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FLORA COSTARICENSIS

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Family #97 Krameriaceae

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Family #98 Oxalidaceae

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Family #99 Geraniaceae

William Burger

Family #100 Tropaeolaceae

William Burger

Family #101 Linaceae

William Burger

Family #101a Humiriaceae

William Burger and Nelson Zamora

Family #102 Erythroxylaceae

Timothy Plowman†

Family #103 Zgyophyllaceae

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Introduction

This is the seventh issue in the Flora Costaricensis series. The first dealt with families numbered 40 and 41, Casuarinaceae and Piperaceae (Fieldiana, Bot. 35, 1971). The second included families 42 through 53, Chloranthaceae through Urticaceae (Fieldiana, Bot. 40, 1977). The third issue covered family 15, the Gramineae, authored by Richard Pohl (Fieldiana, Bot., new series, No. 4, 1980). The fourth issue included families 54 through 70, Podostemonaceae through Caryophyllaceae (Fieldiana, Bot., new series, No. 13, 1983). The fifth issue covered families 200 and 201, the Acanthaceae, authored by L. H. Durkee, and Plantaginaceae (Fieldiana, Bot., new series, No. 18, 1986). The sixth issue covered families 80 and 81, the Lauraceae and Hernandiaceae (Fieldiana, Bot., new series, No. 23, 1990). The alphabetical listing and the sequence of families are given inside the front and back covers.

This issue includes the Geraniales and the families traditionally associated with them in the Engler sequence. Several recent collections representing new species for Costa Rica's flora are included here. However, the most important contribution in these pages is that for the Erythroxylaceae. Timothy Plowman's untimely death cut short his monographic work in *Erythroxylum*, but he was able to complete a number of floristic treatments, and we have the benefit of his insights in these works. We were fortunate to have so gifted, friendly, and conscientious a botanist on our staff

at the Field Museum, and we greatly mourn his loss.

Acknowledgments

Beginning in 1961, fieldwork in Central America by Field Museum staff and their associates in Honduras and Costa Rica was supported in part by grants from the National Science Foundation. The most recent of those grants was DEB-8103184. Collections made with this support together with many other herbarium holdings provide the basis for much of our descriptive and geographic information.

The staff and facilities of the Natural History section of the Museo Nacional de Costa Rica have been a primary resource for this project and have been most helpful in carrying out field programs for more than two decades. Recent work by collectors associated with the Museo Nacional, Duke University, and the Missouri Botanical Garden have greatly expanded our knowledge of Costa Rica's rich flora. Pablo Sánchez, Jorge Gómez-Laurito, Nelson Zamora, Barry Hammel, and Beryl Simpson have been especially helpful in providing information regarding the families included in this issue of the Flora. An anonymous reviewer made many helpful suggestions. Sadly, the publication of this group of families was initiated by Timothy Plowman's contribution of the Erythroxylaceae during the last year of his life.

FLORA COSTARICENSIS

Family #97 Krameriaceae

Family #98 Oxalidaceae

Family #99 Geraniaceae

Family #100 Tropaeolaceae

Family #101 Linaceae

Family #101a Humiriaceae

Family #102 Erythroxylaceae

Family #103 Zygophyllaceae

KRAMERIACEAE

By William Burger and Beryl B. Simpson

REFERENCE—B. B. Simpson, Krameriaceae. Flora Neotropica Monogr. 49: 1–108. 1989.

Perennial herbs, **shrubs**, or rarely small trees, usually vestitured with single-celled hairs, hemiparasitic on the roots of other plants; stipules absent. **Leaves** alternate or fasciculate, simple in Central America (rarely trifoliate), petiolate or sessile, the leaf blades with entire margins. **Inflorescences** of single axillary flowers, terminal racemes (by condensation of internodes and loss of leaves) or open panicles, peduncles with 2 opposite foliaceous bracts, pedicels variable. **Flowers** bisexual, bilaterally symmetrical (zygomorphic), hypogynous, colorful parts pink, rose, or purple, rarely reddish brown to yellow, imbricate, deciduous, sepals (4–)5, free and petaloid, showy, unequal with the 3 outer usually larger than the inner sepals and the petals; **petals** (4–)5, unequal and dimorphic, small, the 3 upper (adaxial) long-clawed, united near the base in some species, the petal-laminae small or absent, the 2 lower (abaxial) petals smaller, thick, sessile, laterally flanking the ovary, glandular on the dorsal surfaces (and called elaiophores); **stamens** (3–)4, usually alternating with the 3 upper petals and angled downward and outward, filaments thick, free or united near the base or adnate to the bases of the adaxial petals, anthers basifixed, dehiscing near the apex by membranous pores, pollen 3-porate (3-colporate), the pores often expanded equatorially; **pistil** 1, of 2 united carpels with one developing and the other vestigial, ovary with 1 locule with 2 pendulous ovules from an axial placenta near the top of the locule, style obliquely terminal, stigma simple. **Fruit** 1-seeded, dry and indehis-

cent, usually covered with spines, the spines often with retrorse barbs; seeds globose with a smooth seed coat, with a straight embryo and 2 thick cotyledons, endosperm absent.

A monogeneric New World family with 17 species ranging from the southwestern United States (with disjunct populations in Florida and Georgia), Mexico, and the West Indies southward to northern Chile and Argentina. Major centers of species diversity are in northern Mexico and central and eastern Brazil. All the species are found on sandy or rocky soils in arid or seasonally dry climates. The family is not now of commercial importance, but the roots have been used medicinally and as a source of yellow and reddish brown dyes. The Krameriaceae were once thought to be closely related to the Leguminosae, but a relationship with the Polygalales is more likely.

Krameria Loefling

With the characters of the family (see above). The genus is quite distinctive because of its zygomorphic flowers, the unique configuration of calyx and corolla, and its unusual fruit. The flowers are usually held erect with the longitudinal plane of the open perianth vertical, somewhat like those of *Senna* or *Cassia* (Leguminosae). This orientation and the unusual morphology of the flowers are part of an interesting pollination syndrome in which the lower petals secrete lipids that are collected by female *Centris* bees. The flora parts were misinterpreted in the past; see the article by B. B. Simpson (1982) and the monograph cited above.

Key to the Species of *Krameria*

- 1a. Leaves with distinct petioles, leaf blades narrowly elliptic to lanceolate and gradually narrowed at the base; flowers pinkish fading to white *K. ixine*
- 1b. Leaves sessile or subsessile, leaf blades linear to linear-lanceolate, abruptly narrowed at the base; flowers yellow and dusky rose *K. revoluta*

Krameria ixine Loebl., Iter hispan. 195. 1758. *K. cuspidata* K. Presl, Reliq. haenk. 2: 103. 1835. Figure 1.

Small **shrubs**, erect to 1(–1.5) m tall, often many branched and to 1 m broad, internodes 1–15(–25) mm long, leafy stems 1–3(–4) mm thick, densely strigillose with thin whitish or grayish hairs 0.2–0.8 mm long. **Leaves** simple, petioles 3–7(–9) mm long, merging gradually with the decurrent lamina-base, strigillose; **leaf blades** 8–20 (–33) mm long, 3–8 mm broad, narrowly oblong or narrowly elliptic to narrowly obovate or lanceolate, acute with a spinose tip 0.5–1.5 mm long, acute at the base and decurrent on the petiole, obscurely palmately 3-veined, densely strigillose. **Inflorescence** in lateral or terminal racemes, peduncles usually shorter than the subtending leaves, with a pair of opposite bracts in the middle, densely strigillose. **Flowers** ca. 8 mm long and 12 mm broad when dry, perianth rose-pink to deep red, magenta or reddish brown, turning white with age, sepals 4–10 mm long, broadly oblong, densely whitish sericeous on the outer surfaces; upper **petals** united in the lower half; **stamens** didynamous with anthers ca. 1 mm long. **Fruit** globose, body of the fruit 4–7 mm in diameter, covered with short (1 mm) whitish hairs and longer (1.6–4.6 mm) orange or reddish spines with thin retrorse barbs distally.

Plants of seasonally deciduous vegetation along the Pacific slope of Mexico and Central America. Growing from near sea level to 400 m elevation in Costa Rica (to 1000 m in Honduras and 1500 m in Guatemala). Flowers and fruits have been collected during the wet season in Costa Rica (late May to December). This species ranges from western Mexico (Sonora) to northwestern Costa Rica, through most of the Greater and Lesser Antilles, and into South America in northeastern Colombia, northern Venezuela, and eastern Guyana.

Krameria ixine is recognized by its short shrubby habit, grayish puberulence, small, petiolate, narrowly elliptic and spine-tipped leaves, unusual pink flowers with the sepals turning white with age, and distinctive rounded fruits with dense whitish hairs and longer barbed spines. The species is known only from northern Guanacaste Province in Costa Rica, where it ranges over a wider area than its congener, *K. revoluta*.

Krameria revoluta Berg, Bot. Zeitung (Berlin) 14: 751. 1856. Figure 1.

Small **shrubs** or herbs with woody bases, to 50 cm tall, with many branches, woody stems 2–5 mm thick, dark gray to blackish and glabrescent, with longitudinal fissures or smooth, leafy internodes 1–4(–8) mm long, 0.6–2 mm thick, grayish white with appressed ascending strigulose hairs 0.9–1.5 mm long. **Leaves** alternate, pale

grayish or grayish white, sessile or subsessile (petioles less than 2 mm long if present); **leaf blades** 6–22 mm long, 1.2–2.8(–3.5) mm broad, linear to linear-lanceolate (narrowly lanceolate), tapering gradually to the acute apex, with a small glandlike tip or spine that dries dark, abruptly narrowed at the base, margins usually revolute when dried, covered with white or pale grayish appressed-ascending strigose hairs ca. 0.5 mm long. **Inflorescences** terminal racemes (but flowers may appear to be solitary in distal leaf axis in early stages because of the leaflike bracts), flowers borne on slender strigulose peduncles 4–12 mm long, usually with 2 opposite leaflike linear bracts in the middle, larger outer sepals 5–9 mm long and ca. 3 mm broad, appressed whitish sericeous on the outside, petaloid (upper) **petals** ca. 6 mm long and 2.5 mm broad, basally connate for 3.4–4 mm, blades yellow or dull red to brownish red, glandular petals orbicular, 2–3 mm in diameter; **stamens** ca. 4 mm long. **Fruits** 4–6 mm in diameter (to 11 mm measuring the spines), globose to ovoid, covered by short dense whitish hairs and slender red and yellow spines to 3.5 mm long, spines with retrorse barbs.

Plants of seasonally very dry deciduous forest and shrub communities, from 50 to 250 m elevation in Costa Rica (to 1400 m elsewhere). Flowers and fruits have been collected in September and October in Costa Rica. The species flowers from July through December elsewhere. The species ranges along the Pacific side of middle America, from southern Mexico to northwesternmost Costa Rica.

Krameria revoluta is recognized by its almost linear alternate leaves covered with whitish hairs, unusual yellow and dusky rose flowers, puberulent fruit with barbate spines, and restriction to very dry habitats. In Costa Rica the species is known only from two collections made in Santa Rosa National Park, Guanacaste (*Salas & Poveda s.n.* [1974] CR, *Callaway* 485 CR).

OXALIDACEAE

By William Burger

REFERENCE—Alicia Lourteig, Oxalidaceae, in R. E. Woodson, R. W. Schery et al., Flora of Panama, Ann. Missouri Bot. Gard. 67: 823–850. 1980.

Herbs, rarely shrubs or small trees; stipules present and adnate to the petiole or absent. **Leaves** alternate, subopposite or closely clustered (sometimes all basal), pinnately or palmately compound, often (in *Oxalis*) trifoliolate, rarely unifoliolate, often folding up at night, petiolate, the **leaf blades** usually entire. **Inflorescences** axillary or cauliflorous, usually cymes, sometimes in compound racemiform or umbelliform panicles, some-

Krameria ixine



FIG. 1. Krameriaceae: two species of *Krameria*.

times densely clustered or reduced to solitary flowers. **Flowers** bisexual, radially symmetrical (plant rarely with apetalous and minute cleistogamous flowers), hypogynous, often with trimorphic heterostyly, sepals 5, united only near the base, imbricate (valvate), persisting in fruit; **petals** 5, free or connate near the middle, contorted or imbricate in bud, narrowed at the base (clawed), nectar glands often present between petals and stamens and alternating with the petals; **stamens** basically 10 in 2 whorls of 5 (15 in *Hypseocharis*), the outer stamens usually shorter and opposite the petals, all the stamens functional or 2–5 not bearing anthers and staminodial, filaments slender and united in the lower half or only at the base, anthers ovoid, versatile, 2-theous, dehiscing longitudinally and introrse; **pistil** 1, (3–)5-carpellate, ovary (3–)5-locular and lobed, each locule with (1–)2–15 ovules pendulous from axile placentae, styles 5 and free (1 in *Hypseocharis*), persisting, stigmas bifid or bicapitate. **Fruit** a 5-lobed capsule (rarely a berry), usually 5-locular, calyx and style persisting, dehiscence loculicidal, seeds often ejected by a basal aril (the elastic outer integument); seed

with fleshy endosperm (rarely endosperm absent), embryo straight.

A family of six genera and about 950 species found throughout the world in cold climates and warm. The largest genus of the family is *Oxalis*, with over 800 species worldwide. *Averrhoa* is widely planted in the tropics for its fruit, and *Biophytum* is pantropical. *Hypseocharis* is endemic to the tropical Andes, but Boesewinkel has recently suggested this genus be transferred to Geraniaceae (see Acta Bot. Neerl. 37: 111–120. 1988). The family is recognized by the compound leaves, 5-parted flowers, obdiplostemonous stamens, pistil with usually five styles and five locules, and loculicidal capsule or berry. The following treatment is based largely on the herbarium annotations and publications of Alicia Lourteig.

Key to the Genera of Oxalidaceae

- 1a. Trees, leaves pinnate; fruit over 5 cm long, fleshy and edible; plants grown in gardens and parks *Averrhoa*
- 1b. Herbs or small (to 3 m) subshrubs; fruit a small dehiscent capsule; ornamental and wild plants 2a
- 2a. Leaves usually 3-foliolate; capsule dehiscing by longitudinal slits, carpels (mericarps) remaining attached to the central axis of the fruit *Oxalis*
- 2b. Leaves long-pinnate with many small leaflets; capsules loculicidal in a radial form, carpels remaining attached only at the base *Biophytum*

Averrhoa Linnaeus

Trees, usually small and widely branching, puberulent; stipules minute or absent. **Leaves** alternate, compound and imparipinnate, petiolate, leaflets short-petiolulate, alternate or subopposite on the rachis, margins entire. **Inflorescences** solitary and axillary or cauliflorous, of cymes in racemiform panicles, bracts and bracteoles subulate and caducous. **Flowers** bisexual and regular, heterostylous, sepals 5, imbricate, united near the base; **petals** 5, free or united near the middle, contorted in bud; **stamens** 10 in 2 series or 5 fertile and 5 staminodial;

ovary 5-lobed, each lobe with 1 locule and 2–7 ovules. **Fruit** an elongate fleshy indehiscent berry, pendant at maturity, usually with 5 longitudinal ridges or lobes; **seeds** 2–several in each locule, endosperm fleshy.

A genus of only two species, probably native to Southeast Asia. Both species are widely planted in the tropics and subtropics. The fleshy, usually yellow or orange fruits have a pleasant but acidic flavor and are used to make drinks or preserves or are eaten raw.

Key to the Species of Averrhoa

- 1a. Leaves with 6–15 leaflets, leaves evenly spaced along the distal branchlets; petals to 9 mm long, fertile stamens 5; fruit longitudinally deeply 5-lobed; commonly planted *A. carambola*
- 1b. Leaves with 14–40 leaflets, leaves clustered near the tips of branchlets; petals 10–20 mm long, fertile stamens 10; fruit smooth or slightly lobed; less common *A. bilimbi*

Averrhoa bilimbi L., Sp. Pl. 428. 1753.

Trees to 15 m tall, trunks to 30 cm thick, branches usually ascending, leafy branchlets ca. 7 mm thick, densely

brownish or yellowish puberulent. **Leaves** clustered at the tips of branchlets, to 65 cm long, petioles 4–13(–17) cm long, ca. 2.5 mm thick and expanded at the base, densely puberulent; **leaf blades** 2.5–8(–15) cm long, 1.2–3(–5) cm broad, oblong to ovate-oblong, asymmetrical,

acuminate at the apex, rounded to truncate at the base, minutely puberulent above and below. **Inflorescences** axillary or cauliflorous on aborted branchlets, racemiform or paniculate, 15–20-flowered, puberulent and glandular, bracts ca. 4 mm long, bracteoles 1.5–2 mm long, subulate, pedicels 4–20 mm long, articulate near the middle. **Flowers** small, sepals 1.5–2.5 mm long, 1.5–3 mm wide, ovate to elliptic (1 internal sepal oblong), pubescence appressed and glandular on both surfaces; **petals** 10–20 mm long, 2–5 mm wide, narrowly spatulate, reddish purple, caducous; **stamens** 10, all fertile, biseriate with longer (10 mm) and shorter (4 mm) filaments; **pistil** 7.5–12 mm long, ovary 4–7.5 mm long. **Fruits** 5–10 cm long, ca. 3.5 cm in diameter, smooth or longitudinally 5-lobed (circular to pentagonal in cross section).

Averrhoa bilimbi has smaller, more sour fruits than its congener, and the fruits are not so prominently ridged. The fruits are used for preserves or for flavoring. This species is not commonly planted in Central America. It is called *mimbro* and *tiriguro* in Costa Rica.

Averrhoa carambola L., Sp. Pl. 428. 1753.

Trees to 10(–25) m tall, much branched, leafy branchlets 2–3 mm thick and minutely (0.1 mm) puberulent with ascending thin whitish hairs, becoming glabrous and brownish. **Leaves** separate along the distal twigs, 10–20 cm long, petioles 15–35 mm long, thickened near the base and minutely puberulent; distal **leaf blades** (leaflets) 5–8 cm long, 2–3 cm broad, ovate to ovate-oblong, short-acuminate at the apex, truncate or rounded at the base, proximal laminae 1.5–3 × 1–2 cm, minutely puberulent on the major veins above and below. **Inflorescences** axillary or cauliflorous, to 8 cm long, of cymes borne on racemiform panicles or fasciculate, peduncle to 1 cm long, pedicels 3–4 mm long. **Flowers** ca. 8 mm long, sepals 2.5–3.5 mm long, 1–2 mm wide, oblong; **petals** 6–9 mm long, 1.5–3 mm broad, spatulate, connate at the middle, papillate-glandular within, violet to purple and white; fertile **stamens** 5 with longer (2–2.5 mm) filaments, 5 inner stamens/staminodes with shorter filaments and usually without anthers; **pistil** 3–4 mm long, cylindrical-ellipsoid. **Fruits** 8–13 cm long, 5–6 cm thick, elliptic-oblong to ovoid, with 5 prominent longitudinal ridges and grooves (strongly pentagonal or star-shaped in cross section), yellowish translucent, mildly acidic to sweet.

Averrhoa carambola is widely planted, both as an ornamental and for its value as a fruit tree. The

acidic fruits are eaten fresh and are used in salads and desserts. The glabrous, 5-ribbed, lustrous yellow fruits are distinctive. The fruit is often called *carambola*, both in Spanish and English.

Biophytum DeCandolle

Herbs or subshrubs, sometimes woody at the base, erect or decumbent, stems usually bearing a ring of stiff retrorse hairs at the apex; stipules obscure. **Leaves** fasciculate at the apex of the stem or at ground level on the rootstock, pinnately compound with many leaflets, short-petiolate, paripinnate (the terminal leaflet has been reduced to a bristle), the **leaf blades** (leaflets) opposite, very short petiolulate and articulate at the rachis, gradually differing in shape from base to apex (along the rachis) with the lower pairs reniform to broadly ovate and smaller than the more distal leaflets, puberulent. **Inflorescences** solitary and axillary, cymose or few-flowered, pseudo-umbellate, peduncles long, pedicels subtended by the spiral and imbricate bracteoles. **Flowers** bisexual and regular, 5-parted, sepals essentially free, imbricate, scarious; **petals** coherent near the middle, white to yellow, orange, pink, or red; **stamens** 10, biseriate with 5 shorter and 5 longer filaments, connate near the base, all fertile or sometimes the shorter without anthers; **ovary** 5-lobed and 5-locular, each locule with 2–6 ovules alternating along 2 rows within each locule, styles 5, free, each with an enlarged bifid subcapitate or papillate stigma. **Fruits** capsular and covered by the persisting sepals, obovoid to subglobose or ellipsoid, each valve (carpel) 1–6-seeded, loculicidally dehiscent, the valves opening upward over the sepals in a 5-pointed star pattern and remaining attached at their base (centrally); **seeds** expelled explosively from the outer integument, usually tuberculate.

Biophytum is a pantropical genus of about 75 species, with one species in northern Central America and five additional species in Panama. Only one species has been recorded in Costa Rica, but it seems likely that a second will be found in Costa Rica. The plants are quite distinctive because of the relatively long, narrow leaves clustered at the ends of unbranched stems, and the many opposite little leaflets that change their shape along the length of the leaf. The plants look like miniature palms or tree ferns. The following account is based on the treatment for the Flora of Panama by Lourteig (Ann. Missouri Bot. Gard. 67: 825–834. 1980).

Key to the Species of *Biophytum*

- 1a. Middle leaflets usually oblong to slightly falcate in outline, the larger leaves usually with less than 22 pairs of leaflets (range: 9–26 pairs); cymes condensed and 2–4 mm broad *B. dendroides*
- 1b. Middle leaflets usually slightly falcate in outline, the larger usually with more than 22 pairs of leaflets (range: 13–34 pairs); cymes ca. 5 mm broad *B. falcifolium*

Biophytum dendroides (H.B.K.) DC., Prodr. 1: 690. 1824. *Oxalis dendroides* H.B.K., Nov. gen. & sp. 5: 194. 1822. Figure 2.

Rhizomatous herbs, with leaves from the apex of an underground stem or from an erect or decumbent stem to 15(–35) cm long and 0.5–3(–5) mm thick, stems unbranched (rarely with 2–4 branches), puberulent with retrorse appressed hairs but glabrescent, roots to 10 cm long, fibrous. **Leaves** pseudoverticillate at the ends of stems, pinnate with 9–18(–26) pairs of leaflets, petioles 1–4 cm long, leaflets sometimes overlapping, rachis 2–10 cm long and hirsutulous, petiolules ca. 0.2 mm long; proximal **leaf blades** (leaflets) 1–2.5 mm long, 1–2.5 mm wide, asymmetrically ovate to triangular, middle leaflets 5–10 mm long and 1.5–4 mm wide, subrectangular to subfalcate, distal leaflets 6–11 mm long and 2.5–5 mm wide, asymmetrically obovate, glabrous to sparsely hirsutulous on 1 or both surfaces, midvein with 8–18 ascending secondary veins on each side, a submarginal vein present but obscure. **Inflorescences** from the axils of the fasciculate leaves, with a distal cluster of flowers but only 1 flower blooming at a time, peduncles 1–8 cm long, minutely puberulent to hirsutulous, pilose beneath the flowers, bracts subulate to 6 mm long, bracteoles 2–7 mm long, 0.3–1.5 mm wide, linear to lanceolate, inner bracteoles equaling or exceeding the pedicels, pedicels 1–5 mm long, articulate in the lower half, glabrous or finely puberulent. **Flowers** whitish pink or lilac, sepals 5–7 mm long, 1–1.5 mm wide, lanceolate and acuminate with a slender tip, glabrous or with ascending hairs, densely hirsutulous at the base, with parallel raised venation; **petals** 6–10 mm long, spatulate to obovate, narrowed at the base, slightly retuse at the apex; **stamens** with filaments enlarged at the base, longer stamens 4.5–5.5 mm long, shorter stamens 3–4 mm long; **pistil** microstylous or macrostylous, puberulent apically, stigmas small and bifid. **Fruits** capsular, 2.5–4 mm long, oblong to subglobose, yellowish to violet, puberulent near the apex, valves 1–6-seeded, short pubescent within; **seed** ca. 1.5 mm long, semiovoid to triquetrous, planar on one side and convex on the other, longitudinally tuberculate.

Herbs of evergreen formations from near sea level to 1200 m elevation. This species ranges from Mexico through Guatemala, Honduras, Nicaragua, and Panama to Ecuador; it has not been recorded from Costa Rica.

Biophytum dendroides is recognized by its unusual habit (resembling miniature palms or tree ferns) with the verticillate long-pinnate leaves arising from the apex of a small, usually unbranched, erect woody stem. The opposite asymmetrical sessile leaflets that change their size and shape along the length of the rachis, and the long, thin, few-flowered peduncles also help make these plants distinctive. This species has fewer leaflets on the mature leaves than does *B. falcifolium*. The apparent absence of *B. dendroides* in Costa Rica is puzzling.

Biophytum falcifolium Lourteig, Ann. Missouri Bot. Gard. 67: 829. 1980. Figure 2.

Erect or decumbent herbs, erect stems 5–12 cm long and branched only near the base, ca. 2 mm thick, puberulent in early stages and drying blackish. **Leaves** pseudoverticillate at the end of the stem, 5–11(–15) cm long and 7–14 mm broad, pinnate with 13–34 pairs of opposite or subopposite leaflets, the leaves linear-cuneate in outline, petioles 4–11 mm long, ca. 0.5 mm thick, rachis minutely puberulent above and hirsutulous beneath, petiolules 0–0.2 mm long, thick; proximal **leaf blades** (leaflets) 3–6 mm long and 1.5–3 mm wide, oblong to rhombic-oblong and slightly falcate (curved forward), central leaflets 5–11 mm long and 2–4 mm wide, falcate and oblong-rhombic, the distal leaflets equal to or shorter than the middle leaflets, usually with a short (1–2 mm) filamentous mucro at the apex, broadly obtuse to subtruncate at the base, glabrous to finely puberulent above, puberulent beneath. **Inflorescences** 1–3, subsessile and subcapitate with the condensed cymes globose to cylindrical, with 1–5 flowers in various stages of development, pedicels 8–16 mm long, minutely puberulent, bracts ca. 2.5 mm long, subulate, purplish, bracteoles 1.5–3 mm long, 1-veined, keeled, spirally overlapping and green, puberulent and glandular. **Flowers** whitish, sepals 4.5–7 mm long, 0.7–1.3 mm wide, linear-elliptic, 5–7 veined, densely glandular; **petals** 6–10 mm long, oblong-spatulate, cream-white with pink veins and yellowish near the base, narrowed at the base; longer **stamens** 3–3.5 mm long and unequal, anthers ovoid and cordate at the base, shorter stamens 1–1.5 mm long, with sterile anthers or reduced to glands; **pistil** 3–4 mm long, ovary pilose near the apex and 5-lobed, each locule with 3–4 ovules, styles glandular-puberulent, styles ca. 1.5 mm long, stigma bifid. **Fruits** capsular, globose, ca. 3–5 mm long, shorter than the persisting calyx, glandular and puberulent at the apex; mature seeds unknown.

Plants of wet evergreen forest formations from about 300 to 1200 m elevation. The species is only known from Costa Rica and Panama.

Biophytum falcifolium is recognized by the larger number of leaflets on each leaf, the narrower, more falcate leaflets, and the whitish petals. The species has only recently been collected in Costa Rica (*L. D. Gómez et al.* 23843 CR, MO) from Río Uren, Limón Province, at an altitude of ca. 1000 m. This species is closely related to *B. panamense* Lourteig, but that species has more oblong leaflets.

Oxalis Linnaeus

REFERENCES—Melinda Denton, a monograph of *Oxalis*, section *Ionoxalis* (Oxalidaceae) in North America. Publ. Mus. Michigan State Univ. 4(10): 459–615. 1973. Alicia Lourteig, Oxalidaceae extra-austroamericanae. I. *Oxalis* L. Sectio *Thamnoxys* Planchon. Phytologia 29: 449–471. 1975;

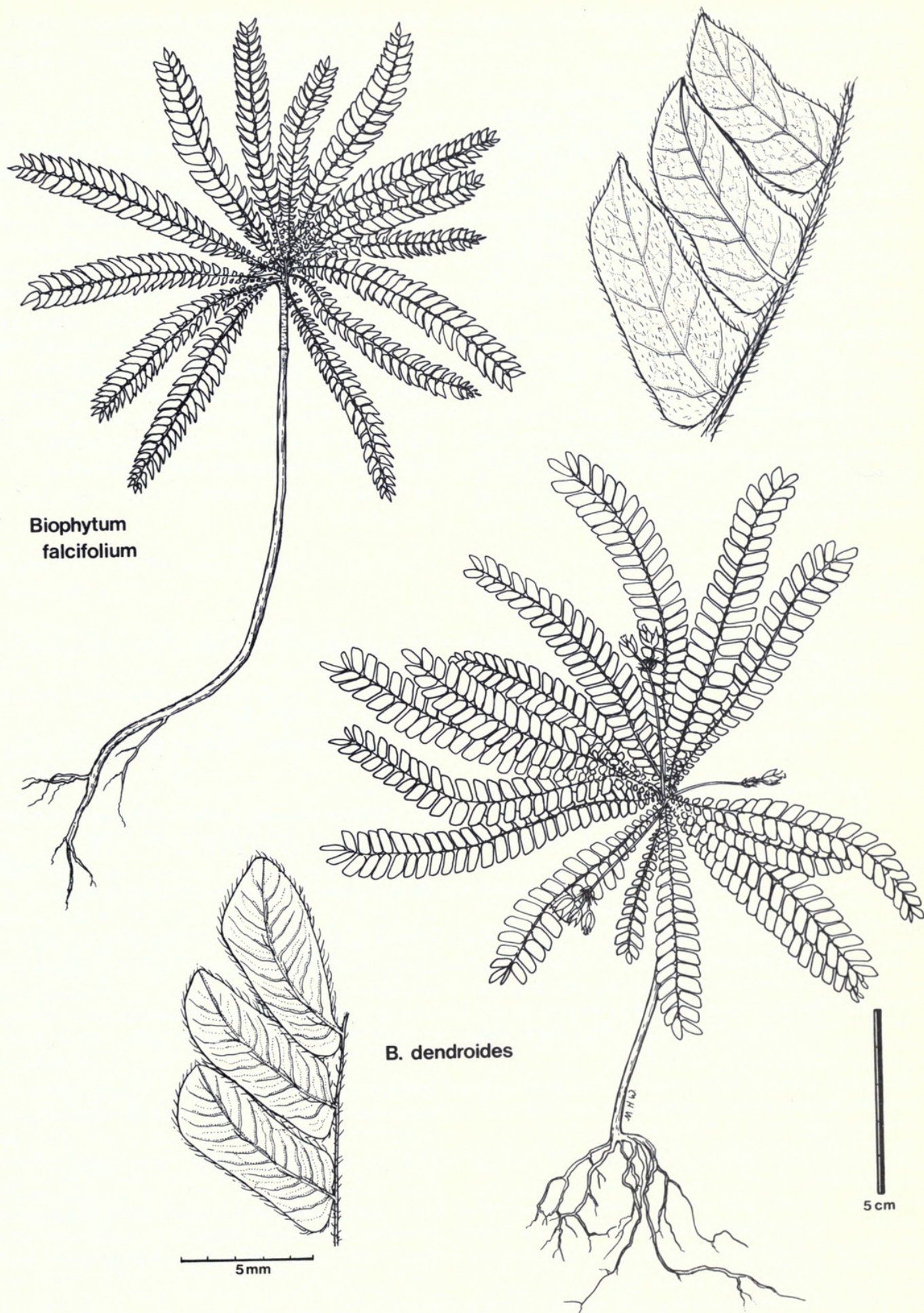


FIG. 2. Oxalidaceae: two species of *Biophytum*.

Perennial **herbs** or subshrubs (rarely vines), stems rhizomatous, bulbous, or aerial, herbaceous or woody, puberulent or rarely glabrous; stipules present or absent, sometimes glandlike or interpetiolar. **Leaves** alternate or subopposite to pseudoverticillate, basal or cauline, pinnately or palmately 3-foliolate (rarely 1-foliolate or 4-foliolate), petiolate, leaf blades (leaflets) usually entire, often obcordate. **Inflorescences** axillary, umbelliform cymes or solitary flowers, bracts small, bracteoles 2. **Flowers** usually showy, often heterostylous (rarely cleistogamous and reduced), sepals 5 (4), free or united near the base, imbricate, persisting in fruit; **petals** 5 (4), free, narrowed at the base, contorted in bud, caducous; **stamens** 10, the outer shorter stamens opposite the petals and alternating with the sepals, filaments slender, united near the base; **pistils** heterostylous and bi- or trimorphic, ovary 5-locular, with 1–15 ovules in each locule, styles 5 and free, stigmas capitate. **Fruits** cylindrical to oblong or globose capsules, glabrous or puberulent, loculicidally dehiscent, each locule with (1–)2–15 seeds, valves connate to the central axis and persisting; **seeds** usually ovoid, flattened on the sides, oblong to apiculate, testa char-

taceous, longitudinally ribbed to transversely striate or sculptured and densely verrucate, external integument fleshy and ariliform, breaking elastically and expelling the ripe seed, endosperm fleshy.

A worldwide genus of more than 800 species in both warm and cold environments. The trifoliate leaves that are narrowed to the base and, together, form an almost circular outline characterize many species. The leaves usually fold together at night and in inclement weather; they are often marked with red or purple. Species of the genus are often cultivated as ornamentals. *Oxalis tuberosa* (Oca) is an important tuber crop in the high Andes. Some species are called *acedera* and *vinagrillo* in Central America. The following work is based on Lourteig's treatment in the Flora of Panama (Ann. Missouri Bot. Gard. 67: 835–850. 1980) and includes three species not yet known to occur in Costa Rica (*O. dombei*, *O. microcarpa*, and *O. tetraphylla*).

Key to the Species of *Oxalis*

- 1a. Leaves pinnately 3-foliolate, the distal leaflet borne on a petiole-like extension of the rachis, laminae rounded apically, never deeply emarginate or obcordate distally 2a
- 1b. Leaves digitately (palmately) 3- or 4-foliolate, all the leaflets arising from the apex of the petiole, laminae usually emarginate to obcordate distally (except in *O. rhombifolia*) 5a
- 2a. Petals pinkish distally (white or yellowish at the base); terminal leaflets ovate to ovate-oblong *O. barrelieri*
- 2b. Petals yellowish throughout 3a
- 3a. Leaflets with small white punctate cystoliths, leaflets broadly ovate to oblong-orbicular; inflorescences often with foliaceous bracts; plants not yet collected in Costa Rica *O. dombei*
- 3b. Leaflets lacking small white punctate cystoliths; inflorescences with small linear bracts; plants known to grow in Costa Rica 4a
- 4a. Inflorescences umbelliform with 2–7(–15) flowers; capsule ovoid to oblong; terminal leaflets often narrowly ovate to narrowly triangular (lanceolate), bluntly obtuse to slightly emarginate at the apex; sepals 2.5–5 mm long; a common species *O. frutescens*
- 4b. Inflorescences elongate, with 5–12(–40) flowers; capsule globose; leaflets usually ovate-elliptic to rhombic, rounded at the apex; sepals 2–3 mm long; a wide-ranging species, but not yet collected in Costa Rica *O. microcarpa*
- 5a. Leaves and inflorescences arising from a single bulbous or woody rootstock, elongate woody or herbaceous internodes absent, petioles and peduncles usually over 10 cm long; flowers pink to lavender 6a
- 5b. Leaves and inflorescences arising from aerial or rhizomatous stems, elongate internodes present; flowers yellow 9a
- 6a. Leaves and inflorescences arising from a short, rhizomatous woody stem covered with the bases of old leaves; leaflets broad distally, rounded and deeply notched *O. articulata*
- 6b. Leaves and inflorescences arising from a basal bulb, bulb with many subulate scales and fibrous roots at the base 7a
- 7a. Leaflets 4, usually with rounded divergent distal lobes *O. tetraphylla*
- 7b. Leaflets 3, deeply notched to slightly emarginate distally 8a

- 8a. Leaflets often broadly triangular with relatively straight margins, usually retuse to slightly obcordate distally; sepals with distal brownish calli 0.3–1 mm long *O. latifolia*
- 8b. Leaflets rounded, broadly obovate in general outline; sepals with distal brownish calli 0.3–0.5 mm long *O. debilis*
- 9a. Petiole base without adnate stipules; stems erect and often climbing, clambering, or shrublike, to 2.5 m tall; distal leaflets often rhombic to ovate-triangular and acute at the apex *O. rhombifolia*
- 9b. Petiole base with adnate stipules (these sometimes difficult to see among the hairs); herbaceous plants rarely more than 50 cm tall; leaflets usually obovate with incised (notched) apex 10a
- 10a. Stems slender and decumbent, outer cortex often splitting off in age; leaflets usually less than 1 cm long; capsules densely and minutely puberulent, sepals usually more than half the length of the capsule; petals 8–14 mm long *O. filiformis*
- 10b. Stems slender and decumbent to erect, outer cortex not splitting off; leaflets (0.5–)1–3 cm long ... 11a
- 11a. Stipules with an abruptly truncated apex or the apex gradually merging with the petiole; distal leaflets broadly obovate to triangular; capsules covered with minute hairs, persisting calyx $\frac{1}{2}$ – $\frac{1}{3}$ as long as the capsule; petals 5–13 mm long *O. corniculata*
- 11b. Stipules with a short acute apex (often difficult to see among the hairs); distal leaflets narrowly obovate to obovate-oblong with a notch (ca. 3 mm deep in large leaflets); capsule with few erect multicellular hairs, persisting sepals equaling the capsule in length; petals 11–18 mm long *O. spiralis*

Oxalis articulata Savigny, in Lamarck, Encycl. 4: 686–687. 1797.

Herbs, to 40 cm high, stem rhizomatous, to 15 cm long and (1–)2 cm in diameter, covered distally with the short bases of leaves and their adnate stipules, roots tuberous, cylindrical, to more than 10 cm long; stipules 4–16 mm long and adnate to the leaf-base. **Leaves** fasciculate from the apex of the stem, 5–15(–30) cm long, erect or ascending, petioles (4–)9–18(–30) cm long, slender, pubescent to glabrate with thin hairs ca. 0.5 mm long, petiolules 0.5–1 mm long, thick, pubescent; **leaf blades** (leaflets) 5–20(–30) mm long, 7–35(–45) mm wide, obcordate and widely obovate in outline, rounded distally and emarginate to retuse at the apex, cuneate at the base, usually with appressed ascending thin whitish hairs ca. 0.7 mm long on both surfaces, with dark or orange punctations or lines (calli) 0.2–0.5 mm long near the margins (less often scattered over the surface). **Inflorescences** umbelliform and cymose with 6–20 flowers, peduncles usually longer than the leaves (2.5–40 cm), pubescence similar to the petioles, bracts and bracteoles 0.5–3 mm long, lanceolate, pedicels 1–3(–5.5) cm long, slender and articulate at the base. **Flowers** violaceous to pink, sepals 2–5(–6.5) mm long, 1–2 mm broad, narrowly elliptic to lanceolate, appressed puberulent with thin straight ascending hairs; **petals** 5–15(–20) mm long, obovate, connate near the middle, areas exposed in bud covered with appressed whitish hairs; longer **stamens** ca. 3.5 mm long, shorter **stamens** ca. 2 mm long, united for more than half their length; **pistil** ca. 5.5 mm long, ovary usually pilose distally, each locule with 4–8 ovules, styles puberulent, the flower with long, medium or short styles, stigma small and capitate. **Fruits** cylindrical to oblong, 8–11 mm long, acute at the apex, with ascending appressed hairs distally on the carpels or all over, the persisting calyx ca. $\frac{1}{2}$ as long; **seeds** 1–1.3 mm long, ovoid to ellipsoid and acute at both ends, with 8 or 9 ribs and 4–8 pits, pale brown.

A cultivated species originally from Uruguay and adjacent areas, escaping and becoming naturalized in some areas. *Oxalis articulata* is recognized by the short, thick stems bearing the closely clustered leaves and inflorescences, the pink to violaceous flowers, and the rounded leaflets punctate along the margin.

Oxalis barrelieri L., Sp. Pl. ed. 2, 624. 1762. Figure 4.

Herbs or subshrubs, to 1 m tall, leafy internodes (0–)0.5–8 cm long, 0.5–3 mm thick, sparsely puberulent with thin whitish hairs, glabrescent, roots fibrous; stipules linear and ca. 3 mm long or absent. **Leaves** alternate to subopposite, petioles 1–4 cm long, ascending, canaliculate, sparsely puberulent with thin hairs, more densely puberulent and articulate near the base, the rachis 3–15 mm long, petiolules 0.5–1 mm long, with thin hairs; **leaf blades** (leaflets) 10–55 mm long, 8–25 mm broad, ovate to elliptic-oblong (rarely suborbicular), bluntly obtuse to acute at the apex, obtuse to rounded at the base, asymmetric at the base in lateral leaflets, sparsely puberulent above and below. **Inflorescences** usually axillary cymes longer than the leaves, (1–)3–11(–30)-flowered, peduncles to 6.5 cm long, 0.5–0.8 mm thick (dry), glabrescent, terminated by a flower and with 2 unbranched secondary branches to 3 cm long, bracts and bracteoles 1–2 mm long, pedicels 1.5–3.5(–5) mm long, articulate above the base. **Flowers** pink, sepals greenish, 3–4 mm long, 1–2 mm wide, linear to narrowly oblong, acute and minutely mucronate, sparsely and minutely puberulent; **petals** 7–9 mm long, ca. 3.5 mm broad, retuse, obovate to spatulate, pink distally, white or yellow in the lower half; longer **stamens** ca. 3 mm long, ligulate at the middle,

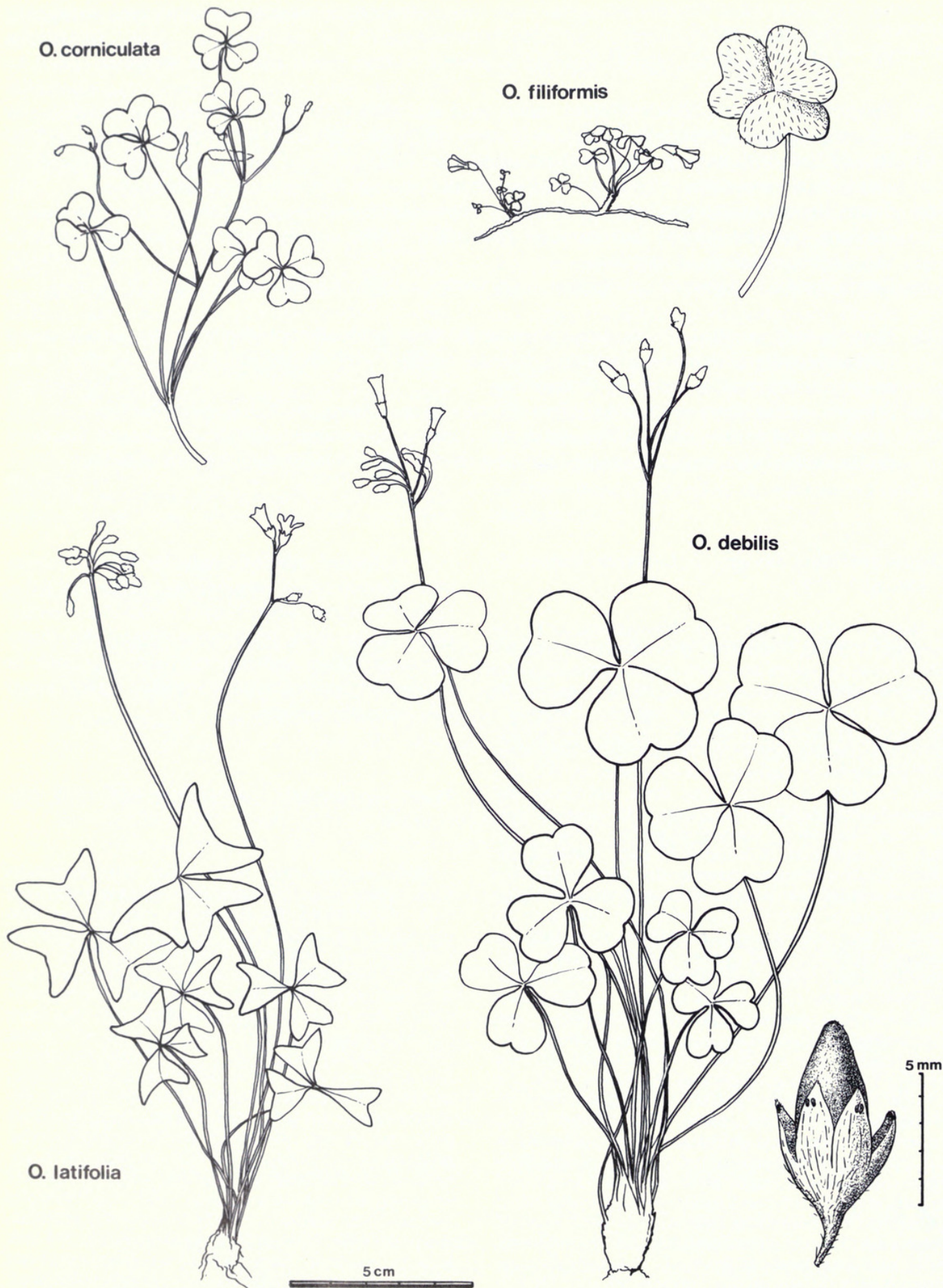


FIG. 3. Oxalidaceae: four smaller species of *Oxalis*.

shorter stamens 1.5–2 mm long; **pistil** 3.5–4 mm long, ovary glabrous and ovoid, each locule with 3 or 4 ovules, styles puberulent, stigma bifid and subcapitate. **Fruits** 5–9 mm long, to 4 mm thick, ovoid, persisting calyx half as long; **seeds** 1.5–2 mm long, ca. 1 mm broad, ovoid with slightly flattened sides, with 6–8 prominent transverse ridges/grooves, and minutely tuberculate, brown.

Plants of the evergreen lowland Caribbean forest formations from near sea level to 1000 m elevation (rarely from as high as 2000 m in the Chiriquí highlands); flowering collections have been made throughout the year. This species is native to tropical and subtropical America and has been introduced into the Old World tropics.

Oxalis barrelieri is recognized by its erect, slightly woody stems, pinnately trifoliolate leaves (terminal leaflet borne on a slender rachis), leaflets acute to rounded distally (neither retuse nor emarginate), and pink flowers.

***Oxalis corniculata* L., Sp. Pl. 435. 1753. Figure 3.**

Annual **herbs**, much branched and with prostrate or decumbent stems to 50 cm long (rarely with erect stems to 40 cm tall), often rooting at the nodes, internodes variable in length (0–)1–4 cm long, 0.3–1.3 mm thick (dry), usually with a few slender whitish hairs ca. 0.5–1 mm long, roots usually fibrous; stipules 0.8–3 mm long and adnate to the petiole-base, 1–2(–3) mm wide and truncated at the apex, ciliate along the margin. **Leaves** alternate to subopposite or often fasciculate, petioles 1–5(–7) cm long, slender and ascending, with thin ascending whitish hairs, petiolules ca. 1 mm long, thick and pubescent; **leaf blades** (leaflets) 4–12(–20) mm long, 5–20 mm broad, broadly obovate and usually wider than long, rounded and retuse to deeply emarginate distally (obcordate) with a notch to 6 mm deep in large leaflets, cuneate to obtuse at the base, margin entire and ciliate, the pubescence variable with sparse to dense slender ascending or appressed hairs 0.5–1 mm long (often glabrous above). **Inflorescences** cymose or umbelliform, (1–)2–7-flowered, peduncles to 2–7(–21) cm long, slender with thin appressed hairs, bracts and bracteoles 0.5–4 mm long, linear to lanceolate, pedicels slender, ca. 10 mm long (lengthening in fruit). **Flowers** yellowish, sepals 2.5–5.5 mm long, elliptic-oblong to narrowly ovate (lanceolate), acute at the apex, translucent, lacking calli; **petals** 5–13 mm long, 1–3 mm broad, often pinkish or whitish within, yellow distally; longer **stamens** 4–6 mm long, shorter stamens 3.5–4 mm long and united in the lower third; **pistils** micro-, meso-, or macrostylous, to 8 mm long, ovary oblong and acute, each locule with 2–15 ovules, stigma 2-lobed and papillose. **Fruits** 5–25 mm long, 1–3 mm thick, subcylindrical and 5-ribbed, acute apically, minutely puberulent or with multicellular glandular hairs, persisting sepals $\frac{1}{5}$ – $\frac{1}{3}$ the length of the fruit; **seeds** ca. 1 mm long, ovoid but flattened on the sides, apiculate at the apex, with 6 longitudinal ribs (3 on each side) and prominent transverse ridges, brown or reddish brown.

A species originating in the Mediterranean area but now distributed worldwide. In Central America it is primarily found between 1000 and 2000 m elevation in open secondary vegetation, flowering throughout the year. The species is weedy and capable of hybridizing with indigenous species.

Oxalis corniculata is recognized by its small stature, trifoliolate leaves with laminae rounded and notched distally, unusual stipules, and yellow petals. The flowers usually open in the morning and close by the middle of the day. This species represents a complex of forms that have been treated as three subspecies and several varieties by Lourteig. It has been called *acederilla* in Costa Rica.

***Oxalis debilis* H.B.K., Nov. gen. sp. 5: 236, t. 466. 1822. *O. martiana* Zuccarini, Denkschr. Königl. Akad. Wiss. München 9: 144. 1825. Figure 3.**

Herbs, arising from a globose, ovoid, or oblong bulb 1–2 cm long, the bulb covered with scales and leaf-bases, the scales 7–13 mm long, 3–5 mm broad near the base, lanceolate and with 3 longitudinal ribs, roots fibrous; stipules to 13 mm long and 2 mm wide, completely connate to the leaf-bases (difficult to see). **Leaves** trifoliolate, petioles to 30 cm long, 0.4–1.5 mm thick, with thin transparent hairs 0.8–1.5 mm long or glabrous, petiolules 0.5–1 mm long; **leaf blades** (leaflets) 1.2–5.5 cm long, 1.5–6 cm broad, broadly obovate to suborbicular in outline, obcordate, broadly rounded distally and emarginate to retuse with a notch 2–7 mm deep, glabrous to sparsely puberulent above, more densely puberulent beneath with thin hairs ca. 1 mm long, minutely (0.1 mm) dark punctate along the margin and more sparsely scattered over the surface. **Inflorescences** bifid cymes (sometimes twice bifid), with 6–15 flowers, to 30(–45) cm long, peduncles similar to the petioles, bracteoles (at the base of the pedicels) 1–3 mm long, often with brownish calli, pedicels to 3 cm long, slender. **Flowers** pinkish to red-violet, sepals 4–7 mm long, 0.7–1.5 mm wide, narrowly ovate-elliptic or oblong, glabrescent, usually with 2 brown or orange antherlike calli ca. 0.5 mm long on the outside of the sepal apex; **petals** 2–3 times the length of the sepals, obovate and narrowed at the base; longer **stamens** 4.5 mm long, puberulent near the apex, shorter stamens ca. 3 mm long and glabrous, connate in the lower $\frac{1}{3}$; **pistil** ca. 7.5 mm long, ovary glabrous, macro- or mesostylous (rarely microstylous), with scattered thin hairs and glandular hairs, each locule with 2–12 ovules. **Fruits** ca. 18 mm long with styles 2 mm long, cylindric, calyx $\frac{1}{4}$ – $\frac{1}{3}$ the length of the capsule; **seeds** ovoid with flattened sides, with 12 longitudinal ribs and 12 transverse ridges, brown.

A weedy species found in evergreen areas from near sea level to 1500 m elevation in our area. The species is originally South American, but it is now widespread.

Oxalis debilis is recognized by its scaly bulbs, lack of visible internodes, rounded trifoliolate leaves with shallow distal notches, pinkish flowers, and unusual brownish calli at the tips of the sepals. These plants fruit infrequently, reproducing by bulblets.

Oxalis dombeii St. Hilaire, Fl. bras. merid. 1: 111.

1825. *O. darienensis* Woodson, Ann. Missouri Bot. Gard. 27: 312–313. 1940.

Herbs, stems erect, to 60 cm tall, leafy internodes to 10 cm long, to 4(–6) mm thick and woody near the base, glabrous to sparsely puberulent (sometimes more densely viscous-puberulent near the base), rhizome cylindrical, roots fibrous; stipules obscure. **Leaves** alternate, subopposite or pseudovercillate, pinnately trifoliolate, petioles 1–4 cm long, 0.2–0.4 mm thick (dry), articulate near the base, glabrescent, canaliculate above, rachis 3–6 mm long, petiolules ca. 0.5 mm long and drying dark; **leaf blades** (leaflets) 9–25 mm long, 5–22 mm broad, obovate to suborbicular, rounded at the apex, cuneate to the base, lateral leaflets often asymmetric, essentially glabrous above and below (fine ciliate on the margin), with whitish minute (0.1 mm) cystoliths usually visible on the dried leaf. **Inflorescences** bifid-cymose (the peduncle terminated by a flower and with 2 racemose branches), 10–25-flowered, peduncle to 7 cm long, 0.5–1.1 mm thick, glabrous, bracteoles 1–2 mm long, linear-lanceolate, pedicels about 3 mm long, articulate near the base, usually glabrous. **Flowers** yellow, sepals 4.5–7 mm long, 1–2.5 mm broad, ovate-oblong, acute, thin, glabrous; **petals** 7–14 mm long, obovate to subspatulate; longer **stamens** 2.5–4.5 mm long, minutely puberulent, shorter **stamens** 1–2 mm long, glabrous; **pistil** 2–5 mm long, ovary ca. 3 mm in diameter, each locule with 7–10 ovules, stigma capitate. **Fruits** 10–12 mm long, oblong to ellipsoid, the persisting styles 1–2 mm long, sepals $\frac{1}{2}$ – $\frac{2}{3}$ of the length of the capsule; **seeds** 1–1.2 mm long, ca. 1 mm broad, obovoid and slightly flattened on the 2 sides, with 5 or 6 weakly developed longitudinal ribs, the transverse ridges weakly developed, orange-brown.

Plants of drier deciduous forest vegetation and in semideciduous areas, ranging from central Panama to Peru and in the Galapagos Islands.

Oxalis dombeii is recognized by its short, erect habit, almost glabrous parts, pinnately trifoliolate leaves, white punctate cystoliths, and yellow flowers. Although not recorded from our area, it may become introduced into the seasonally dry Pacific lowlands.

Oxalis filiformis H.B.K., Nov. gen. sp. 5: 190, t. 460. 1822. *O. bradei* Knuth, Repert. Spec. Nov. Regni Veg. 23: 276. 1927. Figure 3.

Short, creeping **herbs** to 10 cm tall, stems horizontal or rhizomatous, to 50 cm long, internodes 0–5 cm long, 0.5–1 mm thick, dark brown or reddish, sparsely puberulent, outer layers splitting off in age; stipules 1.5–3

mm long, 0.5–1.7 mm broad, adnate to the petiole, ciliate. **Leaves** alternate or fasciculate, palmately trifoliolate, petioles 8–25 mm long, slender, sparsely to densely puberulent with thin ascending whitish hairs, petiolules ca. 0.5 mm long; **leaf blades** (leaflets) 2–10(–15) mm long, 3–15(–20) mm broad, broadly obcordate to obovate and retuse distally, rounded at the notched apex, cuneate at the base, both surfaces with thin, white, appressed hairs 0.5–1 mm long or the upper surface glabrous, ciliate along the edge. **Inflorescences** 1-flowered, 1–4(–8) cm long and exceeding the leaves, peduncles (measured to the bracteoles) about twice the length of the pedicels, filiform and with thin hairs, bracteoles 1–3 mm long, linear, pedicels 0.5–2.5 cm long. **Flowers** yellow, sepals 3–5 mm long, 1–2 mm wide, oblong, obtuse at the apex, usually with thin whitish hairs; **petals** 8–14 mm long, narrowly obovate; longer **stamens** 4–5.5 mm long, shorter **stamens** 3–4 mm long and connate to $\frac{1}{4}$ of their length; **pistils** 5–7 mm long, all longistylous, each locule with 3–6 ovules, style densely puberulent, stigmas bifid. **Fruits** 10–15 mm long, 2–3 mm thick, densely minutely puberulent, calyx $\frac{1}{2}$ – $\frac{2}{3}$ as long as the capsule, persistent styles 2–5 mm long; **seeds** 1–1.5 mm long, broadly ellipsoid and flattened on 2 sides, reddish brown, with 6 longitudinal ribs and transverse ridges.

Small plants of open sites in highland evergreen areas from 1100 to 2000 m elevation in Costa Rica and Panama. Flowering and fruiting material has been collected from December through May. The species ranges from Costa Rica southward to Ecuador at elevations from 1000 to 3000 m.

Oxalis filiformis is recognized by its small stature, creeping stems with older exfoliating surfaces, small obcordate leaflets, single-flowered inflorescences, and yellow petals. It appears to be native, and it prefers open sunny habitats, such as roadsides.

Oxalis frutescens L., Sp. Pl. 435. 1753, subsp. **angustifolia** (H.B.K.) Lourteig, Phytologia 29: 463–471, fig. 3. 1975. *O. angustifolia* H.B.K., Nov. gen. sp. 5: 193. 1822. *O. neaei* DC., Prodr. 1: 690. 1824. *O. coccinea* Woodson & Schery, Ann. Missouri Bot. Gard. 28: 431. 1941. Figure 4.

Herbaceous **subshrubs** or small shrubs to 40 cm tall, usually with several erect or ascending branches from a short (2–10 cm), woody base, leafy internodes 0.8–2 mm thick, with thin, ascending, straight or crooked whitish hairs to 1 mm long (shorter and curved in age); stipules obscure. **Leaves** alternate, subopposite or verticillate, pinnately trifoliolate, petioles 1–4 cm long, ca. 0.3 mm thick (dry), puberulent as the stems, rachis 2–5(–10) mm long, petiolules minute; **distal leaf blades** (leaflets) 7–23(–45) mm long, 3–12(–20) mm broad, about twice as long as the lateral leaflets, narrowly ovate to narrowly triangular or ovate-oblong, tapering to the apex and emarginate (or slightly notched), rounded to obtuse (acute) at the base, the smaller lateral leaflets usually more ob-

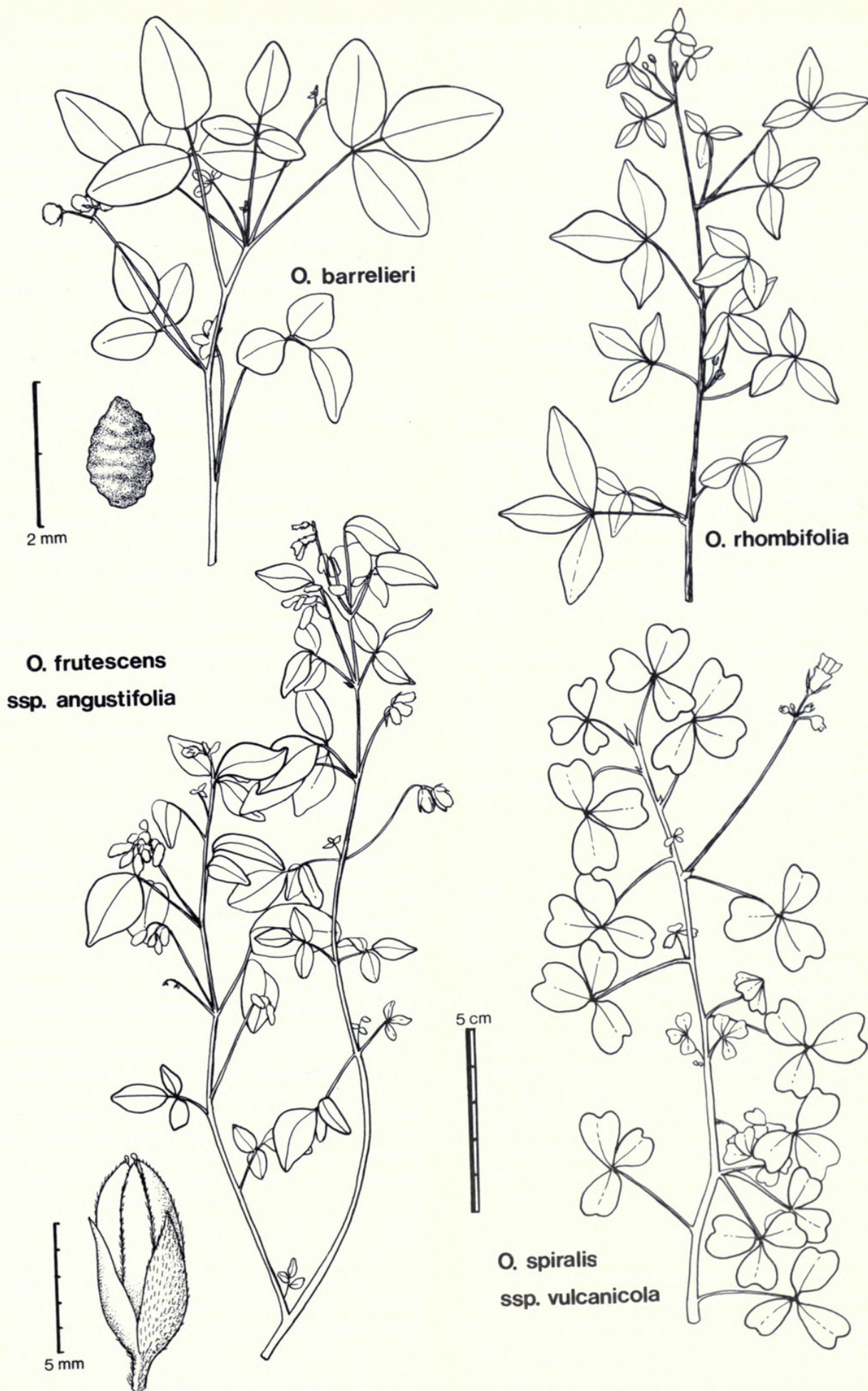


FIG. 4. Oxalidaceae: four larger species of *Oxalis*.

long and asymmetric, densely puberulent on both surfaces or glabrescent above. **Inflorescences** somewhat exceeding the leaves, cymes or umbelliform cymes, (1-)3-7(-15)-flowered, peduncles to 3.5 cm long, ca. 0.3 mm thick, puberulent, bracteoles ca. 1 mm long, pedicels 3-6 mm long, articulate ca. 1 mm above the base. **Flowers** yellow, sepals 2.5-5 mm long, ca. 1 mm broad, narrowly oblong, carpels ciliate on the back, calyx $\frac{1}{2}$ - $\frac{3}{4}$ the length obovate, emarginate at the apex, narrowed to the base; longer **stamens** ca. 3 mm long, shorter stamens ca. 1.5 mm long, connate to the lower $\frac{1}{3}$; **pistil** 3-5 mm long, minutely pilose, each locule with up to 8 ovules, stigmas bifid. **Fruits** 5-8 mm long, ca. 3 mm thick, ovoid to oblong, carpels ciliate on the back, calyx $\frac{1}{2}$ - $\frac{3}{4}$ the length of the capsule; **seeds** 1.5-2 mm long, ovoid and convex on two sides, apiculate, with 6 or 8 longitudinal ribs and 10-12 transverse ridges, pale brown.

Herbs and subshrubs of open and shaded sites in seasonally dry deciduous and partly deciduous forest formations from near sea level to 800(-?1600) m elevation on the Pacific slope of northern and central Costa Rica. Flowering material has been collected throughout the year except October and November. The species ranges from the Mexican-U.S. border through Central America and the West Indies to Argentina.

Oxalis frutescens is recognized by the preference for seasonally dry vegetation, herbaceous or shrublike habit with a slightly woody base, pinnately trifoliolate leaves with the terminal leaflet usually narrowed to the apex, and the yellow petals. It is found in open savannas as well as partly shaded sites.

Oxalis latifolia H.B.K., Nov. gen. sp. 237, t. 467. 1822. *O. ramonensis* Knuth, Notizbl. Bot. Gart. Berlin-Dahlem 7: 313. 1919. *O. chiriquensis* Woodson, Ann. Missouri Bot. Gard. 24: 190. 1937. Figure 3.

Herbs, stems not apparent, leaves and inflorescences from an ovoid or globose bulb to 25 mm long and 20 mm thick, with scales 7-15 mm long and 4-6 mm broad near the base, conspicuously 3-veined and with a long narrow tip; stipules connate to the petioles, often difficult to see among the leaf-bases, translucent brownish, auriculate at the apex. **Leaves** closely clustered on the bulb, erect or ascending, petioles 5-17(-25) cm long, 0.5-1.5 mm thick (dry), glabrous or with scattered thin hairs, petiolules ca. 1 mm long, thick; **leaf blades** (leaflets) 10-25(-45) mm long, 15-45(-75) mm broad, broadly obcordate to triangular in outline, the distal margin rounded and emarginate, slightly notched or deeply V-shaped with divergent lobes, cuneate to obtuse with straight sides at the base, glabrous or rarely with few hairs and cilia. **Inflorescences** exceeding the leaves in length, erect, to 35 cm long, umbelliform cymes with 5-20 flowers, peduncles 10-30 cm long, similar to the petioles, bracteoles

1-2 mm long, at the base of the umbel, pedicels 14-28(-40) mm long, filiform, glabrous. **Flowers** pink to purplish or lavender distally, sepals 3-6 mm long, 0.5-1.5 mm wide, narrowly oblong, thin translucent, glabrous, usually with 2 brown or reddish calli 0.3-1 mm long near the tip (the calli sometimes resembling anthers); **petals** 10-20 mm long, obovate to spatulate; longer **stamens** 4-7 mm long, shorter stamens 3-4 mm long and connate near the base; **pistils** 4-6(-8) mm long, usually microstylous, each locule with 4-8 ovules, stigmas bifid and papillose. **Fruits** 4-9 mm long, oblong and acute, glabrous, calyx $\frac{1}{4}$ - $\frac{1}{2}$ the length of the capsule; **seeds** ca. 1 mm long, ellipsoid and slightly lenticular, with 8-9 longitudinal ribs and 9-12 transverse ridges, pale brown.

Plants of moister situations in evergreen and partly deciduous vegetation from 1000 to 2000(-2700) m elevation. Most of our flowering collections have been made from May through August. The species ranges from Mexico and the Antilles southward along the Andes to Bolivia.

Oxalis latifolia is recognized by the bulbous base (without stems or internodes), largely glabrous parts, long peduncles, palmately trifoliolate leaflets with triangular or V-shaped form, and pink-lavender petals. Denton interpreted *O. latifolia* more narrowly in her monograph (see reference at the beginning of the genus). Central American material here considered *O. latifolia* was placed under *O. galeotti* Turcz. in that monograph.

Oxalis microcarpa Benth., Pl. hartw. 115. 1839.

Herbs or subshrubs, to 0.7(-1.2) m tall, internodes 2-16 mm long, ca. 1 mm thick, with thin, straight or curved whitish hairs 0.2-0.5 mm long, stems becoming slightly woody, 2-3.5 mm thick, gray and glabrescent; stipules obscure. **Leaves** alternate to subopposite, pinnately trifoliolate, petioles 2-4 cm long, filiform (only 0.2-0.3 mm thick when dry), puberulent, slightly thickened and articulate at the base, rachis 4-10 mm long, petiolules ca. 0.7 mm long, thick and puberulent; terminal **leaf blades** (leaflets) 10-24(-38) mm long, 6-14(-20) mm wide, ovate-elliptic to somewhat rhombic or elliptic, tapering to the rounded apex, obtuse to slightly rounded at the base, lateral leaflets smaller and slightly asymmetric at the base, sparsely to densely puberulent with thin appressed-ascending hairs 0.4-0.9 mm long on both surfaces. **Inflorescences** solitary and axillary, to 12 cm long in fruit, bifid cymes with 5-12(-40) flowers, peduncles to 6 cm long, filiform, the 2 branches to 6 cm long in fruit, bracteoles linear, pedicels 1.5-3 mm long, slender, articulate near the base. **Flowers** yellow, sepals 2-3 mm long, 0.5-1 mm broad, narrowly ovate to elliptic, acuminate, glabrous; **petals** 5-7 mm long, obovate to subspatulate; longer **stamens** ca. 2.5 mm long, shorter stamens 1.5-2 mm long; **pistil** ca. 2.5 mm long, ovary glabrous, each locule with 1 or 2 ovules, stigmas slender. **Fruits** 2-3 mm long, oblate to subglobose, glabrous, calyx usually equaling or slightly exceeding the capsule, walls of the

capsule thin; **seeds** ca. 1.5 long and 1 mm thick, ellipsoid, with 6–8 prominent longitudinal ribs and transverse ridges.

A species of seasonally dry areas of the Pacific slope in Central America, to 1500 m elevation, and flowering in the wet season. The species has not been reported from Costa Rica, but is found in Mexico, Honduras, and from Panama to Ecuador.

Oxalis microcarpa is recognized by the small stature, pinnately trifoliolate leaflets that are rounded distally, glabrous yellow flowers, and short, few-seeded capsules. The unusual distribution may imply that the species is not native to Central America. This species resembles *O. frutescens*.

Oxalis rhombifolia Jacquin, *Oxalis* 22, pl. 2. 1794.

O. maxonii Standley, J. Wash. Acad. Sci. 17: 311–312. 1927. Figure 4.

Shrubs, erect or climbing over others, to 2(–6) m high, internodes (1–)3–15(–40) cm long along the main branches, 1–3 mm thick, puberulent with thin curved hairs, dark brown; stipules obscure. **Leaves** alternate or fasciculate on short shoots, palmately trifoliolate, petioles 1–6 cm long, ca. 0.3 mm thick (dry), puberulent, thickened and articulate at the base, petiolules ca. 1 mm long, thick and puberulent; distal **leaf blades** (leaflets) 14–38(–45) mm long, 10–20(–25) mm broad, lateral leaflets slightly shorter, rhombic-ovate to ovate-elliptic, tapering to the obtuse or acute apex, acute to obtuse at the base, glabrescent on both surfaces or ciliate-puberulent with thin hairs ca. 0.5 mm long. **Inflorescences** solitary and axillary, bifid cymes to 9 cm long, 3–5-flowered, peduncles to 6 cm long, resembling the filiform petioles, bracts 3–7 mm long and linear, bracteoles 1.5–2 mm long, pedicels 2–5 mm long, puberulent, articulate at the base. **Flowers** yellow, sepals 4–6 mm long, 1–1.5(–2) mm wide, narrowly oblong, puberulent and densely ciliate at the tip; **petals** 10–18 mm long, obovate to subspatulate; longer **stamens** 5–8 mm long, shorter **stamens** 3–6 mm long, connate for $\frac{1}{2}$ above the base; **pistils** macro-, meso-, or microstylous, 6–10 mm long, ovary and styles puberulent, each locule 3-ovulate, stigmas bifid. **Fruits** 6–9 mm long, oblong or ovoid, densely puberulent, calyx $\frac{1}{2}$ as long as the capsule; **seed** ca. 2.2 mm long, lenticular, with 13 or 14 longitudinal ribs.

Plants of open and partially shaded sites in evergreen forest formations from 1000 to 2300 m elevation in our area. Flowering material has been collected from December to August in Central America. The species ranges from Mexico through Central America to Colombia and Venezuela.

Oxalis rhombifolia is recognized by its shrublike or clambering habit, palmately trifoliolate leaves

with somewhat rhombic leaflets, filiform petioles and peduncles, few-flowered inflorescences, and yellow petals. This species appears to be rare in Costa Rica, though common in the Chiriquí highlands of Panama.

Oxalis spiralis Ruiz & Pavon ex G. Don, Gen. hist. 1: 755. 1831. *O. vulcanicola* J. D. Smith, Bot. Gaz. 23: 241. 1897. *O. spiralis* subsp. *vulcanicola* (J. D. Smith) Lourteig, Ann. Missouri Bot. Gard. 67: 846. 1980. Figure 4.

Herbs, scandent, decumbent, or erect to 50 cm tall or 1.5 m long, internodes 2–30(–80) mm long, succulent, with thin yellowish to brown hairs 0.4–0.9 mm long, often reddish in life; stipules adnate to the petiole, thin and translucent, reddish, 2–5 mm long, narrow and acute at the free apex. **Leaves** alternate, palmately trifoliolate, petioles 1–5(–7) cm long, 0.3–1.2 mm thick (dry), glabrous or puberulent, petiolules 0.5–1 mm long; distal **leaf blades** (leaflets) 8–25(–38) mm long, 5–18(–25) mm broad, oblong-obovate to suborbicular-obovate, with a shallow (1–4 mm) distal notch and rounded distal lobes, cuneate at the base, glabrous or sparsely puberulent above, puberulent beneath with thin whitish appressed-ascending hairs ca. 0.5 mm long, laminae often purplish beneath. **Inflorescences** solitary and axillary or terminal, exceeding the foliage in length, cymes with 3–17 flowers or sometimes with only 1 or 2 flowers, peduncles 1.5–9(–12) cm long, puberulent, bracteoles ca. 1 mm long, linear, pedicels 5–12(–16) mm long, articulate above the base. **Flowers** yellow, sepals 4–8 mm long, 0.7–1.5 mm broad, narrowly lanceolate, gradually narrowed to the acute apex, usually glabrous; **petals** 11–18 mm long, obovate, veins usually red or dark violet; longer **stamens** 4–6 mm long, shorter **stamens** 2–3 mm long and connate for half their length; **pistils** micro-, meso-, and macrostylous, 6 mm long, ovary glabrous, each locule with 3 or 4 ovules, stigmas capitate and minutely papillose. **Fruits** 4–8 mm long, ellipsoid-oblong, glabrous, calyx about the same length as the capsule; **seeds** ca. 1.2 mm long, ellipsoid, somewhat muricate, without prominent longitudinal ribs or transverse ridges, dark reddish brown.

Plants of evergreen montane forests and subparamo formations from 1400 to 3300 m elevation. Flowering material has been collected in all months but June; most flowering collections have been made between November and March. The species is found in the Cordillera de Talamanca, around Volcán Irazú and, in a few collections, as far west as the Alajuela–Heredia border (Vara Blanca). The species ranges from southern Mexico to Peru and is grown as an ornamental.

Oxalis spiralis is recognized by its reddish stems, sparse (less often dense) puberulence, palmately trifoliolate leaves with oblong-obovate leaflets slightly notched distally, yellow petals with reddish veins, and seeds without ribs or ridges. Dif-

ferent plants may differ greatly in the size of their leaves, probably as a result of environmental factors; some have terminal leaflets averaging only 10 mm long, others have terminal leaflets averaging 30 mm. There is also great variation in the degree of pubescence and growth pattern.

All our material belongs to subspecies *vulcanicola*, which is found in the highlands of Chiapas, El Salvador, Costa Rica, and adjacent Panama. This species can be grown in hanging pots; its pendulous reddish stems and yellow flowers make an attractive display.

Oxalis tetraphylla Cavanilles, Icon. descr. 3: 19–20, t. 237. 1794. *O. deppei* Loddiges, Bot. cab. 15, t. 1500. 1828. *O. hayi* Knuth, Notizbl. Bot. Gart. Berlin-Dahlem 7: 316. 1919.

Herbs, stems not apparent, leaves and inflorescences from the apex of an ovoid to globose bulb to 4 cm long and 3 cm in diameter, bulb covered with scales and leaf-bases, outer scales 4–18 mm long, 1–12 mm wide, 3–5-veined, sometimes lost during collection, inner scales with 5–14 prominent veins, acute; stipules adnate to the petioles, 12–30 mm long, 4–13 mm wide at the base, thin or scarious. **Leaves** palmately 4-foliolate (rarely 3-foliolate in young plants), petioles 5–20(–30) cm long, 1–1.5 mm thick (dry), glabrous or sparsely puberulent, petiolules ca. 1 mm long, puberulent; **leaf blades** (leaflets) 20–40(–70) mm long, 25–55(–75) mm broad, broadly obovate to subtriangular (rarely suborbicular or with divergent distal lobes), straight (truncate) to slightly concave distally with rounded corners, cuneate to the base, sparsely puberulent or glabrescent. **Inflorescences** to 50 cm tall, umbelliform or bifid cymes, 3–12-flowered, peduncles 10–45 cm long, similar to the petioles, bracts and bracteoles 2–4 mm long, pedicels to 17 mm long, articulate at the base. **Flowers** pink to lavender or violet, sepals 4–7.5 mm long, 1–2 mm broad, narrowly oblong, bluntly acute at the apex and usually with 2 dark calli ca. 0.5 mm long, glabrous or with a few hairs; **petals** to 3 cm long, usually glabrous; longer **stamens** 2.5–4 mm long, shorter **stamens** 1.5–2.5 mm long, with filaments connate $\frac{1}{4}$ – $\frac{1}{2}$; **pistils** mostly macrostylous, 5–7 mm long, each locule with 3–6 ovules, stigma bifid and papillose. **Fruits** ca. 13 mm long, cylindrical, acute at the apex, styles ca. 1.5 mm long; **seeds** ca. 1.2 mm long, ovoid-lenticular, with 9–14 longitudinal ribs and 12–16 transverse ridges, yellowish brown.

Plants escaped from cultivation in Panama and growing wild; the species is a native of Mexico and Guatemala at elevations from 1000 to 3000 m.

Oxalis tetraphylla is recognized by its bulbous base, long-petiolate, palmately 4-foliolate leaves, almost triangular rounded leaflets with slightly indented distal margins, and pink to violet flowers. This species appears to have become naturalized in the Chiriquí Highlands of Panama, but it has not yet been found in Costa Rica.

GERANIACEAE

By William Burger

REFERENCE—K. R. Robertson, The genera of Geraniaceae in the southeastern United States. J. Arnold Arbor. 53: 182–201. 1972.

Annual, biennial, or perennial **herbs**, subshrubs (rarely small trees), stems sometimes succulent, often puberulent with simple or gland-tipped hairs; rhizomes, tubers, or thickened roots often present; stipules present and paired at the leaf-base. **Leaves** alternate or opposite (and often unequal at the node when opposite), basal or cauline, simple and lobed to deeply divided or pinnately or palmately compound, petioles usually present; **leaf blades** lobed or toothed to deeply sinuate (rarely entire), palmately or pinnately veined. **Inflorescences** terminal or axillary, generally cymose to umbellate, rarely with only 1 or 2 axillary flowers, pedicels usually subtended by subulate stipulelike bracts. **Flowers** bisexual (rarely unisexual), radially symmetrical (bilaterally symmetrical in *Pelargonium*), hypogynous, perianth 5-parted, sepals free or united at the base, imbricate (valvate), often awned or with a narrow tip, persisting in fruit; **petals** 5 (rarely 4, 2, or 0), free, imbricate or convolute in bud, often narrowed at the base and emarginate at the apex, caducous, usually with 5 small nectariferous glands alternating with the petals; **androecium** usually with 10 stamens and the outer opposite the petals (rarely with 15 stamens), all the stamens fertile or some reduced and staminodial, filaments slender, united at the base, anthers attached at the center of the back (versatile), 2-theous and dehiscing longitudinally, introrse; **pistil** 1, of 3–5 (rarely 2 or 6) carpels united by their styles to a central axis (column) and forming a “beak” on the ovary and fruit, ovary superior and 3–5-lobed, 3–5-loculate with 2 ovules pendulous from axile placentae in each locule, style present (rarely, absent), 5-parted near the apex and with 5 slender ligulate stigmas. **Fruit** a schizocarp usually breaking up into 5 mericarps (carpel-bodies) and separating from the persisting central column with a part of the style forming an awn on the apex of the mericarp, dehiscing (often explosively) by the separation and contraction of the long stylar elements; **seed** smooth or minutely reticulate, without endosperm, embryo usually curved.

A family of five genera and 700 species widely distributed in temperate, subtropical, and montane tropical areas. *Geranium* and *Erodium* have native New World species; *Pelargonium* of the Old World has several widely cultivated ornamental species. *Erodium cicutarium* has been used as a forage plant, but has become a weed in many areas. This family is closely related to Vivianiaceae of South America and Dirachmaceae of Socotra, and these taxa are sometimes included in a broader circumscription of the Geraniaceae. The Oxalidaceae are also closely related.

Key to the Genera of Geraniaceae Found in Central America

- 1a. Leaves not deeply dissected, usually ovate to reniform and palmately veined; petals slightly unequal with the upper 2 usually larger than the lower 3, 1 sepal calcarate at the base and with a spur attached to the pedicel, lacking a disc or extrastaminal glands; cultivated ornamentals *Pelargonium*
- 1b. Leaves deeply dissected; petals all the same size and shape, sepals never calcarate and without an adnate spur, a disc or extrastaminal glands present; wild or weedy (rarely cultivated) 2a
- 2a. Leaves palmately or radially dissected or lobed, usually (3–)5–7-parted or lobed, the lobes usually dentate; flowers with 10 stamens and 10 anthers; styles simply coiled in fruit, glabrous on the inner face; with 2 indigenous species *Geranium*
- 2b. Leaves pinnately divided, the pinnate divisions pinnately veined and lobed; flowers usually with only 5 anthers; style spirally coiled in age and pubescent on the inner side; not yet collected in Costa Rica *Erodium*

Erodium L'Héritier

Annual or perennial **herbs**, beginning as acaulescent rosette plants and later with elongate stems, often with several elongate stems arising from unbranched taproots; stipules paired at each leaf. **Leaves** opposite or verticillate, basal and cauline leaves similar, pinnately compound or deeply pinnately lobed (rarely simple or palmately lobed), petioles short; **leaf blades** (leaflets) toothed, lobed, or divided, sessile or petiolulate. **Inflorescences** solitary and axillary, umbellate, the ultimate peduncles usually with more than 2 flowers. **Flowers** bisexual (rarely unisexual and the plants dioecious), radially or slightly bilaterally symmetrical, sepals 5, free, often aristate-awned or mucronate at the apex; **petals** 5, glabrous, equal or subequal, pink to violet or purple, venation often more darkly colored, sometimes with a dark spot at the base of the upper 2 (or all) petals; **androecium** of 5 outer staminodia or scales and 5 inner fertile stamens; **pistil** with a puberulent ovary. **Fruit** a schizocarp, mostly dehiscent downward from the top, mericarps and their awns becoming completely detached from the central axis,

mericarps tapering toward the base and usually with persisting awns, awns puberulent on the inner (adaxial) surface and the lower part coiling into a spiral when freed from the central axis; **seeds** smooth.

A temperate zone genus of 60–80 species, centered in the area of North Africa and Mediterranean Europe to central Asia, with some species in Australia and southern South America. A few species have become weedy throughout the world. The elongate pinnately compound leaves with the leaflets deeply pinnatisect are very distinctive. Material of this genus has not been seen from Costa Rica, but two species have become naturalized in northern Central America at elevations from 1500 to 3500 m. These two species, *E. cicutarium* (L.) L'Hér. ex Aiton and *E. moschatum* (Burm.f.) L'Hér. ex Aiton, can be distinguished by the following key.

Key to the Species of Erodium in Northern Central America

- 1a. Leaflets deeply pinnatisect; tips of sepals with setiferous hairs, inflorescences lacking viscid hairs *E. cicutarium*
- 1b. Leaflets serrate or incised; tips of the sepals lacking setiferous hairs; inflorescences with viscid hairs *E. moschatum*

Geranium Linnaeus

REFERENCE—H. E. Moore, Jr., A revision of the genus *Geranium* in Mexico and Central America. Contr. Gray Herb. 146: 1–108. 1943.

Annual or perennial **herbs** (rarely small shrubs), stems of 2 kinds: (1) herbaceous and leafy flowering stems with

slightly swollen nodes, and (2) thickened basal or underground stems and rhizomes, often with dichotomous branching, with thick taproots or adventitious roots; stipules paired. **Leaves** alternate, opposite or closely congested, often alternate in the inflorescences, cauline or from the basal stem, simple but often deeply lobed or palmately compound, petioles expanded at the base, long in the basal leaves and shorter in the cauline leaves; **leaf blades** mostly circular to pentagonal in outline, palmately to radiately deeply cleft or lobed, the lobes usually lobulate or incised. **Inflorescences** terminal or axillary,

often cymose and umbelliform, ultimate peduncles 1- or 2-flowered and with 2 or 4 stipulelike bracteoles, usually long-pedunculate or long-pedicellate. **Flowers** bisexual and radially symmetrical, small (5 mm) to large (40 mm), sepals 5, free, imbricate, often with a narrow tip or awn at the apex; **petals** 5, free, imbricate, puberulent at the base and often emarginate at the apex, white to pink or reddish purple, a disc and glands present; **stamens** 10 in 2 whorls, often of 2 lengths, filaments slender and connate near the base, anthers versatile; **pistil** with a 5-lobed ovary, often puberulent, with 2 ovules in each locule but only 1 developing, the 5 styles united to the central column, stigmas 5. **Fruit** a schizocarp with a very unusual mode of dehiscence, the basal carpels splitting into 5 (or fewer) mericarps (carpel-bodies) and carried upward (often explosively) by the bending of the revolute styles, which remain attached to the apex of the central column (carpopore), styles and central column form the beak on the pistil and developing fruit, mericarps rounded at the base and with a persisting awn (part of the style) distally; **seeds** usually ejected from the mericarps, surface reticulate or smooth, with little or no endosperm.

Key to the Species of *Geranium* in Costa Rica

- 1a. Leaves essentially glabrous on the upper and lower surfaces, but often minutely ciliate along the edges; short plants with stems covered with persisting and overlapping stipules, the distal internodes not usually visible; sepals glabrous or ciliate along the edge *G. costaricense*
- 1b. Leaves sparsely to densely puberulent on their surfaces; erect or decumbent plants with long, slender, conspicuous distal internodes; sepals puberulent and often with gland-tipped hairs *G. guatemalensis*

Geranium costaricense H. E. Moore, Gentes. Herb. 8: 253. 1951, based on *G. cucullatum* H.B.K. var. *multifidum* Suessenguth, Bot. Jahrb. Syst. 72: 276. 1942 (non *G. cucullatum* L., nec *G. multifidum* Sweet). Figure 5.

Perennial **herbs**, stems short (to 10 cm tall or 30 cm long) and partly horizontal, 5–10 mm thick (including the persisting stipules), arising from a vertical slightly woody rootstock; stipules (6–)8–15 mm long, lanceolate to subulate, thin, brownish and covering the stem. **Leaves** closely clustered at the apex of the stem, petioles (1–)3–10 cm long, 0.5–0.7 mm thick, expanded at the base and united with the stipules, minutely (0.1–0.3 mm) puberulent with whitish retrorse hairs, the hairs dense at the apex of the petiole; **leaf blades** 12–20 mm long, 15–25 mm broad, rounded in outline, deeply divided, the primary divisions forming 3 or 5 parts that are also deeply lobulate or divided, the secondary divisions usually with 3 prominent lobules and each leaf with as many as 25 distal lobules, acute and often reddish at the tips of the lobules, glabrous and the major veins impressed above, glabrous or ciliate along the distal margins, glabrous beneath. **Inflorescences** apparently solitary and axillary from among the crowded leaves, 1-flowered, peduncles (0.5–)3–5 cm long (to the narrowly lanceolate paired bracteoles), bracteoles ca. 8 mm long, pedicels 1.5–5.5 cm long,

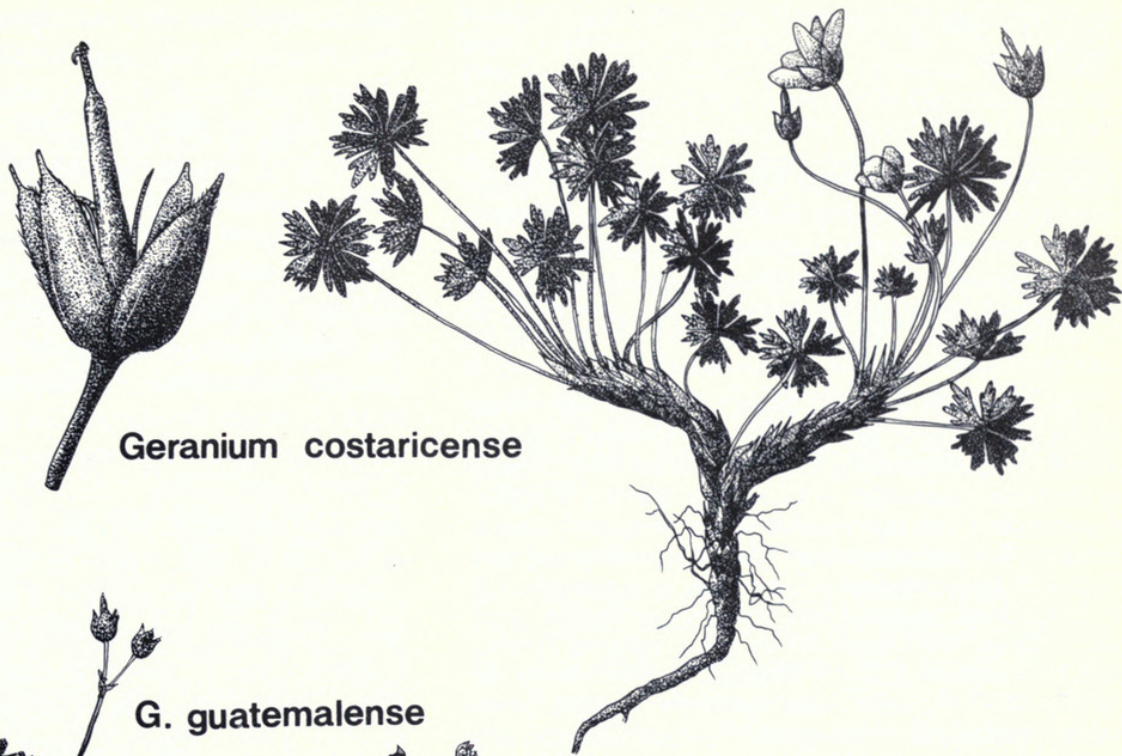
A genus of 250–300 species widely distributed in temperate, montane tropical, and polar regions of the world. Major areas of diversification are the mountains of Europe, the Mediterranean region, and the major cordilleras of South America and western North America. The genus is much in need of a modern revision, both as regards the delimitation of species and their relationships. Only two species are recognized here, and these are likely to become submerged within larger more broadly defined species when the Neotropical taxa are studied more carefully.

Geranium is a very distinctive genus with its herbaceous habit, simple but palmately deeply lobed leaves with incised margins, few-flowered inflorescences, 5-parted hypogynous flowers with usually ten stamens, and beaked fruit with unusual mode of dehiscence.

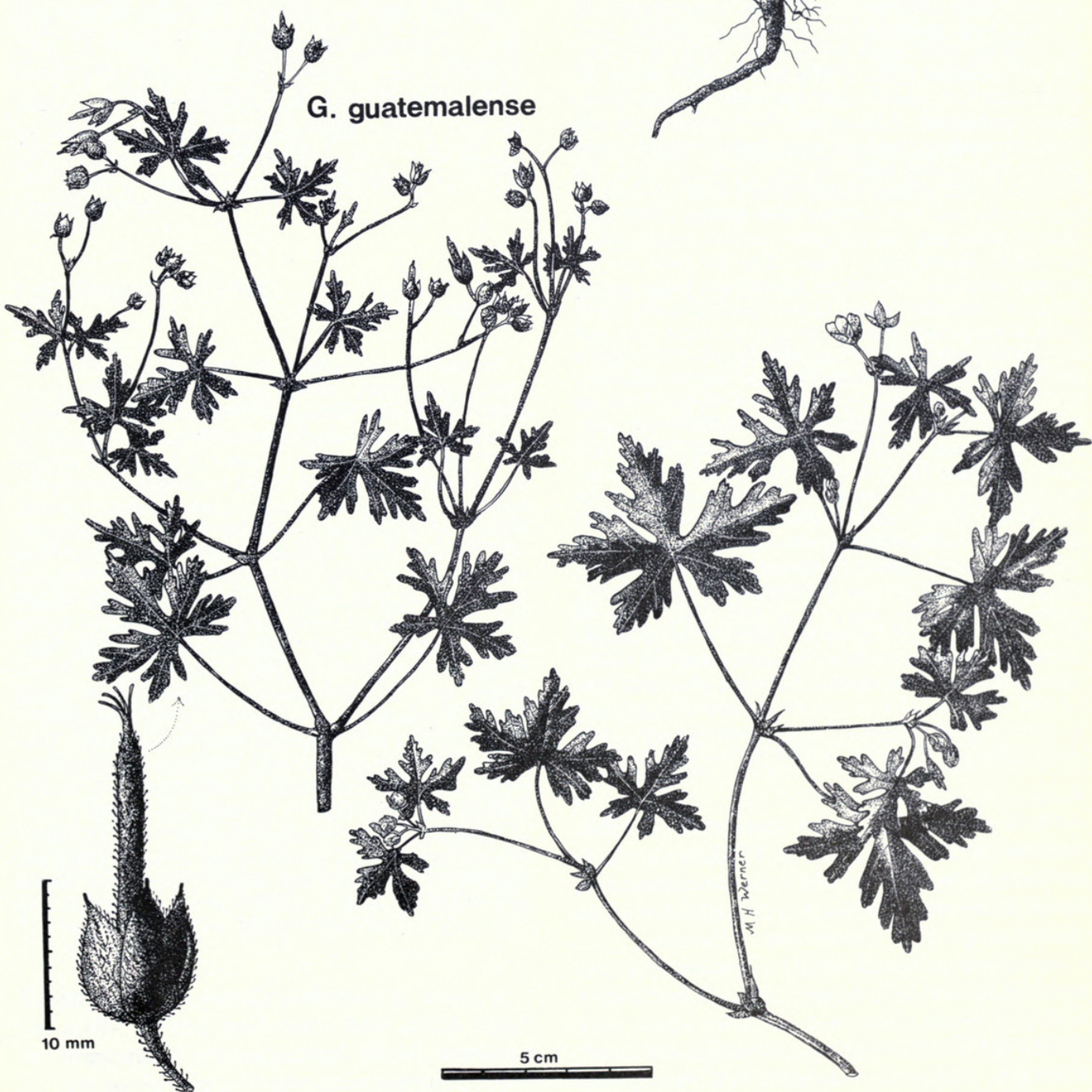
sparsely and minutely puberulent, more densely retrorse whitish puberulent beneath the perianth. **Flowers** ca. 10 mm long, to 24 mm broad, sepals 6–8 mm long, 2–3 mm broad at the base, narrowly ovate, with a short narrow tip, green and glabrous but ciliate along the translucent margin and just beneath the tip; **petals** 9–15 mm long, 5 mm wide, obovate, rounded or truncated distally, white to pink with dark red or purple longitudinal lines; **stamens** ca. 6 mm long; **pistil** 7–8 mm long. **Fruits** (12–)14–17 mm long, united styles (beak) 0.8–1.2 mm thick, free stigmas 1–2 mm long, mericarps (carpel bodies) 2–2.5 mm long, sparsely puberulent.

Plants of evergreen higher montane forest formations from 2600 to 3400 m elevation. Flowers and fruits have been collected from January to August. This species is only known from the Cordillera de Talamanca; it has been collected from the area near El Empalme to the area near Chirripó Grande.

Geranium costaricense is recognized by its deeply divided and many-lobed leaves, short stipule-covered stems, and relative lack of pubescence. This species may prove to be a subspecific element of an Andean species when the genus is properly revised. The smaller leaves with more narrow lobes



Geranium costaricense



G. guatemalense

FIG. 5. Geraniaceae: two species of *Geranium*.

help distinguish this species from *Geranium guatemalense*.

Geranium guatemalense Knuth, in Engler, Pflanz.-enr. 4(129): 200. 1912. *G. repens* H. E. Moore, Contr. Gray Herb. 146: 78. 1943, based on *G. pulchrum* C. V. Morton, Phytologia 1: 147. 1935, non *G. pulchrum* N. E. Brown, 1895. Figure 5.

Perennial **herbs**, stems 10–80(–150) cm long, erect when young, ascending to procumbent in age, lower stems ca. 4 mm thick, distal stems 0.5–1 mm thick, often rooting at the nodes, internodes to 15 cm long, sparsely to densely puberulent with thin whitish (sometimes gland-tipped) hairs ca. 0.5 mm long, roots fibrous to woody; stipules 5–10 mm long, subulate or lanceolate, with a slender tip 1–2 mm long, glabrous and ciliate to puberulent over the surfaces. Basal **leaves** few to many, not long persisting, with petioles 5–25 cm long and laminae deeply divided into 3–7 nearly equal narrowly rhombic lobes; cauline leaves with petioles (1–)2–8(–14) cm long, strigillose to hirsutulous, the hairs more dense beneath the leaf blades; cauline **leaf blades** (1–)2–5.5(–8) cm long, 2–6(–11) cm broad, deltoid to pentagonal or hastate in outline, mostly with 3 or 5 major lobes (parts), distal lobes often rhombic and conspicuously toothed or cleft above the middle, lateral lobes broader than the distal but not as long, usually drying darker above than below, upper surface with slender ascending hairs paralleling the major veins, lower surface densely hirsutulous on the veins and surfaces beneath, the hairs thin, slightly curved or straight and 0.4–0.8 mm long. **Inflorescences** solitary and axillary, each peduncle usually 2-flowered, (1–)3–5(–10) cm long, 0.3–0.5 mm thick (dry), bracteoles 2.5–4 mm long, subulate, pedicels (3–)5–20(–35) mm long, with short pilose and longer (0.7 mm) gland-tipped hairs more dense beneath the flowers. **Flowers** 6–15 mm long and 8–20 mm broad, campanulate to rotate, sepals (4.5–)6–7(–8) mm long (including a slender awn-tip 0.5–1.5 mm long), 1.5–3 mm broad, narrowly oblong, usually with glandular hairs ca. 0.7 mm long on the veins and margins; **petals** (6–)8–14 mm long (3–)4–7 mm wide, narrowly obovate, lilac to pale lavender, apex entire to deeply notched; **stamens** with filaments shorter than the sepals; stigmas ca. 2 mm long. **Fruits** 18–20 mm long, beak 0.8–1.5 mm thick, hispidulous or with thin gland-tipped hairs 0.5 mm long, mericarps 2.5–4 mm long and 1.5–2 mm thick; **seeds** 2–3 mm long, dark brown and reticulate.

Herbs of evergreen higher montane forest formations from (1100–)1700 to 3300 m elevation in Costa Rica. Flowers and fruit have been collected in all months of the year except March. The species ranges from Guatemala to Panama.

Geranium guatemalense is recognized by its puberulent flowers and foliage, deeply lobed leaves with cleft distal lobes, and spreading stems with slender internodes. The specimens placed under this name include a number of different species

according to Moore's monograph, but the flowers are remarkably alike and the distinctions of length of the stylar beak in fruit seem insignificant. It seems best to place this material under a single name until the genus can be carefully revised. However, there seem to be ecologically correlated morphological distinctions among our material.

Specimens from higher elevations (above 2800 m) have smaller, more deeply divided leaves and the leaf-divisions are more deeply incised or lobed. Specimens from below 2200 m often have broader leaves that are less deeply incised and are thinner in texture. These differences can be quite striking in some specimens, but it does not appear that they are correlated with any consistent differences in flowers or fruit. These differences appear to be clinal and may be worthy of subspecific recognition. (Compare the differences between *G. guatemalense* and *G. repens* as outlined by MacBryde in the Flora of Panama, Ann. Missouri Bot. Gard. 54: 202. 1967.) Also included here is material ascribed to *G. mexicanum* H.B.K. by Standley in his Flora of Costa Rica (1937–1938, p. 560).

Pelargonium L'Héritier

Annual or perennial **herbs** to subshrubs or small shrubs, stems usually thick, usually puberulent, often viscid and aromatic; stipules various, often prominent. **Leaves** opposite or alternate, simple (rarely compound) and petiolate; **leaf blades** entire and lobed to crenate or serrate, or palmately to pinnately lobed or incised, often fleshy, venation palmate or pinnate. **Inflorescences** terminal, axillary or leaf-opposed, 2–many-flowered pseudo-umbels (flowers rarely solitary). **Flowers** bilaterally symmetrical, sepals 5, free, imbricate, or valvate, unequal and 1 forming a short spur or nectariferous tube which is decurrent on the pedicel and adnate to it; **petals** 5(0–4), free, imbricate, unequal, usually narrowed to the base, a disc or extrastaminal glands absent; **stamens** 10 but usually with only 5–7 bearing anthers and the others sterile, filaments linear, united only at the base; **pistil** 1, ovary 5-lobed and 5-loculed, each locule with 2 pendulous ovules, styles forming a beak around a persistent central column, puberulent within, stigmas 5, usually filiform. **Fruit** a schizocarp, breaking into 5 basal 1-seeded mericarps, the mericarps acute at the base and rounded at the apex, thrown upward by the spirally coiled style, which is often puberulent or feathery distally, the central axis persisting; **seeds** oblong to ovoid, keeled and with 2 grooves, smooth or foveolate, endosperm absent.

A genus of over 200 species, nearly all from South Africa, with a few from tropical Africa and Australia. Many horticultural hybrids are cultivated as garden and potted plants.

Pelargonium × **hortorum** L. H. Bailey, Stand. Cycl. Hort. 2531. 1916.

Succulent-stemmed **herbs** or subshrubs, to 1.5 m tall; stipules broad and expanded at the leaf-base, to 20 mm long and 15 mm broad. **Leaves** alternate or opposite, petioles 2–20 cm long, puberulent; **leaf blades** 4–12 cm long, 6–15 cm broad, ovate to rounded or reniform, crenate-dentate or scalloped around the edge, cordate at the base, often with zones of dark and light green on the leaf surface, puberulent on both surfaces with slender hairs. **Flowers** with nearly equal petals, double-flowered and other forms sometimes grown, red to pink, salmon, or white.

A popular ornamental of complex hybrid origin used both for garden flower beds and as a pot plant; represented by many varieties. The brightly colored flowers, usually variegated foliage, and succulent aromatic vegetative parts make this a very distinctive plant. It is called *geranio* in Spanish and the “garden geranium” in English. According to Standley (Flora of Costa Rica, 1937–1938, p. 560), *Pelargonium graveolens* (Thunb.) L’Hér. is also grown in our area; it has deeply lobed and crisped leaves.

TROPAEOLACEAE

By William Burger

REFERENCE—B. Sparre, Tropaeolaceae, in Flora of Panama, Ann. Missouri Bot. Gard. 62: 15–20, 1975.

Annual or perennial **herbs**, mostly climbers with long twining petioles, stems often glabrous and semisucculent; stipules present and small or absent. **Leaves** alternate (sometimes opposite near the base of the plant), simple and peltate or subpeltate, the leaf blades palmately (radiately) veined, often palmately lobed or angled (to orbicular or reniform), margin entire. **Inflorescences** of solitary axillary long-pedunculate (pedicellate) flowers, rarely umbellate or fasciculate, ebracteate in nearly all species, bird- or insect-pollinated. **Flowers** bisexual, bilaterally symmetrical (almost radially symmetrical in *Trophaeastrum*), showy and yellow to orange, red, or dark purple, hypogynous to somewhat perigynous (with a floral tube or hypanthium), with a backward-projecting spur which has been interpreted as (1) an extension of the hypanthium or (2) part of the upper sepal(s) (the spur is little developed in *Trophaeastrum*), sepals 5, free or united near the base (and with 5 calyx

lobes), inserted on the floral tube, equal or the lower 2 larger, imbricate in bud; **petals** 5 (or the lower 3 rarely absent), free, imbricate, strongly narrowed to the base (clawed), the upper 2 adaxial petals usually differing from the 3 lower (abaxial) petals, the upper 2 often hairy at the base, with entire to serrate or laciniate distal margins; **stamens** 8 in 2 unequal whorls of 4, filaments free, slender or winged at the base, anthers small, 2-thealous, opening laterally by longitudinal slits, pollen tricolporate or dicolporate; **pistil** 1 (3-carpellate), glabrous, ovary 3-lobed and 3-locular, each locule with 1 pendulous ovule from the apex of the locule, style slender, 3-parted distally, stigmas simple. **Fruits** indehiscent, separating from the central axis into 1-seeded drupaceous or nutlike mericarps (with a single samaroid mericarp in *Magallana*); **seed** with a large straight embryo and 2 thick cotyledons, endosperm absent.

A New World family of three genera. *Tropaeolum* contains 86 species according to Sparre, ranging from Mexico to Chile and southern Argentina. The two other genera have three species and are found only in southernmost South America; they are very similar to *Tropaeolum*. *Magallana* produces winged samara-like carpels, and *Trophaeastrum* has erect peduncles and an almost regular calyx with a very small spur.

Tropaeolum Linnaeus

Characters of the family (see above). The genus is easily recognized because of its usually herbaceous twining habit with long twisted petioles, peltate or subpeltate laminae, and solitary showy flowers with a conspicuous backward oriented nectariferous spur.

Tropaeolum tuberosum R. & P. (añu) is an important tuber crop in the high Andes. *Tropaeolum majus*, *T. minus* L., and *T. peltophorum* Benthham and their hybrids are important ornamental plants (the “garden nasturtiums”) grown throughout the world. *Tropaeolum peregrinum* L. (the “canary-bird flower”) is also an important garden ornamental.

The following treatment follows Sparre, but it is possible that the native species recognized below are in reality only different elements of a single polymorphic species. More and better collections of the rarer taxa (*T. moritziana* and *T. pendulum*) are needed to assess variability within populations and the validity of our present species concepts.

Key to the Species of *Tropaeolum*

- 1a. Flowers 4–7 cm long, petals about the same size, much exceeding the sepals; petioles attached near the center of the lamina; plants grown for ornament and rarely escaping *T. majus*

- 1b. Flowers 2.5–3.5 cm long, petals unequal and only slightly exceeding the sepals; petioles attached about halfway between the margin and the center of the lamina; wild climbers 2a
- 2a. Leaves with 5 major veins, the 3 distal major veins not bifid (except near the margin), the leaves usually with 9 veins radiating from the petiole attachment; lower petals ciliate at the base of the lamina (lateral sepals ca. 10 mm long) *T. moritzianum*
- 2b. Leaves usually with 3 major veins, the 2 lateral veins usually strongly bifid, the leaves usually with 7 or 8 veins radiating from the petiole attachment, usually with 3 major distal veins and 4 or 5 smaller veins; lower petals not ciliate at the base of the laminae 3a
- 3a. Distal edge of the petals deeply serrate to lacinate, rarely extending beyond the sepals, lateral sepals ca. 6 mm long and 5 mm broad, outer parts of the flower usually orange to red; common plants *T. emarginatum*
- 3b. Distal edge of the petals entire to serrate, usually extending slightly beyond the sepals, lateral sepals ca. 10 mm long and 7 mm broad, outer parts of the flower usually yellowish; rarely collected plants *T. pendulum*

Tropaeolum emarginatum Turcz., Bull. Soc. Imp. Naturalistes Moscou 31: 425. 1858. *T. guatemalense* Suess., Repert. Spec. Nov. Regni Veg. 51: 205. 1942. *T. moritzianum* sensu auctores, non Klotsch.

Twining herbaceous **climbers** to 3 m high (to 8 m long?) in shrubs and small trees, internodes to 20 cm long, 0.5–3 mm thick (dry), minutely (0.3 mm) whitish puberulent at the nodes and glabrous elsewhere; stipules 2–3 mm long and linear or absent. **Leaves** peltate, petiole attached 3–12 mm from the proximal margin, petioles 4–8 cm long, 0.4–1 mm thick (dry), glabrous, often twisted in the lower half; **leaf blades** (1.5–)3–8 cm long, (1.8–)3–9 cm broad, bluntly triangular (with rounded corners) to ovate-triangular in outline, usually with a straight base and 3 or 5 distal and lateral lobes, sinuses shallow (2–5 mm) and usually broadly rounded, apex obtusely rounded, sometimes with a small (0.5–2 mm) tip, drying membranaceous to thin chartaceous, glabrous above and below, often glaucous beneath, venation radiating from the petiole attachment and with 3 major distal veins, the 2 lateral major veins usually parallel with the base of the lamina and bifid in the proximal half. **Inflorescence** of solitary axillary flowers, peduncles (= pedicels) 3–12 cm long, filiform, pendant. **Flowers** 2.5–3.5 cm long, orange to reddish orange on the outer parts, spur 12–24 mm long, 1.5–3 mm in diameter, lateral sepals ca. 6 mm long and 5 mm broad, corolla ca. 8 mm long and 4–7 mm broad distally, fimbriate distally, yellow or marked with purple; filaments ca. 7 mm long, anthers ca. 0.7 mm long. **Fruit** a deeply lobed schizocarp 5–8 mm long, the mericarps to 8 mm long (measured parallel to the central axis) and 12 mm broad, rectangular, fleshy.

Plants of open secondary sites in montane evergreen forest formations, from 1300 to 2800 m elevation on the wet Caribbean slope in Costa Rica. Probably flowering throughout the year. The species ranges from Chiapas, Mexico, to Chiriquí, Panama, and Colombia.

Tropaeolum emarginatum is recognized by its slender, twining, almost glabrous stems, long

twisted petioles, peltate leaves with three major veins, long-pendant showy flowers, and colorful rearward-projecting nectariferous spur. The leaf blades are usually broader than long with a straight or convex base and with five broad distal and lateral lobes. This species is very similar to *T. moritzianum*, and the differences in the flowers are very difficult to see in dried specimens. Also, the distinction between five major veins and three major veins breaks down in some collections of *T. emarginatum* where the lateral veins are strongly bifid near the base (see the discussion under *T. moritzianum*).

Tropaeolum majus L., Sp. Pl. 345. 1753.

Small erect **herbs** or climbing annual vines, stems often to 5 mm thick and fleshy, internodes 1–15 cm long, usually glabrous; stipules absent or obscure. **Leaves** peltate with the petiole attached near the center of the lamina, petioles 8–20 cm long, 0.5–2 mm thick, usually glabrous; **leaf blades** (3–)5–10 cm long, (3–)5–10 cm broad, suborbicular with 5–7 rounded (and weakly defined) lobes, often with 3 broadly rounded distal lobes and the sinuses only 1–3 mm deep, drying thin chartaceous, glabrous above, minutely (0.1–0.2 mm) papillate puberulent beneath, venation with 5–7(–9) major veins radiating outward from the peltate base. **Inflorescence** of solitary axillary flowers, peduncles to 25 cm long, often equaling the petioles, glabrous. **Flowers** 4–7 cm long, the spur 25–35 mm long, sepals 13–18 mm long, 4–8 mm broad, sepals and spur often yellowish green; **petals** subequal, upper petals 3–4 cm long with a lamina 15–20 mm long and equally broad and with a narrow clawed base 12–15 mm long, bright orange to yellow or dark purple. **Fruits** to 10 mm long, fleshy.

A species probably of hybrid origin and not known in the wild, having originated in Peru. It is now grown as an ornamental throughout the

world. It has been called *capuchina*, *espuela del gelan*, *mastuerzo*, and "garden nasturtium." The plants are sometimes used for medicinal purposes.

Tropaeolum moritzianum Klotzsch, Allg. Gartenzeitung 6: 241. 1838.

Herbaceous **climbers** to 10 m long, internodes to 25 cm long, 0.5–2.5 mm thick (dry), glabrous; stipules absent. **Leaves** peltate with the petiole attached about halfway between the center and the basal margin, petioles 5–15 cm long, 0.3–1 mm thick, glabrous; **leaf blades** 3–9 cm long, 2.5–8.5 cm broad, broadly ovate-triangular to suborbicular, usually with a straight or rounded (convex) base and 5 or 7 distal lobes, the lobes often weakly defined with shallow (1–3 mm) sinuses, tips of the lobes mucronate to emarginate, the leaf blades drying membranaceous and usually glaucous beneath, glabrous above and below, with usually 9 veins radiating from the petiole attachment, with 5 major veins, the 3 major distal veins unbranched and the 2 lateral veins often bifid. **Inflorescences** of solitary axillary flowers, peduncles 7–20 cm long, ca. 0.5 mm thick, pendant, glabrous. **Flowers** ca. 3 cm long, glabrous, spur 20–25 mm long, straight or slightly curved upward, sepals (calyx-lobes) 10–12 mm long, 4–5 mm broad, broadly elliptic, reddish; upper **petals** 8–9 mm long, 4–5 mm broad distally, lower petals 10–12 mm long, with a narrow ciliate base and distal lamina ca. 7 mm long and 4–5.5 mm broad, the petals yellow to orange or reddish (with darker purple veins) and with a deeply serrate-ciliate distal margin. **Fruits** becoming 10 mm long, triangular, and deeply ribbed before separation of the mericarps.

Plants often clambering over shrubs in open forest edges in evergreen forest formations, from 1000 to 2000 m elevation. Flowering collections are few and range from September to January in our area. The species is said to range from Guatemala to Colombia and Venezuela (but see below).

Tropaeolum moritzianum is recognized by the climbing habit with long twisted petioles, weakly lobed peltate leaves, laminae with five major veins, lack of pubescence, and solitary pendant reddish flowers with long nectariferous spurs. This species seems to be very similar to both *T. emarginatum* and *T. pendulum*, differing in leaf venation and subtle characters of the flowers. It is possible that all three are different forms of a single polymorphic species, for which *T. moritzianum* would be the oldest name. It is highly likely that *T. warscewiczii* Buchenau (Bot. Jahrb. Syst. 26: 582. 1899), based on *Warscewicz 2-15* from "Costa Rica et Veragua" (not seen), is a synonym of this species.

Tropaeolum pendulum Klotzsch, Allg. Gartenzeitung 18: 377. 1850.

Annual herbaceous **climbers** to 5(–8) m long, internodes 3–18 cm long, 0.5–2.5 mm thick (dry), sparsely puberulent at the nodes and glabrous elsewhere; stipules small (0.5 mm) and caducous. **Leaves** peltate with the petioles attached halfway between the center and margin (4–14 mm from the edge), petioles 4–10 cm long, often much twisted in the lower half, sparsely puberulent with thin whitish hairs near the base or glabrous; **leaf blades** 3–7 cm long, 4–9 cm broad, pentagonal to very broadly ovate-triangular (suborbicular), usually 5- or 3-lobed distally, the lobes broadly rounded and separated by very shallow (0–3 mm) sinuses, often short-mucronate with tips 0.3–1.5 mm long, base straight to slightly concave or rounded, lamina drying membranaceous and greenish, glabrous, major veins 3(–5) with the lateral veins usually bifid. **Inflorescences** of solitary axillary flowers, peduncles 2.5–5(–7) cm long, pendant, and filiform (dry), glabrous. **Flowers** 2.5–3 cm long, yellowish, spur 12–16 mm long, 0.7–1.2 mm thick distally, greenish, lower sepals ca. 12 mm long and 3–4 mm broad, upper sepals ca. 10 mm long and 6–8 mm broad; upper (larger) **petals** 8–12 mm long and exceeding the calyx-lobes, with a narrow base ca. 5 mm long and expanded lamina to 8 mm broad, entire to slightly serrate on the distal petal margins. **Fruits** 5–6 mm long, longitudinally ribbed (before separation of mericarps).

Rarely collected climbing plants of montane evergreen forest formations, from 1600 to 2300 m elevation on the Pacific slope and along the central highlands in Costa Rica. Flowering material has been collected in July–September, December, and January. The species ranges from Costa Rica to Colombia and Ecuador.

Tropaeolum pendulum is distinguished by its yellow flowers with greenish spurs, peltate leaves with rounded, often mucronate lobes, long calyx-lobes, and petals with entire to serrate distal margins. This species resembles the more common *T. emarginatum* and *T. moritzianum*, but those species tend to have deep orange flowers with fimbriate petal margins that barely exceed the calyx-lobes. The flowers of *T. pendulum* tend to dry thinner, more whitish, and more translucent than the other two species. However, there is the possibility that all three are part of a single polymorphic complex (see the discussion under *T. moritzianum*). The original description of *T. pendulum* was based on plants grown in Europe from seeds originating in Costa Rica.

LINACEAE

By William Burger

REFERENCE—K. R. Robertson, The Linaceae in the Southeastern United States. J. Arnold Arbor. 52: 649–665. 1971.

Herbs, rarely subshrubs or shrubs, stipules present and small (sometimes glandlike or interpetiolar) or absent. **Leaves** alternate or opposite (whorled), simple, sessile or petiolate, leaf blades entire, often narrow. **Inflorescences** cymose or paniculate, few-flowered to racemose or spicate, axillary or terminal. **Flowers** bisexual, radially symmetrical, hypogynous, 5-parted (4-parted in *Radiola*), sepals 5 (4), free or united near the base, imbricate, persisting; **petals** 5 (4), free, contorted or convolute in bud, narrowed to the base or clawed, fugacious, a disc absent; **stamens** the same number as the petals, alternate with the petals (opposite in *Anisadenia*), sometimes alternating with small staminodes, filaments united to form a short tube or cup, anthers basifixed and 2-theous, dehiscent by longitudinal slits, introrse; **pistil** 1, composed of (2-)3-5 united carpels, ovary superior, (2-)3-5-locular or unilocular near the apex, with 2 axile pendulous ovules in each locule, styles (2-)3-5, free or united below, stigmas capitate. **Fruit** a septicidal capsule, usually 3-5-valved (of 2 indehiscent 1-seeded mericarps in *Anisadenia*); **seed** with a usually straight embryo and with flat cotyledons, endosperm oily, little, or none.

This family is now delimited more narrowly than in the past, and only one genus is represented in Central America. Cronquist (1981) included six genera within the family and estimated 220 species. The largest genus by far is *Linum*, with about 200 species in temperate and subtropical areas of the world. Woody genera formerly considered part of the family have now been separated as Hugoniaceae (Old World tropics), Ixonanthaceae (five pantropical genera), and Humiriaceae (see the following family).

Linum Linnaeus

Annual or perennial **herbs** or small shrubs woody at the base, usually glabrous; stipules absent or reduced to

small paired glandlike structures. **Leaves** alternate, less often opposite or in whorls of 4, simple, sessile or petiolate, leaf blades elliptic or ovate to lanceolate or linear, entire, pinnately veined. **Inflorescences** terminal or axillary, racemose to corymbose, less often cymose to fasciculate or in spicate heads, bracts present and with 2 dark glands at the basal margins. **Flowers** bisexual and radially symmetrical, blue to white or yellow (red), hypogynous, sepals 5, free or united at the base, lanceolate to ovate, usually with long narrow apices, often with gland-tipped teeth, with 1-5 veins and persisting in fruit; **petals** 5, free or slightly united at the base, obovate and narrowed at the base, with 5 small nectar-glands opposite the petals and adnate to the staminal tube; **stamens** 5, alternating with the petals, united at the base to form a short tube or cup, sometimes with small filamentlike staminodia on the edge of the tube, filaments linear, anthers dehiscent introrsely by longitudinal slits; **pistil** superior, ovary 5-locular or 10-locular by the formation of false septa, styles 5, stigmas 5, capitate to clavate. **Fruits** 5-valved or apparently 10-valved, 5-locular with 2 seeds in each locule or 10-locular with 1 seed in each locule, usually dehiscent along the false septa or locules; **seed** with a straight embryo and mucilaginous testa.

A genus of about 200 species in temperate and subtropical regions, especially the Northern Hemisphere. About 40 species are found in North America, and 36 in the Mediterranean. Three species are native to Guatemala, of which one ranges southward into Honduras and Nicaragua and one into Costa Rica. These slender, few-branched herbs can be confused with *Schwenkia* of the Solanaceae or *Evolvulus* of the Convolvulaceae, but those genera have corolla tubes.

Key to the Species of *Linum*

- 1a. Petals yellow, ca. 6 mm long, sepals 2-3 mm long; rarely collected wild plants of higher (ca. 2000 m) elevations *L. guatemalense*
- 1b. Petals blue or white, 10-15 mm long, sepals 5-7 mm long; plants cultivated for ornament, fiber, or oil seeds *L. usitatissimum*

Linum guatemalense Benth., Bot. voy. Sulphur 67. 1844.

Herbs 50-110 cm long, annual or perennial, erect, branched at the base or distally (within the inflorescence), internodes 1-3 mm thick, terete, glabrous or sparsely and minutely (0.2 mm) puberulent, with slightly elevated and slender longitudinal ridges. **Leaves** alternate and ascending (occasionally fasciculate on the short shoots), petioles absent; **leaf blades** 14-30 mm long, 4-8 mm broad, lanceolate to linear-lanceolate, acute at the apex,

contracted or slightly rounded at the base, drying membranaceous and grayish brown, with 3-6 obscure secondary veins on each side, glabrous above and below. **Inflorescences** terminal, 7-30 cm long, 2.5-15 cm broad, racemose to corymbiform panicles, with slender alternate lateral branches subtended by linear-lanceolate leaf-like bracts 6-20 mm long, 0.7-4 mm broad, glabrous. **Flowers** glabrous, sepals 2-3 mm long, 1.5-2 mm broad, ovate with a sharp acuminate or acute apex, margin occasionally with a few minute (0.2 mm) teeth; corolla yellow; **petals** ca. 6 mm long. **Fruits** ca. 3 mm long and 3 mm broad, ovate with a conical apex, appearing to

split into 10 parts; **seeds** 1.3–1.5 mm long, 0.8–1 mm broad, lenticular and lustrous brown.

Linum guatemalense was collected in 1989 by G. Herrera and W. Gamboa (3606 CR, MO) at 1900 m elevation in the Sabanas de Murur-Biruk, north of Buenos Aires, southern Puntarenas Province. This is the first record of the species south of Guatemala. The unbranched erect stems with broad distal inflorescence, alternate sessile lanceolate leaves, lack of pubescence, yellow flowers with five separate sepals and petals, and 10-locular capsules are characteristic.

Linum usitatissimum L., Sp. Pl. 277. 1753.

Annual **herbs**, 20–80(–120) cm tall, single-stemmed or branched only at the base or below the inflorescence, stems slender, internodes 0.5–1.5 mm thick, glabrous; stipules absent. **Leaves** alternate and sessile; **leaf blades** 6–20(–25) mm long, (0.5–)1–4 mm broad, linear to lanceolate, glabrous, with 3 major veins from the base. **Inflorescences** distal corymbs or panicles, pedicels 8–14 mm long, slender and elongating in fruit. **Flowers** to 1.5 cm long, ca. 1.2 cm broad, sepals 5.5–7.5 mm long, ca. 2 mm broad, acuminate at the apex, inner sepals with scarious or denticulate margins but without glandular dentations; **petals** blue or white, 10–15 mm long; stigma clavate. **Fruits** 7–10 mm long, ca. 8 mm in diameter, pale yellowish brown, capsule slightly longer than the persisting sepals, usually 10-locular with 5 thicker walls and 5 thinner walls (false septa).

Linum usitatissimum is recognized by its slender erect stems, narrow sessile leaves, usually bright blue 5-parted flowers, and capsular fruit with usually 10 locules. These plants are not known to be naturalized in Costa Rica, though they are occasionally cultivated. This species has been in cultivation for more than 5,000 years in Europe and western Asia. Today, special varieties are grown for their oil seeds or their excellent fiber. Linseed oil is used for paints, varnishes, and coatings as well as an edible oil. Flax fiber is flexible, strong, and durable and absorbs water, making it very useful for towels and table coverings. The bright blue flowers have made this species an ornamental as well. This species is called *linaza*, *linaza lino*, and *lino* in Spanish, and flax or linseed in English.

HUMIRIACEAE

By William Burger and Nelson Zamora

REFERENCES—J. Cuatrecasas, A taxonomic revision of the Humiriaceae. Contr. U.S. Natl. Herb.

35: 25–214. 1961. A. H. Gentry, Humiriaceae, in Flora of Panama, Ann. Missouri Bot. Gard. 62: 35–44, 1975.

Evergreen **trees** or shrubs, wood hard and often reddish; stipules absent or minute, paired, deciduous. **Leaves** alternate, often distichous, simple petiolate or rarely sessile; **leaf blades** often coriaceous, entire to slightly serrate, pinnately veined, often glandular punctate near the margin on the undersurface. **Inflorescences** axillary or pseudoterminal (rarely terminal), paniculate, often corymbiform with trichotomous, dichotomous, or alternate branching, bracts and bracteoles small, persistent or deciduous, pedicels short. **Flowers** bisexual, radially symmetrical, hypogynous, calyx 5-lobed, united to form a cup or short tube, glabrous to puberulent, equal or the outer 2 lobes smaller, imbricate in bud; **petals** 5, free, oblong-lanceolate to oblong or linear, white to yellowish (red), contorted or imbricate along the edges in bud (but appearing to be valvate); **stamens** 10–30 in 1–2 series or many and multiseriate, filaments united in the lower part to form a short staminal tube, free filaments usually alternating in length, sterile filaments (antherless staminodia) often present, anthers dorsifixed or basifixed, 2-thecous and bilocular with longitudinal dehiscence, or 2- or 4-thecous and unilocular and dehiscing by detachment (the 4 thecae separate on the connective with 2 proximal and 2 distal), connective usually thick and prolonged beyond the thecae, an intrastaminal disc surrounding the ovary and cupular to tubular and dentate to lacinate or of 10–20 free scales; **pistil** 1, composed of (4–)5(–7) united carpels, ovary sessile, ovoid to ellipsoid, with (4–)5(–7) locules and 1 or 2 ovules from axile placentae in each locule, style 1, stigmas (4–)5(–7) and often capitate. **Fruits** drupaceous with a hard, usually plurilocular stone, small (1 cm) to large (12 cm), exocarp pulpy to fibrous and coriaceous in texture, endocarp (stone) hard and woody, the surface smooth to deeply rugose or costate, (4–)5(–7)-locular but with only 1–2(–5) seeds, valves of the endocarp visible as grooves on the surface of the hard stone; **seeds** oblong, embryo straight or slightly curved, endosperm fleshy and oily.

A family of eight genera and about 50 species, ranging from Nicaragua to southern Brazil and with a single species in western Africa. The family includes tall trees of lowland rain forests as well as smaller trees of deciduous forests and savannas. Because our species are tall trees of lowland rain forests, some have been little collected and are poorly known. For this reason, many of the floral details described below are based on the excellent monograph by José Cuatrecasas (see reference above).

The family is recognized by the stiff simple alternate leaves, these glabrous and lustrous with entire to undulate, serrulate, or crenulate margins, the 5-parted flowers with short calyx cup, narrow petals, ten or more stamens with filaments united at the base, cupular or scaly disc, 4–7-locular ovary, and fruit with an unusually sculptured hard

stone. The petals are imbricate only at their edges and may appear valvate. The anthers are quite unusual, with the thecae usually borne on the low-

er part of a thick and distally expanded connective. The wood is very hard and heavy.

Key to the Genera of Humiriaceae

- 1a. Flowers with 50–180 stamens, anthers with 2 bilocular thecae; locules 2-ovulate; endocarp with 5 separate lingulate valves; leaves bluntly obtuse to rounded at the apex, margins usually entire . . . *Vantanea*
- 1b. Flowers with 10–20 stamens, anthers with 2 unilocular thecae; locules 1-ovulate; leaves acuminate or abruptly short-acuminate at the apex, margins undulate to sinuate, bluntly serrulate, or crenulate . . . 2a
- 2a. Stamens 10, anthers with lateral thecae; endocarp with inconspicuous furrows, without dorsal foramina (apertures), alternating ribs thin; leaf margins mostly undulate to sinuate . . . *Sacoglottis*
- 2b. Stamens 20, anthers with basal thecae; endocarp with 5 foramina at the apex, with 5 short opercular valves; leaf margins mostly bluntly serrulate to crenulate . . . *Humiriastrum*

Humiriastrum (Urban) Cuatrecasas

Evergreen trees, stipules small and deciduous or lacking. Leaves petiolate to subsessile, subcoriaceous to coriaceous, entire to denticulate. Inflorescences axillary or pseudoterminal, paniculate and usually with dichotomous or trichotomous (cymose) branching, bracts deciduous or persistent. Flowers with calyx united to form a cup, calyx-lobes broadly rounded and imbricate; petals free, oblong to linear, stiff; stamens 20 and of 2 alternate lengths, glabrous, filaments united at the base, anthers ovate-lanceolate to oblong, basifixed, thecae 2 and unilocular, ellipsoid or rounded, borne at the base of the expanded connective, connective well developed beyond the thecae, thick and acute at the apex, disc a dentate ring around the ovary or of free scales; pistil with carpels (locules) opposite the sepals, ovary 5-locular, 1 pendulous ovule in each locule, style short, stigma smooth and capitate. Fruit a small to medium-sized (1–5 cm) drupe, ellipsoid to subglobose, smooth, exocarp fleshy to hard-carnose, endocarp woody, usually lacking resinous cavities, with 5 foramina (openings) around the apex and 5 oblong germination valves (opercula) on the upper half; seeds oblong, usually 1 or 2 per fruit.

A genus of 12 species, mostly in South America, but with one species reaching Costa Rica and Panama.

Humiriastrum diguense (Cuatr.) Cuatrecasas, Contr. U.S. Natl. Herb. 35: 141. 1961. *Sacoglottis diguense* Cuatr., Trop. Woods 96: 38. 1950. *H. diguense* subsp. *costaricense* Cuatr., Contr. U.S. Natl. Herb. 35: 142. 1961. Figure 6.

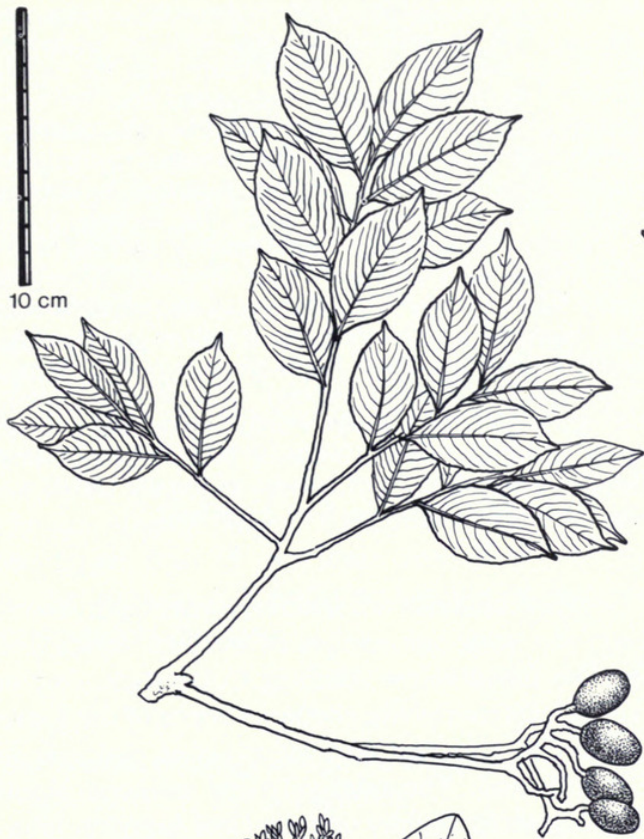
Small to large trees, 25–40 m tall, with trunks 50–70 cm d.b.h., heartwood reddish brown, leafy branchlets 0.7–4 mm thick, internodes 1–6 cm long, glabrescent, becoming grayish; stipules obscure or absent. Leaves al-

ternate, subsessile with petioles only 1–2 mm long; leaf blades (4–)5–8.5(–9.5) cm long, 2–4.5(–5.5) cm broad, elliptic to obovate-elliptic, acuminate (acute) at the apex, cuneate (obtuse) to subtruncate at the base, margin bluntly serrulate or crenulate with 2–5 teeth per centimeter, laminae drying stiffly chartaceous to subcoriaceous and dark brown, glabrous above, with sparse, thin, inconspicuous hairs ca. 0.2 mm long beneath, with 12–25 obscure secondary veins on each side, central secondaries arising at angles of 50–70°, the secondaries difficult to differentiate from the parallel tertiary veins. Inflorescences paniculate to corymbiform, usually with trichotomous branching, (5–)8–15 cm long, peduncles 1–2 cm long, 1–2 mm thick, minutely (0.2 mm) puberulent, rachis with 2 longitudinal ridges, pedicels 0.5–1 mm long. Flowers ca. 3 mm long, greenish white, calyx ca. 0.5–0.7 mm long, calyx-lobes ca. 0.5–1.1 mm broad, glabrous on the surfaces (in ours) and minutely ciliolate along the margin; petals ca. 2.3 mm long and 1 mm broad, oblong, sparsely puberulent with thin whitish ascending hairs; stamens 20, glabrous, filaments connate at the base, unequal, the larger 1.2 mm long and the shorter 0.9 mm long, anthers 0.7–0.8 mm long, ovate-lanceolate, disc made up of small (0.2 mm) scales; ovary ca. 1 mm long and puberulent, stigma 5-lobed. Fruits 20–26 mm long, 11–16 mm in diameter, ellipsoid to obovoid with bluntly rounded or obtuse apex and truncated base, exocarp drying hard, smooth, and glabrous, becoming black at maturity, endocarp hard woody, with 5 rounded apertures near the apex.

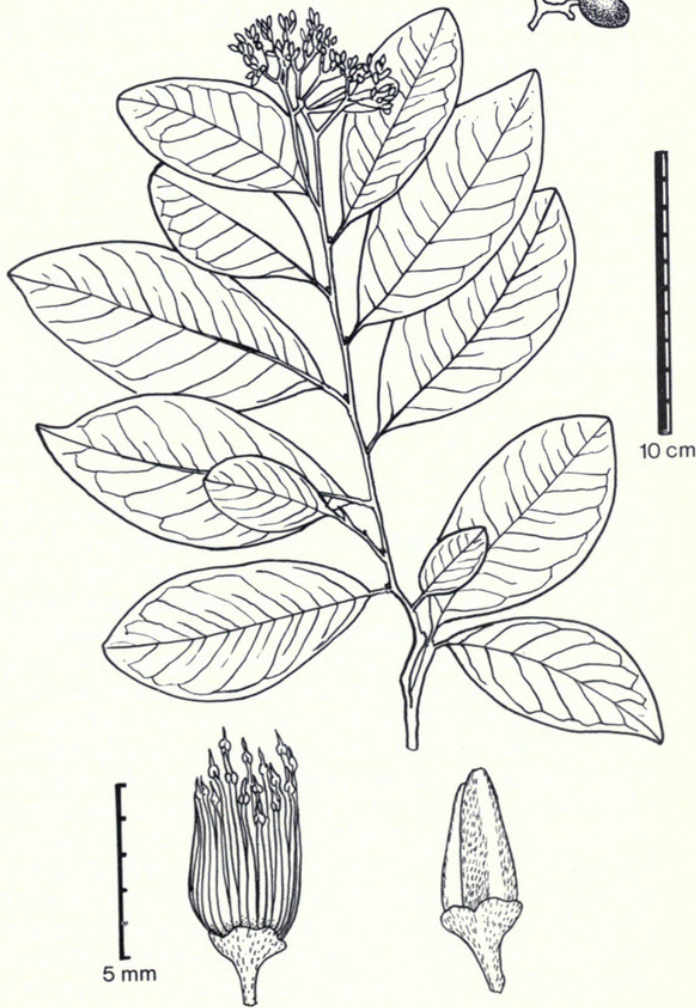
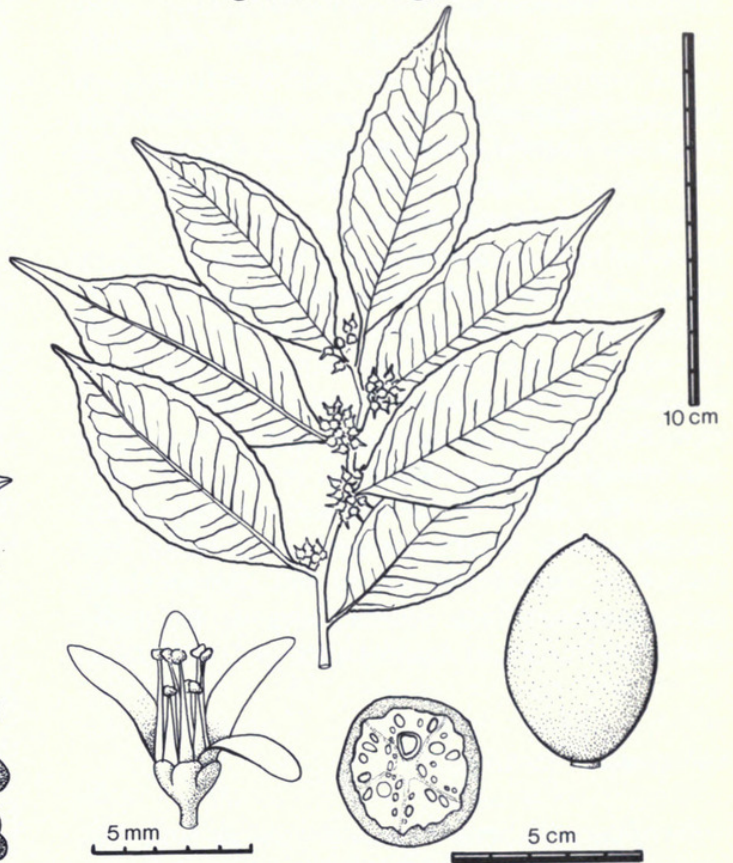
Large trees of lowland rainforest formations from near sea level to 250(–400) m elevation in Costa Rica. Flowers have been collected in January–February and July–November. Fruits have been collected in January–April. This species is found on both the Caribbean slope (near Tirimbina, Heredia) and the southern Pacific slope (General Valley to Osa Peninsula) in Costa Rica; it ranges southward through Panama to western Colombia.

Humiriastrum diguense is recognized by its small

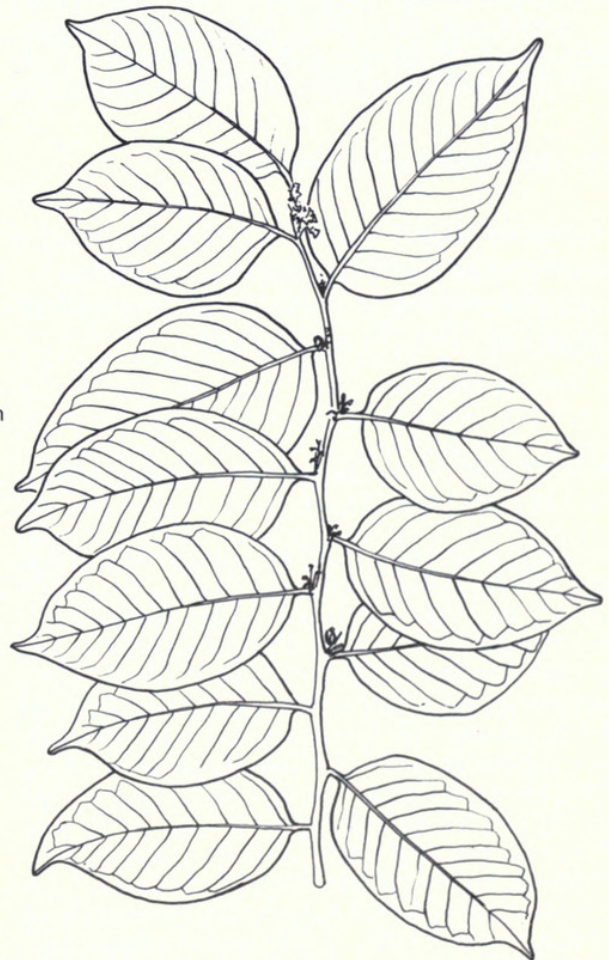
Humiriastrum diguense



Sacoglottis trichogyna



Vantanea barbourii



Sacoglottis holdridgei

FIG. 6. Humiriaceae: four Costa Rican species.

alternate subsessile leaves with bluntly serrulate laminae with many weakly defined secondary veins, small 5-parted flowers with 20 stamens, and unusual drupes with hard outer surface and woody endocarp with five distal apertures. The large size of these trees explains why they are poorly represented in herbaria. They are important timber trees and their hard wood has been used for heavy construction. In Costa Rica the names *chiricano*, *lorito*, *laurelito*, and *níspero* have been used for this species. All our material belongs to subspecies *costaricense*, which is distinguished from other elements of the species by its glabrous calyx-surface, narrow leaves, less puberulent petals, and more puberulent stems. These are not very significant characteristics, but they do seem to be consistent. Paul Allen mistakenly placed this species under the name *Sacoglottis excelsa* Ducke in his book, *The Rain Forests of Golfo Dulce* (p. 317. 1956).

Sacoglottis Martius

Evergreen trees; stipules minute or absent. Leaves alternate, petiolate; leaf blades subcoriaceous to coriaceous, margin entire to crenate. Inflorescences axillary or subterminal, paniculate with dichotomous or trichotomous branching, bracts persisting or deciduous.

Key to the Species of *Sacoglottis*

- 1a. Laminae elliptic-oblong, 2.5–5 cm broad, acute to cuneate at the base, major secondary veins arising at angles of 50–70°; isthmian Costa Rica *S. trichogyna*
- 1b. Laminae oblong, 4–8 cm broad, rounded to truncate at the base, major secondary veins arising at angles of 70–90°; Cocos Island *S. holdridgei*

Sacoglottis holdridgei Cuatrecasas, Ciencia (Mexico) 27: 171. 1972. Figure 6.

Medium to large trees, to 25 m tall and with trunks to 1 m d.b.h., leafy branchlets with internodes 1–3.5 cm long, 1.5–5 mm thick, glabrous, subterete; stipules 0.5–1 mm long, caducous. Leaves alternate and distichous, petioles 4–7 mm long, 2–4 mm thick, with adaxial ridges continuous with the lamina margins, glabrous; leaf blades 7–13(–15) cm long, 4.2–6.5(–8) cm broad, oblong-ovate to ovate-elliptic, abruptly short-acuminate at the apex, rounded to truncate at the base, margin entire or slightly sinuate-crenate, minutely glandular punctate at the margin, drying dark grayish brown to almost black above, paler beneath, glabrous above and below, with 8–11 major secondary veins on each side, the central secondaries arising at angles of 70–90°, weakly loop-connected near the margin. Inflorescences axillary, 0.5–3 cm long, cymose-paniculate, subsessile or sessile (and appearing as several inflorescences in the leaf axil), peduncle 0–4 mm long, branches dichotomous, 1–4 mm long, sparsely and

Flowers with united calyx, calyx-lobes 5, broadly rounded and imbricate; petals 5, free, imbricate (or appearing valvate), stiff; stamens 10, unequal, with the 5 opposite the sepals longer than those alternate with the sepals, glabrous, filaments flattened and united near the base, anthers ovoid to ovoid-oblong, dorsifixed near the base, thecae 2 and unilocular, ellipsoid, attached to the lower side of the expanded connective, dehiscing by detachment, connective prolonged, acute, disc forming a thin cup with a dentate margin, surrounding the base of the ovary; pistil with 5 united carpels opposite the sepals, ovary 5-locular, with 1 pendulous ovule in each locule, style equaling or exceeding the length of the stamens, stigma capitate and lobed. Fruits medium to large drupes, ellipsoid to subglobose, exocarp carnosous and smooth, drying coriaceous, endocarp woody and bullate, without apical openings, usually with 10 obscure longitudinal furrows, resinous cavities present within the woody tissue; seeds oblong, usually 1 or 2 per fruit.

A genus of about ten species, most South American, but with one species in western Africa and the two listed below reaching Costa Rica. One of our species marks the northern limits of the genus in Central America and the other is endemic to Cocos Island. The relatively few stamens, small inflorescences, slightly undulate leaf-margins, loop-connected secondary veins, and woody endocarps without apertures distinguish this genus from our other representatives of the family.

minutely papillate-puberulent, bracts ca. 2.5 mm long, 1 mm broad, deciduous, pedicels ca. 0.5 mm long. Flowers green to greenish yellow, calyx 1.7–2 mm high, calyx-lobes ca. 2 mm broad, broadly rounded and suborbicular, glabrous but minutely ciliolate along the edge; petals ca. 5.5 mm long and 2 mm broad, narrowly oblong; stamens 10, glabrous, the longer filaments 4 mm long and sepal-opposed, the shorter filaments 3 mm long and petal-opposed, anthers ca. 1 mm long, ovate, thecae orange, attached at the base of the connective, annular disc cupulate, ca. 0.8 mm high, with denticulate margin; ovary ca. 1.5 mm long, ovoid, style ca. 2.5 mm long, columnar. Fruits 32–40 mm long, 21–32 mm in diameter, oblong-ellipsoid, sepals persisting at the base, exocarp 2–4 mm thick, endocarp woody, irregularly 5-septate, resin vesicles with lustrous interior surfaces; seeds ca. 12 mm long, 4 mm in diameter, oblong.

A dominant large tree on Cocos Island. Flowers have been collected in January, March, April, and

October. Fruits were collected in January, April, August, and October. This species is said to include the tallest trees on Cocos Island; it is endemic there.

Sacoglottis holdridgei is recognized by its stiff oblong to ovate leaves abruptly rounded at the base and with crenulate-undulate margin, lack of pubescence, small inflorescences, hard endocarp with internal resinous chambers, and isolated habitat. Sterile specimens of this species were originally placed under *S. ovicarpa* Cuatr. in the monograph (pp. 168–169), but additional material has shown the Cocos Island population to merit the status of an endemic species. *Sacoglottis amazonica* Mart. is closely related, but has larger fruit and thinner elliptic leaves. *Sacoglottis ovicarpa* also has larger fruit (5 × 4 cm), and the leaves are similar to those of *S. holdridgei* but not as abruptly truncated at the base.

Sacoglottis trichogyna Cuatrecasas, Ciencia (Mexico) 27: 171. 1972. Figure 6.

Trees to 35 m tall, trunks 40–90 cm d.b.h., lower branches often drooping, leafy branchlets 0.8–3.7 mm thick, glabrous (the terminal bud minutely puberulent), tuberculate-lenticellate, becoming terete; stipules minute (ca. 0.5 mm) and caducous. **Leaves** alternate, petioles (4–)5–11 mm long, 0.9–1.7 mm thick, with adaxial margins continuous with the lamina-margins, glabrous; **leaf blades** (4–)5–12(–15) cm long, (1.5–)2–5(–7) cm broad, elliptic-oblong to narrowly elliptic, gradually narrowed to the acuminate apex, the tip 0.5–2 cm long, acute to obtuse at the base, margin subentire to crenate-undulate with a few reddish glands along the edge beneath, leaf blades drying stiffly chartaceous to subcoriaceous and dark grayish brown above, paler beneath, glabrous above and below, major secondary veins (5–)7–11 on each side, central secondaries arising at angles of 50–70°, arcuate and loop-connected near the margin. **Inflorescences** axillary, paniculate, 1–3 cm long, peduncle and rachis to 1 cm long, minutely puberulent, lateral branches 1–3 cm, bracts 0.7–1 mm long, triangular, deciduous, pedicels 1 mm long. **Flowers** in bud to 4.5 mm long and 2 mm in diameter, calyx ca. 1 mm long, calyx-lobes broadly rounded, 1.5 mm broad, minutely ciliate along the margin, usually eglandular, greenish; **petals** 4–6 mm long, 1–1.6 mm broad, oblong-linear, yellow; **stamens** 10, glabrous, united near the base, longer stamens 3.5–4.3 mm long and 0.5–0.6 mm broad at the base, shorter stamens 3–3.2 mm long and 0.7–0.8 mm broad at the base, anthers 1–1.3 mm long, connective thick and acute, thecae ca. 0.5 mm long, disc closely surrounding the ovary-base, ca. 0.8 mm high, glabrous and minutely denticulate; **ovary** 1.5 mm long, ovoid, minutely puberulent, style ca. 4 mm long, stigma 5-lobed. **Fruits** 3–5 cm long, 2–2.8 cm in diameter, oblong-ellipsoid to oblong-obovate, glabrous, exocarp 1–2 mm thick, endocarp with 5 longitudinal ridges and pitted warty surface, woody

interior with spherical resin cavities 1–4 mm in diameter; **seeds** 1 cm long.

Trees of lowland rainforest formations, from near sea level to 500 m elevation. Flowers have been collected in February, June, and August; fruits were collected in June, August, and December. The species ranges from the Departments of Río San Juan and Zelaya in Nicaragua, the northern Caribbean lowlands, and southern Pacific slopes of Costa Rica through Panama.

Sacoglottis trichogyna is recognized by its stiff alternate, slightly crenulate-undulate, and acuminate leaves with weakly loop-connected secondary veins, small flowers in small axillary inflorescences, ten stamens of two lengths, thecae near the base of an expanded connective, and ellipsoid drupe with unusual woody endocarp. The reddish glands (punctate to linear) terminating small veins in the proximal sinuses beneath the leaf margin can help in the determination of sterile collections. The young foliage has a conspicuous pinkish red coloring, and leaf size can vary greatly. This species is called *campano*, *danto plomillo*, *lorito*, *manteca*, *rosita*, and *titor* in Costa Rica. Material of this species was assigned to *S. amazonica* Mart. in the monograph of the family.

Vantanea Aublet

Tall trees, wood hard; stipules absent or obscure. **Leaves** alternate, petiolate or sessile; **leaf blades** subcoriaceous to coriaceous, usually entire. **Inflorescences** axillary or terminal, paniculate or corymbiform, with alternate or dichotomous branches, bracts deciduous. **Flowers** white or whitish (reddish in *V. guianensis*), calyx cupular, calyx 5-lobed distally; **petals** 5, free, oblong to linear-oblong, stiff, contorted in bud; **stamens** (15–18–)50–120(–180), filaments united at the base, linear, glabrous, anthers ovate-lanceolate, basifixed, thecae 2 and bilocular, attached near the base of the anther, dehiscing by longitudinal slits, connective extended beyond the thecae and acuminate to bluntly obtuse, disc cupular and closely surrounding the base of the ovary, dentate to fimbriate at the margin; **pistil** with 5 carpels opposite the sepals, ovary glabrous or puberulent, 5-locular, each locule with 2 pendulous ovules, the lower ovule with a longer funicle, style simple and straight, stigma thickened and 5-lobed. **Fruit** a medium to large (2–8 cm) drupe, pericarp smooth (tuberculate in *V. tuberculata*), exocarp carnosous and coriaceous when dry, thick or thin, endocarp woody, without resiniferous cavities, opening (when the seeds germinate) by linear or oblong valves or operculae pushed out by the emerging radicle; **seeds** 1(–3) in each fruit.

A genus of 14 species in lowland (below 1000 m) tropical rainforest formations. The genus rang-

es from southeastern Nicaragua to southern Brazil. It is distinguished by its small flowers with cupular calyx, five free (almost valvate), long, narrow petals, many stamens of uniform length, 5-locular ovary with two pendulous ovules in each locule, and the hard (when dry) drupe with unusual woody stone. A species with only 15–18 stamens has recently been described from central Panama (see *Ann. Missouri Bot. Gard.* 75: 1148–1150. 1988). The large number of stamens is probably a derived feature and not primitive as many authors have suggested. The unusual expansion of the connective with the thecae at the base is similar to that in other genera of the family.

Vantanea barbourii Standley, *Trop. Woods* 75: 5. 1943. Figure 6.

Large trees up to 50 m tall, trunks to over 1 m d.b.h., leafy branchlets 2–5 mm thick, glabrous; stipules apparently absent (or reduced to small tuberculae). Leaves with petioles 4–10 mm long, 1–2 mm broad, with lateral margins continuous with the lamina-margins, thickened at the base; leaf blades 5–14 cm long, 2.4–7 cm wide, broadly elliptic to oblong-elliptic, bluntly obtuse to rounded and emarginate at the apex, obtuse to cuneate at the base and decurrent on the petiole, margins entire or slightly undulate, the leaves drying dark brownish above and slightly paler beneath, subcoriaceous, slightly lustrous above, glabrous above and below, with 7–10 major secondary veins on each side, the central secondaries arising at angles of 45–65°, not clearly loop-connected near the margin. Inflorescences axillary or subterminal, cymose and paniculate to corymbiform, 2–8 cm long, often subtended by caducous small leaves, peduncles 1–2 mm thick, branches of the inflorescences dichotomous, very minutely (0.2 mm) puberulent, pedicels 1–2 mm long. Flowers whitish, ca. 12 mm long, calyx 1–1.5 mm high, with rounded ciliolate lobes ca. 0.5 mm broad; petals 7–9 mm long, 1.5–2.5 mm wide, oblong and narrowed toward the apex, glabrous within and appressed retrorse puberulent on the outside except for the thin glabrous margins; stamens ca. 50–60, filaments 5–7 mm long, glabrous, anthers ca. 0.8 mm long, ovate-lanceolate, thecae 0.4 mm long, disc 1 mm high, thick, with short denticulate margin; ovary 1.5–2 mm high, tomentulose-hirsutulous, style ca. 4 mm long, slender. Fruits 2.8–3 cm long, 1.8–2 cm in diameter, ovoid-oblong to ellipsoid, narrowed to the apex, abruptly rounded at the base, smooth, endocarp hard woody, ca. 2.5 cm long and 1.6 cm in diameter, with 5 oblong U-shaped grooves (valves).

Tall trees of lowland rainforest formations on the northern Caribbean and southern Pacific slopes of Costa Rica, from near sea level to 800 m elevation. Flowers are probably produced in November–June; fruits have been collected in June and September. The species ranges from Costa Rica to Panama.

Vantanea barbourii is recognized by its tall stature, stiff glabrous alternate leaves with entire or slightly undulate margins, small flowers with many stamens, unusual anthers, and fruit with woody endocarps that have five longitudinal U-shaped grooves. The short calyx-cup with broadly rounded lobes, narrow petals puberulent along the back, and the apically blunt to emarginate leaves are also distinctive. Paul Allen noted that these trees tend to lose all their leaves for a brief period at the end of the heavy rains in November or December (The Rain Forests of Golfo Dulce, p. 351. 1956). The species has been called *ira chiricana*, *chiricano*, *chiricano triste*, and *níspero*. The very hard and durable wood has been used for bridge timbers. Only the following Costa Rican collections have been seen: Allen 6546 and 6681, Barbour 1018, Dayton & Barbour 3129 (the type), and Hartshorn 2139. *Vantanea occidentalis* Cuatr. of Colombia is very similar to *V. barbourii* and may prove to be a synonym.

ERYTHROXYLACEAE Kunth

By Timothy Plowman

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Glabrous shrubs or small trees, bisexual (hermaphroditic) or rarely dioecious; stipules on twigs persistent or caducous. Leaves alternate (opposite in *Aneulophus*), simple, stipulate, petiolate, entire, pinnately veined. Inflorescences fasciculate at nodes, with 1–many flowers, sometimes short-pedunculate, subtended by small scarious bracteoles, flowers pedicellate. Flowers radially symmetrical, bisexual or unisexual, often heterostylous; calyx persistent, the 5 valvate sepals united below; petals free, 5, alternate with sepals, imbricate in bud, caducous, usually appendaged on the inner (adaxial) surface and narrowed at the base; stamens 10, biseriate, united at the base by the filaments and usually forming a short tube, anthers 2-locular, longitudinally dehiscent; pistil solitary, ovary superior, 3-locular (2-locular in *Nectaropetalum*), usually only one locule ovuliferous; ovules solitary (2 in *Nectaropetalum*), axile, pendulous, styles 3 (2 in *Nectaropetalum*), free or connate from the base, stig-

mas capitellate, rarely sessile. **Fruits** small, drupaceous, and 1-seeded (in *Aneulophus* rarely capsular and 2- or 3-seeded); embryo straight, with or without endosperm.

Four genera with about 230 species; three of the genera, with few species, are restricted to tropical Africa and are incompletely known. *Erythroxylum* is by far the largest genus and occurs in tropical parts of Australia, Asia, Africa, and the Americas.

Erythroxylaceae are recognized by the lack of indumentum, the intrapetiolar stipules, the usually alternate, simple, entire leaves, the fascicled, axillary flowers, the persistent 5-lobed calyx, the appendaged petals, and the small, drupaceous fruit.

Erythroxylum P. Browne

Glabrous **shrubs** or small trees, evergreen or deciduous, rarely dioecious or subdioecious, the twigs compressed at apex, often bearing persistent, distichous, imbricated cataphylls and stipules; stipules intrapetiolar, united and appearing as a single organ, dorsally bicostate, often 2- or 3-setulose at apex, persistent or caducous, often leaving an obliquely transverse scar. **Leaves** alternate, often distichous, petiolate, simple, entire, with involute veneration that sometimes imprints 2 parallel lines and/or a distinct central panel on lower surface, pinnately veined. **Inflorescences** of fasciculate or solitary axillary flowers, rarely short-pedunculate, the flowers arising from small, scarious, often persistent bracteoles, pedicellate. **Flowers** radially symmetrical, small, heterostylous; calyx of 5 valvate sepals, united below, persistent; **petals** 5, free, imbricate in bud, appendaged on the adaxial surface with a 2-lobed ligule, caducous; **stamens** 10 in 2 whorls of 5, the outermost alternate with the petals, the filaments united at base and forming a short tube surrounding the ovary, persistent, anthers 2-locular,

longitudinally dehiscent; **ovary** 3-locular but with only one locule ovuliferous, the ovule solitary in the fertile locule, pendulous from an axile placenta, anatropous, epitropous, styles 3, free or partly connate from base, stigmas capitellate. **Fruit** a small, fleshy, reddish, one-seeded drupe, the endocarp 1- or 3-locular but with only one fertile locule; **seed** with or without endosperm, the embryo straight.

About 230 species, of which at least 180 are found in the Neotropics; the centers of diversity for the genus are found in Venezuela, eastern Brazil, and Madagascar; six species, including one cultivated, occur in Costa Rica. Costa Rica seems to be one of the less diverse areas of Central America in species of *Erythroxylum*, being surpassed even by Nicaragua. Most if not all of the species have originated elsewhere (South America, Antilles) with subsequent dispersal to Costa Rica.

In Costa Rica, *Erythroxylum* species fall into two main groups: those with relatively large, apically acute or acuminate leaves and conspicuously striate-nerved stipules (*E. macrophyllum*, *E. citrifolium*, *E. fimbriatum*), and those with small to medium-sized, apically obtuse or rounded leaves and smooth, nonstriate stipules (remaining species). Identification within either of these groups may be difficult, especially if complete material is not available. I therefore provide multiple characters in the key to help distinguish flowering, fruiting, and/or vegetative material. The important stipule characters should be observed in newly formed (subapical), undamaged stipules or cataphylls. The character of relative positions of calyx and staminal tube is easily observed in flowers whose petals have fallen, or in young fruit.

Key to the Species of *Erythroxylum* in Costa Rica

- 1a. Stipules longitudinally striately veined, caducous or persisting; mature endocarps terete 2a
- 1b. Stipules smooth, not striately veined, persistent (sometimes withering but not caducous); mature endocarps variously ribbed or sulcate, not terete 4a
- 2a. Stipules apically acute or tapered to a long point; bracteoles 2–5.5 mm long; calyx-lobes broadly ovate, oblong or obovate and abruptly acuminate at the apex *E. macrophyllum*
- 2b. Stipules apically obtuse or rounded and 2- or 3-setulose; bracteoles 0.5–2 mm long; calyx lobes triangular to triangular-ovate or ovate-lanceolate, acute or acuminate at the apex 3a
- 3a. Stipules persistent, 1.5–2 mm long (not including seti), the 2 lateral apical seti conspicuous, often fimbriate and strongly recurving, persisting; staminal tube equaling or longer than the calyx; endocarps acute to obtuse at the apex *E. fimbriatum*
- 3b. Stipules usually caducous, 4–12 mm long, the apical seti slender, weakly filamentous, evanescent; staminal tube shorter than the calyx; endocarp obtuse at apex *E. citrifolium*
- 4a. Flowers manifestly unisexual, produced near apex of current season’s shoots, often on short shoots; mature drupe 3-locular with 1 fertile and 2 empty locules; petiole longer than 1/5 the length of leaf blade *E. rotundifolium*

- 4b. Flowers bisexual, produced on year-old twigs of past season; mature drupe unilocular; petiole shorter than $\frac{1}{2}$ the length of the leaf blade 5a
- 5a. Staminal tube less than 50% as long as the calyx; plants completely deciduous; flowers produced on last season's twigs before the leaves, never in leaf-bearing axils; leaf blades never bilineate nor with distinct central panel on lower surface; a native species *E. havanense*
- 5b. Staminal tube 50–100% as long as the calyx; plants evergreen or incompletely deciduous; flowers produced in axils of year-old twigs (in Costa Rica), often with leaves present; leaf blades usually bilineate and/or with distinct central panel on lower surface; cultivated species *E. novogranatensis*

***Erythroxylum citrifolium* St. Hil., Fl. bras. merid.**

94. 1829. *E. citrifolium* St. Hil. var. *minus* O. Schulz, in Engl., Pflanzenr. 4(134): 37. 1907. D'Arcy & Schanen, Ann. Missouri Bot. Gard. 62: 29. 1975.

Evergreen **shrubs** or small trees to 10 m tall, the branchlets smooth, the bark dark reddish or grayish brown, developing a tan suberous outer bark, the lenticels if present minutely punctate; cataphylls scattered at base of shoots, 5–7, early caducous, similar to foliar stipules; foliar stipules caducous, sometimes tardily so, (2–)4–8(–12) mm long, oblong-lanceolate, membranaceous, densely longitudinally striate-nerved, obtuse at apex with three slender, short, often evanescent setae 1–2 mm long. **Leaves** with petiole 4–7 mm long, the leaf blades 8–14 cm long, 2–7 cm wide, oblong, oblong-elliptic or lanceolate, long-acuminate at apex, short-acuminate to rounded at base, coriaceous or subcoriaceous, the upper surface drying dark grayish green or brown, the secondary nerves often obscure, the lower surface drying somewhat ferruginous, not bilineate and a central panel lacking or faint, the lateral nerves prominulous, more or less shiny on both surfaces. **Inflorescence** produced in the axils of leaves or cataphylls on mature twigs of current season, many-flowered; bracteoles 0.5–2 mm long, lightly striate-nerved, strongly keeled, at apex acute or obtuse, 1-setulose; pedicels 3–5 mm long, strongly 5-ribbed. **Flowers** bisexual; calyx ca. 1.5 mm long, triangular to ovate-lanceolate, often spreading after anthesis; staminal tube ca. $\frac{1}{2}$ as long as calyx. **Drupe** 7–10 mm long, 4–5 mm in diameter, red, the endocarp oblongoid, obtuse at apex, terete.

Evergreen forest formations of the Pacific slope, 700–1200 m elevation, the General Valley (*Skutch* 4351 F, *Skutch & Barrantes* 5057 F), and near Las Alturas in Puntarenas Province (*Wilbur et al.* 22658 F). It appears to be uncommon in Costa Rica. Flowering specimens have been collected between June and August. This species is widely distributed, often in secondary forest, from Nicaragua to Bolivia; the Guianas; and southeastern Brazil.

Erythroxylum citrifolium is recognized by its caducous, striate-nerved, apically obtuse, 3-setulose stipules, by relatively large (8–14 cm long), oblong, apically acuminate leaves, and by dense axillary clusters of small (ca. 1.5 mm long) flowers.

***Erythroxylum fimbriatum* Peyr., in Mart., Fl. bras. 12(1): 162. 1878.**

Evergreen **shrubs** or treelets, 2–6(–10) m tall, the branchlets initially with smooth bark without discrete lenticels, becoming superficially suberose, light tan; cataphylls scattered at base of new shoots, 4 or 5, similar to foliar stipules; foliar stipules persistent, 1.5–2 mm long (excluding setae), broadly ovate, subcoriaceous, distinctly longitudinally striate-nerved with 4–6 nerves per side, obtuse or truncate at apex, 3-setulose, the 2 lateral setae persistent, conspicuous, (1–)3–5 mm long, ribbon-like, extending from subulate keels, often fimbriate, manifestly recurved, the medial seta filamentous, evanescent. **Leaves** persistent, scattered on twigs, the petiole 3–5 mm long; **leaf blades** 5–10(–14) cm long, 2.5–5.5 cm wide, elliptic to elliptic-oblong, short- to long-acuminate at apex, rarely acute, the tip itself obtuse or acute, broadly to narrowly cuneate at base, chartaceous, the upper surface drying dark grayish green, the adaxial midrib sometimes impressed-sulcate with a slender medial ridge, the lateral nerves obscure or sometimes impressed-sulcate, the lower surface drying ochreous or ferruginous, without parallel lines, the lateral nerves sometimes conspicuous. **Inflorescences** in axils of leaves or cataphylls on current or year-old shoots, with 1–3(–8) flowers per node; bracteoles ca. 1 mm long, striate-nerved, acute and 1-setulose at apex; pedicels 4–6 mm long, pentagonal in cross section, the fruiting pedicels 5–7 mm long. **Flowers** bisexual; calyx 1–2 mm long, the lobes narrowly triangular to lanceolate, narrowly acute or acuminate at apex; staminal tube equaling or slightly longer than the calyx. **Drupe** 10–12 mm long, 4–5 mm in diameter, red, the endocarp oblongoid, acute or obtuse at apex, terete at maturity.

In Central America known only from Costa Rica, Provincia de Heredia, Finca La Selva, in lowland moist primary forest, 45–100 m elevation (*Hartshorn* 1243 and 1413 F, *Opler* 1740 F, *Kress* 76-526 DUKE). In Costa Rica, *Erythroxylum fimbriatum* flowers in March–May and fruits in April–June. In South America, the species is sporadically distributed throughout the greater Amazon basin, from Colombia to French Guiana, south to Peru and western Brazil.

Erythroxylum fimbriatum is easily recognized by the well-developed (3–5 mm long), persistent, fimbriate, and recurved lateral setae on the striate-

nerved stipules. The Costa Rican and some Peruvian material of this species differs modestly from the typical, lowland Amazonian form in having smaller leaves and the stipular setae much shorter and not so markedly fimbriate and recurved. Moreover, the lower surface of the leaves in the Amazonian collections shows conspicuous secondary nerves diverging at near right angles from the midrib.

Erythroxylum havanense Jacq., Enum. Syst. Pl. 21. 1760. Select. Stirp. Amer. Hist. t. 87, fig. 2. 1763. D'Arcy & Schanen, Ann. Missouri Bot. Gard. 62: 32. 1975. *E. ovatum* Cav., Diss. 404, t. 233. 1789. *E. obtusum* DC., Prodr. 1: 574. 1824. *E. havanense* Jacq. var. *continentis* O. Schulz, in Engl., Pflanzenr. 4(134): 92. 1907. *E. chiapense* Lundell, Wrightia 4: 175. 1971. Figure 7.

Deciduous shrubs or treelets 1–5 m tall, the branchlets 1.5–2.0 mm in diameter, weakly differentiated into long and short shoots, smooth, light grayish brown to dark reddish brown, dotted with whitish punctate or elongate lenticels, becoming longitudinally fissured; cataphylls persistent, produced at base of long shoots or congested on short shoots, similar to foliar stipules, turning dark brown with age; foliar stipules persistent, 2.0–3.5 mm long, triangular-ovate, not striate-nerved, acute and briefly 2-setulose at apex, drying reddish brown. **Leaves** deciduous, sometimes tardily so, scattered on long shoots or 1–3 produced at tips of short shoots, the petiole 2.5–5 mm long; **leaf blades** (3–)3.5–8 cm long, (1.2–)1.5–3(–4) cm wide, obovate or elliptic, rounded, obtuse or slightly retuse at apex, acute at base, chartaceous, strongly bicolorous, the upper surface drying medium green, dull, the lower surface drying very pale green or glaucous to whitish, without parallel lines nor with a distinct central panel, the lateral nerves 12–14, inconspicuous. **Inflorescence** produced in axils of leaves or cataphylls on leafless, year-old twigs just prior to leaf flush, with 1–8 flowers per node; bracteoles 1–1.5 mm long, ovate, acuminate at apex; pedicels slender, 4–9 mm long. **Flowers** bisexual; calyx-lobes triangular-ovate, reflexing after anthesis; staminal tube much shorter than calyx (in Costa Rica). **Drupes** 5–7 mm long, 4–5 mm in diameter, the endocarp ellipsoid to oblongoid, rounded or obtuse at apex, unequally and shallowly 4-sulcate at maturity.

Lowland Guanacaste and adjacent Puntarenas, seasonally dry, deciduous forest and adjacent savannas, often along water courses, sea level to 250 m elevation. This species flowers in March–June and fruits in May–June. It ranges over Cuba, the Lesser Antilles, and Mexico to Panama and the northern coast of South America.

Erythroxylum havanense is recognized by its de-

ciduous habit, with flowers appearing before the leaves, by the relatively small, apically obtuse or rounded, strongly bicolorous leaves that are elineate beneath, by the staminal tube much shorter than the calyx lobes, and by the short, obtuse, sulcate endocarps. The illustrations of *E. havanense* (fig. 7) are based on the following collections: A, E, F, drawn from *Frankie 380c* from Costa Rica; B, C, drawn from *Sandino 2888* from Nicaragua; D, drawn from *Plowman 3597* from Colombia; G, H, I, drawn from *Berry 3502* from Venezuela. All the specimens are represented at F.

In the Flora of Panama (Ann. Missouri Bot. Gard. 62: 32. 1975), D'Arcy and Schanen erroneously placed several species in synonymy under *E. havanense*. *Erythroxylum cumanense* Kunth and *E. hondense* Kunth are distinct species that occur in northern South America, and *E. mexicanum* Kunth is found in dry areas of Mexico, El Salvador, and Nicaragua. *Erythroxylum pringlei* Rose is here considered a synonym of *E. rotundifolium* Lunan sens. lat. (see below).

Erythroxylum macrophyllum Cav., Diss. 401, t. 227. 1789. *E. lucidum* H.B.K., Nov. Gen. sp. 5: 138. 1822. *E. costaricense* J. D. Smith, Bot. Gaz. 23: 240. 1897. *E. ellipticum* Ramirez, Anales Inst. Med.-Nac. Mexico 3: 36. 1897. *E. tabascense* Britton, N. Amer. Fl. 25: 66. 1907. Standl. & Steyerl., Fieldiana: Bot. 24(5): 393. 1946. *E. lucidum* H.B.K. var. *costaricense* (J. D. Smith) O. Schulz, in Engl., Pflanzenr. 4(134): 25. 1907. D'Arcy & Schanen, Ann. Missouri Bot. Gard. 62: 28. 1975. *E. skutchii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 344. 1940. *E. multiflorum* Lundell, Amer. Midl. Naturalist 29: 474. 1943. D'Arcy & Schanen, Ann. Missouri Bot. Gard. 62: 24, t. 1. 1975.

Shrubs 2–3 tall or small trees to 10 m tall; branchlets 2–4 mm in diameter, smooth, becoming tan or light grayish brown, with obliquely transverse scars of fallen stipules and cataphylls, without distinct lenticels; cataphylls produced at base of shoots, caducous, 10–60 mm long, similar to but sometimes larger than foliar stipules; foliar stipules 4–35 mm long, longitudinally striate-nerved, at apex acutely tapered to a point, sometimes with 2–3 filamentous setae, caducous, leaving obliquely transverse scars on twigs. **Leaves** with petiole 3–10 mm long; **leaf blades** (5–)7–30 cm long, (2–)3–15 cm wide, oblong to elliptic-oblong, long- to short-acuminate at apex, the tip itself sharply acute, acuminate to acute, obtuse or rounded at base, the upper surface often drying rather shiny and leaden gray, the lateral nerves inconspicuous, rarely impressed-sulcate, the lower surface drying dull and ferruginous, usually without parallel lines



FIG. 7. Erythroxylaceae: *Erythroxylum havanense*. A, flowering branch; B, fruiting branch; C, leaf showing venation; D, stipule; E, short-styled flower; F, petal; G, drupe with attached calyx; H, cross section of endocarp; I, embryo.

or distinct central panel, the lateral nerves inconspicuous or rarely prominulous. **Inflorescences** produced in the axils of leaves or cataphylls on new shoots, often appearing "knobby" at the nodes, the flowers usually numerous; bracteoles 2.0–5.5 mm long, persistent, 1-keeled, striate-nerved, apically acute, 1-setulose; pedicels 3–10 mm long, 5-ribbed. **Flowers** bisexual; calyx 2.5–5.0 mm long, the lobes broadly ovate, obovate or oblong, often subfoliose, lightly striate-nerved, abruptly acuminate at apex, the margins often overlapping or touching; staminal tube about half as long as the calyx. **Drupes** 8–11 mm long, 4–5 mm in diameter, the endocarp oblongoid or ovoid-oblongoid, obtuse or acutish at apex, terete at maturity.

In Costa Rica, widespread on both Atlantic and Pacific slopes (Guanacaste, Puntarenas, Alajuela, San José, Heredia, Limón) in evergreen moist to wet forests, seasonally dry or cloud forests, sea level to 1600 m elevation. Flowers in January–September; fruits in February–November. The species ranges from southern Mexico to Bolivia and Brazil.

Erythroxylum macrophyllum is recognized by the relatively large (4–30 mm long), apically acute, striate-nerved, caducous stipules that leave obliquely transverse scars on the stem, by the rather thick, apically acuminate leaves, by the persistent, striate-nerved bracteoles, and by the broadly ovate, abruptly acuminate calyx-lobes.

Erythroxylum macrophyllum is a highly polymorphic, complex, and wide-ranging species, occurring from southern Mexico to Bolivia. Many names have been proposed to accommodate the numerous minor and major variants in both Central and South America. I am treating the species here in the widest sense. In Central America, subspecific taxa are difficult to characterize with any degree of constancy. However, in Costa Rica two general forms occur, corresponding to *E. costaricense* J. D. Smith, with leaves generally less than 14 cm long, and *E. skutchii* Standley, with leaves more than 15 cm long. The former, small-leaved form is far more widespread, occurring from sea level to 1600 m elevation in most of Costa Rica.

Erythroxylum skutchii was described from a specimen (*Skutch 4847* F) collected in the General Valley. The leaves are distinguished adaxially by impressed-sulcate nerves and abaxially by prominulous, reticulate venation. Two other collections from Limón Province (*Gómez et al. 20463* F) and the Osa Peninsula (*Gómez 19681* F) more or less match the type of *E. skutchii*. Several other collections from the lowlands of Heredia and Limón Provinces have exceptionally large leaves but without the impressed-sulcate nerves of *E. skutchii* (*Chacon 716*, *Hartshorn 1198*, *Kennedy 3790A*,

Stevens 23797, *23964*, *Wilbur 34408*, all at F). These collections differ from the common highland forms primarily in the larger leaf size and greater number of flowers per node. A number of intermediate specimens connect the extremes of variation. Until this group can be thoroughly revised, I decline to designate formally subspecific taxa in Costa Rica.

Erythroxylum multiflorum Lundell from Panama is also included in synonymy under *E. macrophyllum*. This distinctive plant with large leaves and cataphylls is obviously related to both *E. skutchii* and two distinctive South American varieties: *E. macrophyllum* var. *macrocnemium* (Mart.) Plowman and var. *ecuadorensis* Plowman.

Bawa and Opler (Evolution 29: 167–179. 1975) erroneously reported that "*Erythroxylum lucidum* var. *costaricense*" from Guanacaste is dioecious. This error resulted from a misidentification of *E. rotundifolium* Lunan.

Erythroxylum novogranatense (Morris) Hieron., Bot. Jahrb. Syst. 20, Beibl. 49: 353. 1895. O. Schulz, in Engl., Pflanzenr. 4(134): 85, t. 18. 1907. *E. coca* Lam. var. *novogranatense* Morris, Bull. Misc. Inform. 5, t. 2. 1889.

Evergreen shrubs or small trees to 6 m tall, the branchlets ca. 2 mm in diameter, without short shoots, flexuous, often appearing zigzag, reddish brown, the lenticels punctate or absent, if present rarely breaking the surface; cataphylls lacking or few, if present resembling foliar stipules; foliar stipules 2.5–3.5 mm long, narrowly ovate to triangular, acute to obtuse at apex, minutely 2-setulose, membranous, not striate-nerved, soon withering and disintegrating. **Leaves** persistent, scattered on twigs, the petiole 2–5 mm long; **leaf blades** 2.5–7.5 cm long, 1.2–3.6 cm wide, elliptic to obovate or oblong, at apex obtuse, rounded or retuse, at base acute to attenuate, firm-membranaceous, the upper surface bright yellowish green when fresh, the adaxial midrib flat not ridged, the lower surface very pale green, usually bilineate and/or with a distinct central panel, the laminae drying pale green or yellowish and dull on both surfaces, the lateral nerves 10–15, inconspicuous. **Inflorescence** produced in axils of the previous season's twigs, with or without leaves present, 1–3(–10) flowers per node; bracteoles 1–1.5 mm long, cymbiform-deltoid, acuminate at apex, pedicels 3–7(–12) mm long. **Flowers** bisexual; calyx 1.5–2.5 mm long, divided $\frac{1}{2}$ – $\frac{3}{4}$ its length, the lobes narrowly to broadly ovate; staminal tube half as long as to equaling the calyx. **Drupes** 8–13 mm long, 4–7 mm in diameter, the endocarp ovoid to ellipsoid, rounded to obtuse at apex, unequally 4-sulcate.

Ornamental shrubs cultivated at I.I.C.A., Turrialba, ca. 635 m, flowering in June–August (*Brown CR-221* F, *Rosbach 3570* GH, *Leon 591* US). Na-

tive to Colombia and cultivated throughout the tropics and in Central America as an ornamental or medicinal plant, or as a minor commercial source of the alkaloid cocaine.

Erythroxylum novogranatense is recognized by the relatively delicate, bright yellowish green (when fresh), apically obtuse leaves that are usually bilineate beneath, by the thin stipules that soon disintegrate, and by the sulcate endocarps. This species has long been confused with *E. coca* Lam., which is the commercially important species from which both coca leaves and cocaine are principally derived (Plowman, J. Linn. Soc., Bot. 84: 329–353. 1982. Bohm et al., Syst. Bot. 7: 121–133. 1982). Because it is more difficult to grow, *E. coca* is rarely seen outside of the tropical Andean *montaña* where it is native. No unambiguous collections of *E. coca* are known from Central America. The common name of *E. novogranatense* is “coca.”

Erythroxylum rotundifolium Lunan, Hort. Jamaic. 2: 116. 1814. Standl. & Steyererm., Fieldiana: Bot. 24(5): 393. 1946. *E. obovatum* Macfad., Fl. Jamaica 143. 1837, non Griseb.. *E. pallidum* Rose, Contr. U.S. Natl. Herb. 8: 314. 1905. Standl. & Steyererm., Fieldiana: Bot. 24(5): 392. 1946. *E. pringlei* Rose, Contr. U.S. Natl. Herb. 8: 314. 1905. *E. compactum* Rose, Contr. U.S. Natl. Herb. 8: 313. 1905. *E. suave* O. Schulz, in Urban, Symb. Antill. 5: 197. 1907. *E. suave* O. Schulz var. *compactum* (Rose) O. Schulz, in Engl., Pflanzenr. 4(134): 68, t. 15. 1907. *E. sessiliflorum* O. Schulz, in Engl., Pflanzenr. 4(134): 69. 1907. *E. fiscalense* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22(1): 33. 1940. Standl. & Steyererm., Fieldiana: Bot. 24(5): 391. 1946. *E. tikalense* Lundell, Wrightia 4: 177. 1971.

Semideciduous, dioecious **shrubs** or small trees to 8 m tall, highly variable in habit with branches long and slender, or short and compact with well-developed short shoots, the branchlets dark brown to dark gray, abundantly supplied with lenticels; cataphylls persistent, scattered at base of long shoots or crowded on short shoots, similar to foliar stipules; foliar stipules persistent, 1.5–2.5 mm long, at apex obtuse and briefly 2-setulose, fimbriate at margin. **Leaves** persistent or partly deciduous, the petioles 3–6 mm long, very slender, often drying orange or ferruginous; **leaf blades** 8–30 mm long, 7–25 mm wide, obovate, elliptic, or rounded, rounded or shallowly retuse at apex, acute at base, bicolorous, drying medium green on upper surface, very pale green on lower surface, without parallel lines or central panel on lower surface, the lateral nerves 4–6, inconspicuous. **Inflorescence** produced in the axils of leaves or cataphylls near apex of current season's shoots, the flowers 1 (or rarely

2 or 3) per node; bracteoles ca. 0.8–1.0 mm long, ovate, fimbriate; pedicels 0.5–4 mm long, 5-angled, thickened at the apex into the calyx. **Flowers** unisexual; calyx 1.2–1.5 mm long, the lobes triangular to triangular-ovate, acute at apex; **pistillate flowers** bearing a staminal tube with very short filaments and rudimentary anthers, the ovary with subsessile, flattened stigmas, 0.5 mm long; **staminate flowers** with 10 stamens in two unequal series, the staminal tube about half as long as the calyx, and a pistil rudiment. **Drupe**s 5–8 mm long, 3–5 mm in diameter, the endocarp ellipsoid or curved, rounded at apex, \pm trigonal in cross section, subequally 3-locular with 1 fertile and 2 empty locules.

In Costa Rica, known only from Guanacaste and northwestern San José provinces, in dry forest, often along water courses, 50–900 m elevation. Flowering specimens have been collected in late May and in August–September, fruits in September. This species ranges from the Bahamas, Greater Antilles, and Mexico to Costa Rica.

Erythroxylum rotundifolium is recognized by the small, rounded leaves with long, slender, orangish petioles and by the small, unisexual, solitary, subterminal flowers and trilocular drupes. *Erythroxylum rotundifolium* is treated here in the widest sense as a highly polymorphic species with either slender and open or compact and dense branching habit, and the leaves variable in shape and size of lamina and relative length of petiole. After further study, some of the Central American segregate populations such as *E. pallidum* Rose and *E. compactum* Rose may need to be recognized at least at the varietal level. Much Central American material of this species has been misidentified as *E. brevipes* DC., a species from Puerto Rico and Hispaniola closely related to *E. havanense*.

ZYGOPHYLLACEAE

By William Burger

REFERENCE—D. M. Porter, The genera of the Zygophyllaceae in the southeastern United States. J. Arnold Arbor. 53: 531–552. 1972.

Annual or perennial **herbs**, subshrubs, shrubs, or trees, often strongly scented and with sticky resin, growth usually sympodial, branches often with swollen or articulated nodes, with simple hairs; stipules paired at each leaf base, free, persisting or rarely deciduous, sometimes modified as spines. **Leaves** opposite or less often alternate, often distichous, usually evenly pinnate, occasionally simple to bifoliate or 3–7-parted, petiolate; **leaf blades** (leaflets) petiolulate or subsessile, inequilateral, usually entire, stiff to fleshy in texture, often strongly

resinous. **Inflorescences** racemose or fasciculate (rarely cymose), usually with the flowers solitary on axillary peduncles/pedicels. **Flowers** bisexual (rarely unisexual and dioecious), radially symmetrical or rarely somewhat bilaterally symmetrical, hypogynous, perianth (4–)5(–6) parted, sepals free or united at the base, imbricate or valvate in bud; **petals** imbricate or convolute in bud (rarely valvate), narrowed at the base, a disc usually present and often with extra- or intrastaminal glands; **androecium** usually with twice as many stamens as the petals (rarely 3 × or 1 × as many), free, the outer stamens opposite the petals, filaments with or without appendages at the base, anthers 2-thecous, versatile or basifixed, dehiscent introrsely with longitudinal slits; **pistil** solitary, of (2–)4–5(–6) united carpels, ovary sessile or short-stipitate (with a gynophore), 2–6-locular, with axile placentation and 1–several(–many) ovules in each locule, ovules pendulous or ascending, style slender and terminal, stigma solitary and lobed or 2–6-parted. **Fruit** a 2–6-lobed loculicidal or septicidal capsule, or a schizocarp breaking

up into few to several mericarps or nutlets (rarely berrylike or drupaceous), the mericarps often thickened and spinose to tuberculate on the outer (abaxial) surface; **seed** with a straight or curved embryo, cotyledons linear or oblong, endosperm hard and oily or absent, an aril present or absent.

A family of about 25–30 genera and 250 species, best represented in arid, saline, or seasonally dry tropical and subtropical environments. The family consists of somewhat diverse elements, several of which are often segregated as separate families (such as *Balanites* of Africa–Eurasia and *Nitraria* of the Old World subtropical deserts). This family has been classified with both the Geraniales and the Sapindales; the Rutaceae of the Sapindales may be the most closely related family.

Key to the Genera of Zygothylaceae

- 1a. Trees with very hard heavy wood; petals blue or purplish *Guaiacum*
- 1b. Herbs or subshrubs, usually prostrate on the ground; petals white to yellow or orange 2a
- 2a. Fruiting mericarps armed with spines; each leaf with more than 10 leaflets (in our species) *Tribulus*
- 2b. Fruiting mericarps without spines; each leaf with 8 or fewer leaflets (in our species) *Kallstroemia*

Guaiacum Linnaeus

Small to medium-sized **trees**, wood very hard, heavy and resinous, branches often with thickened nodes; stipules small. **Leaves** opposite, parapinnate, petiolate, leaflets in 2–6 opposite pairs. **Inflorescences** of fasciculate flowers at distal nodes, each flower borne on a slender unbranched peduncle (= pedicel) from the axil of a distal node. **Flowers** 4- or 5-parted, sepals slightly united at the base, petals 4 or 5, blue or purple, strongly narrowed at the base (clawed); **stamens** 8 or 10, filaments slender, anthers cordate or sagittate at the base; **pistil** with a short stipe (gynophore), ovary 2–5-lobed and 2–5-locular, ovules 8–10 in each locule. **Fruits** slightly fleshy when ripe, but drying smooth and coriaceous, with 2–5 prominent longitudinal lobes or rounded ridges (rarely wings); **seeds** ovoid to ellipsoid.

A genus of about six species, ranging from southern Florida, USA, and the West Indies to northern South America. This is the genus of lignum vitae, the hardest of commercial timbers, often used for construction in salt water. The medical resin guaiacum is obtained from these plants by heating. Unfortunately, the usefulness of these trees has resulted in their decimation in many areas. *Guaiacum sanctum* grows wild in northwestern Costa Rica, while *G. officinale* L., with larger more rounded leaflets, occurs in the West Indies.

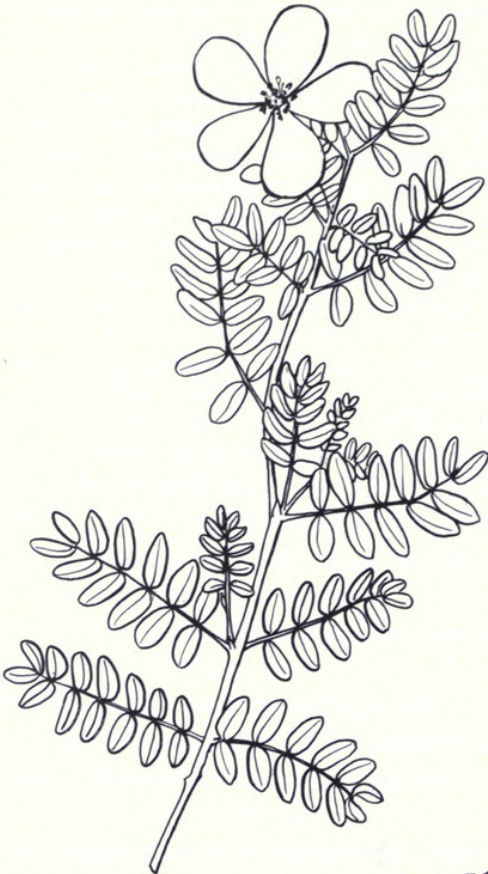
These species are sometimes planted as ornamentals for their showy blue flowers.

Guaiacum sanctum L., Sp. Pl. 382. 1753. Figure 8.

Small **trees** up to ca. 10 m tall, leafy branchlets 0.8–3 mm thick, minutely puberulent with thin ascending hairs ca. 0.2 mm long, becoming pale gray and glabrous; stipules 2–4 mm long, triangular and acute, appressed puberulent distally, thick and persisting. **Leaves** opposite, 3–9 cm long, pinnately compound with (2–)3–5(–6) pairs of leaflets, petiole 3–8 mm long, petiole and rachis to 5 cm long, rachis 0.3–0.8 mm thick, minutely puberulent or glabrescent, deeply sulcate above; **leaf blades** (leaflets) 12–28(–32) mm long, 4–14(–16) mm broad, asymmetric and narrowly oblong to oblong-obovate, the middle leaflets the longest on each leaf, bluntly obtuse to acute at the apex, subsessile and unequal on the thick petiolule, with the proximal side usually rounded at the base and the distal side more straight, leaflets drying stiffly chartaceous, glabrous above and below or sparsely sericeous near the base, venation palmate with 1–3 major veins and more weakly defined lateral veins, all these veins strongly ascending and loop-connected distally. **Inflorescences** fascicles of (1–)4–8 flowers at distal nodes, peduncles (= pedicels) 12–20 mm long, slender (0.3–0.5 mm thick when dry), sparsely and minutely puberulent. **Flowers** ca. 15 mm long and 20 mm broad, sepals 4–6 mm long and ca. 3 mm broad, broadly imbricate in bud;

Kallstroemia maxima

Tribulus cistoides



Kallstroemia pubescens

Guaiacum sanctum

FIG. 8. Zygophyllaceae: four Central American species.

petals 8–12 mm long and 6–8 mm broad, broadly ob-ovate and clawed at the base, bright blue; **stamens** ca. 6 mm long, anthers 1.5–2 mm long, becoming curved; **pistil** ca. 10 mm long, with a short (2 mm) stipe, and slender style 2–3 mm long, ovary obovoid and drying dark. **Fruits** 14–16 mm long and 12–18 mm broad, ob-ovoid and prominently 2–5-lobed or ridged, the longitudinal lobes 7–9 mm thick and rounded, fleshy or moist at maturity but drying to a yellowish and lustrous hard surface; **seeds** ellipsoid, ca. 1 cm long, brown to black and with a red aril.

Trees of the seasonally very dry and deciduous forest formations in northwestern Costa Rica. The species is found from 10–200 m elevation in Costa Rica, and up to 700 m in Nicaragua. Flowering material has been collected in March; fruit has been collected in July. The species ranges from southern Florida and eastern Mexico through the West Indies and Central America to northern South America.

Guaiacum sanctum is recognized by its opposite compound leaves with 2–5 pairs of small subsessile asymmetric leaflets, the bright sky-blue flowers, and the restriction to lowland deciduous forest formations. The leaflets resemble those of some Leguminosae, but the opposite leaves and lobed capsular fruit are quite different. The hard and heavy heartwood is said to become bluish on exposure to air (Janzen & Liesner, Brenesia 18: 90. 1980). For a discussion of uses of this species and the closely related *G. officinale* see the Flora of Guatemala (in Fieldiana: Bot. 24(4): 395. 1946, reprinted 1985).

Kallstroemia Scopoli

REFERENCE—D. M. Porter, The genus *Kallstroemia* (Zygophyllaceae). Contr. Gray Herb. 198: 41–153. 1969.

Annual or less often perennial **herbs**, stems herbaceous or slightly woody, prostrate or decumbent to ascending, often spreading outward from a central taproot, terete and slightly succulent, becoming longitudinally striate when dry; stipules paired at each leaf-base, free. **Leaves**

opposite and parapinnate, petiolate, with 2–10 pairs of opposite subsessile leaflets, the distal leaflets larger and often somewhat falcate and asymmetric, the basal (proximal) leaflets often unequal in size; **leaf blades** (leaflets) entire, pubescent to glabrescent, subsessile on short slender petiolules. **Inflorescences** represented by usually solitary axillary or pseudoaxillary flowers, each peduncle (= pedicel) with a single flower. **Flowers** bisexual and radially symmetrical, sepals 5(–6), free, pubescent, usually persisting in fruit; **petals** 5(–6), free, rotate, white to bright yellow or orange, convolute in bud, broadly ob-ovate and rounded distally, narrowed to the clawed base, fugaceous and quickly withering but often persisting; **stamens** 10(–12), the outer 5(–6) opposite the petals and somewhat larger than the inner 5(–6), these latter often subtended at the base by small lobed glands, filaments filiform (rarely winged near the base), inserted on the disc, anthers ovoid to oblong-linear; a fleshy annular disc present, obscurely 10(–12)-lobed; **pistil** 1, ovary broadly sessile, 10(–12)-ribbed and 10(–12)-locular, globose to conical, glabrous to pubescent, 1 pendulous ovule in each locule, style simple and cylindrical to conical, persisting in fruit, stigma capitate to clavate, with 10(–12) ridges or lobes. **Fruits** broadly ovoid to conical, with 10(–12) longitudinal ridges or lobes and the persisting style (beak), glabrous or puberulent at maturity, breaking septicidally into 10(–12) or fewer mericarps and those separating from the persisting central axis, each mericarp with 1 locule and 1 seed, the mericarps wedge-shaped (triangular in cross section) with a rounded tuberculate or rugose abaxial surface; **seeds** oblong to ovoid, testa membranaceous, endosperm absent.

An American genus of 17 species, ranging from the southern United States, Mexico, and the West Indies through Central America to central Argentina. The genus has become naturalized in western Africa and India. Nearly all the species are found in arid and seasonally very dry environments, or in early stages of open secondary succession. The mericarps are quite unusual in form, and a mericarp may leave an oblong opening in the side of the fruit if adjacent locules fail to develop. In addition, the mericarps can be mistaken for seeds. The two species of *Kallstroemia* found in Costa Rica are quite similar in overall appearance; they appear to be native to Central America. These plants may be mistaken for *Portulaca oleracea* L. (*verdolaga* or purslane), of similar habit but with alternate or clustered leaves.

Key to the Species of *Kallstroemia*

- 1a. Ovary and fruit glabrous or strigose only at the base; sepals lanceolate in fruit, often curved over the fruit; stipules narrowly lanceolate; leaflets as many as 8 per leaf *K. maxima*
- 1b. Ovary and fruit usually with appressed thin pilose hairs; sepals linear-lanceolate with involute margins and usually spreading laterally beneath the fruit; stipules usually linear; leaflets as many as 6 per leaf *K. pubescens*

Kallstroemia maxima (L.) Hook. & Arnott, Bot. Beechey Voy. 282. 1838. *Tribulus maximus* L., Sp. Pl. 386. 1753. Figure 8.

Annual **herbs** or herbaceous vines, stems prostrate to decumbent, to 1 m long, leafy internodes 1–3 mm thick, with thin whitish ascending hairs of varying (0.3–1 mm) length; stipules 3–4 mm long, lanceolate. **Leaves** 1.2–6 cm long and 1–3.5 cm broad, obovate or oblong in general outline, paripinnate with (2–)3–4 pairs of leaflets, terminal leaflets the largest, a slender tip ca. 1 mm long often present at the end of the rachis; **leaf blades** (leaflets) 2–16(–18) mm long, 1.5–7(–11) mm broad, distal leaflets strongly asymmetric, oblong-obovate to obovate-falcate, obtuse at the apex, unequal at the base with the proximal (outer) side rounded and the distal (inner) side straight or concave, surfaces with slender appressed hairs ca. 1 mm long, with 1 midvein and several ascending secondary veins. **Inflorescences** of solitary axillary flowers, peduncles (= pedicels) (7–)12–20(–28) mm long, glabrescent. **Flowers** with sepals 4–5 mm long, ca. 2 mm wide, narrowly ovate, with stiff slender hairs to 1.5 mm long, persisting, petals 4–6 mm long, to 6 mm wide, obovate, pale yellow to orange; **ovary** ca. 1 mm in diameter, style cylindrical, to 2 mm long, stigma capitate. **Fruits** broadly ovoid to broadly conical, 6–9 mm long, 4–7 mm broad near the base, pale yellowish white, glabrous or strigose at the base, the beak 3–4 mm long and darker in color, mericarps 3–4 mm high, 1–1.5 mm wide, abaxially tuberculate and transversely ridged, with pitted sides.

Plants of open recently cleared ground and early secondary growth in seasonally dry and deciduous formations and in evergreen areas; ranging from sea level to 500(–1400) m elevation. The species probably flowers throughout the year in Central America, but has been collected most often in May–August and in November. The species ranges from the southeastern United States through Mexico, Central America, and the West Indies to northern South America.

Kallstroemia maxima is recognized by the low-growing habit on open ground, the opposite evenly pinnate leaves, the 3 or 4 pairs of leaflets with the distal leaflets largest, and the unusual fruit (see discussion under the genus).

Kallstroemia pubescens (G. Don) Dandy, in Keay, Kew Bull. 10: 138. 1955. *Tribulus pubescens* G. Don, Gen. Hist. 1: 769. 1831. *K. caribaea* Rydb., in Vail and Rydb., N. Amer. Fl. 25: 111. 1910. Figure 8.

Annual **herbs**, stems prostrate to decumbent, up to 1 m long, leafy internodes 0.5–2 mm thick, with thin ascending hairs 0.5–1 mm long; stipules 3–4 mm long, linear, with thin straight hairs. **Leaves** opposite, to 4.5

cm long and 2.5 cm broad, often rectangular to obovate in outline, paripinnately compound with 2–3 pairs of subsessile leaflets, the terminal leaflets the largest, petiolules ca. 0.5 mm long; **leaf blades** (leaflets) 5–14(–20) mm long, 3–8(–10) mm broad, proximal (lower) leaflets broadly oblong or ovate-oblong, distal leaflets asymmetric and oblong-falcate or obovate-falcate, rounded at the apex or with an apiculate tip, unequal at the base with the proximal (outer) part rounded and the distal (inner) side straight or convex, with straight slender stiff appressed ascending hairs ca. 0.5–1 mm long on the surfaces and along the edges, midvein with 1–3 diverging secondary veins on each side. **Inflorescences** represented by solitary, axillary flowers, peduncles (= pedicels) 5–15 mm long. **Flowers** with sepals 3.5–5 mm long, 0.5–1.5 mm broad, lanceolate, with thin hairs ca. 1.2 mm long; **petals** ca. 6 mm long and 5 mm broad, obovate, white to yellow, withering but persistent; **pistil** 4–6 mm long, ovary broadly ovoid to conical, densely appressed-puberulent with fine white hairs, style 3–4 mm long, glabrous distally. **Fruits** 5–6 mm in diameter near the base, with 10 longitudinal ridges, the ridges with tubercles or transverse striations, with dense short hairs, mericarps 3–4 mm long and 1 mm thick, the subtending persisting sepals linear-lanceolate with involute margins.

Plants of open sunny early successional sites in seasonally dry deciduous formations and in evergreen areas, from sea level to 200 m elevation in Central America. Flowers and fruits have been collected in March–October in Central America. The species ranges from central Mexico through Central America and the West Indies to Colombia, Venezuela, Ecuador, and Peru. This species has become naturalized in West Africa and India.

Kallstroemia pubescens is recognized by the low habit on open ground, the paripinnate leaves with only four or six leaflets, the yellow flowers, the pubescent ovary and fruit, and the unusual mericarps. All our Costa Rican collections come from lowland Guanacaste.

Tribulus Linnaeus

Annual **herbs** (occasionally perennial, sometimes woody at the base, rarely small shrubs), plants diffusely branched and often spreading radially from a central taproot, prostrate to decumbent or ascending, stems herbaceous to slightly woody, often somewhat succulent, terete and longitudinally striate on drying, densely puberulent to glabrescent; stipules paired at the leaf-bases, leaflike. **Leaves** opposite with one of each pair usually shorter than the other, occasionally alternate when an opposing leaf fails to develop, evenly pinnate (paripinnately compound) with 3–10 pairs of opposite leaflets (rarely 1 leaflet of a pair aborting), petiolules very short or the leaflets subsessile, rachis often extending beyond the terminal pair of leaflets; **leaf blades** (leaflets) oblong to ovate-oblong or elliptic, often somewhat oblique and asymmetric at the base, the terminal pair usually point-

ing forward, puberulent with thin straight whitish hairs, with a single midvein. **Inflorescences** represented by solitary axillary flowers (usually from the axil of the smaller leaf of the node), borne on long peduncles (= pedicels). **Flowers** bisexual, radially symmetrical, sepals 5, free, puberulent, caducous or sometimes persisting; **petals** 5, free, bright yellow (white), spreading to rotate, imbricate in bud, narrowed at the base, deciduous; **stamens** 10 (rarely 5), the 5 outer longer and united to the base of the opposing petals, the 5 inner (antesepalous) stamens with nectariferous glands at the base, anthers cordate to oblong, interstaminal glands free or connate beneath the base of the ovary; **pistil** sessile, globose to ovoid, 5-lobed and 5-locular, densely puberulent, with 3–5 lobules in vertical rows on axile placentae in each locule, style cylindrical, stigma 5-angular or 5-lobed, pyramidal to oblong. **Fruits** usually breaking up into 5 (or fewer) hard mericarps but not leaving a central axis, mericarps broadly triangular, each mericarp divided internally by transverse septa to produce 2–5 1-seeded locules, the mericarps with hard spines or wings (or tuberculate) on their

outer (abaxial) surface; **seeds** oblong-ovoid, testa membranaceous, endosperm absent, embryo straight.

A genus of about 25 species of seasonally dry habitats and desert communities. Originally restricted to the Old World; a few species have become widespread and are now found throughout the tropics and warm-temperate areas of the world. The genus is recognized by the bright yellow flowers with free parts, the somewhat unequal usually opposite leaves with (3–)5–10 pairs of small (4–15 mm) opposite subsessile leaflets, and the fruit breaking up into hard spiny mericarps. Two species (*T. cistoides* L. and *T. terrestris* L.) have been found in Central America, but neither has been collected in Costa Rica. The following key distinguishes these two distinctive species.

Key to the Species of *Tribulus* Collected in Central America

- 1a. Flowers borne on peduncles usually longer than the leaves, sepals 5–12 mm long; intrastaminal glands united and forming a lobed cup at the base of the ovary; stigma oblong, on a short prominent style *T. cistoides*
- 1b. Flowers borne on peduncles equaling or shorter than the leaves, sepals 3–6 mm long; intrastaminal glands free; stigma hemispheric, subsessile *T. terrestris*

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