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# FIELDIANA

## Botany

NEW SERIES NO. 36

### FLORA COSTARICENSIS

William Burger, Editor

### Family #113 Euphorbiaceae

William Burger

Michael Huft

October 31, 1995  
Publication 1469

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### FLORA COSTARICENSIS

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## Introduction

This is the ninth issue in the *Flora Costaricensis* series. The first dealt with the Piperaceae, family number 41 (*Fieldiana*, Bot. 35, 1971). The second included families numbered 42 through 53, Chloranthaceae through Urticaceae (*Fieldiana*, Bot. 40, 1977). The third issue covered the Gramineae (Poaceae) and was authored by Richard Pohl (*Fieldiana*, Bot., n.s. No. 4, 1980). The fourth issue included families numbered 54 through 70, Podostemaceae through Caryophyllaceae (*Fieldiana*, Bot., n.s. No. 13, 1983). The fifth issue covered families 200 and 201, the Acanthaceae, authored by L. H. Durkee, and Plantaginaceae (*Fieldiana*, Bot., n.s. No. 18, 1986). The sixth issue included families 80 and 81, Lauraceae and Hernandiaceae

(*Fieldiana*, Bot., n.s. No. 23, 1990). The seventh issue included families numbered 97 through 103, Krameriaceae through Zygophyllaceae (*Fieldiana*, Bot., n.s. No. 28, 1991). The eighth issue included family 202, the Rubiaceae (*Fieldiana*, Bot., n.s. No. 33, 1993).

In the figures, leaves and leafy stems are drawn to the same scale throughout. Enlarged flowers and fruits are drawn to the same scale on an individual plate unless otherwise noted. The closed scales represent centimeters, and the open scales represent millimeters. The figures are somewhat diagrammatic and represent the senior author's concept of a common or characteristic morphology.

## Acknowledgments

We wish to thank the staff of the Museo Nacional de Costa Rica for their assistance in collecting programs over many years. The National Science Foundation and the National Geographic Society helped support many of these collecting activities. The Missouri Botanical Garden and the Instituto Nacional de Biodiversidad have been especially active in enriching our knowledge of Costa Rica's flora in recent years. Dr. Michael Huft, on the staff of the Missouri Botanical Garden and stationed at the Field Museum, worked with Neotropical euphorbs for more than a decade. His determinations and taxonomic concepts served as

the foundation for the present treatment. The collections of the Field Museum, the Missouri Botanical Garden, Duke University, and the U.S. National Herbarium were consulted in preparing this treatment, and we thank those institutions for the use of their materials.

We have benefited from the annotations and publications of many taxonomists; they are acknowledged in the generic treatments and in the keys to genera. Three anonymous reviewers were very helpful, providing many detailed corrections and useful suggestions.



# FLORA COSTARICENSIS

## Family #113 Euphorbiaceae

### EUPHORBIACEAE

By William Burger and Michael Huft

Trees and shrubs or less often herbs, vines, and lianas, sometimes with thick green cactus-like stems and reduced leaves in African and ornamental species, monoecious (bisexual) or dioecious (unisexual), sap often with colored or whitish latex (sap strongly caustic in *Hippomane* and some *Euphorbia* spp.), glabrous or pubescent, trichomes simple, stellate, scurfy, or rounded and peltate with flat apex (cf. *Croton*), stinging hairs present in some genera (cf. *Cnidioscolus* and *Tragia*); stipules usually 2 and lateral at the petiole base (rarely 1 or 0), often falling early (caducous). Leaves usually alternate (opposite in *Chamaesyce*, *Euphorbia* spp., et al.), simple (rarely trifoliate or palmately compound as in *Dalechampia* spp. and *Hevea*), petioles usually present, often with prominent glands distally or at the base of the blade (*Croton*, *Sapium*, et al.); leaf blades entire to serrate, sometimes palmately lobed (rarely irregularly pinnately lobed as in *Codiaeum*, *Euphorbia* spp.), glabrous to pubescent, venation pinnate or palmate, often with glands along the edge or imbedded in blade, domatia rarely present. Inflorescences terminal, axillary or extra-axillary, usually solitary or few/node, unisexual or bisexual, the bisexual usually with the ♀ flowers proximal and the more numerous ♂ flowers distal, very variable in form (spikes, racemes, cymes, thyrses, panicle or of solitary or fasciculate flowers) but most often with flowers in distal cymes, inflorescences forming pseudo-flowers (pseudanthia) in *Chamaesyce*, *Euphorbia*, and *Pedilanthus* (called cyathia) and with less tightly organized pseudanthia in *Dalechampia* and *Pera*; flowers always unisexual but the pseudanthia usually bisexual, sessile or pedicellate, usually subtended by bracts, bracts sometimes with 2 lateral glands. Male flowers radially symmetrical, perianth whorls 1 or 2 (rarely 0), calyx with 3–6 sepals or calyx lobes, valvate or imbricate in bud, glabrous or puberulent, petals present or absent, a disk usually present (annular, lobed, flat or glandular); stamens (1–2) 3–many, usually as many or twice as many as the perianth parts, filaments free or united into a column (a parasol-like androecium in *Astrocasia*, mushroom-like in *Omphalea*, strobilus-like protuberances in *Hura*, distally branched and with many anthers in *Ricinus*), anthers 2- or 4-theous, usually dehiscing longitudinally, pollen grains of many differing types and often important in determining generic relationships; a pistillode present or absent. Female flowers radially symmetrical, perianth of 1 or 2 whorls (reduced or absent in a number of genera), calyx with 3–8 sepals or calyx lobes, imbricate, valvate or united in bud, corolla usually of separate petals or absent, disk present or absent, annular to lobed or cu-

pulate, staminodes usually absent; ovary superior, locules usually 3 (1–20), styles usually the same number as the locules, free or united into a short or long column, style branches simple or divided to lacinate distally, ovules 1 or 2 in each locule, usually pendulous. Fruits usually capsules (schizocarps), rarely berries or drupes, the capsules characteristically separating septicidally into 2-valved cocci (mericarps) that open loculicidally and explosively on the inner face, a central columella often remaining after dehiscence; seeds often with an adaxial line or scar (ventral raphe), a thickened or fleshy caruncle often present at the micropylar attachment site, surfaces smooth to rugose, endosperm usually copious and oily, sometimes containing poisonous compounds.

The Euphorbiaceae are a large and important family with an estimated 7,700 species (Mabberley, 1987) in 317 genera (Webster, 1994b). Except for the polar regions, the family is worldwide in range but with the great majority of species in tropical and subtropical regions. The family includes important agricultural taxa (*Hevea*, *Manihot*, *Ricinus*), medicinal plants, timber trees, and garden ornamentals (*Acalypha*, *Codiaeum*, *Euphorbia*, *Ricinus*) (see Mabberley, 1987, and other references under Literature Cited). The taxonomy of the Euphorbiaceae was recently the subject of a symposium (in Ann. Missouri Bot. Gard. 81, parts 1 and 2, 1994). The relationships of the Euphorbiaceae have been the subject of many different opinions (Webster, 1987). For a recent overview of the family, see Webster (1994a, b).

The Euphorbiaceae are often difficult to identify, both as to family and as to genera. The small unisexual flowers of great morphological diversity (often on unisexual trees and shrubs) account for some of this difficulty. Flowering material may be difficult to recognize as euphorbiaceous when only ♂ flowers are present. The usually three-parted ovaries, capsular fruits often breaking open explosively, and the characteristic seeds allow many fruiting collections to be quickly determined to family. The presence of milky or colored latex/sap or stellate-lepidote-peltate hairs can aid in determination of some genera. Many species of Euphorbiaceae have flat or elevated glands at or near the junction of the petiole and leaf blade or small glands along the edge of the blade. Specimens of

Euphorbiaceae may be mistaken for species of Flacourtiaceae (but these usually have bisexual flowers), Moraceae (especially *Sorocea* and *Trophis*), and Urticaceae. Ornamental leafless succulent species with spines are often confused with Cactaceae, but the flowers and fruits easily distinguish the two families. Also, succulent euphorbs never have the tiny hooked hairs (glochids) found in many cacti, whereas cacti rarely have the milky sap found in many succulent euphorbs.

To aid in identification, we provide two separate keys to genera. The first is a technical key based on the characteristics that help define the genera,

and this key may be useful over a broader region. This key is based on the key developed by Webster (in Webster & Huft, 1988) and to a lesser extent on one by Gillespie (1993). The second key is an artificial key that is intended to be easy to use but that may not be helpful with atypical material or material new to southern Central America. Hopefully, the illustrations will serve as an additional aid to identification, especially when critical floral features are not available. The illustrations are arranged in a series of artificial "look-alike" groupings.

# Key 1: Key to the Genera of Euphorbiaceae in Costa Rica

(Based on the Key of Webster in Webster & Huft, 1988.)

- 1a. Ovules 2 in each locule of the ovary (seeds 1/locule in *Drypetes* and in *Astrocasia*); seeds 1–2 in each locule of the fruit, often 6/fruit (also 1–4/fruit), without caruncle; whitish latex absent; leaf blades never lobed, usually entire to obscurely serrate, usually lacking imbedded laminar glands, usually pinnately veined; trichomes simple or peltate [subfamily Phyllanthoideae and *Croizatia* of the Oldfieldioideae] ..... 2
- 1b. Ovule 1 in each locule of the ovary; seeds usually 3/fruit, seeds with or without an apical caruncle; whitish or colored latex present or absent; leaf blades often serrate or lobed (also entire), often with glands on blade or petiole, venation pinnate or palmate; trichomes various ..... 10
  - 2a. Petals present in the flowers ..... 3
  - 2b. Petals absent in the flowers ..... 5
    - 3a. Petals equaling or longer than the sepals; filaments connate and forming a parasol-like androecium; ♀ disk forming a thin corolla-like cup; seeds with copious endosperm [rare in southern Central America] ..... *Astrocasia*
    - 3b. Petals much shorter than the sepals; filaments free or connate, not forming a parasol-like androecium; ♀ flower without a thin cupulate disk; seeds with little or copious endosperm ..... 4
    - 4a. Plants monoecious (bisexual); stipules united above the petiole (intrapetiolar); petals glabrous; styles bifid and expanded; columella narrowed toward apex, without apical wings ..... *Amanoa*
    - 4b. Plants dioecious (unisexual); stipules not united above the petiole; petals puberulent; style twice bifid (pistil with 12 style branches); columella expanded distally forming 3 papery wings [eastern Panama and South America, not included in text] .. *Croizatia*
  - 5a. ♂ inflorescences spikes or racemes; ♂ flowers with prominent pistillode; plants dioecious (unisexual) ..... 6
  - 5b. ♂ inflorescences of axillary flower clusters or on deciduous branchlets if racemose; ♂ flowers lacking a prominent pistillode; plants monoecious (bisexual) or dioecious ..... 7
    - 6a. Trichomes simple; calyx deeply lobed (almost of separate sepals); ♂ inflorescences spicate with sessile flower clusters; anther thecae not pendulous; ovary 2–3-locular; fruits dry capsules ..... *Richeria*
    - 6b. Trichomes mostly peltate; calyx with short lobes; ♂ inflorescences with alternate branches; anther thecae pendulous; ovary 2-locular; fruits fleshy and drupaceous ..... *Hyeronima*
  - 7a. ♂ flowers with a central intrastaminal disk; ovary with 1 or 2 locules, stigmas sessile and expanded; fruits drupaceous; ovules 1/locule; dioecious (unisexual) trees ..... *Drypetes*



- 7b. ♂ flowers without a central disk or the disk outside the stamens if present; ovary with 3–6 locules and styles, styles present and bifid, stigmas slender or expanded; fruits mostly capsules; ovules 2/locule; plants monoecious (bisexual) or dioecious ..... 8
- 8a. Ovary with 4 or 5 locules (rarely 3, 6), styles 4 or 5 (3, 6); fruits irregularly dehiscent; seeds with fleshy outer coat and hard bony inner coat; ♂ flower with annular (ring-like) disk and 4 free stamens; distal branchlets persisting, not resembling pinnate leaves; dioecious trees ..... *Margaritaria*
- 8b. Ovary with 3 (rarely 2) locules, styles 3 (2); fruit usually breaking into valves; seeds without both a fleshy and bony layer; ♂ flowers with 2 or 3 stamens, or without a disk when 4 stamens are present; distal branchlets often deciduous and resembling pinnate leaves; monoecious or dioecious ..... 9
- 9a. Common wild trees, shrubs, and herbs with green leaves; seeds dry, ventral faces not invaginated; floral disk usually present ..... *Phyllanthus*
- 9b. Ornamental garden shrubs with variegated leaves; seeds with fleshy exotesta, ventral face invaginated; floral disk absent ..... *Breynia*
- 10a. (from 1b) Floral bracts without glands at the base (present in *Tetrorchidium*); sepals imbricate to valvate, usually covering the anthers completely in bud, rarely petaloid; petals present or absent; disk often present; trichomes various; leaves simple to palmately lobed or compound ..... 11
- 10b. Floral bracts with 2 glands at the base (but sometimes difficult to see, absent in *Hura* and *Senfelerdea*); sepals imbricate or not well developed; anthers mostly exposed in bud; petals absent and the sepals not petaloid, but glands of involucre cup may have petal-like lobes; disk absent or minute; trichomes simple or absent (dendritic in *Mabea*); leaves without lobes [subfamily Euphorbioideae] ..... 37
- 11a. Petals absent, or if petals present the leaf blades with pinnate venation; petioles lacking stalked glands (but glands imbedded in leaf blades often present); seeds lacking caruncles (caruncles present in *Pera* and *Ricinus*); trichomes simple or attached at the center (peltate in *Pera*); flowers in axillary clusters, racemes, or spikes (these sometimes aggregated into panicles); latex usually absent, rarely white (subfamily Acalyphoideae) ..... 12
- 11b. Petals present, at least in the ♂ flowers, or else calyx petaloid (except in *Tetrorchidium*, with raised foliar glands, and in *Croton punctatus*); leaves often palmately veined or lobed; petioles or bases of the leaf blades often with stalked or prominent glands; seeds with caruncles or fleshy (except in *Garcia*); trichomes simple, attached in the center, stellate or peltate; inflorescences various; latex clear, colored or whitish (subfamily Crotonoideae) ..... 29
- 12a. Petals present in both ♂ and ♀ flowers [flowers in racemes; ♂ flowers with 10 stamens; seeds usually foveolate] ..... 13
- 12b. Petals absent (3 petals in ♀ *Caryodendron*) ..... 14
- 13a. Leaves serrulate, 2° veins straight, more than 6/side and clearly parallel; trichomes simple or gland-tipped; ♂ flowers with a pistillode ..... *Caperonia*
- 13b. Leaves entire, 2° veins arcuate-ascending, fewer than 5/side and not clearly parallel; trichomes often attached at the center; ♂ flowers lacking a pistillode. .... *Argythamnia*
- 14a. Flowers sessile within a globose stipitate flower-like inflorescence, at first enclosed by the petal-like involucre; inflorescences resembling globose flower buds borne on leafless nodes below the leaves; seeds smooth and shiny black with caruncle [dioecious trees with peltate or stellate trichomes] ..... *Pera*
- 14b. Flowers not sessile nor enclosed in a stipitate involucre; inflorescences not resembling pedicellate flower buds in early stages; seeds neither black nor shiny ..... 15
- 15a. Flowers in a complex flower-like arrangement (pseudanthium) with 2 usually conspicuous palmately veined bracts often held in a vertical plane [ovary and fruit usually armed with stinging hairs; plants mostly vines or lianas with palmately veined or lobed leaves, or with palmately compound leaves] ..... *Dalechampia*
- 15b. Flowers not in a complex pseudanthium with 2 large palmately veined bracts held in a vertical plane ..... 16
- 16a. Stamens resembling little trees, with many distal branches bearing 80–many anthers;

- leaf blades peltate and palmately lobed; inflorescences with ♀ flowers distal and ♂ flowers proximal; seeds with caruncles [introduced plants] ..... *Ricinus*
- 16b. Stamens not branched and tree-like with so many anthers; leaf blades never peltate or palmately lobed; inflorescences usually with ♀ flowers proximal; seeds with minute caruncle or caruncle absent ..... 17
- 17a. ♂ flowers with 4 sepals imbricate in 2 whorls, stamens 2, completely united and mushroom-shaped with connective enlarged and fleshy; latex reddish or purplish; fruits 8–12 cm diam. [globose; plants usually lianas] ..... *Omphalea*
- 17b. ♂ flowers with 3–5 valvate sepals, stamens 3–many (if 2 then the connective not enlarged); latex not reddish or purplish; fruits less than 7 cm diam. .... 18
- 18a. Stinging hairs present [styles undivided and connate basally; disk absent; seeds smooth, caruncle absent] ..... 19
- 18b. Stinging hairs absent ..... 20
- 19a. Anthers lacking a minute tuft of apical hairs; bisexual vines; leaf blades usually cordate at base, usually with many stinging hairs ..... *Tragia*
- 19b. Anthers with a minute apical tuft of stinging hairs (often difficult to see); unisexual shrubs and trees; leaf blades cuneate at base, glabrescent ..... *Acidoton*
- 20a. Styles basally connate into a long column; inflorescences bisexual and axillary; ovary 4-locular, strongly keeled; lianas [leaf blades with 2 circular glands at base] ..... *Plukenetia*
- 20b. Styles free or basally connate; inflorescences unisexual, various; ovary 2–3-locular, not strongly keeled; trees, shrubs, or herbs ..... 21
- 21a. Styles usually divided into many slender laciniate branches; anthers minute (ca. 0.1 mm wide) with narrow pendulous-vermiform thecae (but difficult to see); ♀ bracts much larger than the ♂ or if not the ovary verrucose [♂ inflorescences usually slender congested spikes] ..... *Acalypha*
- 21b. Styles various, but only divided into slender laciniate branches in *Adelia*; anthers usually more than 0.2 mm wide and the thecae not narrow and pendulous-vermiform; ♀ bracts not conspicuously larger or differently shaped than the ♂ bracts ..... 22
- 22a. Ovary with 2 locules and 2 elongate free entire styles [stamens usually 8, pistillode absent; seeds tuberculate, lacking a caruncle, dry; trichomes often minutely stellate] ..... *Alchornea*
- 22b. Ovary with 3 locules and with 3 bifid styles (or the seeds fleshy if styles are simple) ..... 23
- 23a. Stamens fewer than 10; plants unisexual (dioecious) ..... 24
- 23b. Stamens more than 10; plants unisexual or bisexual (monoecious) ..... 27
- 24a. Herbs with creeping stems; stipules thin and persisting; capsule thin-walled ... *Dysopsis*
- 24b. Trees and shrubs with erect stems; stipules absent or caducous; capsules thick-walled ..... 25
- 25a. Leaves usually tripliveined; stipules absent; seed coat fleshy; a pubescent pistillode present in ♂ flowers [inflorescences axillary; ♀ flowers subsessile] *Alchorneopsis*
- 25b. Leaves pinnately veined; stipules present; seed coat not fleshy; pistillode absent in ♀ flowers ..... 26
- 26a. Leaves without glands; stamens 3, disk absent in ♂ flowers; styles broadly expanded and stigma-like; seeds < 1 cm long ..... *Adenophaedra*
- 26b. Leaf blades with flat laminar glands at the adaxial base; stamens 4–7, disk large in ♂ flowers; styles short; seeds > 1 cm long ..... *Caryodendron*
- 27a. Stamens more than 50 in ♂ flowers, anther connective enlarged; stipules thickened [disk absent in ♀ flowers] ..... *Cleidion*
- 27b. Stamens less than 30 in each ♂ flower, anther connective not enlarged; stipules thin ..... 28
- 28a. Styles much divided and laciniate distally, ♀ flowers with long (> 18 mm) pedicels; fruits long-pendulous; leaf blades without glands ..... *Adelia*

- 28b. Styles once or twice bifid (6 or 12 style branches), not laciniate, ♀ flowers sessile or on pedicels to 6 mm long; fruits not pendulous; leaf blades with conspicuous glands near the base ..... *Bernardia*
- 29a. (from 11b) Flowers without petals; stamens 3/flower, anthers peltate and appearing 4-theous; seeds fleshy, lacking a caruncle [dioecious/unisexual trees and shrubs; leaves with stalked petiolar glands and trichomes attached at the center] ..... *Tetrorchidium*
- 29b. Flowers with petals present, or if petals absent then the calyx petaloid or trichomes peltate; stamens 8 or more per flower, anthers not appearing 4-theous; seeds not fleshy, with a caruncle (except *Garcia*) ..... 30
- 30a. Flowers without petals, but the calyx petal-like [leaves palmately lobed; trichomes simple; sap white; plants monoecious/bisexual; inflorescences terminal and dichasial or paniculate; stamens 8–10] ..... 31
- 30b. Flowers with petals, or if petals absent then the trichomes peltate; sap not whitish .... 32
- 31a. Stinging hairs absent; calyx yellow to greenish or purple and often resembling a rotate corolla; ♂ flowers with free filaments and central interstaminal disk ..... *Manihot*
- 31b. Stinging hairs present (sometimes very few); calyx whitish and not resembling a rotate corolla; ♂ flowers with connate filaments and extrastaminal disk ..... *Cnidosculus*
- 32a. Anthers inflexed in bud; some peltate or stellate trichomes usually present [♂ flowers with 8-many stamens, filaments free; inflorescences spicate or racemose (never branched); plants usually monoecious/bisexual in Central America; seeds with caruncles] ..... *Croton*
- 32b. Anthers usually erect in bud; trichomes not stellate or peltate ..... 33
- 33a. Calyx opening into valvate segments; ♂ flowers with 6–13 petals, stamens 30–100 or more; seeds without caruncles [trichomes simple; bisexual trees or shrubs] ..... *Garcia*
- 33b. Calyx of initially separate imbricate sepals; ♂ flowers with usually 5 petals, stamens 12 or fewer; seeds with caruncles ..... 34
- 34a. Leaves palmately veined or lobed; stamens mostly 8–12, filaments partly united; inflorescences terminal and dichasial, usually bisexual; trichomes simple or with gland-tipped segments ..... *Jatropha*
- 34b. Leaves pinnately veined; stamens 3–40, filaments free; inflorescences terminal or axillary, usually unisexual (unisexual or bisexual in *Sagotia*), spicate to racemose or paniculate; trichomes never with gland-tipped segments ..... 35
- 35a. Stamens 3–7; ♀ flower with petals connate into a tube longer than the calyx; unisexual trees [inflorescences axillary and spiciform; trichomes simple and attached at the center but often difficult to see] ..... *Pausandra*
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- 36a. ♂ flowers without a disk; styles deeply bifid; inflorescences usually terminal, 1–12 cm long; leaves never lobed or with bright variegated colors; native trees ..... *Sagotia*
- 36b. ♂ flowers with a lobed disk; styles simple and unlobed inflorescences usually axillary, 10–20 cm long; leaves often with lateral lobes and brilliant variegated colors; introduced garden shrubs ..... *Codiaeum*
- 37a. (from 10b) Flowers not pseudanthial (as in 37b), without a well-developed involucre cup; flowers in spicate, racemose, or paniculate inflorescences; styles simple; stamens in whorls or united, not in radiating groups of 5 within a calyx cup or calyx tube; shrubs or trees, rarely herbs ..... 38
- 37b. Flowers pseudanthial, actually flower-like inflorescences (called cyathia) in which the involucre bracts are united to form a calyx-like cup, usually with 1–5 glands along the edge of the involucre cup and these often with petal-like structures, central pistil actually a naked ♀ flower on an articulated stipe (pedicel), styles bifid or simple; stamens usually in 5 lateral groups within the cupulate or shoe-shaped cyathium; cyathia often in cymose or dichotomous inflorescences; caruncle small or absent; herbs, shrubs, or small trees; sap usually whitish (often caustic) ..... 47
- 38a. Inflorescences thyrsoid or paniculate (resembling racemes in *Mabea*); ♂ flowers with anthers subsessile on an elevated receptacle ..... 39
- 38b. Inflorescences spicate or racemose; ♂ flowers with anthers borne on well-developed filaments ..... 40



- 39a. Trichomes branched (dendritic); ♀ flower with long styler column; ♂ flowers 2 or more/  
node, long-pedicellate, stamens 10 or more in our species [inflorescences long and  
racemose] ..... *Mabea*
- 39b. Trichomes absent, plants glabrous; ♀ flower with styles nearly free to the base; ♂ flowers  
1/node, subsessile, stamens 5 [eastern Panama and South America; not included in  
text] ..... *Senfelteria*
- 40a. Styler column at least 25 mm long, terminated by a fleshy disk 2–3 cm wide and resembling  
a parasol; ♂ flowers breaking their perianth irregularly in early anthesis, with anthers borne  
in whorls on cone-like columns from the axis of the inflorescence; ovary and fruit with more  
than 10 locules [capsule 5–9 cm diam.] ..... *Hura*
- 40b. Styler column < 25 mm long, styles diverging distally and not forming a flat disk; ♂ flowers  
not rupturing the perianth and not borne on conical projections of the inflorescence axis;  
ovary and fruit with fewer than 10 locules ..... 41
- 41a. Ovary 6–9-locular; fruits drupaceous and not splitting open [seeds lacking a caruncle; ♀  
flowers with 3-parted calyx; petiole with single gland; latex extremely caustic; seaside trees]  
..... *Hippomane*
- 41b. Ovary 2–3-locular; capsules often splitting open explosively ..... 42
- 42a. Seeds lacking a caruncle, seed coat fleshy; petioles usually with a pair of cylindrical glands;  
♀ sepals united at the base [♂ flowers with 2 stamens] ..... *Sapium*
- 42b. Seeds with a caruncle, seed coat dry; petioles without prominent glands; ♀ flowers with separate  
sepals ..... 43
- 43a. Dehiscent fruits with persistent woody 3-pronged stylobase (gynobase), columella present or  
absent; stems usually with much white sap; leaf blades with paired glands near the base [seeds  
with small caruncle in Central American species, rare in our area] ..... *Stillingia*
- 43b. Dehiscent fruits without a persisting woody 3-pronged stylobase, columella usually present;  
stems with little or no white sap; leaf blades without stalked glands ..... 44
- 44a. ♂ part of the inflorescence contracted to less than 1 cm long and ovoid; stamens 2 with  
filaments united, styles distinctly connate; seeds with large cap-like caruncle, seed surface  
foveolate [central Panama to South America and not included in text] ..... *Maprounea*
- 44b. ♂ part of the inflorescence elongated and spicate, not contracted and subglobose; stamens  
usually 3–5, filaments free or partly connate; styles free or partly united in *Actinostemon*;  
seeds with small caruncle, seed coat smooth ..... 45
- 45a. Spikes terminal or opposite the leaves; ♂ calyx 3-lobed, stamens 3; ovary with 3 or 6 distal  
lobes or projections; fruiting pedicels < 5 mm long ..... *Sebastiania*
- 45b. Spikes or racemes axillary or pseudoaxillary; ♂ calyx minute and 1-parted or absent; stamens  
2–6 (in Costa Rica); ovary smooth; fruiting pedicels > 10 mm long ..... 46
- 46a. Stipules and bud-scales < 1 mm long, not forming cap-like structures over shoot-apices and  
early inflorescences, often persisting; inflorescences minutely puberulent or glabrous .....  
..... *Gymnanthes*
- 46b. Stipules and bud-scales ca. 3 mm long, often forming a cap over shoot-apices and early  
inflorescence-buds, caducous; inflorescences essentially glabrous ..... *Actinostemon*
- 47a. (from 37b) Cyathia (flower-like pseudanthia) bilaterally symmetrical with involucre somewhat  
shoe-shaped, often with reddish coloring; involucre glands borne within the nectar spur and not  
visible from the exterior; styles connate into a long column; distal stems often green .....  
..... *Pedilanthus*
- 47b. Cyathia radially symmetrical, involucre usually urceolate or campanulate and round in cross-  
section, usually greenish, yellow or white; involucre glands usually visible at the edge of the  
involucre cup; styles not forming a long column; distal stems green or woody and brown ... 48
- 48a. Involucre without 4–5 distinct glands alternating with lobes of the cyathium, involucre usually  
saucer-shaped, red; few-branched succulent ornamental shrubs ..... *Synadenium*
- 48b. Involucre usually with 4–5 (1–3) distinct glands alternating with the lobes on the rim of the  
cyathium, involucre usually deeply cupulate or urceolate; trees, shrubs, and herbs, succulent or  
not, cultivated and wild ..... 49
- 49a. Leaves alternate, opposite or whorled, if opposite then blades not asymmetric at the base; stipules

- absent or gland-like and small; veins of the leaf blades lacking a sheath of chlorenchyma; main axis of the plant not aborting soon after germination; trees, shrubs, or herbs ..... *Euphorbia*
- 49b. Leaves always opposite, blades usually small and strongly asymmetric at the base; stipules present and often lobed; veins of the leaf blades with a sheath of chlorenchyma (in dried leaves the veins often look translucent in transmitted light, in contrast to the darker areas between the veins); main axis of the young plant aborting just above the cotyledons; herbs and small shrubs *Chamaesyce*

## Key 2: Artificial Key to Genera and Unusual Species

- 1a. Leaves compound with usually 3 leaflets, or the leaves simple and with prominent lobes > 20% the length or width of the leaf blade ..... 2
- 1b. Leaves simple and without prominent lobes, the blades entire to deeply serrate, dentate or crenate, teeth or lobes < 15% the width of the blades (note: simple leaves usually have buds or flowers in the axils of their petioles but leaflets do not) ..... 16
- 2a. Leaves 3-foliolate, petioles with 3 petiolate leaflets at the apex in at least some of the leaves on the plant ..... 3
- 2b. Leaves simple, petioles with a single leaf blade (the leaf blade may be deeply divided but the divisions do not have slender petiolules at their base) ..... 4
- 3a. Slender-stemmed vines; leaves sometimes simple and compound on the same stem; native ..... *Dalechampia* spp.
- 3b. Trees; leaves always 3-foliolate; introduced economically useful plants ..... *Hevea brasiliensis*
- 4a. Venation pinnate, lobes and sinuses along the lateral margins of the leaves ..... 5
- 4b. Venation palmate, lobes and sinuses distal and lateral on the leaf margin ..... 6
- 5a. Weedy herbs to 1 m tall ..... *Euphorbia heterophylla*
- 5b. Garden shrubs to 5 m tall ..... *Codiaeum variegatum*
- 6a. Leaf blades peltate, petiole attached near the center or near the edge of the blade ..... 7
- 6b. Leaves with the petioles attached at the edge of the blade ..... 8
- 7a. Margin of the leaf serrate; petiole attached near the center of the blade ..... *Ricinus communis*
- 7b. Margin of the leaf entire; petiole attached near the edge of the blade ... *Jatropha* spp.
- 8a. Plants slender vines with clambering branches, stems becoming > 1 m long, leaves > 4 cm long ..... 9
- 8b. Plants erect herbs, trees, and shrubs, or if prostrate or procumbent and clambering the stems < 1 m long with leaves usually < 3 cm long ..... 11
- 9a. Plants without stinging hairs; inflorescences racemose with prominent pedicels (to 15 mm long); flowers 6–18 mm long with prominent 5-lobed or 5-parted perianth ..... *Manihot brachyloba*
- 9b. Plants often with stinging hairs (at least near the flowers); inflorescences not clearly racemose; flowers lacking prominent calyx 6–18 mm long, often subtended by 2 large perianth-like bracts ..... 10
- 10a. Inflorescences with 1 or 2 slender axes from a peduncle 1–10 cm long, floral bracts 3–5 mm long, many along the axes ..... *Tragia bailloniana*
- 10b. Inflorescences flower-like with 2 large (1–6 cm) floral bracts usually held in a vertical plane (subtending the flowers) ..... *Dalechampia* spp.
- 11a. Stinging hairs usually present (around the flowers if lacking on the stems) [inflorescences usually dichotomously branched] ..... *Cnidoscylus* spp.
- 11b. Stinging hairs absent ..... 12
- 12a. Trees with broad (8–30 cm) leaves and short (1–5 cm) triangular obtuse lobes, depth of sinuses between lobes < 25% of the blade length ..... 13
- 12b. Herbs, shrubs, small trees, or vines, leaves small to broad (3–25 cm) and with narrow lobes, depth of sinuses > 30% of the length of the blade ..... 14
- 13a. Apex of the petiole with prominent glands, stellate and scurfy hairs present; native forest trees ..... *Croton smithianus*



- 13b. Apex of the petiole without prominent glands, plants glabrous or with simple or scurfy hairs; introduced trees ..... *Aleurites* spp.
- 14a. Stems with stellate hairs; inflorescences lacking lateral branches; herbs to 1 m tall; leaf blades 3–9 cm long ..... *Croton lobatus*
- 14b. Stems lacking stellate hairs, glabrous or with glandular hairs; inflorescences often with short lateral branches; herbs, shrubs, small trees, or vines, leaf blades 5–25 cm long ..... 15
- 15a. Stems usually glabrous or with hairs less than 0.3 mm long; flowers with a single perianth-like whorl, united in the lower part in ♂ flowers; small shrubs, small trees, or vines ..... *Manihot* spp.
- 15b. Stems usually puberulent, often with gland-tipped hairs; flowers with 2 whorls of free sepals and petals; herbs, shrubs, or trees ..... *Jatropha* spp.
- 16a. (from 1b) Plants slender vines with twining branches, shrubs with clambering green stems or woody lianas, stems becoming > 1 m long, leaves > 4 cm long ..... 17
- 16b. Plants erect herbs, trees, and shrubs, or if prostrate or procumbent and clambering then the stems < 1 m long with leaves usually < 3 cm long ..... 21
- 17a. Plants becoming woody lianas with stems usually > 4 mm thick [inflorescences 15–50 cm long, paniculate; leaves often subcoriaceous, 6–24 cm long, palmately veined; stinging hairs absent] ..... *Omphalea diandra*
- 17b. Plants not becoming thick-stemmed woody lianas, leafy stems usually < 4 mm thick ... 18
- 18a. Shrubby plants with clambering terete green branches ca. 3–10 mm thick, sap white; stinging hairs absent; flowers (= pseudanthia) bilaterally symmetrical and shoe-shaped, orange or red [gardens and seasonally dry habitats] ..... *Pedilanthus*
- 18b. Vines, not shrub-like, climbing leafy stems usually < 4 mm thick; flowers not shoe-shaped ..... 19
- 19a. Inflorescences flower-like with 2 prominent bracts usually held in a vertical plane and enclosing unusual flowers; venation palmate [stinging hairs sometimes present] ..... *Dalechampia* spp.
- 19b. Inflorescences not flower-like, bracts not large (> 5 mm wide) or opposite in a single plane; venation palmate or pinnate ..... 20
- 20a. Stinging hairs usually present; inflorescences terminal or leaf-opposed, with 1 or 2 slender unbranched axes; styles united only at base, fruit usually 3-locular ..... *Tragia* spp.
- 20b. Stinging hairs absent; inflorescences axillary or terminal with 1 stiff rachis; styles united into a thick column, fruit usually 4-locular ..... *Plukenetia* spp.
- 21a. (from 16b) Leaf blades consistently < 5 cm long ..... 22
- 21b. Larger leaf blades > 5 cm long ..... 27
- 22a. Leaf blades consistently opposite along the stems ..... 23
- 22b. Leaf blades alternate along the stems, but sometimes opposite below the inflorescences and/or at branching nodes ..... 24
- 23a. Leaf blades usually strongly asymmetrical (unequal) at the base, often very small (5–15 mm) stipules lacinate to ovate; plants erect or prostrate, herbs and subshrubs ... *Chamaesyce* spp.
- 23b. Leaf blades symmetrical (equal) at the base, usually > 10 mm long; stipules usually poorly developed; plants erect herbs, shrubs, or trees ..... *Euphorbia* spp.
- 24a. Fruits with 2 seeds/locule, seeds wedge-shaped and acutely triangular in cross-section; flowers few from the leaf axils, subtending bracts inconspicuous; leaf blades often in a single plane, very small to large (5–50 mm long) [note that cultivated ornamental shrubs with rounded variegated leaves keying here are *Breynia disticha*] ..... *Phyllanthus* spp.
- 24b. Fruits with 1 seed/locule, seeds rounded or angular in cross-section; flowers few to many, axillary, terminal or extra-axillary, usually with conspicuous bracts; leaves usually in a spiral, rarely < 15 mm long ..... 25
- 25a. Stems slender and repent; herbs at high (2000–3000 m) elevation [leaves ovate-orbicular with rounded crenate margins] ..... *Dysopsis glechomoides*
- 25b. Stems not slender and creeping, mostly erect; plants rarely found above 2000 m elevation ..... 26

26a.	Male spikes leaf-opposed; female flowers often on stems between the nodes; fruits subtended by sepals with scale-like processes on the outer surfaces; small-leaved herbs, rarely collected in Central America	<i>Sebastiania corniculata</i>
26b.	Plants without the above characteristics	27
27a.	(from 21b and 26b) Weak-stemmed herbs and subshrubs	28
27b.	Shrubs and trees with strong erect woody stems	32
28a.	Leaf blades entire, glabrous or with thin inconspicuous hairs; sap often whitish; flowers (actually pseudanthia) with calyx-like cup; pistil borne on an articulated stipe within the cup	<i>Euphorbia</i> spp.
28b.	Leaf blades serrate to crenate, densely pubescent when subentire; sap rarely whitish; flowers without calyx cups or urceolate perianth tube; pistils sessile	29
29a.	Inflorescences terminal and spicate, resembling a foxtail or <i>Cenchrus</i> inflorescence, or the ♀ flowers subtended by broadly rounded bracts with toothed margins and enlarging in fruit; style branches usually much divided and lacinate	<i>Acalypha</i> spp.
29b.	Inflorescences not resembling foxtails, bracts subtending the fruit not broadly rounded and exceeding the fruit in size; style branches not lacinate	30
30a.	Plant usually growing in water or at the edge of wet sites, main stems usually hollow; venation pinnate with 5–20 pairs of 2° veins [petioles without stalked glands or stipels at the apex, base of blade without glands, blades ovate to linear-lanceolate]	<i>Caperonia</i> spp.
30b.	Plants not usually growing in or near water, main stems solid; venation usually palmate with fewer than 6 pairs of 2° veins	31
31a.	Stellate or peltate hairs often present, simple hairs not attached at the center when present; stalked glands often present at apex of the petiole; ♂ flowers with stamens inflexed in bud	<i>Croton</i> spp.
31b.	Hairs attached at the center but often appearing simple and appressed, stellate and peltate hairs absent, stipel-like structures usually present at the apex of the petiole; ♂ flowers with stamens straight in bud	<i>Argythamnia guatemalensis</i>
32a.	(from 27b) Ornamental small trees and shrubs cultivated in gardens and parks; leaves green to red, purple, yellowish, or whitish; some with thick succulent green stems	33
32b.	Plants not grown as ornamentals, wild species but sometimes used as hedges; leaves not brightly colored; none with thick succulent green stems	39
33a.	Leaf blades distinctly serrate, often reddish to copper colored; inflorescences pendant, to 40 cm long with reddish fimbriate style branches	<i>Acalypha</i> spp.
33b.	Leaf blades entire to subentire, green to purple, yellow, marked with white or leaves absent and the stems green	34
34a.	Leaf blades usually 3–5 times longer than wide, often variegated with yellow, green, white, and purple, margins often undulate, sinuate, or minutely denticulate [few-branched shrubs]	35
34b.	Leaf blades 1–3 times longer than wide, variegated leaves present or absent, margins entire or sinuate	36
35a.	Stems woody and without white sap; leaf blades subcoriaceous; inflorescences unbranched and yellowish	<i>Codiaeum variegatum</i>
35b.	Stems semisucculent and with whitish sap; leaf blades slightly succulent; inflorescences with dichotomous branches, reddish	<i>Synadenium grantii</i>
36a.	Fruits sweet fleshy drupes, 1-seeded; leaves subcoriaceous and entire; sap not white or caustic; shrubs or subshrubs	<i>Antidesma bunius</i>
36b.	Fruits dry capsules, usually 3-seeded; leaves thin to semisucculent; sap often white and caustic; shrubs, trees, or green-stemmed vines and succulents	37
37a.	Flowers (actually cyathia) shoe-shaped and bilaterally symmetrical, reddish or orange [petals absent; distal stems green and terete and often clambering; plants to 2 m tall]	<i>Pedilanthus</i> spp.
37b.	Flowers not shoe-shaped, radially symmetrical, white, yellow, red, or greenish	38
38a.	Flowers (actually cyathia) urceolate or campanulate, greenish to yellow or red, petal-like	

- appendages small or absent; distal stems green and terete or woody; some plants resembling cacti, others leafy trees and shrubs ..... *Euphorbia* spp.
- 38b. Flowers with separate petals and sepals, not urceolate or campanulate, petals often large and colorful; small trees and shrubs, not cactus-like ..... *Jatropha* spp.
- 39a. (from 32b) Larger leaf blades rounded at the base and cordate to subcordate ..... 40
- 39b. Larger leaf blades acute to obtuse or truncated at the base, not cordate or subcordate ..... 44
- 40a. Plants becoming large trees with broad-based conical spines on the grayish trunk; fruit ca. 6 cm diam. with ca. 15 locules and seeds; staminal column with 2 (3) whorls of sessile anthers ..... *Hura crepitans*
- 40b. Plants shrubs or small to large trees, trunks lacking spines; fruits < 3 cm diam. with ca. 3 locules and seeds; stamens not united into a single column with whorled anthers ..... 41
- 41a. Style branches much divided and fimbriate;  $\delta$  flower buds < 1 mm diam., anthers < 0.2 mm wide; fruits often subtended by a large broad bract ..... *Acalypha* spp.
- 41b. Style branches simple to 2 times bifid, not fimbriate or laciniate;  $\delta$  flower buds ca. 2 mm diam., anthers > 0.2 mm wide; fruits not subtended by a broad bract ..... 42
- 42a. Stamens incurved in bud, mostly 8–30/flower; petioles usually with stalked glands at apex; stellate, scurfy or peltate hairs often present; inflorescences always with a single unbranched rachis ..... *Croton* spp.
- 42b. Stamens straight in bud, 3–5 or 30–60/flower; petioles without stalked glands at apex but stipels may be present; hairs simple or stellate; inflorescences unbranched or paniculate .. 43
- 43a. Minute stellate hairs present on the leaf abaxially;  $\delta$  flowers with 30–60 stamens; fruits fleshy ca. 18 mm long, oblong; tall trees ..... *Conceveiba pleiostemona*
- 43b. Small straight hairs present on the leaf surfaces;  $\delta$  flowers with 3–5 stamens; fruits dry capsules ca. 7 mm long; small trees ..... *Aparisthmium cordatum*
- 44a. (from 39b) Leaf blades with palmate venation, the basal pair of lateral (2°) veins reaching the middle or distal half of the blade ..... 45
- 44b. Leaf blades with pinnate venation, the basal pair of lateral (2°) veins not reaching the distal half of the blade ..... 48
- 45a. Leaves usually tripliveined, the basal pair of veins strongly ascending and reaching the distal third of the blade, midvein with only 1 pair of additional prominent 2° veins, pit domatia often present in the vein axils [ $\delta$  inflorescences unbranched; fruits ca. 4 mm diam.] ..... *Alchorneopsis floribunda*
- 45b. Leaves rarely tripliveined (except in *Alchornea*), the midvein usually with 2 or more pairs of prominent 2° veins, pit domatia rarely present ..... 46
- 46a. Style branches much divided and fimbriate;  $\delta$  flower buds < 1 mm diam., anthers < 0.2 mm long; fruits often subtended by a large broad bract ..... *Acalypha* spp.
- 46b. Style branches simple to 2 times bifid, not fimbriate or laciniate;  $\delta$  flower buds 2–5 mm diam., anthers > 0.3 mm long; fruits not subtended by a broad bract ..... 47
- 47a. Stamens incurved in bud, 8–50/flower; fruits usually 3-locular; style branches usually 3–many; inflorescences with a single unbranched rachis (except in *C. billbergianus*); petioles often with stalked glands at apex; stellate, scurfy or peltate hairs often present ..... *Croton* spp.
- 47b. Stamens straight in bud, usually 8/flower; fruits usually 2-locular; style branches usually 2; inflorescences unbranched or paniculate; petioles without stalked glands at apex but 2–6 flat glands often present in the base of the blade; hairs simple or stellate ..... *Alchornea* spp.
- 48a. (from 44b) Larger leaf blades with more than 10 major secondary veins on each side ..... 49
- 48b. Larger leaf blades usually with fewer than 10 major secondary veins on each side ..... 54
- 49a. Petioles with elevated glands along their length or at the apex (sometimes absent or at the base of the blade, be sure to survey a number of leaves); flowers sessile or short-pedicellate and the inflorescence spicate ..... 50
- 49b. Petioles without elevated glands; flowers on prominent pedicels and the inflorescences racemose ..... 52
- 50a. Leaves narrowly obovate, 18–70 cm long [margin with conspicuous gland-tipped teeth];



- hairs attached at the center; inflorescences axillary; ♂ bracts small, ♀ floral bracts with glands ca. 1 mm diam. .... *Pausandra trianae*
- 50b. Leaves oblong to elliptic-oblong, 6–20 (rarely to 26) cm long; hairs attached at base or leaves glabrous; inflorescences mostly terminal, floral bracts with broad rounded sessile flat glands 1.2–3 mm wide ..... 51
- 51a. Common trees; leaves 2–9 cm wide; leaf margin entire or rarely serrulate, the teeth without prominent glands at their apex ..... *Sapium* spp.
- 51b. Shrubs (rare in our area); leaves 0.7–3(–4) cm wide, leaf margins serrate with gland-tipped teeth ..... *Stillingia zelayensis*
- 52a. Flowers in dense cymes on dichotomously branching inflorescences or crowded in leaf axils; flowers (pseudanthia) with calyx-like cup or tube; leaf margins always entire; small shrubs to small trees ..... *Euphorbia* spp.
- 52b. Flowers in open racemose inflorescences with a single unbranched rachis; flowers without a cup-like or tubular calyx; leaf margins entire or dentate; shrubs to tall trees ..... 53
- 53a. Trees and shrubs, usually with both ♂ and ♀ flowers; inflorescences 10–40 cm long with many closely crowded flowers; petals absent; anthers sessile on a conical receptacle; leaves usually narrowly oblong, serrulate ..... *Mabea* spp.
- 53b. Trees dioecious (unisexual); inflorescences 3–12 cm long with well-separated flowers; petals present; anthers borne on slender filaments in ♂ flowers; leaves usually elliptic-oblong, entire ..... *Sagotia racemosa*
- 54a. (from 48b) Styles much divided and laciniate, with slender filamentous divisions; fruit usually subtended by broad serrate bracts; anthers usually < 0.2 mm wide; inflorescences usually narrow spikes and racemes (the ♀ inflorescence pyramidal-paniculate with slender lateral branches and the fruit not subtended by broad bracts in *A. costaricensis*); trichomes of simple hairs attached at the base; leaf margins serrate ..... *Acalypha* spp.
- 54b. Styles not divided into slender filamentous divisions (except in *Adelia* with tufted domatia in leaf axils); fruits not subtended by broad serrate bracts; anthers > 0.2 mm wide; inflorescences and trichomes various; leaf blades entire to serrate ..... 55
- 55a. Stalked or prominent glands usually present at the apex of the petiole or base of leaf blade; hairs stellate, scurfy, peltate (flat and rounded) or simple; inflorescences with a single unbranched rachis; ♂ flowers with well-developed perianth, the 8–40 stamens incurved in bud; ♀ flowers with style branches usually bifid or twice bifid; fruits dry 3-seeded capsules; seeds with a smooth surface and apical caruncle ..... *Croton* spp.
- 55b. Plants without the above suite of characteristics ..... 56
- 56a. Young leafy stems or leaves with flat rounded hairs, the small (ca. 0.2 mm) appressed hairs (peltate trichomes) often difficult to see [plants unisexual; fruits often with a slightly fleshy covering] 57
- 56b. Young leafy stems lacking flat appressed rounded hairs ..... 58
- 57a. Fruits 3–6 mm long, with a single seed; inflorescences paniculate, usually with few spiciform branches, never globose in bud ..... *Hyeronima* spp.
- 57b. Fruits 12–14 mm long, with 3 seeds; inflorescences with few flowers from a short common peduncle, at first enclosed in rounded bracts and resembling a flower bud .. *Pera arborea*
- 58a. Petioles with raised glands at the apex or along their length, or with raised glands at the base of the blade ..... 59
- 58b. Petioles without raised glands, flat or rounded glands sometimes present at the base of the blade or along the blade margins ..... 63
- 59a. Flowers borne on long (8–50 mm) thin pedicels from the axils of leaves [leaves entire and ovate-rhombic; rarely collected in Costa Rica] ..... *Astrocasia tremula*
- 59b. Flowers borne on axes of inflorescences, flowers sessile or on short thick pedicels [often associated with 2 glands; ♂ flowers with 2–3 stamens but the flowers often crowded and difficult to interpret] ..... 60
- 60a. Leaves glabrous or with appressed straight hairs attached at the middle; plants unisexual (dioecious); flower groups often on short (1–3 mm) lateral peduncles [inflorescences with floral glands not appressed on the rachis; fruits capsules] ..... *Tetrorchidium* spp.

- 60b. Leaves usually glabrous, hairs attached at the base if present; plants bisexual (monoecious); flower groups usually sessile or subsessile on the rachis ..... 61
- 61a. Fruits fleshy and green, usually with more than 4 seeds; sap highly caustic; leaf blades rounded-ovate; trees of ocean shores and swamps ..... *Hippomane mancinella*
- 61b. Fruits dry capsules with 3 or fewer seeds; sap not caustic; leaf blades ellipsoid to oblong; trees of varied habitats ..... 62
- 62a. Glands on the petiole apex or in the middle, prominent and easily seen; floral glands flat, 1.5–3 mm long, rounded and appressed on the inflorescence rachis; leaves mostly thick and oblong ..... *Sapium* spp.
- 62b. Glands at the base of the blade small and often difficult to see; floral glands less than 1 mm diam., borne on the floral bracts; leaves mostly thin and elliptic .. *Sebastiania pavoniana*
- 63a. Leaf blades entire, the margins entire and lacking glands ..... 64
- 63b. Leaf blades minutely serrate to conspicuously dentate or rounded-crenate, with well-defined glands along the margin if subentire ..... 72
- 64a. Petiole distinctly thickened below the blade for 4–8 mm and terete [inflorescences of 1–few terminal flowers; ♂ flowers ca. 3 cm wide with many stamens; fruits 3–4 cm diam.; seasonally dry forests] ..... *Garcia nutans*
- 64b. Petioles without a prolonged thickened terete area beneath the blade, a short thickened area at the apex of the petiole sometimes present ..... 65
- 65a. Leaf blades with a notch (indentation) and terminal gland at the apex [blades elliptic-oblong with a narrowed apex; inflorescences terminal with a few thick spiciform branches; rarely collected in southern Central America] ..... *Caryodendron angustifolium*
- 65b. Leaf blades lacking a notch and terminal gland at the apex ..... 66
- 66a. Fruits 1-seeded and with a thin fleshy cover; unisexual (dioecious) trees [ovary with 2 ovules/locule but only 1 ovule developing; leaves subcoriaceous] ..... 67
- 66b. Fruits usually 3-seeded, dry or with a thin fleshy covering; unisexual or bisexual, trees or shrubs ..... 68
- 67a. Leaf blades elliptic to oblong, often asymmetric at the base; flowers borne in leaf axils on short or long pedicels; fruits axillary, seeds without a red or orange aril ..... *Drypetes* spp.
- 67b. Leaf blades often obovate, symmetric at the base; flowers and fruits borne on spikes or racemes with thick axes; pedicels short or flowers sessile; seeds with red or orange aril ..... *Richeria obovata*
- 68a. Ovules 2 in each locule, fruits usually with 4–6 seeds; leaves usually distichous; flowers on thin pedicels in axillary fascicles ..... 69
- 68b. Ovules 1 in each locule, fruits usually 2–3-seeded; leaves usually in a spiral; flowers borne on short racemes, in cymose groups, or in axillary fascicles ..... 70
- 69a. Plants unisexual (dioecious); leaves deciduous; ♂ flowers with 4 stamens; fruits 9–12 mm diam., seeds 3–5 mm long, with fleshy bluish covering; a common species ..... *Margaritaria nobilis*
- 69b. Plants bisexual; leaves evergreen; ♂ flowers with 3 stamens; fruits ca. 8 mm diam., seeds ca. 7 mm long, without a fleshy covering; rarely collected ..... *Phyllanthus skutchii*
- 70a. Flowers without perianth, borne on short (4 cm) unbranched axillary racemes [leaves narrowly obovate and subcoriaceous] ..... *Actinostemon caribaeus*
- 70b. Flowers with 4–5 sepals, or with a cupulate or urceolate base resembling a calyx cup .. 71
- 71a. Flowers with 4–5 distinct sepals, without a calyx cup; flowers borne in axillary fascicles; fruits pendulous on long slender pedicels; leaves with tufted domatia in vein axils beneath ..... *Adelia triloba*
- 71b. Flowers (pseudanthia) with a cupulate or urceolate base resembling a calyx cup, usually borne in cymes; fruit never pendulous on long pedicels; leaves without tufted domatia in vein axils ..... *Euphorbia* spp.
- 72a. (from 63b) Stipules persisting, triangular to lanceolate, with 3–7 prominent raised veins parallel with the midrib; stinging hairs present or absent ..... 73



- 72b. Stipules caducous or, if persisting, without prominent parallel venation; stinging hairs absent . . . . . 74
- 73a. Shrubs or small treelets 1–7 m tall; leaves with prominent distal serrations, 8–18 cm long; stinging hairs usually present on the anther tips and fruits and sometimes on the leaves . . . . . *Acidoton nicaraguensis*
- 73b. Small single-stemmed subshrubs to 1 m tall; leaves subentire to serrulate, 12–28 cm long; stinging hairs usually absent . . . . . *Dalechampia spathulata*
- 74a. Inflorescences 12–45 cm long, racemose with a single axis and long-pedicellate flowers; ♂ flowers with subsessile anthers on a conical receptacle [leaf blades oblong to narrowly oblong] . . . . . *Mabea occidentalis*
- 74b. Inflorescences not 12–45 cm long and racemose; anthers on a dome-shaped conical androecium only in *Cleidion* (with inflorescences < 12 cm long) . . . . . 75
- 75a. Leaves with small stellate hairs on the upper (adaxial) surface; ♂ inflorescences with overlapping pubescent bracts, catkin-like in leaf axils [fruits 7 × 11 mm; leaf blades 3–12 cm long] . . . . . *Bernardia nicaraguensis*
- 75b. Leaves glabrous on the upper surface or with few simple hairs; ♂ inflorescences of congested flowers in sessile glomerules on slender spikes . . . . . 76
- 76a. Leaves with petioles 13–50 mm long, distinctly thickened at the apex and often slightly bent [leaf margins with prominent gland-tipped teeth] . . . . . 77
- 76b. Leaves with petioles 4–16 mm long, not clearly thickened or bent at the apex [♂ flowers usually with 3 stamens] . . . . . 78
- 77a. Styles usually 2 and simple; fruits with usually 2 seeds and fleshy exterior; ♂ flowers usually with 8 stamens; young stems glabrous . . . . . *Alchornea* spp.
- 77b. Styles usually 3 and bifid; fruits dry capsules with usually 3 seeds; ♂ flowers with ca. 30 stamens on a conical receptacle; young stems minutely puberulent . . . . . *Cleidion castaneifolium*
- 78a. Leaves 12–33 cm long, often oblanceolate; plants unisexual; ♂ flowers with 3 sepals, ♀ flowers with 6 sepals in 2 whorls, style branches broad . . . . . *Adenophaedra grandifolia*
- 78b. Leaves 6–16(–20) cm long, usually obovate; plants usually bisexual; flowers with 0–2 bract-like perianth parts, style branches slender . . . . . *Gymnanthes riparia*



FIG. 1. Shrubs or treelets with deeply lobed leaves: species of *Manihot* and *Ricinus*.

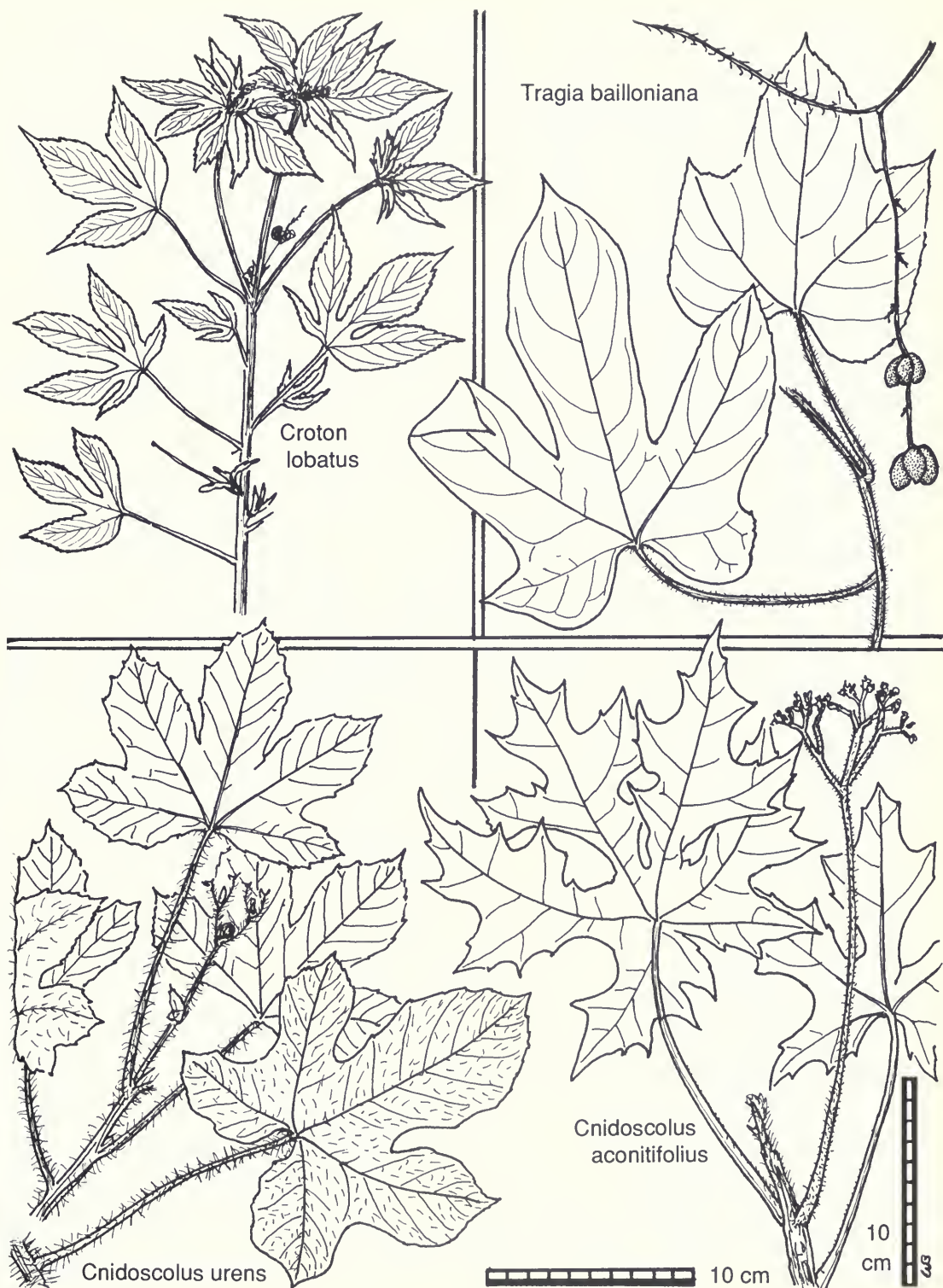


FIG. 2. Vines and subshrubs with lobed leaves: species of *Croton*, *Cnidoscolus*, and *Tragia*.





FIG. 3. Trees and shrubs with deeply to slightly lobed leaves with palmate venation: species of *Jatropha*.

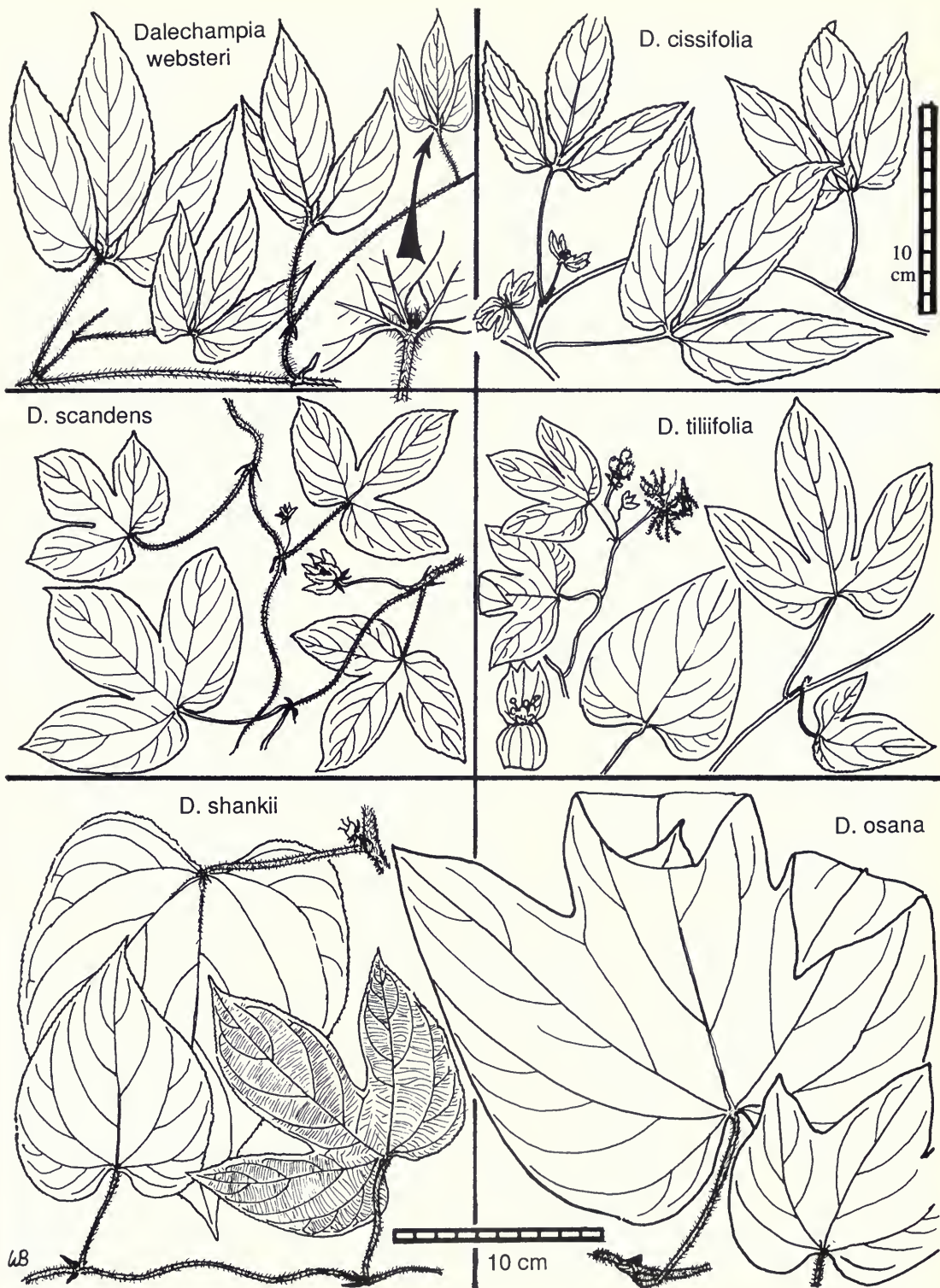


FIG. 4. Slender-stemmed vines with lobed or compound leaves: species of *Dalechampia*.





FIG. 5. Slender-stemmed vines: species of *Dalechampia*, *Plukenetia*, and *Tragia*.



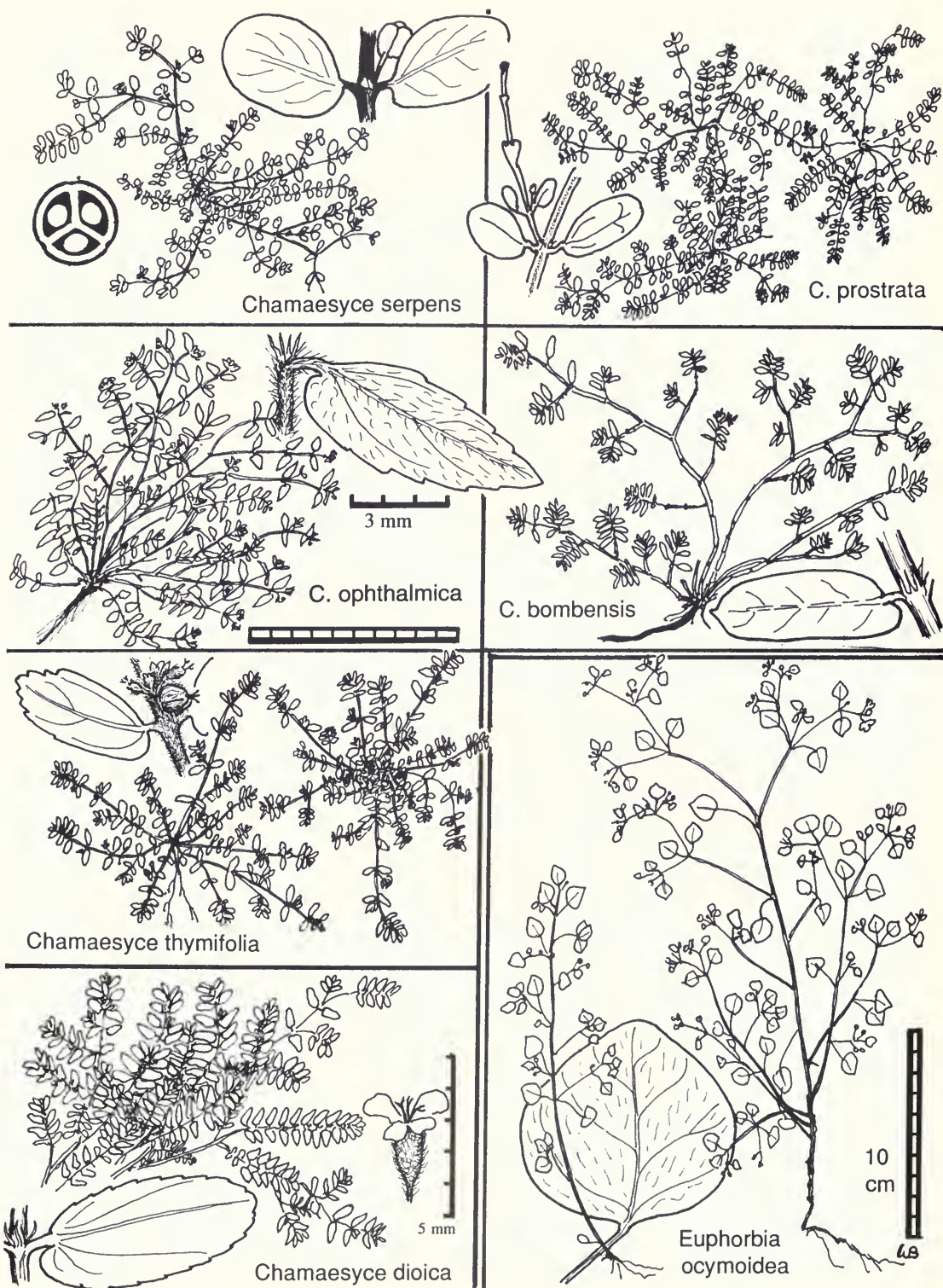


FIG. 6. Plants with very small leaves: species of *Chamaesyce* and *Euphorbia*.



FIG. 7. Plants with small opposite leaves: species of *Chamaesyce*.







FIG. 9. Plants with small alternate leaves: species of *Phyllanthus*.





FIG. 10. Herbaceous or weedy plants: species of *Caperonia*, *Croton*, and *Dysopsis*.





FIG. 11. Herbaceous or weedy plants: species of *Acalypha*, *Argythamnia*, and *Sebastiania*.

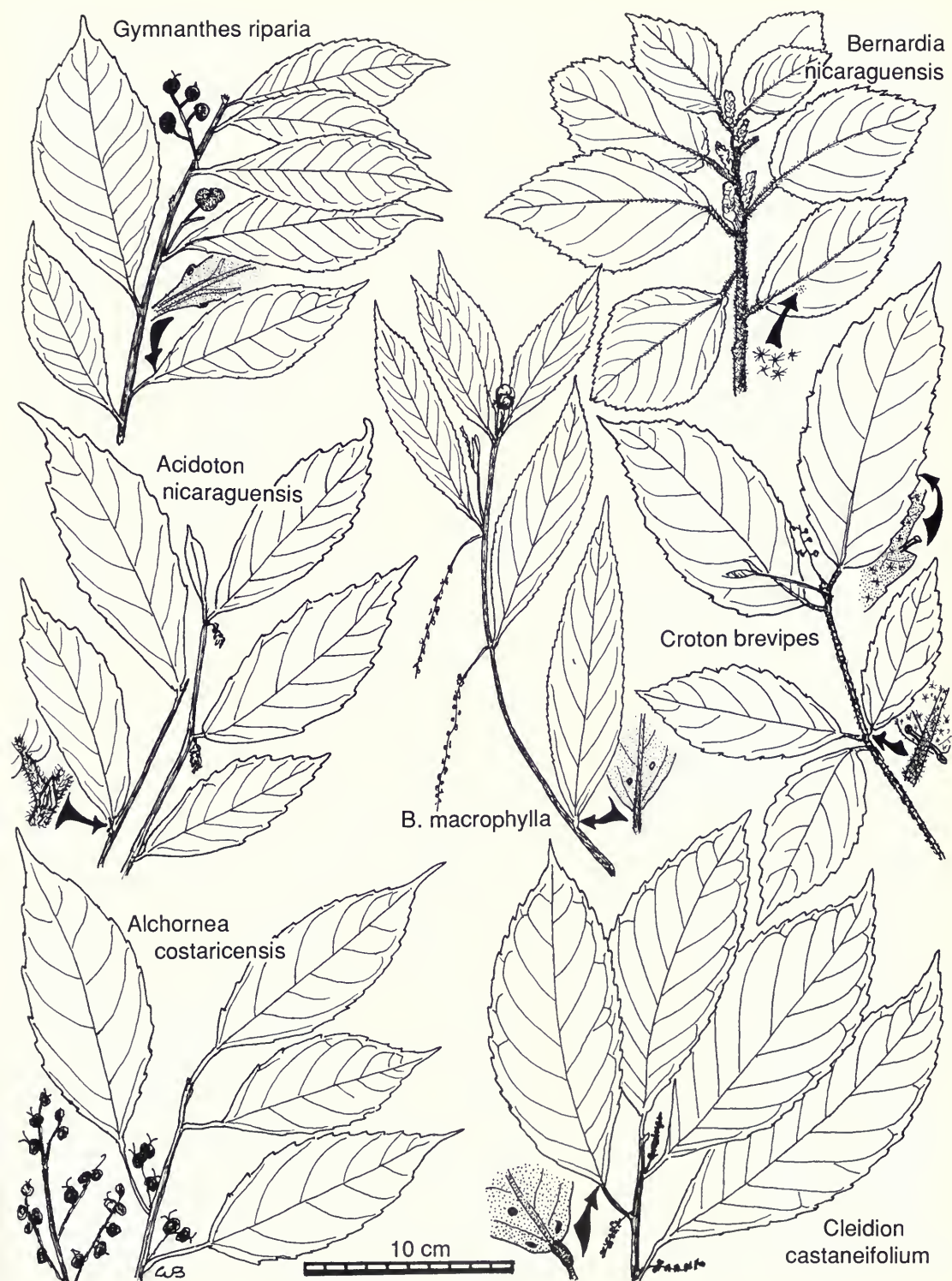


FIG. 12. Trees and shrubs with serrate elliptic leaves: species of *Acidoton*, *Alchornea*, *Bernardia*, *Cleidion*, *Croton*, and *Gymnanthes*.





FIG. 13. Plants with larger oblanceolate serrate leaves: species of *Adenophaedra*, *Dalechampia*, and *Pausandra*.



FIG. 14. Shrubs or herbs with serrate leaves and lacinate styles: species of *Acalypha*.







FIG. 16. Plants with slightly serrate leaves and stellate hairs: species of *Croton*.





FIG. 17. Trees and shrubs with flat peltate hairs: species of *Croton*.



FIG. 18. Trees and shrubs with larger ovate leaves, stellate hairs, and glands at apex of petiole: species of *Croton*.





FIG. 19. Trees and shrubs with larger ovate or oblong leaves and stellate or peltate hairs: species of *Croton*.

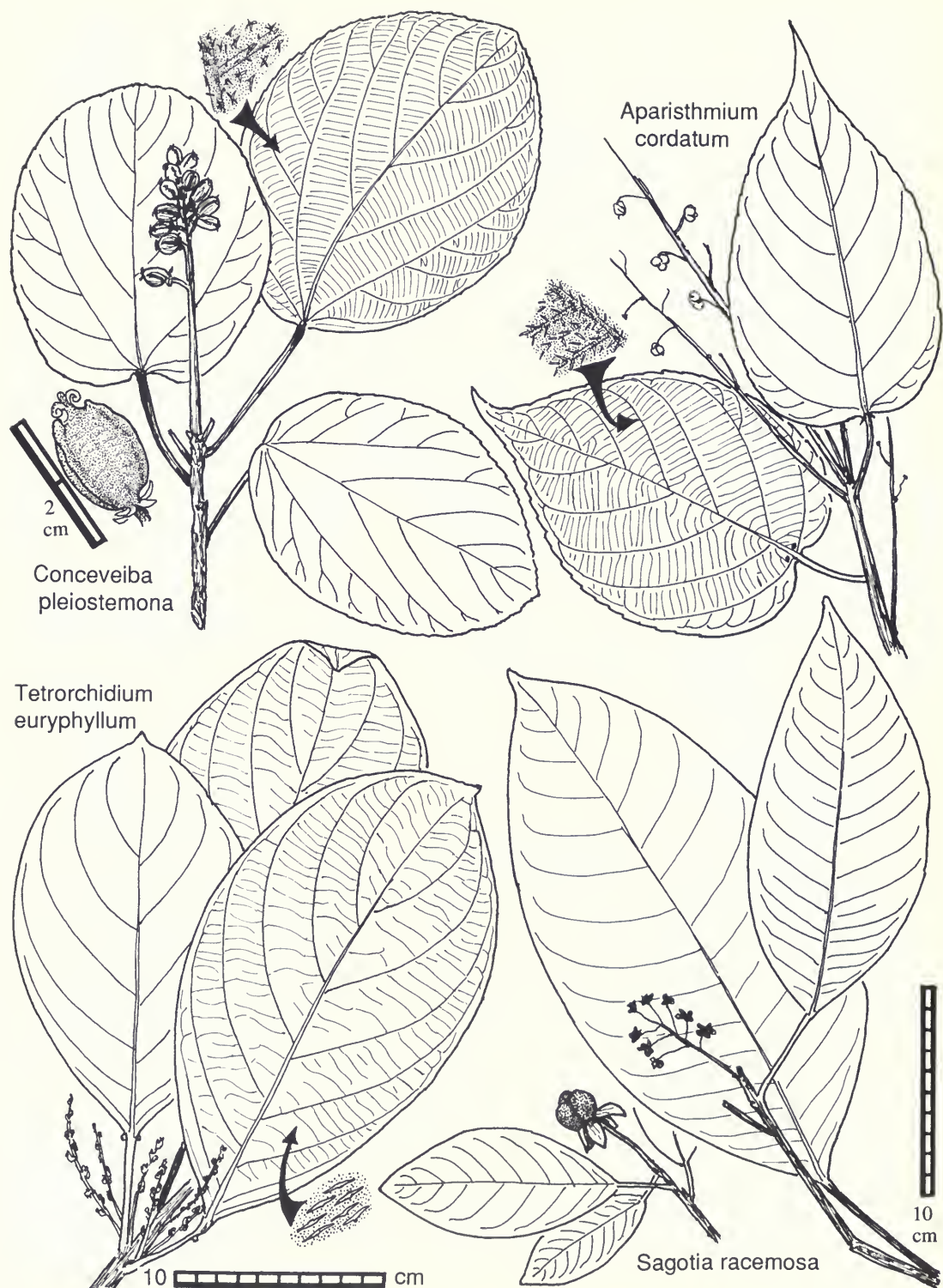


FIG. 20. Trees with larger leaves: species of *Aparisthium*, *Conceveiba*, *Sagotia*, and *Tetrorchidium*.



FIG. 21. Trees with glands on petioles or a thickened petiole apex: species of *Garcia* and *Tetrorchidium*.





FIG. 22. Trees with glands on petioles: species of *Sapium*.



FIG. 23. Trees with glands on petioles (*Sapium* spp.) or shrubs with glands along lamina margins (*Stillingia* sp.).



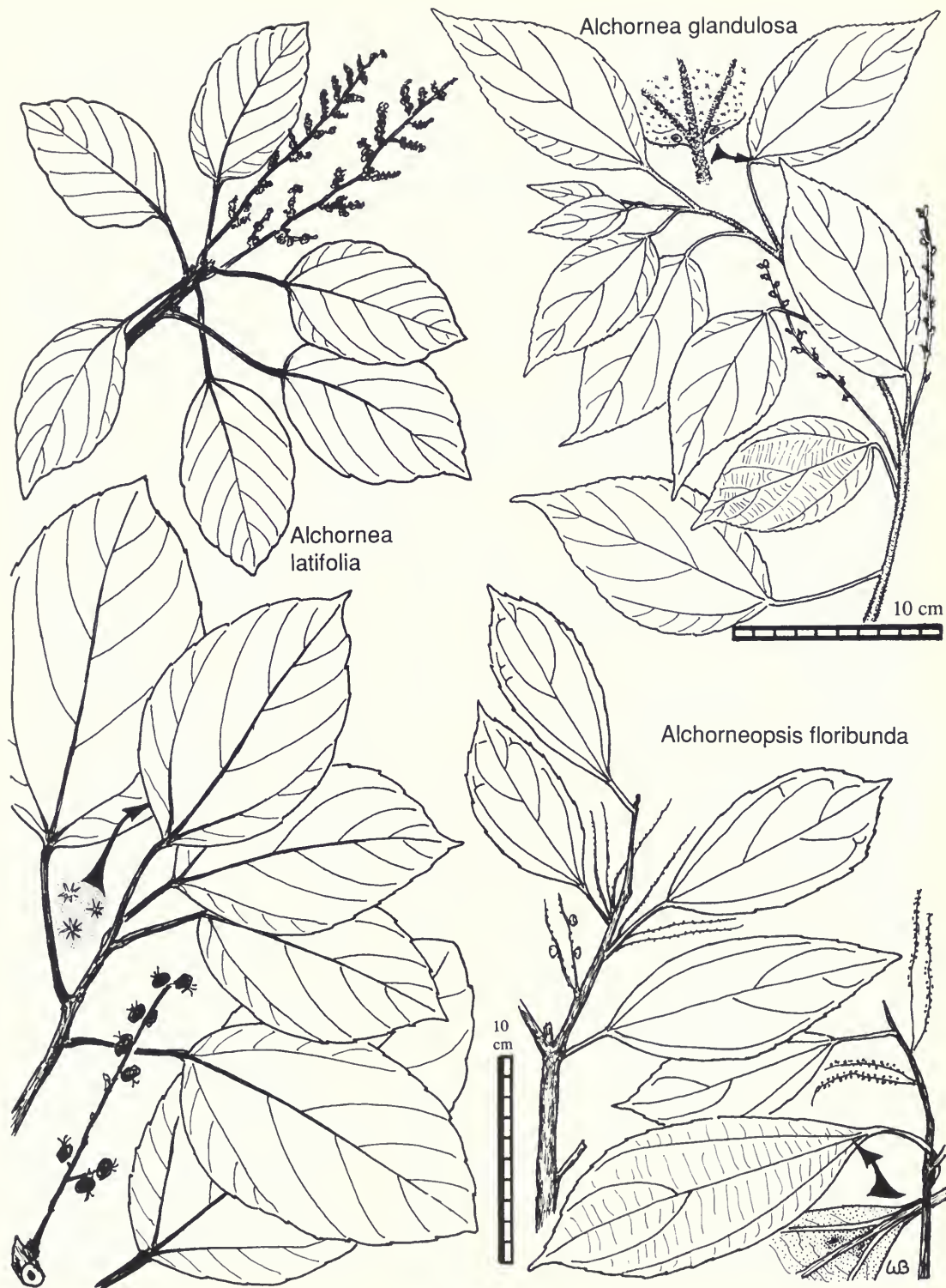


FIG. 24. Trees with slightly serrate leaves and subpalmate or palmate venation: species of *Alchornea* and *Alchorneopsis*.





FIG. 25. Trees and shrubs with entire or serrate leaves: species of *Actinostemon*, *Margaritaria*, *Phyllanthus*, and *Sebastiania*.



FIG. 26. Trees and shrubs with entire elliptic leaves: species of *Gymnanthes*, *Mabea*, and *Pera*.





FIG. 27. Trees and shrubs with entire elliptic leaves: species of *Amanoa* and *Drypetes*.





FIG. 28. Trees with spicate inflorescences or inflorescence branches: species of *Hyeronima* and *Richeria*.



FIG. 29. Herbs or weak-stemmed shrubs with entire leaves and white sap: species of *Euphorbia*.



FIG. 30. Shrubs and trees with small entire leaves and white sap: species of *Euphorbia*.



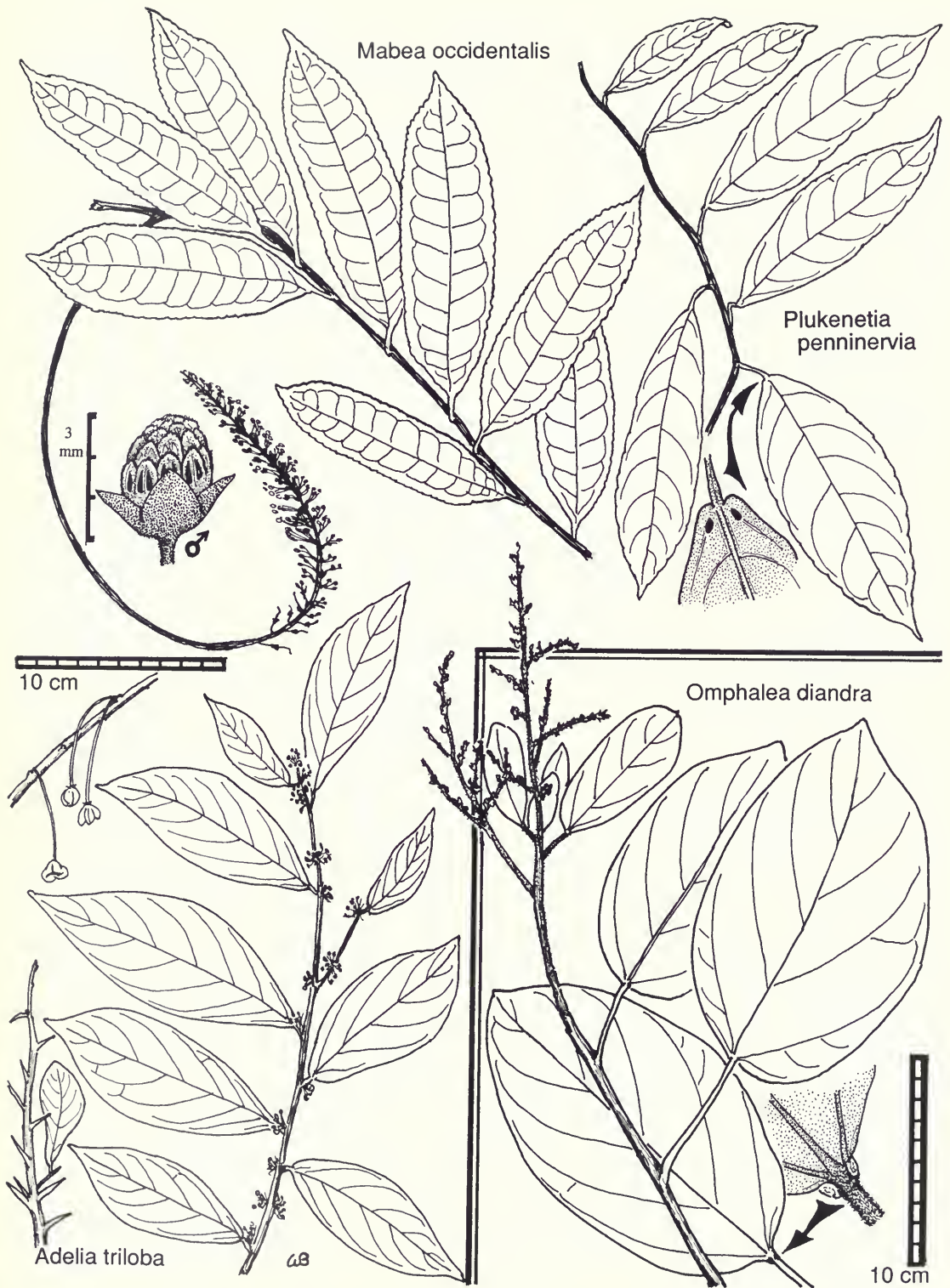


FIG. 31. Climbers and unusual plants: species of *Adelia*, *Mabea*, *Omphalea*, and *Plukenetia*.

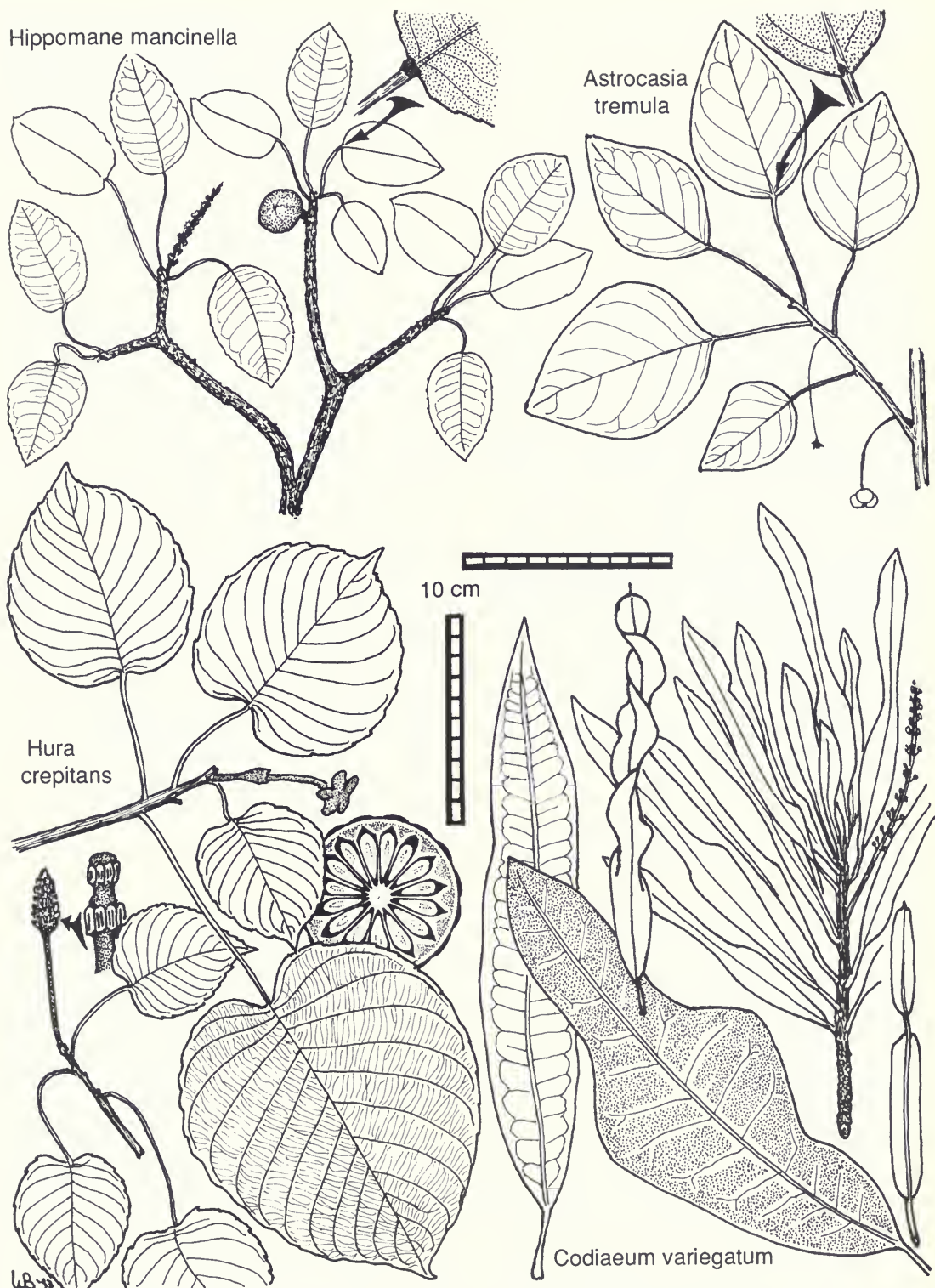


FIG. 32. Trees and shrubs with distinctive leaves: species of *Astrocasia*, *Codiaeum*, *Hippomane*, and *Hura*.



**Acalypha** Linnaeus

REFERENCE—O. Seberg, Taxonomy and phylogeny of the genus *Acalypha* (Euphorbiaceae) in the Galapagos Archipelago. Nord. J. Bot. 4: 159–190. 1984.

Annual or perennial herbs, **shrubs** or small trees, monoecious or less often dioecious, hairs simple or stellate (plants rarely glabrous); stipules paired at the leaf base, ovate to lanceolate or linear, (1–)3–7-veined, often with linear distal awn. **Leaves** alternate, simple, petiolate, glands absent at apex of petiole (stipels rarely present); leaf blades mostly ovate, palmately 3–5-veined or pinnately veined, pubescent or glabrous, margins crenate-serrate or dentate (not lobed). **Inflorescences** terminal or axillary, unisexual or bisexual, solitary, the ♂ axillary (often below the ♀) usually spiciform and slender with flowers in sessile clusters; ♀ inflorescences axillary or terminal, open panicle to spicate or racemose, bisexual spikes usually with ♀ flowers proximal and ♂ distal, floral bracts broadly sessile, often enlarging and enclosing the fruit; ♀ flowers sessile or short-pedicellate. **Male flowers** very small, pedicellate, globose in bud, calyx 4-parted, valvate in bud, petals absent, disk absent, stamens 8 (4, –16), borne on a slightly raised receptacle, filaments free, anthers with divaricate or pendulous thecae, oblong or linear to vermiform; pistillode absent. **Female flowers** with 3–5 sepals, united at or near the base, imbricate or open in bud, shorter than the pistil, petals absent, staminodes absent, disk absent; ovary 3-(2-)locular, surface often muricate, pubescent or papillate, ovules 1/locule,

style column short, each style with many slender laciniate style branches (unbranched in *A. alopecuroidea*). **Fruits** capsular, usually small, 3-lobed and breaking into 3 2-valved 1-seeded cocci, bracts enlarging in fruit (in most species) to envelop the capsule; seeds small, ellipsoid to subglobose, caruncle minute or absent, testa crustaceous, endosperm fleshy or granular, cotyledons broad and flat.

A pantropical genus of 400–500 species with a few species reaching temperate regions. The majority of species are Neotropical and are in serious need of monographic study. Many species are weedy plants of open sites that vary greatly from individual to individual. This large intraspecific variation has made understanding the species-boundaries and the search for important taxonomic characters difficult. Fortunately, southern Central America has relatively few species as compared to Mexico or South America. As in many other genera, the weedy species are often poorly represented in herbaria. These plants often resemble species of *Urticaceae*.

*Acalypha* is recognized by its often long narrow spiciform, usually unisexual, inflorescences, very small ♂ flowers with minute anthers, ♀ flowers with much-divided and slender-laciniate style branches often red or purple, broad floral bracts enlarging to enclose the fruits (in most species) and small three-seeded capsules. The ♂ inflorescences are always axillary. Specimens lacking mature ♀ flowers and fruits may be very difficult to identify.

**Key to the Species of *Acalypha* in Costa Rica**

- 1a. Plants of gardens and hedgerows, with brightly colored leaves or inflorescences ..... 2
- 1b. Plants of natural and disturbed vegetation, not grown for the colorful leaves or inflorescences 3
  - 2a. Plants with conspicuous reddish pendant inflorescences, ♂ inflorescences usually absent; leaves usually green ..... *A. hispida*
  - 2b. Plants with inconspicuous ♂ and ♀ inflorescences often present on the same plant; leaves usually red to purple ..... *A. amentacea* ssp. *wilkesiana*
- 3a. ♀ flowers and fruits pedicellate along the major inflorescence axes, bracts of ♀ flowers remaining small and obscure; leaves > 12 cm long and palmately veined; species of evergreen areas below 800 m elevation ..... 4
- 3b. ♀ flowers and fruits sessile (solitary ♀ flowers sometimes borne on long axillary pedicels in *A. arvensis* and *A. leptopoda*), bracts of ♀ flowers enlarging and enveloping the fruits but sometimes difficult to see because of the pubescence (only enlarging slightly in *A. radinostachya*); leaves larger or smaller, venation palmate or pinnate; species of evergreen and deciduous areas from sea level to 2200 m elevation ..... 5
  - 4a. Plants usually with ♀ flowers in large terminal many-branched narrowly pyramidal panicles; seeds 1.5–1.7 mm long; leaf blades becoming narrower in the lower 1/3–1/4, rarely ovate, venation pinnate ..... *A. costaricensis*
  - 4b. Plants with the ♀ flowers usually on slender axillary unbranched racemes; seeds 0.8–1.4 mm



- long; leaf blades nearly always broadest in the lowest  $\frac{1}{3}$  and ovate, venation palmate or subpalmate ..... *A. villosa*
- 5a. Leaves with pinnate venation, shrubs or small treelets ..... 6
- 5b. Leaves with palmate or subpalmate venation (the basal pair of 2° veins prominent and terminating at or above the middle of the blade), herbs, shrubs, or small treelets ..... 8
- 6a. Leaf blades narrowed to an obtuse or acute base, only rarely slightly rounded at the petiole; ♀ bracts becoming 2–4 mm long with small (< 1 mm) lobes or unlobed in fruit; seeds 1.4–1.6 mm long [♀ flowers few, axillary or at base of ♂ spikes] ..... *A. diversifolia*
- 6b. Leaf blades narrowed to the base and slightly rounded or auriculate at the petiole; ♀ bracts becoming 10–13 mm long with teeth 1–6 mm long in fruit; seeds 2.1–2.6 mm long ... 7
- 7a. Female flowers many in long (to 18 cm) conspicuous terminal inflorescences; ♂ inflorescences few ..... *A. ferdinandii*
- 7b. Female flowers 1–few, in axils of distal leaves; ♂ inflorescences many ..... *A. apodanthes*
- 8a. (from 5b) Plants shrubs or trees, > 1 m tall; ♀ bracts with lobes becoming up to 2 mm long; glands often present at the apex of the petiole ..... 9
- 8b. Plants herbaceous, usually < 1 m tall; ♂ bracts with lobes often 3–7 mm long (except *A. mexicana*); glands rarely present at the apex of the petioles ..... 13
- 9a. Fruiting inflorescence a slender (0.2 mm thick) pendulous rachis with usually only a single terminal bract, to 4 cm long (axillary ♀ flowers may also be present) [stipules 4–15 mm long with a long-awned tip] ..... *A. leptopoda*
- 9b. Fruiting inflorescences with rachis 0.5–2.5 mm thick, with many bracts and fruits along the rachis, to 30 cm long ..... 10
- 10a. Bracts of the ♀ inflorescence 2–3 mm long and not enlarging in fruit; stipule scars becoming thickened, hard and pale colored, 2–3 mm wide [stipules to 7 mm long with a narrowed terminal portion; ♀ inflorescences terminal and solitary; plants of the Caribbean slope, 100–300 m] ..... *A. radinostachya*
- 10b. Bracts of the ♀ inflorescences enlarging (to 6 mm long) in fruit; stipule scars not as above ..... 11
- 11a. Stipules ovate to narrowly lanceolate, without a slender terminal awn; petioles 2–26 cm long; fruiting inflorescences axillary, to 35 cm long, pendant (see also *A. obtusifolia*); common and widespread ..... *A. macrostachya*
- 11b. Stipules narrowed above the base into a long slender (0.3 mm) awn; petioles 2–13 cm long; fruiting inflorescences terminal, to 18 cm long, erect; rarely collected species ..... 12
- 12a. Leaf blades ovate, petioles to 7 cm long; margins of fruiting bracts with prominent teeth, without gland-tipped hairs; semideciduous forests at 100–800 m elevation ... *A. schiedeana*
- 12b. Leaf blades elliptic, petioles to 13 cm long; margins of fruiting bracts entire and with gland-tipped hairs to 1.5 mm long; evergreen forest at 1100 m ..... *A. sp. aff. A. mortoniana*
- 13a. (from 8b) Large-bracted ♀ inflorescences present at nearly all nodes, usually short and subsessile (rarely to 4 cm long), bracts ca. 4 mm long with short (0.5 mm) rounded lobes [rarely collected, 900–2200 m elevation] ..... *A. mexicana*
- 13b. Large-bracted ♀ inflorescences only at the distal nodes; ♀ bracts with lobes 1–6 mm long ... 14
- 14a. Fruiting inflorescences 10–15 mm wide, open or densely flowered and resembling the hairy spikes of a foxtail grass (*Setaria* spp.) [♀ bracts with linear lobes 3–6 mm long, glabrous or with thin straight hairs 1–2 mm long] ..... 15
- 14b. Fruiting inflorescences 5–12 mm wide, not resembling the hairy inflorescences of a foxtail grass ..... 17
- 15a. Flowering and fruiting ♀ spikes with bracts not closely congested, bracts glabrous to very minutely puberulent or with few glandular hairs; larger leaf blades > 8 cm long; seeds > 2 mm long [uncommon in Costa Rica] ..... *A. polystachya*
- 15b. Flowering and fruiting ♀ spikes with bracts closely congested, bracts with thin straight hairs to 2 mm long; leaf blades to 8 cm long; seeds < 1.5 mm long ..... 16
- 16a. Plants lacking gland-tipped hairs on stems but gland-tipped hair often present in the inflo-

rescence; stipules to 5 mm long; ♀ inflorescences axillary on peduncles to 32 mm long; styles with 3–5 branches and bright red (absent in later fruiting stages); seeds 1.1–1.4 mm long; common in Costa Rica ..... *A. arvensis*

16b. Plants usually with gland-tipped hairs on stems, petioles and/or inflorescences; stipules to 2.5 mm long; ♀ inflorescences consistently terminal on peduncles to 10 mm long, styles unbranched and difficult to see; seeds 1–1.1 mm long; uncommon in Costa Rica ..... *A. alopecuroides*

17a. ♀ flowers few and axillary or lacking, distal ♀ flower often on a slender (0.2 mm) rachis 0.5–3 cm long; stipules often terminating in a slender transparent sharp-pointed hair; immature plants of ..... *A. arvensis*

17b. ♀ flowers on spicate inflorescences, distal ♀ flower not borne on a slender filament-like rachis; stipules not terminating in a long, sharp slender hair ..... 18

18a. Stems and leaves with many thin straight hairs 1–2 mm long; ♂ spikes 5–12 cm long, with thin peduncles 1–5 cm long [rarely collected in Central America] ..... *A. triloba*

18b. Stems and leaves with short (0.1–0.4 mm) hairs; ♂ spikes 0.8–3 cm long, with peduncles < 5 mm long ..... 19

19a. Fruiting bracts with rounded or triangular lobes 1–2 mm long, with hairs ca. 1 mm long; stipules triangular to subulate; 1100–1900 m elevation ..... *A. septemloba*

19b. Fruiting bracts with linear lobes to 6 mm long, glabrous or with minute hairs; stipules linear; 10–1000 m elevation ..... *A. setosa*

***Acalypha alopecuroides*** Jacq., Collect. 3: 196.  
1790. Icon. Pl. Rar. 3: 19, t. 620. 1792. Figure 11.

**Herbs** 20–90 cm tall, bisexual (monoecious), leafy stems 0.6–3 mm thick, densely pubescent with thin straight hairs 0.2–1 mm long, also often with gland-tipped hairs 0.6–1.2 mm long; stipules 1–2.5 mm long, 0.3–0.6 mm broad at the base, subulate-linear, sparsely puberulent, persisting. **Leaves** with petioles 4–65(–80) mm long, 0.2–0.5 mm thick, sparsely pubescent with thin hairs, gland-tipped hairs usually present distally, small (0.3 mm) digitate glands sometimes present at the apex; **leaf blades** 1.8–8 cm long, 1.3–5.5 cm wide, ovate to ovate-triangular, tapering to a short-acuminate apex, margins with 14–28 teeth/side, base rounded and truncate (rarely subcordate), drying membranaceous, pubescent above with scattered thin straight hairs 0.2–2 mm long, with shorter hairs along the veins beneath, venation palmate, 2° veins 2–3/side of the midvein. **Male inflorescences** 8–30 mm long, peduncles 2–6 mm long, 0.1–0.2 mm thick, slender and spiciform, gland-tipped hairs usually present, bracts ca. 0.4 mm long, usually obscure; ♂ flower buds ca. 0.4 mm diam., glabrous, perianth 0.5 mm wide at anthesis. **Female inflorescences** terminal, 1.5–6 cm long, flowering portion becoming 8–15 mm wide and ellipsoid to cylindrical, peduncles 2–10 mm long, ca. 1 mm thick, bracts with linear teeth 5–8 mm long, with straight thin hairs to 2 mm long, gland-tipped hairs often present, sometimes with a slender distal rachis and solitary ♀ flower; ♀ flowers 1/bract, sessile, hispidulous and often with gland-tipped hairs, styles 2–7 mm long, unbranched and inconspicuous. **Fruits** 1.2–1.5 mm diam., subtended and enclosed by bracts to 12 mm long with a broad united (4 mm) base and linear lobes 5–8 mm long; **seeds** 1–1.1 mm long, 0.6–0.7 mm diam., grayish, ovoid-ellipsoid, caruncle slightly elevated, ca. 0.4 mm long, whitish.

Weedy plants of open sites in evergreen and seasonally dry habitats in the Pacific lowlands, 0–300 m elevation (to 1400 m in Guatemala). Flowering and fruiting in July–August. While this species can be locally common, collections from southern Central America are few; it has not been collected in the Caribbean lowlands or in the evergreen areas of the Pacific lowlands of Costa Rica. This species ranges from the southern United States and the Bahamas to Venezuela and Peru.

*Acalypha alopecuroides* is recognized by its small weedy habit, presence of gland-tipped hairs, short slender axillary ♂ spikes, bracts with long-linear teeth, thick terminal catkin-like ♀ spikes, and undivided styles. This species is very similar to *A. arvensis*, and the two are very closely related. Nevertheless, the two seem to differ quite consistently by the characters used in the key. This species has been called *chimbombo* in Costa Rica (Orozco 221 F).

***Acalypha amentacea*** Roxb., Fl. Ind. ed. 1832, 3: 676. 1832, subspecies *wilkesiana* (Müll. Arg.) Fosberg, Smithsonian Contr. Bot. 45: 10. 1980. *A. wilkesiana* Müll. Arg. in DC., Prodr. 15 (2): 817. 1866.

**Ornamental shrubs** 2–5 m tall, monoecious, leafy stems 1.5–6 mm thick, sparsely to densely pubescent with minute (0.2 mm) appressed or curved hairs; **stipules** 10–25 mm long, ca. 2 mm wide at the base, narrowly lanceolate. **Leaves** with petioles 1.2–9 cm long, 0.8–2.5 mm

thick, sparsely to densely puberulent; **leaf blades** 9–28 cm long, 4–18 cm wide, ovate to ovate-elliptic, apex acuminate, margin with rounded teeth 22–60/side, base obtuse to rounded and subcordate, drying chartaceous, with few short hairs along the veins above, glabrescent below, venation palmate, 2° veins 5–8/side of the mid-vein. **Inflorescences** mostly axillary, ♂ inflorescences to 25 cm long, ♀ inflorescences 4–14 cm long, bracts subtending ♀ flowers 1–4 mm long, with 1 central lobe and smaller lateral lobes; style branches to 6 mm long.

*Acalypha amentacea* ssp. *wilkesiana* is a very common ornamental shrub with foliage varying from bronze-green to reddish purple or dark red and marked with white or pink. Originally from the western Pacific, the species is now widely planted in gardens of the tropics and subtropics. It is grown at low and middle elevations (0–1500 m) in Central America. Common names are *capa del rey*, *manto de Jesús*, *pastor*, “beefsteak plant,” “copper leaf,” and “Jacob’s coat.”

***Acalypha apodanthes* Standl. & L. O. Williams,** *Ceiba* 1: 241. 1951. *A. ferdinandii* var. *pubescens* K. Hoffm., *Pflanzenreich* 4. 147. 16: 64. 1924. Figure 14.

**Shrubs** or small treelets 1.5–3(–6) m tall, mostly monoecious, bark rough brown, leafy stems 1.2–3.5 mm thick, densely pubescent with straight or curved hairs 0.2–0.6 mm long; **stipules** 3–8 mm long, 0.5–1 mm broad at the base, narrowed ca. 1 mm above the base into a linear awn, with minute appressed hairs. **Leaves** with petioles 4–20(–32) mm long, 0.5–1 mm thick, usually densely hirsute with erect hairs 0.2–0.4 mm long, flat or disk-like glands sometimes present at the apex; **leaf blades** 5–17 cm long, 1.5–5 cm wide, narrowly elliptic to narrowly elliptic-oblong, oblanceolate or elliptic, tapering gradually to an acuminate apex, margins with 20–30 teeth/side ca. 0.5 mm long, tapering gradually to the base and rounded (2–3 mm) at the petiole (subauriculate), sparsely pubescent above with hairs ca. 0.5 mm long, more densely pubescent beneath with hairs 0.2–0.4 mm long, 2° veins 7–12/side. **Male inflorescences** 2–16 cm long, 1.5–2 mm diam., peduncles 4–10 mm long, 0.3–0.5 mm thick, densely pubescent, flower clusters ca. 1.4 mm wide, usually closely approximate, rachis 0.2–0.4 mm thick, bracts ca. 0.6 mm long, acute; ♂ flowers minute, buds ca. 0.4 mm diam., pedicels to 0.7 mm long. **Female inflorescences** axillary to distal leaves, usually only 1 bract/node with 1 ♀ flower, sometimes at the base of a ♂ spike, bracts 1–5 mm long and becoming 5–8 mm long in fruit, with 7–11 prominent linear or triangular teeth 3–6 mm long, flowers sessile; ♀ flowers with ovary ca. 1.3 mm long, densely covered with straight erect hairs, style branches to 6 mm long, separate to base, white to red. **Fruits** enclosed within the cupulate-conuplicate bracts, united base of bracts ca. 3 mm long; **seeds** 2.1–2.2 mm long, 1.6–1.7 mm diam., oblong-rounded.

Plants of evergreen forest formations of the Caribbean slope and adjacent areas, 100–1400 m elevation. Flowering in late January–September. The species is only known from central and northern Costa Rica (but see below).

*Acalypha apodanthes* is recognized by its solitary ♀ bracts in distal leaf axils, long slender ♂ spikes, small narrow pinnately veined leaves with small basal lobes (subauriculate), and larger seeds. This species may prove to be an unusual morphotype of *A. ferdinandii* (q.v.), lacking the characteristic terminal ♀ spikes of *A. ferdinandii* and usually with smaller leaves. The shared habitat (in part) and the similar phenology also suggest that these plants may be conspecific.

***Acalypha arvensis* Poeppig in Poeppig & Endl.,** *Nov. gen. sp. pl.* 3: 21. 1841. Figure 11.

**Herbs** 20–70 cm tall, older plants often with multiple branches from a woody base, leafy stems 0.9–4 mm thick, with thin whitish hairs 0.2–0.7(–1.5) mm long, smaller hairs often recurved; **stipules** 2–5 mm long, 0.5 mm wide at the base, narrowly lanceolate to subulate, often terminated by a thin transparent sharp-tipped hair. **Leaves** with petioles 1–3 cm long, 0.3–0.9 mm thick, sparsely to densely pubescent, lacking glands at the apex; **leaf blades** 1.8–7 cm long, 1.2–4 cm wide, ovate to ovate-elliptic, tapering to an acute or short-acuminate apex, margin with 11–23 teeth/side, cuneate to rounded and truncate at the base, drying thin-chartaceous, pubescent on both surfaces with thin straight hairs 0.2–1.9 mm long, venation palmate, 2° veins 2–4/side along the mid-vein. **Male inflorescences** 3–5 cm long, ca. 1.5 mm thick, peduncles 3–25 mm long, 0.2–0.3 mm thick, puberulent; ♂ flowers pedicellate, perianth 0.4–0.5 mm broad at anthesis. **Female inflorescences** axillary, at first 4–7 mm long with subglobose flowering portion but expanding and 24–80 mm long in fruit, becoming a dense loosely cylindrical spike 6–22 mm wide, sometimes with a distal filiform rachis with several ♂ flowers or 1–3 ♀ flowers, peduncles 6–32 mm long, 0.4–1 mm thick, with thin whitish hairs ca. 1 mm long (gland-tipped hairs present or absent), bracts becoming 4–8 mm long with 3–7 lobes, lobes triangular at base and with linear tips 3–5 mm long; ♀ flowers soon becoming enclosed within the congested bracts, ovary ca. 0.7 mm long, hispidulous, style branches 2–5 mm long, red. **Fruits** deeply 3-lobed, hispidulous, hidden within the expanded and persistent bracts of the cylindrical infructescence; **seeds** 1.1–1.4 mm long, 0.7–1 mm diam., oblong-subglobose, surface grayish and minutely reticulate ( $\times 10$ ), caruncle ca. 0.4 mm long and slightly elevated, whitish.

Common weedy plants of open or partly shaded sites in evergreen and deciduous forest formations; 1–700 m elevation (ca. 1100 m near San Vito and in Chiriquí). Probably flowering primarily in the wet season; fruiting mostly in July–November in



Costa Rica. The species ranges from Mexico to Brazil and Bolivia.

*Acalypha arvensis* is recognized by its herbaceous habit, short-awned stipules, and the short thick catkin-like infructescences. The infructescences have a soft texture because of the thin hairs and long linear lobes of the many imbricated bracts; they are reminiscent of *Cenchrus* (Poaceae). Some plants may also produce small ♀ inflorescences with one to three separate proximal ♀ flowers and one to two distal flowers on a filiform rachis. The axillary inflorescences and lack of glandular hairs on stems help separate this species from the closely related *A. alopecuroides*. Specimens with fruiting infructescences are much more common than those with flowers in anthesis.

***Acalypha costaricensis* (Kuntze) Knobl. ex Pax & Hoffm., Pflanzenreich 4, 147, 16: 16. 1924. *Ricinocarpus costaricensis* Kuntze, Rev. gen. pl. 2: 615. 1891. Figure 15.**

**Herbs** or shrubs 0.6–2(–4) m tall, monoecious or dioecious, leafy stems 1.2–4.3 mm thick, with thin or curved hairs 0.4–1 mm long, terete; **stipules** 2.5–8 mm long, 1–1.3 mm wide at the base, lanceolate to linear, glabrous or pubescent. **Leaves** with petioles 1.5–7(–10) cm long, 0.5–1.8 mm thick, pubescent or rarely glabrous, often with minute (0.5 mm) disk-like or ridged glands at the blade; **leaf blades** 10–22 cm long, 4.5–11 cm wide, elliptic to elliptic-oblong or ovate-elliptic, apex acuminate with narrowed tip 8–15 mm long, margin crenate-dentate with short (0.5–3 mm) teeth 12–28/side, rounded at the truncated base or subcordate at the petiole, drying thin-chartaceous and green, with few hairs ca. 0.6 mm long above, more densely pubescent beneath with hairs ca. 0.3 mm long, venation pinnate, 2° veins 5–10/side. **Male inflorescences** 5–30 cm long, 1.5–3.5 mm wide, peduncles 8–12 mm long, 0.3–0.4 mm thick, flower clusters closely crowded or to 1.5 mm apart, ♂ flower buds ca. 0.8 mm diam. **Female inflorescences** terminal, 15–40 cm long, 4–12 cm wide, paniculate and narrowly pyramidal, peduncles to 11 cm long and 3 mm thick, minutely pubescent, lateral branches 2–9 cm long (becoming shorter distally), 0.2–0.4 mm thick, subtended by bracts ca. 1 mm long; flowers usually 1/bract, subtended by imbricate bracts ca. 0.5 mm long, pedicels 1–5 mm long, ca. 0.2 mm thick, puberulent; ♀ **flowers** purple or dark red, sepals ca. 1 mm long, linear, ovary 1–2.3 mm long, 1.5 mm diam., verrucose hispidulous, style column 0.5–1 mm long, style branches 2–4 mm long, with many filamentous parts. **Fruits** 3–4 mm wide, 3-lobed, with erect narrow verrucose projections 0.2–0.4 mm high; **seeds** 1.5–1.7 mm long, 1.4–1.5 mm diam., subglobose or ovoid, smooth, brown or gray, caruncle minute.

Plants of lowland Caribbean rain forest formations, 20–250(–500) m elevation. (Of the 54 Costa Rican collections seen, only 1 was collected

above 250 m elevation.) Flowering and fruiting throughout the year but collected mostly in February–August. The species ranges from southern Mexico to Panama.

*Acalypha costaricensis* is recognized by the large open terminal ♀ inflorescences with conspicuous reddish purple lacinate styles. The larger long-petiolate leaves, verrucose surface of the ovary, and long narrow ♂ inflorescences are also distinctive. It is a handsome and distinctive species. Because the very small bracts do not enlarge in fruit and the ♀ flowers are pedicellate, this species is placed in subgenus *Linostachys* (as is *A. villosa*, q.v.). This species resembles the rarely collected *Ayenia mastatalensis* Cristobal & Zamora (Sterculiaceae).

***Acalypha diversifolia* Jacq., Hort. Schoenbr. 2: 63, t. 244. 1792. *A. leptostachya* H.B.K., Nov. gen. sp. 2: 96. 1817. *A. panamensis* Klotzsch in Seem., Bot. voy. Herald 101. 1853. *A. tabascensis* Lundell, Lloydia 4: 51. 1941. Figure 14.**

**Shrubs** or small trees, 1.5–5(–15) m tall, monoecious, with many arching branches, leafy stems 1–4 mm thick, sparsely to densely hirsutulous with thin hairs 0.2–0.5 mm long, glabrate, gray to dark brown; **stipules** 3–6(–8) mm long, 0.5–1 mm broad at the base, narrowed 1–2 mm above the base to the linear tip, minutely puberulent, often with a thickened convex base. **Leaves** with petioles 4–17(–30) mm long, 0.7–1.5 mm thick, sparsely to densely pubescent, glabrescent, distal glands absent; **leaf blades** 6–20 cm long, 2–8 cm wide, narrowly elliptic to ovate-elliptic or oblong-lanceolate, apex short- to long-acuminate, tip to 25 mm long, margins with 20–40 teeth/side, 0–0.6 mm high, base obtuse to cuneate and often slightly rounded at the petiole, drying chartaceous, upper surfaces sparsely pubescent to glabrescent, lower surface usually pubescent along the veins with hairs 0.1–0.6 mm long, 2° veins 4–8/side. **Inflorescences** axillary, spicate, mostly ♂ and 2–10 cm long (sometimes on short leafless shoots forming a panicle of spikes), peduncles 0–4 mm long, 0.4–0.7 mm thick, sparsely to densely puberulent, ♀ bracts 1–3 and axillary or 1–3 near the base of bisexual spikes, distal ♂ portion of the spike 2–5 mm wide. **Male flowers** in congested or separated clusters, bracts 0.5–1 mm long, triangular, pedicels 0.6–1 mm long, buds ca. 0.5 mm diam., calyx 0.8–1 mm wide, cupulate; stamen cluster 0.5 mm wide distally, anthers ca. 0.1 mm long. **Female flowers** 1–3/bract, subtending bracts 1–1.5 mm long but hidden by pubescence, enlarging in fruit; ovary 0.9–1.5 mm long, ovoid and covered with short erect hairs, base of styles 1–1.5 mm long with lacinate branches to 4 mm long. **Fruits** 2 × 3 mm, muricate with scattered short (0.1 mm) hairs, subtended by bracts 2–4 mm long, 3–4 mm broad, broadly ovate, lobes small or absent, subglabrous; **seeds** 1.4–1.6 mm long, ca. 1.2 mm diam., oblong-rounded, dark brown, smooth.

Common plants of evergreen formations and shaded sites in deciduous forest formations (often

found along riverbanks), 20–1100 m elevation. Flowering in December–August (primarily February–May); fruiting in March–July. This species ranges from Mexico to Peru.

*Acalypha diversifolia* is recognized by the pinnately veined leaves lacking glands at the petiole/blade juncture, dense ♂ flowers often forming thick (4–5 mm) spikes, few ♀ flowers in leaf axils or at base of rare bisexual spikes, and few fruit subtended by subglabrous bracts lacking well-developed teeth. The paucity of ♀ flowers and rarity of fruit among the many collections of this common Central American species is unusual. This may be due to the late development of the difficult-to-see axillary fruits. The species has been called “*costilla de caballo*” and “*costilla de danto*” in Honduras.

***Acalypha ferdinandii* K. Hoffm., Pflanzenreich 4, 147. 16: 63. 1924. Figure 14.**

**Shrubs** or subshrubs 0.7–3(–6) m tall, usually monoecious, leafy stems 0.7–4 mm thick, with short (0.5 mm) hairs or glabrous; **stipules** 3–11 mm long, ca. 1 mm wide at the base, contracted 1–2 mm above the base into a linear awn, glabrous or with thin appressed hairs 0.1–0.2 mm long. **Leaves** with petioles 4–34(–60) mm long, 0.6–1.5 mm thick, glabrous or with few short hairs in early stages (rarely densely pubescent), small glands or pits sometimes present at the apex; **leaf blades** 6–22 cm long, 2–9 cm wide, narrowly elliptic-obovate to oblanceolate or elliptic, usually broadest at or above the middle, tapering gradually to the acuminate apex, serrations 11–35/side, 0.3–1 mm high, blade narrowed below the middle, rounded at the petiole and often auriculate with small (0–2 mm) basal lobes, drying chartaceous, glabrescent above, glabrous or with thin short (0.3–0.7 mm) hairs beneath, 2° veins 7–10/side. **Male inflorescences** axillary to distal leaves, 4–12 cm long, ca. 3–4 mm diam., yellow-green, peduncles 3–15 mm long, ca. 0.5 mm diam. and glabrous or pubescent, flower clusters closely congested; ♂ **flowers** 0.6–1 mm wide, borne on pedicels 0.5–1 mm long, anthers ca. 0.1 mm long. **Female inflorescences** terminal or near-terminal, 6–18 cm long and spicate, 10–15 mm diam. (including style branches), reddish, bracts 5–8 mm long, subtending 1–3 sessile ♀ flowers, enlarging in fruit, teeth of the bracts 0.5–3 mm long, acute; ♀ **flowers** with ovary ca. 1 mm long, ovoid and covered with erect-ascending hairs, style branches many, lacinate-filamentous, 2–6 mm long, white to red or pink. **Fruits** 2 × 3 mm, strongly 3-lobed, enclosed within the enlarged (10 × 13 mm) conduplicate bracts with 5–11 teeth 1–5 mm long and triangular to linear; **seeds** 2.4–2.6 mm long, 1.4–1.6 mm diam., oblong, surface smooth.

Plants of evergreen and partly deciduous forest formations, 20–1300 m elevation (rarely collected below 500 m on the Caribbean slope in Costa Rica). Probably flowering throughout the year; fruiting in January–July. The species ranges from Guatemala to central Costa Rica.

*Acalypha ferdinandii* is recognized by the long thick terminal ♀ spikes with conspicuous toothed bracts and the usually narrowly obovate leaves with pinnate venation that taper to a rounded small-auriculate base. This species is quite similar to *A. apodanthes* (q.v.) with smaller leaves and solitary ♀ flowers, and it is possible that the two are conspecific.

***Acalypha hispida* Burm., Fl. Ind. 203, pl. 61, f. 1. 1768.**

**Ornamental shrubs** 1.5–3 m tall, dioecious, leafy stems minutely hirsutulous with hairs ca. 0.3 mm long. **Leaves** with petioles 2–5 cm long, ca. 1.5 mm thick, hirsutulous; **leaf blades** 9–18 cm long, 5–11 cm wide, ovate, apex usually short-acuminate, margin with 15–30 teeth/side ca. 1 mm high, base rounded, drying thin-chartaceous, glabrescent above, minutely puberulent on the veins beneath, venation palmate, 2° veins 3–5/side on the midvein. **Inflorescences** ♀ in cultivated material, 15–35 cm long, 6–25 mm wide, pendulous, densely flowered and reddish from the many style branches; ♀ flowers with ovary 1 × 2 mm, densely covered with minute erect hairs, style branches 5–7 mm long; fruits and seeds usually not developing.

*Acalypha hispida* is planted as an ornamental shrub because of its colorful pendant red or reddish purple spikes. Originally from Malaysia, it is now grown throughout the tropics and subtropics. In Central America it is grown at low and middle elevations (0–2000 m). Common names are *cola de gato*, *cola de zorro*, *rabo de gato*, “chenille plant,” “red-hot cattail,” and “red cattail.”

***Acalypha leptopoda* Müll. Arg., Linnaea 34: 39. 1865. *A. lotsii* J. D. Smith, Bot. Gaz. 20: 544. 1895. Figure 15.**

**Shrubs** or small treelets, monoecious, 1–3 m tall, often clambering or leaning over others, leafy stems 0.6–4 mm thick, sparsely to densely pubescent with hairs 0.1–0.5 mm long, usually glabrescent and dark reddish brown; **stipules** 3–15 mm long, ca. 1 mm broad at the base, narrowed 1–2 mm above the base into a linear awn, persisting. **Leaves** with petioles 3–60(–70) mm long, 0.2–1.3 mm thick, sparsely to densely pubescent, with minute (0.3 mm) fimbriate glands at the adaxial apex; **leaf blades** 2–12(–16) cm long, 1–6(–9) cm wide, ovate to ovate-triangular or ovate-elliptic, tapering gradually to the acuminate apex, margins with 22–38 serrations/side ca. 1 mm high, base broadly obtuse or rounded and subcordate, drying thinly chartaceous, sparsely pubescent above, more densely pubescent beneath, venation palmate, 2° veins 4–7/side of the midvein, strongly ascending. **Male inflorescences** 2–11 cm long, 1.5–2 mm thick, peduncles 3–16 mm long, ca. 0.3 mm thick, sparsely to densely pubescent, bracts ca. 1 mm long, pedicels 0.4–0.8 mm long; ♂ flower bud ca. 0.4 mm diam., broadly ovoid,



perianth ca. 0.7 mm broad at anthesis. **Female inflorescences** axillary, pendant on filiform (0.1–0.2 mm) peduncles 11–38 mm long, usually with 1 terminal bract (rarely 2–3), bracts 1.5–3 mm long, subtending 1–3 sessile flowers; ♀ flowers ca. 2 mm long in early stages, ovary 0.7–1 mm long, hispidulous, styles 3–5 mm long. **Fruits** verruculose, subtended by bracts 4–7 mm wide with 7–11 triangular and acute or acuminate teeth 1–3 mm long; seeds 1.6–1.9 mm long, 1.2–1.3 mm long, oblong-ellipsoid, smooth.

Plants of evergreen lower montane forest formations, (100–)500–1700 m elevation. Probably flowering throughout the year but with most collections made in June–January. The species ranges from southern Mexico to western Panama.

*Acalypha leptopoda* is recognized by the slender pendulous ♀ spikes usually with only a single terminal bract and one to two flowers, thin ovate leaves with palmate venation and minute glands at the apex of the petiole, awned stipules, and lower montane habitats. There are sometimes more than one inflorescence per leaf axil, but these appear to be borne on short-shoots. Different collections can vary greatly in the density of pubescence. This species is very similar to *A. unibracteata* Müll. Arg. of southern Mexico and northern Central America.

***Acalypha macrostachya* Jacq., Hort. Schoenbr. 2: 63, t. 245. 1797. *A. seemannii* Klotzsch in Seem., Bot. voy. Herald 102. 1853. *A. pittieri* Pax & K. Hoffm., Pflanzenreich 4, 147, 16: 147. 1924. *A. hicksii* Riley, Kew Bull. 1927: 126. 1927, ex char. *A. fertilis* Standl. & L. O. Williams, Ceiba 1: 146. 1950, ex char. Figure 15.**

**Shrubs** or weak-stemmed treelets 1–3(–5) m tall, monoecious or dioecious, leafy stems 2.5–11 mm thick, densely to sparsely pubescent with hairs 0.3–1.4(–2) mm long, terete; **stipules** 5–16 mm long, 3–7 mm broad, ovate-lanceolate and acuminate or subulate, a slender linear tip to 10 mm long sometimes present, veins 3–5 and parallel with midrib, pubescent to glabrous. **Leaves** with petioles 2.5–26 cm long, 1–3.8 mm thick, sparsely to densely pubescent, small (0.5–0.8 mm) glands sometimes present at the apex; **leaf blades** (10–)15–24 cm long, (5.5–)8–17 cm wide, ovate to ovate-triangular, tapering gradually to the acute or acuminate apex, narrowed tip 6–18 mm long, margin with 30–60 teeth/side ca. 1 mm high, base abruptly rounded and truncated (cordate in larger leaves), drying chartaceous, with straight hairs 0.6–1.3 mm long on the upper surface, more densely pubescent beneath, venation palmate or subpalmate, 2<sup>nd</sup> veins 5–11/side of midvein, 3<sup>rd</sup> veins subparallel. **Male inflorescences** 4–20 cm long, peduncles 3–9 mm long, 0.6–1.5 mm thick, flowering part 2.5–5 mm thick, bracts 0.7 mm long, flower clusters closely crowded, pedicels to 1.5 mm long; ♂ flowers 0.8 mm diam. in bud, 1 mm wide at anthesis, 0.7 mm long, sepals with straight hairs

to 0.4 mm long. **Female inflorescences** axillary, 9–35 cm long, 5–14 mm wide (including styles), peduncles 1–10 mm long, 1–1.9 mm thick, usually densely pubescent, flowers 1/bract, up to 6 mm distant along the rachis bracts ca. 1 mm long at anthesis and covered with whitish hairs, enlarging in fruit, with 5–12 major veins and teeth ca. 1 mm long; ♀ flowers with ovary 1–1.5 mm long, ovoid, covered with straight ascending hairs ca. 0.7 mm long, becoming enclosed within the subtending bract, style branches exserted and 1.5–8 mm long, filiform-laciniate and reddish. **Fruits** 3–5 mm wide, sessile and enclosed within the enlarged (8 × 8 mm) cupulate-conuplicate bracts; **seeds** 1.9–2.2 mm long, 1.4–1.8 mm diam., ovoid-globose, smooth, dark brown, caruncle a whitish area ca. 0.5 mm long.

Plants often found in second growth of evergreen wet forest and partly deciduous forest formations on both the Caribbean and Pacific slopes, 10–1200 m elevation. Flowering throughout the year (mostly January–May); fruiting February–May. This species ranges from southern Mexico to Bolivia and Brazil; it may be present on Cocos Island (see below).

*Acalypha macrostachya* is recognized by the generally larger leaves, long pendant inflorescences, the enlarged fan-like floral bracts (not present at anthesis), and larger seeds. Most plants appear to be monoecious with several spikes of one sex followed by several spikes of the other sex in more distal leaf axils. Rarely, ♀ spikes may have ♂ flowers near the apex. The pubescence is grayish white in life but pale yellowish in herbarium material. Different collections can vary greatly, from sparsely puberulent to densely villous. The separation of such a variable species into varieties based on pubescence serves no useful purpose (cf. Standley & Steyermark, 1949, p. 39). Two type collections from Cocos Island may prove to be this species: *Pittier 16246* (photo B at F), type of *A. pittieri*, and *Hicks 456* (κ, not seen), type of *A. hicksii*. We have seen no material of this genus from Cocos Island.

***Acalypha mexicana* Müll. Arg., Linnaea 34: 41. 1865. *A. indica* L. var. *mexicana* (Müll. Arg.) Pax & K. Hoffm., Pflanzenreich 4, 147, 16: 35. 1924. Figure 11.**

**Herbs** 15–40 cm tall, branched at the base with erect unbranched stems, leafy stems 0.3–1.8 mm thick, with minute (0.2–0.3 mm) curved hairs along 2 longitudinal lines; **stipules** 0.5–2 mm long, filiform, minutely puberulent, deciduous. **Leaves** with petioles 6–45 mm long, 0.2–0.6 mm thick, pubescent with thin straight or curved hairs; **leaf blades** 1–5 cm long, 0.8–3 cm wide, ovate to ovate-rhombic, apex obtuse or bluntly acute, margin with 6–15 teeth/side, base rounded and obtuse to truncate,



drying membranaceous, with scattered straight hairs 0.5–1.2 mm long on the upper surface, with shorter (0.4 mm) hairs along the veins above, venation palmate, 2° veins 2–3/side of the midvein. **Inflorescences** axillary, ♂ spikes 1–2 cm long, slender, falling early, ♀ to 4 cm long with 3–6 distant bracts or 1–2 bracts crowded in the leaf axils, sessile or short-pedunculate, sometimes with a filamentous extension of the rachis and solitary distal ♀ flower. **Fruits** becoming 3 mm diam., subtended by an ovate to reniform bract 3–6 mm long, 5–12 mm wide, with 9–13 rounded distal lobes 0.5–1 mm long, minutely pilose or ciliate along the margin; **seeds** 1–1.2 × 0.6–0.7 mm, ovoid-ellipsoid with acute apex, surface smooth, grayish.

Rarely collected weeds of open sites, at 900–2100 m elevation in Costa Rica. More common in Mexico and Guatemala, the species is probably an introduction in Costa Rica.

*Acalypha mexicana* is recognized by its short erect unbranched stems, palmately veined leaves with serrate margins on slender petioles, short inflorescences at almost all nodes, and foliaceous bracts with short rounded lobes. We have seen only four Costa Rican specimens, from the Valle Central, Cartago, and the lower slopes of Volcán Irazú. This species has also been thought to be a variety of the Asian *A. indica* L.

***Acalypha obtusifolia* Pax & K. Hoffm., Pflanzenreich 4, 147, 16: 147. 1924.**

**Shrubs;** stipules ca. 5 mm long, lanceolate. Leaves with petioles 1–3.5 cm long, slender; blades 10–12 cm long, 6–7.5 cm wide, broadly ovate, apex obtuse or short-acute, margin denticulate, base obtuse, membranaceous, glabrous or subglabrous, palmately 5-veined. **Fruiting inflorescence** 10–15 cm long, short-pedunculate, sparsely pilose, bracts 3–5 mm long, 6–7 mm wide, obovate-truncated, with 13–15 teeth, sepal triangular, styles ca. 5 mm long; seeds 2 mm long.

This species was based on a single collection from Punta Mala along the Pacific coast (*Tonduz* 6823, probably destroyed at B). We have not seen isotypes. It was placed close to *A. macrostachya* Jacq. by Pax and Hoffmann and may be an unusual small-leaved form of that species.

***Acalypha polystachya* Jacq., Hort. Schoenbr. 2: 64, t. 246. 1797.**

**Herbs** 35–90 cm tall, leafy stems 0.7–8 mm thick, sparsely puberulent with curved hairs 0.1–0.3 mm long, glabrescent and terete; stipules 0.3–1 mm long or absent, linear, caducous. **Leaves** with petioles 1–9(–15) cm long, 0.4–1.7 mm thick, glabrous or sparsely puberulent with curved hairs to 0.4 mm long; **leaf blades** 4–11(–16) cm long, 2.5–7.5(–12) cm wide, ovate to ovate-elliptic, apex short-acuminate, rounded to the obtuse or truncate base,

teeth 20–38/side, drying membranaceous, with scattered thin straight hairs to 1.4 mm long on the upper surface, glabrous to sparsely pubescent beneath, venation palmate, 2° veins 2–6/side on the midvein. **Male inflorescences** 9–60 mm long, peduncles 5–20 mm long, 0.2–0.3 mm thick, flowering portion ca. 2 mm wide, pedicels to 0.8 mm long; ♂ flower buds ca. 0.5 mm diam. **Female inflorescences** terminal or in distal axils, 10–30 mm long and 2–3 mm thick in early stages, becoming 4–12 cm long and 1–2 cm thick in fruit, bracts usually subtending 2 sessile flowers, bracts with 7–12 narrow lobes elongating in fruit; ♀ flowers with ovary ca. 0.5 mm long and styles 2 mm long in early anthesis. **Fruits** 2.4 mm broad, 2–3 mm long, with smooth rounded surfaces, subtended by bracts developing elongated linear teeth to 11 mm long; **seeds** 2.4–2.7 mm long, 1.9–2.1 mm diam., ovoid with an acute tip (beak), surface prominently rugose.

Uncommon weedy plants of open sites in both deciduous and evergreen vegetation, 1–400 m elevation. Flowering and fruiting primarily in June–August. The few Costa Rican collections seen come from the Pacific lowlands. The species ranges from Mexico to Ecuador.

*Acalypha polystachya* is recognized by the herbaceous habit, palmate leaves with few hairs, short slender ♂ spikes, ♀ spikes becoming thick with expanded glabrous linear-toothed bracts, and large fruit with somewhat rugose surface. The very small stipules are quite unusual.

***Acalypha radinostachya* J. D. Smith, Bot. Gaz. 54: 243. 1912.**

**Shrubs,** subshrubs or small treelets, 1–3 m tall, leafy stems 2–6 mm thick, minutely (ca. 0.2 mm) appressed-puberulent; stipules 6–13 mm long, lanceolate or subulate with a long narrow apex, caducous with the base becoming thickened and pale colored, ca. 2 mm wide. **Leaves** with petioles 2–23 cm long, 1–2.5 mm thick, appressed puberulent or subglabrous, with sessile glands 0.5–1 mm wide at apex adaxially; **leaf blades** 11–26 cm long, 6–15 cm wide, ovate to ovate-elliptic, apex acuminate, margin strongly serrate with 1–3 teeth/cm, base narrowed and rounded, subcordate to truncate, drying thinly chartaceous and dark green, subglabrous or minutely puberulent beneath at maturity, venation palmate, 2° veins 3–5/side of the midvein. **Male inflorescences** axillary to distal leaves, solitary, 8–22 cm long, spicate, peduncles ca. 1.3 mm thick, flowering portion ca. 2 mm thick, minutely puberulent, bracts 0.5 mm long, difficult to see, glomerules with 3–6 flowers; ♂ flower buds ca. 0.4 mm diam., globose. **Female inflorescences** terminal, solitary, 23–45 cm long, spicate, peduncles 2–2.5 mm thick, densely or sparsely puberulent, bracts 2–3 mm long, becoming 4 mm wide, with 2–3 lobes 0.5–1.2 mm high, green but drying dark, bracts closely clustered or separate; ♀ flower 1/bract, ovary ca. 2 mm long, 2–3 mm wide, broadly ovoid, glabrous, styles 3–6 mm long, lacinate. **Fruits** ca. 2–2.5 mm long, ca. 3 mm wide, sessile, subtended by bracts not exceeding 3 mm in length, to 5 mm wide.

Plants of the wet evergreen Caribbean slope, 100–300 m elevation. Flowering February and May–September. The species is known only from La Selva and the Llanuras de Santa Clara (*J. D. Smith 6849* us the type) in north-central Costa Rica.

*Acalypha radinostachya* is recognized by its long terminal (apparently erect) ♀ inflorescences, ♀ bracts that do not become significantly enlarged, larger ovate leaves with large blunt teeth, and the thick hard whitish base where the stipules were attached. The ♀ inflorescences are described as green, with style branches sometimes becoming white. *Acalypha macrostachya* is vegetatively similar but the blades are broadly rounded at the base, and the stipule scars do not become hard and smooth. Also, *A. radinostachya* is never densely villose as are some collections of *A. macrostachya*.

***Acalypha schiedeana*** Schldl., *Linnaea* 7: 304. 1832. Figure 14.

**Shrubs** 1–3 m tall, much branched, leafy stems, 1.3–5 mm thick, glabrous or with thin whitish hairs 0.2–0.4 mm long; stipules 7–10 mm long, 0.7–1.2 mm broad at the base, filiform (ca. 0.2 mm thick) above the short (ca. 1 mm) base. **Leaves** with petioles 2–7 cm long, 1.1–1.5 mm thick, glabrous or pubescent, usually with small (0.2 mm) digitate glands at the apex; **leaf blades** 6–18 cm long, 4–11 cm wide, ovate to elliptic-ovate, apex usually short-acuminate, margin with 12–35 teeth/side, base rounded and truncate or subcordate, drying membranaceous, with thin hairs 0.3–0.8 mm long on veins above and below, venation palmate, 2° veins 3–4/side along the midvein. **Male inflorescences** 1–13 cm long, ca. 1.5 mm wide, peduncles 2–14 mm long, ca. 0.6 mm thick, pubescent, pedicels ca. 0.5 mm long; ♂ flower with perianth ca. 0.4–0.5 mm wide, anther-clusters 0.4–0.5 mm wide. **Female inflorescences** terminal, 4–18 cm long, becoming 6–14 mm thick in fruit, peduncles 6–14 mm long, 0.7–0.9 mm thick, pubescent, flowers at first with minute bracts and separate along the rachis, sessile, becoming congested; ♀ flowers with ovary 0.5–1.5 mm long, minutely hispidulous, styles 1.5–3 mm long, laciniate distally. **Fruits** ca. 3 mm broad, smooth, solitary within conspicuous bracts 3–12 mm long, with 7–13 lobes 1–2 mm long, triangular to lanceolate, bracts usually with thin hairs 0.4–1.5 mm long; **seeds** 1.7–2 mm long, 1.3–1.5 mm diam., ovoid, grayish, caruncle not elevated, 0.7 mm long.

Uncommon plants of moist evergreen sites in deciduous forest formations on the Pacific slope, 0–800 m elevation in Costa Rica. Flowering in late May–early June; fruiting in June (June–December in northern Central America). This species is known in Costa Rica from Sta. Rosa N.P., riparian forest near Bagaces and Cañas, and San Luis (below Monteverde). The species ranges from

central Mexico to northern Puntarenas Province, Costa Rica.

*Acalypha schiedeana* is recognized by the shrubby habit, ovate leaves with palmate venation, narrow stipules, conspicuous terminal ♀ spikes, and broad bracts with relatively short teeth subtending the fruit.

***Acalypha septemloba*** Müll. Arg., *Flora* 55: 27. 1872. *Ricinocarpus irazuensis* O. Ktze., *Rev. gen. pl.* 2: 616. 1891. *A. irazuensis* (O. Ktze.) Pax & Hoffm., *Pflanzenreich* 85 (IV, 147, XVI): 53. 1924. Figure 14.

**Herbs** or subshrubs, to 1 m tall, leafy stems 0.3–2 mm thick, with thin curved whitish hairs 0.2–0.4 mm long; stipules 0.5–1.5 mm long, triangular to subulate, caducous. **Leaves** with petioles 4–40 mm long, 0.3–0.6 mm thick, pubescent with thin whitish hairs, with minute digitate glands at the apex or adjacent to a gland-like area on the blade; **leaf blades** 1–7 cm long, 1–4 cm wide, ovate to ovate-triangular (suborbicular in very small leaves), apex acute or subacuminate, margin with 12–22 teeth/side, base rounded and obtuse or truncate, drying membranaceous, with scattered appressed straight hairs 0.2–0.9 mm above, with shorter hairs beneath, venation palmate or subpalmate, 2° veins 2–3/side on the midvein. **Male inflorescences** 0.8–2 cm long, 1.5 mm wide, bracts ca. 0.6 mm long, peduncles ca. 3 mm long, pedicels 0.5 mm long; ♂ flower buds ca. 0.4 mm diam. (the mostly ♂ inflorescences often bisexual with 1–2 ♀ flowers at apex or base). **Female inflorescences** terminal, 2–9 cm long and 7 mm wide, enlarging in fruit to 10 mm wide, peduncles 0–4 mm long; ♀ flowers 1/bract, sepals 0.5–0.8 mm long, ovary ca. 0.6 mm long, style branches 2–4 mm long, reddish. **Fruits** ca. 2.6 mm diam., subtended by bracts 3–5 mm long, to 6 mm wide, with short (1–2 mm) triangular or digitate lobes; **seeds** ca. 1.3 × 0.8 mm, ovoid-ellipsoid, smooth.

Uncommon plants of evergreen montane formations, 1100–1900 m elevation. Flowering in July–January; fruiting in November–December. The species ranges from central Costa Rica to western Panama.

*Acalypha septemloba* is recognized by its higher-elevation habitat, short weak-stemmed habit, very small stipules, glandular processes at the junction of petiole and blade, and floral bracts with short acute or rounded lobes. The reddish style branches are conspicuous at anthesis.

***Acalypha setosa*** A. Rich. in Sagra, *Hist. fis. Cuba Bot.* T. XI: 204. 1850.

**Herbs** 0.3–0.8 m tall, usually with a single main stem and few lateral branches, leafy stems 0.8–4 mm thick, with thin curved hairs ca. 0.2 mm long; stipules 1–2 mm long, 0.1–0.2 mm wide, persisting or deciduous. **Leaves**



with petioles 1–7 cm long, 0.3–0.8 mm thick, with thin curved ascending hairs; **leaf blades** 2.5–10 cm long, 1.5–6.5 cm wide, broadly ovate to ovate-triangular, abruptly short-acuminate at the apex (acute), marginal teeth 5–8/cm, base broadly obtuse to truncated, drying membranaceous, with straight appressed hairs 0.4–0.8 mm long on the upper surface or glabrescent, lower surface with inconspicuous hairs along the major veins, venation palmate, midvein with 2° veins 2–4/side. **Male inflorescences** at distal nodes, solitary, 8–25 mm long, flowering portion 1.5–2 mm diam., rachis 0.2–0.3 mm thick, filaments 0.2–0.4 mm long; ♂ flowers ca. 0.4 mm wide at anthesis. **Female inflorescences** axillary to distal nodes or appearing terminal (abnormal ♀ inflorescences often at lower nodes), 3–12 cm long, flowering portion 3–11 mm wide, bracts 2–7 mm long, with 9–13 narrow lobes up to 6 mm long, enclosing 1 ♀ flower; ovary pubescent, styles not conspicuous. **Fruits** 1.5–2 mm long, 2–3 mm wide, 3-lobed, with few erect hairs; seeds 1.2–1.4 mm long, 1–1.2 mm wide, subglobose to ovoid, smooth.

Weedy plants of open or disturbed sites in deciduous and evergreen areas, 5–900 m elevation (in northern Central America). Flowering and fruiting throughout the year in northern Central America. The species ranges from Mexico to northern Costa Rica and from the West Indies to northern South America.

*Acalypha setosa* is recognized by its short herbaceous habit, broadly ovate leaves with truncated base and palmate venation, and the ♀ bracts with long narrow lobes. The small linear stipules and very short ♂ spikes are also characteristic. This species may be mistaken for *A. polystachya*, but the seeds of the two species are very different. This species has only recently been collected in Guanacaste Province (Wilbur *et al.* 23031 & 31203 DUKE) and may be a recent introduction.

***Acalypha triloba* Müll. Arg., Linnaea 34: 23. 1865.**

**Herbs** to ca. 1 m tall, leafy stems 1–4 mm thick, hirsute with thin straight somewhat retrorse hairs 1–2 mm long, shorter (0.1–0.3 mm) hairs also present; stipules 1.5–5 mm long (or absent), linear to narrowly triangular. **Leaves** with petioles 2–7 cm long, 0.5–0.8 mm thick, with thin straight hairs 0.3–2 mm long; **leaf blades** 4–10 cm long, 2–6 cm wide, ovate-elliptic to ovate or ovate-triangular, apex acuminate, margin serrate with ca. 5 teeth/cm (Costa Rica) or 2–3 teeth/cm (Mexico and Guatemala), base obtuse to rounded and truncate, drying chartaceous, surfaces with thin straight hairs 0.5–1.5 mm long, venation palmate, 2° veins 4–5/side of midvein and strongly ascending. **Male inflorescences** solitary, 5–12 cm long, peduncles 8–60 mm long, flowering portion 1.5–2.5 mm thick, flower buds 0.3–0.5 mm diam., pedicels less than 1 mm long; ♂ flowers with anthers 0.2–0.3 mm wide. **Female inflorescences** terminal or axillary to distal leaves, solitary, 3–7 cm long, 3–12 mm wide (including styles), rachis densely pubescent, flowers 2–3/bract (original description) or apparently 1/bract (Costa Rican collection),

sessile, bracts with 3 distal lobes; ♀ flowers with calyx ca. 1 mm long, ovary densely pubescent, styles 4–6 mm long, lacinate, becoming reddish. **Fruits** and fruiting inflorescences not seen; seed foveolate-punctulate (original description).

*Acalypha triloba* is a poorly known species of Mexico and Guatemala with a single Costa Rican collection placed here provisionally. The species is unusual because of its ♂ spikes with long thin peduncles, long slender petioles, and the stems and leaves with straight slender hairs to 2 mm long. A Guatemalan collection (Steyermark 51959 F) was collected at 2500 m elevation, but the Costa Rican collection came from a partly shaded roadside at ca. 100 m elevation near Bahia El Coco in Guanacaste Province in late July (Burger & Burger 7753, distributed as *A. polystachya*?). The Costa Rican collection differs in having more finely serrate leaves and less well-developed stipules, and the ♀ flowers appear to be solitary on the young spike. We thank Geoffrey Levin for the provisional determination of this collection.

***Acalypha villosa* Jacq., Enum. Syst. Pl. 32, 1760; Sel. Stirp, Pl. Amer. 254, t. 183, f. 61. 1763.** Figure 15.

Weak-stemmed **shrubs** or small treelets 0.5–3(–8) m tall, usually monoecious, leafy stems 1.3–5 mm thick, sparsely to densely pubescent with minute (0.1 mm) or villous yellowish hairs 0.3–0.9 mm long; stipules 2–10 mm long, narrowly triangular to lanceolate, acuminate, often with a distinct midvein and thin lateral margins. **Leaves** with petioles 2.5–14 cm long, 0.6–2 mm thick, sparsely to densely pubescent, often with elevated or lanceolate glands 0.5–1.5 mm long at the apex and drying dark; **leaf blades** 8–17(–25) cm long, 5–11(–13.5) cm wide, ovate to ovate-triangular, tapering gradually to the acute or acuminate apex, margin crenate-serrate with 25–75 teeth/side 0.5–2 mm high, usually abruptly rounded to the truncated or cordate base, drying thin-chartaceous, sparsely strigose to glabrate above, more densely pubescent below with hairs 0.3–0.9 mm long (rarely glabrous), venation palmate or subpalmate, 2° veins 4–7/side of the midvein, 3° veins subparallel; minute pellucid dots sometimes present on the lower surface. **Inflorescences** almost always unisexual and unbranched, usually axillary, often with a series of axils bearing the same sex followed by a number of axils bearing the other sex, puberulent. **Male inflorescences** 4–12 cm long, 1.8–3.6 mm diam., spicate, peduncles 4–12 mm long, 0.3–1 mm thick, flower clusters sessile and closely congested, obscuring the rachis until after anthesis, bracts 0.7–1 mm long, broadly triangular, often ciliolate, pedicels 0.5–1.5 mm long; ♂ flowers ca. 1 mm wide, sepals ca. 0.5 mm long, with a glabrous perianth-like inner whorl drying and brownish (ca. 0.4 mm long), anthers ca. 0.1 mm long. **Female inflorescences** becoming racemose, 5–16 cm long, peduncles 5–25 mm long, rachis 0.2–0.3 mm thick, flowers mostly solitary, subtended by minute (0.5



mm) bract and tufted hairs, pedicels 1–2 mm long, to 4 mm in fruit; ♀ **flowers** with sepals ca. 0.5 mm long, persisting in fruit; ovary 0.8–1.3 mm long, style column 0.3 mm long, style branches 1–2 mm long, often drying yellowish (red in life). **Fruits** 1.5 × 2 mm, prominently 3-lobed, muricate with narrow projections 0.1–0.3 mm long, persisting columella ca. 0.7 mm long, expanded apically; **seeds** 0.8–1.4 mm long, 0.7–1.3 mm diam., ovoid or subglobose, smooth, pale brown.

Plants of evergreen forest formations on both Caribbean and Pacific coasts, 1–800 m elevation. Probably flowering and fruiting throughout the year in Central America. The species ranges from Mexico to Brazil and Paraguay.

*Acalypha villosa* is recognized by the slender ♀ racemes with small isolated flowers and the base of the leaf blades consistently broad and rounded to a truncated or cordate base. Occasional collections with near-terminal ♀ inflorescences with many slender lateral branches occur in Honduras and Nicaragua (rarely in Costa Rica) and can be easily confused with *A. costaricensis*. This species is less common in Costa Rica than the closely related *A. costaricensis* (q.v.).

***Acalypha* sp. aff. *A. mortoniana* Lundell, Bull. Torrey Bot. Club 64: 552. 1937.**

**Shrubs** ca. 3.5 m tall, leafy stems 1.2–4 mm thick, densely puberulent with short (0.2–0.3 mm) curved ascending or appressed hairs; stipules 3–4 mm long, linear or setaceous. **Leaves** with petioles 3–13 cm long, 0.8–1.8 mm thick, densely minutely puberulent, apical glands

absent; **leaf blades** 12–18 cm long, 5–8 cm wide, elliptic to elliptic-oblong or narrowly ovate-elliptic, apex acuminate, margin with short (0.5 mm) gland-tipped teeth, base cuneate to obtuse, drying membranaceous or thin-chartaceous, dark, minutely puberulent on the veins above, sparsely puberulent beneath, venation palmate or subpalmate, midvein with 4–5 2° veins/side. **Male inflorescences** 6–12 cm long, 3–4 mm thick (with flowers), rachis 0.2–0.3 mm thick, puberulent, bracts ca. 1 mm long, subtending 3–7 flowers, pedicels ca. 1 mm long; ♂ flowers ca. 1 mm wide. **Female inflorescences** terminal, to 14 cm long in fruit, not seen at anthesis, fruiting bracts 5–6 mm long, broadly conduplicate-reniform, apically emarginate or with a short sinus, margin entire and with prominent gland-tipped hairs 0.5–1.5 mm long, surfaces with few thin hairs, each bract subtending a solitary fruit. **Fruits** 5–6 mm long, ca. 6 mm wide, subglobose, sessile, partly enclosed by the bract; seeds 3.7–4.2 mm long, ca. 3 mm diam., ovoid-ellipsoid, smooth, brown.

Known only from primary evergreen forest at Estación Cacao (10°55'38"N, 85°29'38"W) at 1100 m elevation. Flowering and fruiting in June. This taxon is represented by a single collection (*Delgado 29*) from northwestern Costa Rica.

*Acalypha* sp. aff. *A. mortoniana* is recognized by its larger elliptic leaves on long petioles, slender ♂ spikes, and prominent erect fruiting spikes with floral bracts bearing gland-tipped hairs along their rounded entire margins. Our collection is very similar to material of *A. mortoniana* from Guatemala and may prove to be a southern subspecies. The following key highlights the differences between our collection and the Guatemalan material.

- 1a. Leaf blades mostly elliptic and narrowed gradually to the base, serrations small or obscure; fruiting bracts often emarginate at the apex ..... (*Delgado 29*)
- 1b. Leaf blades mostly ovate and rounded at the base, usually with prominent (0.5–1.5 mm high) serrations; fruiting bracts often with a single apical tooth ..... *A. mortoniana*

## **Acidoton Swartz**

**Shrubs** or small treelets, dioecious, stinging hairs sometimes present, spines absent; stipules paired at the leaf base, small, deciduous or persistent. **Leaves** alternate, simple, petiolate, without glands or stipels; leaf blades entire to crenate or dentate, pinnately veined, domatia often present. **Inflorescences** axillary, racemose with flowers in fascicles along the length of the single rachis, bracts eglandular, ♂ flowers subsessile or pedicellate, ♀ flowers pedicellate. **Male flowers** with 3–5 sepals, valvate in bud, petals absent, disk absent or part of the raised receptacle; stamens ca. 22–60, filaments free, slender, glabrous, anthers dehiscing longitudinally, extrorse, connective with a minute tuft of stinging hairs at its apex; pistillode absent. **Female flowers** with 5–6 sepals, narrow and imbricate, petals and disk absent;

ovary 3-locular, covered with stiff stinging hairs, ovules 1/locule, styles with basal column and 3 papillate branches. **Fruits** capsular, deeply 3-lobed and breaking into 3 2-valved cocci, surfaces with stinging hairs; seeds rounded, ecarunculate.

A small genus of approximately six species centered in the Caribbean. It is related to *Tragia* but differs in having the connective terminated by stinging hairs. One species is found in Central America.

***Acidoton nicaraguensis* (Hemsl.) G. Webster, Ann. Missouri Bot. Gard. 54: 191. 1967. *Cleidion nicaraguense* Hemsl., Biol. centr. amer. Bot. 3:**

130. 1883. *Gitara panamensis* Croizat, J. Arnold Arbor. 26: 192. 1945. Figure 12.

**Shrubs** or small treelets 1–5(–7) m tall, dioecious, leafy stems 0.9–4 mm thick, with thin whitish hairs, glabrescent and gray in age, epidermis exfoliating in longitudinal strips on older stems; stipules 1.5–6 mm long, 0.8–1.8 mm broad at base, triangular to lanceolate, glabrous or puberulent abaxially, persisting and brown, veins parallel and prominent or obscure. **Leaves** with petioles 2–6 mm long, ca. 1 mm thick, densely strigose with stiff ascending or erect hairs 0.2–0.6 mm long; **leaf blades** 8–21 cm long, 3–7 cm broad, narrowly elliptic-oblong, narrowly ovate-elliptic or elliptic, apex acuminate with a narrowed tip 7–25 mm long, margin distally crenate-dentate with gland-tipped teeth 0–4 mm long, base gradually narrowed and cuneate, slightly rounded at the petiole, drying chartaceous and dark green to greenish gray or brown, glabrous or minutely puberulent on the veins above, glabrous beneath but with some hairs along the veins and in the vein axils (domatia), with 4–7 major secondary veins on each side. **Inflorescences** 1–3 on axillary short-shoots, unisexual, axillary or pseudoterminal, ♂ 0.5–5 cm long, ♀ ca. 1 cm long but elongating in fruit, racemose, subtended at the base by a series of imbricate stipules, peduncles 3–8 mm long, 0.3–0.4 mm thick, ♂ flowers in alternate fascicles of 2–4, ♀ flowers 2–4 and alternate along the strigulose unbranched or few-branched rachis, bracts to 2 mm long, acute, ♂ pedicels to 3 mm long, ♀ pedicels ca. 1 mm long. **Male flowers** white or yellowish, sepals 3, 1.5–3 mm long, 0.8 mm broad at the base, pubescent on the exterior, stamens ca. 21, filaments 1.3–2.5 mm long, 0.1–0.2 mm thick, erect, drying orange-brown, anthers 0.2–0.4 mm long, 0.2–0.3 mm broad, connective apex with a minute (0.1 mm) tuft of stinging hairs (difficult to see). **Female flowers** white or yellowish, sepals 1.3–2 mm long, 0.5–0.8 mm broad, narrowly acute; ovary 1–1.7 mm long, covered with stiff ascending hairs, style column 0.4–1.2 mm long, style branches 1.3–2.7 mm long, recurved, papillose. **Fruits** 5–6 mm long, 8–10 mm broad, deeply 3-lobed and breaking into cocci 4–5 mm broad, surfaces with sharp stinging hairs; seeds 4–4.5 mm long, subglobose.

Plants of evergreen forest formations on both the Pacific and Caribbean slopes, 0–700 m elevation (to 1000 m in Nicaragua). Flowering in January–July; fruiting in March–October. While the species is not often collected in Costa Rica, it can be locally common (as at Volcán Orosi). The species ranges from Guatemala to Peru.

*Acidoton nicaraguensis* is recognized by the narrow short-petiolate leaves with prominent gland-tipped teeth, domatia in vein axils, slender axillary spicate/racemose inflorescences, ♂ flowers with many closely congested filaments, minute anthers, and fruits with rounded cocci and stinging hairs. This species appears to be common in eastern Nicaragua; it has been called *mala* in southeastern Honduras, perhaps because of the stinging hairs, which may be present on the foliage as well as on

the flowering parts. The South American *A. venezolanus* (Croizat) Webster may be conspecific.

#### **Actinostemon Martius ex Klotzsch**

REFERENCE—E. Jablonski, Notes on Neotropical Euphorbiaceae 4. Monograph of the genus *Actinostemon*. Phytologia 18: 213–240. 1969.

**Trees** and shrubs, monoecious, stems glabrous or puberulent, inflorescence buds enclosed in a tight series of imbricate stipule-like bud-scales; stipules lateral. **Leaves** alternate, simple, usually short-petiolate, often coriaceous or subcoriaceous, usually glabrous, margins entire, venation pinnate. **Inflorescences** terminal or axillary, solitary or 2–3/node, bisexual or unisexual, racemes with an unbranched rachis, at first subtended by imbricate deciduous bracts; ♂ flowers usually 2–3/bract, each flower borne on a thin pedicel; ♀ flowers 1 (2–3) and proximal on the rachis, borne on long pedicels. **Male flowers** minute, calyx and corolla absent, disk absent; stamens 2–16 or many, filaments free, anthers erect, ovoid, dehiscing longitudinally; pistillode absent. **Female flowers** small, calyx absent or represented by 1–3 minute lobes, corolla and disk absent, staminodes absent; ovary 3-locular, smooth or tuberculate, ovules 1/locule, styles united for a short or longer length, free and recurved distally, simple (undivided). **Fruits** capsules, glabrous to sericeous, breaking into 3 2-valved cocci, columella persisting; seeds subglobose, carunculate, endosperm fleshy, cotyledons plane and flat.

A Neotropical genus of 13 species; most species are found in southeastern South America, with outliers in Cuba, the Lesser Antilles, Venezuela, and the Amazon basin. The strobilus-like inflorescences are at first enclosed in a tight series of imbricate bracts. This, in addition to the virtually naked flowers and restriction to dry deciduous lowlands in Costa Rica, help distinguish our representative of this genus. It appears that the protection of the young floral organs by the bud-scale-like bracts compensates for the loss of a protective perianth. Webster (1994b and earlier) includes this genus in *Gymnanthes*.

**Actinostemon caribaeus** Griseb., Abh. Ges. Wiss. Göttingen 7: 168. 1857. *Excoecaria caribaea* Griseb., Fl. Brit. W. Ind. 51. 1864. *A. concolor* var. *caribaeus* (Griseb.) Müll. Arg. in DC., Prodr. 15 (2): 1193. 1868. Figure 25.

Small **trees** or shrubs 2–5 m tall, to ca. 10 cm trunk diam., leafy stems 1.4–4 mm thick, glabrous, longitudinally striate; stipules ca. 3 mm long, glabrous, quickly caducous and leaving small scars, shoot-apices covered by stipule-like glabrous bud-scales (3–7 mm long) that dry dark reddish brown and leave a circle around the



stem when they fall. **Leaves** glabrous, petioles 3–7 mm long, 0.5–2 mm thick, drying brown; **leaf blades** 5–11 cm long, 1.8–4.7 cm wide, elliptic-ovate to narrowly obovate or narrowly elliptic-oblong, apex obtuse to acute, often with a small (0.3 mm) glandular tip, margin entire and drying slightly revolute, tapering gradually to the cuneate base, slightly (0–3 mm) lobed or auriculate at the petiole, drying subcoriaceous and grayish, 2° veins 8–11/side and loop-connected distally, with usually 4 dark flat glands (0.3–0.4 mm diam.) near the base beneath. **Inflorescences** axillary or pseudoaxillary, solitary, bisexual or ♂, 1.5–4 cm long, with a single unbranched racemose axis, peduncle 1–5 mm long, with a solitary proximal ♀ flower subtended by stipule-like bracts, distal rachis 0.3–0.7 mm thick and winged, yellowish, ♂ flowers subtended by linear bracts 2–4 mm long. **Male flowers** lacking perianth (naked), borne on a pedicel 0.5–3 mm long, with 2–5 slender filaments 0.3–0.8 mm long, anthers 0.3–0.5 mm long. **Female flowers** glabrous, lacking perianth, pedicel 1–1.5 mm long and continuous with the ovary base, ovary ca. 2 mm long, 0.8 mm diam., style base 2–4 mm long (to 5 mm in fruit), style branches 3–5 mm long, papillose adaxially. **Fruits** 10–12 mm long, 9–12 mm diam., greenish in life, borne on pedicels 1–5 cm long, outer wall of cocci 0.5 mm thick, columella 7 mm long, 4 mm wide at apex; seeds ca. 6.8 × 4.5 × 3.5 mm, oblong, caruncle 1 mm high.

Plants of deciduous lowland and adjacent partly deciduous forests, 100–700 m elevation (to 1000 m in Nicaragua). Flowering in June (*Hammel 17777 CR*, *Zamora et al. 1255 CR*, F); fruiting in August (*Q. Jiménez et al. 868 CR*) and September (*Q. Jiménez 385 F*). This species has only recently been collected in northern Guanacaste Province, Costa Rica, and central Nicaragua; this species also occurs in the Lesser Antilles and northern Venezuela.

*Actinostemon caribaeus* is recognized by its lack of pubescence, often narrowly obovate leaf blades with glandular punctations in the lower lamina base, slender little inflorescences with stalked ♀ flowers and clustered ♂ flowers, and flowers lacking calyx or corolla (naked). The ♀ flower exhibits almost no differentiation between pedicel and ovary base or ovary apex and stylar column. Thus, the ♀ flowers appear as stipitate pistils. The narrowly ovoid apical buds with overlapping scales and acute apex are also distinctive. This species is closely related to *A. brachypodus* (Griseb.) Urban of Cuba and *A. concolor* (Spreng.) Müll. Arg. of southeastern Brazil and Paraguay.

#### **Adelia** Linnaeus

**Shrubs** or small trees, dioecious, branchlets often with spines (leafless short-shoots), pubescence simple, glabrescent; **stipules** small and paired at the leaf base. **Leaves**

alternate, simple, petiolate; leaf blades pinnately veined, margins entire, membranaceous to chartaceous, with tufts of hairs (domatia) in the vein axils beneath and along some of the major veins, pellucid-punctate. **Inflorescences** axillary, unisexual, ♂ flowers fasciculate on reduced short-shoots, small, pedicels slender and short to long, often articulate in the middle; ♀ flowers paired in the axils and long-pedicellate. **Male flowers** with calyx of 4–5 parts, valvate in bud, petals absent, disk extrastaminal and annular (rarely of 5 glands), adnate to the calyx; stamens 6–30, filaments free or becoming connate basally, slender, anthers versatile, dorsifixed, with parallel divergent thecae, dehiscing longitudinally, a small pistillode sometimes present at the apex of the staminal column (Croat, 1978). **Female flowers** with 5–7 narrow sepals, reflexed at anthesis, petals and staminodes absent, disk annular and pubescent; ovary usually 3-lobed and 3-locular, styles 3, free, laciniate, ovules 1/locule. **Fruits** capsular, 3-lobed, puberulent, usually separating into 3 2-valved cocci with loculicidal dehiscence; seeds mostly carunculate.

A genus of 10–12 Neotropical species, best represented in the West Indies.

**Adelia triloba** (Müll. Arg.) Hemsl., Biol. centr. amer. Bot. 3: 130. 1883. *Ricinella triloba* Müll. Arg., Linnaea 34: 153. 1866. Figure 31.

Shrubs or small trees, 3–15 m tall, trunk 12–20(–30) cm thick, leafy stems 1–3.5 m thick, minutely (0.1 mm) puberulent or glabrous, yellowish to pale gray, with small (0.3 mm) rounded lenticels, straight spines 8–22 mm long sometimes present, 1–2 mm thick at the base; **stipules** 0.5–3.5 mm long, triangular to linear-subulate, glabrous and lustrous on the exterior, deciduous. **Leaves** with petioles 3–7(–9) mm long, 0.4–1.5 mm thick, minutely puberulent or glabrous, glands absent; **leaf blades** 8–17(–23) cm long, 2.5–7(–9) cm broad, elliptic to elliptic-oblong or narrowly obovate, apex acuminate, gradually narrowed to the cuneate base, often slightly rounded at the petiole, drying chartaceous and greenish or grayish, glabrous and the major veins prominent above (dry), with whitish hairs 0.2–0.4 mm long usually along major veins beneath, 2° veins 3–6/side, vein axils often lined by hairs (domatia) beneath. **Male flowers** in fascicles of up to 50 flowers, bracts to 2 mm long, pubescent at the base, pedicels 3–10 mm long, slender, minutely puberulent, flower buds ca. 2 mm diam., globose; sepals 4–5, 2–2.5 mm long, pale yellowish; stamens 6–30, staminal column short or not apparent, filaments 0.5–1.8 mm long, filiform, anthers 0.4 mm long, 0.5–0.6 mm broad. **Female flowers** pendulous on slender pedicels 1–3 cm long (to 7.5 cm in fruit), 0.3–0.5 mm thick, glabrous or minutely puberulent, sepals 4–6, 3–6 mm long, 0.5–1 mm broad; ovary ca. 2 mm long, 2.5–3 mm wide, 3-lobed, densely puberulent with erect hairs 0.1–0.2 mm long, styles 1.5–3 mm long, laciniate distally. **Fruits** 6–9 mm long, 8–12 mm wide, oblate and slightly to deeply 3-lobed distally, pubescent, pendulous on the slender pedicels, splitting from the top, persisting columella 3–4.2 mm long, 0.7 mm thick, expanded at apex; **seeds** 3.8–5 mm long, subglobose, with or without a mottled color surface, smooth, with a linear longitudinal raphe.



Plants of evergreen and partly deciduous forest formations of both the Pacific and Caribbean slopes, 10–1000 m elevation. Flowering in December–February; fruiting in January–April. The species ranges from southern Nicaragua to eastern Panama.

*Adelia triloba* is recognized by the spiny stems (when present), fruits pendulous on long slender pedicels, persisting columella, the fasciculate ♂ flowers, leaves with pubescent little domatia, and restricted flowering/fruiting period. In addition, the leaves are short-petiolate and pellucid-punctate. Some collections have distinctively long (15–20 cm) narrow (ca. 6 cm) leaf blades. The plants are called *espino de playa* in Nicaragua. This species is closely related to *Adelia barbinervis* Schldl. & Cham. (Mexico to Nicaragua), but that species lives in seasonally dry deciduous and open secondary forests and has smaller leaves than *A. triloba*, and the fruits are not deeply lobed.

#### **Adenophaedra** (Müller Argoviensis) Müller Argoviensis

**Shrubs** or small trees, dioecious, hairs simple, sap not milky; stipules paired at the leaf base. **Leaves** alternate, simple, petiolate, pinnately veined, entire or dentate with gland-tipped vein endings, with laminar glands. **Inflorescences** axillary or terminal, 1–3/node, spiciform, bracts without glands, subtending 1 ♀ flower or several closely congested ♂ flowers, flowers pedicellate. **Male flowers** globose in bud, sepals 3, valvate in bud, petals absent, disk absent; stamens 2–3, alternate with sepals, filaments very short, anthers ovate, dehiscing longitudinally and introrse, connective enlarged distally; pistillode absent or minute. **Female flowers** with 6 sepals in 2 series, interior whorl smaller, imbricate in bud, petals absent, staminodes absent, disk annular and 3-lobed; ovary 3-lobed, 3-locular, style short or minute with broad sessile stigmas, ovules 1/locule. **Fruits** capsular, prominently 3-lobed, depressed at the apex, separating into 3 2-valved cocci; seeds globose, ecarunculate, surfaces smooth.

A genus of three South American species with one reaching central Costa Rica. The pendulous unisexual spike-like inflorescences, minute ♂ flowers with few subsessile stamens, and ♀ flowers with six imbricate sepals and broad sessile stigmas help distinguish the genus.

**Adenophaedra grandifolia** (Klotzch) Müll. Arg. in Mart., Fl. Bras. 11 (2): 386. 1874. *Tragia grandifolia* Klotzsch, London J. Bot. 2: 46. 1843. *Bernardia grandifolia* (Klotzsch) Müll. Arg., Linnaea 34: 173. 1865. *Cleidion denticulatum*

Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 218. 1929. *Bernardia denticulata* (Standl.) Webster, Ann. Missouri Bot. Gard. 54: 200. 1967. Figure 13.

**Shrubs** or small trees, 2–6(–8) m tall, leafy stems 1–6 mm thick, with stiff ascending hairs 0.2–0.5 mm long, glabrescent, becoming dark reddish brown; **stipules** 3–13 mm long, 1–2 mm wide at the base, oblong to narrowly lanceolate, densely strigose to glabrous, deciduous. **Leaves** with petioles 5–18 mm long, 1.3–2.3 mm thick, strigose and glabrescent; **leaf blades** (10–)18–33 cm long, (2–)5–13 cm wide, narrowly obovate-oblong to oblanceolate or elliptic-oblong, apex short-acuminate or caudate-acuminate, narrowed tip 4–14 mm long, margins dentate with 19–28 teeth/side (entire along basal third), teeth 0.5–1 mm high, tapering gradually to a cuneate base with the margin sometimes thickened near the base, flat rounded imbedded glands often present near the lamina base adaxially, drying stiffly chartaceous to subcoriaceous, with thin whitish hairs ca. 0.5 mm long on the upper surface and glabrescent, with hairs 0.2–0.5 mm long beneath, 2° veins 7–11/side. **Male inflorescences** axillary, 1–3, ♂ to 26 cm long with up to 60 glomerules separated by 4–12 mm and with 2–6 flowers/glomerule, fallen flowers leaving stiff persistent pedicels to 1 mm long; ♂ flower buds ca. 0.7 mm diam., 0.5 mm long, sepals 0.8 mm long, 0.6 mm broad at the base, with sharp straight hairs on the outer surface, glabrous within; stamens 3, subsessile, anthers 0.2 mm broad. **Female inflorescences** to 12 cm long with 4–7 flowers, rachis densely hirsute or strigose with stiff whitish hairs 0.2–0.4 mm, bracts 1–1.5 mm long; ♀ flowers with perianth parts ca. 2.2 mm long, 2 mm wide at the base, outer surface with stiff ascending hairs, stigmas ca. 0.5 mm long and equally broad. **Fruits** 6–9 mm long, 13–18 mm broad, deeply 3-lobed, borne on peduncles to 5 mm long, cocci ca. 12 × 8 mm, columella 3–6 mm long, to 7 mm broad distally, with winged erose axis; seeds 7–9 mm long, 6.3–7.5 mm wide, oblong, smooth, with mottled coloring.

Plants of wet evergreen cloud forest formations of the Caribbean slope, (100–)300–900 m elevation. Possibly flowering throughout the year; fruiting in December–May. This species ranges from central Costa Rica (83°28'W) to Venezuela.

*Adenophaedra grandifolia* is recognized by the larger oblanceolate leaves on short thick petioles, gland-tipped dentate leaf margin, unisexual spiciform inflorescences, and minute flowers. Compare the superficially similar *Caryodendron angustifolium*.

#### **Alchornea** Swartz

**Trees** or shrubs, dioecious in Central American species, glabrous or puberulent with simple or stellate hairs; stipules free, small or obscure. **Leaves** alternate, simple, petioles usually thickened near the blade; leaf blades

usually dentate with small rounded teeth, venation pinnate or palmate (tripliveined), usually with glands in the leaf tissue near the base, domatia present or absent. **Male inflorescences** axillary, 1–3/node, spicate or with simple lateral branches, ♂ flowers many, subsessile or short-pedicellate on the spicate axes, bracts subtending 1–6 flowers; ♂ flowers with perianth globose to oblate in bud, splitting into (2–)3–4(–5) valvate calyx lobes, petals absent, disk absent or confluent with stamen bases, stamens usually 8 in Central America, in 2 whorls of 4, filaments free, usually shorter than the anthers, anthers oblong and dorsifixed, dehiscent longitudinally, introrse; pistillode absent. **Female inflorescences** axillary or terminal, usually 1/node, usually spicate with an unbranched rachis or sometimes with a few basal branches, bracts usually subtending solitary (2–3) flowers, pedicels short or absent; ♀ flowers with usually 4 (3–6) imbricate sepals, petals absent, staminodes absent, disk absent; ovary with 2 (3–4) locules, ovules 1/locule, styles 2 (3–4), united

only near the base, style branches rarely bifid at apex. **Fruits** capsules with fleshy exterior, globose, usually splitting into 2 2-valved cocci, columella present but caducous; seeds tuberculate, ecarunculate, with prominent ventral raphe, endosperm present, cotyledons straight.

A pantropical genus of ca. 50 species. The genus is distinguished by its dioecious plants, flat rounded glands near the lamina base, frequent presence of domatia in vein axils, and subsessile flowers and fruits on long slender few-branched axes. The inflorescences are either simple and spiciform or panicle-like with spiciform branches. Individual collections vary considerably within species, and this often makes identification difficult.

### Key to the Species of *Alchornea*

- 1a. Largest leaves < 6 cm long (in Costa Rica) [subcoriaceous and glabrous, rounded or bluntly acute distally, venation tripliveined or pinnate; rarely collected from 900 to 1900 m in Costa Rica and Panama] ..... *A. triplinervia*
- 1b. Largest leaves > 6 cm long ..... 2
- 2a. Leaves drying chartaceous, grayish green to dark green ..... 3
- 2b. Leaves drying coriaceous or subcoriaceous, often yellowish or dark gray [venation pinnate or subpalmate] ..... 4
- 3a. Venation pinnate, basal 2° veins not prominent and not reaching the middle of the blade, leaf blades usually elliptic to oblong; young stems glabrous; 0–800 m elevation .. *A. costaricensis*
- 3b. Venation palmate or subpalmate, basal 2° veins prominent and reaching the center of the blade, leaf blades usually ovate to ovate-elliptic; young stems densely puberulent; 500–1200 m elevation ..... *A. glandulosa*
- 4a. Leaf blades 5–24 cm wide, usually broadly ovate to oblong (elliptic-oblong in the lowlands); style branches to 0.6 mm wide; commonly collected in Central America, 40–2300 m elevation ..... *A. latifolia*
- 4b. Leaf blades 2–7.5 cm wide, usually narrowly ovate; style branches to 1 mm wide; rarely collected in Central America at 1600–2200 m elevation ..... *A. grandiflora*

***Alchornea costaricensis*** Pax & K. Hoffm., Pflanzenreich 4. 147. 7: 235. 1914. *A. costaricensis* f. *longispicata* Pax & K. Hoffm., Pflanzenreich 4. 147. 14: 20. 1920. Figure 12.

**Trees** 4–15(–27) m tall, trunks usually less than 30 cm diam. (to 70 cm), branchlets terete and glabrous; stipules to 0.5 mm long, triangular. **Leaves** with petioles 13–35 (80) mm long, 0.7–1.5 mm thick, to 1.8 mm thick near the blade, glabrous or minutely papillate-puberulent; **leaf blades** 7–18 cm long, 3–6.5 cm wide, elliptic to ovate-elliptic or elliptic-obovate, apex long-acuminate, tip 1–3 cm long, margin prominently serrate with teeth 5–15 mm apart, base acute to obtuse, glands often on the edge at the base, drying chartaceous, glabrous above, glabrous or minutely (0.05 mm) papillate-puberulent beneath, venation pinnate, 2° veins 5–8/side. **Male inflorescences** 1–3/axil, 4–8 cm long, unbranched spikes (rarely with

short basal branches), rachis 0.3–0.5 mm thick, minutely stellate puberulent, flowers in sessile glomerules of 2–5; ♂ flowers white or yellowish, buds 1.2–1.5 mm diam.; filaments short (0.3 mm) and untied at base, anthers 0.5–0.6 mm long, 0.4 mm wide. **Female inflorescences** 1/axil, 2–5(–10) cm long, unbranched (or branched when distal leaves fail to develop), rachis 0.5–0.7 mm thick, minutely puberulent; ♀ flowers solitary, subsessile, calyx lobes 4, ca. 1 mm long, ovary 1–1.5 mm long, 0.7–1 mm diam., densely puberulent, styles 7–10 mm long, ca. 0.4 mm thick. **Fruits** 5–7 mm long, 6–9 mm wide, rounded and bilobed, pinkish green to reddish brown, pedicels to 3 mm long; seeds 4–6 mm diam., subglobose, surface irregularly rugose.

Plants of lowland rain forest formations, 0–800 m elevation. Flowering in January–June; fruiting in March–July. This species ranges from the Ca-

ribbean coast of Honduras to eastern Panama and Colombia.

*Alchornea costaricensis* is distinguished by its chartaceous serrate glabrescent leaves with pinnate venation, simple (rarely branched)  $\delta$  spikes, and lowland habitat. It has been called *fosforo* in Costa Rica. This species is similar to *A. glandulosa*, but that species has palmate venation and 3° veins that are more prominent and often conspicuously parallel. Specimens of two tall (27 m) trees from mangrove forest in Honduras appear to be this species (*Saunders 914 & 931*). These plants are easily mistaken for species of *Sorocea* (Moraceae).

***Alchornea glandulosa*** Poepp. in Poepp. & Endl., Nov. gen. sp. Pl. 3: 18, t. 221. 1841. *A. pittieri* Pax, Bot. Jahrb. Syst. 33: 291. 1903. *A. glandulosa* var. *pittieri* (Pax) Pax, Pflanzenreich IV. 147. VII (Heft 63): 235. 1914. Figure 24.

Trees 8–22 m tall, leafy stems 1.5–5 mm diam., densely hirsutulous with short (0.1–0.3 mm) simple and stellate hairs; stipules 0.5–1.5 mm long, hirsutulous. Leaves with petioles 1.3–5(–7) cm long, 0.7–1.5 mm thick, ca. 1.9 mm thick near the apex, stellate hirsutulous; leaf blades 5–16.5 cm long, 2–9 cm wide, ovate-elliptic to elliptic, ovate or narrowly ovate, tapering gradually to the acuminate apex, tip 4–17 mm long, marginal teeth 8–17/side, rounded, base obtuse to rounded and slightly subcordate, with 2–6 flat rounded glands in the blade near its base, drying chartaceous, glabrescent above except for small hairs on the midvein, minutely (0.1 mm) stellate-puberulent beneath, with tufted domatia in major vein axils beneath, venation palmate with basal 2° veins reaching the middle of the blade, distal 2° veins 2–3/side, 3° veins subparallel. Male inflorescences 5–12 cm long, spicate or with lateral branches to 4 cm long, rachis 0.5–0.8 mm diam., glomerules with 2–5 subsessile flowers;  $\delta$  flower buds 1.2 mm diam., anthers ca. 0.5 mm long. Female inflorescences 4–17 cm long, unbranched spikes (rarely branched), rachis 0.6–1 mm thick, stellate-puberulent, flowers sessile and solitary;  $\eta$  flowers with calyx lobes ca. 0.5 mm long, ovary 1.5–2 mm long, 1.2–2.2 mm diam., ovoid, densely white or yellowish stellate-pubescent, styles 5–7 mm long, 0.3–0.4 mm thick; puberulent along abaxial side. Fruits 5–6 mm long, 7–8 mm wide, bilobed, becoming dark; seeds with reddish covering.

Plants of evergreen lower montane forest formations; 500–1500 m elevation. Flowering occurs in January–March and September–October; fruiting in October–December. This species ranges from Costa Rica to the Amazon basin.

*Alchornea glandulosa* is recognized by the chartaceous ovate leaves with as many as six small glands imbedded in the blade near the base, stellate-pubescent young stems, and mid-elevation

habitats. Collections from Costa Rica and Panama belong to variety *pittieri*, distinguished by smaller glands than those found in typical South American collections.

***Alchornea grandiflora*** Müll. Arg., Linnaea 34: 170. 1865.

Trees 6–25 m tall, leafy stems 1.6–5 mm thick, with scattered minute (0.05–0.1 mm) flat stellate hairs, glabrescent and drying dark; stipules 0.5–1 mm long, triangular. Leaves with petioles 17–65 mm long, 1–2 mm thick, glabrous and drying dark; leaf blades 5–13 cm long, 2–7.5 cm wide, broadly elliptic to ovate, apex obtuse, marginal teeth 7–11/side, prominent, base cuneate to obtuse, margin often recurved near the petiole, drying subcoriaceous, glabrescent above and below, venation palmate with basal 2° veins reaching middle of the blade, distal 2° veins 3–4/side, 3° veins prominent and subparallel, basal vein axils forming cavities beneath, distal vein axils with tufted domatia. Male inflorescences 2–11 cm long, with lateral branches 1–4 cm long, central rachis 0.5–1 mm thick, bracts ca. 1 mm long;  $\delta$  flower buds 1.5–2 mm diam., calyx lobes ca. 1 mm long, triangular, glabrous except on edge, stamens 6–8. Female inflorescences 4–6 cm long, unbranched, rachis 0.6–1.4 mm thick, with ca. 6–12 flowers,  $\eta$  flowers with calyx lobes to 1.8 mm long, acute, ovary 1.5–2 mm long, densely pubescent, style branches 4–18 mm long, ca. 1 mm wide. Fruits 6–7 mm long, ca. 8 mm wide, bilobed, columella ca. 5 mm long, 0.8 mm broad.

Plants of montane and lower montane evergreen forest formations, 1600–2200 m elevation in Panama (400–2300 m in South America). Flowering in June–July in Panama. This species is said to range from Costa Rica to Bolivia (see below).

*Alchornea grandiflora* is recognized by its  $\eta$  flowers with thick style branches, larger fruits, stiff glabrous leaves with prominent domatia, and unusual leaf bases. In larger leaves, the basal secondary veins have deep depressions in their axils and the leaf margin is revolute. We have not seen material from Costa Rica, but a syntype (*Hoffman 530 G*) was collected in Costa Rica and several collections are cited from Panama (Webster & Huft, 1988). This species can be mistaken for *A. latifolia*, but that species tends to grow at lower elevations in southern Central America.

***Alchornea latifolia*** Sw., Prodr. 98. 1788. Fl. Ind. Occ. 2: 1154, t. 24. 1800. *A. platyphylla* Müll. Arg., Linnaea 34. 171. 1865 (fide Standl. 1937 who may not have seen the type: *Oersted*, Tacaca, Centr. Amer., herb. B). *A. cyclophylla* Croizat, J. Arnold Arbor. 24: 166. 1943. Figure 24.

Trees 6–25 m tall, trunks to 45 cm diam., leafy stems 2–7 mm thick, glabrous or with minute (0.1 mm) scurfy



hairs; stipules 1 mm long and triangular or obscure. **Leaves** with petioles 2.5–8(–13) cm long, 1.5–2.7 mm thick, to 4 mm thick below the blade, usually glabrous, drying dark, glands absent on the petiole but 2–4 glands present in the leaf tissue near the base of the blade; **leaf blades** 8–24(–34) cm long, 5–19(–24) cm wide, ovate to ovate-oblong or ovate-orbicular (elliptic-oblong at lower elevations), apex rounded to obtuse, with a small (0–5 mm) acuminate tip, marginal teeth 8–20/side, 1–2 mm high, base obtuse to rounded and truncate or subcordate, drying coriaceous, glabrous above, glabrous or with scattered minute (0.05 mm) flat stellate hairs beneath, venation palmate or subpalmate (pinnate at lower elevations), basal 2° veins reaching middle of blade (at higher elevations), 2° veins 5–7/side, 3° veins subparallel, tufted domatia or gland-like areas sometimes present in the leaf axils. **Male inflorescences** to 30 cm long, paniculate with few to many alternate unbranched lateral branches 1–9 cm long, rachis 1.2–2.2 mm thick, glomerules with 3–7 flowers; ♂ flower buds ca. 1.5 mm diam., anthers 0.8–1.2 mm long, 0.6–0.8 mm wide. **Female inflorescences** 5–20(–50) cm long, unbranched or with few to many branches to 15 cm long, rachis 2–3 mm thick, minutely stellate puberulent, bracts to 1 mm long, triangular, pedicels 0.5–1.5 mm long; ♀ flowers with calyx lobes ca. 1 mm long, acute, sparsely and minutely puberulent, ovary 1.5–2.5 mm long, 1–2 mm diam., style column 2–3 mm long, style branches 7–11 mm long, 0.4–0.5 mm wide, white. **Fruits** 5–7 mm long, 7–11 mm wide, bilobed, becoming red; seeds 5–6 mm long.

Plants of lower montane evergreen forest formations, (40–)300–1600(–2300) m elevation. Flowering in January–July; fruiting in March–September. This is the most commonly collected species of *Alchornea* in Costa Rica, with most specimens from above 800 m elevation. This species ranges from Mexico and the West Indies to Venezuela and Peru.

*Alchornea latifolia* is distinguished by its larger broad coriaceous leaves, larger paniculate ♂ inflorescences with spike-like distal branches, and rounded fleshy fruits terminated by two persisting style branches. The highland collections with their broadly ovate leaves, subpalmate venation, and usually simple ♂ inflorescences differ strikingly from specimens collected below 500 m elevation with elliptic-oblong leaves, pinnate venation, and ♂ inflorescences with many lateral branches. There appears to be an altitudinal cline in southern Central America, with specimens from 500 to 900 m being intermediate between the highland and lowland collections, but this pattern may be obscured by considerable individual variation.

*Alchornea triplinervia* (Sprengel) Müll. Arg. in DC., Prodr. 15 (2): 909. 1866. *Antidesma triplinervium* Sprengel, Neue Entdeck 2: 116. 1821. *A. guatemalensis* Lundell, Wrightia 6: 10, pl. 20. 1978.

**Trees** 6–20 m tall, leafy stems 1.5–5 mm thick, essentially glabrous; stipules rudimentary. **Leaves** with petioles 8–22 mm long, 0.7–1.3 mm thick, slightly thickened at apex and base, glabrous; **leaf blades** 3–6 cm long, 2–3 cm wide, broadly elliptic-oblong to elliptic-obovate, apex rounded to bluntly acute, margin entire or with 4–5 small rounded teeth, base rounded to obtuse, with 2–6 round flat glands near the base, drying subcoriaceous and grayish, glabrous above and below, venation pinnate with prominent basal 2° veins but these not reaching the middle of the blade, 2° veins 3–5/side. **Male inflorescences** to 10 cm long, with lateral branches to 3.5 cm long, rachis 0.5–1 mm thick, stellate-puberulent, glomerules with 1–4 sessile flowers; ♂ flower buds 1–1.5 mm diam., anthers ca. 0.8 mm long. **Female inflorescences** to 8 cm long, rachis 0.6–0.8 mm thick, with minute stellate or scurfy hairs, bracts 0.5 mm long; ♀ flowers solitary, calyx 1.2–1.8 mm long, lobes 0.8–1 mm long, glabrous, ovary 1–1.5 mm long, 0.6–1 mm diam., with minute stellate hairs, style branches 3–7 mm long, 0.4–0.5 mm thick. **Fruits** ca. 3 mm long, to 5.5 mm wide.

Rarely collected plants of montane (1600–1900 m) forests in Costa Rica but from lower (500–900 m) elevations in Guatemala and Panama. Flowering in June–September; fruiting in September. In Costa Rica, the species is only known from near Desamperados, Altos de Tablazo (*Utley & Utley 3039 & 5209 F*), and Monteverde (*Haber 551 CR, F*). It is also known from a single collection in Guatemala (*Lundell & Contreras 21201 F*, isotype of *A. guatemalensis*) and several collections from Panama. The species ranges to eastern Brazil.

*Alchornea triplinervia* is recognized by its small stiff glabrous leaves with three prominent basal veins, short ♀ sepals, and restricted habitat. The decision to place these few Central American collections under *A. triplinervia* and to submerge *A. guatemalensis* should be considered tentative.

### *Alchorneopsis* Müller Argoviensis

**Trees**, often becoming part of the forest canopy, dioecious, hairs simple; stipules absent. **Leaves** alternate, simple, petioles with slightly thickened tissue at base and apex, blades with flat glands near the base, entire or subentire, venation tripliveined, pit domatia sometimes present in the vein axils beneath. **Inflorescences** axillary, 1–3/axil, unisexual, spiciform with long slender unbranched rachis, flowers or glomerules not crowded along the rachis, subtended by minute bracts; ♂ flowers in alternate glomerules of 1–5 pedicellate flowers, ♀ flowers solitary or few along the rachis, pedicellate. **Male flowers** small, globose in bud, calyx splitting into 3–4 valvate parts, petals absent, disk large and annular, hirsutulous; stamens 4–8, often 6 in 2 whorls, filaments free, anthers dehiscent longitudinally and introrse, outer thecae valves larger than the inner, connective enlarged and glandular; pistillode minute, 3-lobed, glabrous. **Female flowers** small, sepals 4–5, petals absent, disk annular (often difficult to

see), hirsutulous and merged with the base of the ovary, staminodes absent; ovary 3-locular, ovules 1/locule, style column short, style branches 3, recurved and undivided, papillate. **Fruits** capsular, small, rounded and breaking into 3 cocci split only at the apex, columella persistent or not; **seeds** flattened, ecarunculate, outer coat fleshy, inner coat striate-reticulate, cotyledons broad and flat.

A tropical American genus of three closely related species. The genus is very similar in appearance to *Alchornea*, but it lacks the stellate hairs of *Alchornea*. In addition,  $\delta$  inflorescences of *Alchorneopsis* are never branched and the  $\delta$  flowers have a small pistillode. Seeds of the two genera are very different, and the three short styles of *Alchorneopsis* differ from the typically two long styles of *Alchornea*.

**Alchorneopsis floribunda** (Benth.) Müll. Arg., *Linnaea* 34: 156. 1865. *Alchornea glandulosa* var. *floribunda* Benth., Hooker's J. Bot. Kew Gard. Misc. 6: 331. 1854. Figure 24.

**Trees** (3–)10–40 m tall, trunks to 1 m dbh, brownish with vertical fissures, leafy stems 1.5–3.5 mm thick, minutely (0.05–0.1 mm) puberulent, glabrescent and pale brown to dark gray; stipules none. **Leaves** with petioles 10–42 mm long, 0.8–2 mm thick, usually glabrous, slightly thickened and drying darker near the base and apex; **leaf blades** 7–18 cm long, 2–7 cm wide, elliptic, elliptic-oblong or oblong-obovate, apex short-acuminate with blunt tip 4–10 mm long, cuneate to acute at the base, margin crenate with 6–12 gland-tipped lobes 0.3–1 mm high, drying stiffly chartaceous to subcoriaceous, glabrous above and below or very minutely puberulent on the midvein, 2° veins 2–4/side with the basal pair strongly ascending and reaching beyond the middle of the blade, 3° veins subparallel and mostly perpendicular to the midvein, flat rounded glands sometimes present near the base, narrow slit-like pit domatia (0.5–1.2 mm long) sometimes present in the basal vein axils beneath. **Male inflorescences** 5–14 cm long, rachis 0.5–0.8 mm thick and minutely puberulent, with alternate fascicles of 1–7 flowers on pedicels 1–2 mm long, subtended by bracts ca. 0.5 mm long;  $\delta$  **flowers** white to pale yellowish green, ovoid in bud and 1.1–1.3 mm long, sepals 1.1–1.5 mm long, reflexed, sparsely puberulent on the exterior, glabrous on the interior, disk 0.3–1 mm high including the erect whitish or yellowish hairs; stamens usually 6, filaments 0.7–1.8 mm long, slender, anthers 0.3–0.6 mm long; pistillode 0.4–0.6 mm long, 3-parted, hidden within the hairs. **Female inflorescences** 4–6 cm long, usually 1/axil, rachis ca. 0.6 mm thick, minutely puberulent, pedicels ca. 1 mm long, densely puberulent;  $\varphi$  **flowers** with sepals 0.3–0.9 mm long, triangular, ovary ca. 2  $\times$  1.8 mm, minutely pubescent, style column ca. 0.2 mm long, style branches ca. 0.6 mm long. **Fruits** ca. 4 mm long, 3–3.5 mm diam., subglobose, smooth and rounded, splitting into 3 cocci

ca. 3 mm broad; **seeds** often adhering to each other, 2.2–2.4 mm long, 2.1–2.5 mm broad, ca. 1.2 mm thick, ovoid-lenticular, pale yellowish, abaxial surface with 10–12 longitudinal ridges, with a red aril-like seed coat.

Large trees in lowland evergreen rain forest formations on both Caribbean and Pacific slopes, 5–500 m elevation. Flowering in January–August; fruiting in March–October. The species ranges from northern Costa Rica to Peru and Brazil.

*Alchorneopsis floribunda* is recognized by its tripliveined gland-tipped crenate leaves, long slender unbranched axillary inflorescences with distant flowers or clusters of flowers, and unusual seeds. Additional characters are the longer petioles drying darker near apex and base and the occasional presence of pit domatia. These trees can become part of the forest canopy.

**Aleurites** Forster & G. Forster

**Trees**, monoecious, with simple or stellate hairs, sap milky; stipules paired at the node or poorly developed, caducous. **Leaves** alternate, simple, petioles long and with 2 glands at the apex, blades of the young treelets or early branches often with large lobes, margins entire or with minute glands or poorly developed serrations (or sinuses), venation palmate or pinnate. **Inflorescences** terminal or axillary, open-branched panicles of few-flowered cymes (thyrsiform), bisexual with proximal flowers mostly  $\delta$  and distal or terminal flowers  $\varphi$ , pedicels short. **Male flowers** with a united calyprate calyx splitting into 2–3 parts at anthesis, petals 5, longer than the sepals, imbricate, narrowed at the base, disk 5-lobed; stamens 5–20, from a conical receptacle in 1–4 series, outer 5 stamens opposite the petals and alternating with glandular lobes of the disk; pistillode absent. **Female flowers** with perianth similar to  $\delta$  but caducous, staminodes absent; ovary with 2–5 locules, ovules 1/locule, styles 2–5, divided to near the base. **Fruits** drupaceous or a dehiscent 2–5-seeded nut, usually with fleshy exocarp and bony endocarp.

A genus of six species of China, Southeast Asia, Malaysia, and the western Pacific. However, *Aleurites* has also been interpreted as a genus of only two species (cf. Webster, 1994b, p. 114). A number of species are now grown throughout the tropics and subtropics for the seeds, which produce drying oils. Two species are commonly planted in Latin America. Larger leaves of young plants are often deeply lobed. The paired glands at the apex of the petiole, palmate venation, spatulate petals, and drupaceous fruits help distinguish the genus.

1a. Puberulence of simple hairs, usually sparse; flower buds 8–12 mm long, glabrous; ovary 3–5-locular ..... *A. fordii*



- 1b. Puberulence of scurfy stellate hairs, often dense; flower buds 2–4 mm long; ovary 2-locular . . . . .  
 . . . . . *A. moluccana*

**Aleurites fordii** Hemsl. in Hook., Icon. Pl. 29: 2801–2802. 1909.

Trees to 8(–15) m tall, much branched, with smooth pale gray bark, leafy stems 3–7 mm thick, glabrous or with few thin hairs to 1 mm long, drying dark with pale lenticels ca. 1 mm long; stipules 2–4 mm long, caducous. **Leaves** deciduous, petioles 7–16 cm long, 1.2–4.8 mm thick, glabrous, glands 1–4 mm long, 1–3 mm broad, sessile or stalked, base of dried petiole often contracted for 3–6 mm; **leaf blades** 7–17(–24) cm long, 4–14(–23) cm wide, ovate or with 3 or 5 prominent lobes (sinuses to 6 cm deep), apex acuminate, margin entire to slightly undulate, base rounded and truncate to subcordate, glabrous and deep green above, glabrous or with thin yellowish hairs to 1 mm long beneath, venation palmate with 3–5 major veins, 2° veins 5–8/side of the midvein. **Inflorescences** dichotomously branched with distal cymes, with relatively few flowers, to 12 × 18 cm, glabrous, central terminal flower ♀ with the others usually ♂. **Flowers** white, ♂ calyx 3–5 mm long, ♀ calyx 8–12 mm long, petals 5–17 mm long, to 6 mm wide, spatulate, marked with pink, with many parallel veins, filaments 12–16 mm long, anthers ca. 2 mm long. **Fruits** 4–6 cm long, 5–7 mm diam., subglobose to ovoid, becoming dark brown, 5-locular.

*Aleurites fordii* originated in western China; it is found in gardens or special plantings in Central America. The seeds are the source of tung oil, a rapidly drying oil that is used for outside protective paints and waterproofing. The seeds average 50% oil; residue seed cake (from oil-extracted seeds) is toxic but has been used as a fertilizer. *Aleurites montana* is similar and originated in the subtropical areas of China and Burma; it is better adapted to the moist tropics than is *A. fordii*.

**Aleurites moluccana** (L.) Willd., Sp. Pl. ed. 4: 590. 1805. *Croton moluccanum* L., Sp. Pl. 1005. 1753. *A. triloba* J. R. Forster, Char. gen. pl. ed. 2, 112. 1776.

Trees 6–20 m tall, with spreading or pendulous branches, wood pale and weak, leafy stems 4–10 mm thick, densely covered with scurfy-stellate hairs 0.2 mm broad, becoming pale grayish; stipules ca. 5 mm long, narrowly triangular, caducous. **Leaves** with petioles 5–22 cm long, 1.8–5 mm thick, glabrescent, apical adaxial glands ca. 1.3 mm wide, disk-like or shallow cups; **leaf blades** 10–23(–30) cm long, 6–17(–27) cm wide, narrowly to broadly ovate, ovate-triangular or with 1–2 large (2–3 cm) lobes on each side, apex acute to subacuminate, rounded and truncated at the base, edge with minute glands in shallow (0.3 mm) sinuses, very sparsely puberulent above, with minute (0.2 mm) stellate hairs beneath, venation palmate with 3 or 5 major veins (subpalmate in smaller leaves), 2° veins 4–6/side. **Inflores-**

cences 6–16 cm long, to 17 cm wide, widely branching with flowers in distal cymes, densely pubescent with scurfy-stellate hairs, ♂ flowers many, ♀ flowers few. **Flowers** densely pubescent, buds ca. 3 mm long, petals 5–6 mm long, 1.3–2.2 mm wide, obovate-oblong; stamens 15–20 (in ♂); ovary ca. 3 mm long, ovoid, densely stellate-pubescent, styles 0.5–1 mm long. **Fruits** 3–6 cm diam., subglobose-oblate to ellipsoid, covered with a dense indumentum of appressed stellate hairs 0.1–0.2 mm wide, olive-green with whitish flesh.

*Aleurites moluccana*, native to south Asia and the western Pacific, is now widely cultivated in tropical regions. It is well adapted to humid tropical environments where *A. fordii* does not grow as well. Though poisonous, the seed is used for making soap and paint. The species is also used as an ornamental and shade tree, appearing whitish from a distance. It is called *nuez* and “candle-nut tree.” (See fig. 324 in Correll & Correll, 1982.)

## Amanoa Aublet

REFERENCE—W. J. Hayden, Notes on Neotropical *Amanoa* (Euphorbiaceae). Brittonia 42: 260–270. 1990.

Trees or shrubs, monoecious, glabrous, heartwood reddish to purple-brown, moderately to very dense; **stipules** intrapetiolar, united above the upper (adaxial) base of the petiole and forming an oblique-decurrent ligule-like structure, persistent. **Leaves** alternate, simple, short-petiolate, without glands, blades subcoriaceous and entire, pinnately veined. **Inflorescences** basically of solitary axillary fascicles or glomerules but these more often alternate on leafless axes that appear spicate or paniculate (with alternate lateral branches), flowers sessile and subtended by a loose involucre of many imbricate small bracts (the bracts larger in African species). **Male flowers** with 5 unequal imbricate sepals, usually larger than the small scale-like petals, disk inconspicuous, extrastaminal, lobed; stamens 5, opposite the petals, filaments free, shorter than the anthers, anthers ovoid, dehiscing longitudinally and introrse; pistillode 3-lobed distally. **Female flowers** with 5 sepals, imbricate and subequal, petals small and often scale-like, disk small and 5-lobed, staminodes absent; ovary 3-locular, globose, ovules 2/locule, styles short and united, stigmas 3, thick and bifid, reflexed. **Fruits** woody capsules or drupe-like, surface muricate, endocarp usually thick, tardily dehiscent into 3 (2, 1) 2-valved cocci, columella large and persisting; **seeds** 1/locule, ovoid to ellipsoid, smooth and ecarunculate, endosperm little or none, cotyledons massive.

A small genus with 13 species in tropical America and 3 in Africa-Madagascar. Only one species



is known to occur in southern Central America. The two ovules per locule place the genus in subfamily Phyllanthoideae.

**Amanoa guianensis** Aublet, Hist. pl. Guiane Fr. 256, t. 101. 1775. *A. potamophila* Croizat, Amer. Midl. Naturalist 29: 475. 1943. *A. macrocarpa* Cuatrecasas, Brittonia 11: 164. 1959. Figure 27.

**Shrubs** or small trees, 2–7 m tall, leafy stems 2–6 mm thick, glabrous, brownish, often with elevated lenticels 0.5–1.5 mm long; **stipules** 0.7–2 mm long, broadly rounded above the adaxial petiole base, reddish brown, persisting. **Leaves** with petioles 4–8 mm long, 0.8–2.5 mm thick, drying dark, glabrous; **leaf blades** 7–14 cm long, 2.5–7 cm wide, elliptic, elliptic-oblong, oblong or obovate, gradually or abruptly narrowed to the short-acuminate apex, base obtuse to rounded or subtruncate, drying subcoriaceous and dark grayish brown, glabrous, 2° veins 7–9/side, arising at angles of 60–80°, weakly loop-connected 5–9 mm from the leaf edge. **Inflorescences** of axillary fascicles or the fascicles often on a leafless terminal stem-like rachis to 16 cm long, unbranched or with 1–2 lateral branches, fascicles separated by 4–12 mm along the rachis, subtended by an involucre of bracts 5 × 8 mm, distal rachis 1.5–3 mm thick, glabrous, bracts ca. 2 × 2 mm. **Male flowers** with sepals 7–9 mm long, ovate, thick, petals 0.7–1 mm long, disk 1.1–1.4 mm diam., cupulate; anthers ca. 5 mm long; pistillode ca. 5 × 2.5 mm, 3-lobed. **Female flowers** with sepals 7–9 mm long, ovate-oblong, petals 1.5–1.7 mm long, 2–2.3 mm wide, suborbicular, minutely denticulate; pistil 2.5–5 × 2–2.5 mm, ovary and thick stylar column not differentiated, stigmas ca. 1.3 × 1.8 mm, sessile, obscurely 2-lobed. **Fruits** 2–3 cm long, 2.5–3 cm diam., subglobose, slightly compressed at base and apex, borne on a thickened pedicel 3–15 mm long, splitting into 3–6 woody parts, outer wall 3–4 mm thick, columella 15 mm long, 7 mm wide; **seeds** 15 × 13 × 9 mm, cordate-triangular in outline, smooth and lustrous, scar 3 × 2 mm.

Plants of lowland seaside forest formations and swamp forests, 0–150 m elevation. Flowering in March and October; fruiting in February–March, October, and December. This species has been collected along the Caribbean coast of Belize, Guatemala, and Nicaragua and in central Panama. It ranges southward to the Guianas.

*Amanoa guianensis* is recognized by its restriction to lowland forests near the seacoast, the flowers in sessile involucre fascicles on inflorescences that appear to be leafless branchlets, and thick-walled woody fruits. The ovaries with two ovules per locule develop into three-seeded fruits by abortion. Although not yet collected in Costa Rica, it occurs in adjacent Nicaragua.

*Antidesma bunius* (L.) Spreng., the “Chinese laurel,” is occasionally cultivated in Central America. These ornamental shrubs have un-

branched unisexual inflorescences and sweet drupaceous fruits with solitary seeds. The ♀ flowers have an annular disc and the ovary is one-locular with one broad stigma. The male flowers have two to five stamens, a small pistillode, and four to five small imbricate calyx lobes. The eglandular leaves are pinnately veined, entire, and subcoriaceous. *Antidesma*, a paleotropical genus of ca. 160 species, is closely related to *Hyeronima*.

### **Aparisthmium** Endlicher

**Trees** or shrubs, dioecious, pubescence of short simple hairs; stipules 2, small, lateral. **Leaves** alternate, petiolate, with 2 stipel-like appendages at the apex of the petiole, blades ovate, pinnately veined, serrulate. **Male inflorescences** mostly terminal, paniculate, bracts subtending small glomerules of sessile flowers, ♂ flowers small, ovoid in bud, calyx splitting into 2–3 valvate sepals, petals and disk absent; stamens 4 (3, 5), filaments united at the base, separate in the distal half, anthers longitudinally dehiscent, connective not prolonged; pistillode absent. **Female inflorescences** racemose (or with a few lateral branches), bracts biglandular, subtending 1 (2) flower; ♀ flowers with 4–6 sepals, petals and disk absent, staminodes absent; ovary 3-locular, ovules 1/locule, styles 3, united at base and thick, minutely 2-lobed at the apex, papillate on interior surfaces. **Fruits** capsules splitting into 3 2-valved cocci, columella persistent; seeds ecarunculate, endosperm carnose, cotyledons flat, oblong.

A monotypic genus, until recently, known only from South America. The recent addition of this species to the Central American flora is another example of an Amazonian species disjunct in southwestern Costa Rica. Continued use of the generic name will need conservation (Webster, 1994b). The genus is currently being studied by Ricardo Secco (MG).

**Aparisthmium cordatum** (Juss.) Baill., *Adansonia* 5: 3–7. 1865. *Conceveibum cordatum* Juss., Euphorb. gen. 43, t. 13, f. 42a. 1824. *Alchornea macrophylla* Mart., Herb. fl. bras. 24 (beibl 2): 31. 1841. Figure 20.

**Trees** or shrubs, 3–10 m tall, leafy stems 4–9 mm thick, minutely puberulent with thin hairs 0.1–0.4 mm long; stipules to 3 mm long, subulate, caducous. **Leaves** alternate or congested beneath distal flowering nodes, petioles 1.2–11 (–18) cm long, 1–2.7 mm thick, minutely puberulent, with 2 stipel-like structures at the adaxial/lateral apex, 2 flat rounded glands 1–1.5 mm diam. present at the base of the blade in the abaxial surface; **leaf blades** (10–)12–24 (–32) cm long, 5–15 (–19) cm wide, ovate-elliptic to broadly ovate or ovate-orbicular (smaller leaves narrowly ovate-elliptic), apex acuminate to caudate-acuminate, the narrow tip 1–2.5 cm long, margin

crenate or serrate with rounded glandular teeth ca. 1 mm high (subentire), base rounded and truncate to subcordate (cuneate in smaller leaves), drying stiffly chartaceous and dark greenish, upper surfaces with minute (0.1–0.2 mm) hairs along the major veins, lower surfaces minutely puberulent or glabrescent, 2° veins 6–11/side. **Male inflorescences** and flowers not seen. **Female inflorescences** not seen at anthesis, solitary and axillary or several from a condensed distal node, 16–40 cm long in fruit, bracteoles ca. 1.5 mm long, triangular, fruits borne on pedicels 10–18 mm long, 0.4–0.9 mm thick, minutely puberulent. **Fruits** 6–8 mm long, 8–11 mm wide, deeply 3-lobed, sparsely puberulent with minute hairs, subtended by persisting triangular calyx lobes 1.5–2 mm long, persisting style branches ca. 3 mm long, 0.4–0.5 mm thick, columella 3.8–5 mm long; seeds 4.5–5.5 mm long, 3.5–4 mm diam., oblong-ellipsoid.

Plants of evergreen forest on the Pacific slope in southern Costa Rica, ca. 300 m elevation. The species is known in Central America from a single collection (*Wilbur et al.* 23958 DUKE) from about 12 km northeast of Quepos; fruiting in August. In South America, the species ranges from Colombia, Venezuela, and the Guianas to Bolivia.

*Aparisthium cordatum* is recognized by the large ovate leaves with bluntly glandular-serrate margins, minute simple hairs on many surfaces, long racemose ♀ inflorescences, capsular fruits, and seeds almost circular in cross-section. The two stipel-like structures at the apex of the petiole (not seen in the Costa Rican collection), two flat rounded glands on the abaxial base of the leaf, and the subparallel 3° veins are additional distinctions. Specimens may resemble *Conceveiba pleiostemonia*, but *Aparisthium* lacks the minute stellate hairs and has dry capsules with smaller seeds.

### **Argythamnia P. Browne**

**Shrubs**, subshrubs, or small trees (herbs), annual or perennial, monoecious (rarely dioecious), stems pubescent with appressed slender 2-parted hairs attached at the center (T-shaped), often with purplish pigment; stipules paired, small, persisting. **Leaves** alternate, simple, short-petiolate, blades dentate or entire, venation pinnate or palmate (tripliveined), eglandular. **Inflorescences** axillary, solitary, racemiform, usually bisexual with 1–3 proximal ♀ and several distal ♂ flowers, subsessile or short-pedicellate, each flower subtended by a small bract. **Male flowers** with ovoid buds, sepals 5, valvate, petals 5, imbricate but narrowed at the base and adnate to staminal column, disk of 5 glands opposite sepals; fertile stamens 5–15 in 1–3 whorls of 5 each (consistently 10 in 2 whorls in subgenus *Ditaxis*), united at the base to form a column, filiform staminodes sometimes present at the apex of the column, filaments united at base, short, anthers ovate, dehiscing longitudinally and introrse; pistillode absent. **Female flowers** with 5 imbricate sepals, petals 4 or 5, imbricate, usually shorter than the sepals,

entire, staminodes absent, disk cylindrical or dissected into sometimes elongate segments, filaments or glands; ovary subsessile, 3-locular, styles 3, free or united at the base, bifid distally, ovules 1/locule. **Fruits** often borne on reflexed pedicels, capsular, 3-lobed, separating into 3 2-valved cocci, leaving a persistent columella; seeds subglobose, ecarunculate, surface reticulate to foveolate.

A genus (in the wide sense) of ca. 80 Neotropical species. Our species has also been assigned to *Ditaxis*, sometimes considered a subgenus of *Argythamnia* (cf. Ingram, 1980, and Webster, 1994b).

**Argythamnia guatemalensis** Müll. Arg., *Linnaea* 34: 145. 1865. *Ditaxis guatemalensis* (Müll. Arg.) Pax & K. Hoffm. *Pflanzenreich* 4, 147, 6: 59. 1912. Figure 11.

Herbaceous **subshrubs**, stems erect or horizontal, 0.5–1 m tall, from a woody rootstock, leafy stems 0.8–2.8 mm thick, sericeous with slender whitish linear 2-branched hairs attached at the center (but difficult to see), 1–3 mm long; **stipules** 1–3 mm long, 0.2–0.5 mm wide at the base, linear, acute, persistent or deciduous. **Leaves** with petioles 0.7–3(–6) mm long, 0.5–1.5 mm thick, densely sericeous; **leaf blades** 17–85 mm long, 8–35 mm wide, ovate-elliptic to ovate-lanceolate or lanceolate, apex acute with minute gland tip, usually cuneate at the base, margin minutely (0.2–0.5 mm) serrate with 12–30 teeth/side, drying chartaceous and grayish, with hairs 0.3–1.3 long on the upper surface and shorter dense hairs beneath, 2° veins 3–4/side and strongly ascending, becoming impressed above. **Inflorescences** 6–15 mm long, subglomerulate with few flowers, peduncle 1–5 mm long, densely sericeous, flowers subsessile or short-pedicellate. **Male flower** buds ca. 4 mm long, sericeous, sepals 1.5–3 mm long, petals 2–2.8 mm long; stamens 10 with 3 small staminodes, anthers orange. **Female flowers** with buds ca. 4 mm long, sericeous, sepals 3.5–4.5 mm long, 0.6–1.3 mm wide, narrowly oblong to oblanceolate, petals 1–2 mm long; ovary 2–2.5 mm long, 3–3.5 mm wide, oblate, short-pubescent, style column 0.7 mm long, style branches 0.7 mm long. **Fruits** 4 × 6 mm, oblate, short-sericeous, columella 2.2 mm high, I-shaped; **seeds** 2.5–3 mm long, 2–2.5 mm wide, surface reticulate with hexagonal depressions 0.3–0.5 mm wide.

Plants of the seasonally deciduous lowlands of northeastern Costa Rica, 0–200 m elevation. Flowering in February, April, August–October, and December. The species ranges from Mexico along the Pacific side of Central America to the Bay of Nicoya in Costa Rica.

*Argythamnia guatemalensis* is recognized by the unusual hairs (attached at the center but difficult to see), short few-flowered axillary inflorescences, unisexual flowers, sepals and petals differing only slightly in length in ♂ flowers, herbaceous habit, and restriction to seasonally deciduous habitats. The description of this species in the Flora of Gua-



temala (Standley & Steyermark, 1949) lists larger floral parts than those seen in Costa Rica.

### **Astrocasia Robinson & Millspaugh**

REFERENCE—G. L. Webster, Revision of *Astrocasia* (Euphorbiaceae). Syst. Bot. 17: 311–323. 1992.

Small trees and shrubs, monoecious or dioecious, glabrous; stipules lateral, ribbed with parallel venation, deciduous. Leaves alternate, petiolate, sometimes peltate, blades entire, pinnately veined, glabrous. Inflorescences axillary, flowers in fasciculate glomerules of few to many ♂ flowers or 1–3 ♀ flowers, subtended by stipule-like bracts, borne on long thin glabrous pedicels. Male flowers glabrous, sepals 5, free, usually unequal with outer smaller and thicker, imbricate in bud, petals 5, free, longer than the sepals, disk annular or patelliform; stamens 3–5, filaments united to form a column, anthers sessile or stipitate on the column, 2-theous, lateral on the flattened apex of the column, dehiscing horizontally or deflexed, pistillode sessile or stipitate on the dilated apex of the staminal column. Female flowers glabrous, sepals 5, free, imbricate in bud, deciduous, petals 5, free, larger than the sepals, staminodes absent; disk annular to cupular, entire or slightly lobed; ovary 3- (rarely 4)-locular, ovules usually 2/locule, anatropous, styles 3 or 4, short and united at the base, branches short and bifid. Fruits capsules, thin-walled separating into 3 (4) 2-valved cocci, columella persisting, slender; seeds 1/locule, smooth, ecarunculate, raphe conspicuous, endosperm copious, cotyledons thin, flat.

A Neotropical genus of five species ranging disjunctly from Mexico and the West Indies to Brazil and Bolivia. The unisexual plants, lack of pubescence, deciduous leaves, flowers from distal stems on long thin pedicels, free petals, peltate androecium, cupulate ♀ disk, and capsular fruits help distinguish this genus. In a ♀ flower we dissected, there was only one ovule per locule, with some indication that the second ovules had failed to develop.

***Astrocasia tremula*** (Griseb.) Webster, J. Arnold Arbor. 39: 208. 1958. *Phyllanthus tremulus* Griseb., Fl. Brit. W. Ind. 34. 1859. *Astrocasia phyllanthoides* Robins. & Millsp., Bot. Jahrb. Syst. 36, Beibl. 80: 19. 1905. Figure 32.

Small trees or shrubs 1.5–6(–10) m tall, dioecious (or monoecious), leafy stems 0.7–3 mm thick, glabrous, becoming pale grayish with elliptic lenticels; stipules 4–9 mm long, ca. 1.5 mm wide at base, narrowly triangular, glabrous, yellowish, venation parallel, caducous. Leaves deciduous, glabrous, petioles (4–)12–68 mm long, 0.5–1.5 mm thick, sometimes thickened (geniculate) at apex and base, with 1 or 2 small (0.3–0.7 mm) glands/stipels

at apex adaxially (at base of mature blade); leaf blades 3.5–10(–14) cm long, 2.5–6(–9) cm wide, ovate to ovate-rhombic or ovate-elliptic, apex obtuse or acute, margins entire (slightly undulate when dried), base broadly obtuse, drying membranaceous (flowering material) to chartaceous, glabrous, 2° veins 3–7/side. Male inflorescences from axillary short-shoots 2–6 mm long, fasciculate with 5–20 flowers, glabrous, bracts 2–3 mm long, with parallel venation, pedicels 8–18 mm long, 0.1–0.2 mm thick; ♂ flowers 3–4 mm wide, sepals 0.7–1.3 mm long broadly elliptic to obovate, entire, petals 1.5–3.5 mm long, oblong, disk often obscure, 0.9–1.8 mm wide; staminal column 0.3–0.4 mm long, ca. 0.2 mm thick, terminated by a peltate flat apex 0.8–1.1 mm wide, with 5 stamens represented by 10 thecae borne along the outer rounded periphery, anthers ca. 0.3 mm high; pistillode sessile on the staminal column. Female inflorescences of 1–5 flowers in axils of leaves or fallen leaves, glabrous, pedicels 2–5 cm long, 0.4–0.7 mm thick; ♀ flowers ca. 4 mm long, glabrous, sepals 1.7–2.5 mm long, petals 3.5–4.2 mm long, 1.3–1.7 mm wide, obovate to spatulate, rounded distally, disk forming a thin cup 0.5–1 mm high and ca. 2.2 mm diam.; pistil ca. 2 mm long, ovary ca. 1.2 mm diam., styles ca. 0.6 mm long. Fruits 8–9 mm long, 10–12 mm wide, oblate, with 3 rounded lobes, glabrous, persisting stigmas ca. 0.4 mm long, columella 3.5–5 mm long, I-shaped; seeds 4–5 mm long, 3.3–4 mm wide, ca. 3 mm thick, irregularly rounded to wedge-shaped, smooth, uniformly yellowish or dark brown.

Plants of the evergreen Caribbean lowlands, 20–500 m elevation. Fruiting in October–March. Known in Costa Rica only from Bajo Rodríguez (north of San Ramón), Alajuela (*Gómez-Laurito 12368* usj). The species is usually found on limestone and ranges disjunctly from southeastern Mexico, Belize, Guatemala, Jamaica, central Panama, and northern South America to eastern Brazil.

*Astrocasia tremula* is recognized by its complete lack of pubescence, usually dioecious plants, few flowers on slender pendulous pedicels arising from the stems or short-shoots, well-differentiated sepals and petals, and unusual peltate androecium on which the thecae form a 10-lobed margin. Flowering appears to occur with the flush of new foliage. This species is closely related to *A. peltata* Standley of Mexico.

### **Bernardia Miller**

Shrubs or small trees, monoecious or dioecious, pubescence of simple or stellate hairs; stipules small. Leaves alternate, simple, petiolate to subsessile, pinnately or palmately 3-veined, margins dentate, often with 2 glandular areas near the base of the blade, without stipels. Inflorescences unisexual and solitary, ♂ axillary or pseudoterminal, short or long spikes, bracts subtending 1–7 sessile or short-pedicellate flowers; ♀ terminal or axillary to distal leaves, flowers aggregated (and few-flowered) or



sessile on spikes, each concave bract subtending 1 ♀ flower. **Male flowers** globose in bud, calyx splitting into 3–5 valvate sepals, petals absent, disk usually of minute elements among stamens bases; stamens 3–30, filaments free, slender, short, anthers 2- or 4-lobed (emarginate), dehiscing longitudinally, thecae subglobose; pistillode small or none. **Female flowers** with 4–6 imbricate sepals (and subtended by similar bracts), petals absent, disk annular or of separate glands, staminodes absent; ovary 3-locular, ovules 1/locule, style column short, branches

2-lobed, simple to lacerate. **Fruits** capsular, breaking into 3 2-valved cocci, columella persisting; seeds carinate, rounded to prismatic, ecarunculate, endosperm carnose.

A tropical American genus of ca. 50 species, with the majority of species in Brazil and a second center of diversity in Mexico. Our two species are quite different in appearance and habitat.

**Key to the Species of *Bernardia***

- 1a. Plants of evergreen montane forest formations; leaves elliptic-oblong to lanceolate, to 20 cm long; pubescence mostly of simple hairs ..... *B. macrophylla*
- 1b. Plants of deciduous forest formations of Guanacaste; leaves ovate, to 11 cm long, pubescence of stems and leaves mostly of stellate hairs ..... *B. nicaraguensis*

***Bernardia macrophylla*** Standl., J. Wash. Acad. Sci. 15: 103. 1925. Figure 12.

**Shrubs** 1.5–3 m tall, monoecious, leafy stems 1–4 mm thick, appressed-pubescent with thin simple ascending hairs 0.2–0.5 mm long; **stipules** 1.2–1.9 mm long, 0.5–1 mm broad at the base, narrowly triangular, persistent. **Leaves** with petioles 3–10 mm long, 0.5–1 mm thick, densely appressed-hispidulous, glands absent; **leaf blades** 6–16(–20) cm long, 1.5–5(–7.5) cm wide, narrowly elliptic-oblong to narrowly elliptic or lanceolate, tapering gradually to the acuminate apex, margin with gland-tipped serrations 0.2–0.7 mm high, 15–40/side, base acute and slightly decurrent on the petiole, drying chartaceous, 2° veins 7–11/side, arising at 30–40°. **Male inflorescences** 2.5–7 cm long, often axillary to older leaves, peduncles 2–3 cm long, appressed-puberulent, 0.7 mm thick, glomerules 1.4–5 mm distant along the rachis, with 3–6 flowers, bracts ca. 1 × 2 mm, pedicels 1–1.5 mm long; ♂ flower buds 1.3 mm diam., sepals 1.2–1.8 mm long, 0.7–1.1 mm wide, lanceolate, disk represented by minute clavate glands; stamens ca. 15, filaments 0.7–1 mm long, slender, anthers 0.2 × 0.4 mm. **Female inflorescences** in axils of distal leaves, 5–25 mm long, densely pubescent, peduncle ca. 2 mm long, flowers few, subtended by bracts ca. 2 mm long; ♀ flowers pubescent, sepals 5, 1.6–1.8 mm long, 0.8–1.3 mm wide, ovate, disk 0.2–0.3 mm high, glabrous; ovary 1–2 mm long, style branches 0.4 mm long. **Fruits** ca. 7 × 8 mm, yellowish, rugulose, sparsely minutely puberulent.

Plants of evergreen forest formations; known from 1800 m elevation in easternmost Costa Rica but collected near sea level in Panama (*Standley 29389* us holotype). Flowering and fruiting in March in Costa Rica (*Davidse et al. 25611* CR, MO). The species is known only from the collection cited above and a few collections in Panama.

*Bernardia macrophylla* is recognized by its long slender ♂ spikes, narrow dentate leaves, simple hairs, and unisexual flowers. Webster and Burch

(1967) describe the species as dioecious, but our material is clearly monoecious. This species should be reexamined when more material becomes available.

***Bernardia nicaraguensis*** Standl. & L. O. Wms., Ceiba 1: 85. 1950. Figure 12.

**Shrubs** or small trees, 2–8 m tall, dioecious, leafy stems 1.5–4 mm thick, stellate-tomentulose with yellowish hairs 0.2–0.8 mm long, glabrescent and dark grayish in age, terete; stipules 2.5–4 mm long, 1 mm wide at the base, lanceolate, deciduous. **Leaves** with petioles 4–17 mm long, 0.8–1.6 mm thick, densely stellate-tomentulous; **leaf blades** 3–12 cm long, 2–8 cm broad, ovate to ovate-elliptic or broadly elliptic, apex obtuse to acute, margin irregularly crenate-dentate with 15–35 teeth/side 0.3–1.5 mm high, base obtuse to somewhat rounded and subtruncate, drying chartaceous and darker above, scabrous with stellate hairs ca. 0.3 mm long above, with dense stellate hairs 0.3–0.8 mm diam. beneath, 2° veins 4–6/side, subpalmate with the basal 2° veins often reaching the middle of the blade, central 2° veins arising at angles of 40–50°. **Male inflorescences** 12–40 mm long, 3–5 mm wide, at first erect and cone-like, bracts 2–3 mm long, broadly ovate, with dense straight hairs ca. 0.3 mm long; ♂ flowers with 4 sepals 2.5 × 1 mm, densely tomentulous on the exterior but glabrous on the inner surface; stamens ca. 20, filaments 1–1.8 mm long, filiform, glabrous, anthers 0.3–0.4 mm long. **Female inflorescences** to 5 cm long with 2–5 sessile flowers, peduncle to 14 mm long, densely stellate-tomentulous, bracts ca. 1.3 mm long; ♀ flowers with sepals ca. 3 × 2 mm, stiff; ovary 3–4 mm diam., globose, densely yellowish hirtellous, style branches 1.5 mm long. **Fruits** ca. 7.5 × 11 mm, deeply 3-lobed, densely stellate-tomentulose, walls of cocci 0.2–0.3 mm thick, columella 4–5 mm long, 2–4 mm wide; seeds 5.5–6.5 mm long, 4.5–4.7 wide, 4.2–4.5 mm thick, ovoid-angular, grayish brown or mottled.

Plants of open savanna formations, deciduous and partly deciduous forest formations, 20–1200

m elevation (to 1400 m in Nicaragua). Flowering in January–May; fruiting in February–August. The species ranges from Honduras to northwestern Costa Rica.

*Bernardia nicaraguensis* is recognized by its seasonally very dry deciduous habitat, dense covering of slender stellate hairs, ovate denticulate leaves with subpalmate venation, and distal leaf axils with tomentulose cone-like ♂ inflorescences (in early stages) or more elongate few-flowered ♀ spikes. The plants may lose their leaves as flowering progresses (Haber & Zuchowski 10483).

**Breynia J. R. & G. Forster**  
(nom. conserv.)

**Shrubs** or small trees, monoecious, distal leaf-bearing stems resembling pinnate leaves. **Leaves** alternate and distichous, simple, short-petiolate, blades entire, pinnately veined, often blackening on drying. **Inflorescences** axillary, flowers small, solitary or few in fascicles (♂), or on leafless unbranched axillary shoots, ♂ pedicels slender. **Male flowers** with a turbinate calyx, calyx lobes 6, imbricate and rounded, petals and disk absent; stamens 3, filaments united, anthers elongate; pistillode absent. **Female flowers** with 6 calyx lobes, imbricate, petals and disk absent; ovary 3-locular, ovules 2/locule, styles 3, free, bifid or simple. **Fruits** somewhat fleshy, incompletely dehiscent; seeds trigonous, with fleshy outer seed coat, ecarunculate.

A genus of 10–25 variable species in eastern tropical Asia and the Pacific. The genus is closely related to *Phyllanthus* but differs in the ventrally invaginated seeds with fleshy exotesta and the lack of a floral disk. Varieties of one species are widely cultivated in the tropics as ornamental shrubs.

**Breynia disticha** J. R. & G. Forst., Char. gen. pl. 146, t. 73. 1776. *Phyllanthus nivosus* Bull, Cat. 9. 1873; W. G. Smith, Fl. Mag. (London) n.s. t. 120. 1874. *B. nivosus* (W. G. Smith) Small, Bull. Torrey Bot. Club 37: 516. 1910. *B. disticha* forma *nivosa* (Bull) A. R.-Sm., Kew Bull. 35: 498. 1980.

**Shrubs** 1–2 m tall, branching often zigzag, leafy branches 0.5–1.5 mm thick, glabrous, lenticellate; stipules 1–2 mm long, triangular-aculeate. **Leaves** distichous, glabrous, petioles 2–5 mm long, ca. 0.7 mm thick, without glands; **leaf blades** 2–6 cm long, 1.5–3.5 cm wide, broadly ovate-oblong to ovate-orbicular or elliptic-oblong, apex rounded, base rounded, drying thin-chartaceous, often variegated in color, 2° veins 2–5/side. **Inflorescences** of solitary ♀ flowers on slender pedicels 4–

15 mm long (flowers sometimes borne in small groups on leafless axillary branches to 3 cm long); ♂ calyx turbinate; ♀ calyx campanulate and lobed.

*Breynia disticha*, native of the New Herbrides, is often planted as an ornamental bush or in hedges in tropical gardens. The reddish stems with many small variegated leaves marked with green, white, red, or pink give a colorful effect. It is called “snow bush” and “leaf flower.”

**Caperonia St. Hilaire**

**Herbs** or subshrubs, annual or perennial, monoecious (in Central America), usually growing in wet places, with simple or gland-tipped hairs; stipules paired at the leaf base. **Leaves** alternate, simple, short-petiolate, blades usually with gland-tipped serrate margins, venation pinnate, laminar glands absent. **Inflorescences** axillary, usually solitary, mostly bisexual (in Central America), spiciform to racemiform, pedunculate with 1–5 proximal ♀ flowers and 2–10 distal ♂ flowers, a broadly sessile stipule-like bract subtending each flower, ♂ flowers usually pedicellate, ♀ flowers sessile or short-pedicellate. **Male flowers** with 5 sepals, valvate or imbricate in bud, petals 5, free, often unequal, disk absent; stamens 10 in 2 superposed whorls of 5, filaments united near the base into a column, free distally, anthers dehiscing longitudinally; pistillode present at the apex of the staminal column, minute, cylindrical or 3-lobed. **Female flowers** with 4–7 unequal sepals (often 3 larger alternating with 3 smaller), united near the base, enlarging in fruit, petals narrow or reduced and sepal-like, staminodes and disk absent; ovary 3-locular, muricate or with broad-based subulate hairs, styles with 3–7 lobes, ovules 1/locule. **Fruits** capsular, 3-lobed, echinate to hispid or verrucose over the outer and distal surfaces, subtended by the persisting perianth, breaking into 3 2-valved cocci; **seeds** globose, ecarunculate, raphe narrow, surfaces with a fine reticulum forming small areolae (foveolate), endosperm carnose, copious.

A genus of ca. 40 species, mostly American but with ca. 6 African species. Our species are easily recognized because of their tendency to grow in shallow water or wet depressions in open sunny sites and the distinctive serrate leaves with many straight parallel 2° veins. Both our species exhibit extraordinary variation in leaf form, varying from linear-lanceolate to ovate-elliptic. However, such variation is rarely seen within an individual plant. Our species live in the same habitats and overlap in many morphological characteristics. Nevertheless, the characters of the key seem to separate specimens consistently. There may be hybridization between the two species represented in Central America.

Key to the Species of *Caperonia*

- 1a. Stems and petioles lacking slender gland-tipped hairs; stems pubescent to subglabrous; stipules ovate-triangular to triangular; seed surface with areolae 0.08–0.17 mm wide; leaves mostly lanceolate to linear ..... *C. castaneifolia*
- 1b. Stems and petioles with few to many slender gland-tipped hairs; stipules narrowly triangular to lanceolate; seed surface with areolae 0.06–0.12 mm wide; leaves ovate to linear-lanceolate ..... *C. palustris*

***Caperonia castaneifolia* (L.) St. Hill., Hist. Pl. Remarq. Brésil, 245. 1824. *Croton castaneifolium* L., S. P. 1004. 1753. *Cap. paludosa* Klotzsch, London J. Bot. 2: 51. 1843. *Cap. panamensis* Klotzsch in Seemann, Bot. voy. Herald 103. 1853. *Cap. panamensis* Pax & K. Hoffm., Pflanz. reich 63 (4, 147, 7): 424. 1914. *Cap. angusta* Blake, J. Wash. Acad. Sci. 14: 288. 1924. *Cap. stenomeres* Blake, J. Wash. Acad. Sci. 14: 288. 1924. Figure 10.**

**Herbs** 0.3–0.8 m tall, basal stems sometimes repent, larger erect stems longitudinally ridged (*Equisetum*-like), hollow and with transverse septa, leafy stems 1.5–11 mm thick, with appressed-ascending whitish hairs 0.2–0.5 mm long, glabrescent; **stipules** 0.7–3 (rarely to 6) mm long, 0.5–2 mm wide at the base, triangular to narrowly ovate, usually glabrous except at the tip, not becoming reflexed. **Leaves** with petioles 2–22 mm long, 0.5–2 mm thick, pubescent in early stages; **leaf blades** 3–12 cm long, 0.7–3(–6) cm wide, linear-lanceolate to ovate-elliptic (in different plants), usually gradually narrowed to an acute or acuminate apex, with 9–30 serrations/side, base slightly rounded to subtruncate, drying membranaceous to chartaceous, glabrous above and below or sparsely pubescent on the midvein beneath, 2° veins 6–15/side. **Inflorescences** 2–7 cm long, spiciform, peduncles to 4 cm long, rachis appressed-hispidulous, bracts 1–2 mm long, ♀ flowers 1–3, on pedicels ca. 1 mm long, ♂ flowers 5–10, subsessile. **Male flowers** white, buds ca. 1.3 mm diam., sepals 1.5–2 mm long, petals 1.2–2 mm long, 0.5–1 mm wide, obovate, equal or unequal; anthers 0.3–0.5 mm long; pistillode 0.4–0.9 mm long, cylindrical. **Females** flowers with 5–6 sepals, the 3 larger becoming 3–4.5 mm long in fruit, smaller sepals 1.2–1.5 mm long, glabrous or rarely with a few simple or gland-tipped hairs, petals 1.2–3 mm long. **Fruits** 4–5 × 5–6 mm, oblate and 3-lobed, broad-based hairs 0.3–0.5 mm long on distal surfaces, columella 1.5–3 mm long; **seeds** ca. 3 × 2.5 × 2.5 mm, subglobose, raphe the entire length of the seed and linear, areolae 0.08–0.17 mm wide, surface often pale colored and with or without transverse scales.

Plants of the margins of lakes, rivers, areas of shallow water, and moist depressions, often in open sunny sites, mostly in the Pacific lowlands, 0–500 m elevation. Probably flowering and fruiting primarily in the wet season (collections seen are from January–February, July, and October–November). The species ranges from Mexico to Brazil.

*Caperonia castaneifolia* is recognized by its open wet lower-elevation habitats, serrate leaves variable in form, and bisexual spikes with unisexual flowers. It is not possible to distinguish this species from its local congener without careful review of pubescence, stipules, and seeds. The use of the Linnaean epithet to include *C. paludosa* was discussed by Webster and Huft (1988).

***Caperonia palustris* (L.) A St.-Hill., Hist. Pl. Remarq. Brésil, 245. 1824. *Croton palustris* L., Sp. Pl. 1004. 1753. *Caperonia palustris* var. *linearifolia* Standl. & L. O. Williams, Ceiba 1: 148. 1950. Figure 10.**

**Herbs** 0.2–1.5 m tall, older stems often slightly inflated, hollow, leafy stems 0.4–7 mm thick, with few to many slender gland-tipped hairs 1–2.2 mm long and shorter (0.3–1 mm) thin sharp-tipped hairs; **stipules** 2.5–6 mm long, 0.4–1 mm wide at base, narrowly triangular to lanceolate, usually becoming reflexed. **Leaves** with petioles 2–24 mm long, 0.5–2 mm thick, usually with gland-tipped hairs to 2.2 mm long; **leaf blades** 3–12(–21) cm long, 0.8–4(–7) cm wide, linear-lanceolate to narrowly triangular or ovate-elliptic (rarely ovate-oblong), tapering gradually to the acute apex, margin with 12–42 serrations/side, base acute to rounded or subtruncate, glabrous above, appressed whitish hairs on the veins beneath, 2° veins 5–17/side, 3° veins subparallel. **Inflorescences** 1.4–9 cm long, racemiform or spicate, with 1–4 proximal ♀ flowers and several distal ♂ flowers, peduncles 6–45 mm long, often with a few glandular hairs, rachis hispidulous; bracts acute, ♂ flowers short-pedicellate, ♀ flowers subsessile. **Male flowers** white, ca. 1.8 × 2.3 mm at anthesis, sepals 1.5–3 mm long, ca. 2 mm broad at base, petals 1.5 × 0.6 mm; anthers 0.3–0.5 mm long; pistillode 0.6–0.8 mm long. **Female flowers** 2.5 × 3 mm in early stages, sepals 5–9 with 3–6 larger outer sepals, becoming 3–5 mm long in fruit, triangular, usually with gland-tipped hairs 1–1.5 mm long, petals 1–2 mm long; style branches 5–7, 0.4–1 mm long. **Fruits** 3–5 mm long, 4.5–7 mm wide, oblate and 3-lobed, broad-based subulate hairs present on the distal surfaces, ca. 0.5 mm long, gland-tipped hairs present or absent on the subtending sepals; seeds 2.8–3 mm long, ca. 2.5 mm diam., subglobose to ovoid, areolae 0.06–0.12 mm broad, often dark and with pale narrow transverse scale-like processes.

Plants of the margins of lakes, rivers, areas of shallow water, and moist depressions, often in open



sunny sites, mostly in the Pacific lowlands, 0–800 m elevation. Flowering in August–November; fruiting in June–December. The species ranges from the southeastern United States to Argentina.

*Caperonia palustris* is recognized by its open wet lower-elevation habitats, variable serrate leaves often with many parallel 2° veins, and bisexual spikes with unisexual flowers. It is not possible to distinguish this species from its local congener without careful review of pubescence, stipules, and seeds. The glandular pubescence of stems is the most consistently useful marker for this species.

### **Caryodendron Karsten**

**Trees**, dioecious, stems glabrous or with simple hairs; stipules lateral, caducous. **Leaves** alternate, petiolate, laminae simple and entire, subcoriaceous, venation pinnate, with 2 flat rounded glands on the adaxial surface at the base. **Male inflorescences** terminal or axillary to distal leaves, solitary, spiciform thyrses with a thick central rachis and a few thick alternate branches, spiciform axes with subsessile groups of 2–5 ♂ flowers subtended by broadly sessile bracts; ♂ flowers with 3 calyx lobes or parts, ovate, valvate, petals absent, disk central and large, pulviniform and often pubescent; stamens 4–7, usually with a central stamen and 1 or 2 whorls of 3 exterior to the disk, filaments free, inflexed near the apex, anthers dorsifixed, dehiscence introrse and oblique, thecae unequal, connective apiculate; pistillode absent. **Female inflorescences** terminal and solitary, with a thick central unbranched rachis and 0–2 short basal branches, axes spiciform (racemose), with subsessile flowers subtended by sessile bracts; ♀ flowers with a thick urceolate calyx with 3 (5–6) short rounded imbricate lobes, petals 3, broadly imbricate and rounded distally; disk forming a cup with subentire margin; staminodes absent; ovary with 3 (2, 4) locules, ovules 1/locule, styles 3, very short, stigma-like and little differentiated from the ovary. **Fruits** capsules, thick-walled with slightly fleshy smooth surfaces, breaking into 3 2-valved cocci; seeds more than 1 cm long, ovoid to globose, ecarunculate.

A Neotropical genus of three species, ranging as far north as western Panama (Webster & Huft, 1988). The terminal few-branched inflorescences with thick spiciform axes are unusual among our species of Euphorbiaceae.

**Caryodendron angustifolium** Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 217. 1929.

**Trees** ca. 6 m tall, leafy stems 3–5 mm thick, glabrous, smooth and yellowish gray; stipules not seen, stipule scars obscure. **Leaves** glabrous, petioles 12–22(–30) mm long, 1.5–2.3 mm thick, geniculate at the apex, petioles without glands but with 2–4 flat rounded glands in the leaf surface at base of blade adaxially; **leaf blades** 18–33 cm long, 5–9 cm wide, narrowly elliptic-oblong to nar-

rowly or oblanceolate, apex acuminate with tip to 5 mm wide and retuse, margins entire and recurved, tapering gradually to the cuneate base, drying stiffly chartaceous, drying yellowish gray, 2° veins 5–8/side, 3° veins subparallel. **Male inflorescences** 9–23 cm long, with a longer central axis and ca. 2 proximal lateral branches, peduncle ca. 1 cm long (to first lateral branch), 2.5–4.5 mm thick, lateral branches 1.2–1.5 mm thick, rachis ca. 2 mm diam., minutely puberulent with ascending hairs 0.1–0.2 mm long, flower clusters 3–5 mm wide, sessile, bracts ca. 2 mm long, triangular and broadly sessile, flowers 3–7, closely congested, sessile; ♂ flower buds ca. 2 mm long, anthers 0.4–0.5 mm long. **Female inflorescences** not seen [the following information from the closely similar *C. orinocensis*: ca. 7 cm long, simple and unbranched or with 1–3 short (15 mm) thick lateral branches near the base, rachis 3 mm thick, flowers mostly solitary; ♀ **flowers** with a thick calyx cup ca. 5 mm long and 4 mm diam., with short (1 mm) broadly rounded distal lobes, petals 3, broadly rounded and equaling the calyx in length, glabrous but with ciliolate distal margin; pistil ca. 4 mm long, ovoid with gradually narrowed apex and minute (0.5 mm) style branches]. **Fruits** not seen, probably similar to *C. orinocensis* where subglobose-obovoid and 3.5–4 cm diam.

Plants of lowland evergreen forest formations near the Pacific Coast of western Panama. Flowering in July–August (*Cooper & Slater 192 F* holotype, US isotype). Known only from Progreso, Chiriquí, but probably also occurring in the Golfo Dulce region of Costa Rica.

*Caryodendron angustifolium* is recognized by its narrow oblanceolate glabrous leaves to 30 cm long, unisexual plants with terminal inflorescences having few spiciform branches, and sessile flower clusters. The leaf tips usually have a notch at the apex with a terminal gland-like area, and the glands at the lamina base are imbedded in the surface. This species is very similar to some collections placed under *C. orinocensis* Karsten of South America. The type material of *C. angustifolium* differs from that species in having stipule scars that are poorly developed and leaf blades narrowly cuneate at the base. More material is necessary to assess the population variability in Panama and to contrast this with a modern interpretation of population variation in *C. orinocensis*.

**Chamaesyce** S. F. Gray

**REFERENCES**—D. G. Burch, Two new species of *Chamaesyce* (Euphorbiaceae), new combinations, and a key to Caribbean members of the genus. Ann. Missouri Bot. Gard. 53: 90–99. 1966. A. Herndon, Notes on *Chamaesyce* (Euphorbiaceae) in Florida. Rhodora 95: 352–368. 1993.

**Herbs** or subshrubs, annuals or with woody base, prostrate to erect, monoecious (dioecious), stems often reddish in color, latex whitish, glabrous or with simple hairs; stipules united at the base and interpetiolar or separate, small and often lacerate, usually persisting. **Leaves** opposite, simple, short-petiolate or sessile, blades usually somewhat asymmetric at the base and cuneate to subcordate, margin serrate or entire, venation palmate or subpalmate, chlorophyll-bearing cells mostly in a sheath around the veins and veinlets with colorless areas between. **Inflorescences** terminal or apparently axillary (terminal on reduced axillary short-shoots), made up of 1–many cyathia, often in cymose clusters or glomerules. **Cyathium** resembling a flower (cf. *Euphorbia*), the involucre often resembling a calyx cup or calyx tube bearing 5 lobes alternating with 4 (5) sessile glands, the glands simple or often with broad flat white or red petal-like appendages. **Male flowers** few to many within the cyathium, each ♂ flower represented by a single stipitate stamen, anthers with 2 divergent thecae. **Female flower** solitary in the cyathium, represented by a stipitate naked pistil (perianth represented by a rim at the apex of the stipe), ovary 3-locular, ovules 1/locule, styles 3, free or united near the base, bifid distally. **Fruits** usually exerted from the calyx-like involucre by elongation of the stipe, capsules separating into 3 2-valved cocci; seeds ovoid to oblong, 3- or 4-sided (terete) in cross-section, surface smooth, ribbed or sculpted, usually ecarunculate, embryo straight, cotyledons flat, endosperm copious.

A worldwide genus of ca. 250 species, with most of the species in the American tropics and subtropics. Many plant taxonomists do not accept this genus, treating it as a subgenus of *Euphorbia* (see discussions in Webster & Burch, 1967; Webster, 1994b, p. 129; McVaugh, 1993, p. 210). Both taxa

possess the cyathium, a flower-like structure made up of a number of reduced ♂ flowers and a single ♀ flower within a calyx-like involucre or floral cup. The reduced ♂ and ♀ flowers consist only of individual stamens or an individual pistil; they usually have no perianth (see the discussion under *Euphorbia*). Both individual stamens and pistils are pedicellate, here called stipitate to avoid confusion. The edge of the involucre usually has a space resulting from the failure of the 5th gland to develop; the ♀ stipe (pedicel) often deflects in this area. As in *Euphorbia*, the latex of these plants may be caustic; they are not eaten by livestock or most insects. The sap is sometimes used medicinally (cf. *C. bahiensis* and *C. hirta*).

Species of *Chamaesyce* are usually easy to recognize because of their small opposite distichous leaves that are clearly asymmetric at the base, stipules usually united between the petiole bases, and milky sap. Stems and leaves are often marked with red or purple. The leaves are often held in a single plane and slightly succulent. In thin leaves viewed by transmitted light, the minor veins are seen as free-ending within clear areas of the leaf. The small-leaved prostrate mat-forming species are usually called *golondrina* in Central America, a name that may also be used for *Alternanthera polygonoides* (Amaranthaceae). *Chamaesyce* species are almost always plants of open sunny or early secondary succession sites, often associated with sandy or gravelly soils.

### Key to the Species of *Chamaesyce*

- 1a. Fruits glabrous (rarely with a few hairs at the base) ..... 2
- 1b. Fruits puberulent (only on the edges in *C. prostrata*) ..... 8
  - 2a. Leaf blades entire or slightly crenate at the apex, not > 16 mm long, blades usually of similar size on main stems and lateral stems; plants erect or prostrate ..... 3
  - 2b. Leaf blades serrulate along the distal margins, to 35 mm long; blades of the main stem often noticeably larger than those of lateral stems; plants rarely prostrate [seeds often dark gray with poorly developed transverse ribs; species appearing very similar] ..... 5
    - 3a. Erect subshrubs to 60 cm tall; leaf blades stiff, ovate-elliptic or elliptic, to 16 mm long [fruits 1.2–2 mm long; seeds 1.1–1.3 mm long; plants of Caribbean seashores] ..... *C. mesembryanthemifolia*
    - 3b. Prostrate herbs; leaf blades not stiff, oblong to suborbicular, to 10(–12) mm long .. 4
    - 4a. Fruits 2–2.2 mm long; seeds 1.2–1.6 mm long, smoothly rounded and with a longitudinal line (raphe) down the adaxial side; plants of the Caribbean seashore .. *C. bombensis*
    - 4b. Fruits 1.2–1.7 mm long; seeds 0.8–1.1 mm long, with 3–4 concave sides and lacking a longitudinal line or ribs; mostly at edge of fresh water lagoons and in wet depressions ..... *C. serpens*
- 5a. (from 2b) Fruits becoming 2–2.6 mm long, ca. 3 mm wide; rarely collected plants of the sandy Caribbean seashore, 0–5 m elevation ..... *C. bahiensis*

- 5b. Fruits 1–2 mm long, ca. 2–2.5 mm wide; plants of open weedy sites and also found near seashores ..... 6
- 6a. Fruits 0.9–1.3 mm long; columella < 1 mm long; transverse ribs on seeds often poorly defined, giving a pitted or irregular surface; inflorescences usually with leafless distal nodes; stipules usually 1–1.5 mm long and conspicuous ..... *C. hypericifolia*
- 6b. Fruits 1.4–2 mm long; columella > 1 mm long; transverse ribs on the sides of the seeds usually prominent and well defined; inflorescences with narrow reduced leaves at distal nodes; stipules usually ca. 0.5 mm long and inconspicuous ..... 7
- 7a. Distal stems glabrous or with narrow lines of hairs along one side; common plants ..... *C. hyssopifolia*
- 7b. Distal stems usually with hairs along one side; uncommon plants ..... *C. nutans*
- 8a. (from 1b) Plants with erect or trailing stems to 1.5 m long [internodes 1–6 cm long; leaf blades to 4 cm long; seeds 0.9–1.2 mm long, often with irregular ribs and dark gray in color; 10–1200 m elevation] ..... *C. lasiocarpa*
- 8b. Plants prostrate to procumbent (erect in *C. hirta*), rarely > 0.4 m high or 0.5 m long ..... 9
- 9a. Cyathia in capitate (leafless) glomerules on short or prominent peduncles; larger leaves 15–38 mm long; internodes to 5 cm long [stems branched mainly near the base, leaf blades usually ovate-elliptic and tapering to the apex; seeds 0.6–0.8 mm long, with transverse ribs; widespread weeds to 1400 m elevation] ..... *C. hirta*
- 9b. Cyathia not in congested pedunculate capitate glomerules, cyathia or glomerules usually subtended by leaf pairs or reduced leaves; larger leaves 5–18 mm long; internodes on distal stems rarely > 2 cm long ..... 10
- 10a. Fruits usually exserted and easily seen on short peduncles or on a stipitate base, not closely subtended by cyathium and leaves; distal leaf axils and inflorescences not obscured by thin cotton-like hairs ..... 11
- 10b. Fruits appearing sessile on the cyathium and closely subtended by subtending leaves, peduncle or stipe rarely visible without removal of adjacent leaves; distal leaf axils and base of inflorescences with thin cotton-like whitish hairs ..... 12
- 11a. Leaves to 14(–19) mm long, narrowed at the apex; cyathia in dense glomerules with subtending leaves only at the base; seeds 0.7–0.9 mm long ..... *C. ophthalmica*
- 11b. Leaves to 7 mm long, usually rounded at the apex; cyathia 1–3 on axillary short-shoots and subtended by reduced leaves; seeds 0.8–1.1 mm long ..... *C. prostrata*
- 12a. Fruits not fully exserted from the cyathial involucre, often splitting the involucre at maturity; petaloid appendages small or obscure, equal in size; seeds 0.6–0.7 mm long [0–1200 m elevation] ..... *C. thymifolia*
- 12b. Fruits closely subtended by the cyathia and not splitting them at maturity; petaloid appendages conspicuous and unequal with 2 larger and 2 smaller on each cyathium; seeds 0.7–0.9 mm long ..... 13
- 13a. Petaloid appendages glabrous above and puberulent beneath; seeds gray or pinkish; 0–2000 m and usually found above 800 m elevation ..... *C. densiflora*
- 13b. Petaloid appendages glabrous above and beneath; seeds gray to pink or brown; 0–200 m ..... *C. dioeca*

**Chamaesyce bahiensis** (Klotzsch & Garcke) Dugand & Burch, Ann. Missouri Bot. Gard. 54: 344. 1967. *Anisophyllum bahiense* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 33. 1859. *Euphorbia bahiense* (Klotzsch & Garcke) Boiss. in DC., Prodr. 15 (2): 24. 1862.

**Herbs** to 0.4 m high, decumbent to erect, often many-branched, annual or perennial, internodes 8–35 mm long,

leafy stems 0.2–2.5 mm thick, glabrous or with thin curved hairs to 0.3 mm long; stipules 0.2–0.8 mm long, united, triangular to lacerate. **Leaves** sometimes dimorphic with those of the lateral branches considerably smaller than those on the main stems, petioles 0.5–1.5 mm long, 0.2–0.5 mm thick, glabrous; **leaf blades** 6–20(–30) mm long, 4–8.5(–12) mm wide, oblong to elliptic-oblong or oblong-obovate, apex obtuse to rounded, margin subentire to minutely (0.1 mm) serrulate with up to 20 teeth/side, base asymmetric with one rounded side and the other more oblique, drying chartaceous, glabrous above, with few thin hairs to 0.8 mm long beneath, venation palmate



with 3 major veins. **Inflorescences** terminal, cyathia usually solitary in dichasia subtended by opposite leaves or narrow bracts, peduncles 0.3–1.5 mm long. **Cyathia** with involucre ca. 0.8 mm long, 0.6 mm wide at the apex, obconic or tubular, glabrous, petaloid appendages  $0.2 \times 0.3$  mm or absent, white; ovary ca.  $0.5 \times 0.4$  mm, oblong, styles ca. 0.4 mm long. **Fruits** 2–2.6 mm long, 2–3 mm wide, ovoid with truncated base and rounded sides, glabrous; seeds 1.3–1.8 mm long, 0.8–1.1 mm wide, oblong to broadly ellipsoid, with 4 rounded corners in cross-section, transverse ribs 1–3 but not well developed and sometimes giving an irregular surface, grayish.

Uncommon plants of sandy seashores, 0–5 m elevation. Probably flowering throughout the year. The species ranges along the Caribbean and Atlantic seashore from Nicaragua to southern Brazil.

*Chamaesyce bahiensis* is recognized by its small stature, seaside habitat, well-spaced leaves often differing in size on main and lateral stems, glabrous cyathia and fruits, and gray seeds with unusual surface. These plants are very similar to *C. hyssopifolia* but differ in the slightly larger fruits and restriction to seaside habitats.

**Chamaesyce bombensis** (Jacq.) Dugand, *Caldasia* 10: 190. 1968. *Euphorbia bombensis* Jacq., *Enum. pl. syst.* 22. 1760. *E. ammannioides* H.B.K., *Nov. gen. sp.* 2: 55. 1817. *C. ammannioides* (H.B.K.) Small, *Fl. Southeastern U.S.* 709, 1333. 1903. Figure 6.

**Herbs**, prostrate or decumbent, forming loose mats to 0.8 m diam. (not rooting at nodes), leafy stems 0.3–2.2 mm thick, internodes 5–35 mm long, glabrous, often reddish; stipules 0.3–1.7 mm long, with a basal transverse ridge and 2–7 linear laciniate segments. **Leaves** often clustered distally, petioles 0.5–1.5 mm long, ca. 0.3 mm thick, glabrous; **leaf blades** 3–10(–12) mm long, 1.2–5(–6) mm wide, oblong, apex obtuse or rounded and often with a mucronate tip ca. 0.2 mm long, margin entire, base slightly subcordate, asymmetric with 1 side more rounded than the other, drying chartaceous, often dark in color, glabrous, surface often reticulate, venation pinnate, 2° veins 3–6/side. **Inflorescences** terminal, of solitary cyathia or dichasia of condensed shoots, glabrous, peduncles to 1.5 mm long; **cyathia** with involucre 1–1.4 mm long, 0.8–1.2 mm wide distally, obconic, glabrous, glands suborbicular, petaloid appendages ca. 0.5 mm long or absent, white; ovary 0.5–0.8 mm long, styles ca. 0.4 mm long, stipe to 2.3 mm long in fruit. **Fruits** 1.7–2.2 mm long, 2.2–3 mm wide, ovoid-triangular with truncated base and rounded sides, glabrous, columella ca. 1.5 mm long; seeds 1.2–1.4(–1.8) mm long, 1–1.3 mm wide, ovoid-subglobose, rounded in cross-section and 3-angled only near the apex, whitish, smooth with a longitudinal line (raphe) on the inner face.

Plants of open sunny sites along the Caribbean seashore, 0–20 m elevation. Probably flowering

throughout the year. The species ranges from Florida, Cuba, and Mexico through Central America to northern South America.

*Chamaesyce bombensis* is recognized by its small leaves, lack of pubescence, lacinate stipules, and unusual rounded seeds. This is our only species of *Chamaesyce* with seeds having a longitudinal line (raphe) clearly demarked on a smooth rounded surface. The thick little leaves with reticulated (dried) surface and pinnate venation are distinctive.

**Chamaesyce densiflora** (Klotzsch & Garcke) Millsp., *Publ. Field Columb. Mus. Nat. Hist., Bot. Ser.* 2: 391. 1914. *Anisophyllum densiflorum* Klotzsch & Garcke, *Monatsber. Königl. Preuss. Akad. Wiss. Berlin* 1859: 28. 1860. *Euphorbia densiflora* (Klotzsch & Garcke) Klotzsch in Peters, *Reise Mossamb.* 94. 1862. Figure 7.

**Herbs** to 0.6 m wide, prostrate, decumbent or erect, much branched, internodes 3–15(–30) mm long, leafy stems 0.4–2 mm thick, usually densely pubescent with thin multicellular hairs to 1 mm long, pubescent throughout, on 1 side, or in 2 longitudinal rows; stipules subulate, bifid or lacerate, slender teeth 1–1.8(–2.5) mm long. **Leaves** subsessile or with petioles to 1 mm long, ca. 0.4 mm thick, glabrous or puberulent; **leaf blades** (4–)7–16(–20) mm long, 1.5–6(–9) mm wide, oblong, to ovate-oblong, apex bluntly obtuse or asymmetrically rounded, margin serrulate with small (0.1–0.3 mm) serrations to 16/side, base strongly asymmetric with a rounded subcordate-auriculate side and a slightly rounded side, drying chartaceous, subglabrous or puberulent on both surfaces with thin whitish hairs ca. 0.3 mm long, venation palmate with 3 major veins, 2° veins obscure. **Inflorescences** terminal or apparently axillary (terminal on axillary short-shoots), 6–12 mm long, cyathia densely crowded and obscured by leafy bracts, with thin whitish hairs to 1 mm long; **cyathia** with involucre ca. 1 mm long, campanulate, glands suborbicular to reniform, petaloid appendages 0.9–1.5 mm long, 0.7–2 mm wide, of 2 unequal pairs, ovate to reniform, usually reddish (white), pilose on the lower surface; stamens with anthers 0.3 mm wide; ovary ca.  $1 \times 1$  mm, densely appressed puberulent, styles ca. 1.5 mm long, united for 0.5 mm, bifid distally. **Fruits** 1–1.6 mm long, 0.9–1.2 mm wide, ovoid with truncated base, minutely pilose, columella 0.6–0.7 mm long; seeds 0.6–0.9 mm long, 0.4–0.6 mm wide, oblong-triangular, 4-angled in cross-section, with 4–5 prominent transverse ribs on each side, pale grayish or pink.

Common weedy plants of open sunny sites in both evergreen and deciduous areas, sea level to 2000 m elevation. In Costa Rica the species is most often found above 800 m elevation. Flowering and fruiting primarily in July–February. The species ranges from northern Mexico to northern South America.

*Chamaesyce densiflora* is recognized by the usually prostrate mat-forming habit, small closely set leaves strongly asymmetric at the base, and cyathia densely crowded (and obscure) within hairy bracts in the small dense inflorescences. The larger, usually red, petaloid appendages of the glands occur in 2 unequal pairs on the cyathium. This is one of the species often called *golondrina*. This species is closely related to *C. dioeca* and is very similar in overall appearance (q.v.).

***Chamaesyce dioeca* (H.B.K.) Millsp. (as *C. dioica*),** Publ. Field Columb. Mus. Nat. Hist., Bot. Ser. 2: 384. 1914. *Euphorbia dioeca* H.B.K., Nov. gen. sp. 2: 53. 1817. Figure 6.

**Herbs**, prostrate or decumbent, with many branches from the base and often forming flat mats, 15–70 cm wide, leafy stems 0.3–1 mm thick, internodes 2–18 mm long, puberulent with thin hairs 0.2–0.5 mm long; stipules 0.5–2 mm long, with 2–5 linear teeth. **Leaves** often marked with red, petioles 0.5–1.5 mm long, 0.2–0.4 mm thick, glabrous or puberulent; **leaf blades** 3–15 mm long, 1.5–7 mm wide, broadly oblong to ovate-oblong or obovate-oblong, apex rounded to obtuse or acute, margin serrate with 3–6 teeth/side, base strongly asymmetric with a rounded to auriculate side and a cuneate or slightly rounded side, drying stiffly chartaceous, green or with purple spots, glabrous or sparsely puberulent, venation subpalmate with 3 major veins. **Inflorescences** terminal (often on axillary short-shoots) and tightly congested within the distal leaves, white pubescent at the base, peduncles short and rarely visible; **cyathia** with involucre 0.8–1.2 mm long, ca. 0.7 mm diam., obconic, appressed-puberulent, glands reniform to narrowly elliptic, petaloid appendages of 2 unequal pairs, reddish to white, glabrous on both sides, the larger 1–1.5 mm long, 1.3–2 mm wide; ovary ca. 0.7 mm long, styles 0.8–1 mm long, united for ca. 0.5 mm. **Fruits** 1–1.4 mm long, 1–1.3 mm wide, ovoid with truncated base, puberulent, columella 0.8–1 mm long; seeds 0.6–0.9 mm long, 0.3–0.5 mm wide, oblong with narrowed tip, 4-sided in cross-section, often with (2–)3–5 transverse ribs separated by pits, pinkish or brown.

Common plants of open sunny sites in the Pacific lowlands and along the seashore, 0–600 m elevation (rarely to 1200 m elevation elsewhere). Probably flowering mostly in the wet season (June–October). The species ranges from central Mexico to South America.

*Chamaesyce dioeca* (also labeled *dioica*) is recognized by its usually prostrate habit, puberulent stems, stipules with two to five slender teeth, very small leaves, densely congested inflorescences with thin white hairs, subsessile puberulent fruits, and restriction to the Pacific lowlands. The cyathia are noteworthy in having conspicuous petaloid appendages in two pairs differing in size. These ap-

pendages are glabrous on both surfaces in contrast to those of the closely related *C. densiflora* where the appendages are puberulent beneath. Compare also the very similar *C. thymifolia*; see the discussion by McVaugh (1993, pp. 214–216). We attempt to maintain a traditional usage and are not convinced that small differences in ribbing of the lateral seed surfaces is significant.

***Chamaesyce hirta* (L.) Millsp.,** Publ. Field Columb. Mus., Bot. Ser. 2: 303. 1909. *Euphorbia hirta* L., Sp. Pl. 454. 1753. *E. globulifera* H.B.K., Nov. gen. sp. 2: 56. 1817. Figure 7.

**Herbs** 0.1–0.4 m tall, decumbent or erect, internodes 0.5–5 cm long, leafy stems 0.4–2.5 mm thick, minutely (0.1 mm) puberulent to densely hirtellous with multicellular hairs to 1.5 mm long; stipules united for ca. 0.5 mm at the base and with lobes or teeth 1–2 mm long. **Leaves** often marked with red, petioles 1.2–3.5 mm long, 0.3–0.7 mm thick, puberulent; **leaf blades** (4–)7–35(–50) mm long, (3–)4–14(–18) mm wide, ovate-rhombic to ovate-elliptic or asymmetrically lanceolate, apex acute to bluntly acute, margin subserrate or serrate with 6–30 teeth/side, 0.1–0.3 mm high, base usually asymmetric with a cuneate side and opposing rounded-truncate side, drying chartaceous, slightly rough or scabrous above with stiff hairs 0.1–0.2 mm long, with longer (to 0.9 mm) thin hairs beneath, venation palmate with 3 (4) major veins, asymmetric, 2° veins 1–3/side of the midvein. **Inflorescences** usually axillary, solitary and 1/node, 4–18 mm long, 5–16 mm wide, peduncle 2–9 mm long, 0.4–0.5 mm thick, puberulent, bifid distally, pedicels ca. 0.5 mm long; **cyathia** with involucre ca. 1 × 0.8 mm, obconic, glabrous to strigose, often reddish, glands minute, orbicular, petaloid appendages usually absent; anthers ca. 0.1 × 0.2 mm. **Fruits** 0.7–1.2 mm long, 1–1.4 mm wide, ovate with truncated base, strigose, persisting styles 0.2–0.4 mm long, borne on a stipe 0.5–1 mm long, columella 0.7–0.8 mm long; seeds 0.6–0.8 mm long, 0.4–0.5 mm wide, narrowly ovoid, 4-sided in cross-section, with 4–5 transverse ribs on each side, grayish to reddish brown or tan.

Common weedy plants of open sunny sites in both wet evergreen and seasonally dry deciduous formations, 0–1400 m elevation. Probably flowering and fruiting throughout the year (but not collected in September–October). This species, now a pantropical weed, ranges from the southern United States to Argentina and the West Indies; it has been collected on Cocos Island.

*Chamaesyce hirta* is recognized by its longer multicellular hairs, leaves usually acute at the apex, compact pedunculate inflorescences (usually axillary and one per node), and puberulent fruits. The peduncles are often short and difficult to see. These plants are often called *golondrina* in Costa Rica. It has been reported that *C. hirta* can cause



ulcerations by the transfer of flagellates, but this is doubtful since the sap is often used to heal wounds (Standley & Steyermark, 1949, p. 105).

***Chamaesyce hypericifolia* (L.) Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 302. 1909. *Euphorbia hypericifolia* L., Sp. Pl. 454. 1753. *C. glomifera* Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 377. 1913. *E. glomifera* (Millsp.) Wheeler, Contr. Gray Herb. 127: 78. 1939.**

**Herbs** 0.2–0.8 m high, prostrate or erect, usually few-branched with internodes 1–7 cm long, reddish or green, leafy stems 0.3–2.7 mm thick, glabrous or with few minute (0.1–0.3 mm) thin hairs; stipules 0.5–1.5 mm long, united and triangular or divided; **leaf blades** (5–)8–38 mm long, (2–)3–16 mm wide, oblong to ovate-oblong or narrowly oblong, apex bluntly obtuse or rounded, margin slightly serrate with 7–15 teeth/side, base asymmetric with a slightly rounded-cuneate side and rounded-truncate side (rarely subcordate), drying membranaceous, glabrous, venation palmate with 3 major veins, slightly asymmetric, 2° veins 1–3/side of the midvein. **Inflorescences** axillary or terminal, borne on monopodial or dichotomous branches with nodes usually lacking reduced leaves, cyathia often crowded in short (6 mm) groups, glabrous; **cyathia** with involucre ca. 0.8 mm long, obconic, glands elliptic to suborbicular, petaloid appendages white to pink (or absent); ovary glabrous, green, styles 0.3–0.4 mm long. **Fruits** 0.9–1.3 mm long, ca. 1.5 mm wide, ovoid with truncated base, glabrous, borne on a stipe 0.5–1 mm long, persisting styles 0.4–0.7 mm long, columella 0.7–0.9 mm long; seeds 0.8–1 mm long, ca. 0.6 mm wide, ovoid, 4-sided in cross-section, with irregular depressions on the surfaces, dark gray to brown or yellowish.

Plants of open sunny sites in both evergreen and deciduous vegetation, 0–500 m elevation. This species is rarely collected in southern Central America. Probably flowering and fruiting throughout the year. This species ranges from the southern United States, West Indies, and Mexico to Argentina and is an adventive in the Old World.

*Chamaesyce hypericifolia* is recognized by its usually glabrous parts, usually oblong sessile leaves separated by conspicuous internodes, irregularly arranged distal cyathia lacking reduced leaves distally, the small fruits, and small seeds with irregular depressions on the surfaces. The distinctions between this species and *C. hyssopifolia* are subtle; fruiting material is necessary to distinguish them. Much Central American material determined as this species is actually *C. hyssopifolia* (q.v.).

***Chamaesyce hyssopifolia* (L.) Small, Bull. New York Bot. Gard. 3: 429. 1905. *Euphorbia* *hyss-***

***sopifolia* L., Syst. Nat. ed. 10, 1048. 1759. *E. brasiliensis* Lam., Encyc. Méth. Bot. 2: 423. 1788. Figure 7.**

**Herbs** 0.3–0.6(–1) m tall, spreading or erect, internodes of the main stems 1–3 cm long, leafy stems 0.2–3.5 mm thick, glabrous or with few minute (0.1–0.3 mm) thin whitish hairs along longitudinal lines, terete; stipules 0.3–1 mm long, triangular, divided or with an erose margin. **Leaves** with petioles 0.4–3 mm long, 0.1–0.4 mm thick, glabrous or with a few thin whitish hairs to 0.3 mm long; **leaf blades** 6–28(–35) mm long, 3–10(–16) mm wide, oblong to elliptic-oblong or oblong-obovate, apex bluntly obtuse or rounded, margin subentire or minutely (0.1–0.2 mm) serrate with 6–20 teeth/side, base usually asymmetric with a cuneate (slightly rounded) side and an opposite more rounded or truncated side, drying membranaceous or thinly chartaceous, glabrous, venation palmate and slightly asymmetric, with 3 major veins, 2° veins 3–5/side of the midvein. **Inflorescences** terminal or pseudoaxillary, monochasia or dichasia, peduncles 0.5–2 mm long, distal nodes usually subtended by reduced narrow leaves; **cyathia** with involucre 1–2 mm long, glabrous, glands oblong to reniform, petaloid appendages 0.1–0.3 mm long and 0.3–0.6 mm wide, rounded distally, white or pink; anthers ca. 0.1 × 0.4 mm, ovary 0.5–0.6 mm long, glabrous, styles 0.3–0.6 mm long, separate to the base. **Fruits** 1.5–2 mm long, 1.8–2 mm wide, ovoid or ovoid-trigonal with a truncated base, glabrous, yellowish, columella 1.1–1.5 mm long, widened at the apex; seeds 0.8–1.3 mm long, 0.6–0.7 mm wide, oblong or ovoid, 3- or 4-sided in cross-section, grayish, with 2–4 prominent transverse ribs or obscurely pitted, gray to black.

Common plants of open sunny sites in evergreen or deciduous forest areas, 0–1100 m elevation. Flowering and fruiting throughout the year (probably primarily in the wet season in deciduous formations). These plants are most often found below 300 m elevation in Costa Rica. This species ranges from the southern United States and West Indies to Argentina; it has become naturalized in the Old World tropics.

*Chamaesyce hyssopifolia* is recognized by its stems with longer internodes, oblong usually glabrous leaves with palmate venation, glabrous ovaries and fruits, and grayish ribbed fruits. The inflorescences usually bear narrow reduced leaves at most distal nodes. Large individuals of this species may resemble *C. lasiocarpa*, but that species has puberulent fruits and consistently erect habit. Central American material of *C. hyssopifolia* has often been misidentified as *C. hypericifolia* or the rarely collected seaside *C. bahiensis*; compare *C. nutans*. These plants have been used as a kidney medicine in Costa Rica (Stevens 24163).



***Chamaesyce lasiocarpa*** (Klotzsch) Arthur, Torreya 11: 260. 1911. *Euphorbia lasiocarpa* Klotzsch, Nov. Act. Leop. 19, suppl. 1: 414. 1843. *E. hypericifolia* L. *sensu* Wheeler in Contr. Gray Herb. 127: 73. 1939, and Fieldiana Bot. 24, pt. 6: 105. 1944. Figure 7.

**Herbs** or subshrubs with woody base and erect or spreading stems, 0.3–1.5 m tall, internodes 0.6–6 cm long, leafy stems 0.3–3 mm thick, minutely puberulent with thin curved hairs 0.1–0.3 mm long, glabrescent, terete; stipules 0.4–1.5 mm long, acute or erose. **Leaves** with petioles 0.7–3 mm long, 0.2–0.4 mm thick, puberulent with thin whitish hairs; **leaf blades** 7–37 mm long, 2–16 mm wide, oblong, oblong-ovate to ovate-elliptic or oblong-obovoid, apex bluntly obtuse or rounded (acute), margin minutely serrate with 6–28 teeth/side, teeth 0.1–0.3 mm high, base usually asymmetric with a cuneate side and rounded side, drying thinly chartaceous, puberulent with thin whitish hairs 0.2–0.6 mm long on both surfaces (glabrate), venation palmate and asymmetric with 3 major veins, 2° veins 2–5/side of the midvein. **Inflorescences** of terminal or axillary cyathia in short-stalked leafy dichasia, peduncles 0.5–4 mm long; **cyathia** with involucre 1.2–2.4 mm long, obconic, ca. 2 mm wide at apex, tomentulose, glands suborbicular, with 3–4 petaloid gland appendages 0.3–0.7 mm long, 0.5–1.4 mm wide, white turning pink; anthers ca. 0.1–0.3 mm long, rounded; ovary ca. 0.7 × 0.5 mm, ovoid, densely whitish pubescent, styles 0.5–0.6 mm long. **Fruits** 1–2.2 mm long, 1–2.2 mm wide, ovoid and 3-lobed, puberulent, styles 0.5–1 mm long, columella 1–1.3 mm long; seeds 0.9–1.2 mm long, 0.5–0.7 mm wide, oblong-ovoid, 4-sided in cross-section, dark reddish brown or dark grayish, with transverse ribs or with irregular ribs and a surface with depressions.

Common plants of open sunny sites of seasonally dry deciduous and partly deciduous vegetation, 10–1200 m elevation. Probably flowering and fruiting throughout the year (a majority of collections were made in July–January). The species ranges from southern Florida, eastern Mexico, and the West Indies to Peru and Brazil.

*Chamaesyce lasiocarpa* is recognized by its usually erect stems, longer glabrescent internodes, short pubescence, oblong leaves serrate along most of their margins, puberulent fruits, and dark grayish or brown four-angled ribbed seeds. Unlike many of its congeners, this species is not found along seashores. Smaller specimens may resemble material of *C. hyssopifolia* (but that species has glabrous fruits).

***Chamaesyce mesembryanthemifolia*** (Jacq.) Dugand, Phytologia 13: 385. 1966. *Euphorbia mesembryanthemifolia* Jacq., Enum. syst. pl. 22. 1760. *E. buxifolia* Lam., Encyc. Méth. Bot. 2:

421. 1788. *E. litoralis* H.B.K., Nov. gen. sp. 2: 54. 1817. *E. flexuosus* H.B.K., Nov. gen. sp. 2: 55. 1817. *C. buxifolia* (Lam.) Small, Fl. South-eastern U.S. 712, 1333. 1903. Figure 7.

Small **shrubs** or subshrubs 0.2–0.6 m tall, stems erect or ascending, perennial with woody stems to 8 mm thick, usually reddish, internodes usually short (3–12 mm) and uniform on distal stems, leafy stems 0.6–2 mm thick, glabrous, nodes often thickened; stipules 1–2 mm long, ca. 1.5 mm broad at the base, triangular to ovate, with erose margin. **Leaves** often in 2 ranks, subsessile with petioles 0.3–0.9 mm long, ca. 0.3 mm thick, glabrous; **leaf blades** 5–16 mm long, 3–8 mm wide, elliptic-oblong to oblong-obovate, apex obtuse or acute, margin entire and often revolute when dried, base slightly asymmetric and auriculate on both sides, drying stiffly chartaceous and gray or yellowish, glabrous, venation palmate with 3 major veins. **Inflorescences** terminal, of solitary cyathia enclosed and hidden by crowded distal leaves. **Cyathia** with involucre 1.3–1.7 mm long, 0.8–1.2 mm wide at apex, obconic, glabrous, glands elliptic, petaloid appendages 0.4–0.8 mm long, ca. 0.7 mm wide, obovate, white, with entire margin; ovary ca. 1 mm long, glabrous, styles ca. 0.4 mm long, stipe 0.5–1.2 mm long and becoming 2.3 mm long in fruit. **Fruits** 1.7–2 mm long, 2–2.7 mm wide, broadly ovoid with truncated base to subglobose, glabrous, columella ca. 1.8 mm long; seeds 1.1–1.3 mm long, 1–1.2 mm thick, ovoid-ellipsoid with rounded surfaces, the 4 longitudinal edges not well developed except at the apex, surfaces smooth or slightly pitted, pale grayish.

Uncommon plants of sandy dunes and ocean shores of the Caribbean, 0–20 m elevation. This species has not been collected in Costa Rica but is known from nearby Nicaragua and Panama. The species ranges around the shores of the Caribbean from eastern Mexico, Florida, and the West Indies to northern South America.

*Chamaesyce mesembryanthemifolia* is recognized by its short shrubby habit, restriction to Caribbean seaside habitats, stiff short petiolate entire leaves often borne in two distichous ranks along the stems, conspicuous “petals,” and unusual seeds. The seeds differ from most of our species in their form and smooth surface.

***Chamaesyce nutans*** (Lag.) Small, Fl. Southeastern U.S. 712, 1333. 1903. *Euphorbia nutans* Lag., Gen. sp. pl. 17. 1816. Figure 7.

**Herbs** or herbaceous subshrubs to 0.6 m tall, leafy stems 0.4–2 mm thick, internodes 4–20 mm long, glabrous or minutely (0.1 mm) puberulent along 1 side; stipules 0.3–1 mm long, triangular to rounded-erose or ciliate, translucent. **Leaves** subsessile, petioles 0.4–1.3 mm long, 0.2–0.4 mm thick, glabrous; **leaf blades** 5–22(–30) mm long, 3–9(–15) mm wide, broadly oblong to

narrowly oblong or ovate-oblong, apex obtuse, distal margin with 5–20 minute teeth, base asymmetric with 2 rounded sides, drying thin-chartaceous, glabrous or sparsely puberulent beneath, venation palmate with 3 major veins. **Inflorescences** usually terminal, solitary at a branch dichotomy or subtended by narrow leaves ca.  $6 \times 2$  mm, glabrous; **cyathia** 0.5–1 mm long, 0.5–0.7 mm wide at apex, obconic or tubular, glabrous, glands elliptic, petaloid appendages present or absent, white to pink; ovary ca.  $0.8 \times 0.7$  mm, styles 0.4–0.5 mm long. **Fruits** (1.3–)1.9–2 mm long, (1.4–)2–2.5 mm wide, ovoid-triangular with rounded sides, glabrous, borne on stipes to 2 mm long, columella 1.1–1.4 mm long; seeds 1–1.3 mm long, 0.6–1 mm wide, ovoid with narrowed apex, rounded with 3 or 4 sides in cross-section, transverse ribs irregular and giving a wrinkled or pitted surface, dark.

Uncommon plants of open sunny sites in both evergreen and deciduous forest areas, 0–500 m elevation. Probably flowering throughout the year. It is rarely collected in Costa Rica. The species ranges from southern Canada, the eastern United States, and Mexico to Costa Rica.

*Chamaesyce nutans* is recognized by its erect or decumbent stems (often puberulent along one side), mostly glabrous parts, larger leaves on main stems, and dark seeds with irregular (apparently pitted) surfaces. The senior author believes that Central American specimens placed here are not specifically distinct from those identified as *C. hyssopifolia* and that *C. nutans* may not be worthy of specific rank.

**Chamaesyce ophthalmica** (Pers.) Burch, Ann. Missouri Bot. Gard. 53: 98. 1966. *Euphorbia ophthalmica* Pers., Syn. Pl. 2: 13. 1807. *E. procumbens* DC., Cat. Pl. Hort. Monsp. 111. 1813. Figure 6.

**Herbs**, prostrate or decumbent, stems 5–50 cm long, leafy stems 0.3–1.8 mm thick, internodes 5–20 mm long, puberulent with thin straight or crooked hairs 0.2–0.8 mm long; stipules 0.3–2 mm long, laciniate or with 2 linear lobes, puberulent. **Leaves** with petioles 0.7–2 mm long, 0.2–0.3 mm thick, puberulent; **leaf blades** 3.5–14(–19) mm long, 2–8(–12) mm wide, ovate-elliptic to narrowly ovate-oblong or oblong, apex obtuse to bluntly acute, margin serrate with 6–18 teeth/side, 0.1–0.3 mm high and most prominent distally, base strongly asymmetric with a rounded side and a cuneate side, drying membranaceous, glabrous or sparsely to densely puberulent with hairs 0.1–0.5 mm long, venation palmate with 3 major veins. **Inflorescences** terminal, to 5 mm long, of congested cyathia and distal leaves, peduncles ca. 0.5 mm long; cyathia puberulent, glands suborbicular, petaloid appendages usually absent; ovary borne on a short (0.5 mm) stipe, styles ca. 0.2 mm long. **Fruits** 1.1–1.4 mm long, 1–1.3 mm wide, ovoid-triangular with truncated base and slightly rounded sides, surfaces puberulent with minute (0.1 mm) whitish hairs, columella 0.8–

1 mm long; seeds 0.7–0.9 mm long, 0.3–0.4 mm wide, oblong with narrowed apex, 4-sided in cross-section, concave or with 2–5 transverse ribs on each side, pale brown to grayish brown.

Uncommon plants of open sunny sites in sandy river margins and weedy sites, 20–1200 m elevation. Probably capable of flowering throughout the year. Known in Costa Rica from a single collection made in the city of San José in April (*Liesner 14176*). The species ranges from southern Florida and the West Indies to Argentina and occurs in the Old World tropics.

*Chamaesyce ophthalmica* is recognized by its congested inflorescences, very short styles, and puberulent fruit.

**Chamaesyce prostrata** (Aiton) Small, Fl. South-eastern U.S. 713, 1333. 1903. *Euphorbia prostrata* Aiton, Hort. kew. 2: 139. 1789. Figure 6.

**Herbs** 5–20(–30) cm long, prostrate or scandent, internodes 1–10 mm long, leafy stems 0.3–1 mm thick, glabrous or minutely puberulent with thin hairs 0.1–0.4 mm long, often in 2 longitudinal lines; stipules 0.2–0.5 mm long, erose or 2-lobed, puberulent. **Leaves** with petioles 0.3–0.9 mm long, ca. 0.2 mm thick, glabrous or puberulent; **leaf blades** 2–9 mm long, 1–5 mm wide, oblong to oblong-obovate or oblong-ovate, apex rounded or bluntly obtuse, margin minutely denticulate distally with 3–9 minute teeth/side, base slightly asymmetric with larger rounded side and a shorter somewhat cuneate side, drying chartaceous, glabrous, venation palmate with 3 major veins. **Inflorescences** axillary or terminal on small axillary short-shoots with reduced (2 mm) leaves, 2–8 mm long, cyathia 1–3, peduncles 0.5–2 mm long, to 2.3 mm in fruit; **cyathia** with involucre 0.6–0.9 mm long, 0.4–0.6 mm wide at the apex, obconic, glabrous or sparsely puberulent, glands suborbicular, petaloid appendages 4, very small, as wide as the glands. **Fruits** 1–1.5 mm long, 1.2–1.4 mm wide, ovoid with truncated base, often with hairs along the 3 longitudinal edges and glabrous on the flattened surfaces, borne on a stipe 0.7–1.7 mm long, columella 0.9–1.3 mm long; seeds 0.8–1.1 mm long, 0.4–0.5 mm wide, ovoid-oblong, sharply tetragonus in cross-section, gray, tan, or pinkish, sulcate or with 4–6 narrow transverse ribs on each side.

Plants of open sunny sites, 0–1200 m elevation. Probably flowering throughout the year in Central America. (In Costa Rica, collected only in March–April, in and near San José.) The species ranges from the southern United States (Texas–Florida), Mexico, and the West Indies to northern South America.

*Chamaesyce prostrata* is recognized by its usually small prostrate habit, very small leaves, mostly glabrous little inflorescences, capsules often with



thin hairs along the edges, and seeds with well-defined transverse ribs.

***Chamaesyce serpens* (H.B.K.) Small**, Fl. South-eastern U.S. 709, 1333. 1903. *Euphorbia serpens* H.B.K., Nov. gen. sp. 2: 52. 1817. Figure 6.

**Herbs** to 30 cm wide, prostrate, much branched, often rooting at the nodes, leafy stems 0.2–1.3 mm thick, glabrous or minutely puberulent with thin hairs to 0.5 mm long; stipules 0.3–1 mm long, mostly triangular with lacerate margins, occasionally with 2 rounded glands at the base, often white. **Leaves** with petioles 0.5–1.5 mm long, 0.2–0.3 mm thick, glabrous; **leaf blades** 1.5–7 mm long, 0.7–4.5 mm wide, ovate-oblong to oblong or ovate-obicular, apex bluntly obtuse or rounded and emarginate, margin entire or subserrate, base slightly asymmetric with 1 side distally rounded or subcordate and the other side less so, drying chartaceous, glabrous, venation palmate or subpalmate, usually obscure. **Inflorescences** terminal or becoming pseudoaxillary, usually of solitary (2) cyathia borne on peduncles 0.3–1.2 mm long, to 2.3 mm long in fruit, bracts glabrous; **cyathia** with involucre 0.8–1.3 mm long, 0.5–1.1 mm wide, obconic, with small deltoid lobes, petaloid appendages ca. 0.3 mm long, 0.4–0.5 mm wide, transversely oblong, white. **Fruits** 1.2–1.7 mm long, 1.3–1.7 mm wide, ovoid with truncated base and somewhat flattened sides, glabrous, borne on a stipe 0.4–1.3 mm long, columella 0.8–1.3 mm long; seeds 0.8–1.1 mm long, 0.4–0.6 mm wide, with 4 rounded corners in cross-section, sides somewhat concave, transverse ribs absent or poorly developed, pale brown.

Plants of open sunny areas along margins of freshwater lakes, lagoons, and dried depressions; 0–200 m elevation. Probably flowering and fruiting throughout the year (collected in Costa Rica in April and July). In Costa Rica, this species has only been collected near the mouth of the Río Tempisque, Guanacaste Province. The species now ranges widely, from the midwestern United States and southernmost Canada to Peru and the West Indies.

*Chamaesyce serpens* is recognized by its prostrate habit, minute closely set leaves, generally glabrous parts, and seeds lacking well-developed transverse ribs.

***Chamaesyce thymifolia* (L.) Millsp.**, Publ. Field Columb. Mus., Bot. Ser. 2: 413. 1915. *Euphorbia thymifolia* L., Sp. Pl. 454. 1953. Figure 6.

**Herbs**, usually prostrate and forming small mats to 40–(60) cm wide, stems often reddish, internodes 1.5–12 mm long (less often to 20 mm), leafy stems 0.5–1.7 mm thick, with thin whitish hairs 0.1–0.5 mm long, often glabrous on the lower surface or with longitudinal lines of hairs; stipules 0.5–1.8 mm long, united at the base, triangular or with linear teeth. **Leaves** with petioles 0.4–1 mm long, 0.2–0.4 mm thick, puberulent or glabrous,

drying reddish; **leaf blades** 3–8(–10) mm long, 1–4(–5) mm wide, oblong to ovate-oblong or ovate-elliptic, apex bluntly obtuse to rounded, margin subserrate or with 3–7 teeth/side 0.1–0.2 mm high, base asymmetric with a straight cuneate side and a rounded truncate or subcordate side, drying stiffly chartaceous, glabrous above, glabrous or sparsely puberulent beneath, venation subpalmate with a midvein and 2 (3) major laterals from the base, 2° veins 1–3/side of the midvein, usually obscure. **Inflorescences** usually axillary and inconspicuous, 2–6 mm long, cyathia 1–3 and congested on short (1 mm) peduncles, bracts minute; **cyathia** with involucre 0.8–1 mm long, 0.6–0.8 mm wide, obconic, glands 0.1–0.2 mm wide, elliptic to suborbicular, petaloid appendages in 2 unequal pairs or absent, reddish; anthers ca. 0.3 mm wide, with 2 rounded thecae; ovary ca. 0.7 mm long with styles 0.3 mm long. **Fruits** 1–1.3 mm long, 0.9–1.2 mm wide, ovoid-oblong or ovoid with truncated base, usually with minute appressed hairs, often with 3 somewhat flattened sides, closely subtended by the calyx-like cyathium (without a developed stipe and splitting the cyathium at maturity), columella 0.7–0.9 mm long, slender; seeds 0.6–0.9 mm long, 0.3–0.4 mm wide, 4-sided in cross-section, with 3–4 prominent transverse ribs on each side, pale brown.

Common plants of open sunny sites in both evergreen and seasonally deciduous areas, 0–600(–1200) m elevation. Probably flowering and fruiting throughout the year (collected mostly in December–August). This species is often encountered near the seashore and in open disturbed sites such as river edges and roadsides. The species ranges widely throughout the tropics and subtropics of the Americas and the Old World.

*Chamaesyce thymifolia* is recognized by its usually prostrate mat-forming habit, usually closely spaced little leaves, small axillary inflorescences with few cyathia, and puberulent fruits lacking stipes. It is often called *golondrina* in Central America.

## Cleidion Blume

**Trees** or shrubs, monoecious or dioecious, glabrous or puberulent with simple hairs; stipules present, free, caducous. **Leaves** alternate, simple, margins usually dentate, venation pinnate, often with 2–many glands or glandular hairs at the base of the blade, domatia of tufted hairs present or absent. **Inflorescences** axillary, usually 1/node, unisexual, spicate (♂) or thyrsoid to racemiform (♀), bracts eglandular, flowers small and pedicellate. **Male flowers** with united calyx splitting at anthesis into 3–4 valvate lobes, petals and disk absent; stamens 30–80, densely crowded on a convex receptacle, filaments short and free, in several vertical series, anthers 4-thealous, connective usually expanded distally into an appendage or gland; pistillode absent. **Female flowers** with 3–6 imbricate calyx lobes, petals absent, disk and staminodes absent; ovary 3–(2-)locular, ovules 1/locule, styles united



only at the base, each style deeply divided and bifid to 2-parted (= 6 long style branches). **Fruits** capsules breaking into 3 (2, 1) 2-valved cocci, columella slender; seeds subglobose and smooth, ecarunculate, endosperm present, cotyledons broad, thin.

A pantropical genus of about 25 species, with a majority of species in Australasia, several species in South America, and a single species in western Africa. One species ranges northward to Mexico, while *Cleidion membranaceum* Pax & K. Hoffm. (= *C. woodsonianum* Croizat) reaches central and eastern Panama.

**Cleidion castaneifolium** Müll. Arg., Linnaea 34: 184. 1865. *Alchornea oblongifolia* Standl., Carnegie Inst. Wash. Publ. 461 (Botany of the Maya Area 4): 66. 1935. *C. oblongifolium* (Standl.) Croizat, J. Arnold Arbor. 24: 166. 1943. Figure 12.

Shrubs or small trees 3–12 m tall, trunks 10–25 cm diam., dioecious, leafy stems 1.5–5 mm thick, at first minutely (0.1–0.2 mm) puberulent, soon glabrescent; stipules 2–4 mm long, 1 mm wide at base, narrowly triangular, acute, appressed-puberulent, caducous. **Leaves** with petioles 14–52 mm long, 0.8–1.8 mm thick, thickened (2–3 mm) at apex and base and often geniculate, glabrous or minutely (0.1 mm) puberulent; **leaf blades** 9–26 cm long, 4.5–12 cm wide, elliptic-oblong, elliptic, elliptic-ovate or oblong, apex acuminate with narrow tip 7–25 mm long, margin subentire or with 15–18 prominent (0.5–2 mm) glandular teeth/side, base obtuse to acute, base often with lateral glands along the edge or with imbedded flat glands, drying thinly to stiffly chartaceous, glabrous above and below (rarely with domatia, Grayum et al. 8961), 2° veins 6–10/side, 3° veins sometimes subparallel. **Male inflorescences** 2.5–13 cm long, rachis 0.6–0.9 mm thick, glabrous or puberulent, glomerules with 2–12 flowers, pedicels 1–4 mm long, 0.1–0.2 mm thick, glabrous; ♂ flowers glabrous externally, buds 1.5–2 mm diam., globose, androecium 1.5–2 mm wide at base, hemispheric, filaments 0–0.4 mm long, anthers closely compressed, 0.3–0.4 mm wide, opening apically. **Female inflorescences** 1–4 cm long with 1–4 flowers, rachis 0.6–1 mm thick, minutely puberulent, bracts 0.4–1 mm long, subtending solitary pedicellate flowers; ♀ flowers with 3 calyx lobes 1–2 mm long, puberulent, ovary ca. 1.4 × 2 mm, oblate, style branches 3.5–9 mm long, 0.3–0.5 mm thick, puberulent on the inner face. **Fruits** 7–10 mm long, 14–18 mm wide, usually with 3 rounded lobes and flattened distal surface, rounded below, woody walls ca. 0.6 mm thick, columella 6–8 mm long, widened distally; seeds 7–9 mm diam., subglobose, smooth and lustrous, dark, or grayish.

Plants of evergreen lowland forest formations, 20–700 m elevation (to 1700 m in Mexico). Flowering primarily in January–October; fruiting in January–April. The species ranges from southern Mexico to Ecuador.

*Cleidion castaneifolium* is distinguished by its larger pinnately veined leaves with denticulate margin and petioles thickened at the base and apex, spiciform ♂ inflorescences with many anthers forming a dome-shaped androecium, few ♀ flowers usually with six style branches, and flesh-covered fruits. The thickened base and apex of the petioles often dry dark. The distribution in Costa Rica is unusual: the Talamanca valley and the moist forests from Volcán Orosí to Upala on the Caribbean slope and in the evergreen Pacific lowlands (Res. Biol. Carara to Osa). These plants may resemble *Sorocea* and *Trophis* of the Moraceae.

### Cnidoscolus Pohl

REFERENCE—G. Breckon, Studies in *Cnidoscolus* (Euphorbiaceae) 1. *Jatropha tubulosa*, *J. liebmannii* and allied taxa from Central Mexico. Brittonia 51: 125–148. 1979.

Herbs, shrubs, or small trees, monoecious, stems usually armed with slender sharp stinging hairs, with whitish latex; stipules free, small. **Leaves** alternate, simple, petioles usually long, with glands at the base of the blade, with stinging hairs, blades usually palmately lobed with shallow to deep sinuses, venation palmate (pinnate). **Inflorescences** terminal or pseudoaxillary, solitary, usually bisexual with proximal ♀ flowers and distal ♂ flowers, paniculate (of open dichasia with cymose branching), bracts and bracteoles small. **Male flowers** with whitish petaloid perianth of 1 whorl (calyx) united to form a distinct tube with 5 distal imbricate lobes, petals absent, disk annular, extrastaminal; stamens 8–10(–25), outer filaments free and inner usually connate (or all united); slender staminodes (= pistillode?) sometimes present at apex of staminal column. **Female flowers** with white petaloid perianth (calyx), calyx usually 4–5 parted to near the base, petals and staminodes absent, disk annular; ovary 3- (5-)locular, ovule 1/locule, styles 3 (5), free, bifid to lacinate. **Fruits** capsules with 3 (5) 2-valved 1-seeded cocci; seeds carunculate, with much endosperm, embryo straight, cotyledons broad.

An American genus of ca. 50 species with centers of diversity in Mexico and Brazil. The North American material was studied by G. Breckon and annotated in 1974. The genus is easily recognized because of its stinging hairs. Standley and Steyermark (1949, p. 59) remark that these may be the most painful of all the stinging plants in Central America; compare *Urera* (Urticaceae), *Wigandia* (Hydrophyllaceae), and *Loasa* and *Mentzelia* (Loasaceae). The plants are also distinctive because of their large lobed leaves with deep sinuses, glands at the apex of long petioles, few-branched stems,

long-pedunculate dichasia, ♂ flowers with corolla-like calyx tube, ♀ flowers with separate corolla-like

perianth parts, and three-lobed capsules covered with stinging hairs.

Key to the Species of *Cnidoscolus*

- 1a. Glands at the apex of the petiole minutely digitate, sometimes lacking or obscure in drying; herbs or succulent stemmed subshrubs 0.5–2.5 m tall, stems and leaves with many stinging hairs to 10 mm long; leaves 3–5-lobed, the margins entire or with small (3 mm) dentate lobes; ♂ perianth lobes ca. 2 mm long [seeds 10–12 mm long, ca. 3 mm thick; deciduous and partly deciduous formations, 0–300 m elevation] ..... *C. urens*
- 1b. Glands at the apex of the petiole 1–2, flat or rounded; shrubs or small trees 1–7 m tall, stems and leaves with stinging hairs to 7 mm long; leaves with 3–5 large lobes and the margins with additional prominent acute to acuminate lobes; ♂ perianth lobes ca. 4 mm long ..... 2
- 2a. Seeds 6–8 mm long, ca. 3.5 mm thick; deciduous or evergreen areas, often planted in hedges, 0–1200 m elevation ..... *C. aconitifolius*
- 2b. Seeds ca. 12 mm long, 4.5 mm thick; rarely collected in southern Central America ... *C. tubulosus*

***Cnidoscolus aconitifolius*** (Miller) I. M. Johnston, Contr. Gray Herb. 68: 86. 1923. *Jatropha aconitifolia* Miller, Gard. Dict. ec. 8, 1768. Figure 2.

**Shrubs** or small trees 1–4(–7) m tall, leafy stems 5–12 mm diam., glabrous or with slender stinging hairs 0.7–3 mm long, sometimes with broad-based thorn-like structures to 8 mm high; stipules ca. 3 × 2 mm, with digitate margin, caducous. **Leaves** with petioles 6–30 cm long, 1.5–9 mm thick, with few or many sharp-tipped stinging hairs 0.5–6 mm long, hairs simple or with basal stalk to 3 mm long, flat disk-like glands ca. 1.5 mm wide at or near the apex; **leaf blades** 11–28 cm long, 14–36 cm wide, usually with 3 or 5 larger distal lobes and 2 smaller basal lobes, apex acuminate or acute, tip 5–20 mm long, margins with similar acute to acuminate lobes, base broadly to narrowly cordate, drying membranaceous, greenish or brown, with a few scattered sharp hairs above and below, venation palmate with 3 or 5 (7) prominent palmate veins. **Inflorescences** 11–40 cm long, to 55 cm in fruit, 2–10 cm wide, broadly unbelliform dichasia, peduncles 1–35 cm long, 2–5 mm thick, with stinging hairs 0.3–6 mm long, ♂ flowers subsessile, ♀ flowers short-pedicellate. **Male flowers** minutely papillate-puberulent, perianth white, calyx tube 3–6 mm long, tubular or funnelform, lobes 2.4–4 mm long, 2.2–3 mm wide, rounded; anthers 1–1.4 mm long. **Female flowers** minutely puberulent or glabrous, calyx lobes 6–11 mm long, 1.5–2.5 mm wide, oblong-obovate, white, deciduous and leaving a truncated cup 0.7 mm long, ovary 2–4 mm long, style branches 2–3 mm long, distally divided. **Fruits** 12–18 mm long, ca. 12 mm wide, oblong, covered with stinging hairs ca. 3 mm long, columella ca. 7 mm long; seeds 6–8 mm long, 4–5.5 mm wide, 3–3.8 mm thick, caruncle ca. 2 mm wide.

Plants of evergreen or deciduous areas, 0–1200 m elevation. Flowering in April–July. Probably native to southern Mexico but often found in

hedgerows and gardens and apparently naturalized in the Guanacaste lowlands. This species now ranges from Mexico to Peru.

*Cnidoscolus aconitifolius* is recognized by larger stature and fewer stinging hairs (compared to *C. urens*), larger deeply lobed leaves with prominent acuminate lobes along the margins, and flat discoid glands above the petiole attachment. The stinging hairs are often few or absent. The young shoots and leaves have been used as a cooked vegetable (Standley, 1937), and the trees are used as fence posts. *Chicasquil* is a common name.

***Cnidoscolus tubulosus*** (Müll. Arg.) I. M. Johnston, Contr. Gray Herb. 68: 86. 1923. *Jatropha tubulosa* Müll. Arg., Linnaea 34: 212. 1865. *J. tubulosa* var. *quinqueloba* Müll. Arg., *J. cordifolia* Pax, Pflanzenreich IV. 147: 107. 1910. *C. cordifolius* (Pax) I. M. Johnston, Contr. Gray Herb. 68: 86. 1923.

**Shrubs** or small trees, 2–7 m tall, trunks to 30–40 cm diam., leafy stems 4–18 mm thick with sharp stinging hairs 1.5–7 mm long, articulated at the base, with or without minute (0.2 mm) thin hairs; stipules ca. 2 mm long and 2.5 mm wide at the base. **Leaves** with petioles 8–35 cm long, 1.5–5 mm thick, with slender sharp stinging hairs and often with minute thin hairs, with 1–2 rounded flat sessile glands near the adaxial apex; **leaf blades** 11–35 cm long, 14–38 cm wide, with 3 prominent distal lobes separated by wide or narrow sinuses 3–12 cm deep, usually with 2 additional lateral/basal lobes, apex of the major lobes acuminate, margins with short (0.5–6 mm) teeth separated by 5–15 mm, base shallowly or deeply cordate, drying thin-chartaceous, greenish or brown, with scattered thin sharp-tipped hairs 1–3 mm



long on both surfaces, venation palmate with 5 major veins, 2° veins 10–15/side of midvein. **Inflorescences** usually bisexual, 6–40(–70) cm long, a compound dichasium with multiple dichotomies, peduncles 4.5–46 cm long, 1.5–8 mm thick, with stinging hairs, ♀ flowers subsessile in axils of basal dichotomies, ♂ flowers on pedicels ca. 1 mm long. **Male flowers** white, 11–15 mm long, minutely and densely puberulent externally, calyx tube ca. 6 mm long, 2–3 mm diam., lobes 4–5 mm long, 2–3 mm wide, rounded at apex; anthers 1.5–1.8 mm long. **Female flowers** white, 10–15 mm long, perianth tube 5–6 mm long, ca. 3 mm diam. near base, lobes 5–6 mm long, persisting; ovary ca. 5 mm long, styles united for 1.5 mm, style branches ca. 4 mm long, twice bifid. **Fruits** 16–18 mm long, with few to many stinging hairs, oblong; seeds 12–13 mm long, ca. 8 mm wide, 4.5–5 mm thick, elliptic in cross-section, broad surfaces smooth, notched at the base, caruncle 1–1.5 mm wide.

Plants of partly deciduous and montane forest formations, 900–1700 m elevation in northern Central America. Probably flowering primarily in the wet season, May–November. The species ranges from Mexico to Nicaragua and in Peru.

*Cnidoscolus tubulosus* is recognized by its deeply lobed and dentate leaves, prominent stinging hairs, tubular perianth in both ♂ and ♀ flowers, and larger seeds. We have not seen material of this species from Costa Rica or Panama. See discussion regarding this species in Breckon (1979; cited above).

**Cnidoscolus urens** (L.) Arthur, Torreyia 21: 11. 1921. *Jatropha urens* L., Sp. Pl. 1007. 1753. *J. adenophila* Pax & K. Hoffm., Pflanzenreich 63 (IV, 147, VII): 400. 1919. *C. adenophilus* (Pax & K. Hoffm.) Pax & K. Hoffm., Naturl. Pflanzenfam. ed. 2, 19c: 166. 1931. *C. urens* ssp. *adenophilus* (Pax & K. Hoffm.) Breckon, Ann. Missouri Bot. Gard. 75: 1114. 1988. Figure 2.

Herbs or shrubs 0.5–2.5 m tall, stems usually succulent, leafy stems 3–10 mm thick, with many sharp stinging hairs 6–9 mm long, ca. 0.2 mm thick near base; stipules ca. 2 × 2 mm, lacinate-dentate, caducous. **Leaves** with petioles, 7–18 cm long, 1.5–3.5 mm thick, with short (0.2–0.3 mm) thin hairs and longer stinging hairs, glands at apex few to many, digitiform, 0.3–1 mm high but often obscure when dried; **leaf blades** 5–19 cm long, 6–19 cm wide, with 3 large often obovate distal lobes and 2 smaller proximal lobes, apex short-acuminate to acute, margins entire or with short (1–3 mm) broad teeth, base broadly cordate, drying membranaceous, with short (0.1–0.3 mm) thin hairs on both surfaces, venation palmate with 5 major veins. **Inflorescences** 4–16(–22) cm long, 3–8(–12) cm wide, umbelliform dichasia, peduncles 3–12 cm long, 1.6–3.5 mm thick, with short (0.2–0.4 mm) thin hairs and stinging hairs to 4 mm long. **Male flowers** to 11 mm long, white, minutely puberulent or sometimes with stinging hairs, calyx tube funnelform or tubular, 4–7 mm long, 2–3 mm diam., lobes 2–4 mm long, ca. 1.8 mm wide; anthers ca. 1.1 mm long. **Female**

**flowers** white, minutely puberulent or glabrous, 5–6 mm long, corolla lobes ca. 5 × 1.5 mm, deciduous; ovary ca. 2.5 mm long. **Fruits** 10–13 mm long, 9–11 mm wide, green with white stripes, with stinging hairs, walls ca. 0.6 mm thick, columella ca. 8 mm long; seeds 8.5–10.5 mm long, 3.8–5 mm wide, 2.5–3.2 mm thick, whitish to gray, black or mottled, caruncle 2.5–3.2 mm wide, base slightly bilobed.

Plants of deciduous or partly deciduous forests, 0–300 m elevation (to 600 m in Guatemala). Flowering in June–January. The species ranges from eastern Mexico to Argentina.

*Cnidoscolus urens* is distinguished by its dense covering of sharp stinging hairs, smaller stature, lobed leaves with usually unlobed margins, and seasonally dry open habitats. The glands above the apex of the petiole are often minutely digitate. The hairs sting severely, the pain sometimes persisting for many hours (Standley, 1937). This species is apparently represented by two distinctive subspecies in Panama (Breckon in Webster & Huft, 1988; Webster & Burch, 1968). These plants have been called *hierba santa* in Costa Rica and *chorrera*, *chamé*, *ortiga*, and *pringamoza* in Panama.

## Codiaeum Adr. Jussieu

**Shrubs** or small trees, usually monoecious, glabrous or with simple hairs; stipules present or absent. **Leaves** alternate, simple, petiolate, entire or lobed, usually coriaceous, pinnately veined. **Inflorescences** axillary to distal leaves, solitary or 2/node, racemose or spike-like with a long unbranched rachis, unisexual or bisexual with 1–2 proximal ♀ flowers, flowers small, ♀ bracts with 1 flower, ♂ flowers 1–6/bract. **Male flowers** with 5 (3–6) calyx lobes or parts, imbricate in bud, petals small or rudimentary, disk of 5–15 free glands; stamens 15–100, borne on the elevated receptacle, filaments free, anthers erect; pistilode absent. **Female flowers** with calyx usually 5-parted, petals absent, disk cupulate, entire or lobed, staminodes absent; ovary 3-locular, ovules 1/locule, styles 3, simple and slender. **Fruits** capsules, globose or 3-lobed, breaking into 3 2-valved cocci, columella persisting; seeds carunculate, endosperm carnos, cotyledons flat.

A genus of ca. 15 species of Australasia and the western Pacific islands. One colorful ornamental species is now widely cultivated throughout the tropics and subtropics.

**Codiaeum variegatum** (L.) Adr. Juss., Euphorb. Gen. Tent. 111, t. 9, f. 30. 1824. *C. variegatum* (L.) Blume, Bijdr. fl. Ned. Ind. 606. 1825. *Croton variegatus* L., Sp. Pl. ed. 3. 1424. 1764. Figure 32.



**Shrubs** and small few-branched treelets 1–5 m tall, leafy stems 3–10 mm thick, glabrous or glabrescent; stipules absent. **Leaves** with petioles 1–4 cm long, glands absent; **leaf blades** 5–35 cm long, 1–13 cm wide, shape extraordinarily variable in different cultivars (also variable on the same plant), usually long and narrow, narrowly obovate to oblanceolate, apex acute to rounded, margin entire, with or without 1–3 rounded lobes and sinuses (with a bladeless petiole-like portion in the center of the blade in some varieties), drying stiffly chartaceous to subcoriaceous, glabrous, lustrous, variously colored. **Inflorescences** 12–40 cm long, usually erect, unisexual, glabrous, spike-like with 1–3 ♂ flowers in sessile fascicles and pedicels 2–4 mm long.

*Codiaeum variegatum* is native to the southwestern Pacific and is now a favorite ornamental cultivar because of its brilliantly colored leaves mottled with dark green, yellow-green, yellow, rose-red, red, or purple. The blades often have paler colored areas around the major veins. The blades vary greatly in shape but are generally long and narrow and have entire margins. The plants are often used as hedges but are restricted to lower (0–900 m) elevations. *Laurel*, *cintillo*, and “garden croton” are common names.

### Conceveiba Aublet

Small to large **trees**, dioecious, minutely stellate-puberulent, glabrescent; stipules paired at the leaf base, deciduous. **Leaves** alternate, simple, petioles often geniculate at the apex and thickened at the base (stipels absent); **leaf blades** slightly crenate-denticulate with gland-tipped lobes or sinuses, minutely stellate puberulent beneath, venation palmate (in our species) or pinnate. **Male inflorescences** terminal or axillary, solitary, simple and racemose or branched and paniculate, often broad, flowers solitary or in sessile groups along the rachis, bracts small (glands not apparent), pedicels short; ♂ flowers with ovoid or spherical buds, calyx opening irregularly or 3–4 parted, corolla and disk absent; stamens ca. 16–many, filaments free, anthers dehiscent longitudinally, thecae rounded; pistillode absent. **Female inflorescences** terminal, solitary, narrowly spiciform racemes with a thick rachis and distant solitary flowers subtended by small broad-based bracts, lateral glands usually present at the base of the bracts, pedicels short and thick, borne directly on the rachis (*C. latifolia*) or on a very short articulated lateral branch of the rachis (*C. pleiostemona*); ♀ flowers with 5–8 narrow stiff imbricated puberulent sepals (alternating with large glands in *C. latifolia*), petals and disk absent, staminodes absent; ovary 3–4 locular, ovules 1/locule, styles united only at base, thick, papillose adaxially, bifid distally. **Fruits** fleshy and large, 3-costate, separating into 3 2-valved capsules; seeds large, carunculate.

A Neotropical genus of seven to nine species; all are South American, except the Costa Rican

endemic, a recently discovered African species and an undescribed Panamanian species. The stellate nature of the pubescence is difficult to see because of the small size of the hairs. Herbarium material of our species was previously filed under *Veconcibea*; compare *Alchornea*.

**Conceveiba pleiostemona** J. D. Smith, Bot. Gaz. 54: 243. 1912. *Veconcibea pleiostemona* (J. D. Smith) Pax & K. Hoffm. Figure 20.

**Trees**, 10–30 m tall, 25–100 cm dbh, large trunks sometimes fluted, leafy twigs 2–8 mm thick, with short (0.1–0.3 mm) appressed-stellate hairs and with longer (0.4 mm) straight or V-shaped hairs attached at the middle; stipules 4–8 mm long, 0.7–1.2 mm wide, linear, appearing densely sericeous with ascending hairs, deciduous. **Leaves** with petioles 2.2–12 cm long, 1–3 mm thick, minutely stellate-pubescent, sometimes drying darker and thinner along the terminal 4–5 mm; **leaf blades** 5–22 cm long, 4–19 cm wide, broadly ovate to ovate-suborbicular, apex obtuse to rounded or with a short- acuminate tip 3–10 mm long, margin bluntly serrulate with 15–23 teeth/side, teeth 0.3–1 mm high and gland-tipped, base rounded to subcordate, drying stiffly chartaceous or subcoriaceous, glabrous or pubescent on the midvein above, minutely stellate-pubescent beneath, venation palmate, 2° veins 4–6/side, 3° and 4° veins subparallel and perpendicular to the higher rank veins. **Male inflorescences** axillary or terminal, 7–20 cm long, simple and spicate or compound and paniculate with lateral branches to 4 cm long, peduncles 2–35 mm long, 0.7–2 mm thick, minutely stellate-puberulent, bracts ca. 1 mm long, pedicels 0.5–1 mm long, drying black; ♂ flowers with spherical buds ca. 2 mm diam., perianth parts 1–2 mm long, mostly glabrous and drying black; stamens 30–60, filaments 0.5–1.9 mm long (not 7–11 mm as in the original description), anthers 0.4–0.5 mm long. **Female inflorescences** terminal, to 22 cm long in fruit, spiciform at first, rachis 2–3 mm thick, minutely stellate-puberulent, bracts 3–5 mm long, 1–2 mm wide at base, subtending a short lateral peduncle (becoming up to 10 mm long in fruit), articulated below the short (1–3 mm) thick (1 mm) pedicels; ♀ flowers with 5 sepals 3–5 mm long, 1 mm wide at base; ovary ca. 4.5 mm long, 3-angular in cross-section, style branches becoming 4–5 mm long and recurved, 0.5–0.7 mm thick. **Fruits** ca. 1.8 × 1.2 cm, oblong with elevated longitudinal ridges and persisting style branches, green and fleshy, pedicels red; seeds ca. 10 × 8 mm, smooth, brown.

Trees of Caribbean rain forest formations on well-drained soils, 50–600 m elevation. Flowering in June–July; fruiting in August–October. The species is known only from Costa Rica, ranging from just north of Tortuguero National Park to Amubri in the Talamanca valley. It probably occurs also in adjacent Nicaragua and Panama.

*Conceveiba pleiostemona* is recognized by its large stature, minute stellate pubescence, broadly ovate palmately veined leaves with subparallel mi-

nor venation, short-pedicellate ♂ flowers with many stamens, and fleshy fruit on long narrow inflorescences. The large size of these trees and their restricted flowering and fruiting season probably account for the paucity of collections. The fruits are eaten by macaws (*Aras ambigua*). Compare the superficially similar *Aparisthmium cordatum*, which lacks the stellate hairs and has smaller capsular fruits.

Croton Linnaeus

REFERENCE—G. L. Webster, A provisional synopsis of the sections of the genus *Croton* (Euphorbiaceae). Taxon 42: 793–823. 1993.

**Trees**, shrubs or herbs, bisexual (monoecious) or unisexual (dioecious), sap often white or colored, stems with simple, stellate, scurfy or flat rounded peltate hairs; stipules small or absent, usually caducous. **Leaves** alternate or sometimes opposite at congested distal or flowering nodes, simple, petiolate, often with glands near the apex of the petiole or at the base of the blade, blades entire to deeply lobed, margins entire to serrate, venation palmate or pinnate. **Inflorescences** terminal or axillary, spicate to racemose (actually a condensed thyrse with a single unbranched rachis, but apparently branched or pseudopaniculate when distal leaves fail to develop), bisexual or unisexual, with 1–10 usually solitary ♀ flowers at proximal nodes and many ♂ flowers distally when bisexual, rachis usually pubescent, bracts and bracteoles small, ♂ flowers often in sessile fascicles (cymules). **Male flowers** with 4–6 valvate or imbricate calyx lobes, petals usually 5 (4, 6, 0), receptacle usually pilose; stamens 8–50, filaments inflexed in bud and free, pistillode absent. **Female flowers** with 5–7 (4–10) calyx lobes, imbricate or valvate, petals 0 or 5 and small, staminodes absent,

disc entire or lobed; ovary with 3 (1, 2) locules, ovules 1/locule, styles 3 (2), bifid or several times bifid. **Fruits** usually capsules with 3 (2) 2-valved cocci, columella usually persisting; seeds oblong in outline, rounded abaxially, carunculate, endosperm present, embryo with broad flat cotyledons.

A very large genus of ca. 800 species of tropical and warm-temperate regions. South America, the West Indies, and Mexico are important centers of species diversity. The stellate or lepidote hairs, narrow unbranched inflorescences, stamens inflexed in bud, divided style branches, capsular fruits, and inapeturate pollen grains help distinguish the genus. The glands near the apex of the petioles of some species can be quite striking, from sessile and saucer-like to stipitate and patelliform. Plants of this genus are sometimes conspicuous because their leaves turn bright yellow or orange before they are shed.

The Costa Rican species of *Croton* include both wide-ranging species and local endemics with remarkably narrow ranges. Many species are poorly represented in herbaria, probably because they are part of open weedy or early secondary vegetation. A few can become tall trees, and these are not well collected. Many species display considerable variation in leaf size, leaf form, pubescence, inflorescences, and floral morphology. Such variation can make the determination of individual specimens very difficult. The genus is rich in alkaloids, and a number of species in Asia and South America have been used medicinally and for teas (cf. *C. niveus*). Some authors recognize the species of section *Julocroton* (Mart.) Webster as a genus.

Key to the Species of *Croton*

- 1a. Young stems or petioles with appressed flat rounded centrally attached (peltate) hairs 0.1–0.5 mm diam., sometimes with united radiating rays separated distally and resembling stellate hairs, stellate hairs present in a few species; stamens 10–15/flower ..... 2
- 1b. Young stems lacking flat rounded centrally attached hairs, hairs sometimes centrally flattened with radiating hairs but these not united along their lateral edges to form a broad flat surface, the hairs stellate to scurfy and rounded, or simple; stamens 8–50/flower ..... 10
  - 2a. Small (< 1 m) shrubs of the Caribbean seashore; leaves not > 4.5 cm long, upper (adaxial) surfaces of leaves with stellate hairs, young stems and lower (abaxial) surface of leaves with peltate-stellate hairs; ♂ flowers apetalous [stipules absent] ..... *C. punctatus*
  - 2b. Shrubs or trees, not confined to the Caribbean seashore; mature leaves usually > 5 cm long, upper leaf surfaces glabrous or with flat rounded peltate hairs (stellate hairs also present in *C. pachypodus* and *C. tonduzii*), young stems and lower leaf surfaces with peltate hairs; ♂ flowers with petals (but sometimes small) ..... 3
  - 3a. Venation palmate (basal 2° veins reaching the midpoint of the leaf margin or more distally) ..... 4

- 3b. Venation pinnate or subpalmate ..... 5
  - 4a. Leaf blades with entire or subentire margin, often silvery beneath with a dense covering of peltate hairs, 4–14 cm long, broadly ovate-orbicular to triangular; plants often grown in hedgerows, 0–1800 m elevation; seeds 6–16 mm long ..... *C. niveus*
  - 4b. Leaf blades with prominently dentate margin, blades not silvery beneath, 9–18 cm long, ovate to ovate-elliptic or ovate-oblong; plants rare on the evergreen Pacific slope, 400–900 m; seeds 5–6 mm long ..... *C. tonduzii*
- 5a. Seeds 20–28 mm long in capsules 3–5 cm long [trees to 30 m tall; leaves to 13 cm long, with 2 lateral glands at the apex of the petiole; inflorescences mostly terminal, to 9 cm long; 300–1000 m] ..... *C. pachypodus*
- 5b. Seeds < 10 mm long, capsules to 1.5 cm long ..... 6
- 6a. Styles much divided with > 20 distal stigmatic branches/flower; leaf blades rounded and truncate to cordate at the base [8–26 cm long, ovate-oblong; evergreen forests] ..... 7
- 6b. Styles 2–3 times bifid, rarely with > 18 distal stigmatic branches/flower; leaf blades rarely rounded at the base, never cordate ..... 8
  - 7a. Petioles without lateral glands at the apex, leaf blade rounded and truncated at the base, secondary veins 9–13 pairs; ♂ flowers solitary on the rachis .. *C. tenuicaudatus*
  - 7b. Petioles with 2 lateral sessile glands at the apex, leaf blade rounded and cordate at base, secondary veins 11–17 pairs; ♂ flowers in groups of 5–11 ..... *C. skutchii*
- 8a. Apex of petiole lacking paired lateral or adaxial glands; wide-ranging and variable trees or shrubs [on both Pacific and Caribbean slopes, usually found at 0–700 m elevation; 2° veins 8–13/side; styles bifid at base and with ca. 18 distal style branches; seeds 7–8 mm long] .. ..... *C. schiedeanus*
- 8b. Apex of petiole usually with 2 distinct stalked adaxial/lateral glands; restricted species .. 9
- 9a. Leaves with few to many stellate-scurfy hairs on the upper surface, 2° veins 3–6/side; styles bifid in the distal half (6 distal branches/flower); seeds 6–7 mm long; known only from the Cordillera de Tilarán near Monteverde, 1400–1600 m elevation ..... *C. mexicanus*
- 9b. Leaves glabrous above, 2° veins 10–22/side; styles 2 times bifid (12 branches); seeds ca. 3.5 mm long; rarely collected trees of the Caribbean slope at 200–800 m .... *C. lanjouwensis*
- 10a. (from 1b) Leaf blades often ovate (ovate-oblong) with the larger leaves usually becoming > 15 cm long, the base usually rounded and truncate to cordate, sessile or stipitate glands usually present near the apex of the petiole; pubescence usually of scurfy-stellate hairs; trees and shrubs not found in dry seasonally deciduous areas ..... 11
- 10b. Leaf blades not ovate if becoming > 13 cm long, the base rounded and truncate to cordate only in leaves < 13 cm long, glands present or absent near the apex of the petiole, pubescence with various types of stellate or scurfy hairs; trees, shrubs, or herbs of both dry deciduous and wet evergreen formations ..... 20
  - 11a. Larger leaves often with 3 distal lobes and broad shallow sinuses (note that smaller leaves are usually unlobed), venation palmate; ♀ calyx lobes 5–16 mm long [rarely collected species] ..... 12
  - 11b. Leaves with a single acute or acuminate apex (rarely with distal lobes), venation palmate to pinnate; ♀ calyx lobes usually < 5 mm long (except in *C. jimenezii*) ..... 13
    - 12a. Stamens ca. 11/flower; ♀ calyx lobes 5–7 mm long, styles much-branched; seeds ca. 5 mm long; leaves, stems, and inflorescences not yellowish white with dense tomentulous pubescence ..... *C. smithianus*
    - 12b. Stamens ca. 50/flower; ♀ calyx lobes 8–16 mm long, styles 2 times bifid; seeds ca. 7 mm long; leaves, stems and inflorescences with a dense tomentum of yellowish white hairs ..... *C. speciosus*
- 13a. Venation pinnate in larger and smaller leaves, length of leaf blade often twice the width, often ovate-oblong and truncated at base ..... 14
- 13b. Venation palmate or subpalmate in larger leaves, length of leaf blade usually less than twice the width, usually ovate and subcordate at the base ..... 17
  - 14a. Plants growing at 0–700 m elevation in Costa Rica; glands at the apex of the petiole



- usually 2, sessile; stamens ca. 14, anthers 1–1.5 mm long; leaf blades often oblong . . . . . *C. billbergianus*
- 14b. Plants at (0) 800–2300 m in Costa Rica; glands at the apex of the petiole 2–7, often stalked; stamens 14–33, anthers 0.6–0.9 mm long; leaf blades often ovate . . . . . 15
- 15a. Leaf blades rarely > 15 cm long; stellate hairs compact (ca. 0.2 mm diam.) and usually flat, petiole with 2 lateral stalked glands at apex; stamens 14–16; seeds 6–7 mm long [Cordillera de Tilarán at 1400–1600 m elevation] . . . . . *C. mexicanus*
- 15b. Larger leaf blades usually > 15 cm long; stellate hairs often elevated and prominent; petiole with 2–9 glands at adaxial base of blade; stamens 14–33; seeds 4–5 mm long . . . . . 16
- 16a. Calyx lobes of ♀ flowers 2.5–9 mm long, oblong; pubescence with many small brownish scurfy hairs and some stellate hairs [♂ flowers sometimes present with proximal ♀ flowers on bisexual inflorescences; seed ca. 4 × 3 mm; 1000–2500 m, Volcán Barva to San Isidro] . . . . . *C. jimenezii*
- 16b. Calyx lobes of ♀ flowers 1.5–4 mm long, usually triangular; pubescence mostly of whitish or yellowish hairs, scurfy to stellate . . . . . 17
- 17a. Seeds 6–8 mm long, surfaces smooth; glands 2 and sessile near the apex of the petiole; stamens ca. 15; ♀ and ♂ calyx united ca. 50% and conspicuous; plants restricted to the eastern Meseta Central and around Cartago, 900–1600 m elevation . . . . . *C. hoffmannii*
- 17b. Seeds 3.5–6 mm long, usually rugulose; glands 2–12 at the apex of the petiole and sessile or stipitate; stamens 15–33; and without the preceding combination of characters . . . . . 18
- 18a. Plants restricted to the Chiriquí Highlands at 1300–2100 m; leaf blades usually less than 14 cm long and cordate [seeds 5–6 mm long; ♂ flowers present with the proximal ♀ flowers on bisexual inflorescences, stamens 25–40/flower] . . . . . *C. pungens*
- 18b. Plants widely distributed and common, 0–2100 m elevation; larger leaf blades more than 15 cm long, cordate or truncate (the following two species are very similar and can be difficult to separate when bisexual inflorescences are lacking) . . . . . 19
- 19a. Male flowers present with proximal ♀ flowers on bisexual inflorescences, flowers usually in glomerules (cymules) along the rachis; ♀ flowers pedicellate, ♂ flowers mostly in fascicles along rachis, stamens 13–22/flower; seeds 2.8–5 mm long . . . . . *C. draco*
- 19b. Male flowers not present with proximal ♀ flowers on bisexual inflorescences, flowers often solitary along the rachis; ♀ flowers subsessile; ♂ flowers usually 1–few/bract along the rachis, stamens 18–31/flower; seeds 4.8–5.7 mm long . . . . . *C. xalapensis*
- 20a. (from 10b) Leaves with 3 prominent distal lobes separated by deep narrow sinuses, 2 additional smaller basal lobes often also present [seeds ca. 5 × 3 mm, oblong; herbs to 1.5 m tall in open sunny sites in seasonally dry lowlands] . . . . . *C. lobatus*
- 20b. Leaves lacking 3 prominent distal lobes and deep sinuses . . . . . 21
- 21a. Plants of seasonally very dry deciduous areas in the Guanacaste lowlands (0–500 m) . . . . . 22
- 21b. Plants of evergreen or partly deciduous forest formations, above 500 m elevation in Guanacaste and in other areas . . . . . 27
- 22a. Leaf blades silvery white or bright grayish white beneath; stipules often rounded and leaf-like in texture; ♀ sepals broadly ovate and often laterally reflexed [stamens 15; glands absent or minute at apex of petiole] . . . . . *C. yucatanensis*
- 22b. Leaf blades not silvery white or bright grayish white beneath, often pale grayish; stipules not rounded or leaf-like; ♀ sepals not broadly ovate . . . . . 23
- 23a. Leaf blades not exceeding 3.5 cm in length [glands absent at the apex of the petiole; plants not exceeding 1 m in height and rarely collected; stamens ca. 11; seeds 4.5–4.8 mm long] . . . . . *C. ovalifolius*
- 23b. Leaf blades often exceeding 3.5 cm in length . . . . . 24
- 24a. Venation pinnate or subpalmate, shrubby plants . . . . . 25
- 24b. Venation palmate, herbs or shrubs . . . . . 27
- 25a. Glands 2–4 at the apex of the petiole, blades lanceolate to narrowly elliptic or ovate, with prominent denticulate margin, venation pinnate; commonly collected in many sites [stamens 11; seeds 3.5–4 mm long] . . . . . *C. jutiaensis*

- 25b. Glands absent at the apex of the petiole, blades ovate to ovate-elliptic, ovate-oblong or ovate-triangular, with subentire margin; uncommon in Costa Rica ..... 26
- 26a. Venation subpalmate, 2° veins 3–6 pairs, blade not cordate at base, thinly chartaceous; stamens 15; seeds 5–5.5 mm long ..... *C. sphaerocarpus*
- 26b. Venation pinnate, 2° veins 5–10 pairs, blade often subcordate at base, stiffly chartaceous; stamens ca. 11; seeds not seen ..... *C. axillaris*
- 27a. (from 21b and 24b) Plants weak-stemmed weedy annuals, rarely > 1 m tall; wide-ranging species [stellate hairs with thin rays, not scurfy; stamens 8–12; seeds 3–4 mm long] ..... 28
- 27a. Plants woody shrubs and trees, 0.3–25 m tall; wide-ranging or locally endemic species ..... 31
- 28a. Stalked or sessile glands absent at the apex of the petiole, leaf blades drying pale greenish above and whitish below with a dense tomentum of stellate hairs, blades 2–15 cm long ..  
..... *C. argenteus*
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***Croton argenteus* L., Sp. Pl. 1004. 1753. *Julocroton argenteus* (L.) Didr., Vidensk. Meddel. Dansk. Naturhist. Foren. Kobenhavn 1857: 134. 1857. Figure 16.**

Annual herbs 0.2–1 m tall, bisexual, leafy stems 0.8–7.5 mm thick, stellate-pubescent with appressed hairs 0.3–0.5 mm diam. or with long rays to 0.9 mm; stipules 4–11 mm long, linear-subulate, simple or divided distally, with hairs to 1.4 mm long. **Leaves** often closely congested beneath the inflorescences (becoming pseudoverticillate), petioles 3–105 mm long, 0.7–2 mm thick, appressed stellate-pubescent, glands absent at apex; **leaf blades** 1.8–10(–15) cm long, 1.2–6(–8) cm wide, ovate to ovate-oblong, apex bluntly obtuse to rounded, margin minutely or obscurely denticulate, base obtuse or cuneate to subtruncate, drying chartaceous and pale grayish green beneath, stellate-pubescent with appressed hairs 0.1–0.4 mm diam., venation palmate with usually 5 major veins from the base, 2° veins 3–4/side of the midvein. **Inflorescences** terminal, bisexual, 1–4 cm long, often subtended by small (15 × 12 mm) leaves, congested and resembling a capitulum, bracteoles ca. 3 mm long, subtending solitary flowers, ♀ flowers proximal, pedicels to 5 mm long in fruit, ♂ flowers with pedicels ca. 2 mm long. **Male flowers** with calyx 1.5–2 mm long, sepal lobes ca. 1 mm long, petals 2–3 mm long, 0.3–0.4 mm wide, glabrous except on the margin; stamens ca. 11, filaments minutely hirsutulous, anthers 0.6–0.8 mm long. **Female flowers** with 5 unequal sepals, 6–8 mm long in fruit, petals absent, disk with 5 unequal lobes, ovary stellate-tomentellous, styles distally 4 times bifid. **Fruits** ca. 5 mm long, borne on pedicels 3–5 mm long, sepals 6–8 mm long and 3.5–6 mm wide, columella 3–4.5 mm long; seeds 3.2–3.8 mm long, 2.4–3 mm wide, ca. 2.2 mm thick, rounded-oblong, caruncle ca. 1.8 mm wide.

Weedy plants of open sunny sites in seasonally dry habitats, 0–300 elevation. Collected with flowers in January–February, May, and August in Costa Rica and Nicaragua. While rarely collected in Central America, it may be locally common. The species ranges disjunctly from Texas to Argentina.

*Croton argenteus* is recognized by its herbaceous habit, the soft grayish green color of the leaves (especially the often whitish undersides), palmate venation with usually five major veins, appressed stellate hairs, short inflorescences often enclosed

within subtending leaves, and restriction to seasonally deciduous vegetation. The paucity of collections from southern Central America suggests that the species is a recent introduction. Superficially, these plants resemble a number of weedy Malvaceae.

***Croton axillaris* Müll. Arg., Linnaea 34: 126. 1865.**

**Shrubs** or small trees 1–3.5 m tall, apparently unisexual, leafy stems 2–4 mm thick, densely pubescent with pale yellowish stellate hairs but soon becoming dark and glabrescent; stipules 4–6 mm long, ca. 1 mm wide at base, linear, densely stellate-pubescent. **Leaves** with petioles 12–23 mm long, 1.2–1.8 mm thick, densely stellate-pubescent, hairs to 1.5 mm long, glands absent at apex; **leaf blades** 6–14 cm long, 3–8 cm wide, ovate-triangular to ovate-oblong or oblong, apex acute to acuminate with a narrow tip, margin subentire, base rounded and truncate to subcordate, drying thick-chartaceous, upper surface with minute (0.2–0.4 mm) stellate hairs on a slightly raised base, hairs with 5–7 lateral rays and 1 longer central ray, lower surface densely covered with short-stalked stellate hairs to 1 mm wide, venation pinnate, 2° veins 8–18/side. **Male inflorescences** terminal on short axillary shoots before the leaves expand, 4–7 cm long, rachis ca. 1 mm thick, whitish stellate-pubescent, bracts 1–3 mm long, caducous, pedicels 1–3 mm long; ♂ flowers ca. 4 mm wide, densely stellate-tomentose on the exterior, calyx lobes ca. 2 mm long, petals ca. 0.8 mm wide, oblanceolate, glabrous abaxially and densely puberulent on the inner face; stamens 11, filaments 3–4 mm long, sparsely puberulent, anthers 1–1.3 mm long. **Female inflorescences** terminal on new lateral shoots, 2–4 cm long, rachis densely stellate-tomentose, pedicels 0.5–2 mm long; ♀ flowers crowded, 5–6 mm long, calyx lobes 2–3 mm long, densely stellate-tomentulose on the exterior, ovary ca. 3 mm long, densely puberulent, style branches 2 times bifid in the proximal half. **Fruits** not seen.

*Croton axillaris* is recognized by its deciduous forest habitat, stiff ovate-triangular leaves with dense covering of stellate hairs, pinnate venation with more than 10 pairs of secondary veins, and compact inflorescences. The short-stalked stellate hairs have approximately five to seven lateral rays and one longer central ray. This species was described from material collected from Granada,



Nicaragua, and is reported from northwestern Costa Rica by Nelson Zamora (pers. comm.). The species ranges northward to Guatemala in deciduous forest formations.

**Croton billbergianus** Müll. Arg., *Linnaea* 34: 98. 1865. *C. grosseri* Pax, Bot. Jahrb. Syst. 33: 290. 1903. *C. pyramidalis* J. D. Smith, Bot. Gaz. 35: 7. 1903. *C. billbergianus* ssp. *pyramidalis* (J. D. Smith) Webster, Ann. Missouri Bot. Gard. 75: 1123. 1988. Figure 19.

Small trees or shrubs 3–15 m tall, bisexual, sap yellow or orange, leafy stems 2–6 mm thick, scurfy-stellate with appressed hairs with 8–20 peripheral rays, 0.2–0.5 mm wide; stipules 4–7 mm long, linear, caducous. Leaves with petioles 1.6–9(–12) cm long, 0.8–2 mm thick, scurfy-stellate, with 2 lateral abaxial sessile saucer-like, patelliform or cupulate glands 0.7–1.5 mm diam. at the apex; leaf blades 9–25(–32) cm long, 4–17(–24) cm wide, ovate-oblong, to oblong or ovate-elliptic, apex acuminate to caudate-acuminate, narrowed tip 4–15 mm long, margin subentire with minute (0.2 mm) glands along the margin, ca. 6–10 glands/cm, base rounded and truncate to cordate with a shallow (0–7 mm) sinus, drying thinly chartaceous and often greenish, surfaces with small (0.1–0.3 mm) stellate hairs and larger hairs along the veins, more densely pubescent beneath, glandular punctate, venation pinnate or subpalmate, 2° veins 6–11/side, basal 2° veins sometimes strongly developed. Inflorescences terminal or axillary, 1.5–16 cm long, sometimes with 2–4 proximal branches to 11 cm long, bisexual or ♂, densely stellate, ♀ flowers 3–8/rachis, solitary, on pedicels 1–8 mm long, 0.8–1.6 mm thick; ♂ flowers in glomerules of 3–5, pedicels 2–8 mm long. Male flower buds 2.5–3.5 mm diam., calyx 3–4 mm long, lobes 5, ca. 2 mm long, 3.5 mm wide at base, triangular, petals 3.4–3.8 mm long; stamens 13–16, filaments ca. 4 mm long, glabrous distally, anthers 1.1–1.5 mm long. Female flowers with 5 sepals, 3–5.5 mm long, 1.2–3.3 mm wide, glabrous on the interior, becoming reflexed, disk with lobes 0.3–0.4 mm thick; ovary 1.5–2 mm long, 2.3–3 mm diam., stellate-hispid, styles united to form a hispid column 0.5–1 mm long, style branches 6–12 (more), 2–4 mm long, glabrous distally. Fruits 7–8 mm long, 9–10 mm wide, hispid, subtended by the prominent 5-lobed flat disk and reflexed calyx, columella 4.5–5.5 mm long; seeds 4.5–5 mm long, 3.5–4 mm wide, 3–3.2 mm thick, oblong, caruncle 0.7–1.5 mm wide.

Plants of lowland evergreen forest formations on both Caribbean and Pacific slopes, 20–800 m elevation. Flowering in April–July; fruiting in July–December. The species ranges from Veracruz, Mexico, to Panama.

*Croton billbergianus* is recognized by its yellow-orange sap, larger thin ovate-oblong leaves often slightly cordate at the base, sessile glands at the apex of the petiole, longer anthers, reflexed ♀ sepals, thick-lobed disk subtending the ovary, and short hispid style column with 12 style branches.

The compound inflorescences, branched near the base, are very distinctive but not common among the collections seen. Leaves often dry greenish, but there is considerable difference in the leaf shape of different collections. Nevertheless, the leaves are usually more clearly oblong than they are in our other large-leaved species. Subspecies *pyramidalis* (Mexico to Honduras) has larger seeds and stipules than those found in ssp. *billbergianus*. Compare *C. hoffmannii*, where the ovary is subtended by a pubescent disc.

**Croton brevipes** Pax, Bot. Jahrb. Syst. 33: 290. 1903. Figure 12.

Shrubs or small treelets 1–5 m tall, bisexual, leafy stems 0.7–5 mm thick, often with long (ca. 12 cm) internodes, stellate hairs short-stipitate, ca. 0.6 mm diam., with ca. 6–8 rays; stipules 2–6 mm long, subulate. Leaves often opposite or subopposite (whorled) at distal or flowering nodes, petioles 5–48 mm long, 0.7–2 mm thick, stellate-pubescent, apex with 2 lateral yellowish glands 0.5–1.7 mm long, usually narrowly stipitate and saucer-like distally, 0.5–1.1 mm wide; leaf blades 5–22 cm long, 2–9 cm wide, elliptic to ovate-elliptic, elliptic-oblong, or narrowly obovate, apex acute or acuminate, margin with broad rounded teeth 2–4 mm high, 5–8/side, sinuses of the margin often with stipitate glands to 1 mm long, base obtuse or cuneate and slightly rounded at the petiole, drying thinly chartaceous, usually dark above and much paler beneath, with scattered small (0.1–0.6 mm) stellate hairs and larger hairs on the veins both above and below, venation pinnate, 2° veins 4–8/side. Inflorescences terminal (pseudoxillary), solitary, bisexual, 1.2–5 cm long, with 1–3 proximal ♀ flowers on short (2 mm) pedicels, ♂ flowers 1–2/bract, pedicels 1–3 mm long. Male flower buds ca. 1.3 mm diam., sepals 5, stellate-pubescent, 1.2–1.7 mm long, petals 1.4–1.8 mm long; stamens 10–12, filaments 1.8–2.5 mm long, glabrous, anthers 0.4–0.7 mm long. Female flowers with sepals 1.7–6 mm long, 1–1.5 mm wide, oblong, glabrous within, often with teeth on the edge; ovary 1.5–3 mm long, 1.8–3 mm diam., glabrous, styles 1–2 mm long, 2 times bifid. Fruits ca. 7 mm long, 5–6 mm wide, smooth, usually glabrous, subtended by persisting perianth, columella 3–4 mm; seeds 3.8–5 mm long, 2.7–3.7 mm wide, 2–2.5 mm thick, slightly striate-reticulate, caruncle 0.5–1 mm wide.

Plants of evergreen forest formations on both the Caribbean and Pacific slopes, 20–800 m elevation. Probably flowering and fruiting throughout the year. The species ranges from northern Costa Rica to Chocó, Colombia.

*Croton brevipes* is recognized by the thin serrate leaves with pinnate venation, broad rounded teeth, and stipitate glands present in some sinuses along the leaf margin as well as at the apex of the petiole. Long internodes, opposite or whorled leaves at some distal nodes, and the short inflorescences are additional characteristics. This species is very

closely related to *C. macrodontus* Müll. Arg. of Mexico, but there are minor distinctions and the two are widely allopatric (cf. Webster & Huft, 1988).

***Croton decalobus* Müll. Arg., Linnaea 34: 80. 1865.**  
*C. pittieri* Pax in Pittier, Prim. Fl. Costar. 2: 338. Figure 16.

**Shrubs** 1–4 m tall, bisexual, much-branched, leafy stems 1–4 mm thick, stellate-pubescent with hairs 0.4–0.8 mm diam., sessile or on short (0.2 mm) stipes, glabrescent and reddish brown in age; stipules 4–8 mm long, linear. **Leaves** with petioles 3–18 mm long, 0.8–1.3 mm thick, densely stellate-pubescent, lacking glands at or near the apex; **leaf blades** 3–10 cm long, 2–5 cm wide, ovate-lanceolate to ovate-triangular or lanceolate, apex tapering gradually and acute or acuminate, margin entire, base acute to rounded or obtuse, drying chartaceous, dark above with simple scabrous or stellate hairs ca. 0.3 mm diam., pale grayish beneath with a dense tomentum of stellate hairs with 6–9 rays, venation pinnate, 2° veins 4–13/side. **Inflorescences** terminal, 1–3 (rarely more on leafless terminal stems), unisexual or bisexual, 3–10 cm long, ♀ flowers subsessile and with viscous glandular hairs, solitary, ♂ flowers 1/bract, pedicels 1–2 mm long (preanthesis). **Male flower** buds 2.5–3 mm diam., densely short-pubescent externally, petals 2–3 mm long, narrowly spatulate; stamens ca. 15, filaments puberulent, anthers 0.7–1 mm long. **Female flowers** ca. 6 mm long, sepals 4–6 mm long, ca. 1 mm wide, densely short-pubescent abaxially, with distinctive slender gland-tipped hairs along the inner margin 0.8–3 mm long; ovary densely pubescent, style branches ca. 2.5 mm long, pubescent, distally bifid. **Fruits** ca. 5 × 5 mm, columella 3.7–4 mm long, reddish, minutely fimbriate or glabrous; seeds 4–5.2 mm long, 3–3.4 mm wide, 2.2–2.4 mm thick, smooth and lustrous, caruncle 0.8–0.9 mm wide.

Rarely collected plants of evergreen forest formations in the central highlands, 1100–1800 m elevation. Flowering in June–July; fruiting in July–August. This species has been collected only in the eastern Meseta Central, from Tibas and Escazú to Cartago and Agua Caliente. The species is also known from central Honduras and Guatemala.

*Croton decalobus* is recognized by its often narrowly ovate-triangular leaves lacking glands at the petiole/blade interface, pinnate venation, and unusual gland-tipped hairs along the inner edge of sepals in ♀ flowers. The apex of the gland-tipped hairs is often elongate, resembling anthers on stamens.

***Croton draco* Cham. & Schldl., Linnaea 6: 360. 1831.** *Cyclostigma panamensis* Klotzsch in Seem., Bot. voy. Herald 105. 1853. *Cy. denticulatum* Klotzsch in Seem., Bot. voy. Herald 105. 1853. *Cr. panamensis* (Klotzsch) Müll. Arg.

in DC., Prodr. 15 (2): 546. 1866. *Cr. steyermarkianus* Croizat, J. Arnold Arbor. 21: 86. 1940. *Cr. triumfettoides* Croizat, J. Arnold Arbor. 21: 86. 1940. *Cr. draco* ssp. *panamensis* (Klotzsch) Webster, Ann. Missouri Bot. Gard. 75: 1120. 1988. Figure 18.

**Trees or shrubs** 2–15(–30?) m tall, bisexual, leafy stems 2–8 mm thick, densely pubescent with scurfy or stellate hairs 0.2–0.5 mm diam. or with longer slender hairs to 1 mm; stipules 3–10 mm long (to 12 × 4 mm in Mexico), linear or lanceolate. **Leaves** sometimes opposite at distal nodes, petioles 4.2–14(–20) cm long, 1–3.5 mm thick, densely stellate-scurfy, adaxial apex with 2–8 patelliform or saucer-like glands 0.4–1.7 mm wide, sessile or stipitate and 0.4–3.5 mm long; **leaf blades** (7–)11–26(–30) cm long, (4–)6–16(–23) cm wide, ovate-triangular to ovate, apex gradually narrowed and acuminate, tip 8–22 mm long, margin minutely (0.2–1 mm) denticulate or subentire, base rounded and truncate to cordate, drying chartaceous, dark above with stellate or scurfy hairs to 0.4 mm diam., grayish beneath with scurfy or stellate hairs 0.3–1 mm diam., stellate hairs with 8–14 rays, venation palmate or subpalmate with 3 major veins, 2° veins 4–10/side of the midvein, 3° veins subparallel. **Inflorescences** terminal, bisexual or ♂, 7–35(–70) cm long, with proximal ♀ flowers or cymules with 1 ♀ flower and 1–several ♂ flowers, or with many cymules of 3–15 ♂ flowers, bracteoles 1–1.5 mm long, ♀ pedicels 1–4 mm long, ♂ pedicels 3–8 mm long, slender. **Male flowers** 3–6 mm wide, calyx ca. 2.2 mm long, calyx lobes 5, 1–2.3 mm long, triangular, petals ca. 2 × 0.5 mm; stamens 13–20, filaments 1.5–3 mm long, glabrous, anthers 0.4–0.8 mm long. **Female flowers** densely pubescent externally, sepals 5, 1.3–2.5 mm long, 1–1.5 mm wide, glabrous within, petals 1–2 mm long, usually filiform, disc inconspicuous; ovary 2.5–4 mm diam., pubescent, styles deeply or partly bifid (6/flower), 2.5–3.5 mm long. **Fruits** 5–6 mm long, 6–8 mm wide, densely yellowish scurfy-stellate, pedunculate, subtended by the closely appressed sepals (rarely rotate), columella 3–4 mm long; seeds 3.8–5 mm long, 2.4–3.6 mm wide, 2–2.5 mm thick, oblong-ellipsoid, with lateral raised ridges (sometimes chevron-like), caruncle ca. 2 mm wide.

Common plants of partly deciduous and evergreen forest formations of the central highlands, (10–)700–2200 m elevation. Probably flowering throughout the year but collected most often in June–September. This species is rarely collected below 700 m but was said to be common near Golfito (Allen 6627). The species ranges from Veracruz, Mexico, to Colombia.

*Croton draco* is recognized by its larger ovate-triangular leaves with as many as 12 glands at the apex of the petiole, long inflorescences, ♂ flowers present with proximal ♀ flowers in bisexual inflorescences, pedicellate ♀ flowers with relatively small calyx lobes and inconspicuous disk, and seeds with raised lateral ridges. The ♂ inflorescences are often



densely flowered with many closely spaced glomerules of 5–11 flowers (distal fascicles may have one to a few ♂ flowers). The complex indument of both scurfy and stellate hairs is not found in all collections. *Targuá* and *copalchi* are common names applied to this and similar *Croton* species. This species is similar to *C. xalapensis* and *C. hoffmannii* in general appearance, but the latter two species do not have ♂ and ♀ flowers together in the same glomerules.

***Croton glandulosus* L., Syst. ed. 10. 1275. 1759.**

**Herbs**, erect or decumbent, to 0.6 m tall, bisexual, leafy stems 1–2.5 mm thick, with appressed stellate hairs 0.4–1.3 mm wide; stipules to 0.5 mm long, gland-like or absent. **Leaves** often opposite below branching nodes, petioles 2–9 mm long, ca. 0.6 mm thick, densely stellate-pubescent, with paired lateral subsessile glands at apex, ca. 0.5 mm diam.; **leaf blades** 7–35 mm long (larger in the northern part of its range), 6–16 mm wide, broadly ovate to ovate-elliptic or narrowly oblong, apex rounded, margin crenate with 3–5 rounded teeth/cm, base obtuse to truncate, drying grayish green, stellate-pubescent above and beneath, venation pinnate or subpalmate. **Inflorescences** terminal and pseudoaxillary, to 2 cm long and 5 mm wide, developing 2–4 fruits/node; ♂ flowers with 7–13 stamens; ♀ flowers with deeply bifid styles (appearing as 6). **Fruits** 4–5 mm long, splitting at the apex but often remaining united beneath, covered with thin stellate hairs ca. 0.8 mm wide, columella ca. 3 mm long, slender; seeds ca. 3 mm long, 2–2.5 mm wide, oblong, lustrous.

*Croton glandulosus* is recognized by the short herbaceous habit, thin stellate-appressed hairs, small leaves with prominent rounded teeth, subsessile saucer-shaped glands at the apex of the petioles, and short inflorescences. Standley (1937) reported this species from Costa Rica, but we have seen no material from southern Central America. The species ranges from the southeastern United States, Mexico, and the West Indies to South America.

***Croton hirtus* L'Hér., Stirp. Nov. 17, t. 9. 1785.**

*C. glandulosus* L. subsp. *hirtus* (L'Hér.) Croizat, Bull. Torrey Bot. Club 75: 401. 1948. Figure 10.

Annual **herbs** 20–90 cm tall, bisexual, leafy stems 0.8–6 mm thick, hispid with stellate hairs having small (0.3–0.7 mm) thin basal rays and 1 central ray 2–3.5 mm long, often dense and retrorse; stipules 2–4.5 mm long, ca. 0.5 mm wide, linear, pubescent. **Leaves** with petioles 3–30 mm long, 0.3–1 mm thick, with thin stellate hairs to 2 mm long, with paired (1–4) stalked yellowish glands 0.5–1.2 mm long near the apex; **leaf blades** 1.3–9 cm long, 0.9–5.8 cm wide, ovate to ovate-triangular or ovate-oblong, apex acute to rounded, margin with 10–25 rounded teeth/side, base rounded and truncate to broad-

ly obtuse, drying thinly chartaceous, greenish to yellow-brown, upper surface with thin simple hairs 0.3–1 mm long, lower surface stellate with small (1 mm diam.) and longer (2 mm) hairs along the veins, venation palmate with 3 major veins, 2° veins 1–4/side of midvein. **Inflorescences** terminal, 1–3, bisexual, 1–10 cm long, often subtended by small leaves, peduncles 0–28 mm long, ca. 0.5 mm thick, stellate-pubescent, ♀ flowers 3–12, subsessile, ♂ flowers 4–9, pedicels 1–3 mm long, slender, rachis with gland-tipped hairs and linear bracts with 1–3 slender gland-tipped segments 0.5–5 mm long. **Male flower buds** ca. 1.8 mm diam., densely pubescent externally, sepals 5, 1–1.5 mm long, stellate externally; stamens 8–12, filaments 0.8–1.5 mm long, glabrous, anthers 0.3–0.5 mm long. **Female flowers** with 4 unequal sepals 3.5–4 mm long, 0.5–1 mm wide, oblanceolate to linear, pubescent; ovary ca. 3 × 2 mm, styles separate above the base, 1.5–2.5 mm long, bifid. **Fruits** ca. 4 mm long, 3.5–4.5 mm wide, stellate-pubescent (glabrous), sepals to 6 mm long, columella 2.8–3.2 mm long; seeds 2.8–3.6 mm long, 2–2.8 mm wide, 1.4–1.8 mm thick, oblong-lenticular, smooth with surface minutely reticulate, lustrous, caruncle ca. 1.5 mm wide.

Weedy plants of open sunny sites in evergreen and deciduous areas, 0–1700 m elevation. Flowering and fruiting material has been collected mostly in March–August in southern Central America. In Costa Rica, it is most often collected on the Pacific slope and lowlands below 1200 m elevation. The species ranges from Mexico to Brazil, mostly in deciduous vegetation.

*Croton hirtus* is recognized by its annual weedy habit, distinctive (usually retrorse) pubescence, stipitate glands at base of the blade (often difficult to see or absent), simple hairs on upper leaf surfaces, and short inflorescences with unusual bracts with slender segments that resemble gland-tipped hairs. The stellate hairs of the stem, with a basal circle of short thin rays and a central erect large ray, are distinctive, but the small basal rays are often difficult to see. Material of this species was often placed under *Croton glandulosus*, but that species lacks the unusual hispid hairs and has sessile petiolar glands and floral bracts without glands.

***Croton hoffmannii* Müll. Arg., Linnaea 34: 86.**

1865. *C. hoffmannii* var. *incana* Müll. Arg., Linnaea 34: 86. 1865. *C. hoffmannii* var. *viridis* Müll. Arg., Linnaea 34: 86. 1865. *Oxydectes turrialva* O. Ktze. and *C. turrialva* O. Ktze. (as syn.), Rev. gen. 2: 614. 1891. Figure 19.

**Shrubs** or small trees 1.5–6 m tall, bisexual, leafy stems 2–6 mm thick, densely stellate-pubescent with short-stipitate (0.1–0.8 mm) hairs 0.3–0.7 mm diam.; stipules 5–7 mm long, linear, caducous. **Leaves** sometimes opposite at distal flowering nodes, petioles 2–15 cm long, 1–3 mm thick, densely stellate-pubescent, usually with



2 lateral/abaxial saucer-like or patelliform sessile glands near the apex, 0.7–1.3 mm wide; **leaf blades** 7–22 cm long, 4–19 cm wide, ovate to ovate-triangular, acute to acuminate at the apex, margin minutely dentate with small (0.3–1 mm) gland-tipped teeth, ca. 3–9 teeth/cm, base rounded and cordate to truncate, drying thinly chartaceous, upper surface with simple or stellate hairs, lower surface more densely pubescent, stellate hairs with 8–14 rays, 0.3–0.7 mm diam., venation palmate or subpalmate with 3 prominent veins from base, 2° veins 3–8/ side of midvein. **Inflorescences** 8–30 cm long (often pendulous in life), terminal, 1–4, usually bisexual with 1–12 proximal solitary ♀ flowers or proximal cymes with 1 ♀ and 2 ♂ flowers, flowers or fascicles usually distant along the rachis, ♀ pedicels 1–2 mm long, ♂ pedicels 1–3 mm long, distal bracts to 6 mm long subtending 3–9 ♂ flowers. **Male flower** buds ca. 3 mm diam., calyx ca. 4 mm long, calyx lobes 1–2.5 mm long, 1.5–2.7 mm broad at base, petals 5, ca. 3 mm long; stamens ca. 16, anthers 0.7–0.8 mm long. **Female flowers** ca. 6–7 mm long, calyx lobes 5, unequal and imbricate in bud, 3–4 mm long, 1.5–5 mm broad, triangular to ovate, glabrous within, disk with dense radiating hairs 0.7 mm long; ovary densely hirsute, ca. 3 mm diam., styles with short (0.5 mm) pubescent column, each style with 4 glabrous branches ca. 3 mm long. **Fruits** ca. 8 × 10 mm, subtended by the rotate or reflexed sepals, columella 6–7.5 mm long; seeds 6–8 mm long, 4.3–5 mm wide, 3.2–4 mm thick, smooth or with some irregular raised areas, caruncle 2.6–3 mm wide.

Plants of open weedy sites in evergreen forest formations 900–1600 m elevation. Flowering in June–August; fruiting in October–December. In Costa Rica, this species appears to be restricted to the area between the eastern part of the Meseta Central and the northern edge of the Cordillera de Talamanca (Río Virilla eastward to the Orosi valley). Specimens determined as this species have also been collected in Mexico.

*Croton hoffmannii* is recognized by its larger ovate-triangular leaves with sessile glands at the apex of the petiole, serrulate margins, long inflorescences with uncrowded flowers, larger ♀ flowers with ovary subtended by a densely pubescent disc (easily seen in fruit because of the rotate or reflexed sepal lobes), larger seeds, and very limited geographic range. Some inflorescences have proximal cymes with 1 ♀ flower and 2 ♂ flowers. The leaves are often ovate-triangular and usually dry yellowish green. The calyx is united almost 50% in both ♂ and ♀ flowers. The restricted flowering period, flowers well separated along the inflorescence rachis, and calyx united to form clearly visible cups help distinguish this species from the vegetatively similar *C. draco*, *C. pungens*, and *C. xalapensis*.

*Croton jimenezii* Standl. & Valerio, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 604. 1937. Figure 19.

**Trees** or shrubs, 3–15 m tall, bisexual or unisexual, leafy stems 2–8 mm thick, densely pubescent with short (0.2 mm) reddish brown scurfy-stellate hairs ca. 0.3 mm wide at the flattened apex, the hairs often with slender central rays to 1.5 mm long; stipules 3–5 mm long, 0.5–2 mm wide at base, pubescent, caducous. **Leaves** with petioles 3.6–14.5 cm long, 0.8–3.5 mm thick, densely brownish scurfy-stellate hirsutulous, often contracted at apex and base when dried, apex with 2–5 glabrous stipitate conical glands 0.5–1.5 mm long, 0.4 mm wide; **leaf blades** 8–24 cm long, 4–13 cm wide, ovate to ovate-triangular or ovate-oblong, apex acuminate with narrow tip 6–14 mm long, margin entire or subentire (glandular-crenate), base rounded and truncate or subcordate, drying chartaceous, upper surface with scurfy-stellate hairs ca. 0.2 mm wide, lower surface with similar hairs 0.2–0.4 mm wide, hairs to 2 mm long sometimes present near base and along midvein, venation pinnate or subpalmate, 2° veins 7–10/ side. **Inflorescences** terminal, usually solitary, unisexual or bisexual, 4–30 cm long, ca. 2 cm wide, peduncle 2–3.5 mm thick, pubescent as the stems, bracts 0.7–3 mm long, subtending 1 subsessile ♀ flower or 1–5 ♂ flowers on pubescent pedicels 2.5–6 mm long, 0.2–0.4 mm thick. **Male flower** 5–10 mm wide at anthesis, pubescent externally, calyx lobes 1.5–2.5 mm long, petals 2–3 mm long; stamens 21–31, filaments ca. 3 mm long, pubescent only at the base, anthers 0.6–0.8 mm long. **Female flowers** pubescent externally, calyx lobes 5, 3–11 mm long, 1–3 mm wide, spatulate to oblong; ovary ca. 3 mm diam., covered with many-pointed stellate hairs 0.5–1 mm wide, styles 3–4 mm long, undivided for ca. 1 mm, twice bifid (12 distal parts). **Fruits** ca. 6 mm long (only 1 seen); seeds 3.7–5 mm long, 3–4 mm wide, ca. 2 mm thick, oblong-lenticular, surface smooth or very slightly rugulose, caruncle 0.8–2 mm wide.

Trees of wet evergreen montane forests near the continental divide of the central volcanic highlands and Cordillera de Talamanca, (1000–)1500–2500 m elevation. Flowers have been collected in December–May and July. This endemic species ranges from near Zarcero eastward to Sta. Cruz de Turrialba and is also known from a single collection from along the Inter-American Highway about 27 km north of San Isidro del General.

*Croton jimenezii* is recognized by the dense pubescence of brownish or yellowish stellate/scurfy hairs, larger ovate-triangular leaves, oblong ♀ calyx lobes that enlarge as the fruit develops, ♂ flowers with 21–30 stamens, and restricted montane habitat. The hairs of the stems often have very short (0.1 mm) stalks and a flattened reddish brown distal portion with short marginal teeth, giving a rufous scurfy-stellate appearance. In addition, the hairs often have one transparent central ray becoming 1–2 mm long. Though little collected, the species has been noted as locally common and called *targua*. Collections with only ♂ flowers may be very difficult to separate from *C. draco*.

***Croton jutiapensis*** Croizat, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 450. 1942. Figure 16.

Small shrubs 0.5–1(–2) m tall, bisexual, leafy stems 0.7–3 mm thick, stellate-pubescent with hairs ca. 0.5 mm diam., sometimes with longer rays 0.5–1.5 mm long, whitish or yellowish, glabrescent and dark in age; stipules 3–8 mm long, linear, caducous. **Leaves** with petioles 3–12(–32) mm long, 0.4–1.3 mm thick, densely stellate-pubescent, with 2 (3–4) lateral/abaxial stipitate conical yellowish glands 0.4–1 mm long, 0.2–0.7 mm wide at apex; **leaf blades** 1.7–9(–11) cm long, 0.8–4.3(–5.5) cm wide, ovate-triangular to ovate-lanceolate or ovate-elliptic, apex acute or acuminate, margins with 7–19 short (0.5–2 mm) teeth/side, base cuneate to rounded and subcordate, drying chartaceous, upper surface usually dark with stellate hairs ca. 0.5 mm diam., lower surface densely stellate and pale colored, venation pinnate or subpalmate, 2° veins 3–8/side. **Inflorescences** terminal or axillary, solitary, 2.5–(7) cm long, usually bisexual, peduncles 5–15 mm long, densely stellate-pubescent, ♀ flowers 1–7, subsessile or short pedicellate, ♂ flowers solitary, pedicels ca. 2 mm long, bracteoles 1–3 mm long, linear. **Male flower** buds ca. 2 mm diam., sepals 5, 1–2 mm long, 0.8–1 mm wide, triangular, petals 5, 1.7–2.2 mm long, ca. 1.1 mm wide, oblong to spatulate; stamens ca. 11, filaments 1.5–3.5 mm long, glabrous, anthers 0.4–0.7 mm long. **Female flowers** 3.5–8 mm long, sepals 1.5–5 mm long, becoming 5–8 mm long in fruit, subequal or unequal; ovary ca. 3 × 4 mm, densely stellate-hispid, styles 2–4 mm long, bifid to the base (6). **Fruits** 4.5–6 mm long, densely hispid, columella 3–4 mm long; seeds 3.3–4 mm long, 2–3.3 mm wide, 1.5–1.8 mm thick, oblong-ellipsoid, smooth, lustrous, caruncle 0.8–1.8 mm wide.

Common plants in open sunny sites in seasonally dry deciduous woodland formations, 0–400 m elevation (to 1100 m in Honduras and Guatemala). Flowering in April–August; fruiting in July–October. The species ranges from the Petén area of Guatemala along the Pacific slope to Guanacaste Province in Costa Rica.

*Croton jutiapensis* is recognized by the short-shrubby habit with older stems becoming blackish and glabrous, seasonally dry habitat, leaves usually ovate-lanceolate with lateral stipitate glands near the apex of the petiole, pinnate venation, and short inflorescences. Many Costa Rican collections have been identified as *C. costaricensis*, but that name is a synonym of *C. ortholobus*, a species of higher elevation.

***Croton lanjouwensis*** Jabl., Mem. New York Bot. Gard. 12: 158. 1965. *C. matourensis* Aublet var. *benthamianus* Müll. Arg., Linnaea 34: 95. 1865. *C. benthamianus* (Muell. Arg.) Lanjouw. Euphorb. Surinam 17. 1931, non *C. benthamianus* Müll. Arg. in Mart., Fl. Bras. 11 (2): 106. 1874. Figure 17.

**Trees** 7–40 m tall, bisexual, leafy stems 1–6 cm thick, covered with flat rounded-appressed peltate hairs 0.3–0.5 mm diam. and yellowish brown dried; stipules 6–10 mm long, ca. 1.2 mm wide at base, covered with peltate hairs, caducous. **Leaves** with petioles 11–55 mm long, 0.7–1.7 mm thick, covered with peltate scales, with 2 adaxial/lateral patelliform glands 0.7–1.6 mm wide at the apex; **leaf blades** 7–16 cm long, 3–6 cm wide, elliptic-oblong to oblong or elliptic, apex acute to short-acuminate with tip 3–8 mm long, margin entire, base acute, drying stiffly chartaceous, dark brown to grayish brown, glabrous above, sparsely to covered beneath with peltate hairs 0.3–0.4 mm diam., venation pinnate with 11–22 veins/side. **Inflorescences** terminal, 1–4, 6–18 cm long, racemose, bisexual, peduncles 12–60 mm long, ca. 2 mm thick, with peltate hairs, with 1–6 proximal ♀ flowers on pedicels to 5 mm long (to 15 mm in fruit), ♂ flowers in distal groups of 3–5, bracts 1–4 mm long, lepidote. **Male flower** buds ca. 2 mm diam., covered with peltate hairs, calyx lobes 5, valvate, 2–2.5 mm long, petals to 2 mm long; stamens ca. 12, anthers 0.6–0.7 mm long. **Female flowers** ca. 6 mm long, 8–10 mm wide, calyx lobes 5, 3–4.5 mm long, triangular, valvate, with stellate hairs on the inner surface and peltate externally, petals absent; ovary ca. 3.5 mm diam., styles ca. 4 mm long, twice bifid. **Fruits** (not seen) ca. 5 mm long, columella ca. 4 mm long; seeds ca. 3.5 mm long, rounded.

Trees of wet evergreen rain forest formations on the Caribbean slopes between 200 and 800 m elevation. Flowering in March and July in southern Central America. This species ranges from near the Costa Rican–Panama border to the eastern Amazon Basin.

*Croton lanjouwensis* is recognized by its large stature, flat rounded-appressed peltate hairs covering many surfaces, paired glands at the apex of the petioles, pinnate venation with many secondary veins, and larger ♀ flowers. We have seen only a single Costa Rican collection (*A. Chacón* 182 CR, F, MO) from 800 m elevation in Parque Internacional La Amistad. The large height attained by these trees may explain why they are not collected more often. This species is closely related to *C. matourensis* Aublet of South America.

***Croton lobatus*** L., Sp. Pl. 1005, 1753. *Astraea seemannii* Klotzsch in Seem., Bot. voy. Herald 103, 1853. *C. lobatus* var. *seemannii* (Klotzsch) Müll. Arg. in DC., Prodr. 15 (2): 669. 1866. Figure 2.

**Herbs** 0.2–0.9(–1.5) m tall, bisexual, often with distal leaves and shoots from congested nodes, leafy stems 1–4.5 mm thick, with sessile-stellate hairs 0.3–1.8 mm long or with only 1 ray of the hair developing and simple; stipules 2–6 mm long, 0.5–0.8 mm broad at base, lanceolate to linear (sometimes deeply split and more than 2/node). **Leaves** with petioles 3–11 cm long, 0.4–1.3 mm thick, sparsely puberulent with mostly simple hairs to 2 mm long, with minute lobed or digitate glands 0.1–0.4



mm long at the adaxial apex; **leaf blades** 3–9 cm long, 2–10 cm wide, 3–5-lobed with deep narrow sinuses (or unlobed and lanceolate), central lobe elliptic to oblanceolate, apices acuminate, margins of the major lobes with 12–20 teeth/side, base truncate to subcordate, drying thinly chartaceous, greenish to brown, with mostly simple hairs 0.3–1 mm long above and below, venation palmate with 3–5 veins (unlobed leaves pinnately veined with ca. 5 veins/side). **Inflorescences** terminal, 2–6(–15) cm long, racemose, bisexual with 1–3(–7) proximal solitary ♀ flowers and 4–12 distal ♂ cymules, bracts ca. 2 mm long below ♀ flowers and 1 mm long below ♂ flowers, ♀ pedicels ca. 1 mm long and densely pubescent, to 3 mm long in fruit; ♂ flowers solitary or in cymules of 2–5, ♂ pedicels ca. 2 mm long and glabrous. **Male flower** buds ca. 1.2–1.8 mm diam., globose, calyx lobes 5, ca. 1.1 mm long, imbricate and rounded, petals 1.2–1.5 mm long, 0.5–1 mm wide; stamens (8–)12–15, filaments to 1 mm long, glabrous, anthers ca. 0.3 × 0.4 mm. **Female flowers** 4–5 mm long, sepals 5, 4–7 mm long, 1–2 mm wide, oblanceolate to spatulate, sparsely pubescent, with minute teeth or stalked glands near the base, disc of 5 segments ca. 0.3 mm long; ovary 3–4 mm long, pubescent with stellate or simple hairs (rarely glabrous), styles 2–4 mm long, 2 times bifid in the distal half. **Fruits** ca. 6 mm long, 6 mm diam., oblong, 3-lobed, columella 4–5 mm long; seeds 4.5–5.5 mm long, 2.7–3.5 mm wide, 2.5–3 mm thick, oblong-rectangular, slightly rugulose with slanted transverse ribs, caruncle 1.4–2 mm wide, reniform-peltate.

Plants of open sunny sites in lowland evergreen to deciduous formations, 0–800 m elevation (in Central America). Often found in sandy stream-sides or in weedy fields and roadsides. Probably flowering and fruiting primarily in the wet season, May–December. Though weedy and wide-ranging, this species is infrequently collected in Central America; it has been collected only a few times in the Pacific lowlands of central and northern Costa Rica (20–350 m). It ranges from Florida and the Bahamas to Peru and Brazil and is found in western and northeastern Africa.

*Croton lobatus* is distinguished by its short weedy habit, deeply lobed leaves, leaf surfaces with mostly simple hairs, ♀ flowers with five to seven long narrow sepals, and unusual seeds. No other species of *Croton* in Costa Rica has leaves with comparably deep sinuses.

***Croton mexicanus* Müll. Arg., Linnaea 34: 113. 1865. Figure 16.**

**Trees** 4–15 m tall, bisexual, leafy stems 1.5–4 mm thick, stellate-pubescent with flat appressed somewhat peltate hairs 0.2–0.4 mm diam., stems becoming grayish or reddish brown; stipules 3–4 mm long, linear. **Leaves** with petioles 15–58 mm long, 0.8–2 mm thick, appressed-pubescent with stellate or peltate-like hairs, 2 lateral glands present near the apex of the petiole, 0.7–1.5 mm long, 0.4–0.7 mm diam. at apex, conical-cu-

pulate; **leaf blades** 5–14(–16) cm long, 2–7(–9) cm wide, ovate-elliptic to narrowly ovate, lanceolate or elliptic, tapering gradually to the acute or acuminate apex, margin minutely dentate with glandular teeth 0.2–0.4 mm high, 3–5 teeth/cm, base cuneate to rounded, drying chartaceous, darker above with sparse stellate-peltate hairs 0.1–0.4 mm diam., paler and more densely pubescent beneath with larger hairs, venation pinnate or subpalmate with basal 2° veins usually reaching the middle of the blade, 2° veins 3–6/side of midvein. **Inflorescences** terminal, 1–4, unisexual (rarely with bisexual glomerules), 2–13 cm long, ♀ flowers 1–3, ♀ pedicels 1.3–3.5 mm long, 1.2–1.5 mm thick, bracteoles ca. 1 mm long, ♂ flowers in glomerules of 2–5 or solitary, stellate-pubescent, ♂ pedicels 2–8 mm long, slender. **Male flower** buds ca. 3 mm diam., calyx lobes 5, 1.5–2 mm long, 1.3 mm wide, petals 5, ca. 2 mm long; stamens ca. 14–16, anthers 0.6–0.9 mm long, almost as wide. **Female flowers** with 5 calyx lobes 2.5–3 mm long, ca. 1.3 mm wide; ovary 2.3–2.7 mm long, 2–3.3 mm diam., densely stellate-pubescent, style branches pubescent in the lower half, glabrous and bifid in the distal half (6). **Fruits** 10–12 mm long, 9–10 mm wide, with stellate-scurfy hairs, columella ca. 8 mm long; seeds 6–7 mm long, 4.5–4.8 mm wide, 2.5–3.2 mm thick, surface smooth but with irregular raised areas, caruncle 2–2.7 mm wide.

Plants of evergreen forest formations on the Pacific slope and continental divide of the Cordillera de Tilarán, 1400–1600 m elevation. Flowering in February and June–October; fruiting in August–November. The preceding description is based on material collected from the area around the Monteverde community and Cloud Forest Reserve in the Cordillera de Tilarán. The material placed here appears to be a disjunct population of a species otherwise only known from Mexico.

*Croton mexicanus* is recognized by its long petioles with two prominent glands near the apex, narrowly ovate-elliptic leaves with prominent basal 2° veins, appressed flat-stellate or scurfy pubescence on many parts, stamens 14–16/flower, and slightly rugose seed surfaces. The distally flattened stellate hairs with more than 15 radiating peripheral rays are distinctive and often have a raised brownish center. The rays may be united near the elevated center and somewhat peltate, but more three-dimensional irregularly stellate (scurfy) hairs may also be present. The trees are often conspicuous because of the silvery undersides of their leaves. Despite the restricted area from which our collections have been made, the Monteverde material exhibits considerable variation; one collection has spikes with bisexual glomerules (*Haber & Zuchowski 10714*). Placement of this material under *C. mexicanus* is tentative; we have seen no authentic material of *C. mexicanus*. *Croton oerstedianus* Müll. Arg. is also closely related but has leaves that are bluntly retuse at the apex and grows



at lower elevations in Honduras and Nicaragua. Collections placed here were earlier determined and distributed as *C. montevertensis*, an unpublished name.

***Croton niveus* Jacq., Enum. pl. syst. 32. 1760. Figure 17.**

**Shrubs** or small trees 2–12(–20?) m tall, bisexual, leafy stems 1.5–4.5 mm thick, whitish, covered with flat rounded peltate hairs 0.2–0.4 mm diam., usually with a small brown center and whitish circumference; stipules 3–9 mm long, linear, caducous. **Leaves** with petioles 7–32 mm long, 0.7–1.8 mm thick, with peltate hairs, glands absent near the apex; **leaf blades** 3–14 cm long, 2–10 cm wide, broadly ovate to ovate-orbicular or ovate-triangular, tapering gradually to an acuminate or acute apex, margin serrate to subentire, base rounded and truncate to obtuse, drying chartaceous, upper surface dark and glabrous or with scattered peltate hairs, lower surface grayish or silvery with a dense covering of peltate hairs 0.2–0.5 mm diam., venation palmate or subpalmate, with prominent basal lateral veins, 2° veins 3–5/side of midvein. **Inflorescences** usually axillary, 2–11 cm long, bisexual or ♂, with peltate hairs throughout, with 1–3 proximal ♀ flowers on pedicels 4–18(–28) mm long, 0.4–1.7 mm thick, distal bracts 0.5–1.5 mm long, subtending solitary ♂ flowers on pedicels 1–6 mm long, ca. 0.6 mm thick. **Male flower buds** 2–3 mm diam., sepal lobes 1.3–2.2 mm long, triangular, petals 2–3 mm long, ca. 1 mm wide, narrowly oblong, with densely ciliate edge and glabrous surfaces; stamens 10–15, filaments 2.2–3.3 mm long, glabrous, anthers 0.6–1.3 mm long. **Female flowers** with sepals 2.5–4 mm long, 2.1–3 mm wide at base, petals 1–3 mm long, 1.2 mm wide, narrowly oblong, with a densely ciliate white edge; ovary 2.5–5 mm long, 2.5–5 mm diam., covered with stellate-peltate hairs, styles 2.5–3 mm long, bifid to multifid distally. **Fruits** 9–24 mm long, 9–20 mm wide, differing greatly in size in different collections, usually becoming covered with short projections terminating with irregular stellate hairs, columella 7.5–16 mm long; seeds 6.5–16 mm long, 5.3–11 mm wide, 3–5 mm thick, oblong, dark brown mottled with white or yellowish brown, caruncle 1.5–2.2 mm wide.

Plants often seen in hedgerows and roadsides in deciduous and partly deciduous forest formations (rare in evergreen areas), 50–1800 m elevation. Flowering material has been collected in March–August and November–December. The species (in a wide sense) ranges from Mexico to Venezuela.

*Croton niveus* is recognized by the flat appressed rounded peltate hairs on almost all outer surfaces, ovate-triangular leaves often with silvery undersurfaces, and larger fruits and seeds. The hairs covering the ovary are usually more stellate (with deeply divided rays) than hairs on other surfaces, and they often become raised on projections as the fruit develops (but see below). This species is often used as a hedgerow plant. Dried leaves and bark

have been used in Guatemala for medicinal purposes (Standley & Steyermark, 1949, pp. 73, 79). The common names *copalchí* and *quisarrá copalchí* are said to be based on the Mayan name *copalché* (Pittier, 1957, p. 59).

Cultivation and use by indigenous peoples over many centuries may account for the great variation in fruit and seed size seen in different collections. For this reason, we prefer a broad interpretation of this species. The senior author at first included *C. reflexifolius* H.B.K., *C. eluterioides* Lotsy, and *C. guatemalensis* Lotsy as synonyms under this species. However, a reviewer pointed out that these species have peltate hairs on the ovary, not stellate hairs as in *C. niveus* (*sensu stricto*). There are a few specimens in which the ovary is covered with hairs that appear intermediate between peltate and stellate. It is on the basis of such collections that it seems likely a broader interpretation of *C. niveus* will prove more useful. The reader should note that the material placed under this name may represent a complex of closely similar species.

***Croton ortholobus* Müll. Arg., Flora 55: 9. 1872. *Oxydictes costaricense* Kuntze, Rev. gen. 2: 614. 1891. *C. costaricensis* Pax in Pittier, Prim. Fl. Costar. 2: 331. 1900. Figure 16.**

Small **shrubs** 0.5–2.5 m tall, bisexual, leafy stems 0.9–4 mm thick, densely stellate-pubescent and apparently hispid with central sharp rays to 2.2 mm long, older stems glabrescent and dark reddish brown or black; stipules 2–5(–9) mm long, 0.2–0.4 mm wide, linear, drying dark, deciduous. **Leaves** with petioles 4–30(–52) mm long, 0.5–0.9 mm thick, stellate-pubescent and hispid, with paired stipitate-cupulate glands at leaf base beneath, 0.5–1.5 mm long, 0.4–0.7 mm diam. at apex, yellow, glabrous; **leaf blades** 1.8–9.4 cm long, 1.3–5.3 cm wide, ovate to elliptic-ovate, apex acute to shortly cuspidate-acuminate, margin subentire or minutely (0.5 mm) denticulate with 8–20 teeth/side, base obtuse to rounded, thinly to stiffly chartaceous, upper surface with simple or stellate hairs 0.2–1 mm long, lower surface stellate-pubescent with hairs 0.3–0.6 mm wide, venation pinnate or subpalmate, 2° veins 3–5/side. **Inflorescences** terminal, ♂ or bisexual, 2–12 cm long, proximal ♀ flowers 1–12, distal part of spike 1–1.7 cm diam., ♂ flowers 1/bracteole, pedicels 2–3 mm long, slender, bracteoles 2–4 mm long, linear, often with glands. **Male flower buds** 2–2.5 mm diam., calyx lobes 1.5–2 mm long, triangular to ovate, pubescent externally, petals 1.8–2.5 mm long, spatulate to narrowly obovate; stamens 9–11, filament 2–3 mm long, glabrous, anthers 0.5–0.9 mm long. **Female flowers** ca. 6 mm long, calyx lobes 2.5–5 mm long, ca. 1.3 mm wide, narrowly triangular, petals subulate or absent, ovary globose, pubescent, styles deeply bifid. **Fruits** 5.5–6 mm long, 4.5–5.5 mm diam., rounded-oblong, densely pubescent; seeds ca. 4.2 mm long, 2.8–3.2 mm wide, 1.5–2 mm thick, oblong, smooth, lustrous, caruncle ca. 1.5 mm wide.

Plants of secondary growth in evergreen lower montane forest formations, 1300–2100 m elevation. Flowering and fruiting collections have only been made in June–August and November. The species is only known from the northeastern part of the Meseta Central, from near Grecia and Zurquí eastward to Cartago and Paraiso.

*Croton ortholobus* is recognized by its short shrubby habit, paired stipitate yellowish glands at the apex of the petiole (mostly abaxial side), leaf blades often with simple hairs above and stellate hairs beneath, very restricted geographic range, and limited flowering period. The sharp hispid hairs of stems and petioles are actually the central rays of stellate hairs with much smaller basal/lateral rays. The type (*Friedrichsthall 1417* ♂, photo ♀) was mislabeled as coming from Guatemala; it was collected near Cartago. The name *C. costaricensis* has been used for this species and also misapplied to collections of *C. jutiapensis* from lowland Guanacaste.

***Croton ovalifolius*** Vahl in H. West, Bidr. Beskr. Ste. Croix 307. 1793. *C. escathos* Croizat, J. Arnold Arbor. 21: 79. 1940. Figure 10.

Herbaceous **subshrubs** 20–90 cm tall, bisexual, leafy stems 0.6–2 mm thick, hairs stellate, 0.5–1.5 mm wide with slender rays or partly stellate with a single long (1–2.3 mm) ray; stipules 1–2.5 mm long, 0.1–0.6 mm wide, usually lacking stellate hairs and with several glandular teeth along the margin, drying brown, caducous. **Leaves** with slender petioles 2–8(–18) mm long, 0.2–0.4 mm thick, densely stellate-pubescent, apical glands lacking; **leaf blades** 9–35 mm long, 4–18 mm wide, oblong to ovate-oblong or elliptic-oblong, apex obtuse or rounded, margin minutely serrate with 10–20 small (0.3 mm) teeth/side, base obtuse to cuneate, drying chartaceous, sparsely stellate-pubescent above with 6-rayed hairs, densely stellate-pubescent beneath with hairs 1–2 mm diam., venation subpalmate, 2° veins 3–4/side with basal pair prominent. **Inflorescences** terminal or axillary, 1–4 cm long, bisexual or ♂, stellate-pubescent throughout, with 1–3 proximal ♀ flowers on slender pedicels 3–8 mm long, ♂ flowers 5–15, solitary in axils of bracteoles 1–2 mm long, with glandular margin, pedicels 1–2.3(–3.5) mm long. **Male flower** buds ca. 2.2 mm diam., 4–5 mm wide at anthesis, sepals 5, 1.2–2 mm long, ca. 1 mm wide, acute, sparsely pubescent, petals 1.5–2.5 mm long, ca. 0.7 mm wide, spatulate-oblong, glabrous except for minute white hairs at the blunt apical margin; stamens 8–12, filaments 1.4–2 mm long, slender, glabrous, anthers 0.5–0.7 mm long. **Female flowers** 4–6 mm long, sepals 5, 4–7 mm long, 0.5–0.7 mm wide, linear-oblong with glandular marginal teeth 0.4–1 mm long and few stellate hairs; ovary ca. 2 mm long, densely stellate-pubescent, styles to 4 mm long. **Fruits** ca. 6 mm long, oblong, 3-lobed, stellate-pubescent, columella ca. 3.5 mm long; seeds (3–)3.6–4.8 mm long, (2.2–)2.7–3.3 mm wide,

ca. 2 mm thick, oblong, lustrous, grayish yellow, caruncle ca. 1 mm wide.

Uncommon plants of open sites in seasonally very dry deciduous areas, 20–300 m elevation (0–1200 m in South America). Flowering and fruiting material was collected in July (*Webster et al. 12475* ♀) and August (*Wilbur 31130* ♀) in Costa Rica. The species appears to range disjunctly from Oaxaca, Mexico, and the West Indies to Colombia and Venezuela.

*Croton ovalifolius* is distinguished by its small stature, small leaves, stellate pubescence, unusual stipules, and ♀ sepals. The stipules, bracteoles, and ♀ sepals have a similar glabrous texture (drying smooth and brown) that suggests succulence in life, and all have distinctive gland-like teeth (with or without distal knobs) along the margins. The North American material usually has broader leaves, and the larger seeds lack the longitudinal striations characteristic of South American material.

***Croton pachypodus*** Webster, Ann. Missouri Bot. Gard. 75: 1119. 1988. Figure 17.

**Trees** 6–30 m tall, bisexual, leafy stems 1.3–4 mm thick, with small (0.1–0.4 mm) flat appressed rounded peltate hairs; stipules 2–4 mm long, lanceolate to subulate, caducous. **Leaves** with petioles 10–45 mm long, 0.8–1.6 mm thick, densely covered with peltate hairs, apex with paired lateral glands 0.4–0.8 mm long, 0.4–0.6 mm wide distally, usually cylindrical to stipitate conic (rarely absent); **leaf blades** 4–13 cm long, 2–6 cm wide, elliptic to elliptic-oblong or ovate-oblong, apex bluntly acute to short-acuminate or caudate-acuminate, margin obscurely crenate with 5–15 small (0.5 mm) sinuses/side, base obtuse to slightly rounded, drying thinly to stiffly chartaceous, dark and glabrous above or with flat stellate hairs, paler beneath with many small (0.1–0.2 mm diam.) flat peltate hairs, venation pinnate, 2° veins 5–8/side. **Inflorescences** terminal (pseudoaxillary), 2–9 cm long, racemiform, usually unisexual (bisexual inflorescences rare, with 1 ♀ flower and 2–3 ♂ flowers in proximal cy-mules), with peltate hairs, ♀ flowers 1–7, proximal, on pedicels 2–7 mm long; ♂ flowers in groups of (1–)2–3, on pedicels 2.5–5 mm long, covered externally with peltate hairs, bracteoles 0.5–1 mm long. **Male flowers** with 5 valvate calyx lobes, 1.2–3 mm long, triangular, petals 2–3.2 mm long, ca. 1 mm wide, elliptic to oblanceolate, glandular punctate, margins tomentulose, glabrous abaxially; stamens 10–13, filaments 2–4.5 mm long, glabrous, anthers 0.6–1 mm long. **Female flowers** 5–7 mm long, calyx lobes 5, 2.2–2.7 mm long, triangular or ovate, disc ca. 2.8 mm wide, petals apparently absent; ovary 2–3 mm long, ovoid, densely yellowish with peltate hairs, styles 2.5–3.5 mm long, distally bifid, glabrous. **Fruits** 3.5–5 cm long, 3–4 cm wide, obovoid, rounded to truncated at apex, walls ca. 2 mm thick and woody, surfaces covered with peltate hairs, columella 25–34 mm long; seeds 20–29 mm long, 11–18 mm wide, 8–9 mm thick,



oblong in outline and slightly convex abaxially, caruncle 3 mm long, 2.5 mm wide, inverted V-shaped, appressed.

Trees of evergreen forest formations on both the Pacific and Caribbean slopes, 300–1000 m elevation. Flowering in March–June; with mature fruit in July–October. This species ranges from Volcán Rincón de La Vieja southward to western Panama.

*Croton pachypodus* is recognized by its tall stature, small but conspicuous flat peltate hairs, average-sized leaves, terminal unisexual racemes, and very large capsules and seeds. The ovary is covered with lustrous yellowish peltate hairs, and these persist but become grayish on the fruits. The flat peltate hairs have 20–50 radiating rays united for most of their length but separated distally ( $\times 50$ ). This can give the impression of a scurfy or stellate form in some instances. *Campano* is a common name. The preceding description is based on Costa Rican material and differs from Panamanian material having smaller leaves that are more densely pubescent beneath, somewhat larger fruits, and fewer stamens/flower. Specimens placed here are the following: *Bello* 1039; *Gómez-Laurito* 12282; *Haber et al.* 4896, 7036, 7106, 7109, 8395; *Hammel & Grayum* 18936; *Herrera* 607; *Holdridge* 6737, 6784; *A. Jiménez* 1953; *Q. Jiménez* 635 & 987; *Stork* 2811; and *Zamora & Poveda* 822. Some of these collections were earlier misidentified as *C. tenuicaudatus* (q.v.).

***Croton punctatus* Jacq., Coll. 1: 166. 1787. Icon. Pl. Rar. 3: 19, t. 621. 1789. Figure 17.**

Small shrubs 0.3–1 m tall, bisexual, leafy stems 1.4–4 mm thick, covered at first with short-stalked flat-topped discoid-stellate hairs 0.3–0.5 mm wide, becoming woody and black; stipules absent. Leaves with petioles 7–28(–37) mm long, 0.6–1.5 mm thick, densely stellate-pubescent like the stems; leaf blades 1.8–4.5 cm long, 1–2.8 cm wide, ovate-oblong to oblong, apex bluntly obtuse to rounded, margin entire, base rounded and slightly truncate, drying stiffly chartaceous or subcoriaceous, pale grayish green or yellowish green and paler beneath, upper surface with stellate hairs 0.1–0.2 mm wide, lower surface with rounded stellate-edged hairs 0.3–0.8 mm wide, venation pinnate with 4–5 veins/side but usually obscure. Inflorescences terminal, bisexual, 1–4 cm long, peduncles to 14 mm long, ca. 1 mm thick, pubescent, ♀ flowers 1–2 and proximal, subsessile, pedicels to 1 mm long in fruit; ♂ flowers 4–7. Male flower buds globose, ca. 2 mm diam., sepals 5, ca. 2.5 mm long, petals absent; stamens 10–12, filaments to 1.5 mm long, anthers 0.8–0.9 mm long. Female flowers ca. 4 mm long, 3.5 mm wide at apex, sepals 5, 3–3.5 mm long, 1.8–2.2 mm wide; ovary with peltate hairs, styles free, 3 times bifid. Fruits ca. 5 mm long, 8–10 mm wide, oblate and 3-lobed, densely stellate-peltate, columella 3.8–4.2 mm long; seeds 4.5–

5.3 mm long, 3.7–4.3 mm wide, 3.2–4 mm thick, ellipsoid to subglobose, dark to pale yellowish or mottled.

Plants of sandy Caribbean seashores, often growing within a few meters of the high-tide mark; 0–20 m elevation. Probably flowering and fruiting throughout the year. The species ranges from North Carolina (U.S.A.) to Panama and is found on Cuba and Bermuda.

*Croton punctatus* is distinguished by its restriction to sandy Caribbean seashores, short dark woody stems, small pale grayish oblong leaves with entire margins, and rounded apex. The vestiture on stems and petioles is unusual. The hairs are short-stalked with a flat rounded top that has a fringe of minute thin rays (resembling stellate hairs). Because of this form the hairs have both a stellate and peltate appearance.

***Croton pungens* Jacq., Coll. 4: 217. 1791. Icon. Pl. Rar. 3: 19, pl. 622. 1794. *Croton standleyi* Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 151. 1940. Figure 18.**

Shrubs or small trees 1.2–7(–20?) m tall, bisexual, leafy stems 2–5 mm thick, hispidulous with scurfy-stellate hairs 0.2–0.5 mm diam. or with longer rays 0.6–1 mm long; stipules 1–4 mm long, linear or subulate. Leaves with petioles 3–13 cm long, 1.3–2 mm thick, stellate-scurfy pubescent, with 2–4 stipitate conic, patelliform or discoid yellowish glands near the apex; leaf blades 5–12(–22?) cm long, 3–9(–13?) cm wide, ovate to ovate-oblong, caudate-acuminate with narrow tip 5–18 mm long, margin minutely (0.3 mm) denticulate or subentire, base rounded and cordate with sinus 3–18 mm deep, basal lobes widely separate to overlapping, drying chartaceous, upper surfaces with stellate hairs 0.1–0.4 mm diam., lower surface with stellate hairs 0.2–0.8 mm wide, venation palmate with 3 major veins, 2° veins 4–8/side of the midvein. Inflorescences terminal (pseudoaxillary), bisexual, 3–24 cm long, rachis ca. 1.5 mm thick and densely stellate, proximal cymules with ♀ and ♂ flowers, distal cymules with 2–5 flowers, bracteoles 1–3 mm long, ♀ flowers subsessile, ♂ pedicels 3–4(–8) mm long. Male flowers stellate-pubescent externally, sepals 5, 2–2.5 mm long, 1.1–1.4 mm wide, petals 1.5–2.3 mm long, spatulate, puberulent only along the distal edge, receptacle villous; stamens ca. 18–40, filaments 2–3 mm long, glabrous, anthers 0.6–0.9 mm long. Female flowers with 5 sepals 2.2–3.7 mm long, 1.5 mm wide, triangular, petals 0.3–0.4 mm long, stellate on both surfaces; ovary stellate, styles pubescent basally, 4–5 mm long, bifid distally. Fruits ca. 7 mm long, scurfy-stellate, columella 5–6 mm long; seeds 5.2–6 mm long, 3.7–4.1 mm wide, ca. 3 mm thick, rounded but with longitudinal or irregular raised areas on adaxial side, caruncle 1.5–1.8 mm wide, round-

Plants of fields, grasslands, and open sites in montane forest formations, 1300–2100 m eleva-



tion. Flowering collections have been made in January–February, April, and July–August. In Central America, this species is restricted to the Chiriquí highlands, Panama, and adjacent Costa Rica; it ranges to Brazil.

*Croton pungens* is recognized by its smaller cordate leaves, inflorescences with proximal cymes having both ♀ and ♂ flowers, many stamens, larger seeds, and restricted occurrence in southern Central America. The hairs of the upper leaf surface have minute (0.1–0.2 mm) stalks and flattened distal surfaces with ca. 12 radiating points. This species is closely related to *C. xalapensis* (q.v.).

***Croton schiedeanus* Schldl., Linnaea 19: 243. 1847.**  
*C. perobtus* Lundell, Phytologia 1: 405. 1940.  
Figure 17.

**Shrubs** or small trees 3–15(–25?) m tall, bisexual, trunk 10–25 cm diam., leafy stems 1.3–6 mm thick, densely covered with flat rounded peltate hairs ca. 0.2 mm diam., often with a brown center; stipules minute or up to 4 mm long, ca. 0.5 mm broad at base, linear, deciduous. **Leaves** with petioles 6–50(–58) mm long, 0.7–1.9 mm thick, slightly thickened at apex and base, covered with peltate hairs, without glands at apex; **leaf blades** 7–19(–29) cm long, 3–8(–11) cm wide, elliptic to ovate-elliptic, narrowly elliptic-oblong or oblong, apex usually short-acuminate with tip ca. 5–7 mm long, margin entire, base obtuse to cuneate (rarely rounded and subtruncate), drying thinly chartaceous, dark brown to grayish brown, sparsely or densely pubescent above (hairs sometimes obscure), more densely pubescent beneath with flat peltate hairs 0.1–0.2 mm diam., venation pinnate, 2° veins (7)–9–13/side. **Flowers** terminal or axillary, 1–2/axil, racemes (pseudopaniculate when distal leaves fail to develop), 3–7(–12) cm long, bisexual or ♂, with 1–9 proximal ♀ flowers on long (8–27 mm) pedicels 0.2–0.7 mm thick; with many distal ♂ flowers solitary in axils of small (0.5 mm) bracteoles, ♂ pedicels 2–5 mm long, ca. 0.2 mm thick, pubescence of peltate hairs. **Male flower buds** 1.2–1.7 mm diam., 3–6 mm wide at anthesis, white, calyx 5-parted, lobes 0.5–1.5 mm long, petals 1–3 mm long, with minute white hairs along the edge; stamens 9–11, filaments 1.2–2 mm long, anthers 0.5–1 mm long. **Female flowers** ca. 2–3 mm long, 3–5 mm wide, calyx lobes 5, 1.5–3 mm long, 1–1.3 mm wide at base, triangular, petals 1.5–2 mm long, broadly elliptic, white; ovary ca. 2 × 2.3 mm, covered with whitish peltate hairs, styles branched near the base, 2–3 mm long, usually 3 times bifid. **Fruits** 9–13 mm long, 9–12 mm diam., oblong or subglobose, 3-lobed in cross-section, with flat hairs 0.2–0.4 mm diam. and conical protuberances ca. 0.5 mm high, columella 6–9 mm long; seeds 7–9 mm long, 4.8–6 mm wide, 2.7–4 mm thick, oblong, caruncle 0.9–2 mm wide, surface lustrous and yellowish brown to mottled dark brown/white.

Common plants of lowland evergreen and partly deciduous forest formations, 0–800(–1200) m elevation (to 1400 m in Chiriquí and adjacent Costa

Rica). Found within forests, on forest edges, and often along streamsides. Flowering in all months, but with a majority of collections made in January–March; fruiting mostly in February–April. The species ranges from Mexico to Peru.

*Croton schiedeanus* is recognized by its vestiture of flat appressed-peltate hairs, lack of petiolar glands, pinnately veined leaves, long-pedicellate ♀ flowers with many style branches, and many individual ♂ flowers along the slender racemose floral axis. The flat rounded-appressed hairs often have a brown or reddish brown center and translucent or whitish periphery. Central American collections were called *C. glabellus* L. (*C. nitens* Sw.) for many years, but Webster and Burch (1967, p. 250) noted that, though closely related, the Linnaean species is restricted to Jamaica and the Cayman Islands. (Compare the closely related *C. tenuicaudatus*, and note that small-leaved specimens of *C. schiedeanus* with more rounded blades can look very much like *C. pachypodus*.) This is the most commonly collected species of *Croton* in Central America; its name in Costa Rica has been recorded as *colpachí*, *colpalchil*, *copalchí*, and *quizarra colpachí*.

***Croton skutchii* Standl., Pub. Field Mus. Nat. Hist., Bot. Ser. 22: 86. 1940.**

**Trees** 10–27(?) m tall, bisexual, leafy stems 4–8 mm thick, with flat rounded-peltate hairs 0.1–0.3 mm diam.; stipules minute or absent. **Leaves** with petioles 7–15 cm long, 1.4–3 mm thick, covered with minute flat or scurfy hairs with brown centers, paired lateral/abaxial sessile pateliform glands present at the apex, to 2 mm wide, thickened tissue ca. 1 mm long also sometimes present at the petiole/blade juncture; **leaf blades** 15–26 cm long, 10–18 cm wide, ovate-oblong to broadly oblong, or narrowly ovate-oblong, apex acuminate to obtuse, margin entire, base rounded and truncate to subcordate, drying chartaceous, drying greenish brown above with scattered appressed hairs (in the type) or subglabrous, pale greenish beneath with flat rounded hairs 0.1–0.2 mm diam., venation pinnate, 2° veins 12–17/side. **Inflorescences** axillary to distal leaves, 1–2/node, bisexual, 15–25 cm long, with peltate hairs throughout, with 1–5 proximal solitary ♀ flowers on pedicels 6–11 mm long, 1–1.5 mm thick, bracteoles subtending the ♂ glomerules ca. 1 mm long, ♂ flowers in groups of 5–11. **Male flowers** only seen in early anthesis, buds 2–3 mm diam., calyx ca. 4 mm long, calyx lobes 1.5–2 mm long triangular, petals ca. 3 × 1 mm, narrowly obovate; stamens ca. 11, filaments 3–4 mm long, anthers 1.2 × 1 mm. **Female flowers** with sepal lobes 4–6 mm long, 3–5 mm diam., oblong, lateral margins occasionally reflexed; ovary 2–3 mm high, 3 mm diam., covered with lustrous peltate hairs, styles hairy at the base, much divided, distal branches more than 20. **Fruits** and seeds not seen.

Plants of evergreen forest formations of the Caribbean and Pacific slopes, 600–1000 m elevation. Flowering in June and August. The species is known only from two collections: *Skutch 4377* (us iso-type), from near El General, San José Province, and *Lancaster Aug. 5, 1923* (us) from Cachi in Cartago Province.

*Croton skutchii* is recognized by the flat round appressed scales on most surfaces, the larger oblong leaves with many secondary veins and usually subcordate base, and the large solitary ♀ flowers with many style branches. The large broad sepal lobes in ♀ flowers are distinctive. The flat rounded appressed hairs often have a brown center. This species superficially resembles *C. tenuicaudatus* (q.v.).

***Croton smithianus*** Croizat, J. Arnold Arbor. 21: 93. 1940. Figure 18.

**Trees** 5–25 m tall, bisexual, leafy stems 2.5–7 mm thick, densely pubescent with sessile or stipitate stellate-scurfy hairs 0.3–0.8 mm diam., on stalks to 1.3 mm long; stipules 5–9 mm long, 1–2 mm broad at the base, lanceolate, caducous. **Leaves** sometimes opposite at distal or flowering nodes, petioles 5–15 cm long, 1.4–3 mm thick, densely scurfy-stellate pubescent, with 2 lateral sessile saucer-shaped or patelliform glands at the apex, 0.9–1.3 mm wide; **leaf blades** 11–26(–35) cm long, 8–25(–30) cm wide, broadly ovate and usually distally trilobed, the broad triangular distal lobes separated by wide sinuses 1–5 cm deep, apex obtuse to short-acuminate, tip to 6 mm long, margin minutely denticulate with teeth 0.1–1 mm high (rarely with broadly triangular lobes 5–10 mm long), base rounded and cordate to subcordate, drying thinly chartaceous, upper surface with stellate hairs 0.3–1 mm in diam., with 6–12 rays, 0.3–1 mm diam., on stalks 0.1–0.5 mm long, more densely pubescent beneath, venation palmate with 3 major veins, 2° veins 3–5/side of the midvein. **Inflorescences** usually unisexual (with 5–15 proximal bisexual cymules and distal ♂ cymules when bisexual), 20–50 cm long, densely yellowish pubescent, ♀ flowers solitary with pedicels 5–9(–14) mm long, ca. 1.5 mm thick ♂ fascicles (cymules) with 3–15 flowers, ♂ pedicels 1.5–5 mm long, stellate. **Male flower** buds 3–4 mm diam., calyx 3.5–4 mm long, calyx lobes 5, 2–3 mm long, triangular, petals 3–4.5 mm long, spatulate, pubescent; stamens 10–12, filaments 3–4.5 mm long, glabrous only distally, anthers 0.8–1.4 mm long. **Female flowers** with 5 valvate sepal lobes, 3–7.5 mm long, 2.5–6.5 mm wide, stellate abaxially and on margins, disk entire, ovary ca. 1.7 mm wide, styles free, hispid, ca. 5 mm long, each style deeply multifid. **Fruits** ca. 8 × 11 mm, yellowish, with scurfy and stellate hairs 0.1–0.3 mm wide, columella 4–4.5 mm long; seeds 4.7–5.1 mm long, 3.7–3.9 mm wide, 2.8–3 mm thick, surface with minute longitudinal raised ridges, caruncle 1.7–2.2 mm wide.

Plants of evergreen rain forest formations on both the Caribbean and Pacific slopes, 20–800 m

elevation (to 1500 m in Colombia). Flowering material was collected in June–August; fruiting in September. It is rarely collected in Costa Rica (La Selva, General Valley, Osa Peninsula). The species ranges from southernmost Nicaragua to Colombia.

*Croton smithianus* is distinguished by its large leaves with three prominent distal lobes (not present on all leaves), stellate-scurfy pubescence with occasional stipitate hairs, cupulate ♂ calyx, solitary ♀ flowers with broad calyx lobes, many style branches, and longitudinally rugulose seeds. Glabrous short-stalked patelliform or saucer-shaped glands are sometimes found on the leaf surfaces in this species. Specimens lacking the three-lobed leaves may be mistaken for *C. draco* and similar species. This species is part of a species complex including *C. palanostigma* Klotzsch, *C. benthamianus* Müll. Arg., and *C. killipianus* Croizat (cf. Webster & Huft, 1988).

***Croton speciosus*** Müll. Arg., Linnaea 34: 83. 1865.

*C. speciosus* subsp. *tacarcunensis* Webster, Ann. Missouri Bot. Gard. 75: 1119. 1988.

**Shrubs** or small trees 3–15 m tall, bisexual, leafy branches 2–12 mm thick, densely villose with soft or stiff stellate hairs 0.5–2 mm long; stipules 6–12 mm long, 0.7–2 mm wide at the base, densely villose abaxially, entire or with laciniate margins. **Leaves** with petioles 1.5–15(–30) cm long, 1.5–2(–4) mm thick, densely stellate-villose, slender stalked glands at apex, usually 2 and 0.7 mm long or absent in ours (5–10, 5 mm long); **leaf blades** 7–15(–35) cm long, 4–16(–33) cm wide, ovate to ovate-triangular or 3-lobed in larger leaves, apex acuminate, margin minutely glandular dentate, rounded at the base and subcordate to cordate, whitish beneath with a dense tomentum of stellate hairs ca. 1 mm wide, venation palmate, 2° veins 4–9/side of the midvein. **Inflorescences** terminal or pseudoaxillary, 2–6 cm long, bisexual, few-flowered, densely pubescent, flowers solitary or closely clustered, bracts 5–10 mm long, ca. 1 mm wide, ♂ pedicels 3–8 mm long, ♀ pedicels 1–3 mm long. **Male flowers** ca. 8 × 12 mm, calyx lobes 3–5 mm long, triangular, petals 4–5 mm long, obovate-spatulate, pubescent abaxially, glabrous adaxially; stamens 40–70(–80), filaments glabrous, anthers ca. 1.5 mm long. **Female flowers** densely tomentulous, calyx 5-parted, 8–16 mm long, valvate, tapering gradually to the acute apex, petals absent, disk inconspicuous; ovary 4–6 mm diam., densely pubescent, styles 6–9 mm long, 2 times bifid to near the base, pubescent except at the tips. **Fruits** 10–14 mm long, subglobose, hispidulous, columella ca. 8 mm long, slender; seeds ca. 7 mm long, 5 mm wide, brown, caruncle 2–3 mm wide.

Rarely collected plants of evergreen forest formations of the Pacific slope above Buenos Aires, at 1500 m elevation. Flowering and fruiting in



March (*Grayum 10265*). The single collection in Costa Rica and several collections from Cerro Tarcuna in eastern Panama are the only records for this species outside of Venezuela.

*Croton speciosus* is distinguished by the dense tomentum on all parts, the large ♀ flowers with valvate sepals, and the ♂ flowers with ca. 50 stamens. In addition, the larger leaves have three distal lobes with narrow acuminate apices, but the smaller leaves are unlobed. The Costa Rican collection is consistent with the description of subsp. *tacarcunensis* in having smaller nonlacerate stipules, and smaller glands at the apex of the petiole than collections from Venezuela. The Costa Rican collection has somewhat smaller leaves than typical of the species (the larger dimensions of Venezuelan material are given in parentheses in the preceding description).

***Croton sphaerocarpus*** H.B.K., Nov. gen. sp., 2: 84, t. 105. 1817. *C. rhamnifolius* var. *caudatus* Pax in Pittier, Prim. Fl. Costaric. 2: 331. 1900. Figure 16.

**Shrubs** 1–2(–4) m tall, bisexual, leafy stems 1–3 mm thick, at first densely pubescent with stellate hairs 0.2–0.9 mm diam., sessile or on short (0.2 mm) stipes, some with thin hairs to 0.8 mm long, glabrescent; stipules 2–3 mm long, linear. **Leaves** with petioles 10–25(–42) mm long, 0.4–1.3 mm thick, stellate pubescent, glands absent at the apex of the petiole; **leaf blades** 4–12 cm long, 2–6.4 cm wide, ovate to ovate-rhombic or narrowly ovate-elliptic, apex acuminate to caudate-acuminate, narrow tip 6–30 mm long, margin entire (rarely with teeth ca. 0.5 mm long), base rounded or obtuse, drying membranaceous or thin chartaceous, dark above with simple or stellate hairs, more densely pubescent and grayish beneath with hairs to 0.8 mm diam., mostly with 6–8 rays, venation palmate or subpalmate, 2° veins 3–5/side of midvein. **Inflorescences** terminal, 1.5–11 cm long, bisexual, ♀ flowers proximal, solitary, ♂ flowers in distal cymes of 1–3, bracteoles 1.3 mm long, ♂ pedicels 1.5–3 mm long, filiform, usually glabrous. **Male flower** buds ca. 2 mm diam., sparsely pubescent on the exterior, sepals 5, ca. 1.3 mm long, triangular and acute, petals spatulate; stamens ca. 15, anthers 0.6–0.8 mm long. **Female flowers** with sepals ca. 1 mm long, triangular, ovary 1.5–3 mm long, 1.3–2.5 mm diam., densely hispidulous with hairs to 0.7 mm long, styles deeply bifid, 2.5–3 mm long, subglabrous. **Fruits** ca. 7.5 mm long, 6.8 mm wide, columella 4.7–5 mm long; seeds 5–5.6 mm long, 3.7–4.2 mm wide, 2.2–2.8 mm thick, smooth, caruncle ca. 1.5 mm wide.

Plants of seasonally very dry deciduous woodlands and open rocky sites, 0–300 m elevation (to 800 m in Nicaragua). Flowering in May–July; fruiting in June–October. It is rarely collected in Costa Rica (*Webster & Poveda 22163*, *Tonduz 2766*

(type of *C. rhamnifolius* var. *caudatus*), *Wilbur 21442*, *Zamora & Chavarría 1028*). The species is found in Mexico and ranges from northern Nicaragua to northern Guanacaste Province, Costa Rica.

*Croton sphaerocarpus* is recognized by its thin ovate leaves often with long narrow acuminate apices, absence of glands at the apex of the usually long slender petiole, often slender inflorescences, and restriction to seasonally very dry deciduous areas. A variety of Nicaraguan collections are placed here, ranging from specimens with short petioles and stiffly chartaceous ovate-lanceolate leaves to specimens with thin broadly ovate leaves on long thin petioles. *Croton morifolius* Willd. of Mexico may be an earlier name for this species; we follow the annotations of Webster.

***Croton tenuicaudatus*** Lundell, Phytologia 1: 451. 1940. Figure 19.

**Shrubs or trees** to 18 m tall, bisexual, leafy stems 2–7 mm thick, covered with peltate rounded hairs 0.1–0.2 mm diam. and small (ca. 0.2 mm) straight hairs; stipules minute or absent. **Leaves** with petioles 3–10 cm long, 1–2 mm thick, covered with appressed flat hairs, often thickened or geniculate at the apex; **leaf blades** 8–25 cm long, 5–12 cm wide, ovate-oblong to broadly oblong, acuminate at the apex with a narrow tip 5–15 mm long, margin entire, base rounded and broadly obtuse to truncate, usually drying dark brown above with scattered peltate hairs, pubescent beneath with rounded peltate hairs 0.1–0.2 mm diam., venation pinnate, 2° veins 8–13/side. **Inflorescences** axillary to distal leaves or terminal (pseudopaniculate when distal leaves fail to expand), 3–16 cm long, ♂ or bisexual with 1–5 ♀ flowers proximally, with peltate hairs throughout, ♀ flowers solitary, pedicels 3–7 mm long, ca. 1 mm thick; ♂ flowers solitary, subtended by linear bracts to 2 mm long, pedicels 2–4 mm long. **Male flowers** ca. 7 mm wide at anthesis, calyx lobes ca. 3 mm long, triangular, petals 5, 3–4 mm long, narrowly obovate; stamens 10–13, filaments to 4 mm long, anthers 1.2–1.5 mm long, narrowly oblong. **Female flowers** 6–8 mm wide at anthesis, calyx lobes 5, ca. 3 mm long, triangular, petals narrowly obovate, 3.5–4 mm long; ovary ca. 4 mm long, covered with lustrous peltate hairs, styles 3 or 4 times bifid, glabrous distally. **Fruits** not seen (see below).

Plants of evergreen forest formations from near sea level to 900 m elevation, Valle del General, to Golfo Dulce. Flowering in November–March. This species is known only from the Pacific slope of southern Costa Rica and western Panama.

*Croton tenuicaudatus* is recognized by the small flat rounded peltate hairs on all parts, the larger leaves rounded at the base, the lack of glands at the apex of the petiole, the solitary flowers, and the restricted range. This species is very similar to



the common and widely ranging *C. schiedeanus* (q.v.), and the two are closely related. It appears that ascribing large seeds to this species (Webster & Burch, 1967, p. 253) was an error, with the result that this name had been incorrectly used for material now placed in *C. pachypodus* (q.v.).

***Croton tonduzii* Pax in Pittier, Prim. Fl. Costar. 2: 330. 1990. Figure 17.**

Small trees ca. 6 m tall, leafy stems 1.7–5 mm thick, young stems with appressed rounded flat peltate hairs ca. 0.2 mm diam.; stipules ca. 1 mm long, caducous. **Leaves** with petioles 3–8 cm long, 1–2.5 mm thick, covered with peltate hairs, apex with 2(–4) adaxial sessile cupulate or patelliform glands 0.7–1.3 mm diam.; **leaf blades** 9–18 cm long, 3–9 cm wide, broadly ovate (in Pittier 3474) to ovate-oblong or oblong (in Pittier 3878), apex bluntly acute to obtuse, margin conspicuously dentate-crenate with teeth 0.5–2 mm high, ca. 3 teeth/cm, drying thinly chartaceous, dark brown above and glabrescent, paler beneath with many appressed flat rounded hairs ca. 0.2 mm diam., venation palmate (Pittier 3474) or subpalmate (Pittier 3878), 2° veins 4–8/side. **Inflorescences** terminal, apparently unisexual, becoming 15 cm long with rachis 2 mm thick, hairs peltate; ♂ flowers not seen; ♀ flowers solitary on short (1–2 mm) thick (1 mm) pedicels, calyx ca. 2 mm long, lobes 0.7 mm long; ovary ca. 1.5 mm high and 2 mm diam., pubescent. **Fruits** ca. 7 × 9 mm, oblate, with rounded lobes, stellate-peltate, columella 6–7 mm long; seeds 5.5–6 mm long, 4.5–4.8 mm wide, 3.5–4 mm thick, pale brown, lustrous and minutely rugose.

Plants of evergreen forest formations on the Pacific slope between 400 and 800 m elevation. Flowering and fruiting in January–February. Known from only four collections: Pittier 3474, 3878 (syntypes), & 12161 and Skutch 4027. Endemic to southern Costa Rica (but see below).

*Croton tonduzii* is recognized by the peltate hairs, leaves with palmate or subpalmate venation and denticulate margin, long petioles, and restricted habitat. This poorly known species appears to be related to *C. pachypodus*, which has much larger fruits and seeds, and to *C. mexicanus*, where the hairs are not so clearly flat and peltate. *Croton lundellii* Standl. of northern Central America may be conspecific. This species resembles *C. niveus* and *C. schiedeanus* and, like them, is called *copalchi*.

***Croton trinitatis* Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 57. 1900. *C. tragioides* Blake, Contr. U.S. Natl. Herb. 24: 12. 1922. Figure 10.**

**Herbs** or subshrubs 0.3–0.9(–1.5) m tall, bisexual, often with many widely branching stems, leafy stems 0.6–

4 mm thick, sparsely to densely pubescent with stellate hairs 0.3–1 mm long, each hair often with many short radiating rays and 1 slightly longer central ray; stipules 0.4–1.2 mm long, linear. **Leaves** sometimes subopposite at branching nodes, petioles (1–)3–35 mm long, 0.3–0.8 mm thick, stellate-pubescent, usually with stalked cupulate glabrous glands 0.4–0.8 mm long at the apex; **leaf blades** 1–6 cm long, 0.6–3.5 cm wide, triangular to oblong or ovate in outline with prominently dentate margin, teeth 5–12/side, 1–5 mm long and 2–6 mm wide, base of blade rounded to truncate (subcordate), drying membranaceous or thinly chartaceous, greenish or grayish brown, sparsely pubescent above with mostly simple hairs to 1.2 mm long, more densely pubescent beneath with stellate hairs ca. 0.3 mm wide, venation subpalmate with 3(5) major veins from near the base. **Inflorescences** terminal or pseudoaxillary, 3–15 mm long, few-flowered, spicate or branched, stellate-pubescent, with 1–3 proximal ♀ flowers, the 3–8 distal ♂ flowers borne on slender glabrous pedicels ca. 1 mm long, ♀ pedicels to 3 mm long in fruit. **Male flowers** globose in bud, ca. 0.7 mm diam., ca. 1.5 mm wide at anthesis, sepals 5, ca. 0.8 mm long, petals 0.6–0.9 mm long; stamens 8–10, filaments to 1 mm long, glabrous, anthers 0.3–0.4 mm long. **Female flowers** 3–5 mm long, sepals 5, 3–4 mm long, 0.8–1.7 mm wide, narrowly oblong to spatulate, petals 0.3–0.4 mm long, subulate; styles 0.7–1.1 mm long, bifid. **Fruits** 4–4.5 mm long, 3.5–4 mm diam., oblong, stellate-pubescent, columella ca. 3 mm long; seeds 3–3.5 mm long, 2.2–2.5 mm wide, ca. 1.2 mm thick, oblong, with a lustrous usually dark minutely reticulate surface, caruncle 1.1–1.3 mm wide.

Plants of open early secondary vegetation in evergreen forest formations on both the Caribbean and Pacific slopes, 0–1100 m elevation. Flowering in April–September; fruiting in April–February. This species ranges from eastern Mexico to Peru.

*Croton trinitatis* is recognized by its short herbaceous habit, distinctive narrowly triangular leaves with prominent teeth, short few-flowered inflorescences, and the stipitate glands at the apex of the petiole.

***Croton xalapensis* H.B.K., Nov. gen. sp. 2: 85. 1817. *C. pseudoxalapensis* Croizat, J. Arnold Arbor. 21: 85. 1940. *C. pseudoxalapensis* var. *cobanensis* Croizat, J. Arnold Arbor. 21: 86. 1940. Figure 18.**

**Shrubs** or small trees 2–15 m tall, bisexual, leafy stems 2–7 mm thick, densely white or yellowish hispidulous with scurfy-stellate hairs 0.3–0.5 mm diam. and often with thin simple hairs to 1.5 mm long; stipules 2–5 mm long, linear, caducous. **Leaves** with petioles 1.5–14 cm long, 1–3 mm thick, densely stellate-hispidulous, with 2(3–7) usually stipitate and conical or sessile saucer-shaped glands 0.6–2.3 mm long, 0.6–0.9 mm diam. at apex; **leaf blades** 5–24(–32) cm long, 2–14(–20) cm wide, ovate to narrowly ovate-oblong, apex long-acuminate to caudate-acuminate, margin minutely (0.3–1.5) denticulate or subentire, base rounded and truncate or shallowly cor-

date (obtuse), drying thinly chartaceous, with scattered small (0.2–0.4 mm) stellate hairs above, more densely pubescent beneath with somewhat larger hairs, venation subpalmate or pinnate, basal secondaries usually prominent, 2° veins 5–10/side. **Inflorescences** 5–25(–40) cm long, unisexual or bisexual, spicate, densely stellate pubescent, ♀ flowers solitary, not associated with ♂ flowers, subsessile; ♂ flowers solitary or in glomerules of 2–7, pedicels to 8 mm long, bracteoles to 4 mm long. **Male flowers** ca. 6 mm wide at anthesis, calyx 2.5–3.5 mm long, sepals 5, 1.5–2.3 mm long, 1.5–2 mm wide, triangular, petals ca. 3 × 1.2 mm; stamens 18–31 (in Costa Rica), filaments 1.8–4 mm long, glabrous distally, anthers 0.5–1 mm long. **Female flowers** with sepals 1.5–4 mm long, ca. 1.3 mm wide at base, up to 7 × 3 mm in fruit; ovary 2–3 mm long, 3–4 mm diam., densely stellate-hispidulous, styles 2.3–3.5 mm long, bifid near the base. **Fruits** 6–7 mm long, ca. 7–9 mm wide, stellate-pubescent, columella 5–6 mm long, ca. 2 mm wide at apex; seeds 4.8–5.7 mm long, 3.7–4.4 mm wide, ca. 3.7 mm thick, with raised transverse-angular areas on both adaxial and abaxial surfaces, caruncle ca. 2 mm wide.

Plants of montane evergreen and partly deciduous forest formations, 700–2100 m elevation. Probably flowering and fruiting throughout the year but collected most often in February–September. The species ranges from Veracruz, Mexico, to the central highlands of Costa Rica (and to 83°03'W on the Caribbean slope of the Talamanca mountains).

*Croton xalapensis* is recognized by its often larger ovate-oblong leaves truncate or subcordate at the base, stipitate glands near the apex of the petiole (not always present), dense pubescence of stellate hairs, ♂ flowers with 14–33 stamens, and seeds with transverse-oblique raised areas. Leaf venation is generally pinnate, unlike most of our other large-leaved *Croton* species. The larger hairs are distinctive in being slightly (0.1–0.2 mm) stipitate and having 8–24(–many) short rays, often giving a somewhat scurfy appearance. This species has been called *targuá*, *targuá blanco*, and *terré* in Costa Rica. This species is closely related to *C. pungens* of the Chiriquí Highlands. Compare also *C. draco* and *C. hoffmannii*.

***Croton yucatanensis* Lundell, Phytologia 1: 408. 1940. Figure 16.**

**Shrubs** 2–3 m tall (rarely to 7 m), bisexual, leafy stems 1–4 mm thick, densely whitish stellate-tomentulose in early stages, hairs stellate or stellate-peltate with a small (0.1–0.2 mm) flat central area; stipules often broader than long and leaf-like (sometimes absent or minute and linear), 3–8 mm long, to 14 mm wide and reniform, caducous or persisting. **Leaves** with petioles 5–32 mm long, 0.6–2 mm thick, whitish with stellate hairs, small (0.3 mm) sessile glands or stipels usually present at the

adaxial apex; **leaf blades** 2–11(–13) cm long, 1.5–5(–7) cm wide, ovate-oblong, ovate-lanceolate, lanceolate or ovate-oblong, apex bluntly obtuse to acuminate, margin entire to subentire, base obtuse to rounded and subcordate, drying chartaceous and dark above, whitish beneath with a dense tomentum of stellate hairs 0.1–0.3 mm wide, venation palmate or subpalmate, 2° veins 2–6/side of the midvein. **Inflorescences** terminal, 1–2, 3–15 cm long, bisexual or unisexual, with whitish stellate hairs throughout, flowers solitary, ♂ bracts ca. 0.7 mm long, pedicels 3–4 mm long; ♀ bracts 1–2 mm long, ♀ pedicels to 6 mm long in fruit. **Male flowers** ca. 4 mm wide, calyx lobes 5, 1.7–2 mm long, acute, petals narrowly oblong; stamens ca. 15, 3–4 mm long, anthers 0.7–1 mm long. **Female flowers** 3–6 mm long, calyx lobes 5, 2–5 mm long, 3 mm wide at base, broad and often with lateral margins reflexed, disk adnate to base of perianth, ovary ca. 2.7 mm long, styles 2–4 mm long, bifid at the base and also bifid distally (ca. 12 style branches/flower), densely pubescent in lower part. **Fruits** 5–6 mm long, 6–7 mm wide, oblate, sparsely stellate-puberulent, columella ca. 3 mm long; seeds 3.8–4 mm long, 3–3.2 mm wide, 2.2–2.4 mm thick, slightly rugose with minute longitudinal ridges on abaxial surface, caruncle 0.7–0.8 mm wide.

Plants of deciduous forest formations of northwestern Guanacaste Province (Santa Rosa N.P. and vicinity), 0–300 m elevation (400–600 m in Nicaragua). Flowering in May–June; probably fruiting in July–August. This species ranges from southern Mexico to northwestern Costa Rica.

*Croton yucatanensis* is easily identified by its broadly rounded leaf-like stipules, but these may not be present in all collections and are often caducous. The white stellate pubescence of somewhat flattened/peltate hairs, short stature, and broad often reflexed ♀ calyx lobes are additional distinctions. The ca. 24–32 peripheral rays of the hair are united laterally only near the center (× 50). Our collections were earlier identified as *C. watsonii* Standl., a similar species of Mexico. See the discussion under the following species.

***Croton* sp. aff. *C. yucatanensis* Lundell, Phytologia 1: 408. 1940. Figure 16.**

**Small trees** 3–10 m tall, bisexual, leafy branchlets 1.3–3.7 mm thick, densely stellate-tomentulose with whitish hairs; stipules absent or minute (sometimes 1.5–4 mm long near the inflorescences). **Leaves** with petioles 11–45 mm long, 0.8–1.4 mm thick, whitish stellate-tomentulose, glands absent or with minute glands on adjacent lamina margin; **leaf blades** 2.5–12 cm long, 1.8–5.5 cm wide, ovate to ovate-oblong or ovate-elliptic, apex acute to acuminate, margin subentire, base obtuse to rounded and subcordate, drying chartaceous and dark above with scattered minute (0.1–0.2 mm) stellate hairs, bright whitish beneath with appressed stellate hairs, venation palmate or subpalmate, 2° veins 3–6/side of 1° vein. **Inflorescences** 5–17 cm long, terminal or axillary to distal



leaves, usually solitary, bisexual with many proximal ♀ flowers and distal ♂ flowers, solitary or crowded, rachis 1–2 mm thick, densely whitish stellate-tomentulose, ♂ pedicels 3–6 mm long, ca. 0.5 mm thick, ♀ pedicels 2–6 mm long, ca. 1 mm thick. **Male flowers** ca. 6 mm wide, sepal lobes 5, 2.5–3 mm long, 2–2.5 mm wide, triangular, obtuse, petals 3.5–4 mm long, ca. 1.5 mm wide, oblong; stamens 11–14, filaments 3–4 mm long, anthers 1–1.4 mm long. **Female flowers** 5–8 mm long, calyx lobes 3–6 mm long, 1.8–4 mm wide, oblong-obovate, apex rounded or obtuse, lateral margins sometimes reflexed; ovary 3–4 mm long, densely tomentulose, styles densely puberulent, with 15–40 distal style branches/flower. **Fruits** ca. 6 mm long, 3.4–3.6 mm wide, 2.6–3 mm thick, surface smooth, caruncle 1.5–2 mm wide.

Small trees of deciduous and partly deciduous forest on the seasonally dry Pacific slope of the Cordillera de Tilarán, 700–1100 m elevation. Flowering in June–July; fruiting in July. Collections placed here are *Bello 2912* and *Haber et al. 1777, 9944, 9986, 10734, & 10735*. These were collected in the upper Río Lagarto and Río Luis drainages below Monteverde, near the border of Guanacaste and Puntarenas provinces.

*Croton* sp. aff. *C. yucatanensis* is recognized by its restricted habitat, bright white stellate hairs covering the lower leaf surfaces and inflorescences, the broadly reflexed ♀ sepal lobes, and the many style branches. While very similar in overall appearance to *C. yucatanensis*, the material placed here differs in lacking the expanded stipules, having fewer stamens, more divided style branches, and larger seeds. The tree habit and higher elevation habitat also separate the two. This material keys to section *Lasiogyne* (Klotzsch) Baillon in Webster's recent review (Webster, 1993) and is also related to *C. tabascensis* Lundell, which ranges from Mexico to Nicaragua. *Croton tabascensis* differs from our material in having 15–16 stamens per flower, slender subglabrous style branches only twice bifid, and leaves with the pubescence less dense beneath. It is possible that all these taxa are actually part of a single polymorphic complex.

#### *Croton* sp. A.

Small tree ca. 9 m tall, bisexual, leafy stems 1–4 mm thick, stellate-pubescent with flat hairs 0.3–0.4 mm diam.; stipules ca. 3 mm long, linear, caducous. **Leaves** subopposite at some nodes, petioles 3–9.5 cm long, 1–2 mm thick, stellate-pubescent, apex with paired lateral sessile cupulate glands 0.3–0.6 mm diam.; **leaf blades** 9–20 cm long, 3–9 cm wide, ovate-elliptic to lanceolate or oblong, apex long-acuminate with narrowed tip to 20 mm long, margin subentire or with few teeth to 3 mm high, base obtuse, drying membranaceous and dark above with scattered stellate hairs, stellate hairs on lower surface 0.5–1 mm diam. and evenly spaced, hairs flat with

usually 7 slender rays, small (0.2 mm diam.) stalked glands present near vein axils, venation pinnate (subpalmate), 2° veins 4–7/side, loop-connected in the distal part of the lamina. **Inflorescences** terminal or pseudoaxillary, ca. 15 cm long, apparently bisexual, rachis 0.7–1 mm thick, stellate-pubescent, ♂ flowers in small glomerules of 1–4, bracts inconspicuous (ca. 0.5 mm); ♀ flowers not seen. **Male flower** buds ca. 2 mm diam., sepals valvate, petals ca. 3 mm long, oblong-obovate; stamens 16, filaments glabrous, anthers 0.8–1 mm long, 0.6–0.9 mm wide. **Fruits** not seen, persisting pedicel 5 mm long, 1.5 mm thick, columella 11 mm long, 1.5 mm wide at apex.

*Croton* sp. A is distinguished by its unusual leaves, which are thin-textured, borne on long petioles, and have pinnate venation and long-acuminate apices. In addition, lower leaf surfaces have flat stellate hairs with fewer than 10 rays and small stalked glands near the axils of both 2° and 3° veins. The leaves are aromatic when crushed. This unusual species is known only from a single collection: *González, Poveda, & Barquero 196* (MO), made on 10 October 1992 near the Río Corinto (10°11'55"N, 83°53'20"W) at 250 m in a Caribbean rain forest (premontane wet forest) formation. This species is being studied by its discoverer, José González, who has found three trees in the only known population.

#### *Dalechampia* Linnaeus

REFERENCES—G. L. Webster & W. S. Armbruster, A synopsis of Neotropical *Dalechampia* (Euphorbiaceae). Bot. J. Linn. Soc. 105: 137–177. 1991. W. S. Armbruster, A new species, section and synopsis of *Dalechampia* (Euphorbiaceae) from Costa Rica. Syst. Bot. 13: 303–312. 1988.

Vines or lianas, rarely subshrubs or small erect few-branched shrubs, monoecious, pubescence of simple unicellular hairs, specialized stinging hairs present in some species; stipules free, lateral, acute, often with parallel venation, persisting or caducous. **Leaves** alternate, simple or palmately compound, often variable on the same plant with distal leaves more lobed or divided, usually petiolate, often with a pair of stipel-like glands at the base of the blade, blades entire to dentate or deeply lobed, venation palmate or pinnate. **Inflorescences** axillary or terminal, usually solitary, bisexual, often borne on axillary stems with reduced leaves, flower-like pseudanthia with 2 large subopposite usually colorful involucre bracts, palmately veined, margin entire to dentate or laciniate, the 2 involucre bracts subtended by 4 small involucre stipules. **Male cymules** with various arrangements (mostly a pleiochasium of several 1–3-flowered cymules), usually with a pedunculate 2-lipped involucre



with a row of stamens facing the ♀ cymule and a sticky resiniferous gland facing the upper involucrel bract (involucrel of 2 alternate decussate bracts in some species). **Male flowers** mostly 8–12, with articulated pedicels, calyx globose in bud and splitting into 3–6 valvate parts, becoming reflexed, disk and petals absent; stamens mostly 20–50 (8–100+), filaments connate in a stiff column, filaments very short, anthers bilocular, dehiscent longitudinally; pistillode absent. **Female cymules** inserted above the lower involucrel bract and below the ♂ flowers, ♀ cymes usually with 3 flowers (1 in *D. ficifolia*), ♀ flowers subtended by an involucrel of 1 lower (proximal) bract and 2 distal bracteoles or a single 2-lipped involucrel formed by fused bracteoles. **Female flowers** subsessile or pedicellate, sepals 5–12, imbricate, mostly pinnatifid with gland-tipped lobes in Neotropical species, expanding in fruit, petals, staminodes and disk absent; ovary 3-(4-)locular, ovules 1/locule, styles united to form a column, often expanded into a peltate stigma (style branches absent). **Fruits** capsules, splitting explosively into 3 (4) 2-valved cocci, endocarp crustaceous or woody, often developing stiff sharp hairs on the surface, columella persisting; seeds subglobose to ellipsoid, sili faces smooth to tuberculate, ecarunculate, endosperm present, cotyledons broad.

A genus of 95 Neotropical and ca. 20 Old World species. The inflorescence is very unusual and functions like a large individual bisexual flower, usually held vertically with the ♀ flowers below the ♂. The large pulviniform nectary is interpreted to be a modification of bracteoles of undeveloped ♂ cymules. (For a recent study of these unique inflorescences, see H. Froebe & N. Magii, Pattern analysis in the inflorescences of *Dalechampia* L., Bot. Jahrb. Syst. 115: 27–44, 1993.) Inflorescences of the same species can differ greatly in appearance during different stages of flowering and fruiting, and this can make identification quite difficult. Neotropical species are largely pollinated by ♀ bees gathering resin from the large gland or by ♂ euglossine bees gathering aromas. Most species are not well represented in herbaria, but it is difficult to determine whether this is due to the difficulty of discerning vining plants, the rarity of the species, or the stinging pubescence in some species.

Key to the Species of *Dalechampia*

- 1a. Plants erect shrubs 0.5–1.5 m tall, central stem usually without lateral branches; leaves simple with pinnate venation, oblanceolate or narrowly elliptic-obovate, to 28 cm long; gland of ♂ involucrel yellow and lacking resin; seeds minutely tuberculate ..... *D. spathulata*
- 1b. Plants climbing or clambering vines and lianas, lateral branches frequent; leaves simple with palmate venation and never oblanceolate, or compound and 3-foliolate; gland of ♂ involucrel absent or producing clear, white, or maroon resin; seeds smooth or minutely rugulose ..... 2
- 2a. Compound leaves with independent leaflets present, simple or lobed leaves sometimes also present ..... 3
- 2b. Compound leaves absent, leaves sometimes deeply 3-lobed but the lobes not narrowed into basal petiolules ..... 5
  - 3a. Trifoliolate leaves and simple ovate leaves often intermixed on stems; hairs of stems often clearly retrorse [♀ sepals 7–11; seeds 3.5–4.2 mm diam., involucrel stipules 2–3 mm long] ..... *D. heteromorpha*
  - 3b. Trifoliolate and simple ovate leaves rarely intermixed along the stems; larger stem hairs erect and the smaller often retrorse ..... 4
  - 4a. Female sepals 7–11; seeds 2.8–4.2 mm diam.; involucrel stipules 2–5 mm long, involucrel bracts greenish at anthesis; 400–1100 m elevation ..... *D. cissifolia*
  - 4b. Female sepals 6; seeds 4–5 mm diam., involucrel stipules 10–14 mm long; involucrel bracts greenish or white at anthesis; 0–400 m elevation ..... *D. websteri*
- 5a. Stems, leaves, and bracts hirsute or lanate with orange or yellow-orange hairs to 2 mm long; larger leaves usually more than 15 cm long, 3-lobed and unlobed leaves often present on same plant; ♂ involucrel with 4 free bracteoles, glandular-laciniate [evergreen lowlands to 200 m elevation] .. 6
- 5b. Stems, leaves, and bracts not densely hirsute with yellow-orange hairs, hairs rarely exceeding 1 mm; larger leaves rarely > 15 cm long, 3-lobed and unlobed leaves not usually present on the same plant (except *D. tiliifolia*); ♂ involucrel with free or united bracteoles but not glandular-laciniate ..... 7
  - 6a. Male flowers usually 13; stigmas ca. 2 mm wide, distinct resin gland absent; margin of leaf blades minutely denticulate; Caribbean lowlands ..... *D. shankii*
  - 6b. Male flowers usually 10; stigmas 2–4 mm wide, distinct gland with white resin present; margins of leaf blades entire or obscurely denticulate; Osa Peninsula ..... *D. osana*

- 7a. Leaves ovate, consistently without lobes, deeply cordate at the base; involucre bracts deciduous before fruits become mature; ♂ involucre of 4 free bracteoles ..... 8
- 7b. Leaves usually deeply 3-lobed, occasionally ovate; involucre bracts often persisting as fruits develop; ♂ involucre with bracteoles united near base or throughout ..... 10
- 8a. Fruiting sepals ca. 4 mm wide, unlobed and with lacinate margins; seeds 4–4.5 mm diam.; stipules 6–12 mm long; stems and leaves sparsely hirsute with hairs 1–2 mm long [rare in Costa Rica] ..... *D. canescens*
- 8b. Fruiting sepals narrow (ca. 1 mm) with slender lateral pinnatifid lobes 1–8 mm long; stipules 2–7 mm long; stems and leaves lacking longer (1–2 mm) hairs ..... 9
- 9a. Pinnatifid lobes of the fruiting sepals 4–12 mm long; seeds 4.8–5.8 mm long and with 3 longitudinal ribs; leaves usually broadly ovate ..... *D. dioscoreifolia*
- 9b. Pinnatifid lobes of fruiting sepals 1–2 mm long; seeds 2.8–4.2 mm long, subglobose with smooth surface; leaves usually narrowly ovate ..... *D. cissifolia*
- 10a. Leaves usually deeply 3-lobed, never 3-foliolate; from both deciduous and evergreen formations on the Pacific slope (in Costa Rica) ..... 11
- 10b. Leaves usually ovate and unlobed (sometimes 3-foliolate in *D. heteromorpha*); from evergreen or partly deciduous formations on both Pacific and Caribbean slopes ..... 12
- 11a. Involucre bracts with 3 short distal lobes ( $< \frac{1}{2}$  length of bract); ♂ bracteoles free for ca.  $\frac{1}{2}$  their length; seeds 4–5 mm diam.; evergreen or partly deciduous areas, 0–500 m ..... *D. tiliifolia*
- 11b. Involucre bracts with 3 lobes  $\frac{1}{2}$ – $\frac{1}{2}$  the length of the bract; ♂ bracteoles united into a cup-like or bilabiate structure; seeds 3.6–4.2 mm diam.; deciduous or evergreen areas, 0–1000 m ..... *D. scandens*
- 12a. Leaf base with a usually shallow (0–1 cm) sinus, leaves narrowly ovate-triangular and unlobed or sometimes 2-lobed; involucre bracts with 5 main veins from base, deeply 3-lobed to unlobed, green as the leaves; evergreen or partly deciduous formations of the Pacific slope, 0–1100 m elevation ..... *D. heteromorpha*
- 12b. Leaf base with a conspicuous basal sinus 1–2 cm deep, leaves ovate and unlobed; involucre bracts with 7–9 main veins, distally 5-lobed, pale green; evergreen Caribbean slopes ca. 500 m ..... *D. arenalensis*

***Dalechampia arenalensis* Armbruster, Syst. Bot. 9: 275. 1984.**

Clambering vines, stems 0.5–1 mm thick distally, pubescence of strigose hairs 0.5–0.8 mm long; stipules 8–10 mm long, 2–4 mm wide, lanceolate, weakly parallel-veined, persisting. Leaves simple, petioles 1–6 cm long, 0.8–1.2 mm thick, pubescent as the stem, stipules 2 at base of blade, 1–2 mm long, 0.8–1.2 mm wide, gland-tipped and with 1–2 marginal glands; leaf blades 6–14 cm long, 3–8 cm wide, ovate to broadly ovate, apex acuminate, margin entire to glandular-sinuate, base cordate, sinus 1–2 cm deep, drying chartaceous, surfaces strigulose, venation palmate with 3–5 major veins. Inflorescences borne on axillary shoots 5–25 cm long, peduncles 3–4 cm long at anthesis (to 6 cm in fruit), involucre stipules 3–8 mm long, 1.5–2 mm wide; involucre bracts subequal, 3–4.5 cm long, 2.5–3.5 cm wide, broadly ovate, 5-lobed distally, middle lobe 1.8–2.5 cm long, rounded-subcordate at base, palmately 7–9-veined, margins glandular dentate, pale green; resin gland 26–38 mm long. Male cymules with peduncles 3–5 mm long, 1.5–2.5 mm thick, involucre shallowly 2-lipped, lower lip (subtending ♂ flowers) ca. 5 mm long, 8–10 mm wide, margin deeply undulate, upper lip subentire; ♂ flowers 10 (1 terminal with 3 lateral 3-flowered groups), with ca. 20 small (2–3 mm) resiniferous bracteoles; ♂ pedicels 5–

7 mm long, calyx splitting into 5–6 ovate parts, 2–3 mm long, ca. 2 mm wide, reflexed, staminal column 3–4 mm long, 0.7–1.5 mm thick, anthers (13–)18–30, filaments ca. 0.5 mm long, anthers ca. 1.5 mm long. Female cymules sessile, involucre of 2 bracteoles, 4–8 mm long, adaxial bracteole 12–15 mm wide, abaxial 4–7 mm wide; ♀ flowers subsessile at anthesis, sepals usually 12 on central flower and 9–10 on lateral flowers, 1–1.5 mm wide, with lacinate eglandular teeth, ovary ca. 1.5 mm diam., stylar column 13–16 mm long, curving upward, ca. 1.2 mm thick, tip slightly discoid. Fruits 10–12 mm diam., borne on pedicels 10–20 mm long, fruiting sepals 15–20 mm long, linear, with gland-tipped teeth along margin, sharp hairs 1–2 mm long; seeds ca. 4 mm diam., globose, minutely rugulose, mottled brown.

Plants of evergreen Caribbean rain forest formations, 300–500 m elevation. Flowering in January and August. Known only from the following collections *Armbruster & Herzig 79-215 DAV* (type) and *Lent 2766 MO*, both from the northern slopes of Volcán Arenal in north-central Costa Rica.

*Dalechampia arenalensis* is recognized by its simple ovate leaves with narrow basal sinus, in-

volucral bracts green at anthesis, yellow floral resin, and restricted range.

***Dalechampia canescens*** H.B.K., Nov. gen. sp. 2: 98. 1817. *D. friedrichsthalii* Müll. Arg., Flora 55: 45. 1872. *D. canescens* ssp. *friedrichsthalii* (Müll. Arg.) Webster & Huft, Ann. Missouri Bot. Gard. 75: 1109. 1988.

Climbing vines, leafy stems ca. 2 mm thick, minutely puberulent and with few straight longer hairs to 1.5 mm long; stipules 6–12 mm long, 2–3 mm wide at base, lanceolate, pubescent, venation parallel, reflexed and persisting. Leaves simple, petioles 5.5–9.5 cm long, pubescent as the stems, stipels 1.8–3 mm long, lanceolate, glandular at the base; leaf blades 7–14 cm long, 5–10 cm wide, ovate to triangular-ovate, apex abruptly short-acuminate, margin subentire or minutely denticulate, base deeply cordate with lobes often overlapping, drying chartaceous, sparsely hirsute above, minutely puberulent beneath, venation palmate with 3 major ascending veins. Inflorescences axillary to leaves, solitary, peduncles (including axillary stem with caducous leaf) 7–10 cm long, involucre stipules 12–13 mm long, 3.5–5 mm wide, pubescent and hispid-ciliate, parallel-veined; involucre bracts white with green veins, ca. 3 cm long, ovate, with 3 short distal lobes, middle lobe ca. 8–9 mm long, acuminate, margins lacerate, 5-veined at base with petiole 1.5–2 mm long. Male cymules with thick peduncle 1.5–2 mm long, involucre of 4 bracts, 4–5 mm long, 7–8 mm wide, broadly imbricate; ♂ flowers ca. 10, pedicels 2–3 mm long, articulate near apex, buds 1.5–2.5 mm diam., sepals 4–5, staminal column 1.3–2 mm long, hispidulous, anthers (18–)25–33. Female cymules with 2 adaxial bracteoles 5–5.5 mm long, abaxial bracteole ca. 4.5 × 6 mm, broadly ovate or reniform, crenate-toothed; ♀ flowers with 5–8 sepals, 1.7–2.2 mm long at anthesis, ovate-oblong, margin fimbriate; ovary deeply 3-lobed, minutely hispidulous, styles 9–10 mm long, stigma 1–1.5 mm wide. Fruits ca. 7 mm long, ca. 9 mm wide, subtended by the persisting involucre stipules and narrow sepals to 12–15 mm long and 4 mm wide, margins lacinate; seeds 4–4.5 mm diam., subglobose, slightly rugose-costate.

Rarely collected plants of evergreen lowland forest formations. The species ranges from the Río San Juan, Nicaragua (*Friedrichsthal* 683, G type of *D. friedrichsthalii*, not from Guatemala as earlier described) to Peru.

*Dalechampia canescens* is recognized by the simple ovate-triangular leaves with conspicuous narrow basal sinus, the broader parallel-veined involucre stipules, the lanceolate lacinate sepals subtending the fruits, and the slightly rugose seeds with weakly developed longitudinal costa. The above description is based on earlier descriptions: we have seen no material from Costa Rica.

***Dalechampia cissifolia*** Poeppig in Poeppig & Endl., Nov. gen. sp. pl. 3: 20. 1845. *D. trifolia* Lam., var. *cissiflora* (Poeppig) Müll. Arg. in DC., Prodr. 15 (2): 1239. 1866. *D. panamensis* Pax & K. Hoffm., Pflanzenreich IV, 147, XII: 19. 1919. *D. cissifolia* ssp. *panamensis* (Pax & K. Hoffm.) Webster, Ann. Missouri Bot. Gard. 54: 193. 1967. Figure 4.

Climbing vines, leafy stems 0.7–3.5 mm thick, pubescent with thin whitish retrorse hairs 0.1–0.5 mm long, with few to many longer erect hairs to 2 mm; stipules 2–6 mm long, 0.3–0.7 mm wide at base, lanceolate to linear, reflexed. Leaves 3-foliolate (rarely 5-foliolate or simple), petioles 1.5–8 cm long, 0.5–1.3 mm thick, pubescent, stipels 2, 1–3.5 mm long, 0.4 mm wide, glandular at base, petiolules of central leaflet 1–6 mm long; leaflet blades (middle leaflets) 4–11 cm long, 1.1–3.5 cm wide, narrowly elliptic-oblong to narrowly ovate-elliptic, apex acute to acuminate, margins subentire or with 2–5 short (0.5 mm) teeth/cm, base acute, lateral leaflets asymmetric at base with a rounded-truncate side and cuneate side, drying thinly chartaceous, sparsely and minutely (0.1–0.2 mm) puberulent on the veins beneath, larger (0.4–0.7 mm) hairs sometime present on the surfaces, venation pinnate, 2° veins 5–7/side, 3° veins subparallel. Inflorescences axillary (short shoots to 5 mm long), peduncles 6–18 mm long (to 25 mm in fruit), 0.3–0.6 mm thick, pubescent, involucre stipules 2–5 mm long, 0.7–1.7 mm wide at base, subulate, involucre bracts 8–18 mm long, 9–23 mm wide, to 25 × 29 mm in fruit, broadly ovate and 3-lobed or unlobed, middle lobe 3–8 mm long, margin with short (0.5 mm) teeth, greenish. Male cymules subsessile, involucre 1.5–2 mm long, 5–8 mm wide, reniform, pedicels 2–3 mm long; ♂ flowers 8–9, buds 1.5–2 mm diam., calyx lobes 4–5, staminal column ca. 1 mm long, anthers 20–36. Female cymule with 3 flowers, sepals 7–11, unequal and slender-pinnatifid with 4–6 slender lobes/side; ovary densely hispid, stylar column 5–6 mm long, stigma 0.6–1 mm wide. Fruits 5–6 mm long, 8–10 mm wide, with 3 rounded lobes, minutely puberulent, subtended by sharp-hispid pinnatifid sepals 7–11 mm long, 0.6–2 mm wide, lobes 0.5–2 mm long, stinging hairs to 1 mm long, columella 2.8–4.2 mm long, 3.7–4.2 wide at apex; seeds 2.8–4.2 mm long, globose, dark to pale brown, smooth, usually mottled.

Plants of evergreen forest formations of the Pacific slope, 400–1100 m elevation (0–1500 in Guatemala). Fruiting in November–March. Collected only on the Cordilleras de Guanacaste and Tilarán and near San Ramón in Costa Rica (but see below). The species ranges from Mexico to Peru.

*Dalechampia cissifolia* is recognized by its palmately three-foliolate leaves (rarely simple and ovate), greenish involucre bracts often with three distal lobes, and the “involucre” of 7–11 stiff narrow sepals with short narrow lateral lobes and stinging hairs subtending the fruits. It is possible



that *D. heteromorpha* will be reinterpreted as an unusual form of this species.

***Dalechampia dioscoreifolia*** Poeppig in Poeppig & Endl., Nov. gen. sp. pl. 3: 20. 1841. Figure 5.

Climbing vines, leafy stems 1.2–4 mm thick, minutely puberulent with thin mostly retrorse hairs 0.1–0.3 mm long, older stems becoming dark brown with rounded lenticels ca. 0.4 mm wide; stipules 3–7 mm long, 1.1–2 mm wide at the base, lanceolate to narrowly triangular, venation parallel, reflexed, persisting. **Leaves** simple, petioles 1.6–10.3 cm long, 0.7–1.4 mm thick, puberulent, with 2 linear stipels at base of blade near petiole attachment, 0.7–4.3 mm long, 0.2–0.5 mm wide; **leaf blades** 6–15 cm long, 4–13 cm wide, ovate to ovate-triangular, apex short-acuminate to acuminate, tip 3–10 mm long, margin entire or minutely (0.3 mm) denticulate, base cordate to subcordate-truncate, drying chartaceous, upper surfaces minutely puberulent on the major veins, lower surface with minute puberulence on all the veins, venation palmate with 3 major ascending veins and 2 lesser laterals, 2° veins 1–3/side of midvein. **Inflorescences** on short (0.5–8 mm) axillary branches, peduncles 3–18 mm long, 0.6–1 mm thick, minutely puberulent, involucre stipules 4–10 mm long, ovate-triangular; involucre bracts 15–50 mm long, 18–50 mm wide, ovate to ovate-triangular, base cordate, often with a thick (1.3–2 mm) petiole 6–11 mm long, pinkish or white with darker red or purple venation, margin with prominent (2–6 mm) teeth, with 5–7 major veins; resin dark purple. **Male cymules** on peduncles to 1.5 mm long, involucre of 4 free broadly imbricate concave bracteoles, ♂ flowers 8–9, pedicels 3–6 mm long, puberulent distally, calyx lobes 4, puberulent on exterior, staminal column 2.5–3.5 mm long, glabrous, anthers 20–30. **Female cymules** with abaxial bracteoles ca. 5 mm long, concave, glabrous with ciliate margin; ♀ flowers with 5–11 narrow pinnatifid sepals with slender lobes, pubescent; ovary densely hispidulous, styles 3–5.5 mm long, stigmas 1.5–4 mm wide, rounded, flat and peltate. **Fruits** 8–10 mm long, 11–16 mm wide, deeply 3-lobed, sparsely pubescent with hairs 0.1–0.4 mm long, thick-walled (to 2 mm), subtended by sepals 10–16 mm long, central rachis to 1.3 mm wide, lateral lobes 4–12 mm long, 0.3 mm wide, hairs ca. 0.4 mm long, columella 4.5–5 mm long, 4–5 mm wide at apex, T-shaped; seeds 4.5–5.8 mm long, 4.5–6 mm wide, 3.3–4.5 mm thick, lenticular-triangular in cross-section, with a distal longitudinal peripheral ridge and 2 parallel longitudinal adaxial ridges, slightly rugose.

Plants of evergreen rain forest formations of the Caribbean and southern Pacific slopes at 10–1100 m elevation. Flowering and fruiting throughout the year. The species ranges from southeastern Nicaragua to Peru.

*Dalechampia dioscoreifolia* is recognized by its simple unlobed cordate leaves, bright pink involucre bracts with dark reddish veins against a paler background, peltate stigmas, fruits subtended by narrow sepals with long lateral lobes and sting-

ing hairs, and unusual seeds with longitudinal ridges. The involucre bracts often have prominent petioles.

***Dalechampia heteromorpha*** Pax & K. Hoffm., Pflanzenreich IV, 147, XII: 26. 1919. *D. guatemalensis* Gandoger, Bull. Soc. Bot. Fr. 66: 286. 1920. *D. molliuscula* Blake, Contr. U.S. Natl. Herb. 24: 12. 1922. Figure 5.

Clambering vines, leafy stems 0.6–1.8 mm thick, with thin retrorse whitish hairs 0.1–0.5 mm long; stipules 2–6 mm long, 0.6–0.8 mm wide at base, narrowly lanceolate-linear, sparsely puberulent, venation obscure, persisting or deciduous. **Leaves** varying on the same stem, simple and ovate to 3-foliate, petioles 1.2–11 cm long, 0.5–1.6 mm thick, sparsely pubescent, stipels often present, 1–4 mm long, ca. 0.4 mm wide, petiolules 0–3 mm long; **leaf blades** of simple leaves 3–14 cm long, 2–8 cm wide, narrowly ovate-triangular with cordate or subcordate base, central blade of 3-foliate leaves 3–11 × 1.4–3.2 cm, narrowly elliptic or narrowly elliptic-oblong to oblanceolate, apices acuminate, margins denticulate to rounded-crenate or subentire, teeth 3–6/cm, base of lateral leaflets asymmetric and rounded on the outer side, drying chartaceous, with thin straight hairs 0.2–1.1 mm long (shorter beneath), simple leaves with palmate venation and 3 (5) major veins and 2° veins 2–3/side, lateral leaflets with 2 major veins, 3° veins subparallel. **Inflorescences** on axillary stems 1–5 cm long, peduncles 0.5–0.9 mm thick, pubescent, involucre stipules 2–3 mm long, 0.4–1 mm wide at base, puberulent; involucre bracts 1–2 cm long at anthesis and green, becoming 16–27 long and 16–30 mm wide in fruit, ovate to broadly ovate, margin undivided with small (0.2 mm) glandular teeth or deeply 3-lobed, sparsely pubescent. **Male flowers** with connate involucre bracteoles; stamens 20–30 and crowded. **Female flowers** with ca. 10 narrow sepals with narrow pinnatifid lobes, with stiff yellowish hairs ca. 1 mm long; ovary pubescent, stylar column 3–4 mm long, slightly expanded at apex. **Fruits** ca. 6 mm long, 7–10 mm wide, with 3 rounded lobes, minutely (0.1–0.2 mm) puberulent, subtended by the pinnatifid sepals 7–10 mm long with narrow (0.5–1 mm) central axis with 3–7 narrow lobes 1–1.4 mm long and stiff sharp hairs 0.8–1.5 mm long; seeds 3.4–4.3 mm diam., subglobose, mottled brown to dark brown, smooth.

Plants often found in secondary growth in evergreen forest areas, 0–1100 m elevation. Flowering throughout the year. First collected in Costa Rica (*Brenes 14414* the type), the species ranges from Veracruz, Mexico, to southernmost Puntarenas (but see below).

*Dalechampia heteromorpha* is recognized by having both ovate-triangular leaves and three-foliate leaves (often on the same short length of stem) and the linear-oblong ♀ sepals with narrow pinnatifid lateral lobes and sharp hairs. The lateral

leaflets of three-foliolate leaves are asymmetric at the base, very much like those of *D. cissifolia* and *D. websteri*. It seems probable that the plants placed here are no more than an unusual form of *D. cissifolia*.

***Dalechampia osana*** Armbruster, Syst. Bot. 13: 303–312. 1988. Figure 4.

Clambering vines, leafy stems 3–9 mm thick, hirsute with straight orange or yellow hairs 0.7–2 mm long (fading to gray), shorter hairs 0.2–0.5 mm long; stipules 7–14 mm long, 4–9 mm wide near base, ovate or triangular, glabrous adaxially, becoming reflexed, persistent. **Leaves** simple, petioles 3–13 cm long, 1–2 mm thick, often geniculate at the base, pubescent as the stems, with 2 stipels at base of blade, 3–5.5 mm long, ca. 0.5 mm wide, glabrous; **leaf blades** 5–28 cm long, 5–25 cm wide, ovate and unlobed to 3-lobed, apices acuminate, margin entire to minutely denticulate with pubescent teeth 0.2–0.5 mm long, base cordate to subcordate, sinus 5–50 mm deep, drying chartaceous, sparsely hirsute with thin hairs above, more densely pubescent beneath with hairs 0.5–1 mm long, venation palmate with 5 major veins, 2° veins 3–4/side of the midvein, 3° veins subparallel. **Inflorescences** on axillary branches 15–40 mm long (subsessile), densely pubescent, involucre stipules 7–14 × 6–11 mm; involucre bracts 16–25 mm long, 15–20 mm wide, white, 3-lobed, middle lobe 2–3 mm long, lateral lobes ca. 2 mm long, narrowed at base and with 3 major veins, hirsute with orange/yellow hairs on both surfaces, a distinct resin gland present on staminate involucre. **Male cymules** with peduncle 3–4 mm long, involucre with 2 pairs of decussate free ovate bracts 8–9 mm long, margins finely glandular-dentate; ♂ flowers 10 (1 terminal and 3 3-flowered groups), subtended by 3–4 bracteoles 3–4.5 mm long with laciniate and resinous margins; pedicels 3.5–5 mm long, calyx splitting into 3–5 parts ca. 4 mm long, 1–3 mm wide, lanceolate, staminal column 4–6 mm long, ca. 1 mm thick, stamens 25–30, filaments ca. 1 mm long, anthers ca. 0.6 mm long. **Female cymes** sessile, subtended by 2 (3) stipule-like bracts with irregular denticulate margins, distal (adaxial) bracts 7–9 mm long, 6–8 mm wide, overlapped by the proximal (abaxial) bracts 10–12 mm wide; ♀ flowers subsessile at anthesis, sepals 5–6, hirsute with orange or yellow hairs, 4–5 mm long, ca. 1.5 mm wide, margin with laciniate teeth 0.2–0.8 mm long, ovary ca. 2 × 2 mm, stylar column curved upward near the base and downward distally, 8–10 mm long, 0.9–1.2 mm thick, dilated at tip and 2.5–4 mm wide. **Fruits** 8–10 mm diameter, densely hispid-laciniate with orange or yellowish hairs, borne on pedicels 5–7 mm long (central fruit) or 2 mm long (laterals), persisting sepals 10–15 mm long and 3–4 mm wide, lanceolate, columella 5.5 mm long; seeds 5 × 4 mm, ovoid to round-oblong.

Plants of rain forests of the southeastern Pacific lowlands, 40–250 m elevation. Flowering in September–November. This species is endemic to the Osa Peninsula.

*Dalechampia osana* is recognized by its hirsute

stems, large ovate to three-lobed leaves, orange or yellowish pubescence on young shoots, short flowering branches, and compact inflorescences. The reflexed persisting stipules, glabrous on the inner face, are also noteworthy.

***Dalechampia scandens*** L. Sp. Pl. 1054. 1753. Figure 4.

Climbing vines, woody at base, leafy stems 0.7–3.5 mm thick, densely pubescent with straight hairs 0.4–1 mm long and minute (0.1–0.2 mm) appressed hairs; stipules 3.5–9 mm long, 1.8–2.8 mm wide at base, ovate-lanceolate to narrowly triangular, reflexed, persistent. **Leaves** simple but 3-lobed with deep narrow sinuses, petioles 1.5–9(–12) cm long, 0.8–1.8 mm thick, densely pubescent, stipels 2, 1–2(–3) mm long, glandular at base; **leaf blades** 4–13 cm long, 5–16 cm wide, middle lobe 3–10 cm long, 1.8–5 cm wide, elliptic-oblong to elliptic or obovate, apices short-acuminate to obtuse or rounded, margins subentire or minutely (0.2 mm) denticulate, base cordate with wide or narrow sinuses 3–17 mm deep, lateral lobes asymmetric with wide outer basal area, drying chartaceous, with (0.1–0.7 mm) straight hairs above, with shorter denser hairs beneath, venation palmate with 5 major veins (lateral lobes with 2 major veins), 2° veins 4–8/side, 3° veins subparallel. **Inflorescences** 1–2, on axillary shoots with small (8–12 mm) leaves or leaves not developed, peduncles 1–6 cm long, 0.3–0.7 mm thick, with thin sharp hairs 0.2–1 mm long (differing in different plants), involucre stipules 5–7 mm long, 1.5–2.5 mm wide at base, ovate-lanceolate to lanceolate, reflexed; involucre bracts 1.6–3(–4) cm long, 1.6–3.5(–4.6) cm wide, pale green to white, ovate-triangular to ovate-orbicular, 3-lobed at apex, lobes 20–50% of bract length, margin with glandular teeth. **Male cymules** on peduncles 2.5–3.5 mm long, involucre 2–4 mm high, 6–8 mm wide (bracteoles completely connate), ♂ flowers 9–10, pedicels to 1 mm long, buds ca. 2 mm diam., sepals ca. 3 mm long, glabrous, becoming reflexed, staminal column ca. 2 mm long, filaments 0.1–0.2 mm long, anthers 25–35, ca. 0.4 mm long. **Female cymules** sessile, 3-flowered, adaxial bracteoles 3–6 mm high, 6–10 mm wide, sericeous on both surfaces, ♀ flowers subsessile at anthesis (central pedicel to 12 mm long in fruit), calyx lobes 8–12, unequal, narrow with 3–5 slender gland-tipped lateral lobes/side; styles 3–8 mm long, often curved, stigmas 0.5–1.3 mm wide. **Fruits** 6–7 mm long, 8–9.5 mm wide, subtended by 8–12 sepals 5–12 mm long with central axis 0.4–0.8 mm wide, edges with sharp hairs ca. 1 mm long and/or gland-tipped hairs, columella ca. 3 mm long, 4 mm wide at apex (T-shaped); seeds 3.6–4.2 mm diam., subglobose, smooth, mottled.

Plants of open sites in deciduous and partly deciduous formations of the Pacific slope, 10–1000 m elevation. Flowering in August–September; fruiting in October–February. This species is widespread in the American tropics.

*Dalechampia scandens* is recognized by the large deeply three-lobed leaves, the usually three-lobed involucre bracts, narrow sepals with short narrow



pinnatifid gland-tipped lobes, and smooth globose seeds often with an intricate pattern of strongly contrasting dark and light mottling. Stinging hairs are usually present, with *mala* the consequent common name.

***Dalechampia shankii*** (A. Molina) Huft, Ann. Missouri Bot. Gard. 71: 541. 1984. *Tragia shankii* Molina, Ceiba 11: 68. 1965. Figure 4.

Clambering vines and lianas, leafy stems 2–6 mm thick, with yellowish or orange hairs to 1.5 mm long and minute (0.1–0.2 mm) appressed hairs; stipules 10–16 mm long, 4–6 mm broad at the base, ovate-triangular to ovate-lanceolate, glabrous within, venation parallel, persisting and recurved. Leaves simple, unlobed or with 1–3 prominent distal lobes, petioles 4–18 cm long, 1.5–3.5 mm thick, pubescent as the stems, 2 adaxial stipels at the base of the blade, 2–5.5 mm long, ca. 0.5 mm wide; leaf blades 11–26 cm long, 9–28 cm wide, ovate to deeply 3-lobed, central lobe up to 70% of blade length, apex acuminate, margin with 6–10 small teeth/cm, base deeply cordate with sinus 1.5–8 cm deep, basal lobes usually divergent, drying chartaceous, upper surface with slightly curved hairs 0.2–0.8 mm long, lower surface with shorter (0.2–0.5 mm) hairs on venation, venation palmate with 5 major veins, 2° veins 2–4/side of the midvein, 3° veins parallel. Inflorescences 1.5–3 cm long, axillary, peduncles to 8 mm long, involucre stipules ca. 6 mm long, reflexed and glabrous within; involucre bracts ca. 13 × 8 mm, densely sericeous with ascending golden-orange hairs ca. 1 mm long, distal margin entire; a distinct resin gland not developed. Male flowers usually 13 on 4 pleiochasial arms, resin gland absent, sepals ca. 3 × 1.2 mm and reflexed, glabrescent, staminal column ca. 6 × 0.3 mm, filaments 0.7–1.2 long, anthers 0.5–0.7 mm long. Female flowers with sepals to 15 mm long in fruit, with lateral teeth ca. 1 mm long; style column ca. 8 × 0.7 mm, stigma 1.3–2 mm wide. Fruits 6–8 mm long, ca. 9 mm wide, densely covered with orange-yellow hairs 0.3–1 mm long, columella ca. 4 mm long, 3–4 mm wide at apex; seeds 4–4.7 mm long, 3.5–4.5 mm wide, subglobose-oblong, brown, smooth.

Plants of lowland Caribbean rain forest formations, 10–200 m elevation. Flowering and fruiting collections were made in June and December. The species ranges from northern Costa Rica to Ecuador.

*Dalechampia shankii* is recognized by its larger leaves and thicker stems, characteristic yellowish or orange pubescence, short flowering stems and compact inflorescences. Compare *D. osana* and *Tragia bailloniana* with very similar foliage.

***Dalechampia spathulata*** (Scheidw.) Baill., Etude Euphorb. 487. 1856. *Cremophyllum spathulata* Scheidw., Bull. Acad. Roy. Sci. Bruxelles 9: 23. 1842. *D. roezliana* Müll. Arg. in DC., Prodr. 15 (2): 1233. 1866. Figure 13.

Erect subshrubs 0.3–1 m tall, stems woody and usually unbranched, leafy stems 2–5 mm thick, densely pubescent with hairs 0.1–0.2 mm long; stipules 7–12 mm long, 4–6 mm wide at the base, triangular to lanceolate with 7–13 parallel veins, minutely and sparsely puberulent, persisting. Leaves subsessile or with petioles to 9 mm long, 1.3–2 mm thick, sparsely puberulent, stipels usually 2, minute; leaf blades 12–28 cm long, 4–10 cm wide, oblanceolate or narrowly elliptic-obovate to narrowly obovate, apex gradually acuminate or abruptly caudate-acuminate, margin entire or with low blunt teeth (1–2 teeth/cm), base long-cuneate and attenuate, often slightly (0.5 mm) auriculate at the petiole, drying thin-chartaceous, glabrous above and below, 2° veins 9–12/side. Inflorescences axillary, peduncles 2–4.7 cm long, 0.7–1 mm thick, minutely puberulent with whitish hairs 0.1 mm long, involucre stipules ca. 4 mm long; involucre bracts 2.5–5 cm long, 2–4 cm wide, ovate-triangular, with serrate edge (3–5 teeth/cm), base obtuse to truncate (subcordate), rose-red to purple-red or yellow, 3-veined, sparsely and minutely puberulent beneath. Male flowers usually 9, sepals 6, reflexed, staminal column ca. 3.4 mm long, filaments short, anthers ca. 15, 0.7–0.9 mm long. Female flowers with 6 linear-lanceolate sepals, ca. 1 mm long, style column 5–8 mm long, ca. 0.3 mm thick. Fruits 5–6 mm long, ca. 9 mm wide, 3-lobed, puberulent, columella ca. 4 mm long, T-shaped, 2.5–4 mm wide; seeds 4–5 mm diam., subglobose, tubercles 0.2–0.5 mm high, scattered or some in longitudinal ranks, brown.

Plants of lowland Caribbean rain forest formations, 50–600 m (to 1100 m in Mexico) elevation. Flowering and fruiting in February–June. Only a few collections from near Tilarán and Upala have been made in Costa Rica. The species ranges from Veracruz, Mexico, to Peru.

*Dalechampia spathulata* is unique among our species of *Dalechampia* with its short erect unbranched habit and long subsessile oblanceolate leaves. The stiff persisting stipules, colorful involucre bracts, lack of resin-producing glands, and tuberculate seeds are also distinctive.

***Dalechampia tiliifolia*** Lam., Encycl. 2: 257. 1786. Figure 4.

Clambering vines, leafy stems 1.4–4 mm thick, puberulent with minute (0.1–0.3 mm) whitish hairs and with few longer (ca. 1 mm) straight sharp hairs; stipules 1.5–9 mm long, 0.3–0.8 mm wide at base, acute, deciduous. Leaves usually 3-lobed (unlobed ovate/cordate leaves with 5 palmate veins or 2-lobed leaves sometimes present), petioles 1–14 cm long, 0.8–1.8 mm thick, minutely puberulent, often geniculate at the base, stipels at apex of petiole usually 2–4, 0.3–4 mm long; leaf blades 4–16 cm long, 4.5–17 cm wide, central lobe more than ½ the length of the blade, obovate to elliptic-obovate, apices obtuse to short-acuminate (rounded), margin subentire or minutely denticulate with 4–6 teeth/cm, base cordate with broad sinuses 4–24 mm deep, drying thinly chartaceous and grayish green, soft thin hairs (0.2–0.3 mm long) more dense beneath, venation palmate with



3 major veins and 2 minor laterals, 2° veins 3–6/side of midvein. **Inflorescences** on axillary stems with smaller (4–8 cm) leaves, peduncles to 3–4 cm long (to 7 cm in fruit or apparently longer when subtending leaves fail to develop), densely pubescent, involucrel stipules 2–7 mm long, 0.5–0.8 mm wide, linear-lanceolate; involucrel bracts 2–5 cm long, 1.7–4.8 cm wide, rounded-ovate, with 3 (5) short (2–7 mm) apical lobes, pale greenish yellow to white, becoming greenish, with 7–11 veins from the base, pubescent with thin hairs 0.2–0.5 mm long on both surfaces. **Male cymules** on peduncles 3.5–6 mm long, 10–12 mm wide; involucrel bract united near base, ♂ flowers 9–10, pedicels 4–8 mm long, basal part 0.5 mm thick, calyx splitting into 3–6 parts, 2–3.5 mm long and reflexed; staminal column 2.5–4 mm long, androecium rounded and 2.5 mm diam., anthers 25–45, 0.5–0.8 mm long. **Female flowers** subtended by bracts 6–8 mm long, with 9–12 narrow pinnatifid sepals (difficult to see at anthesis), the narrow lobes 6–10; ovary ca. 4 mm diam., with sharp straight hairs 1–1.5 mm long, stylar column 7–12 mm long, 0.3–0.7 mm thick, dilated stigmatic apex 1.3–3.5 mm wide. **Fruits** 7–10 mm long, 14–16 mm wide, 3-lobed, densely hispid, subtended by the stiff sepals 8–16 mm long, 0.6–2 mm wide, with pinnatifid lobes 0.5–1.5 mm long and sharp stinging hairs to 1–2 mm long, columella ca. 4 mm long; seeds 4–5 mm long and wide, 3.8–4 mm thick, subglobose and slightly laterally compressed, mottled brown, smooth.

Plants of evergreen or partly deciduous formations of the Pacific slope, 0–1000 m elevation. Flowering in November–February; fruiting in January–March. The species ranges from southern Mexico to Brazil and Bolivia.

*Dalechampia tiliifolia* is recognized by its larger deeply three-lobed (or unlobed) leaves, stinging hairs, rounded involucrel bracts with small distal lobes, and the 9–12 narrow sepals with slender pinnatifid lobes and many stinging hairs subtending the fruit. The fruiting sepals also have minute (0.1 mm) gland-like protuberances on their surfaces. This is one of Central America's most common species of *Dalechampia*, but it has been collected only along the Pacific slope in Costa Rica. It is usually found in drier sites than *D. dioscoreifolia* and in moister sites than *D. scandens* (Armbruster, 1988).

***Dalechampia websteri* Armbruster, Syst. Bot. 9: 272. 1984. Figure 4.**

Clambering vines, leafy stems 0.5–3.5 mm thick, hirsute with thin erect white or yellowish hairs 0.7–2 mm long, and with shorter (0.1–0.2 mm) hairs; stipules 2–12 mm long, 0.3–3 mm wide, lanceolate, with thin hairs and inconspicuous glands, persistent and reflexed. **Leaves** palmately 3-foliolate, petioles 2–6 cm long, 0.5–1.2 mm thick, pubescent as the stems, petiolules ca. 2 mm long, stipels at apex 2–4 mm long, linear; **leaflet blades** 6–12 cm long, 1.5–4.5 cm wide, middle leaflet narrowly ovate-elliptic to elliptic-oblong, lateral leaflets asymmetric with

base rounded on outer side and cuneate on the inner side, apices acute to acuminate, margins glandular denticulate to sinuate, drying chartaceous, with slender slightly curved hairs 0.5–1.5 mm long above, hairs 0.2–0.3 mm long on the veins beneath, 2° veins 4–6/side of middle leaflet, lateral leaflets with an arcuate lateral vein from the base. **Inflorescences** on leafy lateral stems 10–18 cm long, involucrel stipules of proximal bract 10–14 mm long, 3–5 mm wide, stipules of distal bracts similar but broader, hirsute-sericeous; involucrel bracts subequal, 2.5–4 cm long, 2–3.5 cm wide, 3-lobed, middle lobe 1.5–2 cm long, narrowed to base and 3–4 mm wide, palmately 3-veined, white or pale green, resin gland 14–25 mm long. **Male cymules** with peduncles 2.5–5 mm long, 1.5–2 mm thick, involucrel of 4 free decussate bracteoles, 5–6 × 4–6 mm, parallel-veined; ♂ flowers 10 (1 terminal + 3 groups of 3), subtended by linear or spatulate bracteoles 4–5 mm long, margins fimbriate, pedicels 6–10 mm long; ♂ flowers usually with calyx splitting into 4 ovate-acute parts 1–2.5 mm long, 0.7–1.5 mm wide, staminal column ca. 2.5 mm long, anther cluster ca. 2 mm wide. **Female cymules** sessile, involucrel of 2 parallel-veined glabrescent bracteoles, abaxial bracteoles 4–5 mm long, 5–7 mm wide, simple, adaxial bracteoles 2–3 mm long, 4–6 mm wide, bilobed; ♀ flowers 3, subsessile at anthesis, sepals 6, 3–5 mm long, 1–2 mm wide, laciniate with gland-tipped teeth 1–2 mm long, ovary 1.5–3 mm long, 1.5–4 mm diam., minutely papillate-puberulent to strigulose, stylar column 6–14 mm long, 0.5–1 mm thick distally. **Fruits** ca. 8 mm long, 12–14 mm wide, deeply 3-lobed, subtended by sepals 6–12 mm long, 1–2 mm wide, with marginal teeth 1–3 mm long (often minutely gland-tipped), columella ca. 4.5 mm long; seeds ca. 4 mm long, ca. 4.5 mm diam., subglobose.

Plants of lowland Caribbean rain forest formations, 5–400 m elevation. Flowering and fruiting in January–October. The species ranges from northern Costa Rica to central Panama.

*Dalechampia websteri* is recognized by its three-foliolate leaves with very asymmetric (at the base) lateral leaflets sometimes broader than the narrow central leaflet. This species is common at La Selva.

## **Drypetes Vahl**

**Trees** or shrubs, dioecious (rarely monoecious), glabrous or with simple hairs, shoot apex sometimes with bud scales; stipules lateral, small, usually caducous. **Leaves** alternate, simple, short-petiolate, blades often slightly unequal at the base, often subcoriaceous, pinnately veined, margins entire or dentate. **Inflorescences** axillary or at older leafless nodes, unisexual, sessile fascicles of few ♀ or up to 15 ♂ flowers, ♂ flowers sessile or pedicellate, ♀ flowers pedicellate. **Male flowers** with 4–5 (6–7) imbricate sepals, concave and often unequal, ciliate, petals absent, intrastaminal disk annular or lobed to laciniate; stamens 4–12 (3–50), filaments free, anthers usually ovate, basifixed, extrorse to introrse; pistilode absent or minute. **Female flowers** with 4–5 (6–7) imbricate deciduous sepals, petals absent, staminodes absent, disk cupulate or annular (rarely absent); ovary with 1–2 (3–4) locules,

usually pubescent externally, ovules 2/locule, styles short or absent, stigmas 1–2 (3–4), thick and flattened, entire or sometimes bifid. **Fruits** drupaceous, indehiscent, globose to ellipsoid or ovoid, exocarp fleshy or leathery (drying hard), 1-seeded by abortion (sometimes 2-seeded); seed ecarunculate, testa smooth, endosperm carnose, embryo broad and flat.

A pantropical genus of ca. 200 species, with ca. 20 in the American tropics. Fruiting specimens are difficult to recognize as Euphorbiaceae, because the fruits are indehiscent, one- or two-seed-

ed, and usually with sessile undivided stigmas. In addition, the flowers and flower fascicles are small and inconspicuous, resulting in a paucity of collections. A helpful characteristic in determining herbarium material is the tendency of at least some leaves to be slightly asymmetric at the base, with one side more rounded than the other. Dr. Geoffrey A. Levin (ILLS) is studying the American representatives of this genus, and we thank him for his annotations and advice.

Key to the Species of *Drypetes*

- 1a. Mature fruits 1–15 mm diam., on slender pedicels ca. 1 mm thick; stigmas 1 or 2 and borne on the narrow styler column; leaves 1.6–4 cm wide, usually narrowly oblong to lanceolate; partly deciduous or evergreen forest formations ..... 2
- 1b. Mature fruits 14–28 mm diam., on stout pedicels 1.5–2 mm thick; stigmas 1 and sessile on the apex of the ovary; leaves 3–8 cm wide, usually oblong to elliptic-oblong; evergreen forest formations ..... 3
  - 2a. Locules and stigmas 2/fruit, fruits usually symmetric with the stigma apical; leaves with 3° and 4° veins not clearly differentiated but elevated and demarking small (0.3–0.9 mm) areas in an irregular reticulum, often drying pale grayish; 900–1200 m elevation in partly deciduous forests ..... *D. laterifolia*
  - 2b. Locules and stigmas 1/fruit, fruits often distally asymmetric, the stigma often somewhat lateral; leaves with 3° and 4° veins better differentiated, often paralleling the secondary veins, not forming a reticulum of small areas, drying grayish to dark olive green; 0–800 m elevation in evergreen or deciduous areas ..... *D. sp. aff. D. alba*
- 3a. Fruits usually narrowed at the apex, unilocular; leaves with petioles 4–15 mm long; mostly collected at 200–800 m elevation ..... *D. standleyi*
- 3b. Fruits usually rounded at the apex, bilocular (but may be difficult to see); leaves with petioles 3–8 mm long; 10–1400 m elevation ..... *D. brownii*

***Drypetes brownii*** Standl., Trop. Woods 20: 20. 1929. Figure 27.

**Trees** 5–20 m tall, trunks to 45 cm diam., leafy stems 1.2–4 mm thick, glabrous, often with prominent lenticels; stipules minute (0.5 mm) or obscure. **Leaves** with petioles 3–8 mm long, 0.9–2 mm thick, glabrous, sulcate above; **leaf blades** 9–20 cm long, 3.5–8 cm wide, oblong or elliptic-oblong to ovate-oblong, apex acuminate or acute with slightly thickened (glandular) tip, margin entire or slightly undulate, base obtuse to acute, often slightly asymmetric, drying subcoriaceous and usually grayish, glabrous above and below, 2° veins 5–9/side. **Male inflorescences** axillary, few-flowered fascicles, pedicels 3–5 mm long, densely minutely sericeous; ♂ flowers with sepals 3–3.5 mm long, broadly ovate with rounded apex, minutely sericeous; stamens 8–12. **Female inflorescences** axillary, fascicles of 1–3 flowers, pedicels 2–4 mm long, 0.7–0.8 mm thick, sparsely to densely appressed puberulent with hairs ca. 0.1 mm long; ♀ flowers with calyx 2–3 mm long, lobes 1–2 mm long, ca. 2 mm wide at base; ovary 1–2 mm long, 1.2–2 mm diam., broadly

sessile and ovoid, densely velutinous, stigmas sessile and broadly rounded, flat or reflexed, ca. 0.7 mm long, to 1.8 mm wide. **Fruits** 13–28 mm long, 12–25 mm diam., obovoid to subglobose, rounded apically, surface minutely puberulent, bilocular, 1- or 2-seeded; seed ca. 1.5 mm long.

A species of evergreen forest formations, from near sea level to 1500 m elevation. Flowers were collected in February and May; fruits were collected in February, April, July, and September. This species ranges from Chiapas, Mexico, and Belize to western Panama.

*Drypetes brownii* is recognized by the stiff glabrous short-petiolate leaves, axillary fascicles of few flowers, and obovoid to subglobose one- to two-seeded fruits on prominent pedicels. The leaf blades are often asymmetric at the base, and the



2° veins are strongly ascending. An unusual collection from near Palmar Norte (*Hammel & Aguilar 18193*) has larger (32 mm long) pyriform fruits with woody endocarp.

***Drypetes lateriflora* (Sw.) Krug & Urban, Bot. Jahrb. Syst. 15: 357. 1892. *Schaefferia lateriflora* Sw., Prodr. 329. 1788. Figure 27.**

**Trees** 6–20 m tall, trunk to 35 cm diam., leafy stems 0.9–3.5 mm thick, glabrous (rarely minutely puberulent at the nodes), grayish; stipules 0.4–1 mm long, triangular or obscure. **Leaves** with petioles 3–10 mm long, 0.6–1.2 mm thick, glabrous, sulcate above; **leaf blades** 4–10 cm long, 1.5–4 cm wide, lanceolate to narrowly ovate-elliptic or oblong-lanceolate, apex bluntly acute or acuminate, margin minutely dentate with 1–3 teeth/cm or slightly undulate and entire, base acute and often asymmetric, drying grayish and stiffly chartaceous, glabrous above and below, 2° veins 5–8/side, weakly or irregularly loop-connected distally. **Male inflorescences** axillary, sessile fascicles of 5–15 flowers on pedicels 1.5–3 mm long, slightly puberulent; ♂ flowers ca. 3 mm wide, sepals 4, ca. 1.5 × 1.3 mm, minutely puberulent on the exterior, broadly imbricate in bud; stamens ca. 4, anthers 0.4–0.8 mm long, ca. 0.6 mm wide. **Female inflorescences** axillary, fascicles of 1–4 flowers/axil, pedicels 4–11 mm long (to 16 mm in fruit), ca. 0.4 mm thick, glabrous; ♀ flowers with 4 sepals 2–3 mm long, triangular, ovary 2–3 mm long, 1.6–2 mm diam., ovoid-oblong, densely velutinous, style column 0.7–1 mm long, style branches (stigmas) to 1 mm long broad and flat. **Fruits** 12–15 mm long, 11–15 mm diam., subglobose or irregular in shape (ellipsoid), becoming red-orange at maturity with a soft juicy rind, surface minutely (0.1–0.2 mm) velutinous, 1- or 2-seeded.

Plants of partly deciduous tropical moist forest of the Pacific slope, 900–1300 m elevation. Flowering in November–December; fruiting in late January–July. In Costa Rica, this species has been collected on the western slopes of the Cordillera de Tilarán in the upper Río Guacimal drainage, Puntarenas Province. The species ranges from southern Mexico to Costa Rica and occurs in Florida (U.S.A.) and the West Indies.

*Drypetes lateriflora* is recognized by the smaller, glabrous, leaves that dry pale grayish, the small fasciculate flowers, the rounded fruit with minutely velutinous surface, and its restricted range in Costa Rica. The leaves are often quite asymmetric at the base with one side more cuneate than the other. We follow the determinations of Geoffrey Levin, who has tentatively adopted a broad circumscription for this species. This species is easily confused with the following (q.v.). A common name in Costa Rica is *azulillo*.

***Drypetes* sp. aff. *D. alba* (G. Levin, pers. comm., Jan. 1994).**

**Trees** 6–15 m tall, leafy stems 1–2.5 mm thick, glabrous or sparsely minutely puberulent; stipules ca. 0.5 mm long, triangular. **Leaves** with petioles 3–9 mm long, 0.3–1 mm thick, subglabrous, drying dark; **leaf blades** 4–12 cm long, 1.5–4.5 cm wide, lanceolate to narrowly oblong or elliptic-oblong, gradually narrowed to the acuminate apex, margins entire or minutely crenulate, base usually somewhat asymmetric, drying stiffly chartaceous, grayish to dark olive green, glabrous, 2° veins 6–9/side. **Inflorescences** with flowers not seen, axillary, fruits 2–6/node, pedicels 8–12 mm long, 0.4–0.8 mm thick, glabrous and drying dark. **Fruits** 11–16 mm long, 8–11 mm diam., ellipsoid to obovoid, often asymmetric distally with the style somewhat lateral, surface glabrous (but see below).

Plants of evergreen forests or from moist situations in deciduous formations, 0–750 m elevation. Fruiting material was collected in March near Quepos (*Grayum 6614*), April near Upala (*Herrera 1693*), and in June below Monteverde (*Bello et al. 35 & 58, Hammel & Trainer 17046*).

*Drypetes* sp. aff. *D. alba* is recognized by its usually narrow leaves often drying dark, general lack of pubescence, and narrowly obovoid fruits borne on slender pedicels and asymmetric distally. This material is rather similar to *D. lateriflora*, which grows at slightly higher elevations in some of the same forests, but the fruits and the leaf venation are different. The Herrera collection (see above), with densely pubescent fruits and elliptic leaves, is tentatively included here.

***Drypetes standleyi* Webster, Madroño 24: 65. 1977. Figure 27.**

**Trees**, 15–30 m tall, trunks to 1.2 m thick, leafy stems 1.5–4 mm thick, very minutely (0.05–0.1 mm) puberulent or glabrous, terete, lenticellate; stipules to 1 mm long or obscure, caducous. **Leaves** with petioles 4–10(–16) mm long, 1–1.4 mm thick, glabrous, drying dark, sulcate above; **leaf blades** 7–16(–19) cm long, 2.5–6(–7) cm wide, oblong-elliptic to elliptic or broadly elliptic, apex acuminate, margin entire (subentire), base obtuse and often slightly asymmetric, drying grayish or dark, subcoriaceous, glabrous above and below or with a few hairs along the midvein below, 2° veins 6–9/side, irregularly loop-connected near the margin. **Male inflorescences** axillary, fasciculate with ca. 10 flowers, pedicels 6–11 mm long, 0.3–0.4 mm thick, glabrous; ♂ flowers with 4 sepals, 2.5–4 mm long, 1.7–2.2 mm wide, ovate to ovate-oblong, rounded to acute at apex, sparsely puberulent externally, ciliate along the edge, glabrous or with few hairs within, imbricate becoming recurved, disk 1–1.5 mm wide; stamens usually 8 (6, 9) in 2 series, 2.5–3 mm long, anthers 1.2–1.6 mm long, pistillode absent. **Female inflorescences** axillary, fasciculate with usually



2 (1–5) flowers on thick pedicels 3–5 mm long, to 13 mm long in fruit; ♀ flowers with 4 sepals, 2.8–4.4 mm long, 2.5–3.2 mm wide, minutely strigose externally, glabrous within, margin ciliate, disk 2–2.3 mm in diameter, puberulent; ovary ca. 2 mm diam., densely velutinous or sericeous, style branches (stigmas) ca. 1 mm long, 1.5–2.5 mm wide, flat, sessile. **Fruits** 2–3 cm long, 1.3–1.8 cm diam., ovoid to ellipsoid, apex acute or rounded, usually densely velutinous, persisting stigmas borne on a short (1 mm) narrowed tip; seed with woody endocarp ca. 1.5 mm thick.

An uncommon species of evergreen or partly deciduous forest formations on both the Caribbean and Pacific slopes, (50–)200–700 m elevation in Costa Rica. Flowering in May; fruiting in March–July in Costa Rica (July–August in central Panama). The species ranges from northern Costa Rica to western Venezuela.

*Drypetes standleyi* is recognized by the stiff glabrous leaves, few axillary fasciculate flowers, and fleshy fruit puberulent on the exterior with single seed enclosed in a woody endocarp. The leaf blades are often asymmetric at the base with one side more cuneate than the other. The leaves often have several larger 3° veins arising from the midvein between the 2° veins and parallel with them; this feature may help to separate sterile material from that of *D. brownii*.

### Dysopsis Baillon

Weak-stemmed herbs with slightly succulent stems, monoecious, pubescent with simple and multicellular hairs; stipules paired at the leaf base, minute, subulate, caducous. **Leaves** alternate, simple, pubescent, petiolate, without glands, ovate to subreniform, margins of the blades with broadly rounded lobes, membranaceous, venation subpalmate with strongly ascending secondary veins, major veins terminating in small marginal glands. **Inflorescences** of solitary or few axillary flowers at distal nodes, ♂ flowers with long slender pedicels, ♀ flowers on short pedicels, bracts minute. **Male flowers** with 3 narrow minute sepals, apparently valvate in bud, united near the base, petals and disk absent; stamens 3 or 6 in 2 whorls, filaments connate at base, often unequal, anthers ellipsoid, with stiff thecae; pistillode absent. **Female flowers** with 3 narrow sepals, subvalvate in bud, petals absent, disk absent; ovary 3-lobed and 3-locular, ovules 1/locule, styles 3. **Fruits** capsular, breaking into 3 thin 2-valved cocci; seeds subglobose, ecarunculate, surface smooth.

Distinguished by its weak herbaceous habit, thin alternate leaves, very small solitary axillary flowers, and thin capsular fruit. This genus is represented by a single variable species.

**Dysopsis glechomoides** (A. Rich.) Müll. Arg. in DC., Prodr. 15 (2): 949. 1866. *Hydrocotyle glechomoides* A. Rich., Monogr. Hydrocotyle 14, t. 58, f. 17. 1820, Ann. Gén. Sci. Phys. 4: 180. 1820. Figure 10.

Decumbent or prostrate herbs, 5–20 cm tall, stems 0.4–1.5 mm thick (dried), slightly succulent in life, sparsely to densely puberulent with thin curved whitish hairs 0.1–0.7 mm long; stipules ca. 1 mm long, 0.5 mm wide at the base, narrowly triangular, thin translucent. **Leaves** with petioles 6–22 mm long, 0.3–0.4 mm thick, with short thin curved hairs; **leaf blades** 7–25 mm long, 8–23 mm wide, ovate to ovate-triangular, apex rounded with a minute glandular tip, margins with 3–7 rounded-crenate lobes/side, sinuses 0.3–1 mm deep, base obtuse to truncate, drying membranaceous and gray-green, upper surface with scattered straight sharp-tipped hairs 0.4–1.3 mm long, lower surface more densely pubescent with shorter hairs, venation subpalmate with 2–4 major 2° veins/side, arising from the proximal half of the midvein. **Male flowers** on pedicels 6–42 mm long, 0.2–0.3 mm thick, sparsely puberulent, sepals 0.8–1 mm long; staminal column ca. 1 mm long, anthers 0.5 mm long. **Female flowers** on pedicels ca. 1 mm long, sepals 0.6–1 mm long, ovary ca. 1 × 1.5 mm, bilobed, sparsely puberulent, styles ca. 0.5 mm long. **Fruits** 1.4–1.7 mm long, 2–2.3 mm wide, borne on a short (0.2 mm) stipe above the persisting sepals, surface with slender slightly curved hairs ca. 0.5 mm long; seeds 1.2–1.5 mm long, 0.8–1.2 mm diam., subglobose, smooth, lustrous, brownish black.

Understory herbs of wet evergreen montane forests, 2100–3000 m elevation. Fertile collections have been collected in March–April and September in Costa Rica. The species has been collected on Volcán Barva and the Cordillera de Talamanca; it ranges disjunctly through the Andes from Colombia to Chile, with a subspecies on the Juan Fernandez Islands.

*Dysopsis glechomoides* is recognized by its weak herbaceous habit, thin pubescent broadly ovate leaves with rounded-crenate margin, subpalmate venation ending in marginal glands, minute axillary flowers, and high-elevation habitat. These plants resemble some species of *Pilea* (Urticaceae) and *Hydrocotyle* (Apiaceae). The small flowers are probably difficult to see and may account for the paucity of collections.

### Euphorbia Linnaeus

REFERENCE—R. Oudejans, World Catalogue of Species Names Published in the Tribe Euphorbiae (Euphorbiaceae) with Their Geographical Distribution. Oudejans, Utrecht, 444 pp. 1990.

Herbs, shrubs, or trees, monoecious (rarely dioecious), with milky white sap (often caustic), glabrous or with simple hairs, with succulent green stems in some species; stipules absent or present, often reduced or gland-like, modified as spines in some succulents. **Leaves** alternate, opposite or whorled (sometimes on the same plant), early caducous in some succulent species, simple, usually petiolate, entire or rarely lobed or serrate, glabrous or puberulent, venation usually pinnate (veins not sheathed by chlorenchyma). **Inflorescences** terminal or axillary, made up of 1 to many flower-like cyathia in fasciculate to cymose or panicle arrangements, often subtended by opposite reduced leaves, glabrous or puberulent, opposite bracts subtending or adnate to the cyathium or absent. **Cyathia** (singular: cyathium) flower-like structures with a campanulate to obconic or tubular cup with usually 5 lobes on its distal edge, 4–5 (1, 2) nectar glands alternating with the lobes, the glands with or without broad thin petaloid appendages, bisexual or ♂; ♂ flowers usually in 4–5 reduced cymules opposite the lobes within the cyathium, the cymules with or without subtending bracteoles; cyathium with a single central (“terminal”) ♀ flower. **Male flowers** reduced to solitary naked stamens in congested cymules of 1–5 stamens within the cyathium, each stamen representing a single ♂ flower and borne on a slender stipe (= pedicel, appearing as the base of an articulated filament), a reduced calyx rarely present at the apex of the stipe; anther often with 2 divergent subglobose thecae; pistillode absent. **Female flowers** solitary within the cyathium, sessile or stipitate (pedicellate), perianth usually absent (rarely with 3 rudimentary sepals or a minute calyx cup at the apex of the stipe), stipe (pedicel) often elongating in fruit; ovary 3-locular

(rarely 2, 4, or 5), ovules 1/locule, styles 3 (2, 4, 5), free or united near the base, usually bifid distally. **Fruits** capsules (schizocarps, rarely drupaceous) with 3 (rarely 2, 4, or 5) 2-valved cocci, often dehiscing explosively, columella usually persisting; seeds ovoid to terete, with a longitudinal adaxial raphe, surface smooth or pitted to tuberculate, with or without a caruncle, embryo straight, cotyledons flat.

*Euphorbia* is one of the largest genera of plants, with more than 1,000 species, and is extremely diverse vegetatively. It is found in all but the coldest climates, with greatest diversity in the tropics and subtropics. The genus is especially speciose in dryer regions; it is poorly represented in lowland rain forest formations. The shrubby and tree-like species are all tropical or subtropical. The cactus-like succulent species are native to the African region and extending to Arabia and India, with a few in South America. The latex is often strongly caustic, and the plants are often free of herbivory. The cyathium is a unique flower-like structure, apparently evolved by the fusion of bracts subtending an inflorescence of 4 or 5 reduced ♂ cymules and a terminal ♀ flower. Note that *Chamaesyce* species have the same cyathial structure and are considered species of *Euphorbia* subgenus *Chamaesyce* by many taxonomists.

Key to the Species of *Euphorbia*

- 1a. Plants cultivated for ornament or used to make hedges and fences; not known to be naturalized in Costa Rica ..... 2
- 1b. Plants growing wild in natural vegetation or as weeds in cultivated land (hedgerow plants in *E. hoffmanniana*) ..... 7
  - 2a. Stems with longitudinal ranks of sharp paired spines, distal stems quickly becoming > 1 cm thick ..... 3
  - 2b. Stems lacking longitudinal ranks of sharp spines, distal stems usually < 1 cm thick ... 4
    - 3a. Spines 8–18 mm long, stems hard and woody; inflorescences with peduncles 3–7 cm long; cyathia with 2 adnate petal-like bracteoles usually red or pink in color ..... *E. splendens*
    - 3b. Spines 1–4 mm long, stems succulent; inflorescences subsessile; cyathia subtended by free bracteoles, not brightly colored ..... *E. neriifolia*
  - 4a. Inflorescences subtended by colorful (red, pink, white) leaves 5–22 cm long; small shrubs .... *E. pulcherrima*
  - 4b. Inflorescences not subtended by such large or colorful leaves; shrubs and small trees .. 5
  - 5a. Plants leafless or with caducous leaves, stems mostly vertical, terete and green; many-branched shrubs and trees ..... *E. tirucalli*
  - 5b. Plants with colorful leaves, stems spreading and vertical, not terete and green ..... 6
  - 6a. Inflorescences with narrow white bracteoles to 15 mm long; leaves elliptic to oblong, 0.7–3 cm wide, pale greenish or greenish white ..... *E. leucocephala*

- 6b. Inflorescence with linear green to purple bracteoles to 3 mm long; leaves ovate-triangular to suborbicular, 3–9 cm wide, green to dark purple or reddish ..... *E. cotinifolia*
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**Euphorbia colletioides** Benth., Bot. voy. Sulph. 163. 1846. *Aklema colletioides* (Benth.) Millsp., Publ. Field Columb. Mus., Bot. Ser. 2: 416. 1916. Figure 30.

**Shrubs** or small treelets 1–2(–3) m tall, branches sometimes clambering, nodes somewhat thickened and articulate, leafy stems 1–3 mm thick, glabrous, terete, internodes 2–5 cm long, becoming very dark; stipules absent, transverse or round glands 1–1.7 mm wide often present below or between the leaf bases. **Leaves** 2–3/node, petioles 5–9 mm long, 0.4–0.9 mm wide, glabrous or sparsely and minutely puberulent with whitish hairs ca. 0.2 mm long; **leaf blades** 22–45 mm long, 8–23 mm wide, oblong to elliptic-oblong or narrowly ovate-oblong, bluntly obtuse to rounded at the apex, margin entire, obtuse to acute at the base, drying chartaceous, glabrous (minutely puberulent in early stages), 2° veins 5–11/side. **Inflorescences** terminal or axillary, often borne at leafless nodes, 5–10 mm long, dense fascicles of short cymes, peduncles 1–5 mm long, bracts ca. 1 mm long, caducous. **Cyathia** 2–3 mm long, 1.5–2 mm wide, obconic to campanulate, sparsely to densely minutely whitish puberulent externally with minute (0.1–0.2 mm) whitish hairs, glands with petaloid lobes 1 × 1.3 mm; anthers 0.7 mm wide with opposed thecae; stipe 4–6 mm long, ca. 0.3 mm thick, styles 1 mm long. **Fruits** ca. 4 mm long, ca. 4.7 mm wide, sparsely and minutely puberulent; seeds 3.2–3.3 long, 2.1–2.3 mm diam., oblong with truncated base, surface wrinkled-rugulose with irregular pits and depressions.

Plants of rocky terrain in seasonally very dry deciduous forest formations, 0–200 m elevation (to 800 m in Nicaragua). Probably flowering primarily at the end of the wet season (December–February). In Costa Rica, this species is known only from near the Pacific coast in Sta. Rosa National Park. The species occurs in Mexico, Nicaragua, and northwestern Costa Rica.

*Euphorbia colletioides* is recognized by its small opposite or whorled leaves on stems that become dark and smooth, small dense mostly axillary inflorescences, and seeds with unusual surface.

**Euphorbia cotinifolia** L., Sp. Pl. 453. 1753. Figure 30.

**Shrubs** or small trees 2–6(–10) m tall, with a rounded crown, sap very caustic, leafy stems 0.4–6 mm thick, glabrous or with thin whitish hairs ca. 0.2 mm long, terete, nodes thickened; stipules poorly developed. **Leaves** usually 3 (2) at each node, petioles 2–6(–9) cm long, 0.3–1 mm thick, glabrous; **leaf blades** (2)–4–9(–11) cm long, (1.5–)2.5–7(–9) cm wide, broadly ovate-triangular to ovate-suborbicular or broadly elliptic, apex bluntly obtuse to rounded, margins entire, base rounded to truncate, drying membranaceous to thinly chartaceous, dark grayish green to deep purple, glabrous or sparsely puberulent beneath, 2° veins 8–12/side. **Inflorescences** terminal or axillary, 1–4 cm long or becoming large com-

pound cymose leafy panicles to 30 cm long with 2- or 3-branched nodes, minutely puberulent. **Cyathia** ca. 2 mm long, 2–4 mm diam. distally, sparsely puberulent on the exterior, glands 0.3–1 mm long, ca. 1.3 mm wide, petaloid extensions 0.5–1.5 mm long, 1–2 mm wide, white; stamens red, anthers ca. 0.7 mm wide, thecae rounded and divergent; styles ca. 1.2 mm long, thick. **Fruits** ca. 4 mm long, 4–5 mm wide, oblong-rounded and 3-lobed, surface glabrous or minutely puberulent, columella 3–3.5 mm long, widened distally; seeds 2.5–3 mm long, ca. 1.7 mm diam., surface wrinkled or pitted.

*Euphorbia cotinifolia* is recognized by the rounded dark red to purple leaves on long thin petioles. While frequently seen in gardens and hedgerows, this species is not known to be naturalized in Costa Rica. It is grown primarily in evergreen and partly deciduous areas (0–1400 m) and is deciduous in the dry season. The sap is extremely caustic (Standley & Steyermark, 1949, p. 97). The plant is called *barrabás* in southern Central America; Pittier cites *horla* as the Terraba name.

**Euphorbia cyathophora** Murray, Comm. Götting. 7: 81. 1786. *Poinsettia cyathophora* (Murray) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. *E. heterophylla* var. *cyathophora* (Murray) Boiss. in DC., Prodr. 15 (2): 72. 1862.

**Herbs**, annual or perennial, stems erect or spreading to 0.5(–1.5) m high, green and somewhat glaucous. **Leaves** at first alternate but becoming opposite distally, petioles 5–15 mm long; **leaf blades** 5–10 cm long, 1–3 cm wide, pandurate to ovate, lanceolate or sublinear, apex acute, margin entire or with large teeth, base gradually narrowed to the petiole, glabrous or with short (0.3 mm) hairs, 2° veins 6–10/side. **Inflorescences** usually terminal, 1–2 cm long, to 3 cm wide, cymose and congested or of solitary cyathia, closely subtended by leaves usually reddish near the base or throughout, cyathia on peduncles ca. 3 mm long. **Cyathia** 2–3 mm long, narrowly campanulate, externally glabrous or short-puberulent, the solitary gland transversely oblong (elliptic-oblong) ca. 1.4 mm wide and strongly bilabiate. **Fruits** ca. 4 × 5 mm; seeds to 3 mm long, ellipsoid and truncated at the base, rounded or slightly angular in cross-section, surface tuberculate.

Weedy plants of open sunny sites, 0–1000 m elevation. Rarely collected in Costa Rica (Meseta Central: *Grayum* 3921 MO, flowering and fruiting in August). The species ranges from the southern United States to northern South America.

*Euphorbia cyathophora* is recognized by its herbaceous habit, alternate leaves on lower stems, small congested inflorescences closely subtended by foliage leaves marked with red and the solitary oblong glands. This species is closely related to *E.*

*heterophylla*; both species are members of subgenus *Poinsettia* and are currently being studied by M. Mayfield (TEX).

**Euphorbia dwyeri** Burch, Ann. Missouri Bot. Gard. 54: 182, f. 1. 1967.

*Herbs* or subshrubs 0.5–1.5 m tall, leafy stems 0.7–5 mm thick, glabrous, terete; stipules reduced or represented by a small prominence 0.4 mm wide. *Leaves* alternate on lower stems and often opposite at distal nodes, petioles 14–40(–60) mm long, 0.2–0.9 mm wide, glabrous; *leaf blades* 2–6 cm long, 1–3.5 cm wide, ovate-elliptic to ovate-lanceolate or ovate-suborbicular, apex bluntly acute or obtuse, base obtuse to rounded, drying membranaceous or thinly chartaceous, dark greenish above, glabrous or with few minute (0.2 mm) hairs in early stages, 2° veins 6–10/side. *Inflorescences* terminal or pseudoaxillary, 1–2.5 cm long, of 1–7 cyathia in cymes, glabrous except for narrow bracts with puberulent whitish apices, to 1 mm long, caducous, peduncles of the cyathia to 5 mm long. *Cyathia* ca. 2.5 mm long, 2–4 mm wide, glabrous in the lower half but with a distal rim of minute whitish hairs, glands 4, 0.7–2 mm wide; ovary borne on stipes becoming 5 mm long. *Fruits* 4–4.5 mm long, 4–6 mm wide, oblong-rounded, glabrous, smooth, columella ca. 4 mm long; seeds 2.5–3 mm long, ca. 2 mm diam., ovoid-oblong, smooth, caruncle not developed.

Plants of montane forest formations, 1600–1800 m elevation. Flowering in December–January; fruiting in January and March. This species is known only from Cerro Horqueta, Chiriquí, Panama.

*Euphorbia dwyeri* is recognized by its short weak-stemmed habit, restricted montane habitat, small thin rounded leaves, and small cyathia with four glands. The plants resemble *E. segoviensis*.

**Euphorbia elata** Brandeg., Univ. Calif. Publ. Bot. 6: 55. 1914. *E. valerii* Standl., J. Wash. Acad. Sci. 17: 11. 1927.

Few-branched *shrubs* or treelets 1–5 m tall, leafy stems 4–10 mm thick, glabrous; stipules 2–4 mm long, 1–3 mm wide, at first deltoid, becoming thick and rounded. *Leaves* alternate, petioles 1.5–7 cm long, 1.2–5 mm wide, with lateral adaxial margins, glabrous; *leaf blades* 16–48 cm long, 5–13 cm wide, narrowly oblanceolate to narrowly obovate-oblong or linear-oblanceolate, apex bluntly acute to obtuse and slightly emarginate with gland tip, margin entire (sometimes undulate in life), base cuneate and decurrent on the petiole, drying stiffly chartaceous to subcoriaceous, pale yellowish green beneath in life, 2° veins thin and obscure, 15–30/side, arising at right angles from the midvein. *Inflorescences* terminal, solitary, 14–50 cm long, open-cymose with few (2–6) dichotomous nodes, glabrous, peduncles 8–32 cm long, 3–7 cm thick, primary branches 2–15 cm long, distal bracts 5–6 mm long, 2–3 mm broad at the base or the

distal cyathia at first enclosed in opposite caducous obovate-spatulate imbricate bracts 8–9 mm long, 5–6 mm wide, deciduous. *Cyathia* 8–10 mm long, 5–8 mm wide at apex, campanulate with a narrowed base, reddish, externally glabrous, with 5 distal perianth-like lobes 1.5–3 mm long, with rounded usually sessile-appressed glands 2–3 mm diam., internal bracts erose to fimbriate distally; anthers ca. 1.5 mm long, 0.5 mm wide; style column 2–3.5 mm long, style branches 2 mm long. *Fruits* 9–12 mm long, 11–14 mm wide, oblong, 3-lobed in cross-section, smooth, borne on a short (1–2 mm) stipe, columella 8–10 mm long; seeds 5–6.7 mm long, 4.5–6 mm diam., becoming invaginated when dried.

Plants of evergreen forest formations, 10–1500 m elevation. In Costa Rica, the species ranges along the Pacific slope from the northwestern volcanoes to the Osa Peninsula. (Rarely collected on the Caribbean slope and with differing morphology; see below.) Probably flowering and fruiting throughout the year. The species ranges from Veracruz, Mexico, to the Amazon basin.

*Euphorbia elata* is recognized by its woody few-branched habit, very long narrowly oblanceolate and entire leaves, long terminal inflorescences with opposite branching, and reddish cyathia with rounded flat appressed glands. As in other plants with very long narrow leaves, the main stems have few or no lateral branches. Three collections from the Caribbean slope (280–600 m elevation) are unusual in having emarginate leaf apices, longer inflorescences, shorter floral bracts (4–5 mm), and unisexual cyathia (*Herrera 2266* and *Schatz & Grayum 719 & 720*; the latter two were described as dioecious). The relationships of this species are discussed in Webster and Huft (1988, p. 1138).

**Euphorbia graminea** Jacq., Sel. Stirp. Amer. 151. 1763, and Obs. Bot. 2: 5, pl. 31. 1767. *E. picta* Jacq., Coll. 3: 178. 1790. *Adenopetalum boerhaaviifolium* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1860: 47. 1860. *A. discolor* Klotzsch & Garcke, loc. cit. 49. 1860. *A. hoffmanni* Klotzsch & Garcke, loc. cit. 47. 1860. *A. irasuense* Klotzsch & Garcke, loc. cit. 50. 1860. *A. pubescens* Klotzsch & Garcke, loc. cit. 49. 1860. *A. subsinuatum* Klotzsch & Garcke, loc. cit. 48. 1860. *E. graminea* var. *subsinuata* (Klotzsch & Garcke) Boiss. in DC., Prodr. 15, 2: 54. 1862. Figure 29.

*Herbs* 0.3–1.2 m tall, erect or decumbent, often with many distal branches, leafy nodes 0.5–4 mm thick, internodes 2–10 cm long, glabrous or sparsely puberulent with thin whitish hairs 0.1–0.2 mm long; stipules reduced or gland-like. *Leaves* alternate at lower nodes and opposite at distal nodes, petioles 5–50 mm long, 0.4–1.4



mm thick, glabrous or with few thin hairs, sulcate above; **leaf blades** (1.5–)2–7 cm long, (0.8–)1–5 cm wide, broadly ovate, ovate-elliptic to ovate-triangular or narrowly elliptic-oblong at distal nodes (rarely linear in southern Central America), apex acute to obtuse, margin entire, base broadly obtuse to truncate in larger leaves and acute in distal leaves, drying membranaceous or thinly chartaceous, grayish green, glabrous or with few to many thin hairs 0.1–0.4 mm long, 2° veins 4–8/side. **Inflorescences** terminal or pseudoaxillary, 0.5–1.5 cm long with dichotomous branching, with 1–7 (15) flowers in open cymes, glabrous, peduncles 6–80 mm long, distal nodes subtended by spatulate bracts or reduced leaves 0.5–8 mm long. **Cyathia** 1–3 mm long, campanulate cup ca. 1–2 mm long, glands 2–4, petaloid appendages to 0.8 mm long, 0.5 mm wide; ovary borne on a stipe ca. 1 mm long (to 2 mm in fruit), ovary 0.7–1.3 mm long, glabrous, style branches 0.5–0.8 mm long, deeply bifid. **Fruits** 2–2.5 mm long, 2.5–3.5 mm wide, the 3 lobes rounded or angular in cross-section, columella 1.4–2 mm long; seeds 1.5–2 mm long, 1–1.4 mm diam., surface with large (0.2–0.4 mm) angular pits forming a reticulum of irregular rows, brown to gray.

Weedy plants of open sunny sites in evergreen to deciduous formations, 5–1600 m elevation. Probably flowering and fruiting throughout the year in evergreen areas. This species ranges from southern Mexico to coastal Peru.

*Euphorbia graminea* is recognized by its herbaceous habit with many distal branches, longer internodes, larger alternate proximal leaves, smaller narrower distal leaves, and distinctly pitted seeds. The leaves near the inflorescences are often much narrower than those below. These plants are very variable in all parts of their range, appearing to belong to a single polymorphic species. (Klotzsch and Garcke synonyms cited above follow Standley, 1937; they were based on Costa Rican collections but we have not seen the types.) See the discussion by McVaugh in Contr. Univ. Michigan Herb. 19: 220–227, 1993.

***Euphorbia heterophylla* L., Sp. Pl. 453. 1753.**

*Poinsettia heterophylla* (L.) Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 253. 1859. *E. geniculata* Ortega, Hort. Mat. Dec. 18, 1797. *E. morisoniana* Klotzsch in Seemann, Bot. voy. Herald 100. 1853. Figure 29.

Erect herbs to 0.7(–1) m high, with a central taproot, stems usually with few distal branches, leafy stems 1.5–4 mm thick, glabrous or with few multicellular hairs 0.3–1.5 mm long near the nodes; stipules 0.3 × 0.5 mm, obscure. **Leaves** very variable in form on different plants, alternate but opposite below the inflorescences, petioles 6–33(–55) mm long, 0.8–1.5 mm thick, glabrous or with few multicellular hairs, sulcate above; **leaf blades** 2–11 cm long, 1.4–7 cm wide, ovate-elliptic to obovate or narrowly elliptic (rarely linear), often panduriform with

2 broad lobes on the lateral sides separated by rounded sinuses, apex acute, the distal lobes more obtuse than the proximal, margins entire or dentate, base cuneate and decurrent on the petiole, drying membranaceous to chartaceous, glabrous or with simple hairs to 1 mm long, with minute scabrous hairs along the edge, 2° veins 6–12/side. **Inflorescences** terminal, 1–2 cm long, to 3 cm wide, closely subtended by leaves (sometimes with basal whitish markings), cymes fasciculate and crowded, peduncles of the cyathia to 6 mm long, yellowish. **Cyathia** with narrowly campanulate cup 2.5–3 mm long, ca. 2 mm diam., glabrous externally, gland solitary (2), stalked with rounded apex ca. 0.8 mm diam.; anthers ca. 0.7 mm wide; ovary ca. 2 × 2 mm, stipitate, styles ca. 1.3 mm long. **Fruits** 3.5–4 mm long, 4–6 mm wide, 3-lobed, smooth, glabrous, columella 2.8–3 mm long; seeds 2.5–2.9 mm long, 1.9–2.2 mm diam., ovoid-oblong with truncated base and narrowed apex, surface minutely irregularly tuberculate.

Common weedy plants of open sunny sites in both evergreen and deciduous areas (but rarely collected in Guanacaste), 0–2000 m elevation (to 3000 m in the Andes). Flowering and fruiting throughout the year but restricted to the wet season in deciduous areas. The species ranges from Arizona, Mexico, and the West Indies to Peru.

*Euphorbia heterophylla* is recognized by the erect herbaceous habit, alternate leaves on proximal stems, and small inflorescences closely subtended by opposite leaves that usually have white markings at their base. The leaves are very variable in form on different plants. Panduriform leaves with two major lobes on each side separated by a rounded sinus are distinctive, but they may be absent in many collections. This species is closely related to *E. cyathophora*; both are part of subgenus *Poinsettia*, currently being studied by M. Mayfield (TEX).

***Euphorbia hoffmanniana* (Klotzsch & Garcke)**

Boiss. in DC., Prodr. 15 (2): 99. 1862. *Euphorbiastrum hoffmannianum* Klotzsch & Garcke, Monatsb. Deutsch. Akad. Wiss. Berl. 252. 1859. Figure 30.

**Shrubs** or small trees 1–3(–5) m tall, leafy stems 1–4(–6) mm thick, glabrous or with few thin hairs, terete; stipules reduced to short (0.2 mm) ridges 0.3–0.7 mm wide. **Leaves** alternate, petioles 6–40 mm long, 0.3–1.3 mm wide, with thin lateral margins or slightly sulcate, glabrous; **leaf blades** 2–7 cm long, 0.8–3.5 cm wide, ovate-elliptic to ovate or elliptic (obovate), bluntly acute or obtuse at the apex, margin entire, obtuse to cuneate at the base and decurrent on the petiole, drying membranaceous or thinly chartaceous and yellowish, glabrous, 2° veins 8–14/side, loop-connected near the margin but often obscure. **Inflorescences** of solitary axillary flower-like cyathia, 4–10 mm long (rarely with ca. 3 cyathia on leafless axillary stems to 25 mm long), sometimes terminal and racemose by loss of distal leaves on stems to



25 cm long, peduncles 1.5–5 mm long with 1–3 alternate bracts 1–2 mm long, cyathium enclosed by a condensed spiral of appressed imbricate obovate bracts 2–3 mm long, to 2 mm wide, apex broadly rounded or truncated. **Cyathia** with obconic involucre ca. 2 mm long, often hidden within the bracts, glands 5, 0.7–1.2 mm wide, yellow-green to orange in life, petaloid appendages absent; anthers ca. 0.3 mm long, 0.4 mm wide; ovary ca. 1 mm long, styles 0.5–0.7 mm long, bifid at the tips. **Fruits** ca. 4 × 5 mm, surfaces smooth and glabrous; seeds 2.2–2.5 mm long, 1.7–1.8 mm diam., rounded-oblong, with minute tubercles in longitudinal rows or scattered, grayish.

Plants of partly deciduous and evergreen forest formations, 1100–1900(–2300?) m elevation. Flowering in January–March; fruiting in March–June. The species is endemic to Costa Rica and only known from the Pacific slope of the Cordillera de Tilarán (below Monteverde), the Meseta Central, and near Cartago-Paraiso.

*Euphorbia hoffmanniana* is recognized by its inflorescences of solitary axillary flower-like cyathia (appearing racemose when the leaves are deciduous) and the thin-walled involucre enclosed by imbricate bracteoles. The plants are glabrous, and the small alternate thin deciduous leaves are often absent when the plant is in flower. While this species is a small tree in seasonally dry areas, it is often found as a shrub in hedgerows at higher elevations. It is called *lechilla*.

***Euphorbia leucocephala*** Lotsy, Bot. Gaz. 20: 350, pl. 24. 1895. Figure 30.

**Shrubs** or small treelets 1–5 m tall, crown usually much branched and rounded, leafy stems 0.8–4 mm thick, sparsely puberulent with thin hairs 0.2–0.4 mm long at the nodes, internodes glabrescent, terete, nodes thickened; stipules 0.3–0.7 mm long or not apparent, becoming gland-like. **Leaves** 2, 4, or 6 at each node, petioles 6–24(–38) mm long, 0.2–0.7 mm thick, sparsely puberulent near base and apex; **leaf blades** 2.7–5(–6) cm long, 0.7–2(–3) cm wide, elliptic-oblong to oblong or narrowly oblong, apex bluntly obtuse to rounded, slightly emarginate with a small (0.2–0.4 mm) mucronate tip, margin entire, base obtuse, drying thinly to stiffly chartaceous, pale grayish green or with reddish markings, glabrous above, with few to many thin white hairs beneath, 2° veins 11–14/side, weakly loop-connected near the margin. **Inflorescences** terminal or axillary to distal leaves, 2–10 cm long, cymose-paniculate with opposing branches, major nodes subtended by small leaves or leaf-like bracts ca. 10 × 3 mm, distal flowers subtended by petiolate obovate-spatulate bracts 6–11 mm long, white and conspicuous in life. **Cyathia** 3–4 mm long, campanulate, borne on peduncles 1–2 mm long, with lobes ca. 1.5 mm long, puberulent externally beneath the glands, the triangular petaloid appendages 1–3 mm long, 0.5–1 mm wide at the base. **Fruits** 5–6 mm long, 4.5–5.5 mm diam.,

subglobose and shallowly 3-lobed; seeds apparently not produced in Costa Rica and Panama.

*Euphorbia leucocephala* is used extensively in Costa Rica as a garden ornamental. Its dense whitish crown and limited height make it an attractive little tree for gardens. The pale green leaves and many white bracts can make the entire crown appear whitish. This species is called *pasquite* in Honduras, where it is used for making funeral wreaths. It grows naturally in deciduous woodlands from Mexico to Nicaragua.

***Euphorbia neriifolia*** L., Sp. Pl. 451. 1753.

**Shrubs** 1–2 m tall, with cactus-like distal succulent green stems 8–30 mm thick, glabrous, usually with 3–5 angles and often leafless, stipular spines 1–4 mm long, paired from a rounded base 2–5 mm, wide, dark. **Leaves** alternate, deciduous or caducous, petioles 5–20 mm long but poorly differentiated from the lamina, glabrous; **leaf blades** 6–20 cm long, 2–4.5 cm wide, linear-oblong to narrowly obovate-oblong, apex rounded or bluntly obtuse, margin entire, base cuneate and long-attenuate, succulent in life, drying grayish green, glabrous, 2° veins usually obscure. **Inflorescences** axillary, ca. 10 mm long, sessile or subsessile with usually 3 cyathia, peduncles 0–6 mm long, to 1.5 mm thick, bracteoles ca. 4 mm long, to 5 mm wide, opposite and imbricate, at first enclosing the cyathium. **Cyathia** ca. 4 mm long, ca. 6 mm wide, glands 5, to 4 mm wide, lacking petaloid appendages, bracteoles of the ♂ cymules fimbriate distally.

*Euphorbia neriifolia* is often planted in hedges and along walls in warmer dry climates. The thick cactus-like (usually leafless) spiny stems and short axillary inflorescences are distinctive. These plants are commonly planted in the Pacific lowlands of northern Central America, but we have not seen material from Costa Rica. Compare *E. splendens*.

***Euphorbia ocymoidea*** L. Sp. Pl. 453. 1753. *E. astroites* Fish. & Mey., Index Sem. Hort. Petrop. 10: 44. 1845. Figure 6.

**Herbs** 15–60 cm tall, erect annuals, usually with many 1° and 2° branches, leafy stems 0.2–1 mm thick, puberulent with minute (ca. 0.2 mm) simple and gland-tipped hairs, main stems usually glabrate; stipules not developed. **Leaves** alternate, but usually opposite at distal nodes, petioles 1–16(–30) mm long, 0.1–0.3 mm wide, glabrous or sparsely and minutely puberulent; **leaf blades** 4–15(–20) mm long, 4–13(–18) mm wide, broadly ovate-orbicular to ovate-rhombic or ovate-triangular, apex obtuse or rounded, margin entire, base truncate-rounded to broadly obtuse, drying membranaceous, with thin whitish hairs 0.2–0.4 mm long on both surfaces, 2° veins 2–5/side, thin and often obscure. **Inflorescences** terminal or axillary at distal nodes, 2–3 mm long, of solitary cyathia on peduncles 0.5–1.7 mm long, slender, **Cyathia**

with involucre ca. 0.4 mm long, 0.3–0.4 mm wide, narrowly campanulate to obconic, green, with thin whitish hairs ca. 0.2 mm long externally, glands usually 4 (5), with 3- or 4-parted or dentate appendages, styles 0.3–0.4 mm long, bifid to base. **Fruits** ca. 1.5 mm long, 1.6–1.8 mm wide, with thin hairs to 0.3 mm long (rarely glabrous), borne on pedicels 1.4–2(–4) mm long, columella 1–1.1 mm long; seeds 0.9–1.1 long, 0.7–0.8 mm diam., ovoid-ellipsoid, with deep pits in well-defined depressions ca. 0.2 mm wide and tuberculate on the rims between the depressions.

Plants of seasonally dry deciduous or partly deciduous formations, 50–100 m elevation (to 1900 m in Guatemala). Flowering in September–December; fruiting in December–January. The species ranges from western Mexico along the Pacific slope to Panama.

*Euphorbia ocymoides* is recognized by its seasonal habitats, the slender herbaceous stems, lateral branches with gland-tipped hairs and small (ca. 5 × 5 mm) leaf blades, and unusual pitted-tuberculate seeds. *Euphorbia astroites* with glandular hairs and *E. ocymoides* with eglandular hairs are now interpreted to be the same species, with material from southern Central America often having glandular hairs.

***Euphorbia oerstediana* (Klotzsch & Garcke) Boiss.** in DC., Prodr. 15 (2): 59. 1862. *Poinsettia oerstedianum* Klotzsch & Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 253. 1859. Figure 29.

**Herbs** to 1.5 m tall, erect and usually branched from the base with few distal branches, stems not completely articulate, glabrous or with thin hairs to 1 mm long; stipules not developed. **Leaves** alternate or opposite at distal nodes, petiole 5–20 mm long, glabrous; **leaf blades** 2–8 cm long, 1–3.6 cm wide, broadly ovate to ovate-lanceolate or oblong, apex acute to obtuse, margin entire, base obtuse to rounded, drying membranaceous or thinly chartaceous, glabrous or puberulent beneath, 2° veins 6–9/side. **Inflorescences** terminal, 1–3 cm long, cymose with dichotomous branching, glabrous or puberulent, bracts ca. 1 mm long, narrow, peduncles of cyathia 1.5–6 mm long. **Cyathia** 2–2.5 mm long, 0.8–1.5 mm diam., with usually 2 large (ca. 1.3 × 0.8 mm) distal rounded lobes (= glands?), 1–3 smaller also often present; ovary covered with a minute pale grayish puberulent. **Fruits** ca. 4 mm long, 3–4 mm wide, ovoid, surface minutely puberulent; seeds 2.5–2.9 mm long, 1.7–2 mm wide, surface with distinctive rounded papilla-like projections 0.2–0.3 mm diam., minutely carunculate, grayish.

Weedy plants of open sunny sites, 0–1500 m elevation (to 2500 m in Guatemala). Probably flowering primarily in the wet season (June–November). This species is rarely collected in south-

ern Central America. The species ranges from Mexico and the West Indies to northern South America.

*Euphorbia oerstediana* is recognized by its herbaceous habit, ovate-lanceolate leaves, small inflorescences, and seeds covered with unusual papillae.

***Euphorbia peplus* L., Sp. Pl. 456. 1753.**

**Herbs** 10–40 cm tall, leafy stems 0.3–3(–4) mm thick, glabrous, terete, green; stipules absent. **Leaves** alternate near the base, 2–3 at distal nodes, sessile or with slender petioles to 5 mm long; **leaf blades** 6–25 mm long, 4–15 mm wide, broadly elliptic to rounded-ovate or obovate, apex rounded to obtuse, margin entire, base acute to cuneate or broadly obtuse (subtruncate), bright green in life, drying membranaceous, glabrous, 2° veins 2–4/side, strongly ascending. **Inflorescences** terminal or axillary, umbellate, of solitary cyathia subtended by foliage leaves slightly smaller (4–8 mm) than those of distal stems, peduncles 0.6–1 mm long, glabrous. **Cyathia** with involucre 0.8–1.1 mm long, 0.5–1 mm wide at apex, obconic, glabrous externally, glands 4, crescent-shaped and with prolonged linear lobes 0.5–0.7 mm long (petaloid appendages absent). **Fruits** 1.8–2.2 mm long, 2.2–2.5 mm wide, ovoid-oblong, smooth and glabrous, borne on pedicels 1.3–3 mm long, columella 1.3–1.4 mm long; seeds 1–1.5 mm long, 0.8–1 mm wide, oblong with a prominent caruncle, pale grayish with pronounced oblong depressions 0.5–0.7 mm long on the adaxial surfaces, with rounded dark depressions in longitudinal rows of 3–4 on the abaxial surfaces.

*Euphorbia peplus* is originally from Eurasia but has now become a weed in many moist temperate and tropical montane habitats. In Central America, it is known only from elevations of 1500–2500 m in Guatemala and Chiriquí, Panama. The small stature and many thin rounded leaves in dense leafy, closely clustered, distal branchlets give the living plants a distinctive appearance.

***Euphorbia pulcherrima* Willd. ex Klotzsch, Allg. Gartenz. 2: 27. 1834. *Poinsettia pulcherrima* Graham, Edinb. New Phil. J. 20: 421. 1836. *E. erithrophylla* Bertol., Fl. Guat. 419. 1840.**

**Shrubs** or small treelets 0.5–3(–5) m tall, erect, usually with few lateral branches, leafy stems 3–9 mm thick, glabrous, terete; stipules represented by gland-like ridges ca. 1.5 mm wide. **Leaves** alternate (opposite or whorled beneath the inflorescence), petioles 2–8 cm long, 0.8–2 mm thick, glabrous or very sparsely puberulent, narrowly sulcate above; **leaf blades** 8–22 cm long, 4–12 cm wide, narrower (1–2 cm wide) beneath the inflorescences, elliptic to ovate-oblong or pandurate (with 2 prominent tooth-like lobes separated by a rounded sinus on each side), apex acute, margins entire, base obtuse to acute, with thin crooked hairs ca. 0.4 mm long, 2° veins 8–15/



side. **Inflorescences** terminal or leaf-opposed, cymose-corymbose, subtended by brilliant red (pink, white) oblanceolate leaves. **Cyathia** 6–7 mm long, urceolate, glabrous externally, distal margin fimbriate, gland solitary, 4–5 mm wide, transversely oblong, yellow.

*Euphorbia pulcherrima* is widely used as an ornamental shrub in parks and gardens. Its flowering time (November–December) and strongly contrasting bracts (brilliant red) and foliage (deep green) have made it a Christmastime favorite (*flor de pascua*, *pastora*, “poinsettia”). It is thought to be native to southern Mexico and northern Guatemala; see Standley and Steyermark (1949, pp. 111–112). It is not known to grow wild in southern Central America.

**Euphorbia schlechtendalii** Boiss., Cent. Euphorb. 18. 1860. *E. friedrichsthalii* Boiss. in DC., Prodr. 15 (2): 61. 1862. *E. adinophylla* J. D. Smith, Bot. Gaz. 47: 261. 1909. Figure 30.

**Shrubs** or small trees 0.5–5 m tall, trunks to 20 cm diam. at the base, older stems with thin peeling bark, leafy stems 0.4–5 mm thick, often reddish, glabrous or with few minute (0.1 mm) whitish hairs at the nodes, nodes slightly thickened; stipules ca. 0.3 mm long, obscure, becoming gland-like. **Leaves** opposite or verticillate with 4, 6, or 8 leaves/node, petioles 5–35 mm long, 0.2–0.6 mm thick, glabrous or minutely (0.05 mm) puberulent at the base; **leaf blades** 13–40 mm long, 8–18 mm wide, ovate-elliptic to ovate-suborbicular or elliptic, apex rounded to bluntly obtuse or bluntly acute, margin entire, base cuneate to obtuse, drying membranaceous or thin-chartaceous, glabrous above and below, 2° veins 3–8/side. **Inflorescences** terminal or axillary to distal nodes, 1–2 cm long, cymose and often hemispheric with 2–8 cyathia/node, peduncles 2–6 mm long, bracts usually sessile and ca. 0.7 mm long or sometimes leaf-like and narrowly oblanceolate to 4 mm long, 0.8–2 mm wide, glabrous, yellowish. **Cyathia** 2–3 mm long, 3–4 mm wide at the apex, campanulate, glabrous externally; glands 5, 1–2 mm wide; filaments ca. 1.2 mm long, anthers ca. 0.3 mm long, 0.5–0.7 mm wide, thecae subglobose; ovary ca. 1.5 × 1.5 mm, borne on a stipe 1–4 mm long, styles united at the base, 1–2 mm long, bifid for most of their length. **Fruits** 4–5 mm long, 5–7 mm wide, conspicuously 3-lobed, surfaces smooth, columella ca. 3 mm long; mature seeds not seen, apparently 3 mm long and with a wrinkled surface.

Plants of seasonally deciduous forest formations, 10–1300 m elevation (to 1500 m in Mexico). Flowering in November–April, often when leafless. The species ranges from northeastern Mexico to Guatemala and along the Pacific slope to northern Costa Rica.

*Euphorbia schlechtendalii* is recognized by its woody habit, general lack of pubescence, verticillate leaves with thin rounded blades on slender

petioles, and small inflorescences often in bloom when the leaves have fallen. The stems are quite brittle and are easily broken at the nodes. The species has been used as the source of a purgative in Mexico. An unusual leafless collection, with condensed inflorescences and cyathia minutely puberulent on the exterior, from Sta. Rosa National Park is tentatively placed here (*Wilbur 25084 DUKE*).

**Euphorbia segoviensis** (Klotz. & Garcke) Boiss. in DC., Prodr. 15 (2): 58. 1862. *Leptopus segoviensis* Klotz. & Garcke, Abh. Königl. Akad. Wiss. Berlin 46. 1859. *E. chiapensis* Brandegee, Univ. Calif. Publ. Bot. 6: 54. 1914. Figure 29.

Herbaceous **subshrubs** 1–2 m tall, leafy stems 0.4–3.5 mm thick, terete, glabrous or with thin curved hairs ca. 0.5 mm long; stipules minute or absent. **Leaves** alternate (opposite or ternate at branching nodes), petioles 5–35 mm long, 0.2–0.4 mm wide, glabrous; **leaf blades** 1.5–4(–6) cm long, 1–2(–3) mm wide, ovate-elliptic to narrowly ovate-oblong or oblong, apex bluntly obtuse to rounded, minutely mucronate, margin entire, base obtuse, drying membranaceous, venation pinnate, 2° veins 4–7/side, central 2° veins arising at angles of 70–90°. **Inflorescences** terminal or axillary, slender leafy cymes, often umbellate at ends of branchlets, glabrous or minutely puberulent with short (0.4 mm) thin hairs. **Cyathia** with involucre 1–1.5 mm long, minutely puberulent with thin hairs, glands 5, transversely oblong, with 2 linear or narrowly oblong lobes 0.5–0.8 mm long, ca. 0.2 mm wide; styles bifid. **Fruits** ca. 2.5 mm diameter, glabrous; seeds ca. 1.4 mm long, with conspicuous pits, gray.

Rarely collected plants of partly deciduous and evergreen forest formations, 400–1200 m elevation. The species ranges from central Mexico to the Meseta Central of Costa Rica.

*Euphorbia segoviensis* is recognized by its slender herbaceous habit, thin leaves on long slender petioles, and 10 narrow corolla-like lobes (two per gland) on the margin of the cyathium. The name is based on an Oersted collection from Nicaragua. We thank V. W. Steinman, a student at RSA, for suggesting the use of this name in place of *E. chiapensis*; he also points out that it is very unlikely that *E. chiapensis* is a synonym of *E. zieroides* Boiss. (cf. Croizat in J. Arnold Arb. 26: 194, 1945).

**Euphorbia splendens** Hook., Bot. Mag. pl. 2902. 1829. *E. milii* Des Moul. var. *splendens* (Hook.) Ursch & Leandri, Mem. Inst. Scient. Madagascar, ser. B, 5: 144. 1955.

Scandent **shrubs** or subshrubs with woody stems to 1.5 m long, few-branched, stems 4–12 mm thick, gla-



brous, with sharp paired straight stipular spines 4–18 mm long, ca. 1 mm thick near the base, grayish, separated by short (3–5 mm) internodes. **Leaves** alternate, present only at the distal nodes, petioles not differentiated from the cuneate lamina base; **leaf blades** 1.3–7(–12) cm long, 0.6–2(–4) cm wide, narrowly obovate to oblong-spatulate or elliptic, apex with a short (0.7 mm) slender tip, margin entire, base cuneate and long-decurrent, glabrous. **Inflorescences** axillary to distal leaves, 5–14 cm long, with few distant dichotomies, peduncles to 7 cm long, 1–2 mm thick, glabrous, cyathia borne on peduncles ca. 6 mm long. **Cyathia** subtended and closely enveloped by 2 opposite petaloid bracteoles 8–12 mm long, bracteoles expanded distally and broadly rounded, 6–12 mm wide, red, pink, or yellowish, the cyathium with 5 glands around the periphery of cup.

*Euphorbia splendens* (also called *E. milii*) is a popular ornamental species recognized by its many close sharp straight spines, few distal leaves, open dichotomous inflorescences and “flowers” (cyathia) with two large rounded colorful “petals” (appressed bracts). The spiny scandent stems make this a favorite cultivar for garden walls and edgings. The species originated in Madagascar and is now cultivated throughout the tropics and subtropics. We follow Carter (Ann. Missouri Bot. Gard. 81: 368, 1994) in using the widely known name. It is called *corona de Cristo* and “crown of thorns.”

***Euphorbia tirucalli* L., Sp. Pl. 452. 1753.**

Shrubs or small trees 1.5–10 m tall, dioecious, trunks to 15 cm thick, crown with many erect branches, branchlets 1.5–4 mm diam., green, striate on drying, lenticellate. **Leaves** usually absent, alternate and quickly caducous, less than 2 cm long, the smaller and larger branches photosynthetic. **Inflorescences** terminal or axillary to distal leafless nodes, 5–15 mm long, to 15 mm wide, sessile dense fascicles with short (1–2 mm) scarious bracts and subsessile crowded cyathia. **Cyathia** ca. 2 × 1.5 mm, obconic, minutely puberulent externally, with perianth-like distal lobes, glands 5, 1–1.5 mm wide; ovary 2.5–3 mm long, 1.5–2 mm diam., densely puberulent externally, becoming exserted on a thick (0.7 mm) stipe to 4 mm long, style branches less than 1 mm long, recurved.

*Euphorbia tirucalli* is often planted in parks and at the edges of gardens; it is sometimes used in hedgerows. The dense crown of many cylindrical (mostly vertical) green branches and leafless branchlets gives it an unusual appearance. Common names are *pizarrín* and “Indian finger tree.” The species is probably native to eastern Africa and India.

***Euphorbia xalapensis* H.B.K., Nov. gen. sp. 2: 61. 1817. *Poinsettia xalapensis* (H.B.K.) Klotzsch**

& Garcke, Monatsber. Königl. Preuss. Akad. Wiss. Berlin 1859: 253. 1859. *E. enalla* Brandeg., Univ. Calif. Publ. Bot. 6: 54. 1914. *E. amphimalaca* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 313. 1929. Figure 29.

**Herbs** 20–60(–100) cm high, erect or sprawling, leafy stems 0.4–2.5 mm thick, puberulent with thin multicellular hairs 0.4–1 mm long, internodes 2–10 cm long; stipules 0.1–0.2 mm wide, gland-like. **Leaves** alternate at lower nodes and 3/node distally, petioles 5–45 mm long, 0.3–1 mm thick, flattened above, puberulent, often variable in length on the same stem; **leaf blades** 1.5–6(–9) cm long, 1–3(–3.8) cm wide, ovate-elliptic to broadly ovate or narrowly elliptic-oblong, apex acute or obtuse, margin entire, base obtuse to truncate and rounded, drying grayish green and paler beneath, with crooked multicellular hairs 0.5–1.3 mm long above, more densely pubescent beneath, 2° veins 3–6/side. **Inflorescences** terminal, often paired (lateral to an undeveloped apex), 3–12 mm long, with 1–5 cyathia, becoming 1-sided by abortion, subtended by reduced opposite narrow leaves ca. 7 mm long, peduncles 2–5 mm long. **Cyathia** 0.7–1.5 mm long, 0.5–1.3 mm wide, obconic to campanulate, with conspicuous whitish hairs, glands 5, petaloid appendages 0.2–2 mm long, 0.7–1.2 mm wide; ovary ca. 1 mm long, styles 0.7–1.2 mm long, free and deeply bifid, stipe becoming 1.3–2.8 mm long in fruit. **Fruits** 2–2.3 mm long, 2.3–2.6 mm wide, sparsely and minutely puberulent, ovoid with rounded or truncate base, columella 1–1.6 mm long; seeds 1.1–1.7 mm long, 0.8–1.2 mm diam., with deep angular pits 0.2–0.3 mm wide in longitudinal ranks.

Plants of open sites in deciduous or partly deciduous formations, (200–)1300–2100 m elevation. Probably flowering and fruiting primarily in the late wet season, November–December. Interestingly, nearly all the collections from Honduras and southern Central America come from between 1700 and 2000 m elevation. The species ranges from western Mexico to Honduras, with a few collections from Costa Rica and western Panama.

*Euphorbia xalapensis* is recognized by its short herbaceous habit with long internodes, multicellular hairs (× 50), small inflorescences lacking colorful bracts, five involucre glands, and seeds with conspicuous pits. Material of this species has often been mistakenly referred to the rarely collected *E. oerstediana* (q.v.).

**Garcia Vahl**

Shrubs or small trees, monoecious, hairs simple; stipules absent. **Leaves** alternate, simple, petioles thickened (geniculate) at base and apex, without glands, blades entire, pinnately veined. **Inflorescences** terminal, usually bisexual, apparently reduced cymes, with 1–2 ♀ flowers

and several ♂ flowers at a node, pedicels slender (♂) or thick (♀). **Male flowers** globose in bud, pubescent, calyx rupturing into 2–3 valvate parts, persisting, corolla of 6–13 petals longer than the sepals, disk intrastaminal and dissected; stamens 30–100 on a convex receptacle, filaments free; pistillode absent. **Female flowers** with calyx rupturing into 2–3 parts, caducous, corolla similar to ♂, disk deeply lobed, staminodes absent; ovary 3-locular, ovules 1/locule, style column short, style branches thick, reflexed and bifid. **Fruits** capsular, breaking explosively into 3 2-valved cocci; seeds subglobose, ecarunculate, endosperm copious.

A Neotropical genus of two species, *G. nutans* (see below) and *G. parviflora* Lundell of eastern Mexico. The geniculate petioles, relatively large flowers, many stamens, and large fruits help to distinguish this genus. Lundell has claimed that the genus is a potential source of superior quick-drying oil (see Wrightia 1: 1–12, 1945).

**Garcia nutans** Vahl in Rohr, Skr. Naturhist. Selsk. Kjobenhaven 2: 217, t. 9. 1792. Figure 21.

Shrubs or small trees 2–6 (9) m tall, trunks to 50 cm diam., leafy stems 1.5–4.5 mm thick, sparsely to densely hirtellous with yellowish hairs to 0.3 mm long, quickly glabrescent and becoming dark reddish brown. **Leaves** with petioles 1.6–6 cm long, 1–2.8 mm thick, with long (4–8 mm) thickened areas at both apex and base (drying dark), glabrescent; **leaf blades** 7–20 cm long, 2.5–9 cm wide, oblong to elliptic-oblong or oblong-obovate, apex caudate-acuminate with a tip 3–12 mm long, gradually narrowed to a cuneate or rounded base, margin entire and thickened, drying stiffly chartaceous to subcoriaceous, with thin hairs or glabrescent beneath, 2° veins 4–10/side. **Inflorescences** terminal, of 1–5 flowers on 1–3 peduncles, densely velutinous/sericeous, ♀ pedicels to 30 mm long, 0.8–2 mm thick (to 3 mm thick in fruit). **Male flowers** ca. 3 cm wide, sepals 5–8 mm long, 1.5–3 mm wide, densely yellowish pubescent on both surfaces, petals usually 7–10, pink to purple, 4–12 mm long, 1.5–3 mm wide, with thin whitish hairs 1–1.3 mm long, glabrous within near the base; stamens many from a pilose base, filaments 3–5 mm long, 0.1–0.2 mm wide, red, anthers 0.6–0.9 mm long, yellow. **Female flowers** with perianth similar to ♂ but caducous, the annular disk 0.5–1 mm high, deeply lobed; ovary 3.5–4 mm long, 4–5 mm diam., stylar column 1.5–2 mm long, 1.3–2 mm thick, both ovary and style column densely velutinous, style branches 1.5 mm long, equally broad, red drying black, glabrous. **Fruits** 2–2.5 cm long, 3–4 cm broad, densely yellowish velutinous, wall of the cocci 0.8–1.5 mm thick, columella 13–19 mm long, 10–13 mm broad distally, T-shaped; **seeds** 14–17 mm long, 12–15 mm wide, 12–14 mm thick, subglobose with a slight longi-

tudinal ridge from apex to base, surface smooth and pale grayish brown.

Plants of the understory in seasonally very dry or partly deciduous forests of northwestern Costa Rica, 10–200 m elevation (to 500 m in Nicaragua). Probably flowering in all months; fruiting in October–May. The species ranges from central Mexico to northwestern Costa Rica, with a few collections known from Panama and Colombia where the species may have been introduced.

*Garcia nutans* is recognized by its deciduous forest habitat, the oblong leaves with distinctive petioles thickened at both apex and base, the few large terminal flowers with ca. 10 reddish petals, many stamens with red filaments, and larger fruit. The plants have been used medicinally in Colombia as a purgative, with a single seed said to be sufficient to induce vomiting.

### Gymnanthes Swartz

**Shrubs** or trees, monoecious (rarely dioecious), latex scant and not milky, glabrous or with simple hairs; stipules paired at the leaf base, stipule-like bud-scales sometimes present. **Leaves** alternate, simple, lacking glands at the apex of the petioles, pinnately veined, margins glandular or eglandular and entire or crenulate, often coriaceous. **Inflorescences** axillary, bisexual (rarely unisexual), solitary, spiciform, with 1 (–few) proximal sessile to long-pedicellate ♀ flowers and many distal ♂ cymules, bracts mostly biglandular, ♂ flowers pedicellate. **Male flowers** naked or with 1–2 rudimentary calyx lobes, petals and disk absent; stamens often 3 (2–6), filaments free or variously connate near base, anthers dehiscing longitudinally and extrorse; pistillode absent. **Female flowers** usually with 3 small sepals or naked (petals and disk absent); ovary sessile or stipitate, 3-locular, ovules 1/locule; styles free or basally connate, style branches simple. **Fruits** capsular, breaking into 3 2-valved cocci, the columella persistent; seeds subglobose, caruncle present, testa smooth, endosperm copious.

A Neotropical genus with ca. 15 species, ranging from the southern United States and Mexico into Central America. The small flowers with nearly obsolete perianth are distinctive. One species is frequently collected in Costa Rica, but an additional species is likely to be found in the Caribbean lowlands. Webster includes *Actinostemon* within *Gymnanthes* (Webster, 1994b).

### Key to the Species of *Gymnanthes*

- 1a. Ovary minutely puberulent, fruits puberulent to subglabrous; seeds 6–9 mm long; leaf blade 6–16 cm long, chartaceous to subcoriaceous ..... *G. riparia*



- 1b. Ovary and fruits glabrous; seeds ca. 5 mm long; leaf blades to 11 cm long, usually subcoriaceous [not known from southern Central America] ..... *G. lucida*

*Gymnanthes lucida* Sw., Prodr. 96. 1788. *Ateramnus lucidus* (Sw.) Rothm., Feddes Rept. 53: 5. 1944. Figure 26.

Small to medium-sized trees 5–20 m tall, monoecious, leafy stems 1–4 mm thick, glabrous, drying grayish; stipules ca. 1 mm long, caducous, scars 0.3–0.7 mm wide. Leaves articulated at base, petioles 3–11 mm long, 0.6–1.2 mm thick, glabrous, slightly thickened or bent below the blade; leaf blades 2.5–11 cm long, 1–4 cm wide, narrowly obovate to oblanceolate-spatulate, narrowly elliptic-oblong, bluntly acute to rounded at the apex, margin subentire with minute (0.2 mm) gland-tipped teeth, base acute to cuneate and slightly rounded at the petiole, drying subcoriaceous and grayish green, glabrous above and below, often with dark glandular areas 0.4 mm diam. near the base, 2° veins 5–10/side, loop-connected near the margin, major and minor venation prominent above and below. Inflorescences axillary or terminal, bisexual or ♀, usually cone-like in early stages (ca. 4 × 2 mm) and covered with spirals of appressed imbricate scales ca. 0.8 mm wide, sessile or on a short (2 mm) peduncle, 7–28 mm long and ca. 3 mm wide at anthesis, axis glabrous. Male flowers subtended by small (1 mm) bracts, borne on pedicels ca. 0.6 mm long, without a definite perianth; filaments partly united into a column, anthers 3–5, ca. 0.4 mm long, oblong. Female flowers solitary from the base of the raceme or 1–2 in the axils of leaves, peduncles 12–30 mm long (base-to-bracteoles), ca. 0.6 mm thick, glabrous, pedicel (stipe) 5–7 mm long, continuous with the base of the ovary, ovary ca. 3 × 2.7 mm, style column ca. 1 mm long, style branches 1.5 mm long, recurved. Fruits 7–8 mm long, 9–10 mm wide, oblate and 3-lobed, rounded, glabrous; seeds 4.5–5.2 mm long, 4–4.5 mm wide, 3.5–3.8 mm thick, smooth and rounded, dark brown, caruncle 1.5 mm wide, broadly rounded.

Plants of evergreen or partly deciduous forest formations, 0–400 m elevation. Probably flowering and fruiting in the wet season, May–November. The species is found in the southern United States, Mexico, Belize, Guatemala, Cuba, and the Bahamas.

*Gymnanthes lucida* is recognized by its lack of pubescence, small stiff often obovate leaves, cone-like inflorescence buds, glabrous naked ♀ flowers, and solitary fruit. The hard heavy wood has strongly contrasting color in sapwood and heartwood; it has been used for veneers and other uses. While not known from southern Central America, this species may be expected along the Caribbean.

*Gymnanthes riparia* (Schldl.) Klotzch, Arch. Naturgesch. 7: 182. 1841. *Excoecaria riparia* Schldl. Linnaea 7: 386. 1832. *G. guatemalensis* Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 122. 1944. Figures 12 and 26.

Trees 4–20 m tall, trunks 10–49 cm diam., leafy stems 1.5–5 mm thick, glabrous or with a few minute appressed hairs in early stages; stipules 0.7–1.8 mm long, 0.5–0.7 mm broad at the base, triangular, minutely appressed-puberulent, caducous. Leaves with petioles 4–16 mm long, 1–2.7 mm thick, glabrous or with a few minute appressed hairs in early stages, glands absent; leaf blades 6–16(–20) cm long, 2–6.5(–8) cm broad, obovate to elliptic-obovate, oblong-obovate, or narrowly elliptic-oblong, apex acute to caudate-acuminate with narrowed tip 4–14 mm long, serrulate to subentire with 12–16 glands along the margin, base cuneate (obtus) and slightly decurrent on the petiole, drying stiffly chartaceous to subcoriaceous, yellowish to grayish green, glabrous, 2° veins 5–8(–11)/side, distal veins loop-connected. Inflorescences 1–3/axil, bisexual or unisexual, ♂ to 5 cm long, spiciform with 1–3 flowers in glomerules 0.3–4 mm distant along the slender (0.4 mm) puberulent rachis, bracts 0.3–1 mm long, pedicels 1–2 mm long, puberulent; ♀ inflorescences ca. 2 cm long, to 4.5 cm in fruit, pedicels 3–6 mm long, 0.4 mm thick. Male flowers usually of 3 (2–5) stamens subtended by a small (0.3–0.5 mm) bract-like perianth part at the apex of the pedicel, filaments 0.5–1.8 mm long, 0.1 mm thick, glabrous, anthers 0.2–0.3 mm long, 0.3–0.4 mm wide. Female flowers with 0–2 bract-like perianth parts (ca. 0.3 mm long) at the apex of the pedicel, ovary 1.5–2.3 mm long, 1.3–2 mm diam., ovoid, with dense minute (0.1 mm) velutinous hairs, style branches 3, 1.5–3.5 mm long, 0.3 mm thick, smooth, persisting. Fruits 9–12 mm long, 13–16 mm broad, rounded-oblong, 3-lobed, greenish, minutely pubescent, cocci with outer walls 1–2 mm thick, columella 8–10 mm long, 4–6 mm broad in the distal half; seeds 5–8 mm long, 5–6 mm wide, 4.5–5.5 mm thick, rounded-oblong, caruncle slightly (0.5–1 mm) elevated.

Plants of wet evergreen forests on the Caribbean slope, northernmost cloud forests, and Osa Peninsula, (50–)200–1100 m elevation. Flowering in May–November; fruiting in July–December. The species ranges from Veracruz, Mexico, to southern Costa Rica.

*Gymnanthes riparia* is recognized by the stiff glabrous leaves glandular along the edge, short slender inflorescences, naked flowers with minute vestigial perianth parts, rounded fruits with persisting stigmas, and thick-walled cocci. A collection from Puerto Viejo de Limón (Hartshorn 1853) has smaller subglabrous fruits and larger (12–20 cm) thin-textured leaf blades with 10–12 pairs of 2° veins; we place it here in a broader concept of *G. riparia*. Expanding the concept of *G. riparia* to include a greater range of variation is a natural consequence of better sampling over a wide range of habitats. Unfortunately, this may make the differentiation of other species, such as *G. actinotemoides* Müll. Arg. and *G. dressleri* Webster of Panama, more difficult.



## Hevea Aublet

REFERENCES—R. E. Schultes, The history of taxonomic studies in *Hevea*. Bot. Rev. 36: 197–276. 1970. A brief taxonomic view of the genus *Hevea*. Malaysian Rubber Research & Development Board Monograph 14: 1–57. 1990.

**Trees**, monoecious, glabrous or puberulent, with whitish latex; stipules lateral. **Leaves** alternate, trifoliate, long-petiolate, with a gland at apex beneath petiolule attachment; **leaflet blades** with entire margins, usually thin-chartaceous, glabrous or puberulent, pinnately veined. **Inflorescences** axillary, solitary at each node, paniculate, usually puberulent, flowers in distal cymes with a terminal ♀ flower and lateral ♂ flowers, bracts small. **Male flowers** globose to ovoid in bud, calyx cupulate with 5 valvate teeth or lobes, petals absent, disk of 5 small free or connate glands; stamens united into a column, with 1 or 2 whorls of 5 sessile anthers on the staminal column, column extending beyond the anthers; pistillode present at apex of column. **Female flowers** usually larger than the male, calyx 5-lobed, petals and staminodes absent, disk dissected or absent; ovary 3-locular, ovules 1/locule, styles short or stigmas sessile. **Fruits** large capsules, 3-lobed in cross-section, oblate to ovoid in outline, exocarp slightly carnose, endocarp woody; seeds large, mottled, ecarunculate, cotyledons thick.

A genus of 9–10 species, originally found only in the Amazon basin. The following important economic species is grown in Central America.

**Hevea brasiliensis** (Willd. ex Adr. Juss.) Müll. Arg., Linnaea 34: 204. 1865. *Siphonia brasiliensis* Willd. ex Adr. Juss., Euphorb. Gen., t. 12. 1824.

REFERENCE—R. E. Schultes, Studies in the genus *Hevea* III. Notes on infraspecific variants of *Hevea brasiliensis* (Euphorbiaceae). Econ. Bot. 41: 125–147. 1987.

**Trees** up to 30 m tall, leafy stems 4–12 mm thick, glabrous or with short (0.4 mm) thin hairs; stipules ca. 2 mm long, triangular-subulate, thick. **Leaves** quite variable in size, petioles 9–38 cm long, 2–5 mm thick, often becoming constricted at base and apex when dried, apical gland 1.3–4 mm wide, reniform, petiolules 8–18 mm long, 1–2.2 mm thick; **leaflet blades** 8–22 cm long, 3–10 cm wide, elliptic to obovate, apex acuminate, base acute, 2° veins 11–20/side, 3° veins subparallel, 4° veins partly parallel. **Inflorescences** 8–20 cm long, racemose panicles with alternate lateral branches 5–45 mm long, minutely whitish puberulent; ♂ flower buds 3–4 mm long; distal ♀ flowers 4–8 mm long, calyx lobes 2–4 mm long; ovary ca. 1.7 mm long, ovoid with sessile stigmas, densely sericeous. **Fruits** ca. 4 cm long, 4–6 cm wide, oblate and 3-lobed, smooth and glabrous, on peduncles ca. 12 cm long.

*Hevea brasiliensis* (Para rubber, *cancho de Brazil*) is the world's most important source of natural rubber. Malaysia, Indonesia, and Brazil are the major areas of production. For good production, the trees require warm (24–32°C) temperatures and an even annual rainfall of over 1900–2500 mm/year with a short dry period (Cobley & Steele, 1976). In Central America, the species is found in gardens and plantings at 20–1100 m elevation, with flowering primarily in February–March. The long-petiolate trifoliate leaves, milky latex, fragrant yellowish flowers with a basally united calyx (no corolla), unusual androecium, and large three-lobed fruits distinguish these plants.

## Hieronyma

See *Hyeronima*.

## Hippomane Linnaeus

Small or medium-sized **trees**, monoecious, glabrous throughout, with caustic whitish latex; stipules paired at the leaf bases, small, caducous. **Leaves** alternate, simple, petioles with a glandular area at the apex, lamina ovate, subtire with slightly raised gland-tipped serrations, pinnately veined. **Inflorescences** terminal, solitary, spicate, bisexual with 1(–2) subsessile ♀ flowers at the base, ♂ flowers 8–many in alternate sessile glomerules along the thick rachis, bracts biglandular at the base; ♀ flowers subsessile. **Male flowers** with a small calyx usually separating into 2 (3) parts, petals and disk absent; stamens 2, exerted, united at the base to form a short column, anthers dehiscing longitudinally and extrorse; pistillode absent. **Female flowers** with 2–3 imbricate sepals, petals, disk and staminodes absent; ovary with 6–10 locules, styles short united at base, with 2 recurved simple branches, ovules 1/locule. **Fruits** drupaceous, globose to oblate, smooth, green becoming yellowish, indehiscent; seeds ovoid-compressed, ecarunculate.

A genus of three species, one widespread and the others endemic in the West Indies. Our species is quite distinctive, but this genus may be difficult to separate from its close relatives; see the discussion under *Sapium*.

**Hippomane mancinella** L., Sp. Pl. 1191. 1753. Figure 32.

Small or medium-sized **trees**, 2–8(–18) m tall, often with a spreading rounded crown, bark scaly grayish to reddish brown, leafy stems 2–5 mm thick, glabrous, longitudinally striate, lenticles 0.4–1.2 mm diam., rounded with an annular rim and central brownish area, sap whitish, caustic; stipules 1–2 mm long, 1 mm broad at the base, triangular, brown, caducous. **Leaves** evergreen, petioles 12–48 mm long, 0.4–1 mm thick, glabrous, with a

darkened flat or elevated-crateriform gland at the apex; **leaf blades** 3–8 cm long, 2–5 cm broad, ovate to ovate-oblong or ovate-orbicular, apex obtuse to acute with a minute gland tip, margin with 8–20 teeth/side, ca. 0.3 mm high and gland-tipped, drying stiffly chartaceous, lustrous above, glabrous, 2° veins 7–9/side. **Inflorescences** 2.8–7 cm long, 3–6 mm wide distally, glabrous, peduncles 0.5–2 mm long, rachis 1–1.5 mm thick, greenish; ♀ flowers on pedicels 0.3–1 mm long, ♂ glomerules 2–3 mm broad with 3–12 congested subsessile flowers, yellow, distal bracts ca. 0.7 × 1.5 mm with 2 lateral flat glands basally. **Male flowers** ca. 2 mm long, calyx 0.5–0.9 mm long, breaking irregularly into 2 or 3 parts, filaments slightly exerted, anthers ca. 0.5 mm long. **Female flowers** with a cupulate calyx ca. 2 mm high, irregularly dehiscent, ovary ca. 2 mm long and at first enclosed by the calyx, style column 0.2–0.5 mm long, style branches recurved. **Fruits** 1.4–2 cm long, 1.8–2.5 cm wide (dried), oblate to subglobose, resembling a small green apple; seeds ca. 6 mm long.

Found only along ocean shores and swamps on both the Caribbean and Pacific coasts, 0–20 m elevation. This species sometimes forms monospecific stands at the edge of the beach. While frequent along the Pacific, this species has not been collected along Costa Rica's Caribbean shore. Flowering in March–April and September–December; fruiting in August–September and December–May. The species ranges from Florida, the Bahamas, West Indies, and Mexico to Colombia.

*Hippomane mancinella* is recognized by its seaside habitat, toxic sap, small lustrous ovate leaves with finely crenulate-serrate gland-tipped margins, spicate bisexual inflorescences, and fruits resembling small apples. The sap is highly caustic and will cause severe inflammation of sensitive skin or tissues; it may cause blindness. Smoke from the burning wood can be dangerous to the eyes. The tree is common at Playas de Manuel Antonio where visitors are warned of the tree's toxicity. It is called *manzanillo de playa*, *manzanita de playa*, and "manchineel."

## Hura Linnaeus

Small to very large trees, monoecious, larger trunks to over 1 m diam., bark with hard broad-based sharp-tipped conical spines, sap clear; **stipules** paired, imbricate and covering the shoot apex (but not leaving a scar around the stem), caducous. **Leaves** alternate, simple, petioles long and with 2 rounded glands at the apex, blades usually broadly ovate and subcordate, margins bluntly serrate, glabrous or pubescent beneath, pinnately veined. **Inflorescences** unisexual, glabrous, ♂ terminal, long-pedunculate, spicate with a thick-fleshy rachis with crowded sessile flowers in a narrow cone-like arrangement, bracts membranaceous; ♀ flowers solitary in the axils of distal leaves (rarely at the base of ♂ spikes), ped-

icels thick. **Male flowers** at first enclosed by a thin bract and rupturing at anthesis, calyx united to form a membranaceous denticulate cup, petals, disk and pistillode absent; stamens many and united, filaments absent, anthers sessile, verticillate and laterally compressed in 2–10 superposed whorls on a thick central column truncated distally, dehiscing longitudinally and extrorse. **Female flowers** glabrous, calyx cupulate and truncate, corolla, staminodes and disk absent; ovary 5–20-locular, ovules 1/locule, styles united into a long thick column, style branches as many as the locules and separate beyond the truncated webbed radiating lobes. **Fruits** capsular, large and oblate with a depressed apex, with as many lobes as locules, cocci dehiscing explosively, columella persisting; **seeds** laterally compressed, ecarunculate, cotyledons flat, rounded.

A tropical American genus of two species. The cone-like male inflorescences, with flowers having superposed verticels of anthers on a thick axis, are among the most unusual in angiosperms. *Hura polyandra* Baill. differs from our species in having longer male flowers with 5–10 verticels of anthers on the thick staminal column. This makes the ♂ inflorescences look very different from those of *H. crepitans*. In addition, the leaves of *H. polyandra* appear to have more prominent serrations. Both species were stated to occur in Costa Rica (Standley, 1937; Webster & Burch, 1967), but we believe that these reports were based on misdeterminations; we have seen no material of *H. polyandra* from south of Honduras.

## Hura crepitans L., Sp. Pl. 1008. 1753. Figure 32.

**Trees** 5–35 m tall, larger trunks to over 1.5 m diam., with hard conical broad-based spines 1–3 cm high on a pale gray bark, leafy internodes 3–12 mm thick, glabrous; **stipules** 6–12 mm long, 1–4 mm broad at the base, at first enclosing the shoot apex, usually glabrous or minutely (0.1 mm) ciliolate along the margin, drying reddish brown, caducous. **Leaves** deciduous, petioles 4–15(–20) cm long, 1.3–3 mm thick, often drying with a contracted area 6–10 mm long near the base, with 2 raised dark-drying glandular areas at the apex adaxially; **leaf blades** 5–18(–25) cm long, 4–14(–17) cm broad, ovate to broadly ovate or ovate-orbicular (ovate-elliptic), apex acuminate with a tip 5–20 mm long, margin serrate or rounded-crenate with 9–20 gland-tipped teeth on each side, base rounded and cordate to subcordate, drying chartaceous and greenish, glabrous above, with thin straight or crooked hairs 0.5–1.5 mm long on the major and minor veins beneath, venation pinnate with 7–20 2° veins/side, 3° veins subparallel. **Male inflorescences** with peduncles 2–16 cm long, 2–3 mm thick, spikes 2–5 cm long, 12–18 mm thick, conical at first with spirals of 60–80 congested bract-enclosed flower buds, red; ♂ flowers 3–5 mm long, 2–3 mm diam., borne on thick short (1–2 mm) pedicels, cylindrical-obovoid with a thick central axis, truncated and 1–2 mm wide distally, calyx



ca. 1 mm long; stamens in 2 (rarely 3) verticels of yellow anthers with ca. 12–15 anthers/whorl, anthers of smaller whorl 0.3–0.6 mm long, the larger whorl 0.5–1.2 mm long. **Female inflorescences** of solitary dark red flowers, pedicels 1–5 cm long, 3–4 mm thick, becoming woody in fruit; ♀ flowers 4–6 cm long, glabrous, calyx tube 3–8 mm long, entire distally, stylar column 3–5 cm long, 1.3–2 mm thick (larger near base and apex), style branches forming a truncated apex with united radiating tips (parasol-like), free digitate style branches 4–10 mm long. **Fruits** 3–5 cm high, 6–11 cm broad, rounded-oblately depressed in the center around the apex (pumpkin-like), breaking up into ca. 30 woody crescent-shaped segments 2–5 mm thick, columella ca. 3 cm long with broad apex and base; seeds ca. 15/fruit, 1.5–2 cm diam., 5–8 mm thick, lenticular with flattened sides, smooth and pale yellowish.

Trees of both evergreen and deciduous forest formations in both the Caribbean and Pacific lowlands, 0–600 m elevation. Probably flowering throughout the year (mostly October–November in Golfo Dulce [Allen, 1956]; April–December at Barro Colorado Island [Croat, 1978]); fruiting in January–April. The species ranges from Nicaragua to Peru, Brazil, and the West Indies.

*Hura crepitans* is recognized by its large trunks with thick conical spines, long-petiolate broadly ovate-cordate leaves with crenate/serrate margins, large solitary dark red ♀ flowers with little perianth and expanded parasol-like stylar apex, the unique ♂ flowers, and ± 15-seeded fruits. After explosive dehiscence, the fruits produce many C-shaped woody fragments. The sap is inflammatory to sensitive skin; the wood is used for making boxes and inexpensive furniture. The seeds are poisonous but are used in small amounts as a purgative (Allen, 1956; Standley & Steyermark, 1949). These large impressive trees are called *havillo*, *jabillo*, *javillo*, and “sandbox tree.” Pittier (1957) reported the following Indian names: Bribrí: Betshur; Brunka: Tsu-krá; Térraba: Uí (tirub); and Igún.

**Key to the Species of *Hyeronima***

- 1a. Stamens usually 4, pistillode slender and bifid; fruits 3–4 mm long (dried), fruiting mostly in January–June; petioles 2–18 cm long; stipules narrow or broadly rounded, 3–15 mm long; rarely found above 600 m elevation ..... *H. alchorneoides*
- 1b. Stamens usually 5, pistillode stout, not bifid; fruits 4–6 mm long (dried), fruiting mostly in June–January; petioles 0.9–4 cm long; stipules usually absent; 50–2200 m elevation but uncommon below 500 m ..... *H. oblonga*

***Hyeronima alchorneoides*** Allemão, Pl. novas Brasil (icon.) 1848. *Stilaginella laxiflora* Tul., Ann. Sci. Nat. Bot. Ser. 3, 15: 244. 1851. *H. laxiflora*

***Hyeronima* Fr. Allemão**

**REFERENCE**—P. Franco R., The genus *Hyeronima* (Euphorbiaceae) in South America. Bot. Jahrb. Syst. 111: 297–346. 1990.

Trees or shrubs, dioecious, wood hard, surfaces with flat rounded peltate many-rayed hairs, straight hairs also sometimes present; stipules present or absent, deciduous. **Leaves** alternate, petiolate, lacking glands at the apex, margins entire, venation pinnate, usually with peltate and simple hairs. **Inflorescences** axillary, solitary, ♂ usually somewhat larger and with more branches than the ♀, paniculate with alternate 2° branches, 2° branches unbranched and racemose or spicate, bracts small, with peltate hairs, pedicels short. **Male flowers** with cupulate calyx, with 3–6 short imbricate lobes, petals absent, disk cupulate and thick, annular or lobed; stamens 3–6, opposite the calyx lobes and within the disk, filaments free, exerted, anthers with 2 divergent pendulous thecae, dehiscent longitudinally or by pores; pistillode small. **Female flowers** with united calyx, cupulate with 3–6 short teeth, persisting in fruit, petals absent, disk thin, cupulate, entire or lobed, staminodes absent; ovary 2- (3-)locular, ovules 2/locule, styles short, reflexed, slightly bifid. **Fruits** fleshy, indehiscent, usually 1-seeded, small, exocarp thin, endocarp hard; seed without caruncle, endosperm carnose, cotyledons broad flat.

A genus of ca. 20–30 poorly defined Neotropical species. This genus is very closely related to *Antidesma* of the Old World tropics. The flat peltate many-rayed hairs on almost all plant parts, solitary axillary inflorescences with alternate branches that are unbranched, unisexual (dioecious) trees, small cupulate calyx, and fleshy fruits with usually only one seed make this genus distinctive. Some specimens may resemble *Croton*, but that genus usually has unbranched inflorescences and the fruits are not fleshy. We follow recent authors regarding the spelling of this genus, but note that A. Radcliffe-Smith has recently proposed conserving the spelling *Hieronyma* in preference to *Hyeronima* (see Taxon 43: 485–486, 1994).

(Tul.) Müll. Arg., Linnaea 34: 67. 1865. *H. tec-tissima* Standl. & L. O. Wms. (nom. nud.) in Allen, Rain Forests of Golfo Dulce 222, pl. 29.



1956, without latin description. *H. alchorneoides* var. *stipulosa* Franco, Bot. Jahrb. Syst. 111: 321. 1990. Figure 28.

**Trees** to 40 m tall, trunks 20–150 cm diam., with buttresses to 1.3 m high, dioecious, leafy stems 2–15 mm thick, densely covered with peltate appressed hairs 0.1–0.3 mm diam.; stipules 3–15 mm long, ca. 1–2 mm wide and lanceolate or broadly rounded and to 2 cm wide. **Leaves** with petioles 2–9(–18) cm long, 1.2–3.5 mm thick, appressed-pubescent, often sulcate above, often geniculate at the apex; **leaf blades** 8–24(–44) cm long, 5–15(–29) cm wide, broadly elliptic to broadly elliptic-oblong, ovate-oblong, or suborbicular, apex acute to caudate-acuminate, tip 3–20 mm long, margin entire, base obtuse to rounded and subtruncate, drying thinly to stiffly chartaceous and dark above, with scattered flat rounded peltate hairs 0.1–0.2 mm wide, more densely pubescent beneath, thin straight hairs to 1 mm long often present along the midvein beneath, 2° veins 4–11/side, often weakly loop-connected near the margin. **Male inflorescences** 5–15 cm long, open panicle with 4–9 simple racemose branches to 10 cm long, ca. 0.7 mm thick, bracts ca. 0.7 mm long, broad-based, pedicels 0–0.7 mm long, 0.2–0.4 mm thick; ♂ flowers with calyx 1–1.3 mm long, ca. 1.5 mm wide, lobes 4, ca. 0.2 mm long, broadly obtuse, surface covered with minute peltate hairs; stamens usually 4 in Costa Rica (5–6), filaments 1–1.5 mm long, anthers 0.3–0.4 mm wide, appearing to open by pores, disk annular, pistillode 0.7–1 mm long. **Female inflorescences** 4–10 cm long, with 3–9 alternate branches, densely covered with peltate hairs, pedicels 0.5–1 mm long, 0.3–0.5 mm thick; ♀ flowers 1.5–2 mm long, calyx 0.5–0.8 mm long, lobes minute or obscure, ovary ca. 1 mm long, exposed in early stages, glabrous or with few peltate hairs, styles ca. 0.3 mm long, united at the base. **Fruits** 3–4 mm long, 2–4 mm diam. (dried), ovoid or ellipsoid, becoming red, then purple-black, subtended by the persisting calyx ca. 1.5 mm wide; seeds ca. 2 mm long.

Plants of evergreen lowland rain forest formations, 5–700(–900) m elevation. Flowering peaks are in May–July and November–January (Flores, 1993, reference below); fruiting in January–July. The species ranges from southern Mexico to Peru and Brazil.

*Hyeronima alchorneoides* is recognized by its lowland evergreen forest habitats, long petioles and large leaves (on some shoots), flat rounded hairs on leaf surfaces, open panicles with unbranched lateral branches, small unisexual flowers with cupulate calyx, and single-seeded fleshy fruits. The large size of some individuals, their short buttresses, and the hard reddish wood are additional characters. Also, old leaves turn bright red and are scattered through the crown (Allen, 1956). Leaves can vary greatly in size in different collections. Plants having broadly rounded stipules and larger leaves with more 2° veins have been designated

as var. *stipulosa*. The names *nancitón* (Nicaragua), *pilón* (Costa Rica), and *zapatero* (Panama) are commonly used. For a comprehensive summary of names, ecology, morphology, and silviculture of this species, see Pílon, by Eugenia M. Flores, in *Arboles y semillas del Neotropico*, 2: 53–73, 1993.

***Hyeronima oblonga*** (Tul.) Müll. Arg., *Linnaea* 34: 66. 1865, and in DC., *Prodr.* 15 (2): 271. 1866. *Stilaginella oblonga* Tul., *Ann. Sci. Nat. Bot. Ser. 3*, 15: 248. 1851. *S. benthamii* Tul., *Ann. Sci. Nat. Bot. Ser. 3*, 15: 247. 1851. *H. oblonga* var. *benthamii* (Tul.) Muell. Arg. 34: 66. 1865. *H. guatemalensis* J. D. Smith, *Bot. Gaz.* 54: 241. 1912. *H. poasana* Standl., *Field Mus. Nat. Hist., Bot. Ser.* 18: 611. 1937. Figure 28.

**Trees** 4–25 m tall, larger trunks 20–50 cm diam., wood yellowish to reddish brown within, leafy stems 1.4–6 mm thick, densely covered with flat peltate hairs 0.1–0.3 mm diam.; stipules usually absent (rarely to 4 mm long and 1–2 mm wide). **Leaves** with petioles 1–4 cm long, 0.8–1.7 mm thick, densely covered with appressed peltate hairs; **leaf blades** 4–17 cm long, 2–9 cm wide, elliptic to broadly elliptic-oblong or ovate-elliptic, apex short- to long-acuminate (caudate-acuminate), margin entire, base obtuse to slightly rounded, drying grayish green above and brownish beneath, with scattered flat peltate hairs above, sparsely to densely pubescent beneath, the peltate hairs 0.2–0.3 mm diam., midvein often with straight thin hairs to 1 mm long, 2° veins 4–8/side, free or weakly loop-connected near the margin. **Male inflorescences** to 11 cm long, with 1–5 spiciform lateral branches to 9(–11) cm long, 0.5–0.8 mm thick, densely lepidote, pedicels 0.2–1.3 mm long, 0.2–0.6 mm thick; ♂ flowers mostly solitary (2–3), calyx 0.5–1 mm long, 1.2–2 mm wide, cupulate, lobes 5–6, 0.1–0.2 mm long, broadly obtuse; stamens 5 in ours (4–6), filaments 1–2.2 mm long, anthers 0.2 × 0.4 mm, thecae divergent, disk lobed. **Female inflorescences** 2–8 cm long, with 1–7 lateral spiciform branches subtended by oblanceolate bracts 2.5–7 mm long, branches to 5 cm long, ca. 1 mm thick, bracteoles ca. 0.7 mm long, broad-based, pedicels ca. 1 × 0.4 mm; ♀ flowers solitary, calyx 0.4–0.8 mm long, 1–1.5 mm wide, cupulate with 4–5 lobes ca. 0.3 mm long, obtuse; ovary ca. 1 × 0.5 mm, exposed in early stages, surface dark and glabrous, style column 0.2–0.4 mm long, style branches to 0.3 mm long. **Fruits** 4–6 mm long, 3–5 mm diam., ovoid-ellipsoid, fleshy, becoming yellowish, purplish red or dark red, pedicels to 2 mm long.

Plants of evergreen forest formations from (ca. 100–)500–2400 m elevation. Flowering in January–September; fruiting in June–January. This species ranges from Guatemala to Peru and Brazil.

*Hyeronima oblonga* is recognized by its preference for montane habitats, the flat peltate many-rayed hairs on almost all surfaces, small flowers

with cupulate calyx, and fleshy one-seeded fruits. There is considerable diversity in leaf form, density of leaf pubescence, size and branching of the inflorescences, and floral morphology and vesture. This variation appears to be found throughout southern Central America and at all elevations (but low-elevation leaves tend to be larger and thinner). These conclusions are in agreement with those of Franco (cited above), who studied the South America material.

**Jatropha** Linnaeus

REFERENCES—B. Dehgan & G. Webster, Morphology and infrageneric relationships of the genus *Jatropha* (Euphorbiaceae). Univ. Calif. Publ. Bot. 74: 1–73. 1979. B. Deghan, Phylogenetic significance of interspecific hybridization in *Jatropha* (Euphorbiaceae). Syst. Bot. 9: 467–478. 1984.

Trees, shrubs, or perennial herbs with thick rootstocks (annual in *J. gossypifolia*), monoecious or dioecious, hairs simple or glandular, latex clear or colored; stipules present or absent, very variable in form and glandular in some species. Leaves alternate (subopposite when

crowded on lateral shoots), simple, petioles without glands, blades very variable in form, often with palmate lobes (rarely pinnately lobed), margins entire to dentate, often with glands, venation palmate (pinnate), glabrous or puberulent. Inflorescences axillary or terminal, solitary or 2, usually with a prominent peduncle and alternate or dichotomous branches (corymbiform), bracteate, ♀ flowers terminating proximal nodes and fewer than the distal ♂ flowers in bisexual inflorescences, flowers pedicellate and usually in distal cymes. Male flowers with 5 sepals, imbricate in bud, with or without glandular margins, petals 5, free or connate to form a short tube, greenish to white or red, longer than the sepals, disk entire or of 5 segments; stamens usually 8 (6–14) in 2 whorls (5 + 3), anthers dehiscent longitudinally; pistillode small or absent. Female flowers with 5 imbricate sepals, petals as in the ♂ flowers, disk annular or dissected, staminodes absent; ovary with 3 (1–2) locules, glabrous or hirsute, ovules 1/locule, styles free or united, simple or bifid distally. Fruits capsules breaking into 3 (1–2) 2-valved cocci or somewhat fleshy and tardily dehiscent; seed with a usually lobed caruncle, testa crustaceous, smooth, endosperm copious, cotyledons broad.

A genus of ca. 175 species in tropical America, Africa, and south Asia. Neotropical species are usually found in drier vegetation. A few species are popular as ornamentals and some have been used for their medicinal properties.

**Key to the Species of *Jatropha***

- 1a. Leaves peltate with petiole attached 1–3 cm from edge [stipules branched and drying hard; inflorescences bright red; grown as an ornamental but wild in Nicaragua] ..... *J. podagrica*
- 1b. Leaves not peltate, petiole attached to edge of blade ..... 2
- 2a. Leaves deeply palmately lobed, sinuses > 60% of the length of the blade ..... 3
- 2b. Leaves unlobed or with short lateral lobes, sinuses < 30% the length of the blade ..... 4
  - 3a. Leaf lobes 3 or 5, petioles and leaf margins with small (0.3–1.5 mm) stalked glands or gland-tipped hairs; naturalized weeds or planted for ornament ..... *J. gossypifolia*
  - 3b. Leaf lobes 9 or 11, petioles and leaf margins lacking stalked glands or gland-tipped hairs; planted in gardens for ornament ..... *J. multifida*
- 4a. Flowers with dark red petals to 2 cm long; leaves ovate-oblong with pinnate or subpalmate venation; garden trees and shrubs or occasionally naturalized in Central America ..... *J. integrerrima*
- 4b. Flowers with white or yellowish petals < 8 mm long; leaves ovate to 3-lobed with palmate venation; native or naturalized plants in Costa Rica ..... 5
- 5a. Common trees often planted in hedges; petals united only at the base, broadly imbricate; leaves usually glabrous beneath except for the basal vein axils ..... *J. curcas*
- 5b. Rarely collected trees of northwestern Guanacaste; petals united for about 1/3 of their length, only the distal lobes imbricate; leaves usually with thin hirtellous hairs beneath ..... *J. costaricensis*

***Jatropha costaricensis*** Webster & Poveda, Brittonia 30: 265. 1978. Figure 3.

Shrubs or small trees 2–5 m tall, dioecious, trunks to ca. 20 cm diam., latex reddish, leafy stems hirsutulous with brownish hairs ca. 0.3 mm long, glabrescent, terete;

stipules reduced (ca. 0.5 mm) and gland-like. Leaves with petioles (2–)4–9 cm long, 1–1.5 mm thick, without distal glands, hirsutulous; leaf blades (4–)9–18(–21) cm long, (4–)7–18(–21) cm broad, ovate or with 3 shallow obtuse lobes or 3-angled, apex obtuse or acute, margins entire, without glands, base truncate to subcordate (cordate), drying chartaceous, becoming sparsely hirtellous above,



densely hirtellous beneath with thin hairs ca. 0.3 mm long, venation palmate with 3 or 5 (7) major veins. **Male inflorescences** terminal or subterminal, 1 or 2, peduncles 1–8.5 cm long, with several dichotomous hirtellous branches, bracts 0.5–1.5 mm long, lanceolate, entire, hirtellous;  $\delta$  **flowers** on pedicels 0.5–1 mm long, 0.2–0.3 mm thick, hirtellous, articulated at base; calyx lobes 2–3 (4.5) mm long, 0.8–1.5 mm wide, narrowly oblong, obtuse to subacute, entire, greenish, corolla 3–6 mm long, tube ca. 2.5 mm diam., creamy white, glabrous externally, lobes 1–2.5 mm long, disk with 5 segments 0.5–0.9 mm diam.; stamens 10 in 2 whorls of 5, staminal column ca. 2 mm long, filaments 2–3 mm long, anthers 0.9–1.5 mm long, 0.5–0.8 mm wide. **Female inflorescences** a solitary (2) terminal flower, pedicels ca. 1 mm long, to 6 mm in fruit;  $\delta$  **flower** ca. 8 mm long, calyx lobes 5–7 mm long, lanceolate, usually acute, puberulent, corolla tube 4.5–6 mm long, lobes 1.8–4 mm long, disc with 5 large lobes; ovary 2–3 mm long, smooth, 3-ridged, styles ca. 3 mm long, united into a column ca. 1 mm long, distally bifid. **Fruits** 3–3.5 cm diam., columella ca. 2 cm long, narrowly winged; seeds 17–20 mm long, 12–14 mm thick, ellipsoid-globose, caruncle ca. 1.8 mm wide.

Plants of the seasonally very dry deciduous forests near the Pacific shore at 5–50 m elevation. Flowering in June and August; fruiting in August (*Webster & Poveda 22160* MO holotype, CR & DUKE isotypes). The species is known only from Playas del Coco and P.N. Santa Rosa in Guanacaste Province, Costa Rica.

*Jatropha costaricensis* is recognized by its palmately veined ovate or three-lobed leaves hirtellous beneath, short inflorescences, and small flowers. Herbarium material resembles *J. curcas* quite closely, but the latter has glabrous leaves, except for the basal veins beneath. This species and its close relatives are another example of the phyto-geographic link between the dry deciduous vegetation of northwestern Guanacaste and that of similar habitats in Mexico (*Webster & Poveda, 1978*).

***Jatropha curcas* L., Sp. Pl. 1006. 1753. Figure 3.**

**Shrubs** or small trees 1.5–5 (–8) m tall, bark peeling in papery scales, sap white or clear, leafy stems 2–13 mm thick, glabrous or less often minutely (0.2–0.5 mm) puberulent; stipules 0.3 mm high, acicular or gland-like, caducous. **Leaves** with petioles 3–15 cm long, 0.7–2.7 mm thick, usually glabrous except near the base, geniculate or expanded at the base; **leaf blades** 7–25 cm long, 6–21 cm wide, ovate to ovate-triangular, unlobed or palmately 3- (5-, 7-)lobed, lateral lobes 5–35 mm long, apices obtuse to short-acuminate, margin entire or slightly undulate-dentate, base cordate with sinuses 5–22 mm deep, drying chartaceous, glabrous above, minutely (0.3 mm) puberulent along the veins and in the basal vein axils beneath, venation palmate with 3 (5, 7) major veins, 2° veins 2–3/side of midvein. **Inflorescences** 5–18 (–25)

cm long, terminal or axillary, solitary, bisexual or unisexual, peduncles 1.5–10 cm long, 0.8–2 mm thick, glabrous or puberulent, bracts 2–15 mm long, lanceolate, without marginal glands, distal axes puberulent. **Male flowers** on pedicels 1–5 mm long, articulate below flower, puberulent, sepals 2.8–4.5 mm long, 1.3–1.8 mm wide, oblong to obovate, apex rounded, broadly imbricate in bud, petals 5–7.5 mm long, lobes obovate-oblong, tube villous within, disk segments 0.5–1 mm long; stamens 8–10, 3–7 mm long, anthers 1–2.2 mm long, pistillode absent. **Female flowers** on pedicels 5–9 mm long, to 13 mm in fruit, sepal lobes ca. 2.5 mm wide, oblong to lanceolate, apex obtuse to subacute, petals becoming recurved in fruit and 7–9 mm long; ovary ca. 2.5 × 2 mm, glabrous, styler column 0.5 mm long, style branches 1.5–2 mm long. **Fruits** 2.5–3 cm long, 2.2–2.5 cm diam., ovoid, slightly 3-lobed in cross-section, somewhat fleshy; seeds 15–22 mm long, ca. 9 mm diam., dark with minute longitudinal grooves, caruncle 3–4 mm wide, lobed.

Plants of seasonally very dry deciduous forest formations and widely cultivated, 5–800 m elevation (to 1100 m in El Salvador). Flowering and fruiting in May–September. Ranging along the dry Pacific slope in Central America but widely distributed in tropical America.

*Jatropha curcas* is recognized by the ovate or three-lobed leaves with palmate venation and sparse pubescence, the long-peduncled inflorescences, and larger fruit. *Coquillo*, *coquito*, and *tampate* or *tempate* are common names for this species, which is often used for hedges. The Brunka name is Kuubín-uá (Pittier, 1957). The seeds contain an odorless oil useful in paint and soap and as a lubricant; they have been used as emetics or purgatives but are poisonous in large doses.

***Jatropha gossypifolia* L., Sp. Pl. 1006. 1753. Figure 3.**

Herbaceous **subshrubs** or short-lived shrubs 0.5–2.5 m tall, leafy stems 2–7 mm thick, glabrous, terete; stipules 5–12 mm long, simple or with 1–5 filiform gland-tipped segments 0.5–3 mm long, glabrous, persisting. **Leaves** with petioles 1.4–7 (–11) cm long, 0.7–2 mm thick, with simple or branched gland-tipped hairs to 4 mm long, thin hairs ca. 0.5 mm long often present along the adaxial margin; **leaf blades** 5–16 cm long, 3–18 cm wide, deeply 3- to 5-lobed, central lobe 4–12 cm long, 2–5 cm wide at widest part, elliptic to elliptic-obovate, apices acute to acuminate, margin dentate, with regularly spaced stalked glands 0.2–0.9 mm long, base truncate to subcordate, lateral lobes somewhat asymmetric, drying thinly chartaceous, upper surface glabrous or with few thin hairs along the veins, short (0.3 mm) thin hairs along the leaf edge, venation palmate with 3 or 5 major veins. **Inflorescences** terminal, 1–2, 3–12 cm long, peduncles 2–6 cm long, with 1–3 alternate branches, pubescent with straight thin hairs 0.5–1 mm long, bracts 5–8 (–12) mm long, lanceolate, with stalked glands along the edge. **Flowers** with sepals 2–8 mm long, 0.7–1.5 mm wide,



serrate with marginal glands; petals 3–4 mm long, 1.5–3 mm wide, obovate with rounded apex, purple or reddish; ♂ flowers with 8 stamens, filaments 2.2–3 mm long, anthers 0.5–0.7 mm long. **Fruits** ca. 12 mm high, 10–15 mm diam., oblong, 3-sulcate; seeds 7–8 mm long, 4.5–4.7 mm wide, 3–3.5 mm thick, oblong, smooth, caruncle 2.7–3 mm wide.

Plants of open weedy sites or near ocean beaches in both evergreen and deciduous areas (also cultivated in gardens), 0–800 m elevation. Flowering primarily in May–December. The species is probably an introduction in southern Central America and is widespread as a weed throughout the tropics.

*Jatropha gossypifolia* is recognized by its short stature, three- or five-lobed leaves with deep sinuses, unusual stipules with slender gland-tipped axes, and flowers with deep red or purple petals. Called *frailecillo* in Costa Rica; compare species of *Manihot*, which lack the gland-tipped hairs.

***Jatropha integerrima* Jacq., Sel. Stirp. Pl. Amer. 256, t. 183, f. 47. 1763. *J. hastata* Jacq., Sel. Stirp. Pl. Amer. 256, t. 173, f. 54. 1763. Figure 3.**

**Shrubs** or small trees 1–4 m tall, leafy stems 2–6 mm thick, sparsely puberulent with thin straight hairs ca. 0.5 mm long, becoming reddish brown, terete; stipules 0.5–1 mm long, gland-like or broadly triangular. **Leaves** with petioles 3–8 cm long, 0.7–1.8 mm thick, geniculate at base, sparsely puberulent, stipel-like glands to 2 mm long often present at apex or along base of blade; **leaf blade** 6–15 cm long, 3–8(–13) cm wide, oblong or ovate-oblong to ovate but sometimes with 1–2 short (ca. 7 mm) or prominent (1–2 cm) lateral lobes along the margin in the proximal half of the blade, apex acuminate, margin entire or with a few glands along the basal edge, base rounded and truncate or slightly cordate with a narrow sinus 2–6 mm deep, drying chartaceous to stiffly chartaceous, with short (0.5 mm) straight hairs above, glabrous beneath except in the proximal vein axils, venation subpalmate with 3 (5) major veins, 2° veins 2–5/side of midvein. **Inflorescences** terminal or pseudoaxillary, often bisexual, 15–20 cm long, peduncles 10–14 cm long, ca. 2 mm thick, with alternate cymose branches 2–7 cm long, bracts 3–12 mm long, linear with dark glands along the margin, pedicels 5–9 mm long, articulate beneath the calyx. **Male flowers** with calyx 3–5 mm long, lobes 1–2 mm long, triangular with blunt apex, petals 12–22 mm long, 8–10 mm wide, obovate with rounded distal margin, dark red or rose; stamens 10, staminal column ca. 4 mm long, filaments ca. 3 mm long, anthers 2.2–3 mm long. **Female flowers** with perianth like that of the ♂, ovary 2–2.5 mm long, glabrous, stylar column ca. 2.5 mm long, style branches ca. 3 mm long, bifid. **Fruits** 12–13 mm diam., subglobose with truncated apex, longitudinally 3-sulcate; seeds 9–10 mm long, 5–5.8 mm diam., caruncle ca. 3 mm wide, 2-parted.

*Jatropha integerrima* appears to have become naturalized near Limón and Cahuita and in Honduras, Nicaragua, and Panama; it is a native of Cuba often planted as an ornamental. The ovate-oblong leaves with pinnate or subpalmate venation on long petioles and conspicuous red petals are distinctive.

***Jatropha multifida* L., Sp. Pl. 1006. 1753.**

**Shrubs** or small treelets 2–3(–6) m tall, leafy stems ca. 5 mm thick, glabrous; stipules 1–2 cm long, with short (1 mm) base and slender branches. **Leaves** with petioles 8–18 cm long, 1.5–2.5 cm thick, usually glabrous; **leaf blades** nearly orbicular in general outline but deeply lobed, 10–25 cm long, 14–24 cm wide, with 9 or 11 lobes separate almost to the base, central lobe 8–14(–20) cm long, 1.5–4(–9) cm wide, narrowly elliptic-oblong to oblong-linear, apex long-acuminate, margin entire, base of blade deeply cordate, venation palmate with 9 or 11 major veins, webbing often present at the basal vein axils. **Inflorescences** terminal or pseudoaxillary, solitary, 20–26 cm long, umbellate or corymbiform, peduncles 18–23 cm long, 2–3 mm thick, glabrous, flowers in distal congested cymes 2–3 cm long and 4–5 cm wide; flowers with deep red or scarlet corollas.

*Jatropha multifida*, the “coral plant,” is often grown in gardens as an ornamental. It has not been reported as native or naturalized in Central America. The deeply 9- or 11-lobed leaves and red or scarlet flowers are distinctive.

***Jatropha podagrica* Hook., Bot. Mag. 74, t. 4376. 1848.**

**Small shrubs** with swollen base and few branches, 0.3–1(–2) m tall, leafy stems 8–14 mm thick, glabrous, with large leaf scars and persisting stipules producing a complex surface; stipules 3–6 mm long, with 3–10 glandular branches, becoming hard. **Leaves** peltate, petioles 5–20 cm long, 1.5–4 mm thick, glabrous; **leaf blades** 7–20 cm long, 6–16 cm wide, broadly ovate in outline with 3 (5) shallow to deep sinuses, apices of the lobes subacute, margins entire, base rounded with petiole attached 1–6 cm from the proximal margin, glabrous, venation palmate with 5 or 7 major veins. **Inflorescences** to 26 cm long, bright red or orange, peduncle to 20 cm long, flowers in a compact corymb-like arrangement of dichotomous/trichotomous branching, glabrous; ♂ flowers with small (0.5 mm) calyx lobes and oblong petals 3–6 mm long, bright red or orange. **Fruits** ca. 16 mm long, 12 mm diam., oblong with truncated apex, smooth, green; seeds ca. 12 × 6 mm.

*Jatropha podagrica* is often planted in gardens as an ornamental throughout the tropics. The short thick stem from an enlarged base, few lateral branches, slightly succulent peltate leaves, and bright red inflorescences give it a very distinctive

appearance. It is called *copa del rey*, *ruibarbo*, "white rhubarb," and "purging nut." This species is not known from the wild in Costa Rica but is found among rocky outcrops at 800–950 m elevation near Estelí in northwestern Nicaragua. It may also be native to deciduous areas in Guatemala and Honduras.

## Mabea Aublet

REFERENCES—M. J. Huft, Notes on *Mabea* (Euphorbiaceae) in Central America, together with comments on sect. *Apodae* in Brazil. *Phytologia* 62: 339–343. 1987. K. E. Steiner, Pollination of *Mabea occidentalis* (Euphorbiaceae) in Panama. *Syst. Bot.* 8: 105–117. 1983.

Shrubs or small trees, sometimes with scandent branches, monoecious, stems with whitish sap (not toxic), branched hairs sometimes present; stipules present or absent. **Leaves** alternate, simple, petioles without glands, blade with gland-tipped serrations or entire, pinnately veined, often glaucous beneath. **Inflorescences** terminal or axillary, racemose or paniculate, with long flexuous

central rachis, many-flowered, usually bisexual (rarely unisexual open panicles of few ♀ flowers), ♀ flowers 1–15 at proximal nodes of the rachis, bracts subtending solitary flowers, usually biglandular; ♂ flowers long-pedicellate and usually borne on 2° peduncles in umbellate groups of 3 (1–5) and subtended by a biglandular bract (the many ♂ flower groups sessile on a single unbranched racemose rachis in our species). **Male flowers** with 3–5 imbricate sepals, open before anthesis, petals and disk absent; stamens 10–70, anthers appearing to be sessile on a conical or convex receptacle, dehiscing longitudinally and extrorse; pistillode absent. **Female flowers** with 3–6 unequal sepals, imbricate and acute, petals, disk and staminodes absent; ovary 3-locular, stylar column long, style branches 3, simple, ovules 1/locule. **Fruits** capsular, rounded or 3-lobed and separating explosively into 3 2-valved cocci, columella persistent; seeds with a caruncle, smooth or warty, endosperm carnosous, cotyledons broad, flat.

A Neotropical genus of 40–50 species, mostly South American. The genus is distinctive because of its racemose inflorescences and the small cone-like androecium covered with many sessile anthers. This genus has recently been studied by H.-J. Esser (HBG).

## Key to the Species of *Mabea*

- 1a. Anthers 3–6/flower; inflorescences usually more than 1/branchlet, terminal and axillary, < 10 cm long, apparently erect; plants becoming trees to 30 m tall; leaves glabrous beneath, 5–11 cm long ..... *M. excelsa*
- 1b. Anthers 20–30/flower; inflorescences usually solitary and terminal on the branchlet, > 10 cm long, usually pendulous; plants to 7 (rarely 20) m tall; leaves glabrous or scurfy pubescent beneath, 5–23 cm long ..... *M. occidentalis*

***Mabea excelsa*** Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 123. 1944. Figure 26.

Trees 5–30 m tall, leafy twigs 1.2–4 mm thick, glabrous; stipules 0.5–1 mm long, triangular, caducous. **Leaves** with petioles 4–13 mm long, glabrous; **leaf blades** 5–11 cm long, 1.5–4.5 cm wide, oblong to oblong-lanceolate, apex caudate-acuminate to acuminate, margins with minute (0.1–0.2 mm) serrations, base rounded to obtuse, drying chartaceous, lustrous above and glaucous beneath, glabrous on both surfaces, 2° veins 10–18/side, 3° veins conspicuous. **Inflorescences** terminal or axillary, entirely ♂ or bisexual with 1–3 ♀ flowers at the base, panicles of thyrses, thyrses 3–8 cm long, 5–12 cm wide, short-pedunculate, densely puberulent. **Male flowers** in small sessile 3-flowered umbels (triads), subtending bracts with 2 oblong glands 0.7–1 long, not raised above the axis of the thyrse; calyx 5-lobed, lobes to 0.8 mm long, unequal; stamens 3–6. **Female flowers** subtended by oblong eglandular bracts ca. 0.8 mm long, peduncles ca. 5

mm long; calyx 6-lobed, 1.5–2.3 mm long, lobes acuminate; styles 6–8 mm long, connate, ca. ½ their length. **Fruits** 12–14 mm long, 12–15 mm diam., ovoid to subglobose, slightly 3-lobed, minutely and densely puberulent, columella ca. 14 mm long, broadly 3-winged (ca. 4 mm wide) except near the base; seeds 7–10 mm long, 6–7 mm wide, ca. 6 mm thick.

Plants of evergreen forest formations on both the Caribbean and Pacific slopes, 300–900 m elevation. Flowering in May–July; fruiting in November–December. The only Costa Rican collections seen are *Herrera & Martinez* 2273 CR, MO, and *Sáenz & Nassar* 129 USJ. The species ranges from southern Mexico to southern Costa Rica.

*Mabea excelsa* is recognized by its glabrous vegetative parts, paniculate arrangement of distal fruits, and tall stature. It is a rarely collected species.



**Mabea occidentalis** Bentham, Hooker's J. Bot. 6: 364. 1854. Figure 31.

Small *trees* or shrubs, 2–7 (rarely 20) m tall, wood hard and yellowish, branches usually slender, leafy stems 1.2–4 mm thick, glabrous or with short (0.2 mm) branched reddish brown hairs, terete, pale to dark brown; **stipules** not seen (ca. 5 mm long and linear according to Croat [1978]), caducous, stipule scars 0.5–2 mm wide. **Leaves** with petioles 4–14 m long, 1–1.8 mm thick, glabrous or with short reddish hairs; **leaf blades** 5–18(–25) cm long, 2–6(–9) cm wide, oblong to narrowly oblong, elliptic-oblong or ovate-oblong, apex acuminate to caudate-acuminate, narrow tip 8–16 mm long, margins subentire or with rounded serrations 20–43/side, base obtuse to rounded and subtruncate, drying stiffly chartaceous, glabrous and lustrous above, glabrous or with scurfy reddish hairs beneath, 2° veins 8–16/side (more when the prominent intermediate 2° veins are counted), loop-connected 2–8 mm from the leaf edge, central 2° veins arising at angles of 60–80°. **Inflorescences** bisexual and raceme-like panicles with a single unbranched axis (but with occasional unisexual open panicles of 3–8 ♀ flowers), 12–45 cm long and pendulous, peduncles to 30 cm long, glabrous or reddish puberulent; ♀ flowers 3–14, each subtended by a bract 3–9 mm long, lanceolate, 2 basal glands present or absent, pedicels 6–14 mm long; ♂ flowers usually 3 borne on short (1–5 mm) 2° peduncles often enclosed by a narrowly convolute bract with 2 oblong glands 1.2–3 mm long, pedicels 4–22 mm long, 0.2–0.3 mm thick, sometimes articulate, minutely papillate-puberulent. **Male flowers** reddish or purple, 2–3.5 mm long, sepals 3–5, 0.5–1.5 mm long, united at the base and forming a shallow cup for the cone-like androecium; stamens ca. 20–30, closely crowded on a rounded or conical base (1.5–2.5 mm long, 2 mm broad), anthers sessile, 0.4–0.6 mm long, covering the surface of the receptacle. **Female flowers** with ca. 6 sepals 2.5–5 mm long, 1.2–1.5 mm broad at the base, ovate to lanceolate and acute, minutely (0.05 mm) papillate-puberulent; ovary 2–4 mm long, densely papillate-puberulent, style column 11–20 mm long, 0.4–0.6 mm thick, style branches 4–11 mm long. **Fruits** 10–14(–18) mm long, 12–18(–22) mm broad, slightly 3-lobed, green tinged with red, surface minutely papillate-puberulent, outer wall of cocci 0.7–2 mm thick, columella 7–10(–15) mm long, expanded distally above the 2 mm base; **seeds** 7–10 mm long, 6–7 mm broad, 4.5–6 mm thick, oblong, dark and lustrous, caruncle 1–1.5 mm high at apex of seed.

Plants of lowland evergreen rain forest formations of both Caribbean and Pacific slopes and in moist shaded sites in deciduous formations, 0–1000 m elevation (but rarely collected above 200 m in Costa Rica). Flowering throughout the year (mostly in November–May); fruiting throughout the year. The species ranges from Mexico to Amazonian Brazil.

*Mabea occidentalis* is recognized by its pendulous racemose inflorescences, long-styled female flowers and many distal male flowers usually borne in threes on short peduncles subtended by biglan-

dular bracts, and the unusual androecium. The distinctive pendulous inflorescences have been reported to be pollinated by small nocturnal mammals (see references under genus). The foliage is distinctive because of the usually oblong leaf blades with caudate-acuminate apex and 2° veins loop-connected near the margin. Recent collecting has demonstrated that individuals of this species vary greatly, regarding both vegetative and floral morphology. Such a broad pattern of variation contradicts the assignment of some Costa Rican collections to *M. montana* Müll. Arg. This species has been called *higuera* and *kurinwacito* in eastern Nicaragua.

### Manihot Miller

REFERENCE—D. J. Rodgers & S. G. Appan, *Manihot* and *Manihotoides* (Euphorbiaceae), a computer-assisted study. Fl. Neotropica, monogr. 13: 1–272. 1973.

Herbaceous subshrubs, **shrubs**, small trees, or vines. monoecious (dioecious), branching often dichotomous or trichotomous, stems usually with whitish latex, roots often with tubers, hairs simple, vegetative parts often with cyanogenic glycosides; stipules small, deciduous. **Leaves** alternate, simple but often very deeply lobed and almost trifoliate or palmately compound, petiolate to subsessile, blades with stipels at base (foliar glands absent), margins entire to serrate or lobed, glabrous to puberulent, often with abaxial surfaces waxy-glaucous, venation palmate in lobed leaves or pinnate in unlobed leaves. **Inflorescences** terminal or pseudoaxillary, solitary or several, racemose or paniculate, usually bisexual, ♀ flowers usually proximal, ♂ flowers at central and distal nodes, bracts and bracteoles small, flowers usually on prominent pedicels. **Male flowers** glabrous or puberulent externally, calyx petaloid, usually united in the lower part to form a tube, lobes 5, imbricate in bud, petals absent, disk large and intrastaminal, with 5 bifid lobes (often appearing 10-lobed); stamens usually 10 in 2 unequal series of 5 longer and 5 shorter free filaments, anthers versatile, introrse, dehiscing longitudinally, pistillode absent or minute. **Female flowers** protogynous, glabrous or puberulent, calyx petaloid, usually with 5 sepals united only at or near the base, petals absent, disk thick and fleshy, subtending the ovary, entire or lobed, staminodes absent; ovary smooth or ribbed, 3-locular, ovules 1/locule, styles 3, short, united at the base, style branches broadly dilated and multilobed. **Fruits** capsular, smooth or with longitudinal wings, breaking into 3 2-valved cocci, columella often persistent; seeds smooth with thin-crustaceous testa, carunculate, endosperm copious.

A Neotropical genus of 60–90 species with the majority of species in South America. The genus ranges from southern Arizona to Argentina, but the cultivated *M. esculenta* is now found through-



out the tropics and subtropics. *Manihot* is best represented in seasonally deciduous areas, with centers of species diversity in east-central Brazil and central and western Mexico. Unusual variation within species and extensive hybridization between the cultivated plants and wild species have made this a taxonomically difficult genus. In addition to the important tuber crop (*M. esculenta*), *M. glaziovii* is the source of Ceara rubber and oil seeds.

Key to the Species of *Manihot*

- 1a. Vines, lianas, or shrubs with clambering branches; leaf lobes not more than 3; fruit surface smooth; calyx of ♂ flowers 6–18 mm long; uncommon native plants [in evergreen lowlands, usually minutely puberulent] ..... *M. brachyloba*
- 1b. Erect shrubs or treelets, branches not clambering; leaf lobes 3–11; fruit surfaces slightly rugose and often longitudinally ridged; ♂ calyx 5–13 mm long; common cultivated, escaped or less common native plants ..... 2
- 2a. Leaves peltate or subpeltate, 3–5-lobed with deep sinuses [small trees planted for ornament] .... *M. glaziovii*
- 2b. Leaves not peltate (sometimes subpeltate in *M. esculenta*), the petioles usually attached at the lamina edge ..... 3
- 3a. Fruits without prominent longitudinal ridges or wings; nodes not thickened; leaves glabrous, leaf lobes often with prominent sinuses and lobes along the margins, leaf blades never with the margin extending around the apex of the petiole (not subpeltate); wild plants of the deciduous and partly deciduous Pacific slope ..... *M. aesculifolia*
- 3b. Fruits with longitudinal ribs or wings; nodes usually thickened; leaves glabrous or puberulent, leaf lobes lacking prominent lateral sinuses and lobes along the margins, leaf blades sometimes with leaf margin extending around the petiole apex (subpeltate); cultivated and naturalized plants in many habitats ..... *M. esculenta*

***Manihot aesculifolia*** (H.B.K.) Pohl, Pl. Bras. Ic. 1: 55. 1827. *Jatropha aesculifolia* H.B.K., Nov. gen. sp. 2: 85, pl. 109. 1857. *M. gualanensis* Blake, Contr. U.S. Natl. Herb. 24: 13. 1922. Figure 1.

**Shrubs** or small treelets, 1–7 m tall, trunks to 10 cm diam., leafy stems 1.5–6 mm thick, glabrous; stipules 2–9 mm long, often lacinate, caducous. **Leaves** usually palmately lobed, petioles 4–20 cm long, 1–2.5 mm thick, glabrous, often bent at apex and base, often with a rugose gland-like area at the apex (on blade); **leaf blades** deeply divided into (3)–5–9(–11) lobes (sometimes simple near the inflorescences), middle leaflets 5–18(–25) cm long, 1.3–7(–10) cm wide, narrowly elliptic-oblong, narrowly elliptic, obovate or pandurate with prominent lateral lobes, apex acute to acuminate, margin entire or more often with 1–3 lateral lobes and broad sinuses, gradually narrowed to the base of the sinuses, lateral lobes often ½ the size of the middle lobe, drying membranaceous to thin-chartaceous, glabrous above and below (puberulent at the base adaxially). **Inflorescences** terminal or pseudoaxillary, 4–30(–45) cm long, to 25 cm wide, paniculate with racemose lateral branches to 15 cm long, often with

The genus is recognized by the larger flowers with a single corolla-like perianth whorl, presence of palmately lobed leaves (that may appear to be palmately compound with deep narrow sinuses), glaucous waxy surfaces on the undersides of leaves, whitish sap, and presence of cyanogenic glucosides that readily break down to form the poisonous prussic acid (HCN). Compare *Jatropha* and *Cnidoscolus*.

many (> 50) flowers, glabrous, bracteoles 1–3 mm long, ♂ pedicels 7–12 mm long. **Male flowers** pale green to yellowish, buds ca. 8 mm diam., glabrous on the exterior, calyx 9–14 mm long, tubular, lobes 6–8 mm long; stamens 9–13 and 7–8 mm long, anthers 2.3–3 mm long. **Female flowers** yellowish, glabrous externally, calyx 6–12 mm long, lobes 4–6 mm long, disk 2–3 mm diam.; pistil 6–9 mm long, ovary 2.8–4 mm long, 2.2–3.6 mm diam. **Fruits** 13–15 mm long, 14–17 mm wide, rounded-oblong, surface rugose with weakly developed longitudinal ridges; seeds 9–11(–13) mm long, 6.5–8.5(–10) mm wide, 3.8–5.3 mm thick, lenticular in cross-section with prominent lateral margins, surface uniform or mottled, caruncle 3–3.2 mm wide.

Plants of seasonally deciduous and partly deciduous forest formations of the Pacific slope (rarely collected in the evergreen Caribbean lowlands), 0–1100 m elevation. Flowering in May–October. The species ranges from Mexico and Guatemala along the Pacific slope to Panama.

*Manihot aesculifolia* is recognized by its deeply palmately lobed leaves often with pandurate or

lobed margins, lack of pubescence, larger inflorescences with many flowers, larger ♂ flowers, and rugose fruit. This species is closely related to *M. esculenta* (q.v.) but differs in the verrucose waxy surface on the leaf undersides and in characters of the key. It is often called *yuca de monte*. This species probably includes material Standley (1937) ascribed to *M. carthaginensis* (Jacq.) Müll. Arg., a species of northernmost South America and adjacent islands.

***Manihot brachyloba* Müll. Arg. in Mart., Fl. Bras. 11 (2): 451. 1874. Figure 1.**

**Vines**, lianas, or shrubs with clambering branches, 1–12 m high, leafy stems 1.3–6 mm thick, minutely puberulent with thin whitish hairs ca. 0.2 mm long; stipules 0.5–1 mm long, appressed, puberulent. **Leaves** usually with deep sinuses and almost trifoliolate, petioles 4–13 cm long, 0.6–1.4 mm thick, minutely puberulent, often geniculate at base and apex, small (0.5 mm) gland-like structures sometimes present above the apex; **leaf blades** usually deeply 3-lobed, central lobe 5–13 cm long, 2.4–4.5 cm wide, elliptic-ovate to elliptic-oblong or lanceolate, apex acuminate, margin entire, gradually narrowed to the base of the sinuses, lateral lobes slightly asymmetric (simple leaves with base rounded), drying membranaceous to chartaceous, glabrous above, glabrous or minutely (0.1–0.2 mm) puberulent beneath, 2° veins 9–11/side of midvein. **Inflorescences** pseudoaxillary or supraaxillary, 1–3, 3–9 cm long, racemose, minutely puberulent, pedicels to 15 mm long. **Male flowers** yellowish, calyx 6–18 mm long, 4–7 mm diam., lobes 4–9 mm long, disk 1–2 mm high, 2.5–4 mm diam., with 10 rounded lobes; filaments to 5 and 9 mm long. **Female flowers** with sepals 8–12 mm long, yellowish; pistil 5–6 mm long, ovary subglobose, stylar column ca. 1 mm long. **Fruits** ca. 15 mm long, 20 mm diam., globose-oblate, surfaces smooth or muricate; columella ca. 11 mm long; seeds 10–12 mm long, ca. 9 mm wide, 6–7 mm thick, surface lustrous, caruncle 3–3.5 mm wide.

Plants of evergreen rain forest formations on both the Caribbean and Pacific slopes, 20–600 m elevation. Flowering in June–September; fruiting in November. The species ranges from northern Costa Rica to Peru and Brazil and is disjunct in the Dominican Republic.

*Manihot brachyloba* is recognized by its usually vining habit, minute puberulence, never having more than three major leaf lobes, short racemose inflorescences, and smooth fruit. The waxy surface on the leaf undersides is verrucose ( $\times 50$ ). The leaves may appear to be trifoliolate, but the lobes are connected by tissue at the base and do not have petiolules.

***Manihot esculenta* Crantz, Inst. Rei Herb. 1: 167. 1766. *Jatropha manihot* L., Sp. Pl. 1007. 1753.**

*Jatropha dulcis* J. Gmelin, Onom. Bot. 5: 7. 1772. *Manihot utilissima* Pohl, Pl. Bras. Icon. Descr. 1: 32, t. 24. 1827. *M. dulcis* (J. Gmelin) Pax, Pflanzenreich IV, 147, 44: 71. 1910. Figure 1.

**REFERENCES**—D. J. Rogers & H. S. Fleming, Monograph of *Manihot esculenta* Crantz. Econ. Bot. 27: 1–114. 1973. M. A. El-Sharkawy, Drought-tolerant Cassava for Africa, Asia, and Latin America. BioScience 43: 441–451. 1993.

**Shrubs** or slender treelets 1–2.5(–4) m tall, leafy stems 1.5–8 mm thick, glabrous or sparsely puberulent with thin whitish hairs 0.1–0.2 mm long, roots producing tubers; stipules 5–14 mm long, triangular to linear, caducous. **Leaves** with petioles 4–18(–25) cm long, 0.8–2.5 mm thick, often puberulent near apex and base, often bent near apex and base, tissue of blade often united across apex of petiole (subpeltate); **leaf blades** with 3, 5, 7(–11) lobes separated by deep sinuses, middle lobes 6–17(–22) cm long, 1–6 cm wide, narrowly elliptic, elliptic-obovate to oblanceolate or linear-oblong, apex acuminate, margins entire or slightly sinuate, gradually narrowed to base of sinuses, united basal part of blade 5–15 mm long, drying membranaceous to thin-chartaceous, glabrous or less often minutely puberulent, usually glaucous beneath, 2° veins 5–11/side of the midvein. **Inflorescences** terminal or axillary, 2–10 cm long, paniculate, glabrous, bracts and bracteoles 1–3 mm long, linear, caducous, flowers on prominent pedicels. **Male flowers** yellowish, calyx 5–13 mm long, lobes 2–7 mm long, glabrous externally, disk 10-lobed; stamens usually 10 in 2 series, filaments arising from between the lobes, anthers 1.5–2.5 mm long. **Female flowers** reddish green or purplish, calyx 10–12 mm long, 3–4 mm wide, glabrous externally but puberulent along the inner edges, disk 2.5–3.5 mm wide; ovary 3–4 mm long, 2–3 mm diam., with 6 longitudinal ridges, styles 2 mm long, style branches 3 mm wide. **Fruits** 12–17 mm long, oblong-subglobose, usually with a rugose surface and 6 longitudinal fleshy ridges or wings; seeds 7–11 mm long, 4.5–7.5 mm wide, 4–5.5 mm thick, oblong with prominent lateral margins, caruncle 2–3.5 mm wide.

Plants of open sites (often cultivated) or secondary growth in both deciduous and evergreen areas, 0–1500 m elevation. Flowering primarily in July–February. The species may have originated in Mexico and northern Central America but is now grown throughout the tropics.

*Manihot esculenta* is recognized by its palmately lobed leaves with deep narrow sinuses, shorter inflorescences, ovary with fleshy longitudinal ridges or wings, and verrucose fruits. The vegetative parts contain cyanogenic glycosides that readily break down to prussic acid (HCN) and give a characteristic odor. This species is one of the world's most important food plants, with over 200 varieties cultivated for the tubers that are a very im-



portant source of starch in many lowland tropical regions. These tubers can be left in the ground with little deterioration, avoiding storage problems. The plants are easily grown from stem cuttings, are highly productive, and have few insect pests. Some varieties of *M. esculenta* produce no flowers. Varieties with poisonous tubers are called "bitter" and those without poison "sweet." Standley (1937) listed the following indigenous names under *M. dulcis*: ari (Bribri), unkah (Brunka), shku (Cabécar), and ik (Térraba). For *M. esculenta*, he listed ali and ili (Bribri), ungcah (Boruca), shko (Cabécar), shku (Estrella), iya (Guatuso), li (Talamanca), crosho (Térraba), and tázica (Tucurrique). The species is called *yuca*, *yuca amarga* (Spanish), *mandioca* (Portuguese), *manioc* (French), and "casava" and "tapioca" (English).

**Manihot glaziovii** Müll. Arg. in Mart., Fl. Bras. 11 (2): 446. 1874.

Trees 4–10 m tall, leafy stems 2–5 mm thick, glabrous, with copious latex; stipules 4–8 mm long, 1–2.2 mm wide at base, glabrous, caducous. Leaves peltate or subpeltate, petioles (3–)8–20(–45) cm long, 0.8–2.4 mm thick, glabrous, with a narrowed area at the base when dried, attached (2–)5–30 mm from leaf edge; leaf blades 7–15 cm long, 8–17 cm wide, deeply 3- (5-)lobed with sinuses 3–9(–15) cm deep, middle lobe usually obovate, apices acute to rounded, margins entire, base truncated or subcordate, glabrous, venation palmate with 3 or 5 major veins. Inflorescences terminal or pseudoaxillary, 2–5/ node, 5–13 cm long, glabrous, ♂ and ♀ flowers with sepals ca. 15 mm long.

*Manihot glaziovii* is a native of easternmost Brazil and has been cultivated as an ornamental in Central America. This species is also used for the production of latex (Ceara rubber), oil from the seeds; the leaves are eaten as a vegetable in Zaire. The deeply lobed peltate leaves with entire margins are distinctive.

### **Margaritaria Linnaeus filius**

REFERENCE—G. L. Webster, A revision of *Margaritaria* (Euphorbiaceae). J. Arnold Arbor. 60: 403–444. 1979.

**Shrubs** or small trees, dioecious, branches usually distichous, hairs simple, lenticels prominent; stipules entire or denticulate, caducous or persistent. Leaves alternate, simple, usually deciduous, petiolate, margins entire, pinnately veined. Inflorescences usually appearing with the new flush of leaves, axillary, of solitary, paired or fasciculate flowers, usually at proximal nodes on new lateral

shoots or in axils of distal leafy branchlets, flowers subtended by small bracts, pedicellate. Male flowers small and inconspicuous, sepals 4, united at base, unequal and biseriate, imbricate in bud, petals absent, disk annular, flat or slightly lobed; stamens 4, filaments usually free, anthers dehiscing longitudinally and extrorse; pistillode absent. Female flowers with 4 sepals united at the base, petals absent, disk annular, staminodes absent; ovary with 4–5 (2–3, 6) locules, styles 4–5 (2–3, 6), style branches bifid distally, ovules 2/locule. Fruits capsular, breaking apart irregularly into 4–5 (2–3, 6) thin-walled 2-seeded cocci, green exocarp usually separating from the thin papery endocarp; seeds 2/locule, outer coat (exotesta) becoming fleshy and bluish when fully ripe, inner coat (endotesta) hard and woody (achene-like), ecarunculate, endosperm copious, whitish, cotyledons thin and flat.

A genus of 14 species widely distributed in the moist tropics, except in the Pacific islands. Some taxonomists considered it to be a section of *Phyllanthus*, but Webster (see reference above) considers it to be more closely related to *Flueggea*. The seeds have a fleshy exotesta and thin bony endotesta, unlike other genera of Phyllanthaceae. Only the following species is found in Central America.

**Margaritaria nobilis** L. f., Suppl. Pl. Syst. Veg. 428. 1781. *Cicca antillana* Juss., Tent. Euphorb. 108, t. 4, f. 13B. 1824. *Phyllanthus antillanus* (Juss.) Müll-Arg., Linnaea 32: 51. 1863. *P. nobilis* (L.f.) Müll-Arg., in DC., Prodr. 15 (2): 414. 1866. *P. nobilis* var. *hypomalacus* Standl., Carnegie Inst. Wash. Publ. 461: 68. 1935. Figure 25.

**Shrubs** or small trees, 2–10(–20) m tall, dioecious, leafy stems 1–3 mm thick, glabrous or minutely (0.1–0.3 mm) puberulent but glabrescent, terete, with conspicuous lenticels 0.4–0.8 mm long; stipules 2–4.5 mm long, 0.4–1.2 mm wide at base, narrowly triangular to subulate, acute, glabrous, usually persisting. Leaves deciduous, petioles 1.4–6(–10) mm long, ca. 1 mm thick, with thin lateral margins continuous with the lamina base, without glands; leaf blades 4–14(–18) cm long, 2–4.5(–6) cm wide, elliptic or oblong-elliptic to ovate or ovate-lanceolate, gradually tapering to an acute or acuminate apex, acute to cuneate at the base, slightly decurrent on the petiole, drying chartaceous, glabrous above, glabrous or with short (0.2–0.4 mm) thin hairs on the veins beneath, 2° veins 7–11/side. Inflorescences (see genus description), usually in anthesis when the leaves are deciduous and just as the new leaves begin to expand, pedicels unarticulated; ♂ flowers 1–5 arising from small bracteate buds, pedicels 3–8 mm long, ca. 0.1 mm thick (dried); ♀ pedicels 6–10 mm long (to 15 mm in fruit), 0.3–0.6 mm thick. Male flower buds 0.7–1.3 mm diam., glabrous, perianth 2–3 mm wide at anthesis, sepals 0.6–1.5 mm long, disk annular, flat or slightly lobed, 1.4–3 mm diameter; filaments 1–1.8 mm long, anthers 0.5–0.8 mm long. Female flowers with sepals 1.3–2.2 mm long, 1.3–2.5 mm wide, obtuse, glabrous; ovary 1–1.8 mm



long, 1.5–2 mm diam., glabrous, locules 4–5 (3, 6), style column 0.3–1 mm long, style branches usually 4, 1–1.5 mm long, recurved, bifid in distal half. **Fruits** 7–8 mm long, 9–12 mm broad, rounded-oblate with 4–5 (rarely 3 or 6) shallow longitudinal sulci, bright green, glabrous; **seeds** covered at maturity by a dark bluish fleshy coat, interior “achene” 3–5 mm long, 2.2–3.8 mm wide, 2–2.5 mm thick, with 2 flattened lateral sides, acute adaxial edge and rounded abaxial surface, smooth and yellowish (adjacent seeds sometimes coherent).

Plants of both seasonally deciduous and very wet evergreen lowland rain forest formations, 0–1100 m elevation. Flowering mostly in late May–September; fruiting in June–October. Flowering in Guanacaste usually occurs over a 3-day period about 2 weeks after the rainy season begins (Opler et al., 1976). Leaf fall occurs late in the dry season on Barro Colorado Island (Croat, 1978). The species ranges from Mexico and Cuba to Peru and Brazil.

*Margaritaria nobilis* (formerly *Phyllanthus nobilis*) is recognized by the clearly deciduous habit (there are no thick stems with leaves), small axillary unisexual (dioecious) flowers on slender pedicels along distal stems, the minute ♂ flowers, the rounded fruits with 4–5 (3, 6) 2-seeded cocci that break up irregularly, and the achene-like seeds covered with a thin fleshy bluish layer. A vegetative distinction is that the petiole margins usually merge with translucent tissue of the decurrent leaf edge at the base of the blade. In Costa Rica, the collections come primarily from lowland Guanacaste Province and from the Caribbean lowlands. Specimens from evergreen forests tend to have more elliptic leaves with a great number of 2° veins.

## **Omphalea** Linnaeus

Shrubs, trees, or *lianas*, monoecious, hairs simple, latex clear or reddish; stipules present, small. **Leaves** alternate, simple, petioles with 2 lateral glands at the apex, blades entire (in ours) to deeply lobed, often truncate to cordate at base, venation pinnate or palmate. **Inflorescences** terminal (rarely axillary), solitary or several, unisexual or bisexual, spicate, racemose, panicle with a central stem-like rachis and branched or unbranched lateral branches, bracts subtending the flower clusters (cymules) narrow and leaf-like, often biglandular, flowers small, the cymules entirely of ♂ flowers or with a few central ♀ flowers, pedicels short. **Male flowers** with 4–5 decussate sepals, united at the base and imbricate in bud, petals absent, disk absent or small; stamens 2–3, filaments connate, connectives united into a fleshy structure bearing the 2–3 anthers at the periphery, anthers dehiscing obliquely; pistillode absent. **Female flowers** with 4–5 sepals united at the base, imbricate, petals absent,

disk absent, staminodes absent; ovary (2-) 3-locular, styles connate into a column continuous with the ovary, 3-lobed at the tip or obscure, ovules 1/locule. **Fruits** fleshy and large, thick-walled and indehiscent or capsular with 3 2-valved woody cocci; seeds subglobose, ecarunculate, endosperm present, cotyledons broad, cordate at base.

A genus of 15 tropical species, with centers of diversity in the West Indies and Madagascar. This genus was studied by L. Gillespie (A revision and phylogenetic analysis of *Omphalea* (Euphorbiaceae). Ph.D. thesis, University of California, Davis, 1988).

**Omphalea diandra** L., Sp. Pl. ed. 2, 1377. 1763.

*O. diandra* var. *panamensis* Klotzsch in Seemann, Bot. voy. Herald 101. 1853. *Hebecocca panamensis* Beurl., Svensk. Vet. Akad. Handl. 1854 (Prim. Fl. Portob.) 146. 1856. *O. panamensis* (Beurl.) I. M. Johnston, Sargentia 8: 177. 1949. Figure 31.

**Lianas** to over 30 m high, stems to 20 cm diam., sap reddish to purplish, often with leafless distal stems (to 60 cm long) twining around other stems, leafy stems 2.3–7 mm thick, densely yellowish brown pubescent with hairs 0.1–0.5 mm long; **stipules** ca. 2 mm long, 1 mm broad at the base, triangular and acute, densely hirsute. **Leaves** with petioles 1.2–6.5 (–11) cm long, 1–2.3 mm thick, densely hirsutulous, apex with 2 lateral flat rounded (disk-like) glands 1–2 mm wide, pale green in life; **leaf blades** 6–18 (–24) cm long, 3–11 (–14) cm broad, broadly ovate to broadly ovate-elliptic, or ovate-oblong, apex obtuse to rounded or bluntly mucronate (short-acuminate), margin entire, base rounded and obtuse to subtruncate or slightly subcordate, drying stiffly chartaceous to subcoriaceous, grayish and glabrescent above, sparsely to densely pubescent beneath with hairs 0.2–0.4 mm long, 2° veins 4–5/side, strongly ascending near the margin, 3° veins subparallel. **Inflorescences** 15–50 cm long, open-paniculate with alternate lateral branches to 15 (–25) cm long, densely puberulent with hairs 0.2–0.5 mm long, flower clusters sessile or on short (2–7 mm) thick (1.3 mm) 3° branches, subtended by linear-lanceolate bracts 3–24 (–40) mm long, 1–3 mm broad, leaf-like (with petiole-like base, medial glands and distal narrow blade), cymules with all ♂ flowers or with 1 central ♀ and other ♂ flowers (or solitary distal ♀ flower), pedicels 0.5–2 mm long. **Male flower** buds 1.5–2 mm diam., sparsely and minutely puberulent, sepals 1.5–2.5 mm long, the 2 outer ca. 2 × 2 mm, rounded distally, green, the 2 inner reddish within and with thin margins, disk ca. 1.5 mm wide, flattened with a small central opening, reddish (*Grayum* 9820 f); anthers 2 (3), 0.6–0.8 mm long, connate with and a part of the periphery of the broadly rounded and distally flattened connective ca. 1.2 mm diam. **Female flowers** with calyx lobes 1–2 × 1.4 mm, triangular, pistil ca. 3 × 2 mm, pyriform or conical, densely velutinous, styles obscure, stigmas minute. **Fruits** 8–12 cm diam., globose, fleshy but breaking up; seeds 4–5 cm long, compressed rounded, brown or black, slightly rugose.

Lianas of evergreen rain forest and partly deciduous forest formations in both the Caribbean and Pacific lowlands, 0–600 m elevation. Flowering and fruiting in December–April and August–September in Costa Rica. The species ranges from Honduras and the West Indies to Peru and Brazil.

*Omphalea diandra* is recognized by its climbing habit, broadly ovate leaves with few major veins, petioles with two glands at the apex, large inflorescences with small flowers, narrow leaf-like bracts, and large round fruit. The androecium is quite unusual, resembling the peltate cap of a mushroom in outline and with a slender stalk. The two anthers occupy opposing sides on the periphery of the “cap.” Some labels describe the plants as trees, but this may be in error. Large lianas are among the most poorly sampled members of the tropical flora, and it is likely that this species is more common than the few collections would indicate. Specimens from the Osa Peninsula have longer floral bracts than those from the Caribbean slope.

*Ophellantha spinosa* Standl. is a species of northern Central America; Standley’s citation for Costa Rica (Standley, 1938, p. 1557) appears to have been based on a misidentification. Webster (1994b, p. 107) merges *Ophellantha* with *Acidocroton*, and the species name is *A. spinosus* (Standl.) Webster.

### **Pausandra Radlkofer**

**Trees** or shrubs, dioecious, stems with red or yellowish latex, stems with stellate or simple hairs attached at the center; stipules present, caducous. **Leaves** alternate, simple, petioles thickened distally, blades serrate, with glands at the base, venation pinnate. **Male inflorescences** axillary, spiciform (rarely with lateral branches), flowers in sessile glomerules subtended by small eglandular bracts; ♂ flowers subsessile, calyx lobes 5, imbricate in bud, petals 5 (6), connate near the base, villous within (adaxially), disk intrastaminal, cupulate, lobate, glabrous; stamens (3–)5–7, filaments free; anthers dehiscing longitudinally, introrse, connective not enlarged; pistillode absent. **Female inflorescences** axillary, spiciform, bracts eglandular and sessile, subtending solitary sessile (short-pedicellate) flowers; ♀ flowers with 5 imbricate sepals, petals 5, free, villous within, disc cupulate, entire or lobed, glabrous; ovary 3-locular, ovules 1/locule, styles 3, free, bifid. **Fruits** capsules splitting into 3 2-valved cocci; seeds smooth, carunculate, endosperm copious, embryo straight, cotyledons palmately veined.

A South American genus of approximately eight species, with one reaching as far north as Honduras. Note that while the bracts may be eglan-

dular, the ♀ inflorescences of our species may have glands present on the rachis near the sides of the floral bracts.

**Pausandra trianae** Baillon, *Adansonia* 11: 92. 1873.

*Pogonophora trianae* Müll. Arg., *Flora* 47: 434. 1864 (note that Baillon did not refer to Müller’s earlier name when he published this species). *Pausandra extorris* Standl., *Trop. Woods*. 17: 24. Mar. 1929, and *Publ. Field Columb. Mus.*, Bot. Ser. 4: 219. Oct. 1929. *Clavija septentrionalis* L. O. Williams, *Fieldiana Bot.* 32: 205. 1970. Figure 13.

**Trees** 3–30 m tall, trunks to over 30 cm thick, sap yellowish to red or brown, caustic, leafy stems 4.5–10 mm thick, strigose with appressed straight or slightly crooked hairs ca. 0.3 mm long and attached at their center; stipules 5–6 mm long, 1–2 mm wide at base, triangular, thick, appressed to shoot apex, caducous. **Leaves** clustered near the ends of branchlets, petioles 8–60 mm long, 1.8–5 mm thick, thickened near the apex, appressed strigose and glabrescent, with 2–4 cylindrical or crateriform glands 0.5–1.5 mm long near the apex, 0.7–1 mm diam.; **leaf blades** 18–70 cm long, 8–22 cm wide, oblanceolate to narrowly oblanceolate or narrowly elliptic-ovate, apex abruptly narrowed or rounded, short-acuminate, margin with conspicuous rounded gland-tipped teeth 0.5–2.5 mm long, teeth 1–2/cm, base long-cuneate or long-attenuate, sparsely pubescent with appressed hairs 0.3–0.9 mm long above and below, glabrescent between the veins, 2° veins 15–24/side, 3° veins subparallel. **Male inflorescences** 7–15 cm long, densely puberulent with appressed yellowish hairs ca. 0.2 mm long, united at base, lobes broadly overlapping in bud, ca. 0.8–1.5 mm long, broadly rounded; disk ca. 0.8 × 1.2 mm, spreading-cupulate, entire, stamens 6, filaments 2.5–5 mm long, slender, glabrous, anthers 0.8–1.1 mm long. **Female inflorescences** 2–17 cm long, bracts ca. 1 × 1.5 mm, broadly triangular and sessile, with cylindrical glands 0.7 × 1.2 mm long often present near the sides, 0.5–1 mm diam.; ♀ flowers with green sepals and yellow petals, cupular disc ca. 0.8 mm high, ovary 2–3 mm long, 1.5–2 mm diam., ovoid-trigonal, sericeous, style branches ca. 1.8 mm long. **Fruits** ca. 13–14 mm long, strigose, green, woody wall ca. 1.2 mm thick, columella 8–9 mm long, ca. 3 mm wide at apex; seeds 9–11 mm long, 7.2–8.8 mm wide, 6–7 mm thick, rounded-oblong, dark, caruncle irregular and flattened.

Plants of evergreen lowland rain forest formations, 20–800 m elevation. Flowering occurs in December–June; fruiting in March–July. In Costa Rica, the species is usually found above 100 m elevation. The species ranged from Honduras to Amazonian Peru and Brazil.

*Pausandra trianae* is recognized by its large ob-



lanceolate serrate leaves clustered near the ends of unbranched branchlets, unusual pubescence, glands at the apex of the petiole, spiciform inflorescences with unisexual flowers, and broadly imbricate perianth parts. The hairs appear to be simple and appressed, but they are actually two-branched and attached at the center.

**Pedilanthus A. Poiteau,**  
nomen conservandum

REFERENCE—R. Dressler, A monograph of the genus *Pedilanthus* (Euphorbiaceae). Contr. Gray Herb. 182: 1–188. 1957.

**Shrubs** with woody or succulent greenish stems, usually with few distal lateral branches, monoecious, sap usually whitish; stipules small, caducous. **Leaves** alternate, distichous, simple, sessile or petiolate, blades fleshy, margins entire. **Inflorescences** axillary or terminal cymes of few to many flower-like cyathia, bracts opposite, cyathia pedunculate (appearing to be pedicellate). **Cyathia** bilaterally symmetrical, shoe-like in form, outer perianth-like involucre made up of 5 partly united bracts, 2 adaxial bracts with or without glands along the adaxial edge, 2 lateral bracts asymmetric at the base and with glands along the abaxial margins, and an adaxial bract with glands on each edge, usually partly to entirely reddish, bracteoles 0—many and filamentous within the cyathium. **Male flowers** many, each ♂ flower represented by an individual stipitate (pedicellate) stamen completely lacking perianth, disk or pistillode; filament simple, anthers 2-lobed. **Female flowers** represented by a solitary stipitate (pedicellate) naked pistil within the cyathium, perianth and staminodes absent; ovary 3-locular, ovules 1/locule, styles 3, united for most of their length, distally bifid. **Fruits** capsules or indehiscent, 3-lobed; seeds ovoid or rounded-angular, smooth or tuberculate, ecarunculate.

A genus of 15 species centered in Mexico with 1 species circum-Caribbean. The unusual flower-like cyathium is adapted for bird-pollination and probably derived from the more symmetrical cyathium found in *Euphorbia*. The genus may not be native to Costa Rica; the few collections are probably escapes from cultivation. *Pedilanthus millspaughii* Pax & K. Hoffm. (Repert. Spe. Nov. Regni Veg. 19: 174, 1923) (based on *Brade* 2302 from Miravalles, Costa Rica, destroyed at B) is a nomen dubium.

**Pedilanthus tithymaloides** (L.) Poit., Ann. Mus. Natl. Hist. Nat. 19: 390. 1812. *Euphorbia tithymaloides* L., Sp. Pl. 453. 1753.

**Shrubs** with erect or scandent branches, 1–3 m long, distal stems often slightly zigzag, leafy stems 1.5–9 mm

thick, at first with thin whitish hairs ca. 0.2 mm long, glabrescent, greenish and terete; stipules 0.3–1.2 mm diam., spur-like, caducous. **Leaves** subsessile or with petioles to 6(–12) mm long, with lateral wings continuous with the blade; **leaf blades** 4–12(–16) cm long, 1.5–5(–10) cm wide, ovate-elliptic to ovate-orbicular or ovate-oblong, tapering gradually to an acute apex, margin entire or slightly undulate (dried), base obtuse, drying stiffly chartaceous to subcoriaceous, minutely puberulent or glabrous, venation obscure. **Inflorescences** terminal or axillary, 1—many cyathia in cymose groups, cyathia subtended by thin reddish bracts, peduncles (appearing as pedicels) 3–8 mm long, glabrous or puberulent. **Cyathia** 7–15 mm long, 3–6 mm wide, slipper-shaped with curved basal spur or lobe to 4 mm long, glabrous or minutely puberulent externally, tube red above and green or yellowish beneath; ♂ flowers 20–34, stipes 7–14 mm long, filaments 2.5–3 mm long, anthers ca. 1.2 × 3 mm; ♀ flower (solitary naked pistil) on a stipe 4–14 mm long, ovary 1.5–2 mm long, styles 5–11 mm long, style branches 0.5–1 mm long. **Fruits** 5–6 mm diam., deeply 3-lobed in cross-section; seeds 3–4.5 mm long, 2.5–3.5 mm wide, ovoid to angled or subglobose.

*Pedilanthus tithymaloides* is recognized by its arching greenish stems, semisucculent leaves, and unusual slipper-shaped cyathia that function as flowers. The species is probably an escape from cultivation in Costa Rica; it is often planted in gardens and hedges. *Bítamo*, *bítamo real*, *pie de niño*, *pie de santo*, and *zapatilla* are names used in Central America.

**Pera Mutis**

**Trees** or shrubs, dioecious (rarely monoecious), flat appressed lepidote hairs usually present on young stems and leaves (simple or stellate hairs may also be present); stipules small or absent. **Leaves** alternate (rarely opposite), simple, petiolate, eglandular, pinnately veined. **Male inflorescences** axillary, glomerules at leafless nodes or from leafless short-shoots, 1–15, pedunculate and at first resembling an individual flower bud with globose involucre enclosing 3–10 sessile flowers, involucre subtended by 1–2 bracts; ♂ flowers not all developing, calyx united and splitting into 2–4 acute lobes (or reduced), petals absent, disk absent; stamens 2–8, filaments short and free or longer and basally connate, anthers basifixed, dehiscing longitudinally; pistillode absent. **Female inflorescences** axillary, 1–2 or more/node, at first resembling a flower bud with a pedunculate globose involucre enclosing 2–5 pistils; ♀ flowers lacking perianth, disc absent, staminodes absent; ovary short-stipitate, 3-locular, ovules 1/locule, styles 3, short, connate at the base. **Fruits** capsules splitting into 3 2-valved woody cocci, columella not persisting; seeds ovoid to obovoid or oblong, compressed, smooth, lustrous, carunculate.

A Neotropical genus of ca. 30 species, mostly Amazonian. *Pera barbellata* Standl., with smaller leaves and fruits, ranges from Veracruz, Mexico,



to northern Honduras. The involucrate inflorescences enclosing reduced  $\delta$  or  $\varphi$  flowers may be mistaken for individual flowers.

***Pera arborea*** Mutis, Kongl. Vetensk. Akad. Nya. Handl. 5: 299, t. 8. 1784. Figure 26.

Trees 5–25 m tall, dioecious, trunks 12–40 cm diam., leafy stems 1–5 mm thick, sparsely to densely lepidote with flat rounded appressed brownish hairs 0.1–0.3 mm wide, mostly glabrescent; stipules absent. **Leaves** with petioles 4–14(–22) mm long, 0.8–1.7 mm thick, sulcate or slightly winged above (adaxially), lepidote; **leaf blades** (4–)5.5–14(–16) cm long, (1.5–)2.5–6(–7) cm wide, elliptic to elliptic-oblong or oblong, apex obtuse or cuspidate-acuminate, margin entire, base obtuse to cuneate, usually drying dark grayish or brown, glabrous or sparsely lepidote above, with scattered lepidote hairs 0.1–0.2 mm wide beneath, 2° veins 7–12/side. **Male inflorescences** 5–15, mostly at older leafless nodes or on leafless short-shoots, peduncles (appearing to be pedicels) 4–6 mm long, ca. 0.4 mm thick, lepidote, involucre at first globose, 2–3 mm diam., subtended by 2 opposite unequal bracts 0.5–1.3 mm long, involucre (resembling a calyx) lepidote and splitting into usually 3 broad lobes;  $\delta$  flowers difficult to distinguish, perianth ca. 1 mm long, with narrow lobes, stamens 4–6, filaments 0.7–1 mm long, anthers 0.8–1.1 mm long, ca. 0.7 mm wide. **Female inflorescences** axillary or at older leafless nodes, 2–5, peduncles 4–12 mm long, ca. 0.4 mm thick, lepidote, involucre breaking into usually 3 sepal-like parts 2–3 mm long, to 4 mm broad, lepidote externally, glabrous and drying black adaxially;  $\varphi$  flowers usually 3, ovary ca. 2  $\times$  1 mm, narrowly ovoid, glabrous and drying black, style branches broad with erose margins. **Fruits** 12–14 mm long, oblong and rounded or slightly trigonous in cross-section, surface glabrous or covered with scurfy hairs, fleshy and drying with wrinkled sharp-edged reticulated ridges, borne on stipes and peduncles ca. 4 + 4 mm long, woody walls ca. 1 mm thick; seeds 6–7 mm long, 4.5–5.7 mm wide, 2.2–3 mm thick, ovoid-triangular with rounded proximal margin, dorsoventrally flattened, black and lustrous, the expanded thin yellowish caruncle partly covering the seed.

Plants of evergreen wet forest formations, 5–1000 m elevation. Flowering primarily in August–January; fruiting in October and January–March. This species is uncommon in Costa Rica; it has been collected only at La Selva, in the General Valley, and near Golfito. The species ranges from Belize to Colombia.

*Pera arborea* is recognized by the lepidote hairs on shoot apices and other parts, entire leaves lacking glands, groups of unisexual inflorescences that resemble globose flower buds, naked  $\varphi$  flowers, fruits with wrinkled surfaces, and glossy black seeds partly covered by the expanded aril-like caruncle. The male inflorescences are easily misinterpreted as individual flowers. The hairs have a central (usually dark) attachment and many radiating

translucent rays that are united for most of their length into a flat disk ( $\times$  50). The fruits vary from being densely stellate tomentose to almost glabrous. Further evaluation of the General Valley plants is needed to assess the significance of these differences.

## **Phyllanthus** Linnaeus

REFERENCES—G. L. Webster, A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arbor. 37: 91–122, 217–268, 340–359. 1956. 38: 51–80, 117–198, 295–373. 1957. 39: 49–100, 111–212, 1958.

Herbs, shrubs, or trees, monoecious (dioecious), branches regular or specialized with axes of 2 kinds (persisting axes with spiral leaves and no flowers, and deciduous axes with distichous leaves often with axillary flowers), hairs simple or dendritic; stipules small, lateral, deciduous or persisting. **Leaves** alternate (rarely opposite), simple, short-petiolate, petioles without glands, blades usually thin-textured, margin entire, venation pinnate; scale-like cataphylls may be present. **Inflorescences** usually axillary (cauliflorous or terminal), usually simple and unbranched, flowers solitary or in sessile fascicles (reduced cymes),  $\delta$  flowers on slender unarticulated pedicels,  $\varphi$  flowers subsessile or on unarticulate pedicels. **Male flowers** small, perianth free or united at base, sepals 4–6 in 2 equal or subequal series, imbricate, petals absent, extrastaminal disc usually present and lobed or divided; stamens 3–6 (2–15), filaments free or united, often forming a column, anthers dehiscent variously, thecae parallel or divergent; pistillode absent. **Female flowers** small, perianth free or united at the base, sepals 5–6 in 2 series, equal or unequal, imbricate, petals and staminodes absent, disk usually saucer-shaped or divided into segments or lobes (absent); ovary usually with 3 locules (4, 5), ovules 2/locule, styles 3 (4), free or united, bifid or variously divided. **Fruits** usually capsules dehiscent explosively into 2-valved cocci, less often indehiscent and baccate or drupaceous, columella persisting; seeds usually 2/locule, 3-angled or rounded and convex dorsally, sometimes with the 2 seeds of a locule dispersing as a single unit, ecarunculate, seed coat drying crustaceous, smooth or sculptured, endosperm cartilaginous or fleshy.

A diverse pantropical genus of 750–800 species, best represented in wet evergreen and seasonally moist areas. In South America, some species are used to make a fish poison, and there is a *Salvinia*-like aquatic (*P. fluitans* Müll. Arg.) unique in the family. Many of our species are weedy plants of open early secondary sites and are poorly represented in herbaria.

*Phyllanthus* is unusual in having many species in which the distal lateral stems are unbranched, deciduous, and with distichous small leaves. These

branches resemble pinnate or bipinnate leaves. However, the leaflet-like leaves on these deciduous stems often subtend axillary flowers or fruits, distinguishing them from the leaflets of a truly compound leaf. The entire (usually small) leaves and small flowers in axillary clusters help make most of the species easy to recognize. Note that the unequal sepals in two whorls can be mistaken for two perianth whorls. The stamens are often united over much of their length, producing a sta-

mental column supporting sessile and partly united anthers. The morphology of the pollen grain is important in determining the subgeneric placement of species. For a general review of the morphology of this genus, see L. Bancelhon, Contribution à l'étude taxonomique du genre *Phyllanthus* (Euphorbiacées), Boissiera 18: 1–81, 1971. A closely-related ornamental with white-mottled leaves is *Breynia disticha* (q.v.).

Key to the Species of *Phyllanthus*

- 1a. Leaves usually in a spiral and present on all distal stems, including the stems bearing the ultimate lateral leafy twigs; plants to 0.8 m tall [rarely collected in Costa Rica] ..... 2
- 1b. Leaves usually distichous (in 2 opposing ranks) and restricted to the unbranched distal lateral stems which often resemble pinnate leaves, leaves usually absent on the stems that bear the distal lateral branches; plants 0.1–40 m tall [various habitats] ..... 4
  - 2a. Fruits 2.5–3 mm wide; seeds 1.4–1.6 mm long, smooth and lustrous; leaf blades usually narrowly elliptic and acute at the apex [moist habitats] ..... *P. hyssopifolioides*
  - 2b. Fruits 1–2 mm wide; seeds 0.7–1.2 mm long, smooth but minutely rugulose; leaf blades usually oblong with bluntly obtuse or rounded apex ..... 3
  - 3a. Female sepals usually 6 and narrowly oblong; distal stems usually terete and with or without winged ridges; 2° veins not or weakly loop-connected; stipules lacking basal lobes ..... *P. caroliniensis*
  - 3b. Female sepals usually 5 and obovate; distal stems flattened and conspicuously winged; 2° veins often loop-connected but difficult to see; stipules often with basal auriculate lobes ..... *P. compressus*
- 4a. Plants shrubs or trees, woody throughout, usually > 1 m tall ..... 5
- 4b. Plants herbs or subshrubs, if woody then only at the base, plants usually < 1 m tall ..... 11
  - 5a. Largest leaf blades < 10 mm wide; seeds 1.7–2 mm long [leafy stems with persisting stipules 2–4 mm long; plants to 5 m tall] ..... *P. valerii*
  - 5b. Largest leaf blades > 10 mm wide; seeds 1.9–3.3 mm long ..... 6
  - 6a. Leaves with 11–17 pairs of 2° veins [blades usually oblong-lanceolate in form, rare (?introduced) shrubs at ca. 1800 m elevation] ..... *P. salviifolius*
  - 6b. Leaves with 3–10 pairs of 2° veins ..... 7
  - 7a. Stamens 4/flower; plants introduced and cultivated for their acidic fleshy fruits . *P. acidus*
  - 7b. Stamens 3/flower (or the 3 stamens united and with 6 thecae); plants indigenous, with dry fruits (fleshy in *P. skutchii*) ..... 8
  - 8a. Leaf blades 5–11 cm long; fruits 7–9 mm diameter, globose, with a fleshy covering, seeds 8/fruit, separate; trees 8–40 m tall [100–900 m elevation] ..... *P. skutchii*
  - 8b. Leaf blades to 6 cm long; fruits less than 6 mm diam., dry, seeds 6/fruit or remaining as seed pairs and 3/fruit; shrubs or trees to 8 m tall ..... 9
  - 9a. Seeds 2.6–3.3 mm long; ♀ sepals 1.1–1.7 mm long; leaves elliptic to ovate-lanceolate, to 6 cm long; 0–1700 m elevation ..... *P. acuminatus*
  - 9b. Seeds 1.9–2.5 mm long; ♀ sepals 1.5–2.5 mm long; leaves broadly elliptic to ovate or sub-orbicular, to 4 cm long; 100–1400 m elevation ..... 10
  - 10a. Staminal column bearing 6 rounded thecae, the thecae from 3 slightly separated bases or from a single conical apex; leaves glabrous ..... *P. mocinianus*
  - 10b. Staminal column with a flat top and 6 narrowly oblong thecae along the edge; leaves glabrous or puberulent [Mexico to El Salvador; see discussion under *P. mocinianus*] . *P. mcvaughii*
- 11a. Fruits 3.5–4 mm wide, seeds 1.7–2 mm long, minutely punctate or rugulose or sometimes appearing

- smooth with  $\times 10$  lens; stipules 0.5–2.7 mm long, distally filiform; 900–2500 m elevation [leaves to 16 mm long] ..... *P. niruri*
- 11b. Fruits 1.3–2.7 mm wide, seeds 0.8–1.4 mm long, transversely or longitudinally ridged or with longitudinal lines; stipules 0.4–2 mm long, not filiform distally; 0–1400 m elevation ..... 12
- 12a. Leaf blades usually minutely puberulent along the edges (glabrous on the broad flat surfaces), to 25 mm long; seeds transversely ridged abaxially, often with rounded pits on the lateral sides ...  
..... *P. urinaria*
- 12b. Leaf blades glabrous throughout, to 12 mm long; seeds longitudinally ridged or with faint longitudinal lines, transverse ridges minute ( $\times 50$ ) between the longitudinal ridges or lines, lateral walls often with concentric C-shaped ridges, never with pits ..... 13
- 13a. Female sepals narrow and acute at the apex; seeds with 4–7 prominent longitudinal ridges on the dorsal (abaxial) surface, 0.8–1.2 mm long; fascicles bisexual with 1  $\delta$  and 1  $\eta$  flower; moist to dry sites (not usually inundated) ..... *P. amarus*
- 13b. Female sepals broadly obtuse to rounded at the apex; seeds with 5–11 slightly elevated longitudinal ridges or lines on the abaxial surface, 0.9–1.4 mm long; fascicles unisexual,  $\delta$  flowers 3–10/fascicle; plants often growing in moist soil or in standing water ..... *P. stipulatus*

**Phyllanthus acidus** (L.) Skeels, U.S. Dept. Agric. Bur. Pl. Ind. Bull. 148: 17. 1909. *Averrhoa acida* L., Sp. Pl. 428. 1753. *Cicca disticha* L., Mant. Pl. 124. 1767. *P. distichus* (L.) Müll. Arg. in DC., Prodr. 15 (2): 413. 1866.

Small trees or shrubs, 2–6(–8) m tall, leafy stems 0.7–2 mm thick, borne on woody branchlets 3–8 mm thick, glabrous; stipules 0.3–1 mm long, triangular, appressed, deciduous. **Leaves** distichous on slender stems, petioles 1.5–4 mm long, 0.4–1.1 mm thick, glabrous, drying dark; **leaf blades** 2.5–7 cm long, 1.5–4.5 cm wide, ovate-elliptic to oblong-orbicular, acute to rounded at the apex, base obtuse or rounded-truncate, glabrous, varying from chartaceous and glaucous to thinner and greenish when dried, 2° veins 5–6/side. **Inflorescences** terminal or borne from older leafless nodes,  $\delta$  6–16 cm long,  $\eta$  to 3 cm long, racemose, glabrous, floral bracts 0.5–1 mm long;  $\delta$  flower with 4 sepals and stamens. **Fruits** 6–10 mm long, 7–20 mm diam., oblate, fleshy and with longitudinal ridges, only 1 or 2 locules usually developing, edible.

*Phyllanthus acidus* is recognized by the thicker branchlets bearing slender stems with short-petiolate leaves (resembling a rachis with pinnate leaves), lack of pubescence, racemose  $\eta$  inflorescences and fleshy fruits. The leaves are sometimes ovate-suborbicular. This native of South Asia has become naturalized in parts of seasonally dry northern Central America; it is often grown for the acidic fruits, which are cooked and used in preserves. It is called *grosea* and *grosella* in Central America.

**Phyllanthus acuminatus** Vahl, Symb. 95. 1791. *P. conami* Sw., Prodr. 28. 1788, as to descrip. not as to type. *P. brasiliensis sensu* auct., non *P. brasiliensis* (Aubl.) Poir. (See Webster in J. Arnold Arbor. 38: 366, 1957). Figure 9.

**Shrubs** or small trees 2–8 m tall, monoecious, with distal pinnatifid unbranched twigs 0.5–3.5 mm thick, minutely (0.05–0.2 mm) papillate-puberulent, greenish; stipules 0.4–1.3 mm long, deciduous. **Leaves** with petioles 1–3 mm long, 0.3–0.6 mm thick, minutely puberulent; **leaf blades** 1.6–5.8 cm long, 0.8–2.5 cm wide, ovate, ovate-elliptic, ovate-lanceolate or lanceolate (elliptic), tapering abruptly or gradually to an acuminate (acute) apex, base obtuse to acute (rounded), drying thinly chartaceous, very minutely papillate-puberulent or scabridulous above, smooth and glabrous beneath, 2° veins 3–5/side, arcuate-ascending. **Inflorescences** usually bisexual with fascicles of 5–25  $\delta$  flowers and 1  $\eta$  female flower, fascicles sometimes borne on short (1–2 mm) peduncles, the  $\delta$  flowers developing sequentially (often after anthesis of the  $\eta$ ),  $\delta$  pedicels 1.5–4 mm long,  $\eta$  pedicels to 17 mm long in fruit. **Male flowers** 1–1.5 mm wide, sepals 6 in 2 unequal whorls, outer sepals ca. 1  $\times$  0.5 mm and narrowly oblong, inner sepals 0.9–1.2 mm long, rounded or obtuse, disk segments 3, reniform, ca. 0.3 mm high; stamens 3, staminal column 0.1–0.3 mm long, ca. 0.7 mm wide at the flat 3-angled apex, anthers ca. 0.2 mm long, ovate, dehiscing laterally. **Female flowers** with 5 sepals in 2 unequal whorls, outer 1.1–1.5 mm long, 0.5–0.9 mm wide, ovate to obovate, inner sepals 1.5–1.7 mm long, 1–1.3 mm wide, disk 3-lobed, ovary ca. 0.9 mm long, on a stipe 0.2–0.4 mm long, styles 3 (4), 0.4–0.6 mm long. **Fruits** 3.7–4 mm long, 4–5 mm diam., with smooth rounded surfaces and 3 (4) sulci, columella 1.7–2.5 mm long, narrowed toward the apex; seeds often connivent in seed pairs, 2.6–3.3 mm long, 2.5–2.9 mm wide, 1.8–2.4 mm thick, ovoid-subglobose, lustrous, usually brown, with a longitudinal sulcus when connate in a seed pair.

Common plants of open secondary growth in both evergreen and deciduous forest formations, 0–1700 m elevation. Flowering primarily in May–July; fruiting primarily in June–August. The species ranges from Mexico and the West Indies to Argentina.

*Phyllanthus acuminatus* is recognized by the consistently smaller leaf blades that are usually



ovate to ovate-lanceolate with narrowed acuminate apices and the minutely papillate-puberulent (scabridulous) upper surfaces, which contrast with the glabrous lower (abaxial) surfaces. The seeds of the same locule tend to remain together as a seed pair. Despite its broad geographic range, this species has a sparse and weedy distribution in Costa Rica, suggesting that it may have been introduced. *Chilillo* and *gallina* are common names.

**Phyllanthus amarus** Schum. & Thonn., Beskr. Guin. Pl. 421. 1827; Kongl. Danske Vidensk Selsk. Skr. 4: 195. 1829. (See J. Arnold Arbor. 37: 6–8, 1956, and 38: 313–315, 1957.) Figure 8.

**Herbs** or subshrubs with woody base, 15–90 cm tall, monoecious, usually with a single main stem and pinatifid lateral branches 3–12 cm long with 10–36 leaves, internodes 1.5–6 mm long, leafy rachis 0.2–0.5 mm, glabrous, smooth and terete; stipules 0.5–1.3 mm long, linear-subulate, often unequal. **Leaves** with petioles 0.2–0.5 (–0.7) mm long, 0.1–0.2 mm thick, glabrous, articulate at base; **leaf blades** (2.5–)4–12 mm long, 2–5 mm wide, oblong to oblong-obovate, apex rounded to bluntly obtuse, base asymmetric, rounded or cuneate, drying thinly chartaceous, glabrous, 2° veins 3–5/side. **Inflorescences** axillary, bisexual or of solitary ♀ flowers, each fascicle usually with 1 ♀ and 1 ♂ flower, ♂ pedicels 0.6–1 mm long, ♀ pedicels to 2 mm long in fruit. **Male flowers** with 5 (6) sepals, 1.2–1.7 mm long, 0.3–0.7 mm wide; stamens 3 (2), staminal column 0.2–0.3 mm long. **Female flowers** with 5 sepals, 0.7–1 mm long, ca. 0.3 mm wide, narrowly oblong or oblong-obovate, rotate or becoming reflexed; ovary smooth, styles 0.1–0.2 mm long. **Fruits** 1–1.3 mm long, 1.3–2 mm wide, smooth, columella 0.7–0.9 mm long, 0.1–0.2 mm thick, cylindric; seeds 0.8–1 mm long, 0.5–0.7 mm wide, wedge-shaped (trigonus), yellowish, with 3–6 longitudinal ribs on the curved dorsal (abaxial) surface, inner lateral surfaces smooth or with concentric C-shaped ridges.

Plants of open sites in evergreen and partly deciduous forest regions, 0–300 m elevation. Collected with flowers and fruit in February–September. This species, probably native to the Americas, is now a pantropical weed.

*Phyllanthus amarus* is distinguished by its low-elevation habitats (in Costa Rica), small oblong leaves, few-flowered bisexual fascicles, small sepals subtending the yellowish fruit, and unusual

seed surfaces. The longitudinal ridges on the dorsal surface of the seeds have very minute transverse pitting between them ( $\times 50$ ). Superficially, this species is easy to confuse with *P. niruri*, *P. urinaria*, and *P. stipulatus*.

**Phyllanthus caroliniensis** Walter, Fl. Carol. 228. 1780. Figure 8.

**Herbs** 4–40 (–60) cm tall, monoecious, usually with 1 main stem and few to many erect lateral branches, both main and lateral stems with leaves, leafy stems 0.2–2 mm thick, glabrous, terete or with slightly elevated longitudinal ridges terminating at the petioles; stipules 0.5–1 (–2) mm long, lanceolate-triangular, persisting. **Leaves** longer on the main stems than on the laterals, petioles 0.4–1.3 mm long, ca. 0.2 mm thick, glabrous; **leaf blades** 5–14 (–18) mm long, 2–6 (–8) mm wide, elliptic to broadly elliptic, elliptic-oblong or elliptic-obovate, apex obtuse to rounded, base obtuse to cuneate, drying membranaceous or thinly chartaceous, glabrous, 2° veins 3–5/side, usually readily visible. **Inflorescences** axillary, bisexual or unisexual, sessile, with 1–2 ♂ flowers and 1–2 ♀ flowers, ♀ pedicels to 1.2 mm long in fruit. **Male flowers** with 6 (5) sepals 0.5–0.7 long, disk with 6 segments; stamens 3, filaments free, short. **Female flowers** with usually 6 sepals, 0.5–1.4 mm long, 0.1–0.3 mm wide, linear to narrowly oblong, style ca. 0.5 mm long. **Fruits** 0.9–1.3 mm long, 1.5–2 mm wide, oblate, rounded and smooth, columella ca. 0.4 mm long; seeds 0.7–1 mm long, 0.4–0.7 mm wide, wedge-shaped, smooth, dull brown, minutely rugulose (barely visible at  $\times 10$ ) with minute (0.02 mm) dark lustrous spots in poorly defined longitudinal ranks on all surfaces.

Plants of open sunny sites or in early secondary vegetation, 20–1400 m elevation. Probably flowering and fruiting primarily in the wet season or in wet sites. The species ranges from the eastern United States (Pennsylvania) to Argentina.

*Phyllanthus caroliniensis* is recognized by its small weedy habit, small leaves on both 1° and 2° axes, few-flowered fascicles of minute flowers, and small seeds with unusual surface ( $\times 50$ ). The species has rarely been collected in Costa Rica. Compare the very similar *P. compressus*, which is also infrequently collected in Central America. Webster and Burch (1968) distinguish two subspecies of *P. caroliniensis* in Panama; the following key follows their discussion.

- 1a. Stems terete or slightly flattened distally but not distinctly winged; main stems usually with a number of lateral branches; plants of open weedy habitats. . . . . ssp. *caroliniensis*
- 1b. Stems terete with sharp and narrowly winged ridges ca. 0.1 mm high distally; plants with no, few, or many lateral branches; plants of wet soils in open sites . . . ssp. *stenopterus* (Müll Arg.) Webster

**Phyllanthus compressus** H.B.K., Nov. gen. sp. 2: 109. 1817. Figure 8.

**Herbs** 6–30 cm tall, monoecious, often many-branched, all stems with leaves, leafy stems 0.5–1.5 mm thick, glabrous, distally flattened and with thin longitudinal ridges terminating beneath the petioles; stipules 1–2 mm long, narrowly triangular or subulate, often with basal auriculate lobes, persisting. **Leaves** with petioles to 1 mm long, glabrous; **leaf blades** 6–15 mm long, 3–8 mm wide, broadly elliptic to elliptic-oblong or oblong-obovate, apex broadly obtuse or rounded, drying chartaceous and often grayish, glabrous, 2° veins 3–5/side, often loop-connected near the margin but usually obscure. **Inflorescences** axillary, usually bisexual fascicles with 1–2 ♂ flowers and 1–2 ♀ flowers, glabrous, ♂ pedicels to 1 mm long, ♀ pedicels to 1 mm long, often becoming reflexed. **Male flowers** with usually 5 calyx lobes 0.5–0.7 mm long, 0.5–0.7 mm wide, disk segments 5; stamens 3, filaments ca. 0.5 mm long, partly united, anthers opening horizontally. **Female flowers** with 5 (6) calyx lobes 0.6–0.8 mm wide, obovate, disk entire; ovary smooth, styles ca. 0.4 mm long. **Fruits** 1.7–2 mm wide, oblate, columella 0.5–0.7 mm long; seeds 0.9–1.2 mm long, wedge-shaped, brown.

Weedy plants of open moist sites. The species has not been collected in Costa Rica but is known from many other areas of Central America.

*Phyllanthus compressus* is very similar to *P. carolinensis*, which is also infrequently collected in Central America. The two species are separated by the characters used in the key to species. They share the unusual surface of the seeds (see under *P. carolinensis*) as well as a very similar appearance.

**Phyllanthus hyssopifolioides** H.B.K., Nov. gen. sp. 2: 108. 1817. Figure 8.

**Herbs** 12–40 cm tall, monoecious, with few lateral branches, all stems bearing leaves, 0.4–2 mm thick, glabrous, slender longitudinal ridges ca. 0.2 mm high from the base of the petioles; stipules 0.5–1.5 mm long. **Leaves** with petioles 0.2–0.8 mm long, 0.2–0.3 mm wide, glabrous, base continuous with stem ridges; **leaf blades** 5–16 mm long, 1.5–5 mm wide, elliptic-oblong to narrowly elliptic or narrowly ovate-elliptic, apex acute, base obtuse to acute, drying chartaceous and dark, glabrous, 2° veins 2–4/side, usually obscure. **Inflorescences** axillary, unisexual, ♂ fascicles with few flowers, ♀ flowers solitary, ♀ pedicels 1–2 mm long. **Male flowers** ca. 1.2 mm wide, sepals 5, 0.4–0.7 mm long, 0.4–0.7 mm wide, ovate to obovate; stamens 3, filaments ca. 0.1 mm long, anthers 0.1–0.2 mm wide. **Female flowers** with 6 sepals, 0.5–1 mm long, ca. 0.4 mm wide, oblong to narrowly ovate, with pale margins; style branches ca. 0.2 mm long. **Fruits** 1.8–2 mm long, 2.6–3 mm wide, oblate, rounded and smooth, yellowish; seeds 1.3–1.6 mm long, 1.1–1.2 mm wide, wedge-shaped, brown and lustrous, lateral faces often slightly concave.

Plants of moist sites in lowland evergreen forest and seasonally wet savanna formations, 0–400 m elevation. Flowering and fruiting in July–August. Locally common but rarely collected in Costa Rica and Panama, the species is disjunct in the Dominican Republic, southern Central America, and northern South America.

*Phyllanthus hyssopifolioides* is recognized by its short stature, preference for wet sites, narrow leaves usually tapering to an acute apex, few-flowered inflorescences, and dark lustrous seeds. We have seen only one Costa Rican collection (*Zamora & Chacón 1389*) from Refugio Caño Negro, Alajuela, where it was common at the edge of a seasonal lake.

*Phyllanthus leptobryosa* J. D. Smith is *Hyperbaena leptobryosa* (J. D. Smith) Standl. of the Menispermaceae.

**Phyllanthus mocinianus** Baill., *Adansonia* 1: 35. 1860. *P. anisolobus* Müll Arg. in DC., *Prodr.* 15 (2): 382. 1866, ex char. *P. pittieri* Pax, *Anal. Inst. Fis.-Geogr. Nac. Costa Rica* 9: 195. 1898; and in Pittier, *Prim. Fl. Costar.* 2 (5): 327. 1900. Figure 9.

**Shrubs** or small trees 1–4(–8) m tall, monoecious, deciduous leafy branches to 55 cm long, appearing bipinnatifid with 5–12 alternating pinnatifid branchlets to 30 cm long, leafy stems 0.3–3 mm thick, glabrous, with 2 longitudinal ridges in early stages, terete; stipules 0.5–1.3 mm long, triangular, thin, persisting. **Leaves** with petioles 2–3 mm long, 0.2–0.4 mm thick, glabrous; **leaf blades** 11–40 mm long, 9–28 mm wide, broadly ovate to broadly elliptic or suborbicular, obtuse to rounded at the apex, base obtuse to rounded and subtruncate, drying grayish green, membranaceous or thin-chartaceous, glabrous, 2° veins 4–7/side. **Inflorescences** axillary, usually fasciculate with 1–12 ♂ flowers and 1 ♀ flower or with solitary ♀ flowers, ♂ pedicels 3–10 mm long, filiform, ♀ pedicels 6–13 mm long. **Male flowers** whitish with green center, sepals 6 (5), 1.2–2.5 mm long, outer 0.7–0.8 mm wide, inner sepals 1–1.5 mm wide, disk ca. 1 mm wide, of 3 (6) large rounded parts; stamens 3, united into a column 0.4–1 mm long, apex of the column and anthers 0.5–1 mm wide, anthers 0.3–0.4 mm long, thecae separate. **Female flowers** 1.8–2.5 mm wide, sepals 6, slightly larger than the ♂, disk usually confluent to form a 3-lobed cup 0.5 mm high; ovary 0.9–1.7 mm long, 1–1.6 mm diam., smooth, style column 0–0.4 mm long, branches ca. 0.5 mm long, held horizontally. **Fruits** 2.5–3 mm long, 3–4.5 mm wide, oblate, columella 1.3–1.7 mm long; seeds 1.9–2.3 mm long, 1.3–1.7 mm wide, seed pairs ca. 2 mm wide, surfaces pale or dark brown with longitudinal ridges or smooth.

Plants of evergreen and partly deciduous forest areas (often found along streams), 100–1300 m elevation (20–2100 m in Mexico and Guatemala).



Flowering in April–August; fruiting in July–October. The species (in a wide sense) ranges from Mexico to Peru.

*Phyllanthus mocinianus* is recognized by the small rounded glabrous leaves, seeds often remaining as seed pairs, and whitish ♂ flowers with completely united filaments. Leaf blades vary from small (ca. 12 mm) ovate-orbicular to longer (3–4 cm) ovate-elliptic in different plants. The anthers are unusual because the thecae are divergent and form six peripheral rounded lobes on the apically flattened staminal column. This species has the stamens more closely connate than does *P. micrandus* Müll. Arg. of northern South America. Specimens earlier determined as *P. micrandus* in Mexico and Central America are this species or *Phyllanthus mcvaughii* Webster (southern Mexico to El Salvador). That species is virtually identical in appearance to the material placed here; however, *P. mcvaughii* has six narrowly oblong thecae peripheral on the margins of the flat-topped edges of the umbrella-like androecium and appears to grow only at higher elevations (see Brittonia 18: 336–342, 1966). It is possible, as a reviewer has suggested, that we are incorrect in submerging *P. anisolobus* under *P. mocinianus* and that the lower right section of Figure 9 is characteristic of *P. anisolobus* (including *P. pittieri*).

***Phyllanthus niruri* L., Sp. Pl., 981. 1753. *P. lathyroides* H.B.K., Nov. gen. sp. 2: 110. 1817. Figure 8.**

**Herbs** or subshrubs with woody base, 10–120 cm tall, monoecious, usually with a single main stem and slender pinnatifid lateral branches 3–12 cm long with 16–36 leaves and internodes 3–6 mm long, leafy rachis 0.3–0.6 mm thick, glabrous; stipules 0.5–2.7 mm long, linear-subulate to filiform, often unequal, persisting. **Leaves** with petioles 0.2–0.5 mm long, ca. 0.2 mm thick, glabrous; **leaf blades** (4–)5–12(–16) mm long, (1.5–)2.5–5(–8) mm wide, oblong or elliptic-oblong (rarely obovate, elliptic), apex broadly obtuse or rounded, often apiculate at the tip, base broadly cuneate or obtuse and slightly unequal, drying thinly chartaceous, glabrous above and below, 2° veins 4–7/side, ascending along the margin to form a submarginal vein. **Inflorescences** axillary, unisexual, glabrous, proximal nodes with 3–5(–7) ♂ flowers, distal nodes with solitary ♀ flowers, ♂ pedicels 1–2 mm long, ♀ pedicels to 6 mm long in fruit. **Male flower** buds 0.7–1 mm diam., to 3 mm wide at anthesis, sepals 5 (6), free or connate to 50%, lobes 0.5–1.5 mm long, disk ca. 0.8 mm wide, with 5 rounded parts; stamens 3, filaments free or united, 0.4–1 mm long, anthers 0.2 mm long. **Female flowers** with 5 sepals, enlarging in fruit to 2.5–3 mm long, 1–2 mm wide, yellowish or marked with red; ovary smooth, styles 0.5–0.6 mm long, bifid in the distal 0.2–0.3 mm. **Fruits** 2.5–3 mm long, 3–4 mm wide, ob-

late, surfaces smooth, yellowish, columella 0.5–1.2 mm long, narrowly conical; seeds 1.7–2 mm long, 1.1–1.3 mm wide, wedge-shaped (trigonal), surface minutely rugulose or punctate with minute rounded projections in longitudinal ranks ( $\times$  50).

Plants of open sites in lower montane evergreen forest areas, 1000–2500 m elevation. Flowering and fruiting throughout the year. The species ranges from Texas to Argentina.

*Phyllanthus niruri* is distinguished by its montane habitats, persisting filiform stipules, small oblong glabrous leaves, few-flowered ♂ fascicles, conspicuous sepals subtending the fruit, and larger darkly colored seeds with unusual surface. The secondary veins are loop-connected near the margin, but this is often difficult to see. These characteristics help to distinguish this species from the superficially rather similar *P. amarus*, *P. stipularis*, and *P. urinaria*.

***Phyllanthus salviifolius* H.B.K., Nov. gen. sp. 2: 117, pls. 107, 108. 1817.**

**Shrubs** or small trees 3–5(–8) m tall, monoecious, leafy stems 0.7–6 mm thick, usually densely puberulent with short (0.2 mm) multicellular hairs (rarely subglabrous); stipules 4–7 mm long, 0.3–1.5 mm wide, linear to lanceolate, persisting. **Leaves** distichous on distal branchlets that may be deciduous (as in a pinnate leaf), petioles 2–4 mm long, usually puberulent; **leaf blades** 3–12 cm long, 1.8–4 cm wide, oblong-lanceolate to narrowly ovate-triangular, tapering gradually to the acute apex, base rounded to truncate or subcordate, drying chartaceous and brownish green, with short (0.2 mm) hairs on both surfaces but the hairs denser and more curled beneath (rarely subglabrous), 2° veins 11–17/side, parallel and strongly ascending. **Inflorescences** bisexual or unisexual, of 5–15 flowers in dense axillary clusters, often small corymbs with short (0–4 mm) peduncles and short 2–5 mm few-branched rachis; pedicels of ♂ flowers 3–5 mm long, glabrous, pedicels of ♀ flowers becoming 4 cm long in fruit, ca. 0.3 mm thick, glabrous. **Male flowers** greenish yellow or reddish, calyx in 2 subequal whorls of 3 each, 1.5–2 mm long, oblong and rounded distally, disk a short cup; stamens 3–9, filaments united into a short column. **Female flowers** reddish or purplish, sepals 6, subequal, 4–5 mm long, 2–2.8 mm wide, ovate-oblong, rounded at apex, disc forming a short cup; ovary ca. 1.3  $\times$  2 mm, glabrous, styles ca. 3 mm long, united only near the base, stigmas ca. 0.5 mm long, twisted, red. **Fruits** 4–4.5 mm long, 5–6 mm wide, oblate to rounded-oblong, surfaces smooth, subtended by the persisting perianth; seeds 2.5–2.8 mm long, ca. 2 mm wide, wedge-shaped, with fine longitudinal ridges abaxially and concentric C-shaped ridges on the sides.

Known only from the Cerros de Escazú, south of San José (*G. Vargas* 679 F, USJ) in Costa Rica.



The species grows from 1800 to 3500 m elevation in the northern Andes, Venezuela, to Peru.

*Phyllanthus salviifolius* is recognized by its short-petiolate leaves with usually lanceolate blades, many parallel ascending secondary veins, and axillary clusters of ♀ or ♂ flowers. With only a single collection made in Central America, not far from a densely populated region, it seems likely that this species is a recent introduction.

***Phyllanthus skutchii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 347. 1940. Figure 25.**

Trees 8–45 m tall, trunks to 1 m diam., bark lightly fissured to deeply furrowed and rough brown, wood pale and soft, monoecious, leafy stems 0.7–3 mm thick, glabrous, terete; stipules 0.5–2 mm long, narrowly triangular, acute to acuminate, glabrous or minutely puberulent, persisting. **Leaves** distichous, petioles 2–6 mm long, 0.7–1.2 mm thick, glabrous, drying dark and wrinkled; **leaf blades** 5–11 cm long, 1.7–4 cm wide, ovate-elliptic to oblong-lanceolate or narrowly elliptic-oblong, apex acuminate with narrow tip, margin slightly thickened at the petiole, base obtuse or slightly rounded, drying chartaceous, glabrous or with few minute hairs near the base beneath, 2° veins 6–10/side, ascending. **Inflorescences** axillary, glabrous, unisexual, proximal fascicles of 15–30 ♂ flowers, distal fascicles with 1–9 ♀ flowers, each ♂ flower subtended by a series of imbricate bracts, peduncles 1–3 mm long, ♂ pedicels to 5 mm long, fruiting pedicels 3–7 mm long. **Male flower** buds ca. 1.5 mm diam., sepals usually 6, outer ca. 1.7 × 1 mm, inner ca. 1.2 × 0.7 mm, broadly obovate to oblong, rounded distally, glabrous, disc with ca. 12 peripheral lobes; stamens 3, free, filaments ca. 0.4 mm long, thick, anthers ca. 0.4 mm wide, dehiscing horizontally. **Female flowers** with 6 (7) unequal sepals, 2–2.8 mm long in fruit, 1–2.7 mm wide, narrowly oblong to obovate, disc flat or a thin cup with rounded lobes ca. 0.5 mm long, ovary 4- (5-)locular. **Fruits** 7–9 mm diam., globose, with a thin fleshy smooth covering, persisting style base ca. 0.5 mm high, walls of the cocci thin; seeds ca. 7 × 3.5 mm, wedge-shaped, trigonous in cross-section.

Rarely collected trees of evergreen forest formations, 20–900 m elevation. Flowering in January and May; fruiting material was collected in May–June and December. This endemic species is known only from the General Valley (*Skutch* 4325 the type, 5427, 5491), near Golfito (*Aguilar* 746, *Schmidt* 594), and in the Braulio Carillo National Park (*Hammel et al.* 17820).

*Phyllanthus skutchii* is recognized by its tall stature and normal-sized foliage (unusual in *Phyllanthus*), lack of pubescence, usually unisexual fascicles, six-parted perianth, free stamens, four-locular ovary, and eight-seeded fleshy fruits. The leaves resemble some other genera of Euphorbiaceae (e.g., *Margaritaria*) and some Flacourti-

aceae. This species is another example of Alexander Skutch's important contribution to our knowledge of Costa Rica's flora.

***Phyllanthus stipulatus* (Raf.) Webster, Contr. Gray Herb. 176: 13. 1955. *Moeroris stipulata* Raf., Sylva Tellur. 91. 1838. Figure 8.**

**Herbs** or slender shrubs 10–90 cm (to 2 m?) tall, monoecious, often with 1 main stem and alternate lateral pinnatifid leafy stems 2–7 cm long with 10–30 leaves, 0.2–0.4 mm thick, glabrous; stipules 0.5–0.8 mm long, linear to lanceolate, persisting. **Leaves** closely (0.7–3 mm) spaced, petioles 0.3–0.6 mm long, ca 0.2 mm thick, glabrous; **leaf blades** 2.5–7(–8) mm long, 0.8–3(–4) mm wide, narrowly oblong to narrowly elliptic-oblong, apex bluntly obtuse to slightly rounded, base cuneate to rounded and somewhat unequal, drying thinly chartaceous, grayish beneath, glabrous, smooth or slightly scabridulous, 2° veins 3–6/side, usually obscure. **Inflorescences** axillary, unisexual, proximal nodes with 3–10 ♂ flowers, distal nodes with solitary ♀ flowers, ♂ pedicels 0.3–0.7 mm long, ♀ pedicels becoming 2 mm long in fruit. **Male flowers** with 5 sepals, 0.5–1 mm long, disk entire or lobed; stamens 3 (2), united into a column 0.2–0.3 mm long, anthers dehiscing horizontally. **Female flowers** with 5 sepals, 0.7–1.8 mm long, 0.4–1.2 mm wide, usually obovate and bluntly obtuse to rounded at the apex; styles 0.2–0.3 mm long, free. **Fruits** 1.2–2 mm long, 2–2.7 mm wide, surfaces rounded, columella 0.7–0.8 mm long, ca. 0.2 mm thick; seeds 0.9–0.14 mm long, 0.7–0.9 mm wide, wedge-shaped (trigonous), abaxial surface with 5–11 thin longitudinal ridges or lines and many minute parallel transverse ridges (× 50) between them.

Plants of moist sites or growing in shallow water in evergreen forest areas, 0–1200 m elevation. Probably flowering and fruiting throughout the year. This species ranges widely through the American tropics.

*Phyllanthus stipulatus* is recognized by its preference for wet sites, lack of pubescence, small oblong leaves, solitary female flowers, and seeds with unusual abaxial surface. Plants growing in water often develop spongy (aerenchymatous) stems and roots. The stems are often reddish. Compare *P. amarus* with very similar seeds but few-flowered bisexual inflorescences.

***Phyllanthus urinaria* L., Sp. Pl. 982. 1753. Figure 8.**

**Herbs** or shrubs 10–90 cm high, erect or arching over, monoecious, usually with 1 main stem and shorter pinnatifid lateral stems with 20–35 leaves, leafy stems 0.3–0.7 mm thick, minutely (0.1–0.3 mm) ciliolate along the slender longitudinal ridges (glabrous); stipules 1–1.5 mm long, lanceolate to subulate, persisting (stipule-like structures at base of leafy branchlets to 2 mm long). **Leaves**

with petioles 0.3–0.5 mm long, ca. 0.3 mm thick, usually glabrous; **leaf blades** 4–14(–25) mm long, 1.5–5(–9) mm wide, narrowly oblong to narrowly oblong-obovate, apex obtuse to rounded-truncate, base often asymmetrical, rounded or slightly auriculate at the petiole, drying thin-chartaceous, grayish green to yellowish green, glabrous except for the minute (0.05–0.1 mm) hairs along the edge, 2° veins 3–5/side, ascending. **Inflorescences** axillary, sessile, unisexual, proximal nodes with solitary ♀ flowers, distal nodes with fascicles of 5–7 ♂ flowers, ♂ pedicels ca. 0.5 mm long, ♀ pedicels 0–0.05 mm long. **Male flowers** with 6 sepals, less than 0.5 mm long, disk crenulate; stamens 3, united into a column, anthers dehiscing vertically. **Female flowers** with 6 sepals, 0.5–1 mm long, 0.2–0.4 mm wide; ovary 0.7–1 mm long, subglobose, with scale-like processes on the surface, styles connate, bifid at apex. **Fruits** 1.3–1.7 mm long, 2.2–2.5 mm wide, oblate and rounded with 3 or 6 sulci, columella 0.7–1 mm long, darker at the acute apex; seeds 1.1–1.4 mm long, 0.7–0.9 mm wide, wedge-shaped, dorsal surface with ca. 10 transverse ridges, often with 1–3 pits on the lateral side.

Plants of open sunny sites in moist evergreen areas, 0–1400 m elevation. Fruiting throughout the year in Costa Rica. A native of tropical Asia now widely naturalized in the American tropics.

*Phyllanthus urinaria* is recognized by its small oblong leaves usually with minute hairs along the margins and seeds with transverse ridges across the back. The leaves are reported to be “sensitive,” folding up after contact. This species has been used as a medicinal herb and called *chancapiedras* (Bel-lo & Rojas 2302) and *riñoncillo* (Sánchez & Zamora 150) in Costa Rica.

*Phyllanthus valerii* Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 619. 1937. Figure 9.

**Shrubs** or small few-branched treelets 0.5–5 m tall, monoecious, with distal unbranched pinnatifid lateral stems 5–30 cm long and 10–40 leaves, leafy stems 0.4–2 mm thick, sparsely to densely minutely (0.05–0.2) papillate-puberulent, terete; stipules 2–4 mm long, 0.3–0.5 mm wide at the base, linear-lanceolate, persisting. **Leaves** with petioles 0.5–1.5 mm long, 0.3–0.4 mm thick, glabrous or sparsely papillate-puberulent; **leaf blades** 5–22(–30) mm long, 2.5–9(–12) mm wide, oblong-obovate to elliptic oblong or oblong, apex obtuse to rounded (acute), base obtuse and slightly assymmetric, drying chartaceous, glabrous, 2° veins 4–8/side, ascending and often weakly connected near the margin. **Inflorescences** axillary, unisexual or bisexual, fascicles with 3–5 ♂ flowers or solitary ♀ flower, glabrous, bracts stipule-like, ♀ pedicels to 3 mm long in fruit. **Male flowers** whitish, sepal lobes 5, 1–1.5 mm long, 1–1.5 mm wide, rounded distally, disk with 5 stalked glands 0.5–0.6 mm long with stipules ca. 0.3 mm long; staminal column ca. 1.2 mm long, 0.7–0.8 mm wide at the apex with 2–3 sessile anthers dehiscing horizontally. **Female flowers** with usually 6 sepals, 0.8–1.5 mm long, 0.6–1.1 mm wide, oblong to narrowly ovate (enlarging slightly in fruit); ovary ca. 0.8

mm diam., styles ca. 0.5 mm long. **Fruits** 1.7–2.2 mm long, 2.7–4 mm wide, oblate, rounded and slightly 3-lobed, smooth, yellowish, columella 1.3–1.7 mm long, 0.3–0.4 mm thick, narrowed distally; seeds 1.7–2 mm long, 1.3–1.4 mm wide, wedge-shaped with rounded edges, surface smooth ( $\times 10$ ) but with minute lustrous rounded punctations in poorly defined longitudinal rows ( $\times 50$ ).

Plants of wet evergreen montane forest formations along the central highlands, 1100–2100 m elevation. Probably fruiting throughout the year. The species is endemic to Costa Rica, ranging from the Cordillera de Tilarán eastward to the western slopes of the Cordillera de Talamanca (Tapantí).

*Phyllanthus valerii* is recognized by its restricted montane habitat, leaves that are somewhat larger than most of our other species of *Phyllanthus* with narrowly oblong leaves, minute pubescence on leafy stems, slender persisting stipules, and few-flowered inflorescences. Characteristics of seed surface and flowers suggest a relationship with *P. niruri*.

## Plukenetia Linnaeus

REFERENCE—L. J. Gillespie, A synopsis of Neotropical *Plukenetia* (Euphorbiaceae) including two new species. Syst. Bot. 18: 575–592. 1993.

Vines or lianas, young stems with short thin simple hairs; stipules small, deciduous. **Leaves** alternate, petiolate, blades entire or minutely dentate, venation pinnate or palmate, sessile glands usually present near the petiole. **Inflorescences** terminal, leaf-opposed or axillary, narrowly panicle to thyrsoid or racemose, bisexual or ♂, ♀ flowers 1–2 and basal, ♂ flowers in distal glomerules along an unbranched rachis, bracts small and without glands. **Male flowers** pedicellate, calyx divided into 3–5 parts, petals absent, receptacle slightly to distinctly conical, interstaminal disk of segments or absent; stamens 10–40, filaments free or united at base, anthers 4-theous, connective apiculate; pistillode absent or minute. **Female flowers** pedicellate, calyx 4-parted, slightly imbricate, petals and disk absent, staminodes absent; ovary with 4 locules, ovules 1/locule, styles connate for  $\frac{1}{2}$  or more of their length, often thick, simple or obscurely bifid. **Fruits** capsules, cocci smooth to carinate or winged; seeds lenticular to globose, smooth or ridged, ecarunculate, endosperm present, cotyledons ovate.

A tropical genus of about 16 species, absent from Australia. The slender vining stems, gland-bearing denticulate leaves, minute ♂ flowers with many stamens, and unusual oblate four-lobed, four-seeded capsules help distinguish our material. The two species included here are uncommon in Central America.



## Key to the Species of *Plukenetia*

- 1a. Leaf blades mostly ovate with palmate or subpalmate venation, stipels (glands) present at apex of petiole; inflorescences usually terminal or leaf-opposed; capsules 25–35 mm wide ... *P. stipellata*
- 1b. Leaf blades mostly oblong with pinnate venation, stipels or glands absent at apex of petiole; inflorescences axillary; capsules ca. 15 mm wide ..... *P. penninervia*

***Plukenetia penninervia* Müll Arg., Linnaea 34: 158. 1864. *P. angustifolia* Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 314. 1929. Figure 31.**

Vines, woody near the base, leafy twigs 0.8–3.5 mm thick, with minute (0.1–0.2 mm) thin erect hairs, soon glabrescent; stipules ca. 1 mm long. **Leaves** with petioles 4–14 mm long, 0.9–1.6 mm thick, often thickened near the apex, minutely puberulent; **leaf blades** 6–16 cm long, 2–6 cm wide, narrowly elliptic-oblong to oblong or oblong-lanceolate, apex acute to acuminate (rounded and short-acuminate), margin minutely (0.2 mm) glandular denticulate, base rounded to obtuse, with flat elliptic glands or glandular thickenings near the petiole on the adaxial surface, drying chartaceous, greenish, 2° veins 6–10/side. **Inflorescences** axillary, bisexual or ♂, 5–30 mm long, rachis unbranched and minutely puberulent, ♀ flower proximal and solitary, borne on slender pubescent pedicels 8–20 mm long, ♂ flowers with slender puberulent pedicels to 8 mm long. **Male flowers** with 3 sepals, 1–1.5 mm long, broadly elliptic or obovate; stamens ca. 14–18, dimorphic, outer 4–5 stamens with filaments ca. 0.2 mm long, inner 10–12 anthers sessile on the globose receptacle, anthers ca. 0.2 mm long. **Female flowers** with sepals 1–1.2 mm long, triangular, puberulent along the middle abaxially; ovary ca. 1.7 long, 2.5–3 mm diam., stylar column 1.6–2 mm long, ca. 0.8 mm thick. **Fruits** ca. 1 × 1.5 cm, oblate and prominently 4-lobed, tuberculate around the middle; seeds ca. 5 mm long, 3–4 mm thick.

Plants of evergreen lowland forest formations, 0–600 m elevation. Known in Costa Rica from only a single collection near Golfito (*Moreno et al.* 122 MO); flowering in January. The species ranges from southern Mexico to Venezuela and Peru.

*Plukenetia penninervia* is recognized by its slender-stemmed vining habit, oblong pinnately veined leaf blades glandular at the base, small unbranched inflorescences, and four-lobed oblate fruits.

***Plukenetia stipellata* L. J. Gillespie, Syst. Bot. 18: 588. 1993. *P. volubilis* auct. non L. (for Central American material, see below). Figure 5.**

Slender herbaceous vines or lianas, monoecious, leafy stems 0.7–3 mm thick, minutely (0.1 mm) papillate-puberulent, glabrescent; stipules 0.5–1 mm long. **Leaves** with petioles 20–60(–80) mm long, 0.6–1.3 mm thick, minutely puberulent, sulcate above, often geniculate at the base, usually with 2 small (0.3–1 mm) glands at the adaxial apex; **leaf blades** 6–15 cm long, 3–13 cm wide,

ovate to ovate-triangular, tapering gradually to the acuminate or caudate-acuminate apex, tip 4–20 mm long, margin minutely (0.2 mm) serrulate, base broadly obtuse to truncate or cordate, basal sinus 0–2 cm deep, with narrow oblong glands 1–2.2 mm long along the proximal basal edge 2–5 mm from the petiole, drying membranaceous to chartaceous, greenish, usually glabrous above, with minute (0.1 mm) hairs along the veins beneath, venation palmate or subpalmate, with 3 major veins, 2° veins 2–4/side of the midvein. **Inflorescences** terminal on short-shoots (axillary), solitary, 2.5–10 cm long, usually bisexual with 1 proximal ♀ flower and glomerules of ♂ flowers along a slender (0.5 mm) minutely puberulent unbranched rachis, ♂ pedicels 0.3–1 mm long, ♀ pedicels 2–8 mm long (to 25 mm in fruit). **Male flowers** buds ca. 1.5 mm diam., calyx lobes 5 (4), 1.8–3 mm long, triangular, stamens 25–40, filaments 1–1.2 mm long, anthers 0.3–0.4 mm long, with a gland at the apex of the connective. **Female flowers** ca. 8 mm long, sepals 1–2 mm long, 0.9–1 mm wide, narrowly triangular; ovary 2–7 mm diam., stylar column 6–11 mm long, ca. 1.3 mm diam., drying dark, glabrous, with 2 thick distal styles 1.3–2 mm long. **Fruits** 13–26 mm long, 22–35 mm wide, truncated at apex and base, with 4 prominent lateral lobes, surface smooth, columella 8–10 mm long, 6–8 mm wide at the apex; seeds 11–14 mm long, 9–12 mm wide, 5–6 mm thick, lenticular with an acute circumference, surface with raised ridges and minor reticulation.

Plants of evergreen forest formation, 0–800(–1200) m elevation. Flowering and fruiting primarily in the wet season, June–November. The range of the species in Costa Rica is unusual: collections have been made only north of the Río Pacuare in the Caribbean lowlands and from the Osa Peninsula area. The species is found in eastern and southern Mexico, Guatemala, and Nicaragua to Panama.

*Plukenetia stipellata* is recognized by the slender-stemmed vining habit, ovate leaf blades with distinctive glands at the lamina base, slender inflorescences with unusual ♀ flowers, and oblate prominently four-lobed fruits. The glabrous ovary with its thick stylar column may be mistaken for an immature corolla tube. Our material was formerly considered part of *P. volubilis*, but Gillespie (reference above) notes that *P. volubilis* lacks the glands at the apex of the petiole and has fewer stamens (16–30), thicker filaments, and a longer stylar column, and the staminate sepals are consistently four. However, with possible interme-



diate forms in Colombia and Venezuela, our material might also be interpreted as a subspecies of *P. volubilis*.

### *Richeria* Vahl

REFERENCE—R. Secco & G. L. Webster, *Mareriais para a flora amazonica IX. Ensaio sobre a sistemática de genero Richeria*. Bol. Mus. Para. Emilio Goeldi, Bot. 6: 141–158, 1990.

**Trees** or shrubs, dioecious, glabrous or with simple hairs; stipules enclosing the shoot apex, caducous. **Leaves** alternate, petiolate, margins entire or crenulate distally, pinnately veined, sometimes with glands at the base of the blade. **Male inflorescences** axillary, spicate with sessile flowers or racemose with sessile flowers in pedunculate glomerules, bracts subtending several small flowers;  $\delta$  **flowers** with 3–5-lobed calyx, lobes imbricate in bud, petals absent, disk segments 3–5, interstaminal; stamens 3–6, filaments free, exserted, anthers  $\pm$  versatile, oblong, dehiscing longitudinally, introrse or extrorse; pistillode minute. **Female inflorescences** axillary, solitary from the axil of a bract, shorter than the  $\delta$ , racemose, flowers solitary and pedicellate;  $\varphi$  **flowers** with 3–5-lobed calyx, lobes imbricate in bud, persisting in fruit, petals absent, disk cupulate or undulate, ovary 2- or 3-locular, glabrous or puberulent, ovules 2/locule, styles 2 or 3, short, thick, bifid at the tip. **Fruits** capsules but somewhat fleshy and dehiscing late, breaking into 2-valved cocci, 1-seeded, columella slender, dilated distally; seeds ecarunculate, outer testa fleshy, endosperm present, cotyledons broad, plane, basally cordate.

A Neotropical genus of five species, one reaching Costa Rica. See Webster and Huft (1988) for a short discussion of relationships of the genus and differentiation of the species found in Panama. Despite the bicarpellate ovaries, we take a broad view and include all Costa Rican material under *R. obovata* (see below).

*Richeria obovata* (Müll. Arg.) Pax & K. Hoffm., Pflanzenreich IV. 147. XV (Heft 81): 29. 1922. *Richeria grandis* var. *obovata* Müll. Arg. in DC., Prodr. 15 (2): 468. 1866. Figure 28.

**Trees** 9–30 m tall, trunks to 80 cm diam., leafy stems 2–5 mm thick, glabrous or with short (0.2–0.4 mm) thin hairs; stipules 4–6 mm long, 2–4 mm wide at the base. **Leaves** often crowded distally, petioles 7–40 mm, 1–2.5 mm thick, glabrous or puberulent with short hairs, without glands; **leaf blades** 6–22 cm long, 2.5–10 cm wide, obovate to elliptic-obovate or oblong-obovate, apex bluntly obtuse to rounded, margin entire or slightly crenate distally with minute glands in shallow (0.2 mm) sinuses, tapering gradually to the cuneate base and slightly decurrent on the petiole, often with 2 narrow glandular areas along edge near base, drying dark brown and stiffly chartaceous or subcoriaceous, glabrous or very sparsely

puberulent in early stages, 2° veins 5–8/side. **Male inflorescences** 1–4 at older or leafless nodes, 3–8 cm long, 0.5–1 mm thick, glabrous or with short irregular hairs 0.2 mm long, glomerules sessile, ca. 2 mm wide, subtended by minute irregular bracts ca. 1 mm long;  $\delta$  **flowers** with 3–5 calyx lobes, puberulent, filaments 1.3–2 mm long, 0.1 mm thick, glabrous; anthers 0.2–0.4 mm long, 0.2–0.3 mm wide. **Female inflorescences** from older leafless nodes (axillary), solitary, 2.5–12 cm long, rachis 1–1.5 mm thick, hirtellous, flowers subtended by 1–3 bracts (sometimes resembling a calyx) 1–1.5 mm long, triangular, acute, glabrous, pedicels 0.5–1 mm long;  $\varphi$  **flowers** with calyx ca. 3 mm wide, 5-parted, to 1.5 mm long, ovary 1.5–3 mm long, ovoid, covered with short yellowish hairs, 2-locular in Costa Rica (usually 3-locular in South America), style column ca. 1 mm long, 0.6 mm thick, style branches 0.5–1 mm long and recurved. **Fruits** 10–13 mm long (not including the 1–2 mm high style column), ca. 6–9 mm diam., ellipsoid or narrowly obovoid, glabrous or sparsely puberulent, smooth; seeds 6–10 mm long, covered with an orange or red aril.

Plants of evergreen forest formations on both the Caribbean and Pacific slopes, 50–900 m elevation (to 1200 m in western Panama). Flowering in June–July; fruiting in August–October. The species (in a wide sense) ranges from Costa Rica to southern Brazil.

*Richeria obovata* is recognized by its stiff subglabrous leaves with minute or linear glands along the entire margins, spicate inflorescences with sessile glomerules,  $\delta$  flowers with minute anthers, and ellipsoid fruits with colorful arillate seeds. In contrast to collections of this species from Amazonia, our plants have ovaries and fruits with two locules rather than three. This does not appear to be a significant distinction and can be found in some collections from Colombia (cf. Zarucchi *et al.* 7214). Amazonian material has considerably thicker leaves with more rounded apices, but Colombian material appears to be intermediate with ours. Some Costa Rican collections were misidentified as *R. dressleri* Webster, but that species has larger leaves with more secondary veins and larger foliaceous stipules. Collections placed here include Hammel *et al.* 18499; Hartshorn 1034, 1070, & 1305; Herrera 4452; and Zamora *et al.* 1443.

### *Ricinus* Linnaeus

Weak-stemmed **shrubs** or small trees, annual or persisting for several years, glabrous, often with extra-floral nectaries at the nodes; stipules united and solitary at the node, large and enclosing the shoot apex, entire, with parallel venation, deciduous. **Leaves** alternate, simple, long-petiolate and peltate, glabrous; leaf blades palmately lobed with serrate gland-tipped margins, venation palmate. **Inflorescences** terminal or axillary to distal

leaves, solitary, with a single thick rachis, bisexual (rarely ♀), ♂ flowers solitary or in alternate small fascicles along the rachis proximally, ♀ flowers distal on the rachis, short-pedicellate, subtended by stipule-like bracts, glabrous, pedicels articulated in the middle (♂) or near the apex (♀). **Male flowers** globose in bud, sepals 3–5, valvate, deciduous or reflexed, petals and disk absent; stamens more than 50, filaments united but separate and branched distally, each bearing 2–12 anthers, thecae attached separately on the connective and divergent, biloculate; pistillode absent. **Female flowers** with calyx spathaceous or 3–5-parted (valvate), deciduous, petals, disk and staminodes absent; ovary usually covered with conspicuous ascending spine-like hairs, 3 locular, ovules 1/locule, style short with 3 deeply bifid stigmas, the 6 elongate stigmatic branches erose-plumose. **Fruits** capsules, separating into 3 2-valved cocci, with longitudinal loculicidal dehiscence, surface echinate to smooth; seeds large with a rounded caruncle, surface smooth, lustrous, usually with complex patterned coloration.

The genus consists of a single species, now found throughout the tropics and widely cultivated. The colorful inflorescences (and leaves in some ornamental cultivars) with ♀ flowers distal to the ♂, and the branched stamens with many anthers make the species and genus easily recognizable. The large peltate deeply lobed leaves with serrate margins are unique among Euphorbiaceae found in Central America.

***Ricinus communis* L., Sp. Pl. 1007. 1753. Figure 1.**

Weak-stemmed **shrubs** or small trees 1–4(–8) m tall, leafy stems 3–16 mm thick, hollow or with soft pith, glabrous; stipules 9–22 mm long, 4–6 mm broad at the base, ovate-lanceolate, pale brown, leaving a scar around the stem (except beneath the petiole base). **Leaves** peltate, petioles 7–35 cm long, 2.5–12 mm thick, glabrous, terete, often with glands at the apex and near the base; **leaf blades** 12–48 cm long, equally wide, with (5–)7–11 lobes, the distal lobes larger and narrowly ovate-elliptic, marginal teeth 0.5–3 mm broad, drying chartaceous, with (5–)7–11 palmate 1° veins, the central vein with 10–24 2° veins/side. **Inflorescences** 6–40 cm long, 2–8 cm wide, racemose, peduncle 2–20 mm long (much longer in fruit), ♂ flowers sessile or on pedicels to 15 mm long, ♀ flowers usually congested distally, subtended by linear to ovate bracts 1–3 mm long, short-pedicellate. **Male flowers** 4–6 mm diam. in bud, calyx lobes 5–8 mm long, ovate; stamens 4–8 mm long, anthers 0.3–0.5 mm long, pale yellowish. **Female flowers** with sepals ca. 5 × 2 mm, ovary ca. 3 mm diam., covered with slender-tipped hairs becoming 1–6 mm long, pale bluish green to bright red, style branches 3–5 mm long, orange to red. **Fruits** 1.4–2.5 cm long, 1–2 cm diam., oblong with persisting stiff spines or smooth, borne on pedicels 2–7 cm long; seeds 7–16 mm long, 5–10 mm wide, oblong-obovoid, often with mottled brown and white patterns on the smooth surface, caruncle 2–3 mm wide.

Occasional plants of weedy secondary vegetation and planted in parks and gardens, from near

sea level to 1800 m elevation. The species is probably native to northeastern Africa; it is now grown or naturalized throughout the tropics.

*Ricinus communis* is recognized by the larger peltate palmately lobed leaves with glandular-serrate margins. The unique inflorescences, colorful unisexual flowers, and distinctive fruits with mottled seeds further distinguish this species. Extrafloral nectaries (glands) are usually present on stems and leaves. This species has been cultivated in the eastern Mediterranean for more than 5,000 years. The seeds contain oils (35–55% by weight) which have been used for illumination, lubrication, paints, varnishes, plasticizers, soaps, and printing cotton goods (Cobley & Steele, 1976). The oil is also used medicinally as a purgative. The seeds also contain the poisonous alkaloid ricin, with two to six seeds sufficient to kill a person (Mabberley, 1987). Standley and Steyermark (1949) report that a larger black-seeded variety is used in Guatemala for machinery oil, while a light and dark brown-seeded variety is used for medicinal purposes. The expressed seed remains are used as a fertilizer; stems have been used for making paper. Indicative of the range of variation found within this species are ornamental varieties with leaves ranging from glaucous-blue to dark metallic-red or bright green with white venation. *Higuerilla* and “castor oil plant” are common names; the Brunka name is *sii-krá* (Pittier, 1957). The oil is called *aceito de ricino*, *aceito de castor*, and *aceite de palma-Cristi*.

***Sagotia* Baillon**

Shrubs or **trees**, monoecious or dioecious, latex clear or yellowish; stipules enclosing the shoot apex, caducous. **Leaves** alternate, petiolate, margins entire, venation pinnate, mostly glabrous. **Male inflorescences** terminal or axillary, racemose (or branched near base and paniculate), bracts caducous, flowers borne on long distant pedicels; ♂ flowers with 5 sepals, united near base, lobes rounded, imbricate in bud, petals 5, longer than the sepals, apex rounded, imbricate in bud, disk absent; stamens more than 20, free, closely clustered on the receptacle on very short filaments, anthers elongate with parallel thecae, dehiscing longitudinally; pistillode absent. **Female inflorescences** terminal or axillary, racemose with distant flowers on long pedicels, bracts caducous; ♀ flowers with 5–6 sepals, free to the base, recurved, petals absent, disk absent; ovary with 3 locules, styles 3, united near the base and bifid distally, ovules 1/locule. **Fruits** capsules, rounded and 3-lobed, subtended by the persisting calyx, breaking into 3 2-valved cocci; seeds ovoid to subglobose, endosperm carnosous, cotyledons flat.

A tropical South American genus of two species,



one recently discovered in southern Costa Rica and adjacent Panama.

**Sagotia racemosa** Baillon, *Adansonia* 1: 54. 1860. Figure 20.

**Trees** 5–18 m tall, dioecious (rarely monoecious with bisexual inflorescences), with clear sap becoming white or yellowish with oxidation, leafy stems 1.5–7 mm thick, glabrous (rarely minutely puberulent at first); stipules 4–8 mm long, 1.5–2 mm wide at base, acute. **Leaves** with petioles 1.3–5(–7.2) cm long, 1–2.3 mm thick, glabrous, sulcate adaxially, thickened and often geniculate at the apex; **leaf blades** 10–24(–28) cm long, 4–12(–14.5) cm wide, elliptic-oblong to oblong or ovate-oblong, apex bluntly acute to short-acuminate, margin entire, base obtuse to acute, drying stiffly chartaceous and brownish, glabrous above and below, 2° veins 9–19/side. **Male inflorescences** 3–12 cm long, racemose or paniculate, with 10–many flowers on long (6–18 mm) slender articulated pedicels; ♂ flowers with calyx lobes 1–2 mm long, ca. 1.5 mm wide at base, rounded distally and ciliate, surfaces glabrous, petals 3–5 mm long, obovate, broadly rounded distally, white at first and turning red, drying black; androecium 4–8 mm diam., anthers ca. 1.2 mm long, subsessile. **Female inflorescences** solitary, 4–8 cm long, racemose, rachis 1–2.5 mm thick, glabrous or rarely minutely puberulent (pubescent in South America), drying dark, with 6–15 flowers, bracts 3–4 mm long, lanceolate, pedicels 16–45 mm long; ♀ flowers with usually 6 sepals 4–10(–14) mm long, 1.5–4(–6.5) mm wide, narrowly oblong to obovate or ovate, apex rounded, green and stiff, with parallel venation; ovary 2–3 mm long, 2.5–3.5 mm diam., covered with short dense yellowish white hairs, styles united for ca. 1 mm, branches to 4 mm long, 0.4 mm thick. **Fruits** 14–20 mm long, 16–26 mm wide, 3-lobed and rounded, bright green; seed 16 × 15 × 14 mm (based on *McPherson 12476*), subglobose.

Trees of evergreen lowland rain forest formations, 10–1200 m elevation (in South America). Flowering in May, August, and November–December; fruiting in March–April. In southern Central America, this species has been collected only at 200–300 m elevation, on the Osa Peninsula (*Hammel et al. 16784 & 16799, Marín 100, 301*) and in Bocas del Toro (*McPherson 11823 & 12470*). The species ranges disjunctly from southern Costa Rica and adjacent Panama to the Amazon basin.

*Sagotia racemosa* is recognized by its restricted habitat (in Central America), general lack of pubescence, petioles thickened near the apex, ♂ flowers with sepals, petals, and dome-like androecium, larger ♀ flowers that dry black, and large seeds.

**Sapium** P. Browne

**REFERENCES**—M. J. Huft, Four new species of *Sapium* (Euphorbiaceae) from Central and South

America. *Phytologia* 63: 443–448. 1987. E. Jablonski, Notes on Neotropical Euphorbiaceae, 3. Synopsis of Caribbean *Sapium*. *Phytologia* 16: 393–434. 1968. R. C. Kruijt, Monographic studies on *Sapium* (Euphorbiaceae, Hippomaneae) and related genera. Thesis, Instituut voor Systematische Plantkunde der Rijksuniversiteit Utrecht. 1989. H. Pittier, The Mexican and Central American species of *Sapium*. *Contr. U.S. Natl. Herb.* 12: 159–169. 1908.

**Trees** or shrubs monoecious (dioecious), stems with milky latex, nearly always glabrous; stipules small, often becoming thickened and persistent. **Leaves** alternate, simple, petiolate, usually with 2 prominent adaxial glands at the apex of the petiole or base of blade, glabrous, entire or glandular-serrate, apex sometimes cuculate-reflexed, glabrous, pinnately veined. **Inflorescences** terminal (rarely axillary), solitary (rarely 2–5), bisexual or unisexual, rachis unbranched, usually thick and glabrous, bracts usually with 2 (3) large flat appressed lateral glands, ♀ flowers proximal and 1/bract, ♂ flowers in distal sessile glomerules of 2–16. **Male flowers** sessile or pedicellate, glabrous, calyx united at the base, 2-lobed, open or subimbricate, corolla and disk absent; stamens usually 2, exerted. Filaments free or united at base, anthers 2-theous, dehiscing longitudinally, extrorse; pistillode absent. **Female flowers** glabrous, calyx united near the base (rarely more), 2- or 3-lobed or parted or irregular, corolla and disk absent; ovary sessile or stipitate, locules 1–3, ovules 1/locule, styles (1) 2–3, usually united at base, simple, distally recurved. **Fruits** capsules (sometimes indehiscent), with 3 (2) 2-valved cocci, woody or somewhat fleshy, columella usually persisting; seeds rounded in outline, lenticular to wedge-shaped, often rugulose, with a thin fleshy red or white aril, ecarunculate.

A genus recently interpreted as having 21 Neotropical species (Kruijt, reference above) but also interpreted as being pantropical with 90–100 mostly Neotropical species (Webster, 1994b). Regardless of circumscription, *Sapium* has been considered one of the most difficult genera of Euphorbiaceae as regards the identification and separation of species. This appears to be due in part to great morphological variation among different individuals of what are probably the same species. In addition, flowering and fruiting inflorescences differ greatly on the same tree, and vegetative morphology can vary greatly within a single population. Rather than create more confusion, we have decided to follow Kruijt's approach (reference above) with only a few exceptions. Thus, the vast majority of Costa Rican collections are now placed under *S. glandulosum* (q.v.). Unfortunately, Kruijt did not see material at F or US, some of his descriptive terminology is unconventional, and his thesis work has not been published. We thank the



library of the Missouri Botanical Garden for loan of Kruijt's thesis.

Specimens of *Sapium* are usually easy to recognize because of their glabrous parts, white latex, petioles with prominent glands near the apex, stiff leaves, thick spicate inflorescences, floral bracts with paired rounded flat appressed glands, proximal ♀ flowers (1/bract) and distal sessile glomerules of ♂ flowers with two stamens, and seeds with an aril. The flowering spikes can be quite long

but the ♂ portion breaks off and fruiting spikes are usually less than 10 cm long. A number of South American species have latex that has been used as a source of rubber. *Triadica sebifera* (L.) Small (formerly *Sapium sebiferum* (L.) Roxb., the "Chinese tallow tree") from China and Japan is planted as an ornamental in subtropical areas. Members of the genus are frequently called *yos* in Costa Rica. Compare *Stillingia*.

Key to the Species of *Sapium*

- 1a. Inflorescences axillary, infructescences borne laterally at leafless nodes [leafy stems to 12 mm thick with rough persisting stipules, leaf blades with 15–28 2° veins/side; 10–1200 m elevation on the evergreen Pacific slope of southern Costa Rica] ..... *S. allenii*
- 1b. Inflorescences terminal, infructescences never below leafless nodes of the same axis (but new lateral shoots are often present and may arise from the base of the inflorescence or infructescence ... 2
- 2a. Inflorescences and infructescences 2–5 at the apex of the stems [bracts deciduous beneath the older ♀ flowers, fruits ca. 8–10 mm diam.; venation arising at 70–90° from the midvein, with 15–30 veins/side] ..... *S. laurifolium*
- 2b. Inflorescences and infructescences solitary at the apex of stems ..... 3
- 3a. Secondary veins dichotomizing 2–5 mm from the leaf margin, Y-shaped distally and arising from the midvein at angles of 80–90° [blades 3–11 cm long; fruits on short (2–4 mm) stipes; montane forest trees at 1200–2200 m elevation] ..... *S. rigidifolium*
- 3b. Secondary veins not dichotomizing distally, arching upward near the margin with only minor distal lateral branches ..... 4
- 4a. ♀ flowers subtended by 3 thin erect rounded bracts in addition to the biglandular bract; seeds 6.5–9 mm long; distal flowering stems thick (3–9 mm) and knobby with raised leaf scars and thickened stipules [inflorescences axes 2–8 mm thick, fruits sessile; montane forests 1100–2200 m] ..... *S. pachystachys*
- 4b. ♀ flowers subtended by only 1 sessile biglandular bract; seeds 3.8–7.6 mm long; distal flowering stems usually not so thick and knobby ..... 5
- 5a. Fruits stipitate on stipes 3–8 mm long, often pyriform or ellipsoid, distant along the rachis, 10–14 mm diam., seeds 7–7.6 mm long; perianth not reddish; leaf blades often oblong and acute at both apex and base ..... *S. macrocarpum*
- 5b. Fruits sessile or short-stipitate (stipes to 3 mm long), oblate to globose, never pyriform or ellipsoid, to 12 mm diam., usually closely crowded on the infructescence, seeds 3.8–6.7 mm long; perianth sometimes reddish; leaf blades variable, entire to serrulate, acute to rounded at apex or base [widespread species, frequently collected] ..... *S. glandulosum*

*Sapium allenii* Huft, Phytologia 63: 443. 1987.  
Figure 22.

Trees 12–25 m tall, monoecious, leafy stems 5–12 mm thick, glabrous, becoming rough and knobby with thickened persisting stipules; stipules 5–7 mm long, 3–4 mm wide at base, triangular, glabrous, becoming thickened. Leaves clustered near the apex, petioles 3–5.5 cm long, 1.3–2 mm thick, glabrous, glands opposite or subopposite and adaxial near the apex, 0.5–2 mm long, cylindrical; leaf blades 11–21 cm long, 4–9 cm wide, oblong to elliptic-oblong, apex short-acuminate or obtuse, flat or

often folded, margin entire or slightly undulate with minute (0.2 mm) glandular areas along the edge, often revolute, base obtuse, drying stiffly chartaceous, glabrous, 2° veins 15–28/side (intersecondaries often prominent). Inflorescences lateral, borne at 45–90° angle from leafless nodes, 2.5–6 cm long in fruit (not seen at anthesis), rachis 3–5 mm thick, glabrous, bracts ca. 2 mm long, 3 mm broad at the base, smooth and rounded, ♂ flowers not seen, ♀ flowers with stipes becoming 4–5 mm long and 1–1.5 mm thick in fruit. Fruits 7–9 mm long, 5–11 mm wide, smooth and green, glabrous, columella, ca. 6 × 1.4 mm, 2–3 mm wide at the apex, slightly winged; seeds 4.5–6 mm long, 4–5.2 mm wide, 3–3.5 mm thick, some-

what lenticular with circular outline, tuberculate, with thin ridged margin around the periphery, reddish.

Plants of evergreen rain forest formations of the Pacific slope, 10–1200 m elevation. Fruiting in January–March. Now known from three collections: *Allen 5773* (the type) from near Palmar Sur de Osa, *Gómez-Laurito 11916* from the Jardín Botánico Wilson, and *Skutch 4821* from the General Valley. The species is known only from southern Costa Rica.

*Sapium allenii* is recognized by its short lateral inflorescences from leafless nodes, stipitate fruits, and usually oblong leaves with many secondary veins. Note that the perianth or perianth scars are at the base of the fruit stalk; it is a stipe, not a pedicel. The thick stems with persistent stipules resemble those of *S. pachystachys* (q.v.). *Sapium lateriflorum* Hemsl. of Mexico and northern Central America is the only other species in this region with lateral inflorescences, but it has more slender stems with the smaller stipules usually deciduous, 2° veins that are more strongly ascending, usually more numerous spikes on a branchlet, and somewhat larger fruits. Kruijt did not see material of *S. allenii*.

***Sapium glandulosum* (L.) Morong**, Ann. New York Acad. Sci. 7: 227. 1893. *Hippomane glandulosa* L., Sp. Pl. 1191. 1753. *S. aucuparium* Jacq. Enum. pl. syst. 31. 1760. *S. pittieri* Huber, Bull. Herb. Boissier, Sér. 2, 6: 350. 1906. *S. oligoneurum* K. Schum. & Pittier, Contr. U.S. Natl. Herb. 12: 168. 1908. *S. sulciferum* Pittier, Contr. U.S. Natl. Herb. 12: 169. 1908. *S. biglandulosum* (L.) Müll. Arg. var. *oligoneurum* Monach., Bull. Torrey Bot. Club 67: 772. 1940. *S. biglandulosum* (L.) Müll. Arg. var. *sulciferum* (Pittier) Monach., Bull. Torrey Bot. Club 67: 772. 1940. *S. schippii* Croizat, Amer. Midl. Nat. 29: 477. 1943. Figures 22 and 23.

**Trees** (3–)5–20 m tall, sap white and thick, leafy stems 1.8–7 mm thick, glabrous; stipules 2–3 mm long, 1–2 mm wide, triangular-ovate, appressed, often rounded at base. **Leaves** often clustered distally, petioles 6–30 mm long, 0.7–1.3 mm thick, glabrous, sulcate above, paired lateral glands opposite or subopposite at apex, to 1 mm high, 0.5–0.9 mm diam., cylindrical, rarely borne on the lamina base; **leaf blades** 3–14(–18) cm long, 1.8–5(–8) cm wide, elliptic-oblong to oblong (broadly elliptic or broadly oblong in smaller leaves), apex acuminate or less often rounded, the tip rounded, folded or cucullate, margin entire or subentire with minute glands along the edge, often revolute on drying, base obtuse to acute, drying stiffly chartaceous or subcoriaceous, glabrous, 2° veins 6–14(–20)/side. **Inflorescences** terminal, solitary (2–3),

spiciform, 3–15 cm long, rachis 1.5–2 mm thick, glabrous, both ♂ and ♀ bracts small and inconspicuous but with large (1.5–2.3 mm diam.) circular or oblong flat appressed bracts, bracts and perianth greenish, ♀ flowers solitary, ♂ flowers 3–9/bract, pedicels < 0.5 mm long, thick. **Male flowers** with calyx 1.2–2 mm long, united to form a conic tube, 0.7–1.5 mm long, 2-lobed, translucent; stamens with filaments 1–1.4 mm long, anthers 0.4–0.8 mm wide. **Female flowers** subsessile, sepals 0.7–1 mm long, thin, often obscured by bracts and glands; ovary 2–2.5 mm long, 1.8–2.8 mm diam., styles 3, column 0.5–1.5 mm long, style branches 3, 1.5–2.5 mm long and recurved. **Fruits** 6–10 mm long, 8–13 mm wide, oblate, smooth, green with purple distally, sessile or on short (2.5 mm) stipes, columella 4–6 mm long, ca. 0.7 mm thick; seeds 4.5–6.5 mm long, 3.8–6 mm wide, 2.8–4 mm thick, rounded in outline and often thick-lenticular, surface muricate or warty, red (drying whitish).

Common trees found in evergreen and deciduous forests, 2–2200 m elevation. In Costa Rica, the species is collected most often between 900 and 2000 m. Flowering in February–June; fruiting primarily in June–October. The species (in a wide sense) ranges from Mexico to Paraguay and the West Indies (except Cuba and Haiti).

*Sapium glandulosum* is recognized by its entire (rarely serrulate) leaves, solitary inflorescences, three-style branches, and smaller subsessile or short-stipitate fruits often crowded on the infructescence. The leaf tips may be distinctively cucullate or folded at higher elevations. Also, the leaves are generally smaller but with relatively broader blades and with abruptly rounded leaf apices at higher elevations, helping distinguish this species from the very similar *S. macrocarpum*, but fruiting material is necessary to be certain. In the type of *S. pittieri* (Pittier 4344 us), the glands are along the base of the leaf blade and not at the apex of the petiole. But this character is seen in a few other highland collections and does not appear to be significant. A few collections from the Osa Peninsula have leaves with abruptly rounded apices. Plants of the La Selva area are distinctive in often lacking the many 2° veins arising at right angles from the midvein, and the ♀ calyx is often completely connate to form an urceolate reddish tube. The senior author's attempts to separate these many variants into meaningful "species" were not successful, and he has chosen to follow Kruijt in placing all this diverse material under the Linnaean name. However, our description is based only on Costa Rican material. This is our most commonly collected species of *Sapium* and, like the others, often called *yos*.

***Sapium laurifolium* (A. Rich.) Griseb.**, Fl. Brit. W. Ind. 49. 1859. *Stillingia laurifolia* A. Rich., His.



Fl. Cuba 11: 201. 1850. *Sa. jamaicense* Sw. (nom. illeg., fide Kruijt), Adnot. Bot. 62. 1829. *Sa. anadenum* Pitt., Contr. U.S. Natl. Herb. 12: 164. 1908. *Sa. pleiostachys* K. Schum. & Pitt., Contr. U.S. Natl. Herb. 12: 164. 1908.

**Trees** 8–25 m tall, monoecious, leafy stems 2–10 mm thick, glabrous; stipules 1–3 mm long, triangular, becoming thickened and rounded with thin lateral margins, persisting. **Leaves** with petioles 15–35(–52) mm long, 1–1.5 mm thick, usually with 2 small (0.7 mm) lateral glands near the apex; **leaf blades** 6–15(–20) long, 3–6(–9) cm wide, elliptic-oblong to narrowly oblong, apex usually short-acuminate, margin entire or with a few marginal glands, base acute to obtuse, drying stiffly chartaceous, glabrous above and below, 2° veins 20–30/side, arising at angles of 70–85°. **Inflorescences** apical, usually 2–5, unisexual or bisexual, 2–12(–28) cm long, peduncles very short, bracts subtending ♀ flowers often quickly caducous and leaving a round scar, ♂ bracts subtending 3–6 flowers, glands 1–2 mm long and flat, rounded to oblong. **Male flowers** sessile or subsessile, calyx ca. 1.4 mm long, with 2 lobes ca. 4 mm long, yellowish to red; filaments free, ca. 1.8 mm long. **Female flowers** with calyx ca. 1.5 mm long, trilobed, ovary ca. 1–2 mm long, subglobose, style branches 3, deciduous and leaving a rounded whitish scar. **Fruits** 7–8 mm long, 7.5–10 mm wide, oblate to broadly ovate with 3 longitudinal sulci; seeds 4–6 mm long, 3–5 mm wide.

Plants of evergreen rain forest formations, 0–1200 m elevation on the Caribbean slope and in the Golfo Dulce area. Flowering in March; fruiting in September. The species ranges from Costa Rica to Brazil and the greater Antilles.

*Sapium laurifolium* is recognized by the usually clustered terminal spicate inflorescences, bracts deciduous beneath the ♀ flowers, and small fruits with thin capsule wall. A short flowering season may explain why there are so few collections of this species from Costa Rica. Vegetatively, this species is very similar to *S. glandulosum*, and the two may be indistinguishable in the absence of inflorescences. It is possible that they are conspecific.

***Sapium macrocarpum* Müll. Arg., Linnaea 32: 119. 1863. *S. mexicanum* Hemsl. in Hooker, Icon. Pl. 2680. 1901. *S. thelocarpum* Schum. & Pittier, Contr. U.S. Natl. Herb. 12: 166, pl. 13. 1908. Figure 23.**

**Trees** 8–35 m tall, leafy stems 1.4–5 mm thick, glabrous, (rarely minutely puberulent); stipules 1–2.8 mm long, ovate-triangular, acute, often with thin undulate margins, persistent. **Leaves** distant or closely clustered distally, petioles 7–40 mm long, 0.7–1.4 mm thick, glabrous, distal paired glands 0.7–1 mm long, 0.4–0.7 mm diam., cylindrical to conical; **leaf blades** 4–15 cm long,

1.7–4.5 cm wide, narrowly elliptic-oblong to narrowly oblong or lanceolate, usually tapering gradually to an acute apex, tip rounded and often adaxially recurved, margin subentire or obscurely serrulate with teeth 0.1–0.3 mm high, base acute to obtuse and rounded, drying stiffly chartaceous and often yellowish beneath, glabrous, 2° veins 6–13/side. **Inflorescences** terminal, solitary, bisexual, (3–)7–15(–22) cm long, rachis 2–3.5 mm thick, glabrous, ♀ flowers 3–10 at proximal nodes, ♂ flowers 7–11(–16)/bract, bracts 1.5–3 mm long, flat, appressed, round or oblong. **Male flower** buds ca. 2 × 1.5 mm, obovoid, subsessile at anthesis, calyx 2–2.5 mm long, lobes ca. 0.5 mm long, anthers ca. 0.6 mm long, ca. 0.9 mm wide. **Female flowers** sessile, calyx parts 1–3 mm long, ovary 2–5 mm long, 1.5–4 mm diam., ellipsoid, narrowed at the base and often becoming stipitate, style column 0.5–1 mm long, free styles ca. 2 mm long and recurved. **Fruits** to 2 cm long, 1–3 cm diam., stipitate and usually pyriform or obovoid, distant on the rachis; seeds 7.2–7.6 mm long, 5.8–7 mm wide, 5.2–5.5 mm thick, whitish or reddish.

Plants of both evergreen and partly deciduous forest formations (rarely collected in deciduous forest in Costa Rica), (100–)700–1800 m elevation. Flowering in April–July; fruiting in May–November. The species ranges from Mexico to central Costa Rica.

*Sapium macrocarpum* is characterized by the distant stipitate pyriform to ovoid and smooth fruits. Additional characteristics are the usually narrowly oblong leaves tapering to both apex and base and the often recurved leaf tips. This species can become a huge tree (*Bello* 1499). Herbarium specimens of this species may be impossible to separate from those of *S. glandulosum* (*sensu lato*) in the absence of mature fruit. We follow Kruijt's nomenclature for this species.

***Sapium pachystachys* Schum. & Pittier, Contr. U.S. Natl. Herb. 12: 168, t. 16. 1908. Figure 22.**

**Trees** 8–25 m tall, monoecious, leafy stems 2.7–9 mm thick, glabrous, older stems with thick stipules and raised leaf scars; stipules 4–8 mm long, triangular, appressed, persistent, becoming thickened. **Leaves** usually closely clustered distally, petioles 1.7–6(–11) cm long, 1–2.7 mm thick, glabrous, glands opposite or subopposite near apex, to 1.5 mm long, 0.5–0.9 mm thick, cylindrical or conical; **leaf blades** (8–)10–20(–26) cm long, (2.0–)3–7(–8.5) cm wide, elliptic, elliptic-oblong, to oblong, apex bluntly acute to obtuse (subacuminate), tip flat or cucullate, margin entire or slightly crenate with lobes 0.3 mm high, base obtuse to rounded, drying chartaceous to stiffly chartaceous, often yellowish or grayish, glabrous, 2° veins 8–20/side. **Inflorescences** terminal, solitary, bisexual or ♂, 8–25 cm long, rachis 2–5 mm thick (to 8 mm thick in fruit), glabrous, ♀ bracts ca. 3 × 6 mm, broadly sessile, with 2 lateral flat rounded or oblong glands 2.5–4 mm diam., ♂ bracts subtending 5–11 flowers, glands sessile and appressed, ♂ pedicels ca. 1 mm long. **Male flowers**



with calyx 1.2–2 mm long, united and 2-lobed; stamens free, filaments 0.7–2 mm long, anthers 0.7–1 mm long, 1–1.5 mm wide. **Female flowers** subtended by 3 thin rounded bracts (in addition to the sessile biglandular bract), perianth 2–5 mm long, to 3 mm wide, 3-lobed, resembling the subtending bracts in texture; ovary globose, style column 1.5–4 mm long, to 1.3 mm thick, style branches 2–3 mm long, recurved and coiled. **Fruits** 8–16 mm long, 10–16 mm diam., subsessile, columella ca. 8 mm long, 2.5 mm thick and 3–4 mm wide at the apex; seeds 6.5–9 mm long, 6.5–8 mm wide, 4–5 mm thick, ovate to orbicular in outline, lenticular with a narrow circumferential margin, rugulose or verrucose, aril white to red.

Plants of lower montane evergreen forest formations, 1100–2200 m elevation (700–2100 m in Panama). Flowering in October and December–May; fruiting in June–October. The species ranges from Costa Rica's central volcanic chain (Volcán Poas) to western Panama.

*Sapium pachystachys* is recognized by its highland habitats, thick stems with prominent leaf scars and thickened persisting stipules, three thin rounded bracts between the glandular bract and the ♀ calyx, and subsessile fruits. Leafy stems can be very similar to *S. allenii*, which is a lower elevation species. Specimens of this species with immature inflorescences may be very difficult to separate from *S. glandulosum*. Our interpretation of this species agrees with that of Kruijt.

***Sapium rigidifolium*** Huft, *Phytologia* 63: 444. 1987. Figure 23.

**Trees** 8–30 m tall, trunk to 80 cm diam., monoecious, leafy stems (1.5)–2–6 mm thick, glabrous, dark brown, becoming bumpy with thickened stipules and raised leaf scars; stipules 2–3.5 mm long, 1.3–1.8 mm wide, ovate, usually with thin margins and thick center. **Leaves** clustered near the ends of branchlets, petioles 8–28 mm long, 1–1.7 mm thick, glabrous, drying dark, sulcate above, with 2 apical adaxial glands, opposite or subopposite, to 1 mm long, 0.6–1 mm diam.; **leaf blades** (3)–4–11 cm long, (1.4)–1.8–4.5 cm wide, oblong to elliptic-oblong (lanceolate, elliptic-obovate), apex rounded or emarginate, glandular and often recurved, margin subentire or slightly crenulate (4–6 teeth/cm), base acute or obtuse, thickened and decurrent at the glands, drying stiffly chartaceous, glabrous, lustrous above, 2° veins 16–40/side, arising at 80–90°, dichotomizing 2–5 mm from the edge and irregularly loop-connected, 3° veins prominent. **Inflorescences** terminal, solitary, bisexual, 5–9 cm long, spicate, rachis ca. 1.5 mm thick, glabrous, drying dark, bracts ca. 0.7 mm long, with 2 lateral thin flat appressed rounded glands 1.4–2 mm diam., ♂ bracts subtending 3–8 flowers. **Male flowers** with cupular calyx 1.5–2 mm long, 2-lobed; stamens with filaments ca. 1.2 mm long, anthers ca. 0.5 × 0.9 mm. **Female flowers** with thin bract-like perianth, 0.7–1.5 mm long; stipe 2–3 mm long, to 1 mm thick, ovary 2–3 mm long, 1–1.4 mm diam.,

ellipsoid, styles 3, column 0.8–1.3 mm long. **Fruits** ca. 6 × 8 mm, broadly ovoid to subglobose, drying dark, smooth and glabrous, borne on a stipe 2–4 mm long; seeds 4.3–5 mm long, 3.5–4 mm wide, 2–2.2 mm thick, oblong in outline, surface tuberculate or with short longitudinal ridges.

Plants of lower montane evergreen cloud forest formations, (1200–)1500–2200 m elevation. Flowering in June–July; fruiting in August. The species ranges from the Cordillera de Tilarán to the Chiriquí Highlands of Panama.

*Sapium rigidifolium* is recognized by its lower montane habitat, lack of pubescence, stiff smaller leaves with unusual secondary veins, stipitate ovary, and apparently articulated style column. Note that the fruit is borne on a stipe with perianth or perianth scars at the base (not a pedicel). This species, like its congeners, is called *yos* in Costa Rica. Kruijt (cited above) included this species within *S. stylare* Müll. Arg., and it may prove to be a subspecific element of that species. We maintain it here on the basis of its smaller fruits, more uniform foliage morphology, and distant allopatry.

## Sebastiania Sprengel

**Shrubs** or trees (rarely annual herbs), monoecious or dioecious; stipules minute, usually caducous. **Leaves** alternate (rarely opposite), short-petiolate, blades serrate to rarely entire, pinnately veined, with or without glands at the base. **Inflorescences** terminal or leaf-opposed, rarely axillary or from the internodes, solitary (rarely fasciculate), unisexual or more often bisexual with 1 (2–5) proximal ♀ flower and a single unbranched rachis with alternate bracts with ♂ floweres, bracts with 2 lateral glands or glandular areas, ♂ flowers 1–3/bract, sessile or pedicellate. **Male flowers** small, calyx united at the base, 2–3-lobed, often open before anthesis, corolla and disk absent; stamens 3 (2, 4), filaments free or united at base, anthers small, longitudinally dehiscent, extrorse; pistilode absent. **Female flowers** with calyx 3-parted or 3-lobed, corolla and disk absent, staminodes absent; ovary with 3 (2) locules, ovules 1/locule, styles 3 (2), free or united at the base, simple. **Fruits** capsules, globose or 3-lobed, breaking into 3 2-valved cocci, surface smooth or armed with projections, usually with 3 (2) seeds, columella persisting; seeds subglobose to cylindrical, carunculate.

A genus of 90–100 species, nearly all Neotropical, with a few in Asia, North America, and Australasia. The genus is distinguished by its locules with solitary ovules, biglandular bracts, ♂ flowers usually with three stamens and three calyx lobes, and fruit often with projections on the lateral surfaces.

## Key to the Species of *Sebastiania*

- 1a. Herbs of open sites in lowland evergreen or partly deciduous areas, to 0.6 m tall; ♀ flowers often solitary on the internodes ..... *S. corniculata*
- 1b. Shrubs or trees, usually > 1 m tall; ♀ flowers never borne on the internodes ..... 2
- 2a. Plants of deciduous areas in northwestern Costa Rica, 0–300 m elevation; 2° veins not loop-connected near the margin ..... *S. pavoniana*
- 2b. Plants of montane evergreen forests in western Panama, 900–1500 m elevation; 2° veins loop-connected near the margin ..... *S. panamensis*

***Sebastiania corniculata*** (Vahl) Müll. Arg. in DC., Prodr. 15 (2): 1168. 1855. *Tragia corniculata* Vahl. Eclog. Amer. 2: 55, pl. 19. 1798. Figure 11.

**Herbs** 15–60 cm tall, monoecious, erect or decumbent, few- or many-branched, sometimes forming clumps, occasionally with opposite branching near the base, leafy stems 0.4–2 mm thick, with thin straight or curved hairs 0.4–1.8 mm long; stipules obscure. **Leaves** alternate (except at base), petioles 1.5–7(–11) mm long, 0.2–0.6 mm thick, hirsute; **leaf blades** 11–40 mm long, 3–18 mm wide, lanceolate to ovate-lanceolate (linear-lanceolate), gradually narrowed to the acute apex, margin minutely serrulate or subentire, base obtuse or rounded (rarely cordate), drying thinly chartaceous, with thin straight hairs above and below (rarely glabrous), venation pinnate, 2° veins 5–8/side. **Inflorescences** opposite the leaves and solitary, bisexual with a single basal ♀ flower or ♂, the ♂ flowers subsessile and alternate along a slender spike 4–12 mm long, rachis with short (0.2–0.3 mm) thin hairs, solitary ♀ flowers also arising from the stems between the nodes. **Male flowers** subtended by serrate bracts ca. 0.5 mm long, pedicels 0–0.5 mm long, calyx lobes ca. 0.5 mm long; stamens 3, anthers 0.3–0.4 mm long. **Female flowers** with inconspicuous basal calyx lobes ca. 0.3 mm long, ovary ovoid or urceolate in form, with 6 horn-like lobes at the apex and with similar scale-like processes on the surface. **Fruits** 4–5 mm long, ca. 4 mm wide, with the distal lobes ca. 1 mm long and additional scale-like processes (1 × 1.3 mm) on the sides, usually glabrous, columella 2.7–3.4 mm long, 0.8–2 mm wide, distally; seeds 2.4–2.6 mm long (not including the caruncle), 1.8–2.2 mm wide, ca. 1.5 mm thick, oblong with truncated apex, smooth, caruncle distal and slightly stipitate, 0.5–0.7 mm long, knob-like.

Weedy plants of open sunny sites in lowland evergreen or partly deciduous areas. This species has been collected in Costa Rica only near the Caribbean shore at Barra del Colorado; flowering and fruiting in January–March (*Stevens 24165 & 25040* MO). This species ranges from Cuba and Hispaniola to southern Brazil; it is rarely collected in southern Central America.

*Sebastiania corniculata* is recognized by its small weedy habit, narrow hirsutulous leaves, leaf-opposed ♂ spikes, and unusual ♀ flowers often borne on the stem between nodes. The fruits bear several

triangular acute projections on the surfaces that dry dark against the paler yellowish color of the capsule wall. The slightly stipitate caruncle is also noteworthy. The stem hairs are multicellular, but this is difficult to see (× 50).

***Sebastiania panamensis*** Webster, Ann. Missouri Bot. Gard. 75: 1128. 1988.

**Shrubs** or small treelets, (0.5–)1–4(–6) m tall, monoecious, leafy stems 0.7–3.5 mm thick, with erect or appressed hairs 0.1–0.4 mm long, glabrescent; stipules 0.4–1.2(–2.5) mm long, 0.8–1.5 mm wide at base, caducous. **Leaves** with petioles 2–8 mm long, 0.4–1.8 mm thick, minutely pubescent or glabrous, sulcate adaxially; **leaf blades** 3–16 cm long, 0.6–5 cm wide, lanceolate to elliptic-lanceolate, elliptic-oblong, or oblong-lanceolate, tapering gradually to an acute or acuminate apex, tip 3–16 mm long, margins minutely (0.2–0.3 mm) denticulate with 1–5 teeth/cm, base cuneate or slightly rounded, drying stiffly chartaceous, glabrous above and below except for small hairs along the midvein, 2° veins 5–10/side, loop-connected 1–4(–6) mm from the edge. **Inflorescences** leaf-opposed or pseudoterminal, solitary, 1–5 cm long, usually bisexual with 1 proximal ♀ flower, rachis with minute hairs, bracts subtending ♀ flowers with oblong glands 1.3 mm wide, bracts subtending ♂ flowers with rounded disk-like glands ca. 0.8 mm diam. **Male flowers** on pedicels 0.7–1.5 mm long, calyx 3-lobed; stamens 3–4, filaments ca. 0.7 mm long, anthers 0.3–0.4 mm long. **Female flowers** subsessile or on short (1.5 mm) pedicels, calyx 0.7–1 mm long, covering the ovary in bud, ovary ca. 1.3 × 1.2 mm, styles united for 0.6 mm, branches ca. 2 mm long. **Fruits** 6–7 mm long, ca. 7 mm wide, with 6 subapical projections to 0.7 mm long, columella 4–4.5 mm long, ca. 3 mm wide at apex; seeds 4.6–5 mm long, 3.5–4 mm wide, 3.2–3.5 mm thick, truncated at the base and ovoid, caruncle 1.2–1.4 mm wide.

Plants of evergreen cloud forest formations, 900–1500 m elevation. Probably flowering and fruiting throughout the year. This species is found only in the highlands of western Panama.

*Sebastiania panamensis* is distinguished by its montane forest habitat, leaves with loop-connected secondary veins, leaf-opposed inflorescences, and floral bracts with conspicuous thick flattened glands.



**Sebastiania pavoniana** Müll. Arg. in DC., Prodr. 15 (2): 1189. 1866. Figure 25.

Shrubs or small trees, 3–15 m tall, sap whitish, leafy stems 0.8–2 mm thick, glabrous; stipules 0.3–0.8 mm long, leaving a scar ca. 0.3 mm wide. **Leaves** with petioles 3–11 mm long, 0.4–1.2 mm thick, glabrous, sulcate adaxially, usually with 1–4 minute (0.2 mm) glands at the apex adaxially; **leaf blades** 3–9(–12) cm long, 1.4–3.5(–4.8) cm wide, elliptic-oblong to ovate-elliptic, elliptic or oblong, apex acuminate with narrow tip 3–10 mm long, margin minutely (0.2–0.4 mm) denticulate and sometimes with dark glandular tips 0.1–0.2 mm long, base obtuse or acute, drying chartaceous, greenish, glabrous above and below, 2° veins 4–7/side, distally arcuate-ascending. **Inflorescences** terminal or leaf-opposed, bisexual inflorescences 1.4–7 cm long, ca. 4 mm wide with distal flower groups closely approximate or separate, rachis 0.4–1 mm thick, glabrous, ♀ inflorescences 6–11 mm long, with 1–3 flowers, rachis ca. 0.8 mm thick, bracts broadly sessile, with glandular areas, stinging hairs often present near the flowers. **Male flowers** subtended by bracts ca. 1 mm long, 1.4 mm broad at the base; stamens usually 3/flower, filaments 0.4 mm long, anthers 0.3–0.4 mm long. **Female flowers** subtended by bracts ca. 1 × 1.4 mm, perianth parts to 1.4 mm long and bract-like, broadly imbricate, ovary ca. 1.3 × 1.1 mm, styles 1–2 mm long, recurved. **Fruits** rarely collected, externally smooth, coiled dehiscent valves ca. 11 mm long, columella 5–7 mm long; seeds 4 mm long, globose, smooth, dark and mottled.

Plants of seasonally very dry deciduous forest formations, 0–300 m elevation. Flowering collections have been made in February–June and September. The species is known only from Mexico and Guanacaste Province in northwestern Costa Rica.

*Sebastiania pavoniana* is recognized by its deciduous forest habitat, lack of pubescence, small leaves, small leaf-opposed or terminal inflorescences, and minute ♂ flowers subtended by broadly sessile bracts. Stinging hairs are often present near the flowers. The minute glands at the apex of the sulcate petiole are useful in determining sterile collections. Specimens of this species had been incorrectly identified as *Gymnanthes lucida* (in herb.), *Stillingia* sp. and *Ophellantha spinosa* Standl. (Standley, 1938, p. 1557). This is one of the species whose fruit, when inhabited by a larva, are called “jumping beans” (Mabberley, 1987).

*Skutchia caudata* Pax & K. Hoffm., proposed as a new genus and species of Euphorbiaceae, is a synonym of *Trophis mexicana* (Liebm.) Bureau of the Moraceae.

**Stillingia** Garden ex. Linnaeus

**Shrubs**, small trees, or perennial (rarely annual) herbs, monoecious (bisexual), stems glabrous; stipules usually

filiform and glandular or reduced. **Leaves** simple, alternate, opposite or whorled, petiolate, often with 2–3 cyathiform or scutelliform glands at the apex of the petiole or base of blade; leaf blades glandular serrate, glabrous, venation pinnate. **Inflorescences** terminal or leaf-opposed (axillary), solitary, bisexual or ♂, spiciform with a thick rachis (often with short basal lateral branches) glabrous, bracts small, broadly sessile with 2 prominent lateral glands; ♀ flowers proximal, 1/bract, sessile; ♂ flowers distal, 1–15/bract, subsessile. **Male flowers** glabrous, calyx 2-lobed, membranous, corolla and disk absent; stamens 2 (3), exserted, filaments free but united at the base, anthers longitudinally dehiscent and extrorse; pistillode absent. **Female flowers** glabrous, calyx usually of 3 separate sepals (reduced or absent), corolla and disk absent, staminodes absent; ovary (2–)3-locular, ovules 1/locule, styles connate at base, simple. **Fruits** capsules, usually 3-lobed and splitting into 3 2-valved capsules, columella absent but a 3-horned woody gynobase persisting after dehiscence; seeds subglobose, with or without caruncles, seed surface smooth or rugose.

A genus of 25–30 tropical and warm-temperate species with centers of diversity in Mexico and Brazil, with a few additional species in the Mascarene Islands, Malaysia, and Fiji. The lack of hairs, thick spikes, and leaves with glandular-serrate margins help distinguish the genus. *Stillingia* differs from *Sapium* in the smaller size of the plants, separate ♀ sepals (or none), hard seed testa, and glands of the leaves that are less prominent and not cylindrical. The genus is known in southern Central America from only two collections of the following species.

**Stillingia zelayensis** (H.B.K.) Müll. Arg., Linnaea 32: 87. 1863. *Sapium zelayensis* H.B.K., Nov. gen. sp. (quarto ed.) 2: 65. 1817. *Stillingia microsperma* Pax. & K. Hoffm., Pflanzenreich 2, 147, 5: 187. 1912. Figure 23.

**Shrubs** 0.5–2 m tall, often with many distal branches, leafy stems 1.2–4.5 m thick, terete; stipules 0.3–1 mm long or absent, filiform, minutely triangular or broadly rounded and flat to 1.2 mm diam. **Leaves** alternate, opposite or whorled (often on the same branchlet), petioles 2–10(–14) mm long, 0.4–1.2 mm thick, glabrous, with 2–3 discoid, cupulate or patelliform glands at the apex or lamina base, ca. 0.5 mm high, 0.3–1.3 mm diam.; **leaf blades** (2.5–)3–8(–11) cm long, 0.7–3(–4) cm wide, narrowly elliptic to narrowly ovate-elliptic or elliptic-oblong, apex acute to acuminate, margin with slender (0.1–0.2 mm) gland-tipped teeth 0.2–0.8 mm long, ca. 10–15 teeth/cm, base acute, drying stiffly chartaceous and often dark above, glabrous, 2° veins 6–14/side. **Inflorescences** 4–16 cm long, simple and spiciform or with short (4 mm) proximal lateral branches, glabrous, peduncles 6–36 mm long, 1.5–3 mm thick, distal spike 3–6 mm wide, bracts to 2 mm long, broad at the base, often obscured by the large flat rounded to saddle-shaped glands 1–2.4 mm wide, flowers subsessile or short (1–2



mm) pedicellate. **Male flowers** in glomerules of 7–11 closely congested flowers, calyx ca. 1.3 mm long; filaments 1–1.5 mm long, anthers ca. 0.4 long and 0.8 mm wide. **Female flowers** with sepals ca. 3 mm long; ovary ca. 3 mm long, styles recurved. **Fruits** 8–12 mm long, to 15 mm wide, persisting woody gynobase 7–11 mm wide, with 3 acute lateral projections; seeds 5–7 mm long, 4.5–6 mm wide, ca. 4 mm thick, smooth and lustrous, caruncle ca. 1.5 mm wide.

Plants of open semideciduous vegetation, 1000–2000 m elevation. Flowering in May–July in northern Central America. The species ranges from Mexico to Honduras and is known only from two collections in western Panama.

*Stillingia zelayensis* is recognized by the small shrubby habit, lack of hairs, small leaves with prominent glands at the base of the blade, and spiciform inflorescences with thick rachis and sessile glomerules of ♂ flowers. It appears that the Panamanian collections represent a disjunct population since this species has not been collected in Nicaragua or Costa Rica.

### **Synadenium Boissier**

**Shrubs** and small trees, monoecious or dioecious, distal stems fleshy and terete, sap white; stipules represented by small glands. **Leaves** alternate, simple, petiolate, blades semisucculent and entire. **Inflorescences** axillary or terminal, pedunculate, panicles or umbels of flower-like cyathia in dichotomizing cymes, each cyathium subtended by 2 bracts. **Cyathium** radially symmetrical, with a cup-shaped or saucer-like involucre, with a spreading or rim-like gland around the periphery of the involucre, with 5 thin subquadrate lobes within. **Male flowers** in 5 groups opposite the lobes of the involucre, surrounded by membranous fringed-toothed lobes. **Female flowers** present or absent in the center of the cyathium, sepals reduced to a rim or of 3 lobes, ovary 3-locular, ovules 1/locule, styles 3 united near base, bifid distally. **Fruits** capsular; seeds minutely carunculate.

A genus of 13–19 species of eastern and southern Africa. One species is planted in gardens in Central America. For a more detailed discussion of the cyathium, see *Euphorbia*.

**Synadenium grantii** Hook. f., Bot. Mag. t. 5633. 1867.

**Shrubs** or small trees to 3(–10) m tall, with few thick erect branches, stems succulent, leafy branchlets 3–10 mm thick, terete, glabrous. **Leaves** with petioles merging with the decurrent leaf bases; leaf blades 5–17 cm long,

2–6 cm wide, narrowly obovate to oblong-obovate or oblanceolate, apex obtuse, margin entire or minutely denticulate, base cuneate, green or often reddish beneath, glabrous except along the margins or near the base, 2° veins 9–14/side, strongly ascending. **Inflorescences** 1.5–10 cm long, red or green, peduncles to 5 cm long, branching dichotomous, bracts below the cyathium ca. 3 mm long; cyathia ca. 4 mm diam.

Garden ornamentals cultivated for their short few-branched habit and succulent leaves; originally from eastern and central Africa. Common names are *bítamo*, *Bítamo-zapatillo*, and “African milk bush.”

### **Tetrorchidium Poeppig**

**Trees** or shrubs, dioecious (monoecious), stems with simple hairs or hairs attached at the middle; stipules paired, often glandular along the lateral margins. **Leaves** alternate (opposite), simple, petiolate, prominent paired glands often present at or near the apex of the petiole, blades entire or dentate, venation pinnate. **Male inflorescences** axillary, spiciform (racemiform) or sometimes branched, flowers usually 3–7 in sessile glomerules; ♂ flowers small and subsessile, calyx lobes 3, imbricate in bud, opening early, ribbed on the inner (adaxial) face, petals and disk absent; stamens 3, opposite the calyx lobes, free, filaments usually very short, equal, anthers peltate and rounded, 4-theous; pistillode small or absent. **Female inflorescences** axillary, short racemes (or branched panicles), solitary; ♀ flowers subsessile or pedicellate, calyx lobes 3, petals absent, staminodia absent, disk cupulate or 3-lobed and narrow or broad; ovary with 2–3 locules, ovules 1/locule, styles short, free, bifid, often with broad stigma-like style branches. **Fruits** capsular, thin-walled, 2- or 3-lobed; seeds rounded, caruncle absent (present), outer seed coat fleshy, inner coat foveolate, endosperm present, cotyledons broad and flat.

A genus of ca. 20 American and 5 African species. The anthers, borne on very short filaments and with four separate thecae, form an androecium in which it is difficult to distinguish three stamens. The broad styler branches form thick lobes that often cover the entire apex of the young ovary. Note that the thin erect disk of the ♀ flower, whether as three narrow elements or an entire cup, can be mistaken for a reduced corolla whorl. The hairs are often attached at the center, but this may be difficult to see. There is considerable variation within species, and this can make determination of individual collections difficult (cf. Webster & Huft, 1988). Two of our species can exceed 30 m in height.

## Key to the Species of *Tetrorchidium*

- 1a. Shoot apices and young stems glabrous [petioles usually with flat glands near the middle or in the distal half; disk represented by 3 narrow petal-like elements in ♀ flowers, ♀ flowers pedicellate, 0–1200 m, Mexico to Costa Rica] ..... *T. rotundatum*
- 1b. Shoot apices and young stems puberulent to strigose ..... 2
- 2a. Glands usually near the middle of the petiole [disk of the ♀ flower represented by 3 slender segments; 1200–1700 m elevation] ..... *T. costaricense*
- 2b. Glands usually near the apex of the petiole or at the base of the leaf blade ..... 3
- 3a. Leaf blades 2.7–7 cm long, 1–2 cm wide; plants of the Chiriquí Highlands at 1900–2300 m ..... *T. microphyllum*
- 3b. Leaf blades 9–25 cm long, 4–15 cm wide; Costa Rica and Panama at 20–1200 m elevation ..... *T. euryphyllum*

***Tetrorchidium costaricense*** Huft, Ann. Missouri Bot. Gard. 75: 1112. 1988. Figure 21.

**Trees** 8–16 m tall, older stems often with raised leaf scars, leafy stems 2.3–8 mm thick, with straight or crooked thin whitish hairs to 0.8 mm long; stipules 1.5–2.5 mm long, 1.3–1.8 mm wide at base, triangular, pubescent, often becoming thickened at the base after leaf fall. **Leaves** with petioles 1.5–6 cm long, 0.7–1.8 mm thick, glabrous or minutely strigulose, paired glands 0.3–1 mm high, 0.5–1 mm diam., opposite or subopposite and lateral near the midpoint of the petiole; **leaf blades** (5–)7–18 cm long, 2.5–7 cm wide, narrowly elliptic to elliptic-lanceolate, narrowly elliptic-obovate or obovate, tip acuminate or caudate-acuminate, tip 5–10 mm long, margin entire, base acute to cuneate, drying chartaceous and dark green, sparsely pubescent with thin straight or V-shaped hairs 0.3–0.8 mm long, upper surface glabrescent, 2° veins 5–7/side, arcuate-ascending. **Male inflorescences** 2–12 cm long, spiciform or panicleiform with lateral branches to 3 cm long, rachis pubescent, bracts ca. 1.5 × 1.5 mm, broadly sessile, glomerules sessile or on peduncles to 2 mm long, with 2–5 flowers; ♂ flowers 2–3 mm wide, sepals obovate, cucullate, glabrous externally, pilose within, stamens subsessile, anthers 0.7–0.9 mm long, ca. 1 mm wide, rounded. **Female inflorescences** 1–5 cm long, usually spiciform, rachis sparsely puberulent, pedicels to 3 mm long in fruit (flowers at first subsessile); ♀ flowers ca. 2.5 mm long, calyx 1.5–2 mm long, lobes ca. 0.5 mm long, triangular, glabrous externally, disk segments free, ca. 2 mm long and narrowly ligular, ovary smooth, stigmas 0.5–0.8 mm high, 1.4–1.8 mm diam. (at first wider than the ovary), flattened distally. **Fruits** 4–6 mm long, 6–9 mm wide, oblate, 2–3-lobed; seeds 4–6 mm long, ca. 5 mm wide, ovoid, reddish and with wrinkled surface (dried).

Plants of montane evergreen rain forest formations, 1200–2000 m elevation. Flowers have been collected in March–April and November–January; fruiting in May–October. The species ranges from the Cordillera de Tilarán to western-most Panama.

*Tetrorchidium costaricense* is recognized by its lower montane evergreen cloud forest habitat, pu-

bescent stems, prominent paired glands near the middle of the petiole, and slender disk elements in the ♀ flower. The small hairs attached at the center are distinctive, but their attachment is difficult to see.

***Tetrorchidium euryphyllum*** Standl., Publ. Field Columb. Mus., Bot. Ser. 4: 219. 1929. Figures 20 and 21.

**Trees** 6–30 m tall, trunks 10–75 cm diam., sap whitish, leafy stems 3–9 mm thick, pubescent with thin straight appressed hairs 0.2–0.6 mm long; stipules 0.5–1.5 mm long, often obscure. **Leaves** with petioles (1–)2–6.5 cm long, 1–3.3 mm thick, minutely appressed-puberulent, with paired rounded/tubular glands ca. 1 mm long on the abaxial lamina margins above the petiole apex; **leaf blades** 10–26 cm long, 4–15 cm wide, elliptic to broadly elliptic or broadly elliptic-obovate, apex often abruptly narrowed and usually short-acuminate, margin entire or slightly dentate with few (3–7/side) sessile cupuliform glands 0.3–0.6 mm diam., base cuneate to obtuse and slightly decurrent on the petiole, drying stiffly chartaceous and often yellowish green or yellowish brown, with minute (0.3 mm) appressed straight hairs attached at the center, 2° veins (3–)5–8/side, prominent beneath, distal veins arcuate-ascending. **Male inflorescences** often 3/axil, 3–12 cm long, spike-like or racemiform (rarely paniculate with lateral branches to 20 mm long), glomerules sessile or pedunculate, rachis 0.7–1 mm thick, pubescent with yellowish hairs, bracts 1–1.5 mm long, broadly sessile, minutely (0.2–0.5 mm) pubescent, each with 2 rounded flat lateral glabrous glands 0.6–1.2 mm diam., subtending 1–3 flowers; ♂ flowers with 3 anthers sessile on a short (0.3–0.7 mm) thick column. **Female inflorescences** 1–2/axil, to 5 cm long, rachis 0.6–1 mm thick, pubescent, flowers solitary and distant, subsessile (sometimes pedicellate in fruit); ♀ flowers with calyx 1–1.5 mm long, calyx lobes 3, cupular disk 0.3–1 mm high, thin and resembling a corolla cup, ovary 1–1.5 mm long, ovoid, subglabrous, stigmas sessile, 0.7–1 mm wide distally. **Fruits** 3–4 mm long, 5–6 mm wide, oblate and 2- or 3-lobed, green, columella ca. 3 mm long, rarely persisting; seeds ca. 4 × 3 mm, seed coat reddish.



Plants of evergreen rain forest formations of the Caribbean slope and central highlands, 50–1000 m elevation (to 1200 m near Fortuna Dam in Chiriquí). Flowering in December–May and July; fruiting in March–July. The species ranges from the Caribbean slope of northern Costa Rica to northern Colombia.

*Tetrorchidium euryphyllum* is recognized by its larger entire or slightly dentate leaves with two to four glands along the decurrent base of the lamina (sometimes at the apex of the petiole). These glands are sometimes erect and cylindrical with a round distal opening (urn-like). In addition, the ovary is partly enclosed in a cupulate corolla-like disk, and the lateral glands of the floral bracts are often as large or larger than the bracts themselves. The slender hairs are distinctive because they are attached at the center, but this is often difficult to see. This species is similar to *T. gorgonae* Croizat of Panama and Colombia, but that species has smaller leaves with narrow petiolar glands, fewer 2° veins and pedicellate ♀ flowers.

***Tetrorchidium microphyllum* Huft, Ann. Missouri Bot. Gard. 75: 1110. 1988.**

Small usually slender trees 6–10 m tall, distal branches with raised knobby leaf scars, leafy stems 1.2–4 mm thick, densely strigulose with yellowish hairs ca. 1 mm long; stipules 0.5–2 mm long, triangular, strigulose, becoming thickened and glabrous at the base after leaf fall. **Leaves** clustered near the ends of stems, petioles 5–16 mm long, 0.6–1.2 mm thick, sparsely puberulent, glabrescent, yellowish, with 2 opposite/subopposite cylindrical or cupuliform glands near the apex, 0.5–0.8 mm diam.; **leaf blades** 2.7–7 cm long, 0.9–2 cm wide, oblanceolate to narrowly elliptic-ob lanceolate or narrowly elliptic, apex acuminate, margin entire, base gradually narrowed and acute or cuneate, drying stiffly chartaceous, yellowish, at first minutely strigulose with appressed hairs 0.2–0.3 mm long, glabrescent, 2° veins 4–5/side. **Male inflorescences** 1–3 cm long, spiciform, rachis ca. 0.6 mm thick, strigulose with short (0.3 mm) yellowish hairs, bracts 1–1.5 mm long, broadly sessile, mostly glabrous; ♂ flowers 1.5 mm wide, calyx lobes 0.7–1.2 mm long, triangular, anthers ca. 0.7 mm wide, anthers subsessile, 0.8–0.9 mm long. **Female inflorescences**, flowers and fruits unknown.

Plants of evergreen cloud forests, 1900–2300 m elevation. Flowers were collected in February (*Hammel 6039*) and November (*Hammel 5721*, the type). The species is known only from northeast of Boquete, Chiriquí Province, Panama.

*Tetrorchidium microphyllum* is recognized by its restricted higher-elevation habitat and smaller narrow glabrescent leaves. The distal stems below the leaves are conspicuously knobby, due in part

to the enlargement of the lateral bases of the stipules.

***Tetrorchidium rotundatum* Standl., Trop. Woods 16: 44. 1928. Figure 21.**

Trees 8–35 m tall, larger trees often with buttresses, distal stems with prominent leaf scars, leafy stems 3–9 mm thick, glabrous and often lustrous, yellowish, becoming knobby; stipules ca. 1.3 × 1.3 mm, triangular, persisting and becoming thickened after leaf fall. **Leaves** with petioles 25–60 mm long, 1.4–3 mm thick, glabrous, paired lateral glands usually present near the middle of the petiole, flat, 0.5–0.7 mm wide, 0.2–0.4 mm high; **leaf blades** 9–26 cm long, 3.5–10 cm wide, elliptic to narrowly elliptic-oblong or elliptic-oblong, apex bluntly obtuse to subacuminate, margin entire or slightly undulate (glands along the margin minute), gradually narrowed to the cuneate base, drying chartaceous and dark green or yellowish green, glabrous, 2° veins 6–8/side, flat beneath, ascending. **Male inflorescences** 4–20 cm long, spiciform, rachis 0.7–1.5 mm thick, glabrous or sparsely puberulent distally, glomerules sessile with 3–7 flowers, bracts usually obscured by the flowers; ♂ flowers ca. 1 mm wide. **Female inflorescences** usually 1/axil, 2–6 cm long, glabrous at the base but rachis and pedicels densely puberulent, pedicels becoming 4–8 mm long in fruit, to 1 mm thick; ♀ flowers 2–3 mm long, calyx ca. 1.5 mm long, lobes ca. 0.5 mm long, obtuse, exterior densely and minutely (0.1–0.2 mm) puberulent, disk segments ca. 1 × 0.3 mm, oblong; ovary ca. 1 mm diam., glabrous, stigmas 0.3–0.6 mm thick, 1.3–1.5 mm wide, flattened distally. **Fruits** 5–7 mm long, 8–11 mm wide, oblate and usually 2-lobed, columella not usually separating from both valves; seeds ca. 7 × 6 mm, with wrinkled reddish surface (dried).

Plants of lowland evergreen forest formations, 0–1200 m elevation. Flowering in November–April and August; fruiting primarily in May–October. The species is known only from four collections in Costa Rica: *Grayum & Herrera 4843* from ca. 500 m elevation east of the Río Tenorio, *Oersted 5819* from Monte Aguacate, *Rivera 935* from P.N. Rincón de la Vieja, and *Zúñiga 250* from the Reserva Biológica Carara with fruits in May. The species ranges from Veracruz, Mexico, to central Costa Rica.

*Tetrorchidium rotundatum* is recognized by the lower elevation habitats, generally glabrous leaves and stems, the flat (not prominent) lateral glands usually in the distal half of the petiole, larger leaf blades, and pedicellate ♀ flowers with narrow disk segments (resembling narrow petals). The ♀ inflorescence, glabrous at the base and quickly becoming pubescent distally, is distinctive. This species is very similar to *T. brevifolium* Standl. & Steyererm. (including *T. molinae* L. Wms.) of northern Central America, but that species has smaller leaves,



glabrous ♀ inflorescences, and glands at the apex of the petiole and has not been collected from below 1200 m elevation.

Tragia Linnaeus

Herbs, vines, or shrubs, monoecious, hairs simple, often stinging; stipules paired, entire or lobed, usually persisting. **Leaves** alternate, simple, petiolate, entire to serrate, sometimes deeply lobed, venation pinnate or palmate. **Inflorescences** opposite the leaves or terminal on short lateral branches (also axillary), usually solitary, mostly bisexual, simple or bifurcate, ♀ flowers usually 1–several and proximal, ♂ flowers many and alternate along the unbranched rachis, bracts small, subtending 1–3 ♂ and solitary ♀ flowers. **Male flowers** borne on articulated pedicels, sepals 3–6, valvate in bud, corolla and disk absent; stamens 2–5(–40), filaments free or united

at the base, short, anthers dehiscing longitudinally; pistillode small or absent. **Female flowers** with pedicels often elongating in fruit, sepals 3–6, imbricate; petals and disk absent; ovary usually 3-locular, hispid with stinging hairs, ovules 1/locule, styles 3, united at base, slender, undivided. **Fruits** capsules, often covered with stinging hairs, usually breaking into 3 2-valved cocci, columella persisting, with 3 broad wings at the apex; seeds subglobose, smooth or slightly ridged, ecarunculate, endosperm carnose, cotyledons broad flat.

A tropical genus of ca. 125 species, mostly African and American. The herbaceous vining stems, stinging hairs, and unbranched or two-branched inflorescences arising from opposite the adjacent leaf base make our species quite distinctive. Poor representation of these plants in herbaria may be a reflection of their urticating pubescence and slender twining habit.

Key to the Species of *Tragia*

- 1a. Leaves 8–26 cm wide, cordate at the base with a conspicuous sinus 15–20 mm deep; inflorescences bifurcate, rachis 1–3 mm thick; ♂ flowers with 30–40 conspicuous stamens; evergreen Caribbean slope, 0–800(–1500) m elevation ..... *T. bailloniana*
- 1b. Leaves 1.7–6.5 cm wide, rounded and truncate to cordate at the base with a short (to 6 mm) sinus; inflorescences simple, rachis ca. 0.3 mm thick; ♂ flowers with 2 minute stamens; Meseta Central and Pacific slope, 0–1300 m elevation ..... 2
- 2a. Pistillate flowers long-pedicellate, styles partly connate; stems herbaceous, often green or yellowish; plants of partly deciduous vegetation, 700–1300 m elevation in Costa Rica (0–1500 m elsewhere) ..... *T. volubilis*
- 2b. Pistillate flowers subsessile, styles free; stems slightly woody and often reddish brown; rarely collected plants of evergreen vegetation 20–500 m elevation in southern Costa Rica and Panama ..... *T. correae*

*Tragia bailloniana* Müll. Arg., *Linnaea* 34: 178. 1865, and in DC., *Prodr.* 15 (2): 927. 1866. *Zuckertia cordata* Baill., *Etud. Euphorb.* 496, p. 4. 1858, not *Tragia cordata* Mich. Figures 2 and 5.

Herbaceous vines and climbers, 2–4(–6) m high, leafy stems 2–4 mm thick, with stiff straight to slightly curved stinging hairs to 2.5 mm long; stipules 7–13 mm long, lanceolate to narrowly ovate-triangular, acute. **Leaves** variable in shape on the same plant, petioles 6–12(–25) cm long, 1.3–2.7 mm thick, often thickened and geniculate at the base, with hairs 0.5–2.5 mm long; **leaf blades** 13–33 cm long, 8–26 cm wide, unlobed and ovate to broadly ovate or prominently 3-lobed with sinuses 1–9 cm deep, (rarely also with lateral basal lobes), apices acuminate with slender tip 5–22 mm long, margin with small (0.3–0.5 mm) teeth, 1–4 teeth/cm, base cordate, basal sinus 1.5–5 cm deep, drying membranaceous and greenish, upper surface with straight slender stinging hairs

0.7–2 mm long and minute hairs above the major veins, larger hairs to 1.4 mm long beneath, venation palmate with 3 (5) major veins, 2° veins 3–5/side of the midvein, 3° veins often subparallel. **Inflorescences** 5–13 cm long, usually bifid from a peduncle 1–10 cm long, 1.5–4 mm thick, branches unisexual, ♂ racemes 5–13 cm long, bracts 3–5 mm long, ovate-lanceolate and subglabrous, subtending 1–3 flowers, ♀ axis to 18 cm long, spiciform, ♀ bracts 3–8 mm long, lanceolate, smaller distally. **Male flowers** borne on pedicels 8–10 mm long, ca. 0.2 mm thick, buds pyriform-obovoid, sepals usually 4, 6–7 mm long, 1.3–2 mm wide, oblanceolate, glabrous or ciliate on the margin, stamens 28–40, filaments 3–3.5 mm long united near the base in groups of ca. 3, anthers 0.7–1 mm long. **Female flowers** borne on pedicels 1–4 mm long (hidden by bracts), hirsutulous, sepals 3–5 mm long, 1.7–2.7 mm wide, lanceolate, mostly glabrous abaxially; ovary covered with stiff straight stinging hairs ca. 1 mm long, styles 6–9 mm long, 0.6–1.2 mm thick, separate distally for 2.5–4.5 mm. **Fruits** 8–13 mm long, 12–22 mm wide, prominently 3-lobed, glabrescent, columella ca. 6 mm long, distal wings to 5 mm wide; seeds ca. 6 mm long, subglobose.

Plants of lowland evergreen rain forest formations of the Caribbean slope, 10–800 m elevation (to 1500 m in Chiriquí). Probably flowering throughout the year (collected in September in Costa Rica). The species ranges from Veracruz, Mexico, to western Panama.

*Tragia bailloniana* is distinguished by its slender climbing habit, large cordate leaves on long petioles, inflorescences with two long unbranched axes (1 ♂ and 1 ♀), and stinging hairs on many parts. The more deeply lobed leaves resemble those of *Gurania* (Cucurbitaceae), but the stinging hairs will quickly alert the unwary (compare also *Daléchampia shankii*). Because of its distinctive features, this species is placed in the monotypic section *Zuckertia* (Baill.) Müll. Arg.

***Tragia correae*** Huft, Ann. Missouri Bot. Gard. 75: 1107. 1988. Figure 5.

**Vines** or slender lianas with brown or reddish brown stems, leafy stems ca. 2 mm thick, with both minute (0.2 mm) and longer straight stinging hairs to 1.5 mm long; stipules 4–10 mm long, narrowly triangular to narrowly ovate, pilose. **Leaves** with petioles 25–65 mm long, 0.7–1 mm thick, with slender erect hairs 1–1.5 mm long; **leaf blades** 5–12 cm long, 2–6 cm wide, elliptic-oblong to oblong-triangular or narrowly oblong, apex acuminate or subacuminate, margin minutely denticulate with 15–30 teeth/side, base rounded and cordate to subcordate, sinus 3–6 mm deep, drying membranaceous, surfaces with straight hairs 0.2–0.8 mm long, venation pinnate or subpalmate, 2° veins 5–7/side. **Inflorescences** opposite the leaves, solitary, greenish yellow, 3–6 cm long (to 16 cm after fruiting), rachis ca. 0.3 mm thick, pubescent, ♀ flower solitary and proximal, subtended by a 3-lobed bract, ♂ flowers 20–60, distal, subtended by bracts ca. 2.5 × 1.3 mm, ovate-lanceolate and entire, margins ciliate. **Male flowers** short-pedicellate, calyx lobes 3, ca. 1.3 × 1.2 mm, obovate and acute, hispidulous externally; stamens 3, free, filaments ca. 0.8 mm long, thick, anthers 0.2–0.3 mm long, elliptic, extrorse. **Female flowers** on pilose pedicels 2–4 mm long, calyx lobes 5, 2–3 mm long, ca. 0.7 mm wide, lanceolate; ovary 2–3 mm diam., densely hispidulous with stinging hairs, styles free, 2–3 mm long, spreading, recurved. **Fruits** not seen at maturity.

Plants of evergreen forests of the Pacific slope, 40–600 m elevation. Flowering in January and September; with old inflorescences in November. This species is known only from near Sierpe, Puntarenas, in southern Costa Rica (*Aguilar* 872, *Herrera* 4581 & 4784) and in the province of Panamá, Panama (*Sucre et al.* 9832 the type).

*Tragia correae* is recognized by its Pacific slope habitat, reddish brown slightly woody stems, stinging hairs, simple inflorescences, and oblong or somewhat triangular leaf blades shallowly cordate at the base, thin and drying translucent.

***Tragia volubilis*** L., Sp. Pl. 980. 1753. Figure 5.

Herbaceous vines to 3 m high, stinging hairs present on stems and leaves, leafy stems 0.5–3 mm thick, with curved or straight slender hairs 0.3–1 mm long; stipules 2–4 mm long, 0.7–1 mm wide at base, narrowly triangular, sparsely pubescent. **Leaves** with petioles 5–70 mm long, 0.4–1 mm thick, with stinging hairs 0.4–1 mm long; **leaf blades** 2.5–10 cm long, 1.7–5(–6.5) cm wide, ovate-triangular to triangular or oblong-triangular, apex acute to short-acuminate, margin with acute teeth 0.5–3 mm long (6–18 teeth/side), base rounded and cordate or truncated at 90° to the petiole, drying chartaceous, often much paler beneath than above, surfaces with straight slender hairs 0.3–1.5 mm long, venation pinnate or subpalmate, 2° veins 3–6/side. **Inflorescences** opposite the leaves or axillary, usually solitary, 2–5 cm long, ♀ flowers usually solitary and proximal, on a slender pedicel to 3 cm long, subtended by a 3-parted bract 1–2 mm long, rachis ca. 0.3 mm thick, strigulose, ♂ bracts 1–1.6 mm long, entire, alternate along the rachis, with 1 ♂ flower, pedicels to 1.6 mm long, slender and articulated below the middle, base persisting. **Male flowers** ca. 0.7 mm wide, sepals 3, 0.6–0.9 mm long, 0.4–0.6 mm wide, ovate; stamens 2, filaments thick, short, anthers 0.3–0.4 mm long, 0.1–0.2 mm wide. **Female flowers** with 6 sepals in 2 series, 1.6–2.5 mm long, 0.4–1 mm wide (enlarging in fruit); ovary covered with stiff slender hairs ca. 1 mm long, styles 2.5 mm long, style column 0.5–1.5 mm long, branches recurved. **Fruits** ca. 4 mm long, ca. 6 mm wide (sometimes dimorphic) densely covered with sharp stinging hairs, borne on slender pedicels to 25 mm long, columella 1.4–2 mm long, with distal wings 1.7–2 mm wide; seeds 2.2–3 mm diam., subglobose, with irregular raised reddish ridges on a paler surface.

Plants of deciduous or partly deciduous forests on the Pacific slope and around the Meseta Central, 20–1300 m elevation (to 1500 m in Guatemala). Flowering and fruiting in April–December. The species ranges from Mexico and Cuba to Peru and Argentina; also widespread in tropical Africa.

*Tragia volubilis* is recognized by its slender vining habit, the often triangular and clearly serrate leaves, and small unisexual flowers. More important in recognition are its stinging hairs, which are found on most parts. Local names are *pica-pica* (Costa Rica), *chichicaste de ratón* (Guatemala), and *chimbira* (Nicaragua).

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## List of Accepted Species

Key: CULT = cultivated; END = endemic to Costa Rica; CR + WP = endemic to Costa Rica and western Panama; WP = endemic to western Panama; ?? = not collected in Costa Rica but known from nearby areas. The treatment includes 188 species, of which 150 are native or naturalized and 23 are cultivated. Those endemic to Costa Rica number 10, with 7 additional species endemic to Costa Rica and western Panama. Fifty-two genera are included, of which 45 are native.

- Acalypha alopecuroides*  
*Acalypha amentacea* ssp. *wilkesiana* CULT  
*Acalypha apodanthes* END  
*Acalypha arvensis*  
*Acalypha costaricensis*  
*Acalypha diversifolia*  
*Acalypha ferdinandii*  
*Acalypha hispida* CULT  
*Acalypha leptopoda*  
*Acalypha macrostachya*  
*Acalypha mexicana*  
*Acalypha obtusifolia* ??  
*Acalypha polystachya*  
*Acalypha radinostachya*  
*Acalypha schiedeana*  
*Acalypha septemloba* CR + WP  
*Acalypha setosa*  
*Acalypha triloba*  
*Acalypha villosa*  
*Acalypha* sp. aff. *A. mertoniana*  
*Acidoton nicaraguensis*  
*Actinostemon caribaeus*  
*Adelia triloba*  
*Adenophaedra grandifolia*  
*Alchornea costaricensis*  
*Alchornea glandulosa*  
*Alchornea grandiflora*  
*Alchornea latifolia*  
*Alchornea triplinervia*  
*Alchorneopsis floribunda*  
*Aleurites fordii* CULT  
*Aleurites moluccana* CULT  
*Amanoa guianensis*  
*Antidesmia bunius* CULT  
*Aparisthium cordatum*  
*Argythamnia guatemalensis*  
*Astrocasia tremula*
- Bernardia macrophylla*  
*Bernardia nicaraguensis*  
*Breynia disticha* CULT
- Caperonia castaneifolia*  
*Caperonia palustris*  
*Caryodendron angustifolium* CR + WP  
*Chamaesyce bahiensis*  
*Chamaesyce bombensis*  
*Chamaesyce densiflora*  
*Chamaesyce dioeca*  
*Chamaesyce hirta*  
*Chamaesyce hypericifolia*
- Chamaesyce hyssopifolia*  
*Chamaesyce lasiocarpa*  
*Chamaesyce mesembryanthemifolia*  
*Chamaesyce nutans*  
*Chamaesyce ophthalmica*  
*Chamaesyce prostrata*  
*Chamaesyce serpens*  
*Chamaesyce thymifolia*  
*Cleidion castaneifolium*  
*Cnidoscolus aconitifolius* CULT  
*Cnidoscolus tubulosus*  
*Cnidoscolus urens*  
*Codiaeum variegatum* CULT  
*Conceveiba pleiostemona*  
*Croton argenteus*  
*Croton axillaris*  
*Croton billbergianus*  
*Croton brevipes*  
*Croton decalobus*  
*Croton draco*  
*Croton glandulosus* ??  
*Croton hirtus*  
*Croton hoffmannii* END  
*Croton jimenezii* END  
*Croton jutiaensis*  
*Croton lanjouwensis*  
*Croton lobatus*  
*Croton mexicanus*  
*Croton niveus*  
*Croton ortholobus* END  
*Croton ovalifolius*  
*Croton pachypodus*  
*Croton punctatus*  
*Croton pungens* WP  
*Croton schiedeana*  
*Croton skutchii* END  
*Croton smithianus*  
*Croton speciosus*  
*Croton sphaerocarpus*  
*Croton tenuicaudatus* CR + WP  
*Croton tonduzii* END  
*Croton trinitatis*  
*Croton xalapensis*  
*Croton yucatanensis*  
*Croton* sp. aff. *C. yucatanensis* END
- Dalechampia arenalensis* END  
*Dalechampia canescens* ??  
*Dalechampia cissifolia*  
*Dalechampia dioscoreifolia*  
*Dalechampia heteromorpha*  
*Dalechampia osana* END  
*Dalechampia scandens*
- Dalechampia shankii*  
*Dalechampia spathulata*  
*Dalechampia tiliifolia*  
*Dalechampia websteri* CR + WP  
*Drypetes brownii*  
*Drypetes lateriflora*  
*Drypetes* sp. aff. *D. alba*  
*Drypetes standleyi*  
*Dysopsis glechomoides*
- Euphorbia colletioides*  
*Euphorbia cotinifolia* CULT  
*Euphorbia cyathophora*  
*Euphorbia dwyeri* CR + WP  
*Euphorbia elata*  
*Euphorbia graminea*  
*Euphorbia heterophylla*  
*Euphorbia hoffmanniana* END  
*Euphorbia leucocephala* CULT  
*Euphorbia neriifolia* CULT  
*Euphorbia ocymoides*  
*Euphorbia oerstediana*  
*Euphorbia peplus* CULT  
*Euphorbia pulcherrima* CULT  
*Euphorbia schlechtendalii*  
*Euphorbia segoviensis*  
*Euphorbia splendens* CULT  
*Euphorbia tirucalli* CULT  
*Euphorbia xalapensis*
- Garcia nutans*  
*Gymnanthes lucida* ??  
*Gymnanthes riparia*
- Hevea brasiliensis* CULT  
*Hippomane mancinella*  
*Hura crepitans*  
*Hyeronima alchorneoides*  
*Hyeronima oblonga*
- Jatropha costaricensis* END  
*Jatropha curcas*  
*Jatropha gossypifolia*  
*Jatropha integerrima* CULT  
*Jatropha multifida* CULT  
*Jatropha podagrica* CULT
- Mabea excelsa*  
*Mabea occidentalis*  
*Manihot aesculifolia*

*Manihot brachyloba*  
*Manihot esculenta* CULT  
*Manihot glaziovii* CULT  
*Margaritaria nobilis*

*Omphalea diandra*

*Pausandra trianae*  
*Pedilanthus tithymaloides* CULT  
*Pera arborea*  
*Phyllanthus acidus* CULT  
*Phyllanthus acuminatus*  
*Phyllanthus amarus*  
*Phyllanthus caroliniensis*  
*Phyllanthus compressus* ??  
*Phyllanthus hyssopifolioides*  
*Phyllanthus mocinianus*

*Phyllanthus niruri*  
*Phyllanthus salviifolius*  
*Phyllanthus skutchii* END  
*Phyllanthus stipulatis*  
*Phyllanthus urinaria*  
*Phyllanthus valerii*  
*Plukenetia penninervia*  
*Plukenetia stipellata*

*Richeria obovata*  
*Ricinus communis* CULT

*Sagotia racemosa*  
*Sapium allenii* END  
*Sapium glandulosum*  
*Sapium laurifolium*  
*Sapium macrocarpum*

*Sapium pachystachys*  
*Sapium rigidifolium* END  
*Sapium thelocarpum*  
*Sebastiania corniculata* ??  
*Sebastiania panamensis* WP  
*Sebastiania pavoniana*  
*Stillingia zelayensis* WP  
*Synadenium grantii* CULT

*Tetrorchidium costaricense*  
*Tetrorchidium euryphyllum*  
*Tetrorchidium microphyllum* CR + WP  
*Tetrorchidium rotundatum*  
*Tragia bailloniana*  
*Tragia correae* CR + WP  
*Tragia volubilis*

# Index

The index includes all accepted names (in Roman type), synonyms (*italics*), common English names (Roman), and vernacular Spanish names (*italics*). Page numbers of illustrations are in **boldface**. The text does not include new names or combinations.

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