Costa Rica. These supposedly disjunct distributions are most likely the result of a lack of exploration of the wet lowlands throughout the region.

6. *Clusia quadrangula* Bartlett (= *C. cooperi* Standl.)

Epiphytic shrub; sap creamy. *Leaf* blades elliptic, (7)12–19(26) cm long, 3–6(9) cm wide, both apically and basally acute with the base sometimes decurrent; midrib plane above, prominent beneath, distinct to the apex; lateral

veins 5–7 per cm, arising at an angle of 40–45°, submarginal vein about 1 mm from margin; petiole 1–1.5(3.5) cm long. *Staminate inflorescences* small, 3–9-flowered; flowers 4-merous, subtended by 4–5 pairs of green, decussate bracts; sepals green, coriaceous, similar to the bracts; petals about 1 cm long, thick and rubbery; stamens numerous, about 1.5 mm long, nearly sessile, distinct. *Pistillate inflorescence* a solitary flower; bracts, sepals and petals as above; pedicel about 1 cm long; ovary globose, surrounded at the base by about 16 anther-bearing stamens, stigmas foot-shaped (9)15–20, raised (in fruit) on styles 3–4 mm long and arranged in a circle at the apex of the ovary. *Fruit* ovoid, (2)3–4 cm long, 2–3 cm in diameter, longitudinally ribbed with as many ribs as carpels, green at maturity. Probably flowering mostly in the dry season, fruiting by the end of May. Mexico south into Panama.

Rare at La Selva where known from only two or three individuals, one of them from primary forest and the others from trees left in pastures. *Clusia quadrangula* clearly belongs to a group of related species including *C. cylindrica*, *C. flava*, *C. gracilis*, and *C. oedematopoidea*. At La Selva it is distinctive because of its ribbed fruits, elevated stigmas, and its elliptic, acute, close-veined leaves. Previously unreported for Costa Rica.

7. *Clusia stenophylla* Standl.

Epiphytic shrubs or often free standing trees at higher elevations; latex bright yellow. *Leaf* blades obovate, mostly about twice longer than wide, (9)15–18(22) cm long, (5)7–9(14) cm wide (the juvenile leaves much longer, up to 30 cm long), apically obtuse to rounded, basally gradually narrowed to the winged petiolar region; lateral veins alternating, more and less obscure, the less obscure 3–4 per cm, arising at an angle of 60–70(80)°; submarginal vein about 1 mm from margin, evident in dried material; leaf surface drying darker brown above, the midrib often reddish; petiolar area 1–1.5 cm long. *Inflorescences* congested in about 9–30-flowered cymes; peduncle (1)3–5(9) cm long, the individual flowers nearly sessile. *Flowers* strictly unisexual; petals 5–6, about 1–1.5 cm long; sepals 4, subtended by 1–2 pairs of sepal-like bracts; stamens numerous, about 1 cm long, the anthers somewhat shorter than the filaments; *pistillate flowers* with 3–10, inconspicuous, deltoid to ligulate staminodia irregularly distributed around the base of the ovary; stigmas 5–7(10). *Fruit* ovoid to globose, (1)1.5(2.5) cm in diameter; styles often separate distally but forming a narrow column about (2)5 mm high. Fruiting collections from June and November. Guatemala south into Panama.

Rare at La Selva where found only as a canopy epiphyte in the primary forest. One individual drops leaves and fruits on the Suampo Trail between Q. Pantano and Q. El Salto. Among the species at La Selva, *Clusia stenophylla* can be recognized by its oblong, nearly spatulate leaves with short, winged petioles. The fruits are distinctive because of their long uncinatate styles. Leaves of immature plants are much longer than those of mature individuals.

Clusia stenophylla and closely related species are more common at higher elevations. It is the only member at La Selva of a complex group of species characterized by membranous petals, long stamens with the filaments usually longer than the anthers, globose fruits often with divergent styles, and especially by the inconspicuous whorl of toothlike staminodia that fall off as the ovary matures. The petioles of most species in this group are short and broadly winged.

8. *Clusia uvitana* Pittier (= *C. erectistigma* Maguire)

Large epiphytic shrub; latex white. *Leaf* blades obovoid, 12–15 cm long, 5.5–7(9.5) cm wide, apically obtuse to rounded, basally attenuate; lateral veins 3–5 per cm, arising at an angle of 20–35(40)°, very obscure in fresh material; petioles 1–2 cm long. *Inflorescences* similar in both sexes, 4–7 cm long, 5–10 cm wide, the rachis and especially the pedicels often white; flower buds 1–1.5 cm in diameter. *Staminate flowers* large, 3–4 cm in diameter, subtended by 2 small bracts at the base of the pedicel; sepals 4, rounded, 1–1.5 cm in diameter, decussate, white with green margins; petals 5 or 6, narrowed to a claw at the base, 1–1.5 cm wide, 1.5–2.5 cm long, membranaceous, pink with deeper red markings towards the center and on the claw; stamens fused into a low pentagonal mass covered in sticky resin at anthesis. *Pistillate flowers* as above but with a resinous sticky staminodial ring or cup surrounding the base of the ovary; ovary with 8(10) triangular stigmas about 5 mm long elevated on a crown about 5 mm tall. *Fruit* ovoid, 3–3.5 cm long, 2.5–3 cm wide. Flowering and fruiting mostly from February through July. Nicaragua south into Panama.

Known only from trees left standing in pastures and a few individuals in old secondary forest along the Rio Puerto Viejo. It is unusual in this respect since most other species at La Selva are known also from primary forest. *Clusia minor* has a similar distribution, apparently being restricted to open habitats or trees along the river.

In the Flora of Panama this species was not recognized as an entity separate from *Clusia minor*. However, when variation within *C. minor* is understood, the identity and integrity of *C. uvitana* becomes clear. It has larger, thicker leaves with indistinct lateral veins, larger fruits with elevated and usually more stigmas, and is mostly restricted to the wet Caribbean lowlands of Costa Rica and Panama. Both are members of a diverse group, including *C. valerii*, characterized by resin producing flowers. *Clusia uvitana* also occurs on Barro Colorado Island in Panama where it is called *C. odorata*.

9. *Clusia valerii* Standley

Large, epiphytic or rarely terrestrial shrubs; bark dark reddish brown to black; sap thick, white. *Leaf* blades obovate-elliptic, (10)12–15(24) cm long, 5–7(12) cm wide, leathery, apically acute to rounded, basally acute to attenuate; lateral veins very indistinct even when dry, 5–7(8) per cm, arising at an angle of 55–75°; petioles 2–4(8) cm long, slender and unwinged. *Staminate inflorescence* 5–7 cm long and as wide, 3–7-flowered; flowers large and showy, 3–6 cm across, the buds white, 1–2 cm in diameter, subtended by 2 or 3 pairs of bracts grading into the sepals, the rachis, bracts and sepals all white; petals 5–7, more or less narrowed into a basal claw, 1.5–2.5 cm long, 1–2 cm wide, somewhat fleshy, white abaxially, reddish pink within; stamens many, connate into a low 5–7-sided dome, 1–1.5 cm in diameter, becoming fused by a resinous exudate that covers the surface of the androecium; anthers monothecate, dehiscing by doughnut-shaped apical pores, each pore surrounded by a thin, minutely corrugated ring of tissue. *Pistillate inflorescence* as above but usually only 1–3-flowered; flowers as above but the ovary subtended by a staminodial ring or cup 5–7 mm high, exuding a sticky resin; stigmas 5, large, sessile, triangular, forming a dark cap on the fruit 1–1.5 cm in diameter. *Fruit* ovoid, 3.5–5 cm long, 2.5–3.5 cm wide, reddish pink; inner wall of the fruit valves forming a thick, white, bony endocarp. Flowering and fruiting at least from February through September, perhaps throughout the year. Nicaragua south into Panama.

Widespread in the forest as a canopy epiphyte where it can be located by the large, rose red fruits that fall beneath the parent tree. Like many other species of *Clusia*, however, *C. valerii* also grows low on trees left standing in pastures. This *Clusia* has the largest and visually most striking flowers of any at La Selva. The large pink and white rotate corolla resembles that of the related and sympatric *C. uvitana*, but differs in its pure

white rather than pink and green flower buds and pedicels.

3. *CLUSIELLA* Planch. & Tr.

Epiphytic shrubs; sap clear, resinous. *Leaf* blades elliptic, lateral veins often very indistinct; lower surface of blade obscurely glandular punctate; petioles short. *Inflorescences* axillary or terminal, short, 1- or few-flowered and basally branched, the flowers subtended by several pairs of small, decussate bracts dispersed on the pedicel. *Flowers* with 5 small imbricate sepals and 5 larger contorted petals; *staminate flowers* with the filaments connate basally into a narrow column but more or less free apically, subtended by a collar of clavate, resinous, yellow staminodia; *pistillate flowers* with the ovary subtended by a resinous collar bearing on the periphery numerous staminodia similar to the stamens of the staminate flower; stigmas sessile, 5–7 circular and distinct or about 10 fused into a disc topping the ovary. *Fruit* a small, many-seeded berry with as many locules as stigmas, its pulp clear, mucilaginous; seeds with a transparent, featureless outer integument attached only at the hilum; inner integument black at maturity and shallowly foveolate.

Clusiella is a genus of seven species of epiphytic shrubs restricted to southern Central America and northwestern South America with one species in the Amazon Basin. The genus was only recently reported from Central America and is now known from only about 20 collections in the region, half of them from four sites in Panama (Veraguas to Darién) and the others from La Selva. This is the first report of the genus for Costa Rica.

1. *Clusiella elegans* Planch. & Tr.

Wiry-stemmed, epiphytic shrubs of the forest canopy; sap clear, resinous. *Leaf* blades elliptic, (6)8–14 cm long, (2)3–4 cm wide, apically long-acuminate, basally acute or mostly rounded; midrib prominent on both surfaces, lateral veins very indistinct, 4–7 per cm, arising at an angle of 45–60°; glandular dots very small, visible especially on lower leaf surface; petiole 2–3 mm long. *Inflorescences* terminal or seemingly axillary, mostly 1-flowered; pedicel 0.5–1.25 cm long; bracts 2–4, about 1 mm long; sepals about 2 mm long; petals about 6 mm long, white but basally yellow internally. *Staminate flowers* (not seen at La Selva) with a staminal column about 6 mm tall subtended by a whorl of glandular staminodia, the filaments reddish, the anthers more or less globose, the connective transparent. *Pis-*

tillate flowers with the staminodial ring about 5 mm tall, the ring bright yellow; stigmas apparently 10 but forming an apical disk and difficult to distinguish; ovary 10-celled. *Fruit* about 1 cm in diameter at maturity, translucent white; seeds ovoid, 0.5–0.7 mm long, enclosed in a clear mucilaginous integument, the testa pitted, dark gray to black. Apparently flowering and fruiting throughout the year. Costa Rica south into Peru.

Common canopy epiphyte in the primary forest at La Selva. *Chusiella elegans* can be recognized by its somewhat leathery, short-petiolate leaves with long, slender, acuminate tips, small white berries and wiry stems. Although staminate material has been frequently collected in Panama, none was found at La Selva. This suggests that the species is perhaps hermaphroditic or apomictic at La Selva. More careful examination and preferably, manipulation, of plants in the field is necessary to determine the nature of the breeding system. On herbarium sheets the anthers of the staminodial ring are reduced compared to those of staminate plants and appear sterile. The flowers produce a strong, sweet vanilla-like fragrance at anthesis and exude a sticky resin on the face of the staminodial collar; they are most likely visited by bees.

4. DYSTOVOMITA (Engler) D'Arcy

D'ARCY, W. G. 1978. *Dystovomita*, a new genus of neotropical Guttiferae. *Ann. Missouri Bot. Gard.* 65: 694–697.

Dioecious trees; sap resinous and clear or tardily becoming creamy. *Leaves* broadly elliptic; midrib and lateral veins prominent above and beneath; tertiary venation inconspicuous; petioles with large, axillary, prow-shaped protuberances. *Inflorescences* cauliflorous, axillary at leafless nodes or sometimes terminal, sessile, cymose panicles with minute bracts and bracteoles. *Flowers* small, less than 5 mm in diameter at anthesis; sepals 2–4, decussate, the outer pair half the length of the bud or less, membranaceous to somewhat coriaceous, pale green; petals 4, decussate, membranaceous, only slightly different from the sepals, pale green to white; *staminate flowers* with numerous stamens surrounding a conical disk; *pistillate flowers* with numerous stamens (staminodia?) surrounding the pyriform, 4- or 5-locular ovary, the 4–5 stigmas ligulate, sessile but flaring, ovules 1–2 per locule, pendent. *Fruit* a small, globose, apically dehiscent, fleshy capsule; seeds reniform, completely enclosed in a membranous aril.

Dystovomita is a genus of three species known from Costa Rica, Panama, Colombia, Venezuela and Brazil. Because of its only partially dehiscent

fruits and axillary inflorescences this genus may belong to the tribe Garcinieae (including only *Rheedia* in the New World) rather than to the Clusieae as has been supposed. In general appearance, *Dystovomita* seems to be somewhat intermediate between the two tribes of the Clusiaceae.

1. *Dystovomita pittieri* (Engler) D'Arcy

Dioecious trees 10–20 m tall, 15–40 cm in diameter, the trunk reddish brown, bearing numerous stilt roots; sap resinous and clear or tardily becoming creamy. *Leaf* blades broadly elliptic to nearly orbicular, coriaceous, 23–29 cm long, 13–20 cm wide, apically rounded, basally broadly acute and slightly decurrent; leaf surface dark to yellowish green and lustrous above, paler and dull beneath, glabrous; midrib and lateral veins prominent above and beneath; lateral veins 2.5–3.5 cm apart, 10–12 per side, arising at an angle of (50)60°, curved upward and becoming obscure near the margin; tertiary venation obscure in fresh material; petioles 3–5 cm long, the axillary structure 0.5–1 cm long. *Inflorescences* axillary, borne mostly at leafless nodes along the branches, 15–30-flowered, buds about 2 mm in diameter, the flowers 4–5 mm in diameter at anthesis; perianth 6-parted, decussate, membranaceous, pale green, only slightly differentiated, the outer pair (sepals) about ½ as long as the inner 4 (petals) and somewhat coriaceous. *Staminate flowers* with numerous stamens 2–2.5 mm long, anthers globose, about 0.2 mm in diameter; ovary about 1 mm long, apically 4-lobed and sterile. *Pistillate flowers* with numerous staminodia 0.5–1 mm long, the ovary pyriform, about 2 mm long, capped by 4(5) sessile but flaring, ligulate or deltoid stigmas. *Fruit* globose, 1–1.5 cm in diameter, green, usually 1 seed per locule; seeds about 6 mm long. At La Selva flowering material collected in April, fruiting material in April. Costa Rica south into Colombia.

Apparently restricted to the primary forest in the southern half of the property, where it is most frequently encountered on slopes and ridges. Several individuals grow near the top of the steep slope along the north side of plot III. Its often nearly round, leathery leaves, petiolar appendages, and reddish, stilt-rooted trunk make *Dystovomita pittieri* very distinctive.

5. MARILA Sw.

Shrubs or trees with clear, white, yellow or brown latex. *Leaves* oblong-elliptic, somewhat coriaceous, glabrous or pubescent, obscurely pellucid-punctate beneath; lateral veins impressed

above, prominent beneath and boldly loop-connected near the margin, tertiary veins closely parallel and more or less perpendicular to the lateral veins. *Inflorescences* axillary or rarely terminal racemes or panicles, often borne on leafless nodes along the branches. *Flowers* perfect or (reportedly) unisexual; perianth 5–10 parted, the sepals quincuncial, reflexed at anthesis, persistent in fruit, petals more or less convolute, fugacious; stamens numerous, the filaments free, anthers linear and with an apical appendage; ovary 3–5-celled with numerous ovules per cell and axillary placentation; stigma conical or globose, on an elongate style. *Fruit* a capsule, longitudinally dehiscent into 3–5, often twisting valves; seeds minute, comose at each end.

Although *Marila* is usually treated as a member of the Guttiferae in regional floras, it has also been placed in the Bonnetiaceae, a tropical South American and Asian family, itself sometimes treated as part of the Theaceae. The genus contains approximately 20 species, four of them occurring in Central America. It is known from Guatemala to Bolivia and the West Indies.

1. *Marila laxiflora* Rusby

Tree about 10 m tall (–20 m elsewhere), the twigs minutely pubescent; sap resinous, clear or somewhat brownish. *Leaf* blades oblong-elliptic, 9–28 cm long, 2–12 cm wide, apically acute with a short acumen, basally acute or occasionally rounded, the surface glabrous, minutely pellucid punctate beneath, the very young, unopened leaves densely brownish puberulent; midrib and lateral veins impressed above, prominent beneath, lateral veins (10)12–14(15) pairs, very regularly spaced, mostly 1–1.5 cm distant, arising at an angle of 60–70°, the tertiary veins closely parallel about 1.5 mm apart and more or less perpendicular to the lateral veins; petioles 1–2 cm long, grooved above. *Inflorescence* racemose, pendent, (12)20–35 cm long, many-flowered; pedicels 5–8 mm long. *Flowers* narrowly ovoid, 6–8 mm long in bud, 1–1.5 cm wide at anthesis, green, fragrant; sepals 5, pubescent, thicker and drying reddish where exposed, the covered portions thinner, glabrous and green; petals 5 or fewer (sometimes lacking), very thinly membranaceous; anthers with a linear appendage; ovary and style about 3 mm long. *Fruit* narrow, 4–7 cm long, turning brown. Specimen with flowers and young fruits collected at the end of March. Guatemala south into Bolivia.

Rare at La Selva. The single fertile collection is from the steep bank along the Río Sarapiquí at the crossing on the Western Annex where several individuals occur.

6. *RHEEDIA* L.

Dioecious trees; sap milky, mostly bright yellow, sometimes white. *Leaves* opposite or verticillate; midrib and lateral veins prominent, the major lateral veins numerous, more or less parallel and often difficult to distinguish from intermediate, prominent but more reticulate veins; marginal or submarginal vein often present; petioles with an axillary, prow-shaped structure. *Inflorescences* of 1 to many pedicellate flowers, fasciculate in the axils of leafy or leafless nodes. *Flowers* small with globose buds, perianth 6-parted, decussate, sepals 2, usually smaller than the petals, glabrous, greenish yellow to white; *staminate flowers* with numerous stamens inserted on or around a capitate, ovary-like disk, the filaments free and the anthers small, globose; *pistillate flowers* with the stamens fewer and smaller, the ovary ovoid with 3–4 locules and 1 ovule per locule, the stigmas sessile or with a style. *Fruit* a globose or ovoid, 1–4-seeded berry with a papery or leathery smooth or warty pericarp; seeds large, enveloped in a pulpy aril.

Rheedia is known from Central and South America, the West Indies, Madagascar, and possibly Africa. It contains perhaps two dozen species with five to six of them occurring in Central America. The genus is apparently more diverse in the West Indies than in Central America; more species have been described from Cuba alone than from all of Central America. Although species of *Rheedia* are described as having perfect flowers, the stamens in pistillate flowers examined are small and apparently bear no pollen and pollen producing flowers lack an ovary.

1. *Rheedia edulis* (Seem.) Planch. & Tr.

Dioecious trees 10–15 m tall, trunk dark brown; sap bright yellow. *Leaf* blades elliptic, thinly coriaceous, 14–18(30) cm long, 4.5–7(10) cm wide, apically acute to acuminate, basally acute; leaf surface dark to yellow green above, paler beneath with both surfaces dull, glabrous; midrib, lateral and tertiary veins prominent to prominent (even in fresh material) on both surfaces, main lateral veins about 2–4 per cm, mostly about 5 mm apart, arising at an angle of 55–70°; leaf margin recurved and obscuring the fine marginal vein; petioles 1–2 cm long, deeply channeled above, the foveola rather inconspicuous. *Inflorescences* of fasciculate flowers in the leaf axils, pedicels 1–2 cm long. *Flowers* globose, in bud about 3 mm in diameter, 4–5 mm wide at anthesis, glabrous, greenish white; *staminate flowers* with a capitate ovary-like disk; *pistillate flowers* with the stamens smaller than those of the staminate flowers and apparently sterile, the

ovary pyriform to ovoid, the stigmas sessile. *Fruit* ovoid, 2–3 cm in diameter, soft (pulpy) and fleshy, bright orange at maturity, tasty, 1- or 2-seeded; seeds ovoid, 1.5–2 cm long. Flowering and fruiting in the dry season. Mexico south into Panama.

Although *Rheedia edulis* is known from very few mature individuals at La Selva, saplings are relatively common and found scattered throughout the primary forest.

7. SYMPHONIA L. f.

Trees or shrubs; sap yellowish. *Leaves* elliptic; lateral veins numerous, closely parallel; petioles channeled above. *Inflorescences* globose, condensed racemes or fascicles, terminal on leafy branches or on leafless axillary shoots. *Flowers* perfect, globose in bud, depressed-globose at anthesis; sepals 5, imbricate, pink; petals 5, contorted, bicolorous, red or pink and white; stamens monadelphous, the tube surrounded at the base by a disk, apically split into 4–5 segments each bearing 2–5 linear anthers; ovary 5-celled with 2–8 ovules per locule, style elongate and apically 4- or 5-parted, the lobes alternating with the segments of the staminal column. *Fruit* a 1- or 2-seeded berry with a thin exocarp; seeds with no aril.

Symphonia is known from Central and South America, the West Indies, tropical Africa and Madagascar. It is the only Central American member of Engler's subfamily Moronoiboideae.

1. *Symphonia globulifera* L. f.

Trees or shrubs 4–15(30) m tall; sap bright yellow. *Leaf* blades elliptic to oblong-elliptic, 8–13.5 cm long, (2)3.5–5.5 cm wide, apically acute and abruptly narrowed to an acuminate tip, basally acute; leaf surface dark green above, paler beneath, with a subdued lustre on both surfaces, glabrous; midrib indistinct above, prominent beneath, lateral veins indistinct in fresh material, prominent beneath when dry, 5–7 per cm, arising at an angle of (60)70–80°, forming an inconspicuous submarginal vein; petioles 0.5–1 cm long, flattened and 2-ridged above. *Inflorescences* 5–20-flowered, pedicels about 1 cm long, red. *Flowers* 0.7–1 cm in diameter in bud, 1–1.5 cm in diameter at anthesis, brightly bicolored, red and white; anthers borne on the outer surface of the flaring segments of the staminal column, bright yellow. *Fruit* ovoid, 2–2.5 cm long, brownish at maturity; seeds ovoid, shallowly furrowed, burgundy. Flowering mostly during the dry season (February to May) but sporadically throughout the year. Known from throughout the range of the genus.

Common at La Selva on ridges in primary forest in the southern part of the property. Its bright yellow sap and leaf shape make it similar to the sympatric *Rheedia edulis* but its flush rather than elevated midrib on the upper surface is sufficient to distinguish the two species. Although *Symphonia globulifera* is elsewhere often a large canopy tree, none above 15 m tall was seen at La Selva. The chamber formed by the corolla of this species contains abundant nectar at anthesis and the self-incompatible flowers are visited by hummingbirds.

8. TOVOMITA Aubl.

Dioecious trees; sap usually clear and resinous, sometimes milky. *Leaves* membranaceous to coriaceous, glabrous. *Inflorescences* terminal, usually few-flowered, cymose panicles; *flowers* unisexual but the pistillate flowers with staminodia; sepals 2–8, the outer pair either fused or valvate in bud and overtopping the bud, usually differing in texture and color from the petals, sometimes accrescent in fruit; petals 2–8, imbricate in bud, membranaceous, pale green to translucent white; stamens numerous, the filaments free, staminodia slightly smaller than the stamens. *Fruit* a fleshy capsule, the valves strongly reflexed at dehiscence, inner fruit wall and fruit axis dark red; stigmas either sessile or with styles; seeds 1–2 per locule, bearing a fleshy, usually orange aril.

Tovomita is known from Costa Rica south into South America as well as the West Indies. As here circumscribed, it contains perhaps 20 to 30 species with five or six of them Central American. The whole *Tovomita* group (including *Chrysochlamys*, *Tovomita*, and *Tovomitopsis*) probably contains fewer than 60 species with about 20 occurring in Central America.

1. *Tovomita weddelliana* Planch. & Tr. (= *Clusia pithecobia* Standl.)

Dioecious trees 4–20 m tall, often with a few stout adventitious roots; sap resinous and clear to somewhat milky. *Leaf* blades spatulate, 14–20(47) cm long, 3–5(8) cm wide, apically acute, basally gradually narrowed into a winged petiolar region, membranaceous, glabrous; midrib prominent above and keeled beneath; principal lateral veins indistinct, 1–2(4) mm apart, numerous, often difficult to distinguish from intermediate veins, arising at an angle of 65–85°, true petiole 0–3 mm long. *Inflorescences* terminal, few-flowered cymes, 5–11 cm long and as wide; *flowers* seemingly perfect with numerous staminodia, the buds 6–7 mm in diameter at maturity; outer pair of sepals valvate and covering the bud, green and

coriaceous, accrescent in fruit; open flowers 1–1.5 cm in diameter, the petals membranaceous, translucent, white. *Fruit* pyriform, 3–3.5 cm long, topped by 4–6, small, sessile stigmas, green or reddish, at maturity splitting and the valves reflexed; fruit wall within and the axis dark red; seeds covered by an orange aril. Flowering and fruiting specimens from La Selva in November, February and March. Costa Rica south into Bolivia.

Rare at La Selva where, except for Arboretum plantings, it is known from just two individuals at the southeast corner of the property. Both plants produced fruit and were thought to be hermaphroditic, but closer examination of the stamens showed their anthers to be without pollen and only about one-quarter the size of those of staminate plants.

9. TOVOMITOPSIS Planch. & Tr.

Dioecious, terrestrial shrubs or small trees; sap often resinous and clear, sometimes milky. *Leaves* usually membranaceous, glabrous to puberulent along the nerves; resin canals often evident as fine linear streaks in dried material. *Inflorescences* terminal or rarely lateral cymose panicles. *Flowers* seemingly staminate or perfect; sepals imbricate, light pink to red, membranaceous, difficult to distinguish from the petals but at least 1 sepal (usually both) of the outer pair less than half as long as the inner series; petals imbricate, white to pink, often streaked with canals, membranaceous; *staminate flowers* with no gynoecium (at La Selva), stamens numerous, the filaments free or slightly connivent at the base; *pistillate flowers* with stamens but these at least sometimes and perhaps always without pollen and smaller than in staminate flowers; ovary ovoid, surmounted by (4)5(6), rectangular, sessile but usually radiating stigmas. *Fruit* a fleshy capsule, splitting down from the apex into as many valves as stigmas, the valves rather thick, the fruit wall and axis usually pale pink to white; seeds 1(2) per locule, reniform, green, covered at least partially by an orange aril.

Tovomitopsis is here considered distinct from *Tovomita* by virtue of the relatively reduced outer pair of sepals and the thick, more or less erect valves of the dehiscing fruit.

Tovomitopsis is known from Guatemala south into South America. As here circumscribed, it contains perhaps 15 to 20 species mostly from Central America. Members of this genus are common and accessible shrubs at La Selva. The flowers have a strong sweet fragrance and are visited by bees. The seeds are dispersed by birds and possibly ants.

KEY TO THE SPECIES

1. Leaves widest above the middle; secondary veins bold and distinct, 5–10(11) pairs; flower buds pink to white; sap clear, resinous; plants of low areas, swamp margins or stream sides.
 2. Flower buds 2–4 mm in diameter; leaves dull or at most semilustrous on both surfaces, minutely puberulent along the veins beneath, mostly 5–6 cm wide; inflorescences slender, pendent. 1. *T. glauca*.
 2. Flower buds 4–6 mm in diameter; leaves glossy above and beneath, glabrous, mostly 7–9 cm wide; inflorescences stout, erect. 2. *T. nicaraguensis*.
1. Leaves widest at the middle; secondary veins faint, difficult to distinguish from intermediate veins, 10–16 pairs; flower buds red, 4–5 mm in diameter; sap milky; plants of slopes and ridges. 3. *T. silvicola*.

1. *Tovomitopsis glauca* Planch. & Tr.

Dioecious shrubs or small trees to 4 m tall; sap of leaves and twigs resinous, clear. *Leaf* blades elliptic to oblong, 12–21 cm long, 3.5–7 cm wide, apically abruptly acute, basally acute to acuminate, the surfaces dull both above and beneath; midrib prominent and minutely puberulent beneath, the lateral veins (6)7–10(11) readily visible pairs, arising at an angle of 60–70(80)°, resin canals also visible, especially in young (dried) leaves, as fine, sometimes dense, wavy lines; petioles 1–2.5(3.5) cm long. *Inflorescences* usually pendent, pyramidal, about as wide at the base as long (9–20 cm), many-flowered, minutely puberulent. *Flower* buds ovoid, 2–4 mm long, outer pair of sepals smaller than the inner, inner sepals and petals striate, white to pink; *staminate flowers* with the stamens 1–1.6 mm long, anthers about 0.2 mm long; *pistillate flowers* with the stamens and anthers somewhat smaller. *Fruit* obovoid, 1–2 cm in diameter, pink to red, often streaked with white, the infructescence pendent. Apparently flowering throughout the year but fruiting mostly during the dry season (January to April). Costa Rica and Panama.

Common along streams and in low areas within the primary forest. The other common species at La Selva, *Tovomitopsis nicaraguensis*, has a similar habitat preference but is found more often at the edges of swamps, has larger, glossy leaves with more distant lateral veins and stouter usually erect inflorescences.

2. *Tovomitopsis nicaraguensis* Planch. & Tr.

Dioecious shrubs or small trees to 6 m tall; sap of leaves and twigs clear, resinous. *Leaf* blades oblong-obovate, 14–24(27) cm long, 6–

10(12.5) cm wide, apically acute to obtuse or nearly rounded, basally acute to acuminate, leaf surface glossy above and beneath; midrib prominent beneath, glabrous, lateral veins of 5–8(10) readily visible pairs, arising at an angle of 50–70°, the resin canals not visible; petioles 1–3 cm long. *Inflorescences* erect, pyramidal, about as wide at the base as long (3–19 cm), many-flowered, nearly glabrous; buds 4–6 mm in diameter, outer pair of sepals smaller than the inner, the perianth striate, white or pink; *staminate flowers* with stamens 2–4 mm long; *pistillate flowers* with the staminodia smaller. *Fruit* obovoid to globose, 1.5–3 cm in diameter, pale pink to red; infructescence branches stout, erect. Flowering mostly April to September, fruits maturing July to February. Nicaragua, Costa Rica and Panama.

Common and widespread at La Selva but found most often at the edges of swamps and low areas in the forest. In general, it is distinguished from other Central American species of *Tovomitopsis* by its large, distantly veined, glossy leaves, lack of visible resin canals in dried material, large flower buds, and stout erect infructescences.

Tovomitopsis nicaraguensis has previously been broadly interpreted as a widespread and common species ranging from Guatemala into South America. However, examination of the type specimen (collected along the Río San Juan not far from La Selva) reveals that the name *T. nicaraguensis* has been misapplied. Although locally common, this species is actually quite rare in collections, and is known mostly from the wet Caribbean lowlands of southern Nicaragua, Costa Rica, and Panama. The plants on Barro Colorado Island and many of the specimens cited as *T. nicaraguensis* in the Flora of Panama are *Chrysochlamys eclipses* L. O. Wms., which has thick, succulent petals, monodelphous stamens, and pollen with an echinate rather than psilate-foveolate exine.

3. *Tovomitopsis silvicola* Hammel

Dioecious shrubs or small trees to 6 m tall; sap distinctly milky. *Leaf* blades oblong, mostly (13)16–22 cm long, 4–6.5(8) cm wide, apically broadly acute with a short acumen to acuminate, basally narrowly acute, the leaf surface dull or somewhat lustrous above and beneath; midrib prominent beneath, glabrous, major lateral veins about 10–16, difficult to distinguish from the minor intermediate veins, arising at an angle of (60)70°, with numerous, fine resin canals visible in dried material; petioles 1–2.5 cm long. *Inflorescences* more or less pendent, pyramidal, 6–10 cm long and as wide, many-flowered, minutely puberulent to glabrous; buds 4–5 mm in diameter, the outer pair of sepals

often unequal with the larger overtopping the bud and the smaller about half the height of the bud or smaller, perianth not striate, red abaxially, white adaxially; *staminate flowers* with the stamens 1.5–3.5 mm long; *pistillate flowers* with the staminodia only about 1 mm long. *Fruit* ovoid, 1.5–2.5 cm in diameter, red, infructescence branches pendent. Flowering during the rainy season, June to September, fruits maturing mostly in the dry season, January to June. Caribbean lowlands of Costa Rica.

Restricted to ridges in the primary forest in the southern half of the property. In habitat *Tovomitopsis silvicola* contrasts sharply with *T. glauca* and *T. nicaraguensis*, which are restricted to streamsides or swampy areas. The oblong, obscurely but many-veined leaves, the red flower buds, and above all the milky rather than merely resinous sap distinguish this species from the other two at La Selva.

10. *VISMIA* Vandelli

ROBSON, K. 1978. Hypericaceae. In R. E. WOODSON, R. W. SCHERY ET AL., Flora of Panama. Ann. Missouri Bot. Gard. 65: 9–26.

Trees or shrubs, the bark often flaking; sap resinous, yellow to orange. *Leaves* with numerous but rather widely spaced, parallel lateral veins, the tertiary venation reticulate, midrib impressed above; leaf surface usually stellate pubescent and pellucid-punctate beneath; petioles deeply channeled. *Inflorescences* many-flowered, terminal and sometimes axillary panicles. *Flowers* perfect, homostylous or heterostylous; sepals 5, quincuncial, the exposed portions thicker and usually tomentose, persistent in fruit; petals 5, convolute, soon deciduous, glabrous externally, woolly pubescent within, white, greenish white to yellow; stamens in 5 fascicles opposite the petals, alternating with 5 staminodial fascicles, the filaments connate to above the middle, the anthers ovoid to globose with a gland on the connective; ovary pyriform, 5-locular with 5–many ovules per cell, stigmas capitate to bilobed, elevated on 5, elongate, free or basally connivent styles. *Fruit* a smooth fleshy berry or rarely 5-lobed elsewhere with a thin pericarp and then apparently dehiscent when dry, many-seeded; seeds small, usually reniform, finely reticulate, lacking an aril.

Except for *Marila laxiflora* species of *Vismia* are the most unusual members of the Guttiferae at La Selva. Their stellate pubescent leaves and woolly pubescent petals are notable; all other Guttiferae at La Selva are either glabrous or only minutely puberulent. Other than *Marila* and *Symphonia*, species of *Vismia* provide the only

strictly hermaphroditic Guttiferae at La Selva. Their heterostyly is also unique. Only *Clusiella*, which shares a number of other unusual features with *Vismia*, also has fruits that are many-seeded berries. *Vismia* is often treated in the Hypericaceae, a segregate from the Guttiferae.

Vismia is known from tropical Central and South America, the West Indies and Africa and contains about 55 species of which six are African. From Central America, seven to eight species are known. The flowers in this genus are visited by bees and the fruits are eaten by birds and possibly bats.

KEY TO THE SPECIES

1. Stamen and staminodial fascicles deciduous soon after flowering; lower leaf surface obscured by appressed stellate pubescence; lateral veins mostly 10–14 pairs; leaves seldom over 20 cm long.
 2. Petals glandular-dotted, green; sepals strongly reflexed in fruit; leaves elliptic, basally narrowly acute; aeroles of visible reticulate venation large (2–4 mm in diameter). 1. *V. billbergiana*.
 2. Petals glandular-lined, pale yellow; sepals spreading to slightly reflexed in fruit; leaves ovate, basally broadly acute to rounded or truncate; aeroles of visible reticulate venation small (less than 1 mm in diameter). 3. *V. panamensis*.
1. Stamen and staminodial fascicles persistent in fruit; lower leaf surface not obscured by the stalked stellate or dendroid pubescence; lateral veins mostly more than 20 pairs; leaves often over 20 cm long. 2. *V. macrophylla*.

1. *Vismia billbergiana* Beurl.

Shrub or treelet mostly 3–5 m tall, branchlets densely to sparsely stellate pubescent. *Leaf* blades elliptic, widest just beneath the middle, (7)14–19 cm long, (1.5)5–8(11.5) wide, apically acuminate or acute and abruptly narrowed to an acumen, basally narrowly to broadly acute; leaf surface glabrous, dark green above, densely stellate pubescent and paler grayish brown beneath, pellucid dots rather large, conspicuous; main lateral veins (7)10–13 pairs, arising at an angle of 60–70°, faintly loop-connected 3–10 mm from the margin; reticulate venation obscure; petioles 1–1.5 cm long. *Inflorescences* 4- to many-flowered, terminal or sometimes axillary, broadly pyramidal, the buds globose, 4–5 mm in diameter, pale brown. *Flowers* heterostylous; sepals with the exposed surface stellate pubescent; petals with conspicuous reddish glandular dots, green; fascicles with 14–20 stamens; ovary globose, glandular-punctate. *Fruit* globose to ovoid, about 1 cm in diameter with orange glandular dots, dark reddish purple; seeds dark reddish brown, 3–4

mm long. Flowering and fruiting May to September and perhaps throughout the year. Costa Rica south into Colombia.

Common in open secondary areas such as recently abandoned pastures as well as in light gaps in the forest. The La Selva population has leaves that are larger than some collections of the species from elsewhere. The smaller leaved form, typified by *Vismia viridiflora* Planch. & Tr., apparently also has more markedly reflexed tepals. However, these are presumed to be extremes of variation within a single polymorphic species.

2. *Vismia macrophylla* H.B.K.

Trees or rarely shrubs (2)5–25(43) m tall, branchlets densely ferruginous pubescent. *Leaf* blades narrowly ovate, widest near the base, 10–40 cm long, 6–16 cm wide, apically broadly to narrowly acute and abruptly acuminate or apiculate, basally cordate to rounded, sometimes asymmetric; leaf surface glabrous above except pubescent in the midrib, lustrous or dull, sparsely stellate pubescent beneath, the trichomes rusty red with the green lamina and dark pellucid dots visible through the pubescence; main lateral veins (12)18–31 pairs, arising at an angle of 60–75°, distinctly loop-connected very near the margin; reticulate venation conspicuous beneath; petioles 1–2.5 cm long. *Inflorescences* many-flowered, terminal, pyramidal, the buds globose to ovoid, reddish brown. *Flowers* heterostylous; sepals with stellate-dendroid pubescence on the exposed surface; petals distally glandular punctate, white, greenish white to cream; stamen fascicles each with about 25 stamens; ovary globose, distally glandular punctate. *Fruits* globose to ovoid, 1–1.5 cm long, green to olive brown or reddish; seeds dark reddish brown, 2.5–3.5 mm long. Flowering and fruiting April(?) through July. Mexico(?) south into central Brazil.

Rare at La Selva where it was for a long time mistaken for the more common, or at least more accessible, *Vismia panamensis*. It grows to be much taller than the two other species of *Vismia*, and is found most often in gaps on ridges in the forest.

3. *Vismia panamensis* Duchass. & Walp.

Shrubs or trees 6–15(22) m tall, branchlets densely to sparsely grayish to reddish stellate pubescent. *Leaf* blades narrowly ovate, widest at the base, (9)13–17(26) cm long, (3)5–8(11) cm wide, apically acuminate, basally broadly acute to rounded or truncate; leaf surface glabrous above or minutely puberulent in the midrib, densely appressed stellate pubescent with rusty or grayish trichomes beneath, the pubescence ob-

scuring the leaf surface and the punctate dots; main lateral veins 10–15 pairs, arising at an angle of 50–60°, faintly loop-connected near the margin; reticulate venation prominent; petioles 1–2 cm long. *Inflorescences* 9- to many-flowered, terminal and occasionally axillary, pyramidal, the buds globose, reddish brown. *Flowers* heterostylous; sepals with the exposed surface stellate pubescent; petals with glandular lines and sometimes also with dots, pale yellow; stamen fascicles with about 40–50 stamens; ovary ovoid or pyriform, glandular punctate and striate. *Fruits* broadly ovoid, about 1–1.5 cm long, green; seeds dark brown, about 2 mm long. Flowering at the end of the dry season (April to May), fruiting by the end of May. Known from Nicaragua, Costa Rica and Panama.

Common to abundant on ridges in the abandoned pastureland in the northern part of the Western Annex. It also grows in the successional strips on the original property. The fruits of this species are quite tasty at maturity, reminiscent of dried figs.

Vismia baccifera (L.) Tr. & Planch. is also very common in Costa Rica and should be sought at La Selva. In general appearance it is apparently very similar to *V. panamensis* but is homostylous instead of heterostylous. In addition *V. baccifera* has longer pedicels (4–7 mm), more brownish (instead of reddish) pubescence, abruptly rather than gradually acuminate leaves, paler flowers, and black fruits.