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# ILLINOIS DIANA Botany

Published by Field Museum of Natural History

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Volume 40

## FLORA COSTARICENSIS

WILLIAM BURGER, Editor

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Families of seed plants known or expected to occur in Costa Rica and adjacent areas, listed alphabetically and numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

200	Acanthaceae	102	Erythroxylaceae	82	Papaveraceae
136	Actinidiaceae	113	Euphorbiaceae	150	Passifloraceae
67	Aizoaceae	96	Fabaceae, see Leguminosae	195	Pedaliaceae
11	Alismataceae			66	Phytolaccaceae
64	Amaranthaceae	50	Fagaceae	5	Pinaceae
30	Amariyllidaceae	148	Flacourtiaceae	41	Piperaceae
117	Anacardiaceae	82	Fumariaceae, see Papaveraceae	171	Pyrolaceae
77	Anonaceae	45	Garryaceae	201	Plantaginaceae
184	Apocynaceae	183	Gentianaceae	176	Plumbaginaceae
119	Aquifoliaceae	99	Geraniaceae	3	Podocarpaceae
19	Araceae	198	Gesneriaceae	54	Podostemonaceae
166	Araliaceae	7	Gnetaceae	187	Polemoniaceae
4	Araucariaceae	15	Gramineae	111	Polygalaceae
59	Aristolochiaceae	142	Guttiferae	62	Polygonaceae
185	Asclepiadaceae	29	Haemodoraceae	26	Pontederiaceae
61	Balanophoraceae	165	Halorrhagaceae	68	Portulacaceae
127	Balsaminaceae	93	Hamamelidaceae	9	Potamogetonaceae
69	Basellaceae	81	Hernandiaceae	175	Primulaceae
48	Batidaceae	124	Hippocastanaceae	55	Proteaceae
153	Begoniaceae	121	Hippocrateaceae	158	Punicaceae
74	Berberidaceae	101	Humiriaceae, see Linaceae	140	Quiniaceae
49	Betulaceae	13	Hydrocharitaceae	60	Rafflesiaceae
194	Bignoniaceae	188	Hydrophyllaceae	73	Ranunculaceae
145	Bixaceae	142	Hypericaceae, see Guttiferae	86	Resedaceae
133	Bombacaceae	123	Icacinaceae	128	Rhamnaceae
189	Boraginaceae	33	Iridaceae	160	Rhizophoraceae
24	Bromeliaceae	47	Juglandaceae	94	Rosaceae
91	Brunelliaceae	27	Juncaceae	202	Rubiaceae
38	Burmanniaceae	97	Krameriaceae	104	Rutaceae
106	Burseraceae	191	Labiatae	126	Sabiaceae
12	Butomaceae	43	Lacistemaceae	44	Salicaceae
115	Buxaceae	80	Lauraceae	125	Sapindaceae
154	Cactaceae	159	Lecythidaceae	177	Sapotaceae
96	Caesalpinjiaceae, see Leguminosae	96	Leguminosae	90	Saxifragaceae
		20	Lemnaceae	193	Scrophulariaceae
114	Callitrichaceae	199	Lentibulariaceae	105	Simarubaceae
207	Campanulaceae	28	Liliaceae	192	Solanaceae
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156	Elaeagnaceae	17	Palmae		
130	Elaocarpaceae				
143	Elatinaceae				
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# FIELDIANA: BOTANY

*A Continuation of the*

BOTANICAL SERIES

*of*

FIELD MUSEUM OF NATURAL HISTORY

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VOLUME 40



FIELD MUSEUM OF NATURAL HISTORY  
CHICAGO, U.S.A.

1977



FLORA COSTARICENSIS



# FIELDIANA

## Botany

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Volume 40

### FLORA COSTARICENSIS

FAMILY #42,	CHLORANTHACEAE
FAMILY #43,	LACISTEMACEAE
FAMILY #44,	SALICACEAE
FAMILY #45,	GARRYACEAE
FAMILY #46,	MYRICACEAE
FAMILY #47,	JUGLANDACEAE
FAMILY #48,	BATAACEAE
FAMILY #49,	BETULACEAE
FAMILY #50,	FAGACEAE
FAMILY #51,	ULMACEAE
FAMILY #52,	MORACEAE
FAMILY #52a,	CANNABACEAE
FAMILY #53,	URTICACEAE

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*Field Museum of Natural History*

*Library of Congress Catalog Card Number: 78-172358*

US ISSN 0015-0746

PRINTED IN THE UNITED STATES OF AMERICA



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# Flora Costaricensis<sup>1</sup>

## CHLORANTHACEAE

WILLIAM BURGER

Trees, shrubs, or herbs, usually aromatic when crushed. Leaves opposite and simple, petioles with thin adaxial margins sheathing the stem and connate to form a short or long tube at first including the shoot-apex, stipule-like structures often present on the leaf-sheath. Inflorescences terminal or axillary, spicate, thyrse-like, or capitate; flowers unisexual or bisexual, with or without a perianth, stamens 1 or 3, free or adnate to the side of the pistil, anthers free or connate, 2-theous or the lateral anthers 1-theous, dehiscent longitudinally; pistil solitary, ovary enveloped by a minutely 3-lobed perianth and inferior by adnation, 1-locular, ovule solitary and pendulous from the apex of the locule, stigma 1 and sessile or on a short style. Fruit a small drupe or drupe-like, seed with abundant oil-containing cellular endosperm and a minute embryo.

A small family of five genera and about 50 species in the tropics and subtropics. The family is of phylogenetic interest because it contains one of the very few woody angiosperm genera lacking vessels in the xylem, *Sarcandra* of Southeast Asia. *Hedyosmum* is the only genus of the family native to the Americas. The female flowers of *Hedyosmum mexicanum* have recently been studied by Peter Endress (Bot. Jahrb. 91:39-60. 1971), who interprets the ovary to be monocarpic and compares the family with woody families of the ranalian alliance.

## HEDYOSMUM Swartz

Bisexual or unisexual trees or shrubs, branches articulate at the nodes and exuding a gelatinous aromatic exudate when cut. Leaves evergreen, petioles grooved above and vaginate at the base with the adaxial margins united with those of the opposing leaf to form a tube sheathing the stem, with or without small stipule-like structures on the distal margin of the sheath; laminae generally elliptic and serrate, the serrations often with whitish tissue forming a disc-like gland near their apex (probably a hydathode), venation pinnate. Inflorescences terminal or axillary, sometimes united with the stem near the base, the individual inflorescence unisexual but the compound inflorescences often with female flowers above and male flowers on lower branches; male inflorescence of one to several spikes elongating at

<sup>1</sup>Supported in part by National Science Foundation grants GB 28446, GB 42250, and BMS 74-08757.

anthesis, the male flower without a perianth or subtending bracts, each flower represented by a solitary stamen, filament absent or very short, connective usually produced beyond the two thecae; female inflorescence spicate, thyrselike, or capitate, female flowers subtended by bracts, the perianth tubular and 3-lobed, adnate to the ovary and enlarging in fruit, stigma sessile or subsessile on a very short style, deciduous. Fruit drupe-like with the fleshy wall formed by the accrescent perianth in part, ellipsoid to globose or ovoid, usually trigonous, exocarp juicy, the 3 minute perianth lobes often persisting and whitish at the apex of the fruit.

A genus with probably fewer than 30 species in the Neotropics and with a single species in southeastern Asia. The genus is primarily South American with several species in the West Indies and only one species reaching Mexico. The male flowers are perhaps the most reduced among angiosperms, lacking bracts and perianth, and represented by a single, almost sessile, anther. The expanded connective, usually broad and flat above, serves to protect the reproductive parts in early stages before expansion of the spike. Except for *Hedyosmum mexicanum*, our species are here interpreted as having rather narrow ecological limits. I believe that our collections are sufficiently large to indicate that these narrow patterns of distribution are real and not merely artifacts of inadequate sampling. Our species are found only in areas that are quite moist throughout the year. No Costa Rican species is known to grow in the flat Caribbean Coastal Plain; all species here appear to require the drainage of hilly sites.

- 1a. Leaf-sheath with conspicuous distal fimbriate structures 4-12 mm. long, leaves glabrous and smooth; plants unisexual with the female flowers in compact heads, male flowers (anthers)  $3 \times 1$  mm. on spikes 3-16 cm. long; at elevations of 1100-2800 m. (in Costa Rica). . . . . *H. mexicanum*.
- 1b. Leaf-sheath entire or with subulate or very short (1-4 mm.) fimbriate processes distally; female flowers solitary or in small groups of 2 to 4 . . . . . 2a.
- 2a. Leaves linear-lanceolate to very narrowly elliptic, leaf-sheath entire distally, leaves glabrous and smooth; plants bisexual with the female flowers sessile and solitary, often in a cincinnus-like form, male flowers (anthers)  $1 \times 0.7$  mm.; 1000-1300 m. on the Pacific slope (in Costa Rica). . . . . *H. brenesii*.
- 2b. Leaves broader, plants of the wet Caribbean slopes and the Central Highlands and Cordilleras . . . . . 3a.
- 3a. Leaves with 12 to 20 (30) secondary veins on a side, glabrous and usually smooth; inflorescences free of the stem above the leaf-sheath, male flowers (anthers)  $1.5 \times 0.7$  mm., the plants bisexual or (?) occasionally unisexual; 900-1600 m. . . . . *H. costaricense*.
- 3b. Leaves with 5 to 10 secondary veins on a side, often scabrous; inflorescences usually united with the stem to above the leaf-sheath, plants unisexual . . . . 4a.
- 4a. Female flowers solitary within a subtending cupulate or open bract, male flowers (anthers)  $1.4 \times 0.5$  mm.; elevations of 500-1000 m. *H. calloso-serratum*.

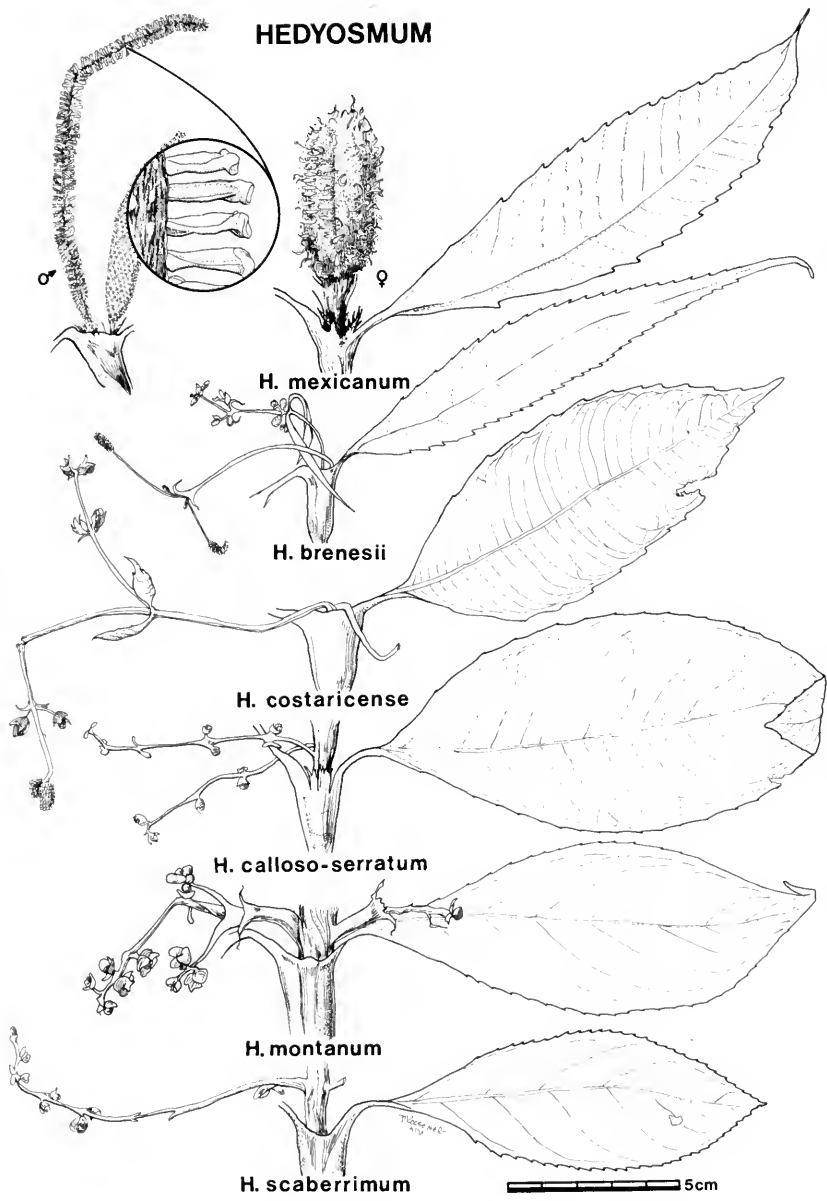


FIG. 1. Chloranthaceae: Costa Rican and Panamanian species of *Hedyosmum*; note the opposite leaves with tubular sheathing leaf-bases.

- 4b. Female flowers usually in groups of 2 or 3 within the subtending bracts . . . 5a.  
 5a. Plants of higher (1800-2700 m.) elevations along the Caribbean side of the Central Highlands and in the Cordillera de Talamanca; male flowers (anthers)  $1.7 \times 0.6$  mm. . . . . *H. montanum*.  
 5b. Plants of lower (0-1000 m.) elevations on the Caribbean slopes of western Panama; male flowers (anthers)  $2.5 \times 0.5$  mm. . . . . *H. scaberrimum*.

***Hedyosmum brenesii* Standl., Field Mus. Bot. 18:371. 1937.**

**Figure 1.**

Bisexual shrubs 1-2 m. tall, often with many branches, leafy internodes (1) 2-7 cm. long, 1-3 mm. thick, glabrous, leaf-scars inconspicuous and narrow around the stem. Leaves with the free portion of the petiole absent or very short (1-3 mm.), margins of the lamina continuous with the vaginate leaf-base, tube of the leaf-sheath 4-10 mm. long with the distal margin usually entire; laminae 7-19 cm. long, 1-2 (3) cm. broad, linear-lanceolate to very narrowly elliptic, broadest at or below the middle, gradually long-acuminate at the apex, attenuate at the base, acutely serrate along the margins, laminae glabrous and drying chartaceous, smooth above and below, the 6 to 12 pairs of secondary veins obscure above and below with only the midvein prominent. Inflorescences usually unisexual with the male borne at nodes directly below those with female inflorescences; male inflorescence usually of opposite pedunculate spikes borne on an unbranched common peduncle 1-3 cm. long, peduncles of the spikes 5-12 mm. long and subtended by a bract, the spikes 5-15 mm. long and about 3 mm. thick, stamens becoming 1 mm. distant on the rachis, anthers sessile, 0.9-1.3 mm. long and 0.5-0.7 mm. thick, connective projecting acutely forward 0.5 mm. beyond the thecae; female inflorescence of paired or solitary flowers often on a cincinnus-like rachis, bracts subtending the lower inflorescence-branches 1-3 cm. long and 2-4 mm. broad, each flower subtended by a bract 1-3 mm. long, female flowers sessile, 2-3 mm. long, 1-2 mm. thick, stigma very short. Fruit 3-4 mm. long and 2-3 mm. thick, ellipsoid and trigonous, drying brown.

This species is known in Costa Rica only from the collections of Alberto Brenes (3731, 4027, & 4620 the type) made between August and November in the area of La Palma de San Ramon, Alajuela Province, at altitudes of 1150 to 1250 m. The species has also been collected in the Province of Bocas del Toro, vicinity of Chiriquí Lagoon, Panama, and near Lake Yojoa, Honduras.

*Hedyosmum brenesii* is easily distinguished from our other species of the genus by the very narrow subsessile leaves, usual presence of a few male inflorescences below the female, and consistently solitary female flowers. This species is closely related to *H. nutans* Sw. of the West Indies.

***Hedyosmum calloso-serratum* Oersted, Vidensk. Meddel. Kjoebenhavn 1856:40. 1857. Figure 1.**

Unisexual shrubs or small trees 3-12 m. tall, leafy internodes 2-10 cm. long, 1.5-6 mm. thick, essentially glabrous, leaf-scars usually absent with the leaf-base persisting and encircling the stem. Leaves with the free portion of the petiole 5-25 mm.

long and 1-2 mm. thick, glabrous or with irregular short or long hairs, tube of the leaf-sheath 1-2.5 cm. long, usually with 2 small (1-3 mm.) aculeate or distally fimbriate structures on each distal margin, usually remaining entire and not tearing distally; laminae 7-22 cm. long, 2.5-8.5 cm. broad, narrowly elliptic to oblong or slightly obovate, abruptly short-acuminate, acute to obtuse at the base, finely serrulate along the margins, drying stiffly chartaceous to subcoriaceous, glabrous and slightly rough to scabrous above, scabrous and often with irregular brownish hairs 0.2-1 mm. long on the midvein beneath, minute (0.1 mm.) epidermal projections sparse or inconspicuous, the 6 to 9 pairs of major secondary veins flat above and prominent beneath. Inflorescences usually united with the stem to above the leaf-sheath; male inflorescence of spikes usually borne in 2 or 3 opposite pairs on a short (1-3 cm.) axis terminated by a single spike, subsessile or terminal on bracteate peduncles 4-12 mm. long, the subulate bracts 5-9 mm. long, spikes expanding to about 3 cm. long and 4-6 mm. thick, each anther subsessile or on a slight projection of the rachis, 1.2-1.6 mm. long and 0.4-0.6 mm. broad, the connective produced about 0.2 mm. beyond the thecae, flat above and acute on one side (toward the apex of the spike); female inflorescences thyrse-like or racemose, 3-8 cm. long, branches of the inflorescence originating from the stem or from a short (1-2 cm.) common rachis, floral bracts opposite or alternate and pedicellate or subsessile, the floral bract cupulate or open on one side, 2-3 mm. long and usually 3-lobed, becoming white but drying brown, each bract subtending and partly enclosing a single female flower (rarely with more than one), female flower about 2 mm. long and 1.5 mm. thick with perianth-lobes about 0.3 mm. long. Fruit 2-3 mm. long and 1.4-2 mm. thick, ellipsoid and trigonous.

Plants of the premontane wet forest and its transition to the tropical wet forest formation between (0) 500 and 1000 m. elevation in Costa Rica. The species ranges from the area of Ciudad Quesada, Alajuela, along the Caribbean slope to the Río Grande de Orosi, Cartago, and from the General Valley on the Pacific slope to Central Panama; apparently flowering throughout the year, but collected most often between February and August.

*Hedyosmum calloso-serratum* is distinguished by the usually solitary female flowers and the lowland habitats above the coastal plain (no Costa Rican collections are known from below 500 m. elevation). The type collection is described as having come from Volcán Irazú at an elevation of 9000 ft. (2760 m.), but I am sure that this is incorrect. Type material very closely matches all the other material placed here, and none of this material was found at altitudes above 1000 m. This species is very closely related to *H. scaberrimum* and *H. montanum*; see the discussion under the latter species.

*Hedyosmum costaricense* C. E. Wood in Burger, *Phytologia* 26:132. 1973. Figure 1.

Bisexual or (?) unisexual shrubs and small trees 3-7 m. tall, essentially glabrous, leaf-scars absent with the leaf-base persisting and encircling the stem. Leaves with the free portion of the petiole 4-15 (25) mm. long, 0.8-2 mm. thick, tube of the leaf-sheath 3-8 (12) mm. long, the distal margins entire or with 2 minute (1 mm.) linear structures on each distal margin; laminae 7-16 cm. long, 2.5-5 (6) cm. broad, very narrowly to broadly elliptic or oblong, abruptly acuminate, obtuse to acute at the base, serrulate with teeth 4-8 mm. distant on the margin, laminae drying stiffly chartaceous to subcoriaceous, smooth and glabrous above and below, the 12 to 20 (30) pairs of major secondary veins flat or becoming impressed above, serrulate with the teeth about (4) 8 mm. distant on the margin. Inflorescences occasionally bisexual (as in the type), usually free from the stem above the leaf-sheath; male inflorescences usually of spikes borne in 1 to 3 opposite pairs on an axis 3-8 cm. long, terminated by a pair of spikes, each spike subtended by an aculeate bract about 3 mm. long, spikes sessile or occasionally short (15 mm.) pedunculate, 6-18 mm. long, 4-5 mm. thick, stamens becoming 2 mm. distant on the expanded rachis, anthers sessile, 1.3-1.8 mm. long and 0.6-1 mm. broad, connective about 0.5 mm. broad and flat above; female inflorescences thyrselike, racemose, or spicate with groups of (1) 3 to 6 female flowers in opposite pairs, sessile or on short (1-8 mm.) peduncles, each group of flowers about 4-8 mm. long and 3-6 mm. thick, each flower subtended by a broad bract about 2.5 mm. long and united with the other bracts only at the very base, female flower about 2 mm. long with perianth-lobes about 0.5 mm. long, the lower half of the flower enclosed within the subtending bract. Fruit 2.5-4 mm. long, about 2 mm. thick, thickest at or above the middle, trigonous.

Plants of the very wet lower montane (premontane wet and pre-montane rain) forest formations between 900 and 1600 m. elevation and known only from areas of the Central Highlands subject to the wet Caribbean winds (see below); flowering and fruiting throughout the year. The species is endemic to Costa Rica.

The leaf-venation, occasional bisexual inflorescence, and floral details readily distinguish this species from all our other species of the genus. The plants are uncommon and known only from the following collections: Los Angeles de San Ramon (*Brenes 4772, 13127, & 13589*), below Zarcero (*A. Smith H566*, the type) in Alajuela Province, near Tapanti (*Lent 990*), above Platanillo (*Wilbur & Stone 10627*) in the Province of Cartago at 1,100 m. near Balsa de San Ramon (*Lent 3502*), and 1,100 m. from Río Hondura-Río Cascajal (*Lent 3783*). In addition, two rather unusual collections are placed here: *J. León 133* from Capellades and *Valerio 1348* from Santa Cruz de Turrialba, Cartago. These differ from the others in having thicker leaves with many more (16-30 pairs) prominent secondary veins and the closer (4 mm.) serrations, but I believe they are only an unusual form of the species; they lack well-preserved flowers. Vegetatively, the species and especially the latter two col-



lections resemble *H. scabrum* (R. & P.) Solms of South America and *H. arborescens* Sw. of the West Indies.

***Hedysomum mexicanum*** Cordemoy, *Adansonia* 3:307. 1862-63. Figure 1.

Unisexual shrubs or small trees 2-8 (12) m. tall, the stems strongly angled, leafy internodes 0.5-4 cm. long, 2.5-5 mm. thick, glabrous in all stages, older stems encircled by leaf-scars at each node. Leaves with the free portion of the petiole 3-10 mm. long, 1-2 mm. thick, adaxial margins continuous with the margins of the lamina and leaf-sheath, tube of the leaf-sheath 1-4 cm. long, widening apically to 14 mm. broad, usually with 2 fimbriate stipule-like structures 4-12 mm. long on each distal margin, the leaf-sheath not persisting after the leaves have fallen; laminae 9-18 (27) cm. long, 2.5-4.5 (7) cm. broad, very narrowly elliptic to very narrowly oblong, broadest at the middle, gradually acuminate, acute to attenuate at the base, the laminae slightly succulent but drying stiffly chartaceous to subcoriaceous, glabrous throughout, smooth on both surfaces, the 12 to 20 pairs of major secondary veins often prominent beneath, conspicuously serrate with the blunt teeth 4-8 mm. distant. Male inflorescences rare in collections, made up of spikes paired or terminal on short leafless axillary branches 3-20 mm. long, spikes 3-8 (16) cm. long, about 8 mm. thick, stamens crowded but becoming 2 mm. distant on the rachis, anthers sessile, about 3 mm. long and 1 mm. thick, connective forming a flat disc-like apex 0.5-1 mm. broad; female inflorescence capitate, 2-4 cm. long and 12-30 mm. thick, the numerous female flowers densely congested and free but appearing to be united basally, perianth about 4 mm. long with lobes 1 mm. long, style 2-4 mm. long and minutely papillate-puberulent. Fruit compound of basally united drupes, the seeds about 3 mm. long and partly immersed in the fleshy head.

This is an uncommon species in Costa Rica, restricted to wet montane forests between 1100 and 2800 m. elevation and collected only between Volcán Barba and the western edge of the General Valley in the Cordillera de Talamanca. The species flowers from February to May in Costa Rica and from December to August in northern Central America, ranging from Costa Rica to southern Mexico.

The deciduous leaf-sheath, with its conspicuous fimbriate structures distally, capitate female inflorescences, and elongate anthers, distinguishes this species from other Costa Rican members of the genus. The female flowers of this species have been studied recently by Peter Endress (1971), who states that these flowers are free. In herbarium material the flowers usually appear to be united basally.

***Hedysomum montanum*** W. Burger, *Phytologia* 26:133-135. 1973. Figure 1.

Unisexual shrubs or trees 3-10 (20) m. tall, leafy internodes 2-6 cm. long, 2-5 mm. thick, essentially glabrous but with a very rough surface and occasional rows of hairs on the leaf-sheath, leaf-scars usually absent with the leaf-base persisting and

encircling the stem. Leaves with the free portion of the petiole 5-14 mm. long, 1.5-2.5 mm. thick, glabrous or with irregular hairs 0.2-1 mm. long in rows, tube of the leaf-sheath 1-2.8 cm. long, with 2 (several) slender, often fimbriate, stipule-like structures 1-3 mm. long on each distal margin, the distal margin occasionally becoming torn in age; laminae 6.5-13 (17) cm. long, 2-5 (7) cm. broad, narrowly elliptic to oblong, widest near the middle, gradually or abruptly short-acuminate, obtuse to acute or sometimes attenuate at the base, drying stiffly chartaceous to subcoriaceous, slightly scabrous or smooth above, glabrous above and often with irregular brownish hairs 0.2-1 mm. long on the midvein beneath, minute (0.1 mm.) epidermal projections obscure or prominent on both surfaces, the 5 to 8 (10) pairs of major secondary veins flat above and slightly raised beneath, serrulate with the teeth 2-4 mm. distant on the margin. Inflorescences usually united with the stem to above the leaf-sheath; male inflorescences usually of 1 or 2 pairs of opposite spikes and a solitary terminal spike on a short (1-2 cm.) rachis, opposing spikes subsessile, the terminal pedunculate, subtended by subulate bracts 3-6 mm. long, the spikes becoming 3-6 cm. long, 4-6 mm. thick, stamens sessile and becoming 2-3 mm. distant on the rachis, anthers 1.4-1.8 mm. long, 0.6-0.7 mm. thick, connective produced 0.1-0.2 mm. beyond the thecae, flat above and often acute on one side; female inflorescences of racemose or spike-like branches arising from the stem or from a short rachis in opposing pairs and thyrselike in form, the female flower clustered in small sessile or short-pedunculate groups, each group with 1 to 4 flowers (usually 3) and about 4 mm. long and 4 mm. thick, each flower subtended and partly enclosed by a bract 3-4 mm. long, the bracts variously united at the base to form a cupulate involucre enclosing all the flowers of the group, flower about 2 mm. long with perianth-lobes about 0.5 mm. long, stigma 2-3 mm. long (? apically bifurcate) and soon deciduous. Fruit about 2.8 mm. long and 1.8 mm. thick, ellipsoid and trigonous with the apical perianth-lobes persisting.

A species of the montane rain forest most often found on slopes subjected to the wet Caribbean weather and collected only between 1800 and 2700 m. elevation in Costa Rica. The species ranges southward to the upper Río Chiriquí Viejo in Panama and may be represented at its northernmost limits by somewhat different plants (not included in these descriptions) on Volcán Mombacho and the Island of Ometepe in west-central Nicaragua. In Costa Rica the species has been collected from the area of Palmira (*A. Smith* 4337, 4186A, & 4187) and Alto Palomo (*Lent* 1829) in Alajuela Province, on the eastern slope of Volcán Barba (*A. Jimenez* 2269, *Burger and Liesner* 6366, the type, & 6416) and La Carpintera (*Allen* 639) in San José Province, and in the Cordillera de Talamanca near Empalme (*Burger* 7919, *A. Jimenez* 2758, *Williams et al.* 25018) and below Chirripo (*Burger and Gomez* 8370) in the provinces of Cartago and San José. The species appears to flower throughout the year; collections with male inflorescences are very rare.

Specimens placed here were previously thought to be *H. callososerratum*, but the latter species has solitary female flowers and is

separated, in Costa Rica, from *H. montanum* by an altitudinal disjunction of about 800 m. I believe that we have enough material to indicate that this ecological separation is real and not an artifact of poor sampling. *Hedyosmum montanum* is also closely related to *H. scaberrimum*, which differs in anther-size and lower elevation habitat. The lack of intermediates between these entities and a very consistent correlation between their morphology and habitat lead me to believe that these taxa are better treated as species than as subspecies or varieties. The material that I have seen from Nicaragua and have mentioned above (*Friedrichsthal 1031, Grant 795 & 811*) differs slightly in morphology from material placed here and occurs in a rather different habitat. *Hedyosmum montanum* has not been collected in the Cordillera de Guanacaste, where one might expect to find intermediates (if such exist) with the Nicaraguan material. I suspect that when the Nicaraguan population is better known, it will also prove to be worthy of specific rank.

***Hedyosmum scaberrimum* Standl., Field Mus. Bot. 4:200-201. 1929. Figure 1.**

Unisexual small trees 3-7 m. tall, leafy internodes 1-7 (10) cm. long, 1.5-5 (8) mm. thick, the surface muricate-scabrous and often with very short (0.3 mm) irregular hairs, leaf scars absent, with the persisting leaf-base encircling the stem. Leaves with the free portion of the petiole (3) 6-12 (22) mm. long, 1.3-3 mm. thick, muricate-scabrous and often irregularly torn on the adaxial margins, tube of the leaf-sheath 1-2.5 cm. long, usually with 2 small (1-3 mm.) aculeate or fimbriate structures on each distal margin, the sheath often tearing and very irregular distally; laminae 9-20 cm. long, 3-8 cm. broad, narrowly elliptic to broadly oblong or slightly obovate, acuminate at the apex, acute to obtuse at the base, finely serrate, the lamina drying stiffly chartaceous to subcoriaceous, conspicuously muricate and scabrous on both surfaces with a very few short hairs, the epidermal projections about 0.1 mm. broad, the 6 to 10 pairs of major secondary veins flat above and prominent beneath. Inflorescences often united to the stem above the leaf-sheath; male spikes usually in 2 or 3 opposing pairs on a short (2-4 cm.) rachis terminated by a single spike, lower spikes subtended by dentate bracts 12-18 mm. long and about 4 mm. broad, subsessile or the terminal pedunculate, spikes about 6 mm. thick and expanding to 6 cm. long with the stamens becoming 1-2 mm. distant on the rachis, anthers subsessile, 2.3-2.8 mm. long, 0.4-0.6 mm. thick, connective produced about 0.5 mm. beyond the thecae, acute; female inflorescences thyrses-like, racemose, or spicate, flowering branches originating from the stem or from a common rachis 2-4 cm. long, floral bracts opposite or alternate and sessile or short-pedunculate, the floral bract cupulate or open on one side, 2-3 mm. long and usually 3-lobed, each bract subtending and partly enclosing 2 (occasionally 4, 3, or 1) female flowers about 2 mm. long and 1.5 mm. thick, perianth-lobes about 0.3 mm. long. Fruit about 2.5 mm. long and 2 mm. thick, ellipsoid and trigonous.

Plants of the wet Caribbean slopes and cloud forests of western Panama, between sea level and about 1000 m. elevation. This species has not been collected in Costa Rica but is known from adjacent Panama (*Cooper 595*, the type, from above Almirante and *von Wedel 1943 & 2910* near Chiriquí Lagoon) in Bocas del Toro Province and also from near El Valle in Coclé Province (*Allen 2148 & 2284*, *Duke 12119*, and *Wilbur et al. 11139*); apparently flowering throughout the year.

The larger male spikes with larger anthers, grouping of female flowers, and unusual surface on both leaves and stems serve to distinguish this species from the very closely related *H. callososerratum* and *H. montanum*. These three species could be considered subspecific elements of a single taxon, but I prefer to keep them separate; see the discussion under *H. montanum*.

## LACISTEMACEAE

WILLIAM BURGER

Trees or shrubs. Leaves alternate and simple, petiolate, the lamina pinnately veined, stipules present. Inflorescence a spike, raceme, or paniculate, often fasciculate in the leaf-axils, subtended by 2 bracts; flowers bisexual or unisexual, subtended by a bract or bracteoles or both, with or without a perianth, the perianth a single whorl of 6 or fewer parts free or variously connate below, a fleshy disc present and lobed or cleft; stamen solitary and arising from near the center of the disc, usually inflexed in bud, anthers 2-theous, dehiscent longitudinally; pistil solitary and superior in the center of the disc, sessile or short-stipitate, ovary 1-locular with 3 parietal placentas, the ovules 1 or 2 and pendulous on each placenta, style short or absent, stigmas 3 or solitary and 3-lobed; fruit capsular, ovoid or subglobose and opening by usually 3 valves, seeds usually 1 (3) by abortion.

This small neotropical family has been recognized and placed among the Amentiferae by a number of authors. The family was recognized and so placed in the "Flora of Panama" (Nevling, Ann. Missouri Bot. Gard. 47:84-87. 1960) and the "Flora of Guatemala" (Standley and Steyermark, Fieldiana Bot. 24, pt. 3:340-342. 1952). Diels, in reworking Engler's Syllabus der Pflanzenfamilien (11th edition, 1936), considered the plants placed here as no more than a tribe within the Flacourtiaceae. A superficial examination of the flowers of our species of *Lozania* leads me to concur with the view that these plants belong with the Flacourtiaceae. Even in the absence of flowers and fruit, the dried leaves and stems of *Lozania* bear a striking resemblance to herbarium material of *Casearia* and other members of the Flacourtiaceae. Our species of *Lacistema*, with its short spikes (aments) with minute flowers largely hidden by the imbricate bracts, appears to be very different from most Flacourtiaceae, but it is clearly related through *Lozania*.

A key to the species and a figure is included here; these, together with full descriptions, will be provided under the account of the Flacourtiaceae in a future issue of this Flora. *Lozania pittieri* (Blake) L. B. Smith and *Lozania mutisiana* Roem. & Schult. are earlier names for *L. pedicellata* (Standl.) L. B. Smith and *L.*

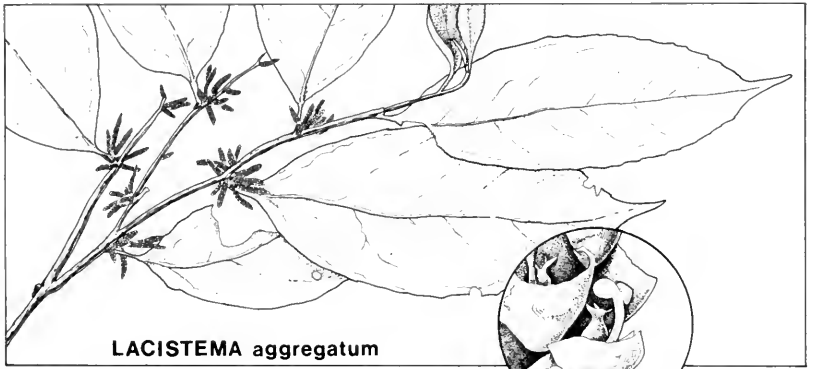


FIG. 2. Lacistemaceae: Costa Rican species of *Lacistema* and *Lozania*; plants closely related to the Flacourtiaceae.

*monatana* Standl., respectively, according to Getulio Agostini.<sup>1</sup> *Lacistema aggregatum* (Berg) Rusby is a very common small tree, more often encountered than the other two species in our flora (see fig. 2).

COSTA RICAN SPECIES ASCRIBED TO THE LACISTEMACEAE

- 1a. Flowers subsessile and partly hidden by the imbricate floral bracts; inflorescences of short spikes borne in clusters of 4 to 12, less than 2 cm. long at anthesis, densely flowered and the rachis not visible; common plants of wet forest formations from sea level to 1600 m. elevation . . . *Lacistema aggregatum*.
- 1b. Flowers clearly visible on distinct pedicels above the minute floral bracts; inflorescences of racemes 3-9 cm. long and 1 to 4 per axil, loosely flowered and the rachis easily visible from early stages; uncommon plants of wet forest formations . . . . . 2a.
- 2a. Plants of montane areas between 1000 and 2000 m. elevation, leaves drying stiffly chartaceous; racemes 1 to 3 per axil, stamen with a very short broad filament . . . . . *Lozania mutisiana*.
- 2b. Plants of lowland areas between sea level and 500 m. elevation, leaves drying thinly chartaceous; racemes solitary, stamen with a slender filament.  
*Lozania pittieri*.

<sup>1</sup>(Acta Bot. Venez. 8: 167-175. 1973).

## SALICACEAE

LUIS DIEGO GÓMEZ P.

Unisexual (rarely bisexual) trees and shrubs with light wood and bitter bark. Leaves alternate in a spiral, simple and stipulate, laminae entire or more often serrulate. Inflorescences dense spikes or racemes (catkins or aments) borne in the leaf-axils; flowers small and unisexual, each subtended by a thin bract, without sepals or petals and the perianth represented by a cup-like disc (in *Populus*) or by 1 or 2 minute glands or scales (in *Salix*); male flower with 2 to many stamens, filaments borne on the base of the bract and free or united near the base, anthers 2-theous, dehiscent longitudinally, a pistillode present or absent; female flower without staminodes, pistil solitary and sessile or stipitate, ovary unilocular, ovules many and erect on 2 to 4 parietal or somewhat basal placentas, style 1 with 2 to 4 stigmas, the stigmas simple or bifid. Fruit a capsule breaking into 2 to 4 parts, seeds small with a coma of long soft usually white hairs, endosperm little or none.

A family of two genera and about 300 species, very common in the arctic and north temperate regions of both the Old and New World but represented in our area only by introduced species. Only one species is commonly encountered in Costa Rica; others are occasionally seen in cultivation. The family is quite isolated by virtue of the much-reduced flowers, but it is probably related to the Tamariaceae.

Laminae usually broad and on conspicuous, often flattened petioles, buds with several usually resinous scales; inflorescences usually drooping or pendulous, each flower with a basal cup-like disc; often planted in gardens and along streets.

*Populus.*

Laminae very narrow and on short terete petioles, buds with 1 scale; inflorescences usually erect, each flower with 1 or 2 minute basal glands; often planted or escaped along streams and lakes and in wet cool areas . . . . . *Salix.*

## POPULUS Linnaeus

Trees, bark on young trunks often pale gray and quite smooth becoming rough and gray in age; buds at first enclosed by several imbricate scales, the scales usually resinous. Leaves persistent or deciduous, petioles usually long and flattened laterally to form an adaxial groove, laminae often broadest below the middle and truncate to rounded at the base, usually serrate to sinuate along the edge; stipules narrow and deciduous. Inflorescences usually pendulous or drooping in anthesis



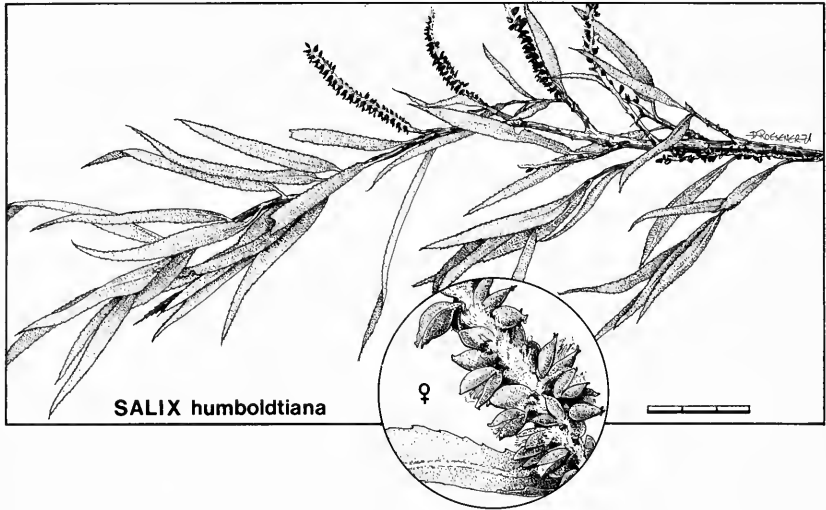


FIG. 3. Salicaceae: *Salix humboldtiana*, twig with fruiting inflorescence.

and fruit; each flower with a cup-like disc, the disc symmetrical or oblique, fleshy or membranous, edge of the disc entire to dentate or lobed; male flower with (4) 8 to 50 or more stamens, filaments free; female flower with a sessile or stipitate pistil, style 1 or none, stigmas 2 or 4. Fruit a 2- or 3-valved capsule.

A genus of about 30 species of the northern hemisphere not ranging further south than Mexico (in North America) but occasionally planted as ornamental trees throughout the Neotropics. None of the introduced species is common in Costa Rica, but *Populus alba* L. with the laminae downy-white beneath is often seen in gardens.

### SALIX Linnaeus

Shrubs or trees often growing near fresh water lakes and streams, young trunks with brown or dark gray bark; bud enclosed within a single scale, the scale with an inner adherent membrane. Leaves persistent or deciduous, usually short-petiolate and with very narrow and serrulate laminae; stipules persistent or deciduous, paired, scale-like or large. Inflorescences usually erect or spreading, floral bracts entire or minutely serrulate, each flower with 1 or 2 minute basal glands or scales; the male flowers with 1 to 2 or 3 to 12 stamens, filaments free or united; female flowers with a sessile or stipitate pistil, style 1 or none, stigmas 2 and simple or bifid; capsule usually 2-parted.

A genus of more than 200 species but with only a few entering the tropics. The following is the only species commonly found in Costa Rica; several others, both native and introduced, have been re-

ported in Guatemala and are treated in the "Flora of Guatemala" (Fieldiana: Bot. 24, pt. 3:343-348. 1952).

***Salix humboldtiana* Willd. in L., Sp. Pl. ed 4, 4:657. 1806. Figure 3.**

Shrubs or trees becoming 10 (18) m. tall, branches often drooping, stems at first puberulent with crooked whitish hairs 0.1-0.3 mm. long, leafy internodes 3-18 mm. long, 0.4-1.8 mm. thick; bud scales 1-2 mm. long. Leaves evergreen, petioles 2-5 mm. long, about 0.5 mm. thick, puberulent; laminae 4-10 (15) cm. long, 4-8 (12) mm. broad, lanceolate to linear, tapering gradually to the slender and acute apex, acute at the base, each margin with 40 or more minute teeth 0.5-1.5 mm. distant, the laminae drying stiffly chartaceous, smooth and glabrous on both surfaces, venation pinnate with many slender secondary veins occasionally joining distally to form a submarginal vein; stipules vestigial. Inflorescences subtended by small leaves; (staminate plants not known from Costa Rica and the description based on Central American material) male spikes 3-6 cm. long with the puberulent flowers crowded, bracts 1-2 mm. long and densely whitish tomentose at the base adaxially, each flower with 3 to 5 (7) stamens, filaments 2-3 mm. long, anthers about 0.4 mm. long and equally broad; female spikes 3-7 cm. long, peduncle about 4 mm. long and 0.8 mm. thick, puberulent, the flowers 0.3-2.5 mm. distant on the rachis, bract 1-2 mm. long and densely white tomentose adaxially, pistil glabrous, 2-3 mm. long with a stipe about 1 mm. long, ovary narrowly ovoid, 0.5-0.8 mm. thick (dry), stigmas 0.4-0.7 mm. broad on a very short style or sessile. Fruit with valves 3-5 mm. long, 1.5-3 mm. broad, seeds 0.5-1 mm. long with many soft whitish hairs 2-3 mm. long.

This species is widely planted by vegetative propagation in the cool and wet areas of the country. Populations of this species have become established in the rivers of the Caribbean lowlands in nearby Nicaragua, and naturalized populations can be expected in Costa Rica throughout the wet and cooler areas of the country between sea level and 2000 m. elevation. The species ranges from Mexico southward to Costa Rica and from Colombia to Argentina and Chile.

The first record of the genus *Salix* in the New World is probably that of Fernandez de Oviedo (Historia General y Natural de las Indias, Book 9, Chap. 32, 1535-1557.), who refers to the "salces so common in the southern lands of New Castile, which are very much like those seen in Europe." Nevertheless, it strikes one as rather awkward for a man of Oviedo's curiosity and fine insight, that although he described many trees peculiar to Central America, he does not mention "salces" nor "sauces" as occurring in places such as Guatemala.

*Salix humboldtiana* is known only from sterile and pistillate collections in Costa Rica, and it is generally thought to have been introduced by the Spanish settlers. However, the species seems to

be native in northern Central America and over a wide area in South America. The very narrow leaves, often slightly curved, and the wet habitat distinguish this species.

The only other species of the genus that is commonly planted in Costa Rica is *Salix babylonica* L., with long hanging branches that may touch the ground. The name *S. chilensis* Molina (Sagg. Storia Nat. Chil., 169. 1782) has been used for this species but is a *nomen dubium*, as according to Schneider (Bot. Gaz. 65:6. 1918) is based on material that may not be *Salix*.

## GARRYACEAE

WILLIAM BURGER

REFERENCE: Walther Wangerin in Engler, Pflanzenreich IV, 56a. Garryaceae. 1-18. 1910.

Unisexual shrubs and small trees, young stems somewhat quadrangular and with an interpetiolar ridge. Leaves opposite, simple and evergreen, petiolate; lamina usually coriaceous and entire, stipules absent but the leaf-bases continuous and united by an interpetiolar ridge. Inflorescence composed of 1 to 4 individual flowers in the axils of leaves or undeveloped leaves and often subtended by conspicuous bracts in a racemose or spicate form or occasionally producing a terminal thyrselike inflorescence; male flowers usually pedicellate, sepals 4, valvate and separating or occasionally remaining connate at the apex, petals absent, stamens 4 and alternate with the sepals, filaments short and free, anthers 2-thealous, basifixed, dehiscing longitudinally and introrse, narrow, a minute pistillode present or absent; female flower without apparent perianth but 2 to 4 small lobes sometimes present at the apex of the ovary (and the ovary probably inferior by adnation), ovary 1-locular with 2 ovules pendulous from the apex of the locule, styles and stigmas 2 and divergent. Fruit baccate, ovoid to globose, seeds 2 or 1 by abortion, seed ovoid to globose with a fleshy covering, embryo minute at the apex of the endosperm.

This family, represented by a single genus, is closely related to the Cornaceae but has become adapted to wind pollination. While placement of the Garryaceae here (between the Salicaceae and Myricaceae) is clearly incorrect, it is perhaps easier for most people to associate these reduced unisexual flowers with those of the ameniferous families. The Garryaceae follow the Cornaceae in the "Flora of Guatemala" (Fieldiana: Bot. 24, pt. 8:69-72. 1966).

### GARRYA Douglas

A genus of about 15 species restricted to North America and ranging from Oregon to the western United States southward through Texas and Mexico to Costa Rica with a single species (*G. fadyeni* Hook.) in Jamaica and eastern Cuba. The following is the only species known from Costa Rica; an additional species is known in Guatemala. They are not known to be useful in Central America, but members of the genus are occasionally planted as ornamental shrubs in California.

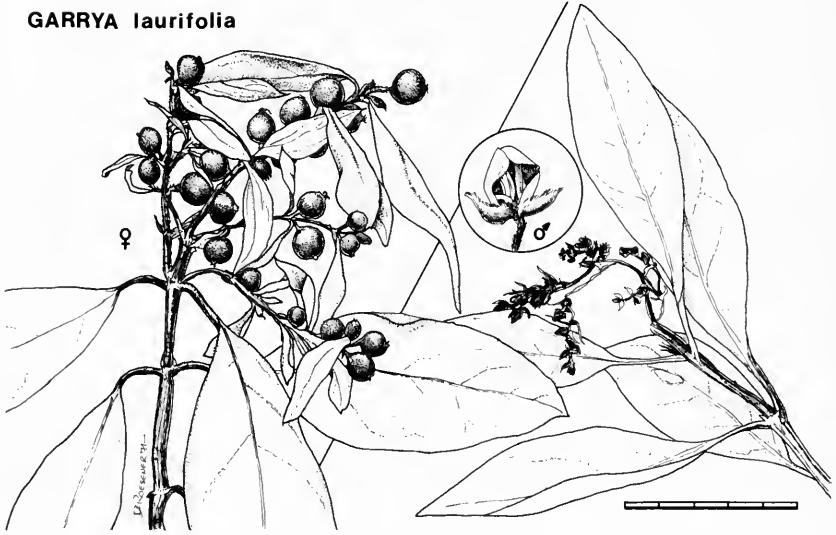
**GARRYA** *laurifolia*

FIG. 4. Garryaceae: *Garrya laurifolia* with fruiting female specimen (left) and male twig (right).

***Garrya laurifolia* Hartweg ex Bentham, Pl. Hartw. 14. 1839.**  
Figure 4.

Diocious shrubs or small trees 2-6 (12) m. tall, often branched from near the base and with many vertical stems, leafy internodes 5-30 mm. long, 1.5-5 (7) mm. thick, with slender whitish hairs 0.3-0.7 mm. long or glabrescent, usually drying dark, interpetiolar ridges prominent. Leaves in decussate pairs, often held erect, petioles 4-18 mm. long, 1-2 mm. thick, minutely puberulent but becoming glabrous, sulcate above with the adaxial ridges continuous with both the lamina-margin and the interpetiolar ridge; laminae (2) 4-11 cm. long, (0.8) 1.5-4 cm. broad, elliptic to oblong or occasionally narrowly obovate, rounded to abruptly obtuse (rarely acute) at the apex, occasionally minutely (1 mm.) mucronate at the tip, acute to attenuate at the base, margins entire and revolute on drying, the lamina coriaceous to subcoriaceous, smooth and often lustrous above, sparsely puberulent above and very sparsely puberulent beneath with straight appressed and ascending whitish hairs 0.1-0.3 mm. long, becoming glabrous in age, the 5 to 9 pairs of major secondary veins slightly impressed above. Inflorescences axillary or apparently terminal, spicate, thyrse-like, or rarely racemose, the flowers solitary and terminal or in opposite axillary pairs, the rachis and branches of the inflorescence probably representing stems with reduced leaves subtending the opposed flowers, branches and rachis often densely whitish sericeous in early stages; each male flower subtended by a narrow bract 4-7 mm. long, sepals (tepals) 2-4.5 mm. long and 1-2.5 mm. broad, usually remaining connate at the apex, stamen with very short (0.5 mm.) filaments, anthers 1.5-2.5 mm. long, about 0.8 mm. thick; each axillary female flower subtended by a small

leaf-like bract 3-15 mm. long and about 3 mm. broad, the terminal flowers subtended by 2 bracts or without bracts, each flower sessile or on a short (1-4 mm.) pedicel, perianth and perianth-lobes not apparent, pistil about 6 mm. long and 3 mm. thick, surface of the ovary sparsely and very minutely puberulent with slender whitish hairs 0.2-0.5 mm. long, style branches 1-3 mm. long, 1 mm. broad at the base, minutely papillate-puberulent on the inner stigmatic surface. Fruit globose or ellipsoid, becoming about 10 mm. long and 8 mm. thick, dark olive-green but drying very dark gray or black.

Plants of the high montane rain forests and paramo formations between 2200 and 3400 m. elevation in Costa Rica; flowering and fruiting throughout the year but most commonly in flower in the wet season, May through December. This species has only been collected along the Caribbean watershed of the Central Highlands and in the western part of the Cordillera de Talamanca along the Inter-american highway and on Cerro Chirripó in Costa Rica. The species ranges northwards to Mexico.

These unisexual woody plants are easily recognized by the very stiff opposite leaves with interpetiolar ridges, reduced flowers, and high montane habitat. This species exhibits what may be transitional stages in the development of complex inflorescences from what were originally solitary flowers in the axils of leaves.

## MYRICACEAE

WILLIAM BURGER

REFERENCE: T. S. Elias, The genera of the Myricaceae in the Southeastern United States, *Journ. Arnold Arb.* 52:305-318. 1971.

Small trees, shrubs, or suffruticose, unisexual or bisexual, usually aromatic and often pellucid-punctate; roots often with nitrogen-fixing nodules. Leaves alternate in a spiral, evergreen or deciduous, simple, entire to dentate or rarely pinnatifid; with or without stipules. Inflorescences spicate to paniculate, axillary or from a short-shoot; flowers unisexual, small and lacking both sepals and petals, solitary in the axil of a large bract, with or without smaller bracteoles; male flowers with 2 to 30 anthers borne on short, free or united filaments, anthers 2-thecous and dehiscent longitudinally, a pistillode usually absent; female flowers with a solitary pistil and unilocular ovary with a single ovule, style short with 2 (3) style-branches, stigmas 2 (3). Fruit drupaceous or nut-like, endocarp hard, exocarp often producing wax, embryo straight with plano-convex cotyledons.

A small family of three genera and probably fewer than 50 species widely distributed in the north-temperate zone and in Africa and Southeast Asia but usually restricted to highland habitats in Central and South America. The family has an extensive fossil record dating from the late Cretaceous and is an old and phylogenetically isolated family. Relationships with the Juglandaceae, Fagaceae, Casuarinaceae, and Hamamelidaceae have been suggested by various authors.

### MYRICA Linnaeus

Small shrubs to small or medium sized (12 m.) trees, unisexual or less often bisexual, often branching near the ground, stems usually with pale grayish lenticels broadly elliptic and bisected by a longitudinal depression; roots usually with nitrogen-fixing nodules. Leaves simple and with pinnate venation (in ours), short-petiolate, laminae stiffly chartaceous to coriaceous, subentire to dentate or serrate, aromatic when crushed; stipules absent. Inflorescence a simple stiff spike arising in the leaf-axils (in ours), flowers alternate in a spiral on the rachis; male flower subtended by 1 broad bract and usually with 2 linear bracteoles, stamens (2) 4 to 8 (20) with free or variously united filaments, the thecae often slightly unequal and divergent on the short thick connective; female flower subtended by a single broad bract with or without smaller bracteoles, the ovule erect from the base of the locule. Fruit

drupe-like with a surface of tubercles or projections which usually become covered with whitish wax in late stages.

The genus may be represented in Central America by no more than the species listed here. Of these, *M. cerifera* (as here interpreted) is very unusual in its wide geographic range. The relationship of these plants with nitrogen-fixing bacteria is an important element in determining their ecological amplitude and role in forest succession. Our species possess the yellowish pellucid peltate glands, concave above, that are so characteristic of the genus. The wax extracted from the fruit has been used for making candles that burn with a pleasing aroma, but this use of the wax is becoming rare in Central America. The ability to grow in poor soils makes these plants useful in erosion control. The names Bayberry or Myrtle (in English) and *Arrayan* or *Arbol de la cera* (in Spanish) are commonly used for the genus.

- 1a. Plants bisexual, spikes usually with male flowers beneath and female flowers distally, fruit on the distal part of the spike; leaves usually densely puberulent beneath with 10 to 25 major secondary veins on each side; plants of montane wet forest formations from 1300 to 2800 m. elevation. . . . . *M. pubescens*.
- 1b. Plants unisexual or rarely with terminal male flowers on a female spike; leaves sparsely puberulent to glabrous beneath . . . . . 2a.
- 2a. Laminae usually oblanceolate, entire or with 3 or 4 blunt teeth distally on each margin, major secondary veins usually less than 9 on each side and often obscure, minute pellucid dots numerous on both surfaces ( $\times 20$ ); plants rarely found above 1800 m. elevation. . . . . *M. cerifera*.
- 2b. Laminae elliptic to narrowly oblong, usually with more than 4 conspicuous teeth on each side, secondary veins prominent beneath and becoming impressed above; plants commonly found above 1800 m. elevation . . . . . 3a.
- 3a. Lamina lacking pellucid peltate glands above or very sparsely glandular, the laminae usually less than 5 cm. long and broadly elliptic; plants endemic to Central Costa Rica . . . . . *M. phanerodonta*.
- 3b. Lamina with numerous yellowish peltate glands on the upper surface ( $\times 20$ ), the laminae often becoming more than 7 cm. long and narrowly elliptic to narrowly oblong; plants not recorded from Costa Rica (see discussion under *M. cerifera*) . . . . . *M. lindeniana*.

**Myrica cerifera** L., Sp. Pl. 1024. 1753. *M. mexicana* Humboldt & Bonpland ex Willd., Enum. Pl. 2:1011. 1809, fide auctores. *M. xalapensis* H.B.K., Nov. Gen. & Sp. 2:16. 1817, ex char. Figure 5.

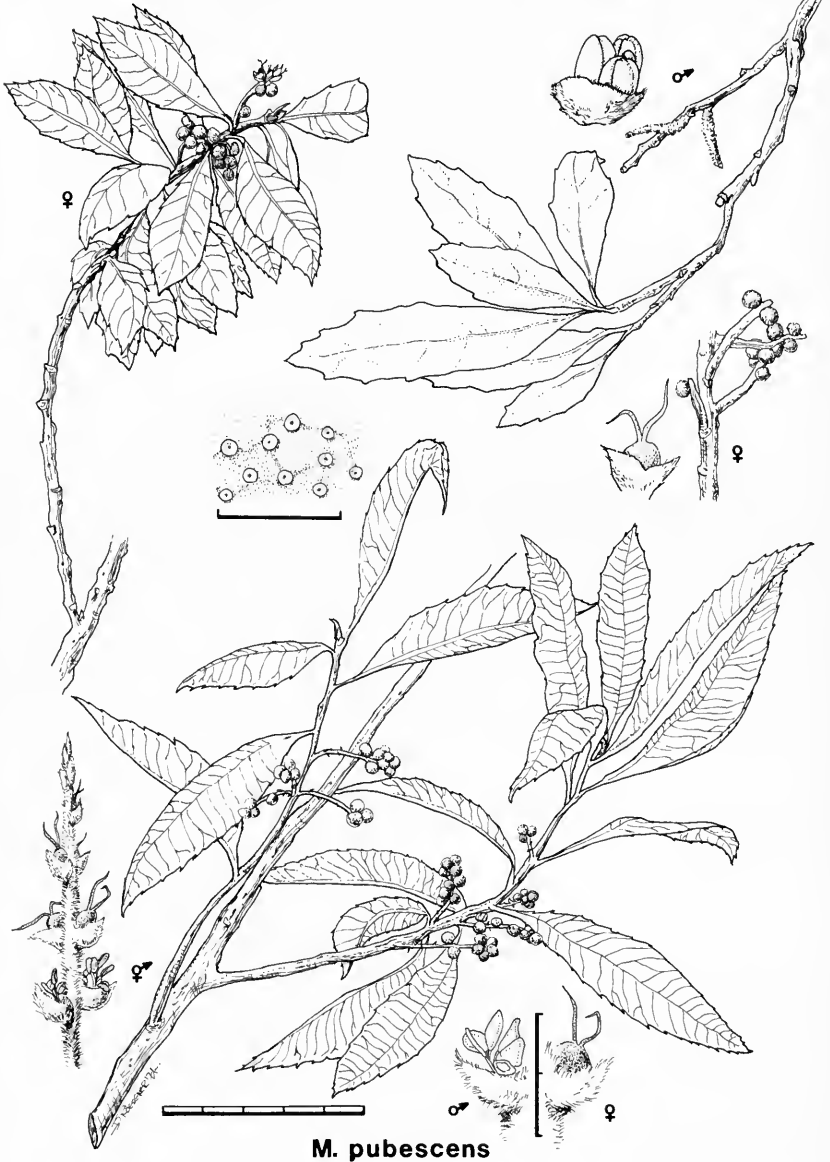
Unisexual shrubs or trees, (0.5) 1-5 (9) m. tall, leafy internodes 2-10 (15) mm. long, 0.8-3 (5) mm. thick, densely to sparsely puberulent with soft gray or brown straight and crooked hairs 0.3-1 mm. long, peltate pellucid glands present but the stems becoming glabrescent and dark brown in age with lenticels 0.3-1 mm. long. Leaves



# MYRICA

*M. phanerodonta*

*M. cerifera*



*M. pubescens*

FIG. 5. Myricaceae: the Costa Rican species of *Myrica*; note the peltate pellucid glands (left-center).

evergreen; petioles 1-3 (8) mm. long, about 0.8 mm. thick, terete or flattened adaxially; laminae 2-7 (9) cm. long, 1-2 (3) cm. broad, oblanceolate to narrowly obovate or less often elliptical, abruptly acute or obtuse at the apex, acute to attenuate at the base, distal half of each margin with 3 to 6 teeth or entire, often revolute on drying and stiffly chartaceous to subcoriaceous, the 4 to 9 pairs of major secondary veins often obscure above and below, smooth and occasionally slightly lustrous above, puberulent on the midvein above and below or essentially glabrous but with peltate pellucid glands about 0.1 mm. broad on both surfaces and these sometimes drying black. Inflorescences unisexual, arising and maturing in the axils of leaves or fallen leaves, peduncle and rachis about 0.8 mm. thick, puberulent and often densely pellucid-glandular; male spike 1-3.5 cm. long with 15 to 40 flowers, usually borne in the axils of persisting leaves, the superposed flowers usually less than 2 mm. distant on the rachis, male bracts about 1 mm. long and 1.5 mm. broad, sparsely puberulent and pellucid-glandular abaxially, anthers 3 to 5 (12) on usually very short (0.5 mm.) filaments, thecae 0.8-1.2 mm. long; female spike 1-3 cm. long with 8 to 30 flowers, usually maturing in the axils of fallen leaves, superposed flowers becoming 2-4 mm. distant on the rachis, female bract about 1.2 mm. long and equally broad, sparsely puberulent and densely pellucid-punctate abaxially, pistil about 3 mm. long with the style-branches 2 mm. long and the ovary about 1 mm. Fruit becoming 2.8-4 mm. long and usually equally thick, globose, the tubercles 0.2-0.5 mm. broad and often remaining contiguous when dried. (Measurements based on Central American material but excluding material ascribed to *M. lindeniana*.)

Plants of seasonally dry evergreen montane forest formations between (500) 800 and 1800 (2000) m. elevation in Costa Rica; probably flowering throughout the year. The species, as here understood, ranges from New Jersey in the eastern United States to the West Indies, western Panama, and possibly to Colombia.

This species is recognized by the generally small oblanceolate leaves entire or serrulate only in the distal half and often clustered at the ends of branches, aromatic parts, and small unisexual spikes. This species possesses an extraordinary geographic and ecological range for a perennial woody plant. The plants are known to grow in montane bogs and in well-drained pine forests in Guatemala (Standley, *Fieldiana: Bot.* 24, pt. 3:349-350. 1952). Populations are known from near sea-level along the Caribbean coast from Nicaragua northward, but it is apparently an uncommon occurrence and the material that I have seen lacks flowers and fruit. Plants from the West Indies bearing this name differ from ours by the much narrower leaves usually without serration. The material from the United States differs from Central American collections in the usually less serrulate leaves and the female spikes more often maturing in the axils of persisting leaves. These geographic distinctions may be worthy of subspecific rank but the species and its relations are not well understood (see below).

There are two taxa in Central America that are very closely related to *M. cerifera*: *M. lindeniana* C.DC. and *M. phanerodonta* Standley. With the variation and range ascribed to *M. cerifera*, it may seem inconsistent to consider these closely related taxa as separate species. In the case of *M. phanerodonta*, the plants are easily separable ecologically and morphologically with no real evidence of intergradation. However, the situation with *M. lindeniana* is not as clear. Material referable to *M. lindeniana* occurs throughout much of the range of *M. cerifera* in Central America and appears to grow in moister situations and at higher altitudes. Typical material of *M. lindeniana* has conspicuously longer (6-12 cm.) laminae than *M. cerifera* with more numerous (9-16 pairs) and more prominent secondary veins and serrations. The ecological and morphological distinctions are bridged by some collections that appear to be intermediate, but these collections are few in number and may prove to be unusual variants rather than true intermediates. Because there is a correlation between ecology and morphology, and until the species are actually studied in the field, I prefer to treat them as separate. *Myrica pringlei* Greenman is probably a small-leaved form of *M. cerifera*.

***Myrica phanerodonta* Standley, Journ. Wash. Acad. Sci. 17:164. 1927. Figure 5.**

Unisexual or rarely bisexual shrubs and small trees 1-5 (7) m. tall, stems with minute peltate glands and sparsely to densely puberulent with short (0.3 mm.) gray or yellowish-brown hairs, becoming glabrous and dark brown with conspicuous lenticels 0.5-1.8 mm. long, leafy internodes 2-10 (15) mm. long, 1-6 mm. thick. Leaves evergreen, petioles (1) 2-7 mm. long, about 1 mm. thick, slightly sulcate adaxially; laminae 1.8-5 (8) cm. long, 0.8-2 (2.8) cm. broad, broadly elliptic to oblong or obovate, abruptly obtuse or rounded at the apex, acute to attenuate at the base, each margin with 4 to 12 teeth, teeth with a gland-like tip about 0.5 mm. thick, slightly revolute on drying, subcoriaceous, the major secondary veins (4) 6 to 10 (14) on each side, usually impressed above and prominent beneath, smooth and slightly lustrous above, puberulent on the proximal half of the midvein above, sparsely puberulent or glabrous on the midvein beneath, hairs about 0.2 mm. long, peltate pellucid glands about 0.1 mm. broad, absent or very sparse above, present but often inconspicuous beneath, small dark pits or depressions often present on both surfaces. Inflorescences unisexual but rarely the female with a terminal male flower (as in *Gómez 2292* and *Molina et al. 17115*), axillary, peduncle and rachis about 1 mm. thick, densely to sparsely puberulent, the flowers at first congested but becoming distant; male spike 1-3.5 cm. long with 15 to 40 flowers, bracts of the male flowers 2 mm. long and equally broad, very sparsely puberulent but with pellucid glands abaxially, anthers 4 to 6 (8) on filaments becoming 1 mm. long and variously united beneath, thecae 0.8-1.4 mm. long; female spike becoming 2-5 cm. long with 10 to 40 flowers, superposed flowers becoming 3-8 mm. distant on the

rachis, female bracts 2-3 mm. long and 0.5-1 mm. broad at the base, sparsely puberulent and pellucid-glandular abaxially, pistil about 2 mm. long with style-branches 1-2 mm. long. Fruit becoming 3-4 mm. thick and equally long or slightly longer, globose to broadly ellipsoid, tubercles 0.2-0.4 mm. thick and usually remaining contiguous on drying.

Plants of montane rain forests between 1800 and 2700 m. elevation and apparently restricted to those areas subject to the wet Caribbean winds between Zarcero, Alajuela, in the west and the Cerros de Zurqui, Heredia. Probably flowering throughout the year but most commonly collected in flower or fruit between September and February. The species is known only from the small area described above and is common near the summit of Volcán Poas.

*Myrica phanerodonta* is characterized by its small, conspicuously serrate leaves with prominent venation and restricted range. It is very closely related to *M. lindeniana* C.DC. but differs in its usually much shorter leaves and the apparent lack of intermediates with typical *M. cerifera*. I believe that this species has become differentiated from *M. cerifera* (sensu lato) in a way that is more complete than but very similar to the differentiation of *M. lindeniana*; both are adapted to higher elevations and both possess serrulate leaves with rather conspicuous venation. A similar situation may exist in Colombia, where several taxa are found that are closely related to *M. cerifera* (sensu lato) but that differ in their smaller leaves and high-altitude habitats.

***Myrica pubescens* Humboldt & Bonpland ex Willd., Sp. Pl. 4:746. 1806. *M. arguta* H.B.K., Nov. Gen. & Sp. 2:17, tab. 98. 1817. Figure 5.**

Bisexual shrubs or trees 1.5-7 (10) m. tall, leafy internodes 3-15 mm. long, 1.5-4 (6) mm. thick, densely soft-puberulent with straight and crooked gray or brown hairs 0.2-0.8 mm. long, pellucid glandular, becoming glabrescent and dark brown in age with conspicuous lenticels 0.5-1.3 mm. long. Leaves evergreen, petioles 3-8 mm. long, about 1 mm. thick, deeply grooved adaxially, densely puberulent; laminae 4-14 cm. long, 1-3 cm. broad, narrowly elliptic to narrowly oblong or rarely oblanceolate, acute at the apex, acute to the base, margins serrate or doubly serrate with 6 to 26 small or prominent teeth on each side, drying stiffly chartaceous to subcoriaceous, upper surface smooth and sparsely puberulent, more densely puberulent on the veins beneath with gray or pale brown hairs 0.1-0.4 mm. long, pellucid glands about 0.1 mm. broad, present on both surfaces, the 10 to 25 pairs of major secondary veins becoming slightly impressed above. Inflorescence usually bisexual, 12-46 mm. long, arising in the axil of a leaf and often persisting after the leaf has fallen, peduncle and rachis 0.6-1 mm. thick, densely puberulent, the superposed flowers becoming 1-4 mm. distant on the rachis, the 3 to 7 male flowers borne below the 6 to 12 female flowers, floral bracts densely puberulent and pellucid-punctate

abaxially; bracts of the male flowers 2-3 mm. long and about 1.5 mm. broad at the base, anthers 4 to 9, thecae 0.6-1.2 mm. long; bracts of the female flowers 2-5 mm. long and 1-2 mm. broad at the base or occasionally leaf-like and larger, the lateral bracteoles about 1 mm. long, pistil 1-2 mm. long with 2 style-branches 0.5-1 mm. long, slender but soon becoming globose. Fruit globose to ellipsoid, 2.5-3.5 mm. thick and 3-4 mm. long (dry), tubercles about 0.3-0.5 mm. long and equally broad, sparsely puberulent, often becoming quite separate on drying.

The species is common on and around the western parts of the Cordillera de Talamanca and in the higher parts of the Central Highlands as far west as Palmira, Alajuela, between 1300 and 2800 m. elevation. Usually growing in or at the edge of montane rain forests or in open bogs and secondary growth; collected in flower from January to August. The species ranges from Costa Rica and Colombia southward to Bolivia.

This species, often called *encinillo* in Costa Rica, is easily recognized by the narrow puberulent leaves with many secondary veins and the presence of bisexual spikes. In plants with poorly developed spikes or with fruiting spikes, the bisexual condition may be difficult to see, but a few clearly bisexual spikes can usually be found by careful searching. The stamens appear to come into anthesis while the pistils are still quite small. A small seedling collected by Margery Carlson (3502, F) in a sphagnum bog on the Cerro de la Muerte clearly shows the root nodules so characteristic of the genus.

## JUGLANDACEAE<sup>1</sup>

DONALD E. STONE<sup>2</sup>

REFERENCES: T. S. Elias, The genera of Juglandaceae in the Southeastern United States, *Journ. Arnold Arbor.* 53:26-51. 1972. J. F. Leroy, Étude sur les Juglandaceae, *Mém. Mus. Nat. Hist. Nat., Sér. B, Bot.* 6:1-246. 1957. W. E. Manning, The morphology of the flowers of the Juglandaceae: I. The inflorescence. *Amer. Journ. Bot.* 25:407-419. 1938; II. The pistillate flowers and fruits. *Amer. Journ. Bot.* 25:407-419. 1941; III. The staminate flowers. *Amer. Journ. Bot.* 35:606-621. 1948. W. E. Manning, Juglandaceae, *In Flora of Guatemala, Fieldiana, Bot.* 24:352-359. 1952. W. E. Manning, Juglandaceae, *In Flora of Panama, Ann. Missouri Bot. Gard.* 47: 90-92. 1960. P. C. Standley, Juglandaceae, *In Flora of Costa Rica, Field Mus. Nat. Hist., Bot. Ser.* 18:372-373. 1937. D. E. Stone & C. R. Broome, Juglandaceae A. Rich. ex Kunth. *World Pollen and Spore Flora* 4:1-35. 1975.

Trees or rarely large shrubs; bark tight or exfoliating, pith solid [or chambered];<sup>3</sup> buds naked [or protected]. Leaves evergreen [or deciduous], opposite, whorled, or

<sup>1</sup>Fieldwork for this project has received generous financing from the National Science Foundation, beginning with my first trip to Costa Rica in January, 1963. Over the years the Organization for Tropical Studies has played a crucial role in providing logistic support, and for this help I particularly wish to thank the Resident Director, Jorge Campabadal. I am indebted to William H. Hatheway, Leslie R. Holdridge, Paul Opler, and Luis Poveda for information about local field sites. Many of the fieldtrips benefitted from the companionship of my good friend Arthur L. Welden and my wife Beverly Larson Stone. Also to my wife I pay thanks for her encouragement and forbearance, at a time when family life would have enjoyed a resident father. William Louis Culberson kindly provided the Latin diagnoses and Wayne E. Manning, as always, lent his expertise to a review of the manuscript. Thomas Daniel has been most helpful in bringing the manuscript into its final form. The drawings are the artistry of Susan Carlton Smith and they were sponsored by the Duke University Council on Research.

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<sup>3</sup>Bracketed descriptions apply to species not found in Costa Rica.

alternate, estipulate, even-pinnate [or odd-pinnate]; leaflets sessile or petiolulate, margins entire or serrate, dotted below with peltate scales [sometimes aromatic]. Trees monoecious (bisexual) [or dioecious]. Inflorescences of several types: terminal androgynous panicle with central female catkin subtended by 1-6 male catkins or, rarely, with central male catkin subtended by several female flowers; terminal female catkin solitary; terminal cluster of 1-10 male catkins [or lateral solitary or clustered male catkins]. Flowers unisexual. Male flowers with 3-lobed [or unlobed] primary bract; floral segments 4-7 [to 14]; stamens 6-19 [or 3-100] in 1-2 series [or many?]; receptacle round to elongate; filaments short; anthers basifixed, erect, 2-locular, longitudinally dehiscent; rudimentary pistil occasionally present. Pollen grains tripororate-isopolar [stephanopororate to anizonipororate], non-pseudocolpate [pseudocolpate], subtriangular [triangular to spheroidal]; pores circular [meridionally elongate]; exine tectate; sculpturing spinulose. Female flowers consisting of a floral cup formed by an abaxial 3-lobed [or unlobed] primary bract that is fused with 2 adaxial bracteoles [or variously fused and divided]; sepals 4 [to 7], fused below and free above as oblong-linear lobes [or modified into a stigmatic disk], adnate at base to bract-bracteolar cup and ovary; syncarpous gynoecium of 2 [rarely 3 or 4] carpels, ovary inferior, 1-8 [1-4]-locular; ovule with single integument, orthotropous, erect at apex of incomplete septa; style obsolete to long tapering, bifurcate, stigma 4[2]-parted, carinal [or commissural]. Fruit a drupaceous nut with 3[1]-lobed [or unlobed] primary bract expanded to form persistent leathery wings, or reduced to a small circular tab at base of nut [or fused with floral parts to form the husk]; pair of bracteoles adnate to circular tab or fused to form protective lobe over nut in species with winged fruits [or fused with floral parts to form the husk]; husk thin to thick, fleshy or hardened, indehiscent [or dehiscent], formed from fused sepals [or various combinations of primary bract, bracteoles, and sepals]; nut 8[2, 4]-chambered at equator, septa without lacunae [or with]. Seed solitary and large [or small], 8[2, 4]-lobes; endosperm absent; nut-meat has bitter [or sweet] taste. Seedling with hypogeous [or epigeous] cotyledons; first two aerial leaves opposite or alternate, simple or compound [or reduced to scale leaves], leaves and leaflets entire or serrate. Chromosome number  $n=16$ [or 32].

The family of seven genera and approximately 60 species is concentrated in the temperate regions of Asia and North America, but extends southward into the montane areas of southeastern Asia, Central and South America, and the West Indies. Members of the Juglandaceae have a well-marked Tertiary history (Berry, 1912), and there is good evidence that several of the genera now confined to Asia were well represented in North America and Europe prior to the Pleistocene (Nichols, 1973). Three genera (*Engelhardia*, *Platycarya*, *Pterocarya*) are extant in the Old World. The Costa Rican representatives of *Alfaroa* and *Oreomunnea* are strictly tropical American elements, whereas the hickories (*Carya*) and walnuts (*Juglans*) have a north temperate concentration in the Americas and Asia. The 13 New World species of *Carya* extend only as far south as the State of Veracruz in Mexico. *Juglans*, on the other hand, is distributed more or less continuously from Canada

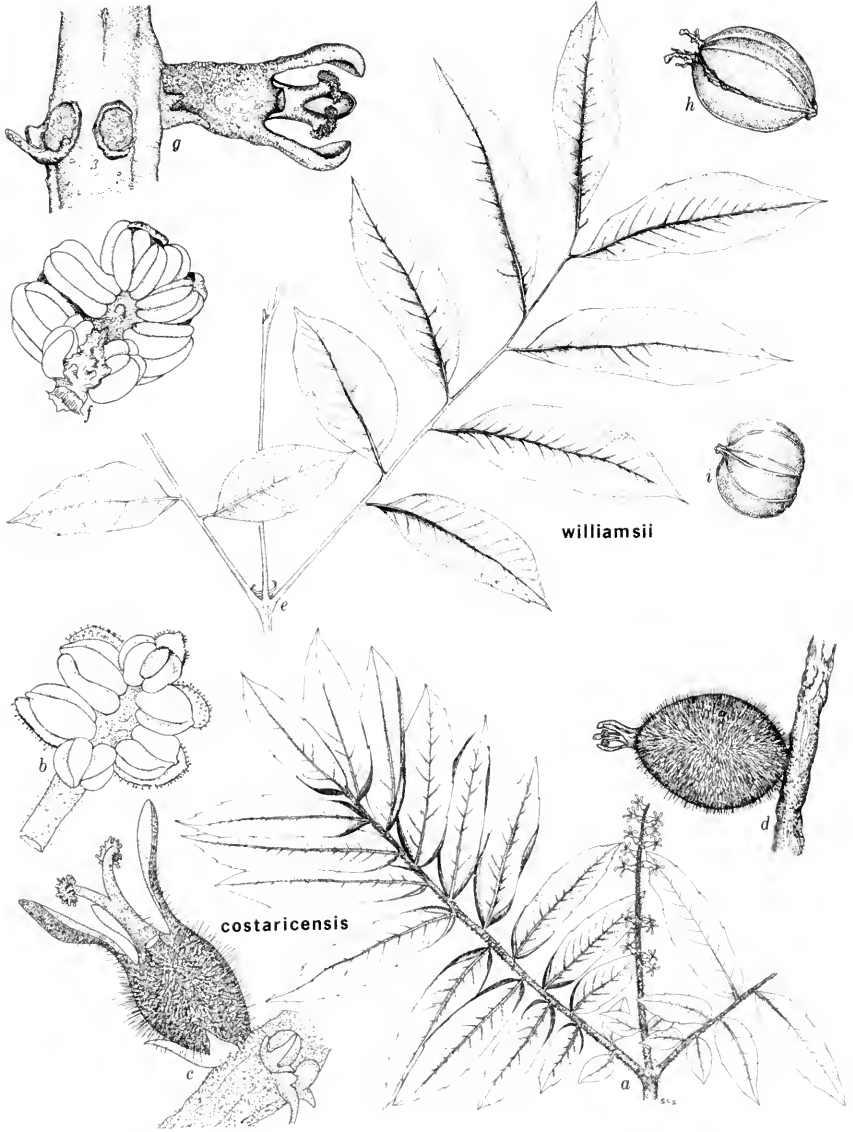
south through the West Indies and Central America to Argentina (Manning, 1957a, 1960a), but is conspicuous by its absence from Costa Rica and Panama. *Juglans boliviana* (C.DC.) Dode was introduced into cultivation at the Instituto Interamericano de Ciencias Agrícolas (IICA) in Turrialba in 1948 (Manning, 1957b), and more recently was established successfully in San José. Evidence from fossil walnuts from Ecuador suggests that the southward migration reached South America only in late Neogene time (Brown, 1946).

The family is coherent and natural with a striking similarity in vegetative characters (de Candolle, 1862), including peltate scales and pinnately compound, estipulate leaves, and a diversity of floral and fruiting features (Manning, 1938, 1941, 1948) that are readily interpretable in terms of evolutionary shifts in the mode of pollination (Whitehead 1969), and seed dispersal and establishment (Conde and Stone, 1970; Stone, 1970, 1973). The monotypic Rhoipteleaceae from China appears to be a primitive member of the Juglandales (Cronquist, 1968; Stone and Broome, 1971; Takhtajan, 1969; Withner, 1941). Recent suggestions (Hutchinson, 1959; Cronquist, 1968) of close affinity with the Picrodendraceae are unfounded (Stone, 1973), though Thorne's placement of the two families near the Anacardiaceae-Burseraceae-Sapindaceae (Rutales

*Opposite:*

FIG. 6. Vegetative and floral features of two wide-spread species of *Alfaroa*. a-d, *A. costaricensis*: a, shoot with opposite, pinnately-compound leaves, pubescent stem, petiole, rachis and midrib, leaflets numerous, serrate, truncate and revolute at base, female inflorescence terminal, bearing numerous, alternate flowers (Stone 2174)  $\times 1/3$ ; b, adaxial view of male flower, pubescent, pedicel elongate (1.9 mm. long), 6 stamens subtended by 6 floral segments (mainly obscured), segments mostly flat (Stone 3621),  $\times 5$ ; c, female flower pubescent, 3-lobed bract sessile, bracteolar rim essentially obsolete, sepal lobes broad, elongate style deeply cleft, stigma lobes horseshoe shaped (Stone 2352),  $\times 4$ ; d, fruit ellipsoid, pubescent, calyx beak persistent at apex, bract-bracteolar cup obscure at base (Stone 2173),  $\times 3/4$ . e-i, *A. williamsii* subsp. *tapantiensis*: e, shoot with opposite, pinnately-compound leaves, glabrous, leaflets 8, mostly entire, occasionally with a small tooth on margin, obtuse and flat at base (Stone 3633),  $\times 1/3$ ; f, adaxial view of male flower, glabrous, sessile, 8 stamens subtended by 4 floral segments, segments tend to cup around tips of anthers, proximal segment not reflexed as in b (Stone 3633),  $\times 5$ ; g, female flower glabrous, sepal lobes broad, elongate style deeply cleft, stigma lobes horseshoe shaped (Stone 3633),  $\times 4$ ; h, fruit ellipsoid, glabrous, sculptured with faint longitudinal ridges, calyx beak persistent at apex, bract-bracteolar cup obscure at base (Stone 2678 A),  $\times 3/4$ ; i, fruit ovoid, similar to h in other aspects (Stone 3624),  $\times 3/4$ .





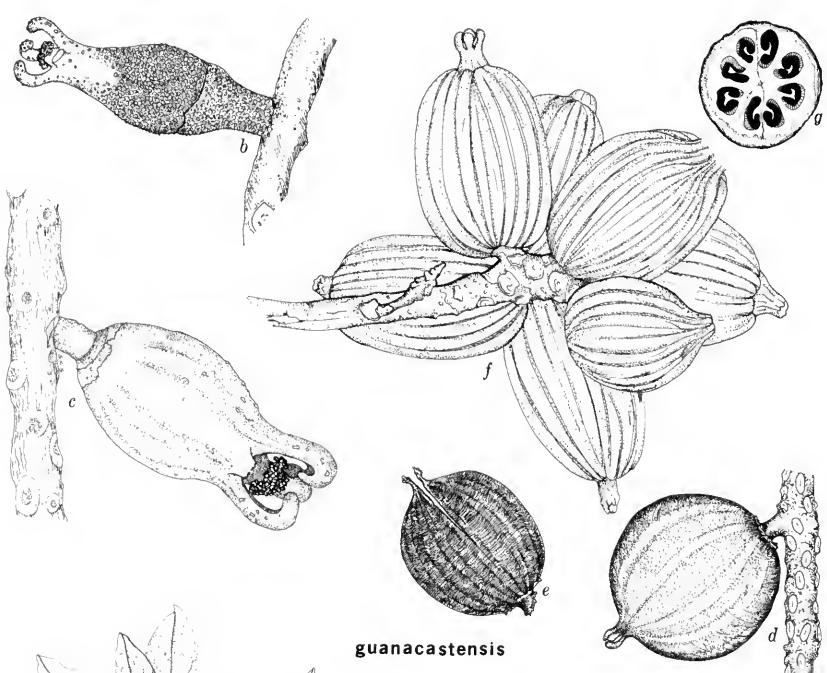
of Thorne, 1973; Sapindales of Cronquist, 1968) seems to be gaining acceptance (Stebbins, 1974; Wolfe, 1973).

Costa Rica is the center of species diversity for the two native genera. Four of the six species of *Alfaroa* and the two species of *Oreomunnea* grow within a 50 km. radius of San José. Cartago Province, the type locality for both genera, has the richest concentration of species. The possibility of finding new species of Juglandaceae is certainly good. The disjunct mountain tops and isolated valleys provide many suitable habitats for local endemism. Costa Rica should be a haven for alpha and omega taxonomists for many years to come. This is particularly true insofar as both genera have had such special significance in interpretation of the phylogeny of the family, because of their possession of a host of primitive features: long vessel members and occasional presence of scalariform perforations (Heimsch and Wetmore, 1939); terminal androgynous panicles (Manning, 1938); and small pollen grains that are basically triplicate, isopolar, suboblate in equatorial view, and subtriangular in polar view (Whitehead, 1965; Stone and Broome, 1975).

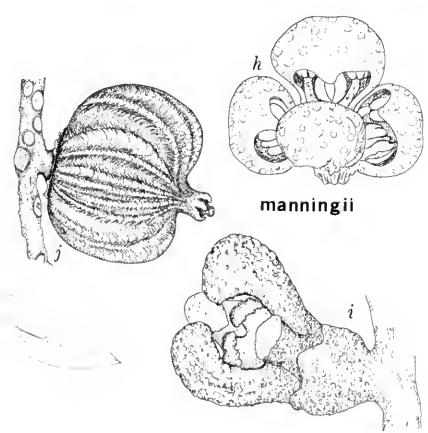
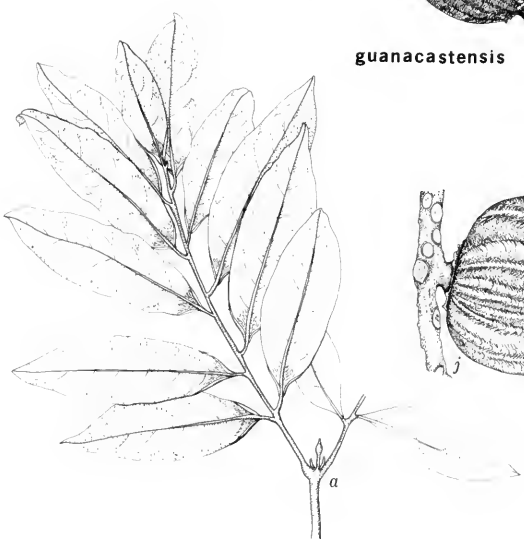
In the following treatment, the species *Alfaroa* and *Oreomunnea* are keyed under the family.

*Opposite:*

FIG. 7. Vegetative and floral features of two endemic species of *Alfaroa* from Costa Rica. a-g, *A. guanacastensis*: a, sterile shoot with opposite, pinnately-compound leaves, leaflets subopposite, entire, decurrent on petiole, revolute at base with a few stiff hairs between the margin and midrib (Stone 3259),  $\times 1/3$ ; b, female flower, floral cup well developed, style obsolete, sepal lobes partially reflexed to expose stigma (Stone 3259, Miravalles),  $\times 2$ ; c, young fruit, bract-bracteolar rim of floral cup split by enlarged ovary, sepal lobes arched over stigma from flowering through fruit maturation (Stone 2753, San Ramón),  $\times 2$ ; d, fruit spheroid, faint longitudinal ridges (Stone 2716, San Ramón),  $\times 3/4$ ; e, ellipsoid fruits, faint longitudinal ridges (Stone 3259, Miravalles),  $\times 3/4$ ; f, inflorescence with oblong fruits, faint longitudinal ridges (Stone 2167, Tenorio),  $\times 3/4$ ; g, transverse section of fruit at equator, secondary partition oriented in north-south direction, husk thin, shell thick, 8-chambered (Stone 2167, Tenorio),  $\times 3/4$ . h-j, *A. manningii*: h, adaxial view of male flower, sessile, 4 hooded floral segments each enclosing 3 stamens (Stone 2220, Platanillo),  $\times 5$ ; i, young female flower, floral cups not fully elongated, style obsolete, sepal lobes arched over stigma (Stone 2170, Platanillo),  $\times 4$ ; j, obloid fruit with deeply corrugated surface, large basal bract-bracteolar tab (Stone 2170, Platanillo),  $\times 3/4$ .



**guanacastensis**



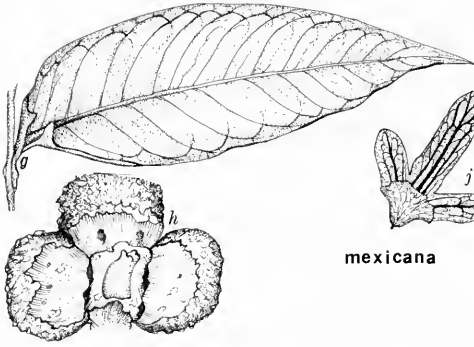
**manningii**

## KEY TO JUGLANDACEAE

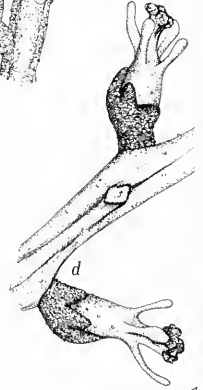
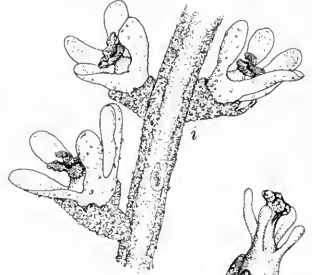
- 1a. Leaflets serrate on seedlings, and serrate to entire on saplings and sucker shoots of adult trees; female flowers sessile (except 5). . . . . 2a.
- 1b. Leaflets always entire; female flowers pedicellate on an elongate bract-bracteolar floral cup . . . . . 4a.
- 2a. Outer bark exfoliating, inner bark orange; leaflets commonly with basal auricles; male flowers compact, hooded with 4 floral segments, each tightly cupped around a pair of stamens, 8 stamens total; female flowers pedicellate, subtended by a bract-bracteolar floral cup with a well-developed 3-lobed bract and adaxial bracteolar lobe; fruit medium size, 3-winged, lateral wing span to 5 cm. . . . . 5. *Oreomunnea mexicana* subsp. *costaricensis*.
- 2b. Outer bark tight, inner bark pink to red; leaflets without auricles; male flowers elongate, not hooded, 4-7 floral segments only loosely enclosing 6-11 stamens, female flowers sessile, bract small, acutely 3-lobed, bracteolar rim obsolete; fruit medium size (1.5-3 cm.), wingless nut with obscure, circular bract-bracteolar tab at base . . . . . 3a.
- 3a. Petiole short, 0.4-2(3.5) cm.; petiole and rachis densely pubescent; leaflets (8)12-18(30), sessile or nearly so, mainly truncate at base; basal leaflets moderately to greatly reduced, often less than one-fourth the length of the longest leaflets; male flowers with short but conspicuous pedicels, 1-2(8) mm.; fruit pubescent . . . . . 1. *Alfaroa costaricensis*.

*Opposite:*

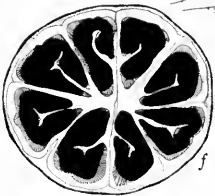
FIG 8. Vegetative and floral features of the Costa Rican species of *Oreomunnea*. a-f *O. pterocarpa*: a, terminal shoot displaying decussate phyllotaxy, leaflets revolute at base, secondary veins curve upward toward tip and end without conspicuous branching (Stone 1016),  $\times 1/3$ ; b, portion of male catkin (Stone 1346),  $\times 3$ ; c, abaxial view of male flower with 5 floral segments subtending 19 stamens (Stone 1346),  $\times 5$ ; d, female flowers with well-developed bract-bracteolar floral cup, sepal lobes linear, style elongate and stigma horseshoe shaped (Stone 1346),  $\times 3$ ; e, fruit with 3-lobed bract, primary vein nearly continuous to tip, pair of lateral secondary veins parallel for short distance, forming looping connections distally, adaxial bracteolar lobe enclosing nut (Stone 1346),  $\times 1/4$ ; f, transverse section of fruit at equator, secondary partition oriented in north-south direction, husk thin, shell thin, cartilaginous, 8-chambered (Stone 1346),  $\times 2$ . g-j, *O. mexicana* subsp. *costaricensis*: g, leaflet with auricles at base, slightly revolute, secondary veins curve upward toward tip, then branch and fuse near margin (Stone 2680),  $\times 3/4$ ; h, adaxial view of sessile male flower with 4 hooded floral segments (proximal segment removed), aborted pistil in center, and 8 stamens borne in one series removed to expose slightly raised, rectangular receptacle (Stone 2680),  $\times 10$ ; i, female flowers with spreading sepals, essentially obsolete style, and horseshoe shaped stigma (Stone 2680),  $\times 5$ ; j, fruit with 3-lobed bract, central lobe with primary and two secondary veins extending nearly to the tip, secondaries looping only in the distal one-third, two lateral lobes with strong primary vein and faint, looping secondaries, adaxial bracteolar lobe enclosing nut (Stone 3632),  $\times 1/2$ .



mexicana



pterocarpa



- 3b. Petiole long, (1.4)2.5-5.5 cm.; petiole and rachis glabrous; leaflets (6)8-12(16), short-petioluled (1-3 mm.), obtuse at base; basal leaflets smaller than median ones, but never less than one-fourth their length; male flowers sessile, pedicel (if present) less than 0.75 mm.; fruit glabrous.  
4. *Alfaroa williamsii* subsp. *tapantiensis*.
- 4a. Petiole often hairy at base; leaflets (4)6-8, petiolules 5-15 mm.; male flowers elongate, with 3-4 floral segments only loosely subtending 16-19 stamens; fruit large, 3-winged, lateral wing span to 13 cm.  
6. *Oreomunnea pterocarpa*.
- 4b. Petiole glabrous; leaflets 6-12(18), petiolules 1-5(10) mm.; male flowers compact, hooded, with 4 floral segments each tightly cupped around 3 stamens, 12 stamens total; fruit large (to 3 cm.), wingless nut with prominent circular tab at base . . . . . 5a.
- 5a. Petiole (4)5-9(11) cm.; leaflets (6)8-12(18); fruits medium size (to 3.5 cm.), obloid, surface deeply corrugated with pronounced longitudinal ribs and grooves and thick husk (1-7.5 mm.) . . . . 3. *Alfaroa manningii*.
- 5b. Petiole (1)2-5(7.5) cm.; leaflets (6)8-10(16); fruits variable in size, spheroid (2.5 cm.) to oblong (1.7 x 3.8 cm.), surface nearly smooth, faint longitudinal ribs and thin husk (0.3-1.5 mm.)  
2. *Alfaroa guanacastensis*.

### ALFAROA Standley

REFERENCES: P. C. Standley, *Alfaroa*, a new genus of trees of the family Juglandaceae from Costa Rica, Journ. Wash. Acad. Sci. 17:77-79. 1927. W. E. Manning, The genus *Alfaroa*, Bull. Torrey Bot. Club 76:196-209. 1949. W. E. Manning, *Alfaroa* and *Engelhardtia* in the New World, Bull. Torrey Bot. Club 86:190-198. 1959.

Trees or rarely large shrubs; bark tight, or with small chips exfoliating, surface reddish-brown with congested lenticels, interior of bark pink with white streaks or orange-yellow; sapwood white, heartwood pink, fine, straight grained; buds glabrous or pubescent. Leaves glabrous or pubescent, decussate, occasionally whorled, infrequently alternate; petioles short to long; leaflets 6-18(30), sessile to short petiolulate, margins entire, or serrate on young plants and sucker shoots. Inflorescences borne terminally with flush of new growth of pink leaves, or occasionally terminal on axillary shoots of old wood; female and male inflorescences either separate and terminal, or combined into an androgynous panicle with central female catkin flanked by one or more pairs of male catkins, or rarely with central male catkin subtended by female flowers. Male flowers numerous, alternately arranged, compact or elongate; floral segments 4-7, flat or hooded; stamens 6-12 in one series. Pollen triporate (2-8), isopolar, suboblate-oblate; amb triangular to rounded triangular, 20-26  $\mu$ m in diameter, pores circular, nexine thick, from one-third to equalling tectum in thickness. Female flowers numerous, alternately arranged; floral cup sometimes elongated into a pedestal consisting of a 3-lobed abaxial bract and an adaxial bracteolar rim; calyx tube fused to floral cup at base, distinct above,

4 broad sepal lobes reflexed at time of pollination to expose stigma, or arched to form sheltered chamber; style obsolete to long tapering, bifurcate with shallow to deep cleft separating stylar arms; stigma weakly 4-parted, horseshoe shaped, carinal, verrucose stigmatic surface confined to rim and outer surface. Fruit medium to large drupaceous nut, ellipsoid to obloid, without wings, 8-chambered at equator; calyx and style persistent at apex; bract-bracteoles persisting as a small to large circular tab at base; husk leathery or hard, indehiscent, sometimes with pronounced corrugations; shell brittle to hard. Seedling with hypogeous cotyledons; first two aerial leaves alternate or opposite, simple or compound, leaves and leaflets entire or serrate. Chromosome number  $n=16$ .

Four Costa Rican species of *Alfaroa* are recognized, including one new species (*A. guanacastensis*) and subspecies (*A. williamsii* subsp. *tapantiensis*). *A. costaricensis*, which is the most distinctive member of the genus, has the widest range, extending from Mexico to Panama. It is sympatric in Costa Rica with the closely related *A. williamsii*. *A. williamsii* Molina subsp. *williamsii* is the only species of *Alfaroa* reported from Nicaragua. In addition, Alfarosas are known from Mexico (*A. mexicana* Stone), Guatemala [*A. guatemalensis* (Standley) Williams], and Honduras (*A. hondurensis* Williams). A single immature specimen from Colombia (Killip & Smith 19285) was tentatively identified by Manning (1959) as *A. manningii*. However, the surface of the fruit is not deeply corrugated and ridged as that of *A. manningii*, and it seems likely that the South American collection represents a new, undescribed species.

The species of *Alfaroa* in Costa Rica are trees of mid-elevations occurring in the premontane rainforests that extend from the borders of Nicaragua to Panama. Their disjunct distribution coincides with the many volcanoes and well-defined mountain ranges in northwest and central Costa Rica. The trees are often locally abundant, and they are readily recognized in the growing season by flushes of pink or dull red shoots. Locating Alfarosas in virgin rainforest is aided considerably by the distinctive saplings in the understory. The leaves are even-pinnate and at first are alternately arranged, but the later formed leaves have a distinctive decussate phyllotaxy. During the growing season the central leader displays a terminal apex with golden-yellow buds flanked by a pair of reddish young leaves with conduplicate leaflets. The adult trees are characterized by moderate size buttresses, tight bark with congested lenticels, generally pink interior, and fine grained wood that is white to pink. The lumber is of cabinet quality, so this is often one of the first species to be logged when new roads are opened. The flowers

are inconspicuous in the field, though a thorough search of the litter often uncovers dried remains of male catkins. The fruits are walnut-like with a thin or thick fibrous husk and a cartilaginous to hard shell. The fruits are similar to those of *Oreomunnea* in having a distinctive 8-chambered nut.

The Costa Rican species of *Alfaroa* fall into two groups: (1) *A. costaricensis* and *A. williamsii* subsp. *tapantiensis*—leaflets entire or serrate, the first pair of aerial seedling leaves opposite, pinnately compound, and leaflets serrate, young leaflets conduplicate at first but flattening out in primoidal stage (leaflet less than 1.5 mm. wide); (2) *A. guanacastensis* and *A. manningii*—leaflets always entire, the first pair of aerial seedling leaves alternate, or opposite and simple or compound, young leaflets conduplicate throughout early stages of leaf expansion (leaflet over 10 mm. wide). There is probably sufficient additional evidence to recognize these groups formally, but I am postponing a decision on this matter until more collections are available.

1. *Alfaroa costaricensis* Standley, Journ. Wash. Acad. Sci. 17:78. 1927. Figure 6a-d.

Trees, or large shrubs, to 23 m. tall and 90 cm. dbh; buttresses small or absent; bark tight, to 1 cm. thick, interior pink with white streaks or infrequently pale orange; buds and shoot usually covered with long (1.5 mm.), coarse hairs, wearing thin as season progresses. Leaves mainly decussate, occasionally alternate, or whorled; petioles 0.4-2(3) cm., pubescent; rachises 10-15(30) cm., pubescent; leaflets (8)12-24(30), opposite to subopposite, lower ones conspicuously reduced, mainly entire, sometimes serrate on apical portion, coarsely serrate on sucker shoots and seedlings, truncate to obtuse and flat to broadly revolute at base, waxy green and glabrous above, except along costa, dull green below, hirtellous along nerves and often puberulent between, sessile or essentially so. Female inflorescences terminal on new growth, stiff and erect, with or without male catkins or individual male flowers at base, to 65 flowers per spike, often found persisting in dried state several weeks after flowering; male catkins alternate or decussate, to 16 cm. long and 10 catkins per branch, up to 40 or 50 forming congested terminal panicle on new growth; androgynous panicles less common, female spike central, subtended by 1-4 short (5-7.5 cm.) lateral male catkins, or with a few sessile male flowers at base or, rarely, with a central male catkin subtended by female flowers. Male flowers with a conspicuous pedicel, 1-2(8) mm.; 3-lobed bract short and blunt to tapered; floral segments 4-7, reflexed at maturity and not enfolding the stamens; stamens 6-11. Pollen subtriangular in amb (polar) view,  $24.8\mu\text{m}$  in diameter. Female flowers sessile; 3-lobed bract not elongated into pedestal, central lobe pronounced, acute to tapered; adaxial bracteolar rim essentially obsolete; sepal lobes 4, reflexed to expose stigma at pollination; style elongate, bifurcate with deep cleft; stigmatic lobes rounded to horseshoe shaped, bright red at maturity. Fruit ellipsoid to ovoid, sometimes slightly compressed in the plane of carpel fusion, up to 2 cm. diameter



and 3 cm. long; calyx beak 2-5 mm. long, persistent at apex; bract-bracteolar tab small (3-5 mm.), appressed to nut at base, the bract sometimes distinguished by retention of a tapered central lobe (up to 2 mm. long) flanked by 2 blunt (less than 1 mm. long) lateral lobes; husk essentially absent, less than 0.5 mm. thick, surface hirtellous (2 mm. long hairs), becoming glabrous and smooth on weathering; shell extremely thin, less than 1 mm., cartilaginous. Seedling with first two aerial leaves opposite, compound, leaflets coarsely serrate; succeeding several leaves alternate, pinnately compound with serrate leaflets; leaves becoming decussate with mostly entire leaflets in sapling stage.

This species is distributed more widely than any other member of the genus. It is known from Mexico, Guatemala, Costa Rica, and Panama, and has an elevational range in Costa Rica from 600 m. (Turrialba, *Keith 371*) to 2220 m. (Río Negro, *Mora CMV-21*). Several local names are used—*goalín* in Turrialba (*Keith 371*), *gualín* at Muñeco (*Standley 33501*), and *campano chile* on the Río Negro (*Mora CMV-21*). Herbarium records indicate that this species was once a fairly common forest tree in Costa Rica. Collections have been made in the Provinces of Alajuela, Cartago, Guanacaste, Heredia, and San José. The tree, which is prized for its timber, is often the first removed when virgin forests are logged. Attempts to relocate early collection sites have been partially successful. Trees from "La Palma de San Ramón," Alajuela, were sampled in 1928 (*Brenes 6300*) and again in 1966 (*Stone 2326*). Most of the area around San Ramón has been converted to pasture and farmland for sugarcane. Only two remnant trees were located on a windswept ridge-top about 10 km. north of the city. Records by Skutch from Heredia (*Skutch 4684, 4686*) have been confirmed by repeated visits to Vara Blanca from 1967 (*Stone 2173*) through 1975 (*Stone 3621*). The trees are scattered in broken pastures and virgin forest at approximately 1700 m. elevation. The record from San José Province was first recorded by *Stork 1700* from Santa María de Dota. I relocated a few trees south of the city in 1968 (*Stone 2679*) on a steep mountain ridge above a pasture broken with oaks, dogwoods, and tree ferns. The report from Guanacaste is based on my 1972 collection (*Stone 3383*) from the exquisite cloud forest near the Quaker community at Monteverde. Some of the largest trees that I have seen once formed stately groves in the mountains south of Muñeco in Cartago Province, but extensive logging in the past several years has reduced the population considerably.

Vivid reddish flushes of new growth appear in January at the beginning of the dry season. February seems to be the month for peak flowering, though at least sporadic flowering occurs in

March, June, and November. Immature to mature fruits have been collected in February, March, April, June, and August. While the trees are monoecious, there is some evidence that one sex may predominate in a particular season, and often whole branches will display either congested panicles of male flowers or elongate female spikes with highly reduced male catkins at the base.

*Alfaroa costaricensis* is the most distinctive member of the genus. The Mexican and Guatemalan trees tend to have longer petiolules and a somewhat less truncate leaflet than the Costa Rican and Panamanian specimens, but the taxon is easily identified by its highly reduced petiole and lower leaflets, and the pubescent stems, leaves, and fruits. This species is most closely related to *A. williamsii*. Plants of both taxa produce at least some leaflets with toothed margins. The first pair of aerial leaves of the seedlings are normally opposite and pinnately compound with coarsely serrate leaflets. The male and female flowers also have much in common, though there are subtle, distinctive differences. *A. costaricensis* has a short to long pedicel supporting the male flower, and the female flower is hirsute. *A. williamsii* has staminate flowers with an extremely short pedicel; the female flowers are covered with peltate scales but are without hairs. The two species also have several distinctive vegetative differences. The former has a pubescent petiole and rachis, an extremely short petiole, and leaflets that are mainly truncate at the base, whereas the latter is glabrous throughout, the petiole is relatively long, and the leaflets are mainly obtuse at the base. Intermediates between these species have been collected. Hybridization, which is suspected, is discussed under *A. williamsii*.

## 2. *Alfaroa guanacastensis* D. Stone, sp. nov. Figure 7a-g.

Arbor usque ad 27 m. alta. Folia pinnata decussata; foliola (6)8-10(16), coriacea, elliptica vel oblongo-lanceolata, basi symmetrica, indumento in pagina inferiore saepe praesenti sed sparsissimo, petiolulis 2-7(10) mm. longis. Inflorescentiae masculinae et femineae terminales sed separatae. Flores masculini ca. 3 mm. lati, bracteis 3-lobatis, perianthio 4-partito, staminibus 12. Flores feminei 7-8 mm. longi, perianthio 4-partito, lobi perianthii cucullati, stylo obsolete, stigmatibus subglobosa. Fructus sphaerici (ad 2.5 cm. diam.) vel ellipsoidi (1.7 x 3.8 cm.), in longitudinem dilute parcati, pagina fere laevi, vagina aliquantum tenui (0.3-1.5 mm. crassa). Germinatio hypogaea. HOLOTYPUS: *Stone 2167*, Duke University; ISOTYPI: A, CR, F, US.

Trees to 27 m. tall and 90 m. dbh; buttresses small to large, extending to 3 m. or more up trunk; bark tight or with small chips exfoliating, to 1 cm. thick, reddish-brown exterior, interior pink throughout or pink toward surface and orange toward

center; buds and shoot glabrous. Leaves decussate, glabrous; petioles (1)2-5(7.5) cm.; rachises commonly 4-16(22) cm.; leaflets (6)8-10(16), opposite to subopposite, entire, obtuse at base, symmetrical, slightly decurrent on petiolule, flat to moderately revolute, glabrous except for occasional presence of a few short hairs at base between midrib and margins; petiolules 2-7(10) mm. Female inflorescences terminal on new growth, stiff and erect up to 45 flowers per spike; male catkins 2-6 per branch, forming congested terminal panicle on new growth, or arising from axillary buds on old wood; terminal androgynous panicles with 1-2 decussate pairs of male catkins subtending 1-4 female flowers in a terminal catkin. Male flowers with gardenia-like odor, sessile or essentially so; 3-lobed bract short, wide, and blunt; floral segments 4, hooded, each segment partially enclosing 3 stamens; stamens 12. Pollen subtriangular in amb (polar) view, 21.8  $\mu\text{m}$  in diameter. Female flowers stalked; pedestal formed by fusion of a faintly 3-lobed abaxial bract with an adaxial bracteolar rim; sepal lobes 4, arched over stigma to form sheltered chamber at pollination (*Stone 2167*) or reflexed (*Stone 3629*); style essentially obsolete to short; stigma lobes horseshoe shaped. Fruit variable in shape, spheroid (to 2.5 cm.) to oblong (1.7  $\times$  3.8 cm.); calyx beak (4-6 mm.) persistent at apex; bract-bracteolar tab large (8-10 mm.), appressed to nut at base; husk relatively thin, 3 mm. or so in fresh state, 0.3-1.5 mm. dried, surface nearly smooth, faint longitudinal grooves and ridges; shell 1-2 mm. thick, hard even in fresh state. Seedling with first two aerial leaves variable, opposite to subopposite, simple (*Stone 2716*) or opposite-compound (*Stone 3254*), leaflets entire (*Stone 2716*), rarely with a few minute teeth (*Stone 3254*); succeeding several leaves alternate, pinnately compound with entire leaflets; leaves becoming decussate in the sapling stage.

*Alfaroa guanacastensis* is known only from the Cordillera de Guanacaste, including Volcán Orosí, Volcán Miravalles, Volcán Tenorio, and the San Ramón area on the southeastern terminus of the Cordillera de Tilarán. This species is present in the premontane rainforest, 650-1000 m., occurring at the lower elevations on the wet Caribbean slopes and nearer the crest and in mountain passes where the moist eastern air spills over to the Pacific side. Peak flowering occurs from February (*Stone 3629*) through May (*Stone 3259*); fruits develop in May (*Stone 3259*) and June (*Stone 2753*) and mature in January (*Stone 2327*), April (*Stone 2167*), and November (*Stone 2327, 2716*).

Populational differences among the four collection sites are apparent. At one time I had considered describing at least one additional species from this complex, but then decided that the vegetative material was too similar for routine identification. In addition, the various fertile collections which look different may, in fact, represent slightly different developmental stages. The leaflets of trees from Orosí, Tenorio, and San Ramón are on the average larger and more coriaceous than those from Miravalles. The sepal lobes are reflexed at pollination (and through fruit maturation) in the

Miravalles specimens (*Stone 3629*), whereas they are arched over the stigma in trees at the other sites (e.g., San Ramón, *Stone 2753*). The mature fruits are variable in shape: those from Orosí and Tenorio are more oblong; fruits from Miravalles vary from oblong to spheroid, but tend to be compressed in the plane of carpel fusion; the trees from San Ramón produce spheroid fruits of uniform size. The seedlings were at first thought to be highly distinctive in the Miravalles population. The first aerial leaves are uniformly opposite and compound, a condition previously encountered only in *A. costaricensis* and *A. williamsii*, although the latter two have serrate instead of entire leaflets. The single seedling from Tenorio (*Stone 2167B*) has opposite-simple first leaves as found in *A. manningii*. Somewhat later I discovered that Orosí seedlings from under the same parental tree may have either opposite-compound (*Stone 2333*) or opposite-simple leaves (*Stone 2553*). Greenhouse-germinated seed confirmed this condition for the San Ramón population (*Stone GH-117*). The type of variability witnessed in *A. guanacastensis* is probably commonplace in tropical trees, but not often realized because of the paucity of samples.

This species is closely related to *A. manningii* and is vegetatively very similar to *A. guatemalensis* and *A. mexicana*. The leaves are generally smaller, the petioles shorter, and the leaflets fewer than those of *A. manningii*. The fruits are also reasonably distinctive. In contrast to the thick, deeply corrugated husks of *A. manningii*, fruits of *A. guanacastensis* are basically smooth in outline with faint longitudinal ridges and a relatively thin husk.

### 3. *Alfaroa manningii* León, Ceiba 4:44. 1953. Figure 7h-j.

Trees to 24 m. tall and 90 cm. dbh; buttresses small to medium; bark tight, reddish brown exterior, pink interior, becoming orange to yellow toward center; buds and shoots glabrous. Leaves decussate, glabrous; petioles (4)5-9(11) cm.; rachises commonly (50)90-230(290) cm.; leaflets (6)8-12(18), opposite to subopposite, entire, obtuse at base, symmetrical, decurrent on petiolule, very slightly revolute, glabrous; petiolules (1)2-5(10) mm. Female inflorescences terminal on new growth, stiff and erect, up to 40 or 50 flowers per spike; male catkins alternate or decussate, 1-6 per branch, forming congested terminal panicle on new growth or arising from axillary buds on old wood, up to 18 cm. long and pendent at maturity; androgynous panicles less common, terminal on new growth, female spike central with 1-4 lateral male catkins at base. Male flowers with gardenia-like odor, compact, sessile or essentially so; 3-lobed bract subtending 4 hooded floral segments, each of which partially encloses 3 stamens; stamens 12. Pollen subtriangular in amb (polar) view, 21.7  $\mu\text{m}$  in diameter. Female flowers stalked; pedestal formed by fusion of a faintly 3-lobed abaxial bract with an adaxial bracteolar rim; sepal lobes 4, arched over stigma to form sheltered chamber at pollination; style essentially obsolete; stigma

lobes horseshoe shaped. Fruit obloid, up to 3.5 cm. in diameter and 3 cm. long, apex slightly concave; calyx beak (4-5 mm.) persistent; bract-bracteolar tab at base large (to 16 mm.), more or less circular; husk of irregular thickness, 1-7.5 mm., surface deeply corrugated, 8-12 pronounced longitudinal ribs or flanges that extend from apex to equator, diminishing toward base; shell 1-2 mm. thick, hard even in fresh state. Seedling with the first two aerial leaves simple, alternate or opposite, and entire; succeeding several leaves compound; later formed leaves decussate with entire leaflets.

*Gavilan colorado* is a valued lumber tree of the Platanillo area of northeastern Cartago Province. This species grows to be a very large tree (up to 90 cm. dbh) in the premontane rainforest between 650-1,200 m. Fertile specimens are recorded only from the vicinity of Río Platanillo. *Oreomunnea pterocarpa*, *gavilan blanco*, is a common associate in this area. Sterile samples of what appear to be the same species, along with *Oreomunnea mexicana*, have been collected near the headwaters of the Río Sapo, about 28 km. north-east of the village of Platanillo. Peak flowering occurs in March and April, though the presence of a range of fruit sizes in April as well as August suggests a more prolonged flowering period. Occasionally, trees bear only male flowers (Stone 2220, 25 March 1967), but most commonly both sexes are present. These trees appear to be truly bisexual, rather than polygamodioecious as reported by Skutch (in Manning, 1949). The exclusive production of male flowers is encountered in young trees, whereas adults display a great deal of variability in the type of inflorescence that is produced on a particular branch. I suspect also that the same tree shows seasonal and yearly differences in the frequency of production of male and female flowers.

This narrow Costa Rican endemic has characteristics in common with *A. guanacastensis*. The leaves of *A. manningii* are generally larger with longer petioles and often have more leaflets. The fruits are also large, quite heavy, and deeply corrugated with 8-12 longitudinal ribs or flanges, and they bear a persistent calyx beak at the apex and a large, more or less circular, bract-bracteolar tab at the base. Manning (1959) tentatively referred a Colombian collection (Killip & Smith 19285) to this species, but has since changed his mind (pers. comm.). Though the fruits are small and possibly immature, they do not display the prominent ridges characteristic of the Costa Rican species. Besides *Juglans*, the Killip & Smith collection of *Alfaroa* is the only member of the family known from South America.

4. *Alfaroa williamsii* Molina subsp. *tapantiensis* D. Stone, subsp. nov. Figure 6e-i.

Arbor usque ad 30 m. alta. Folia pinnata decussata vel alterna, glabra, petiolis (1.4)2.5-5.5 cm. longis; folia 6-12 (16), basi obtusa, petiolulis stamina includentes. Fructus glabri. Germinatio hypogaea. HOLOTYPE: *Stone 3119*, Duke University; ISOTYPI: A, CR, F, US.

Trees to 30 m. tall and 90 cm. dbh; buttresses small to moderate; bark tight, interior pink; buds glabrous, or rarely with a few coarse trichomes. Leaves mainly decussate or alternate; petioles (1.4)2.5-5.5 cm., glabrous; rachises 7.5-12 cm., glabrous; leaflets (6)8-12(16), opposite to subopposite, approximately of equal size, lower ones greatly reduced only rarely, mainly entire, occasionally with a few small teeth on apical end, coarsely serrate on sucker shoots and seedlings, mainly obtuse at base, sometimes truncate, often asymmetrical with basiscopic side decurrent on petiolule, only slightly revolute if at all, glabrous on both surfaces; petiolules 1-3 mm. Female inflorescences terminal on new growth, stiff and erect, to 15 cm. long, 27 or more alternate flowers; male catkins alternate or decussate, 6-9 catkins per branch, more or less erect, to 8.5 cm., forming congested terminal panicle on new growth; androgynous panicles terminal on new growth of two kinds; female catkin central with 1-2 individual male flowers sessile at base of inflorescence, or, more commonly, central female spike flanked at base by 1-11 male catkins. Male flowers sessile or essentially so (pedicel not exceeding 0.75 mm. long); 3-lobed bract short and blunt, or moderately tapered; floral segments 4, each one slightly curved at the tips to enfold (1)2(3) stamens, (6)8(9) stamens total. Pollen subtriangular in amb (polar) view, 23.9  $\mu$ m. in diameter. Female flowers sessile; 3-lobed bract not elongated into pedestal, central lobe pronounced, acute to tapered; adaxial bracteolar rim essentially obsolete; sepal lobes 4, reflexed to expose stigma at pollination; style elongate, bifurcate, shallow to deep cleft; stigmatic lobes rounded to horseshoe shaped. Fruit ellipsoid (1.5 cm.  $\times$  2 cm.) to ovoid (1.5 cm. diameter), sometimes compressed in the plane of carpel fusion; calyx beak 2-3 mm. long, persistent at apex; bract-bracteolar tab inconspicuous at base; husk essentially absent, less than 0.1 mm. thick, surface nearly smooth, with 8 or so very faint ridges; shell extremely thin, less than 0.5 mm., cartilaginous. Seedling with first two aerial leaves opposite to subopposite, simple or, more commonly, compound leaves or leaflets coarsely serrate; succeeding several leaves alternate, pinnately compound with serrate leaflets; leaves becoming decussate with mainly entire leaflets in sapling stage.

Sterile trees and one fruiting specimen have been observed above Monteverde (1300 m.) on the Cordillera de Tilarán (*Stone 3384, 3627, 3628*). The best representation comes from the terminus of the Cordillera de Talamanca south of the city of Cartago where *Alfaroa williamsii* subsp. *tapantiensis* is associated with *A. costaricensis* and *Oreomunnea mexicana*. Flowering specimens have been collected in March (*Stone 3119, 3633*) and April (*Poveda 851a*); however, since green fruit has also been observed at these times, the initiation of flowering probably coincides with the flush of new growth in mid-January. Germination occurs immediately following

fruit maturation, as evidenced by the range of green fruits to seeds with exposed radicles found nestled in the rich litter on the moist forest floor.

Until now *Alfaroa williamsii* has been reported only from the Departments of Jinotega and Matagalpa in central Nicaragua. The recent Costa Rican collections from Tapantí (*Stone 3119*) and the vicinity of San Isidro de Cartago (*Poveda 851, 851a; Stone 3630, 3631, 3633*), correspond closely to the Nicaraguan specimens (*Williams et al. 20143, 23176, 23717; Stone 2178, 2179a, 2180, 3249, 3250*). The new Costa Rican subspecies is distinguished from *A. williamsii* subsp. *williamsii* primarily on the basis of the male flower. Subspecies *tapantiensis* has a well defined, oblong receptacle bearing (6)8(9) stamens. Each pair of stamens is subtended by a floral segment (4 total) that forms a partial hood over the tips of the anthers at anthesis. Subspecies *williamsii* has a more or less elongate receptacle with 6-11 stamens, subtended by 4-7 floral segments that are variable in position and shape; they open flat and do not enfold the stamens at maturity. Because no male flowers have been collected at Monteverde, the assignment of these specimens to subsp. *tapantiensis* is speculative at this time. Field identification of the species is based on the glabrous leaves, long petiole (on the average somewhat longer in subsp. *williamsii* than in subsp. *tapantiensis*), lower leaflets approximating upper leaflets in size, and occasional serrations on the leaflet margins.

A discussion of the close relationship of *Alfaroa williamsii* to *A. costaricensis* is included under the latter species. Not surprising perhaps is the discovery of a putative hybrid between these species from Estrella, Cartago Province (*Stone 3379: 6 July 1972; 2 January 1973*). The tree was sterile, even though it was reasonably large with a 23 cm. dbh and a height of 15 m. The specimen appears intermediate in several respects: the shoots range from glabrous (cf. *A. williamsii*) to moderately pubescent (cf. *A. costaricensis*); the petioles are of medium-length (ca. 2-3.5 cm.); leaflet number is most commonly 10 (8-14; cf. *A. williamsii*); the leaflets range from obtuse to truncate at the base (cf. *A. costaricensis*); the lowermost leaflets may be reduced, but are never less than one-fourth the size of the upper leaflets (cf. *A. williamsii*). The "Alto de la Estrella" was visited by Standley in 1924 at a time when *A. costaricensis* was a common tree of the "wet forest" (*Standley 39122, 39217*). The putative hybrid was located on cut-over land on the lower reaches of the mountain. *A. williamsii* subsp. *tapantiensis* grows today within

2 km. of Estrella, and both putative parents might still be sympatric on the upper slopes. *Alfaroa costaricensis* Standley var. *elongata* Manning, which was described by Manning (1949) from a single male-flowered collection (*Skutch 4685*), is probably a hybrid also. Manning had questioned the taxonomic placement of the variety and correctly pointed out that it differs from the species by having glabrous foliage, distinctly petioled leaves, and sessile staminate flowers with hooded floral segments (cf. *A. williamsii*; see Manning, 1949, Figs. 1, 16, 17: *Skutch 4685*), but does have the truncate leaflet bases as in *A. costaricensis*. In contrast to *Stone 3379*, specimens from this tree have a larger number of leaflets (14-18[22]), as in *A. costaricensis*. If *Skutch 4685* is, in fact, a hybrid, the enormous size of the tree (90 m. dbh and 30 m. tall: *Skutch*, in Manning, 1949) indicates that the hybridization occurred when the forest was virgin. Attempts to relocate "*elongata*" at Vera Blanca have not been successful. *A. williamsii* has not been collected in this area, although *A. costaricensis* is still fairly common in the open pastures at 1700 m. elevation. This is the first report of hybridization in *Alfaroa*.

### OREOMUNNEA Oersted

REFERENCES: P. C. Standley, The American species of *Engelhardtia*, *Trop. Woods* 12: 12-15. 1927. D. E. Stone, New World Juglandaceae, III. A new perspective of the tropical members with winged fruits. *Ann. Missouri Bot. Gard.* 59:297-321. 1972.

Trees or rarely large shrubs; buttresses moderate to well developed; bark exfoliating or tight, surface reddish-brown, interior bright orange to yellow-orange; wood white throughout or heartwood sometimes pink, fine, straight grained; buds studded with yellow peltate scales, without hairs. Leaves occasionally puberulent in young shoots but glabrous at maturity, mainly decussate, occasionally alternate; petioles short to long; leaflets 4-12, generally long petiolulate, mainly entire, or serrate on young plants and sucker shoots. Inflorescences borne terminally with flush of new growth of yellow-red or pink leaves, or occasionally terminal on axillary shoots of old wood; female and male inflorescences either separate, or combined in androgynous panicles with central female catkin flanked by 1-6 male catkins. Male flowers numerous, alternately arranged, sessile or essentially so, compact or elongate, floral segments 4-6, flat or hooded; stamens 8(9) in one series, or 16-19 stamens in two series. Pollen triporate (2-8), isopolar, suboblate-oblate; amb triangular to rounded-triangular, 20-26  $\mu\text{m}$  in diameter; pores circular; nexine thick, from one-third to equalling tectum in thickness. Female flowers numerous, alternately arranged, sessile or nearly so; bract-bracteolar floral cup forms a pedastal with 3-lobed bract abaxial, bracteolar rim adaxial, calyx tube fused to floral cup



at base, forming distinct tube above; sepal lobes 4, narrow or broad, extending to summit of stigma or beyond, reflexed at time of pollination, or arched to form sheltered chamber; style short or long-tapering, bifurcate with deep cleft separating stylar arms; stigma weakly 4-parted, horseshoe shaped, carinal, verrucose stigmatic surface confined to rim and outer surface. Fruit medium to large, 3-winged; adaxial bracteolar lobe covering nut at maturity; nut small, globose, 8-chambered at equator; husk essentially obsolete; shell cartilaginous. Seedling with hypogeous cotyledons; first two aerial leaves opposite and simple or compound, with leaves or leaflets entire or serrate. Chromosome number  $N=16$ .

The genus *Oreomunnea* is extant in the New World with two species: *O. pterocarpa*, an endemic to Costa Rica; and *O. mexicana*, which ranges from southern Mexico to Costa Rica. This genus superficially resembles the Old World taxon *Engelhardia* and is treated by some taxonomists as *Engelhardia* Sect. *Oreomunnea* (de Candolle, 1862, 1864, 1914; Standley, 1927a; Manning, 1959; Jacobs, 1960). However, in spite of the disparity between the winged fruit in *Oreomunnea* and the nut-like fruit in *Alfaroa*, these two genera have more characters in common with each other than either one does with the southeastern Asian *Engelhardia* (Oersted, 1870; Stone, 1972).

In Costa Rica, *Oreomunnea* is a tree restricted for the most part to the rainforests of Cartago Province. *O. pterocarpa* is apparently endemic to the Río Reventazón Valley and its tributaries, although there is one unconfirmed report of *O. pterocarpa* from Laguna Hule in Alajuela Province (see Stone, 1972). *O. mexicana*, which occurs in scattered sites at higher elevations in Cartago Province, grows as far west as the Pan American Highway, extending into San José Province. Surprisingly, there are no reports of this species occurring between Jinotega, Nicaragua, and Cartago, Costa Rica, a distance of about 650 km. Fruiting material of both species is distinctive because of the 3-winged bract. Sterile trees are less easily identified, though the exfoliating platelets of bark found in *O. mexicana* are not common in tropical forests. As in *Alfaroa*, seedlings and saplings of the understory give the best clues. *O. mexicana* has pinnately compound leaves, alternate at first, later opposite, and leaflets that are coarsely serrate and vivid pink when first unfolding. Seedlings and saplings of *O. pterocarpa* are less distinctive. However, the leaves are glaucous below, often hairy on the petiole base, alternate-simple-entire in the early stages, becoming opposite-compound with entire leaflets.

5. *Oreomunnea mexicana* (Standley) Leroy, Bull. Mus. Hist. Nat. (Paris) Sér. 3. 23:127. 1951. *Engelhardtia mexicana* Standley, Trop.

Woods 12:15. 1927. *E. nicaraguensis* Molina, Fieldiana, Bot. 31:358. 1968.

*Oreomunnea mexicana* (Standley) Leroy subsp. *costaricensis* Stone, Ann. Missouri Bot. Gard. 59:320. 1972. Figure 8g-j.

Trees to 32 m. tall and 76 cm. dbh; buttresses moderately developed; bark exfoliating, reddish-brown surface, bright orange interior; buds and shoots studded with bronzy-yellow, peltate scales, without hairs. Leaves decussate, puberulent in bud, glabrous at maturity; petioles 1-3 cm.; rachises 2-12 cm.; leaflets 4-12, opposite to subopposite, mainly entire, coarse serrations on distal half of stump sprouts and some shoots on the upper branches, symmetrical to asymmetrical at base, revolute on one or both margins, but most pronounced on basiscopic side, auricles often present on one or both margins; petiolules to 3 mm. Female inflorescence terminal on new growth, one to several in a cluster, erect at anthesis, with 30 or more flowers per catkin, becoming pendent at maturity with cluster of fruits; male inflorescence forming congested terminal panicle with 1-6 pendent catkins; terminal androgynous panicles common, with central female spike flanked at base by 1-3 pairs of decussate catkins. Male flowers small; 3-lobed abaxial bract cupped; floral segments 4 (rarely 5), hooded, each segment partially enclosing 2, or rarely 3 stamens at anthesis; stamens 8(9) in one series. Pollen not examined. Female flowers sessile or nearly so, oriented at 45° to axis of catkin; floral tube short, sepal lobes and stigma not raised much beyond floral cup at anthesis; sepal lobes 4, broad, spread at maturity, extending well beyond style and exposing stigma at pollination; style short with deep cleft separating stylar arms. Fruit of medium size, 3-winged, lateral wing spread to 4.5 cm., central wing to 3.5 cm. long; adaxial bracteolar lobe covering small (to 10 mm.), globose nut; husk papery thin (.03 mm.); shell cartilaginous, thin (.11 mm.). Seedling with first two aerial leaves opposite and pinnately compound, with coarsely serrate leaflets; succeeding several leaves alternate, pinnately compound, with serrate leaflets; leaves becoming decussate in sapling stage with leaflets mostly entire in more mature trees.

This species, along with *Alfaroa costaricensis*, ranges from Mexico southward to Costa Rica. As presently defined, *Oreomunnea mexicana* subsp. *mexicana* is known from Mexico, Guatemala, and Nicaragua. *O. mexicana* subsp. *costaricensis* has been reported only from Costa Rica, although the Boquette area in Chiriquí Province, Panama, is a promising locality for future investigation. This subspecies ranges from 1100 to 1860 m. (Stone 3620) in the provinces of Cartago and San José. Trees from the virgin forests above Tapantí and El Muñeco are situated on fog-shrouded ridges. A few trees are still standing on the steep, hillside pastures above the Pan American Highway just south and west of the city of Cartago (Stone 3632). This subspecies is often sympatric with *Alfaroa williamsii* subsp. *tapantiensis* and is occasionally associated with *A. costaricensis* (Tapantí, Cartago) and *A. manningii* (Valle Escondido, Cartago). Field identification is relatively simple. Seedlings

and young saplings have odd-pinnate leaves that are at first alternate, later opposite. The new leaves are pale to vivid pink, and the narrow leaflets are numerous (18-20) and coarsely serrate. Shoots from saplings can be confused with *A. costaricensis*. However, the petiole and rachis of *O. mexicana* are puberulent, rather than pubescent, tiny auricles may be evident; and, particularly, the upper leaflet surface is light green and the lower one almost silvery, rather than dull green. Large trees show a flush of new leaves in March-June, August, and again in November. The new leaves on older trees are more of a yellowish-red than the vivid pink shoots of its saplings or trees of *Alfaroa*, but, most distinctively, large, reddish-brown platelets of bark exfoliate from the larger trunks (over 45 cm.). Smaller trees have relatively smooth bark on the lower trunk and evidence of incipient exfoliation in the vicinity of the first major branches. Flowering occurs with a flush of new growth; records are available for 29 April (Stone 2177B), 1 June (Stone 3287), and 29 August (Stone 2680). The only record of fruiting material of this species in Costa Rica was made on 1 March (Stone 3632), though young seedlings with the cotyledons still attached have been collected on 20 January (Stone 2335), 29 April (Stone 2177A), 8 June (Stone 2746), and 13 November (Stone 2718A).

The two subspecies of *Oreomunnea mexicana* that are recognized (Stone, 1972) apparently cannot be separated on the basis of vegetative characters, and even the diagnostic floral differences are subtle. The Costa Rican subspecies has female flowers that are sessile, or nearly so, and oriented away from the floral axis (45° angle), and the sepal lobes are spread at anthesis. Subspecies *mexicana* has female flowers with conspicuous pedicels to 3 mm. long, the bract-bracteolar cup is somewhat recurved so that the flower is oriented more or less parallel to the axis of the catkin, and the sepal lobes are incurved to form a chamber around the stigma at pollination. The mature fruits are also very similar: those of subsp. *costaricensis* are sessile or have pedicels reaching a maximum of 2 mm. and the sepals, enclosed by the bracteolar lobe, are spread; the pedicels of subsp. *mexicana* commonly range to 3 or 4 mm. and the sepals arch over the stigma. This species is quite different from the only other member of the genus, *O. pterocarpa*. In some respects *O. mexicana* combines certain vegetative features of *Alfaroa costaricensis* (i.e., serrate leaflets) with floral features characteristic of *Engelhardia roxburghiana* (floral morphology).

6. *Oreomunnea pterocarpa* Oersted, Vidensk. Meddel. Dansk Naturhist. Foren Kjøbenhavn 3:34. 1856. *Engelhardtia pterocarpa* (Oersted) Standley, Trop. Woods 12:15. 1927. Figure 8a-f.

Trees to 46 m. tall and 83 cm. dbh; buttresses well-developed; bark tight, surface gray or reddish-brown, interior yellow-orange; buds studded with butter-yellow peltate scales, without hairs. Leaves decussate, generally glabrous, pubescent at base of petiole and nodal area in saplings and sucker sprouts; petioles 3.5-6 cm.; rachises 7-10 cm.; leaflets (4)6-8, long petiolulate (5-15 mm.), opposite to subopposite, always entire, symmetrical to asymmetrical at base, revolute on one or both margins, but most pronounced on basiscopic side, auricles absent. Inflorescences borne laterally on old wood or at junction of old and new wood; androgynous panicles with central female catkin of 15-20 flowers, erect at anthesis, becoming pendent at maturity with cluster of fruits, flanked at base by 2-3 pairs of decussate male catkins. Male flowers with 3-lobed abaxial bract long, narrow, and flat; floral segments 5-6, flat, irregularly positioned, stamens 16-19 in two disorganized series. Pollen subtriangular in amb (polar) view, 22.0  $\mu\text{m}$  in diameter. Female flowers sessile or nearly so, oriented at 45° to axis of catkin; floral tube elongate, sepal lobes and stigma raised well above floral cup at anthesis; sepal lobes 4, narrow, spread at maturity, extending to level of stigma but not beyond; stigma exposed at pollination; style elongate, with deep cleft separating stylar arms. Fruit large, 3-winged, lateral wing spread to 13 cm., central wing to 11 cm. long; adaxial bracteolar lobe covering medium size (to 15 mm.), globose nut; husk papery thin; shell cartilaginous. Seedlings with first two aerial leaves opposite, simple and entire; succeeding several leaves alternate, simple and entire; followed by transition to compound leaves, and later abrupt shift to decussate phyllotaxy and entire leaflets.

*Gavilan blanco*, as it is known locally in the Plantillo area, is endemic to the Atlantic watershed of Costa Rica, occurring along tributaries flowing into the Río Reventazón in Cartago Province (Pittier, 1957). The tree has been reported to range from 200 to 1500 m. elevation. Herbarium vouchers, however, only verify collections between 550 and 820 m., although a cultivated tree in the Botanic Garden of the Universidad de Costa Rica in San José (1168 m.) is healthy and producing flowers, fruits, and viable seeds. This species is sympatric with *Alfaroa manningii*. Trees of the rainforest around Platanillo and Tuís commonly have plank buttresses extending to 2.5 m. in diameter at the base. The bark is tight, often gray and the leaves are dark green above. The lower leaflet surface, rachis, petiole, and stems of new growth are glaucous. Flushes of new growth are usually vivid pink. Flowering overlaps with fruit maturation. Male and/or female flowers are recorded for the months of January (*Stone 1346*), March (*Stone 1346*), April (*León 1523*), and September (*León 1819*), while mature fruits are present in January (*Stone 1016*, *Stone 1346*), March (*Stone 2222*), April (*León 1523*, *Tonduz 18000*), and July (*Lankester*, *Stevens 468a*, *Stork 2808*).

*Oreomunnea pterocarpa* is a very distinctive species and not easily confused with other members of the family. The fruits are three-winged as in its closest relative, *O. mexicana*, but the wing span is 2-3 times larger. Certain aspects of the male and female flowers are characteristic of *Alfaroa costaricensis*, in much the same way that the latter species shows certain vegetative similarities to *O. mexicana*.

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## BATACEAE (Batidaceae)

WILLIAM BURGER

Glabrous much-branched little shrubs to 1.5 m. tall with both prostrate horizontal and erect succulent stems, the plants unisexual or bisexual. Leaves opposite and decussate, simple and sessile, fleshy and entire; stipules minute and caducous, represented by gland-like bodies. Inflorescences of cone-like spikes or short-shoots, floral bracts with minute stipule-like appendages; male flowers in the axils of decussate bracts or terminal and arranged in cones, each flower with a perianth-like tube opening irregularly into 2 to 4 parts, 4 spatulate petal-like structures alternating with the stamens and often referred to as staminodes, stamens 4, filaments free, anthers dorsifixed and introrse, center of the flower raised and possibly a pistillode; female flowers sessile and axillary, solitary or grown together at the base, each flower with 1 pistil subtended by a single bract and without perianth, ovary 4-loculed with a single epitropous ovule borne from the base of each locule on enlarged placentas (perhaps parietal in origin), stigmas 2 and sessile. Fruit drupaceous or compound, seeds without endosperm, embryo straight, cotyledons large.

### BATIS Linnaeus

The family is represented by the solitary genus with two species: *Batis maritima* L. on the tropical and subtropical coasts of the Americas and *B. argillicola* van Royen on the southern coast of New Guinea. The systematic position of the genus is not clear, and a wide variety of relationships have been suggested. Modern phylogenists have considered this family related to the Chenopodiaceae (Centrospermae or Caryophyllales) but *Batis* lacks betacyanins and betaxanthins (T. J. Mabry and B. L. Turner, *Taxon* 13:197-200. 1964), which suggests that they are not related to the Centrospermae. More recently the detection of "Myrosinase" in extracts of *Batis maritima* has suggested a relationship with the Cappari- dales (Schraudolf, Schmidt, & Weberling in *Experientia* 27:1090-1091. 1971). The floral diagrams in our illustration are from Eckardt (Ber. Deut. Botan. Gesell. 72:416. 1959).



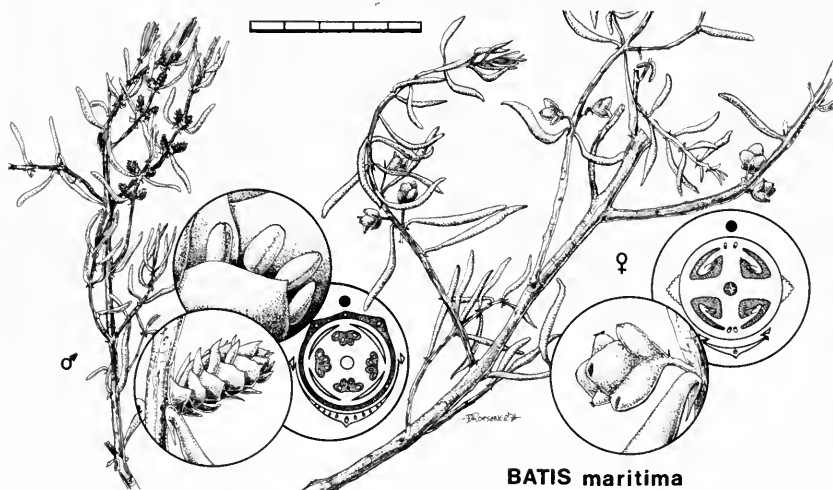


FIG 9a. Bataceae: *Batis maritima*, male parts on the left and female parts on the right.

***Batis maritima* L., Syst. edit. 10, 1289. 1759. Figure 9a.**

Unisexual little shrubs or subshrubs 0.3-1.5 m. tall, stems becoming woody, leafy internodes 1-10 (15) mm. long, 0.7-2.8 mm. thick, glabrous, succulent and drying pale green or grayish. Leaves almost terete, petioles absent, laminae 8-30 (40) mm. long, about 2 mm. thick (dry), linear or linear oblong, abruptly obtuse at the apex, slightly narrowed and prolonged basally about 1 mm. below the point of attachment to the stem, the two basal lobes becoming recurved on drying, venation not visible. Male spikes sessile or very short pedunculate, 5-10 mm. long, bracts about 2 mm. broad, tightly imbricate in 4 ranks, persistent with usually more than 12 bracts and flowers per spike, filaments about 2 mm. long, anthers about 1.2 mm. long; female spikes on short stalks, becoming 15 mm. long, bracts and flowers 4 to 12, bracts round and peltate, 2-2.5 mm. broad, separate and deciduous, pistil about 6 mm. long and 2.5 mm. thick, united below with the free apices bearing the minutely papillate-puberulent 2-lobed stigmas. Fruit fleshy and compound by the union beneath of the pistils, the compound fruit (spike) about 8 mm. long, and 6 mm. thick.

*Batis maritima* is a strand plant ranging along the ocean shores from Florida and Texas in the United States to the West Indies and southward to Brazil along the Atlantic and from California to Peru on the Pacific. While the species has not been recorded from Costa Rica or adjacent countries, it is known from both the Caribbean and Pacific coasts of Honduras. Because the species grows both on sandy shores and near mangrove formations, it very likely is to be found in Costa Rica.

## BETULACEAE

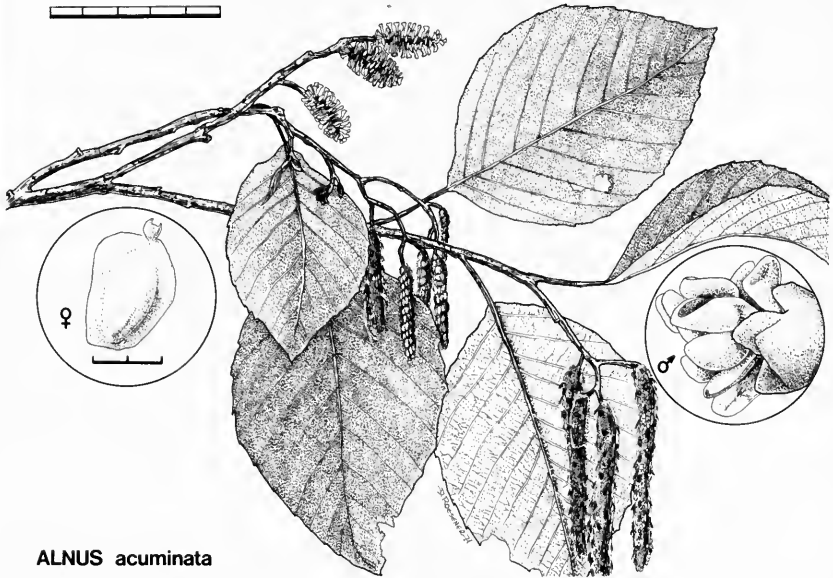
JOHN J. FURLOW

Trees and shrubs, leaves alternate and simple; stipules present, free, and deciduous. Plants unisexual, monoecious; inflorescences usually composed of reduced cymules in a spiral on an elongate axis forming aments (catkins) or in congested dichasia; staminate flowers usually in pendulous aments, the flowers subtended by large bracts with or without bracteoles, perianth of 1 whorl or absent, free or united, often of 4 separate parts, the stamens (1) 2, 4, 5, or 6 (20), borne on slender filaments or sessile, anthers 2-thealous, the thecae separate or connate; pistillate flowers usually in groups of 2 or 3 within a subtending bract with or without bracteoles, the perianth absent or adnate with the ovary, pistil with a 2- or 3-locular ovary (sometimes 1-locular above) with 2 pendulous ovules, styles and stigmas 2 (3). Fruit a nut, often winged, sometimes with the perianth persisting above or subtended by the persistent bracts, seed 1 by abortion, endosperm absent.

The Betulaceae are a family of six genera and about 100 species of the north temperate zone with a few species reaching Central and South America at higher elevations. The family is represented by a single native species in our area; two other genera, *Carpinus* and *Ostrya*, have their southern limits in El Salvador and Honduras. The family is characterized by the very reduced flowers in complex inflorescences and is adapted to wind pollination. Recent studies (Endress, 1967) show that this family is very closely related to the Hamamelidaceae.

### ALNUS Miller

Monoecious trees and shrubs, leaf buds usually stalked and with few scales, roots often with nodules of nitrogen-fixing endophytes. Leaves alternate, simple, petiolate, and pinnately-veined, usually at least somewhat pubescent and glandular below. Staminate aments in terminal clusters or solitary in the axils of leaves, produced during the previous growing season or on growth of the present season; staminate flowers usually in groups of 3 (rarely 6) on each short-stalked peltate bract, bracteoles present, the perianth of 4 (1-6) free or basally connate parts, stamens usually 4 and opposite the perianth parts, anthers with 2 partially separate thecae, dehiscing longitudinally. Pistillate inflorescences congested, ovoid to ellipsoid or cylindrical, solitary or racemose, arising from leaf axils, sometimes on special short shoots, produced during the previous or present growing season, the bracts



**ALNUS acuminata**

FIG 9b. Betulaceae: *Alnus acuminata* with enlarged view of male flower (right) and individual fruit (left).

thick, each subtending 2 flowers and 4 bracteoles, perianth absent or reduced to small adnate glands, ovary laterally compressed. Fruit a small flattened nut, usually with 2 winged margins, 1-locular by abortion; the fruiting spike cone-like, with persistent 5-lobed woody scales derived from the bracts and bracteoles.

A genus of about 20 species, mainly of the Northern Hemisphere but extending into South America along the Andes. Several species occur in northern Central America and Mexico.

*Alnus acuminata* H.B.K. Nov. Gen. Sp. 2: 20. 1817. *A. arguta* (Schlecht.) Spach, Ann. Sci. Nat. ser. 2, 15: 205. 1841. *A. jorullensis* auct., non H.B.K. Nov. Gen. Sp. 2: 20. 1817. Figure 9b.

Trees 5-20 (30) m. tall, leafy internodes 0.5-2.5 cm. long, 1-4 mm. thick, glabrous or sparsely puberulent with slender whitish to yellowish hairs 0.2-0.5 mm. long or with minute brownish peltate glands or both, becoming glabrescent in age, often dark brown and lustrous, lenticels yellowish, oval to circular, 0.5-2.0 mm. long, 0.3-1.0 mm. wide. Buds with 2 or 3 resinous-coated stipular scales, obtuse to acuminate at the apex, stalked, body 4-8 mm. long, 2.0-3.5 mm. thick, stalk 2-8 mm. long, 1-2 mm. thick. Leaves borne in a spiral, petioles 7-25 mm. long, 1-2 mm. thick, deeply grooved adaxially, glabrous or with hairs, glands, or both; laminae 5-17 cm. long, 3-9 cm. wide, broadly elliptic to oblong or somewhat ovate, obtuse or abruptly short-acuminate to acuminate at the apex, acute, abruptly obtuse, and rounded to truncate at the base, unequally doubly serrate along the margin, the teeth smaller near

the apex and base than at mid-leaf, closer near the apex and more distant near the base than at mid-leaf, larger teeth terminating the veins, margin moderately to strongly revolute, lamina drying stiffly chartaceous and usually much darker above, smooth and glabrous to very sparsely pubescent along the veins above, sparsely to moderately glandular above, sparsely to densely puberulent with slender yellowish to brownish hairs 0.2-0.6 mm. long beneath, sparsely to densely covered with whitish to yellowish-brown peltate glands below, the lower surface becoming glabrescent in age, venation often impressed above, secondary veins in 9-16 pairs, 4-9 mm. apart at mid-leaf, prominent beneath with the tertiary veins often conspicuous and sub-parallel. Staminate aments in racemose clusters of 3-6, produced the previous growing season, 4-12 cm. long, 5-9 mm. thick, borne on short glabrous peduncles 4-12 mm. long, 1-2 mm. thick, each cluster (cymule) of flowers subtended by a bract about 1.5 mm. broad, the 3 flowers congested and difficult to distinguish, perianth about 1.3 mm. long, anthers 1.0-1.5 mm. long, 0.8-1.1 mm. broad on filaments 0.4-1.0 mm. long; pistillate spikes (cones) in racemose clusters of 3-6, produced the previous season, 7-10 mm. long, 6-8 mm. thick at anthesis, on short peduncles 0.4-0.7 mm. long, bracts thick and fleshy, tightly imbricate, 3-4 mm. broad distally, pistil about 2 mm. long, styles 0.5-1.0 mm. long. Fruit a 2-winged nutlet (samara), thin and slightly obovate or orbiculate, body 2.2-3.0 mm. long, 1.0-1.5 mm. broad, each wing 0.8-2.1 mm. long, 0.5-0.7 mm. broad, the fruiting cones becoming 1.2-2.5 cm. long, 9-12 mm. thick, peduncles 1-10 mm. long, 1.2-1.5 mm. thick, scales 3.5-4.5 mm. long, 3.5-4.5 mm. broad at the widest point.

Plants of montane forest formations from 1500 to 3100 m. elevation and often occurring in almost pure stands, perhaps as secondary growth on old clearings and landslides. In Costa Rica the species has only been collected between the slopes of Volcán Barba and the Cordillera de Talamanca as far eastward as the slopes above San Isidro del General. It is found in the highlands of Western Panama and ranges northward through central Mexico and southward into South America.

Distinctive plants because of the cone-like infructescences, pendulous staminate aments, unusual glands on the lower leaf surface, and tendency to be found in stands.

The taxonomic status of this species has long been confused. Although the Costa Rican alders show considerable affinity with *Alnus acuminata* of South America, they nevertheless appear somewhat more similar to *A. arguta* of Mexico and Guatemala. Both of these species may be better considered the same species, however, which is the view taken here, in which case *A. acuminata* is the valid name. They are markedly distinct from *A. jorullensis* H.B.K. of Mexico, which name has frequently been misapplied to them. The name commonly used in Costa Rica is *Jaul*.

## FAGACEAE

WILLIAM BURGER

REFERENCE: Thomas Elias, The Genera of Fagaceae in the Southeastern United States. Journ. Arn. Arb. 52: 159-195. 1971.

Trees or shrubs, bisexual or rarely unisexual (in *Nothofagus*). Leaves simple, deciduous or evergreen, usually alternate in a spiral, entire to deeply lobed, pinnately veined; stipules present and deciduous. Flowers unisexual (rarely bisexual); male flowers with 4 to 8 perianth parts (tepals) united basally, stamens usually 6 or 12 (4 to 40), filaments slender, anthers 2-locous, dehiscing longitudinally, a pistilode usually absent; female flowers subtended by bracts forming an involucre or cupule, flowers 1 to 3 per involucre or cupule, perianth 3- to 8-lobed and adnate to the ovary, staminodes usually absent, ovary inferior with 2 or 3 (6) locules, each locule with 2 pendulous ovules, placentation axile, styles and stigmas as many as the locules. Fruit 1 to 3 and subtended by or enclosed within an involucre or cup, each fruit a single-seeded nut, endosperm absent, embryo with thick cotyledons.

A family of eight genera with around 500 species in the temperate zones of both northern and southern hemispheres and in the tropical highlands, but absent in Africa south of the Sahara. The family has had a long and independent history but appears to be related to the Betulaceae and Hamamelidaceae. The Fagaceae are represented in Central America by the genus *Quercus*. The chestnut or *castaño* (*Castanea sativa* Miller) is occasionally planted in the Valle Central; its narrowly oblong leaves with many (12-20) pairs of secondary veins and prominent serration are distinctive.

### QUERCUS Linnaeus

REFERENCES: William Trelease, The American Oaks. Mem. Nat. Acad. Sci. 20. 1924. Cornelius Muller, The Central American species of *Quercus*. U.S. Dept. Agric. Misc. Publ. no. 477. 1942.

Shrubs or trees, older bark pale in color and scaly or dark and furrowed, the wood usually hard, new growth from buds enclosed by imbricate brownish bud-scales. Leaves deciduous or persisting, arising in a spiral, petiolate or sessile, the lamina entire to deeply lobed, veins often extending beyond the margin as bristles; stipules associated with the bud-scales below the leaves, narrow, and usually deciduous. Inflorescences axillary and emerging with the new leaves, male inflorescences long-

pendulous spikes (aments) from the axils of leaves or the inner bud-scales, male flowers solitary or in clusters of 2 or 3 on the rachis, bracts present or absent, perianth of 3 to 6 tepals united below, stamens (2) 4 to 12 from a slightly raised receptacle, filaments free; female flowers solitary and pedicellate or several on erect spikes and arising from the axils of leaves of the current season, each flower enclosed by an involucre of many appressed scales, perianth difficult to distinguish, minutely 6-lobed and adnate to the ovary, pistil with usually 3 locules and styles. Fruit a nut (acorn, or *bellotá*) enclosed or subtended by the cupulate involucre and developing to maturity in 1 or 2 years, ovoid to subglobose or turbinate, flattened and with a circular scar basally, pericarp hard, glabrous or with appressed whitish hairs on the interior surface.

The oaks (*Quercus* spp.) are not represented by many species in Costa Rica, but they are often a dominant group in our highland forests, achieving both great individual size and great numbers. They form large stands in the Cordillera de Talamanca above 2500 m. elevation and occasionally at lower elevations on some of the slopes of the Pacific watershed. Only one species (*Q. oleoides*) is found below 500 m. elevation, while several occur above 3000 m. (*Q. costaricensis*, *Q. copeyensis*, and *Q. seemannii*). Our knowledge of these trees is still poor as their size makes collecting difficult and the populations are poorly sampled. The hard wood has had many uses, but it is especially prized for making charcoal in Costa Rica. The production of charcoal has caused the destruction of many oak forests containing large trees.

The genus is usually easy to recognize because of the buds, covered by bud-scales, and crowded toward the ends of the often fluted stems, the stipules associated with the buds rather than the leaves (but often caducous), the leaves in a spiral, the male flowers on slender pendant spikes (catkins), and the small often obscure female flowers in leaf-axils. The hard wood usually with distinct rings of larger pores, rough light gray to dark gray bark, and the very characteristic acorn and acorn-cup further distinguish the genus. Some species may become more than 30 m. tall, and many species regularly produce trunks more than 1 m. thick.

The North American species of the genus *Quercus* fall into two natural subgenera. Species of the subgenus *Quercus* (formerly called subgenus *Lepidobalanus*) are often referred to as white oaks because of the pale color of their bark and branchlets. Species of subgenus *Erythrobalanus* are endemic to North and Central America and are referred to as black oaks because of their dark bark and branchlets. The two full-page figures illustrate the Costa Rican species of the two subgenera. The following dichotomy outlines the major differences between the two subgenera, but the distinctions

are often difficult to see in herbarium specimens. The key to species does not use this dichotomy in its early parts.

KEY TO THE SUBGENERA (Figures 10 and 11)

- 1A. Bark of the trunk usually gray and forming flat scales, relatively soft, branchlets usually rough and grayish after the first year, wood pale yellowish; leaves entire to lobed and the lobes rounded or if serrate then with short mucronate tips; styles short and abruptly diverging; fruit produced in one year, interior surface of the pericarp glabrous . . . . . subgenus *Quercus*.
- 1B. Bark of the trunk usually very dark and furrowed longitudinally, relatively hard, branchlets usually smooth, lustrous, and dark after the first year, wood often reddish; leaves entire to lobed and the lobes acute or if serrate then usually with aristate tips; styles longer and gradually diverging; fruit produced in one or two years, interior surface of the pericarp tomentose.  
subgenus *Erythrobalanus*.

Both subgenera have closely related species that are often difficult to identify. In our white oaks (subgenus *Quercus*), *Q. insignis*, *Q. oocarpa*, and *Q. pilarius* may present problems unless properly identified herbarium material is available for comparison. Among our black oaks (subgenus *Erythrobalanus*), *Q. seemannii* and its close allies, *Q. gulielmi-treleasei* and *Q. rapurahuensis*, may be impossible to separate convincingly without mature acorns. All these species, within the same subgenus, are probably capable of hybridizing and this factor may account for the difficulty in separating them.

Dr. Cornelius Muller has recently mentioned (pers. comm.) his intention of reviewing the oaks of Costa Rica. At present, his view of the Costa Rican species differs from the one presented here in the following ways. Dr. Muller believes that *Q. gulielmi-treleasei* and *Q. rapurahuensis* are not distinguishable from *Q. seemannii*. He also believes that what are here called *Q. insignis* and *Q. pilarius* are both elements of *Q. oocarpa*. Dr. Muller interprets *Q. tonduzii* as a local population of *Q. eugeniaefolia*. He also recognizes *Q. panamandinea* and an undescribed species. Thus, Dr. Muller finds ten species of *Quercus* in Costa Rica, of which eight represent the twelve species recognized in the treatment given here. The student of Costa Rica's flora should not be disturbed by these differences in interpretation. As mentioned, the oaks are notorious for their ability to hybridize, and they produce populations of considerable variability. Also, these large trees have been poorly sampled, and mature fruit are rare in collections. These factors contribute to differing species-concepts in the work of different authors. Actually, all the species in this Flora should be viewed as scientific hypo-

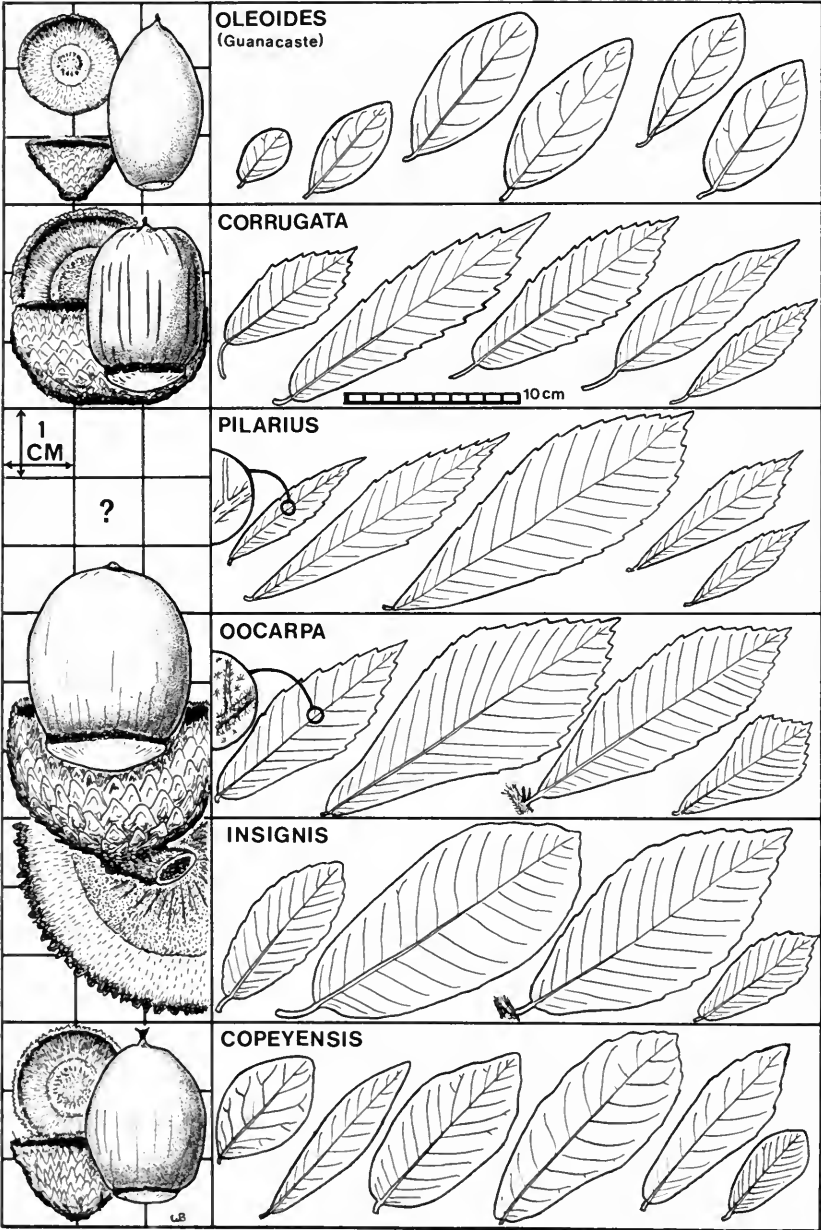


FIG 10. Fagaceae: the Costa Rican species of *Quercus*, subgenus *Quercus*, the white oaks.



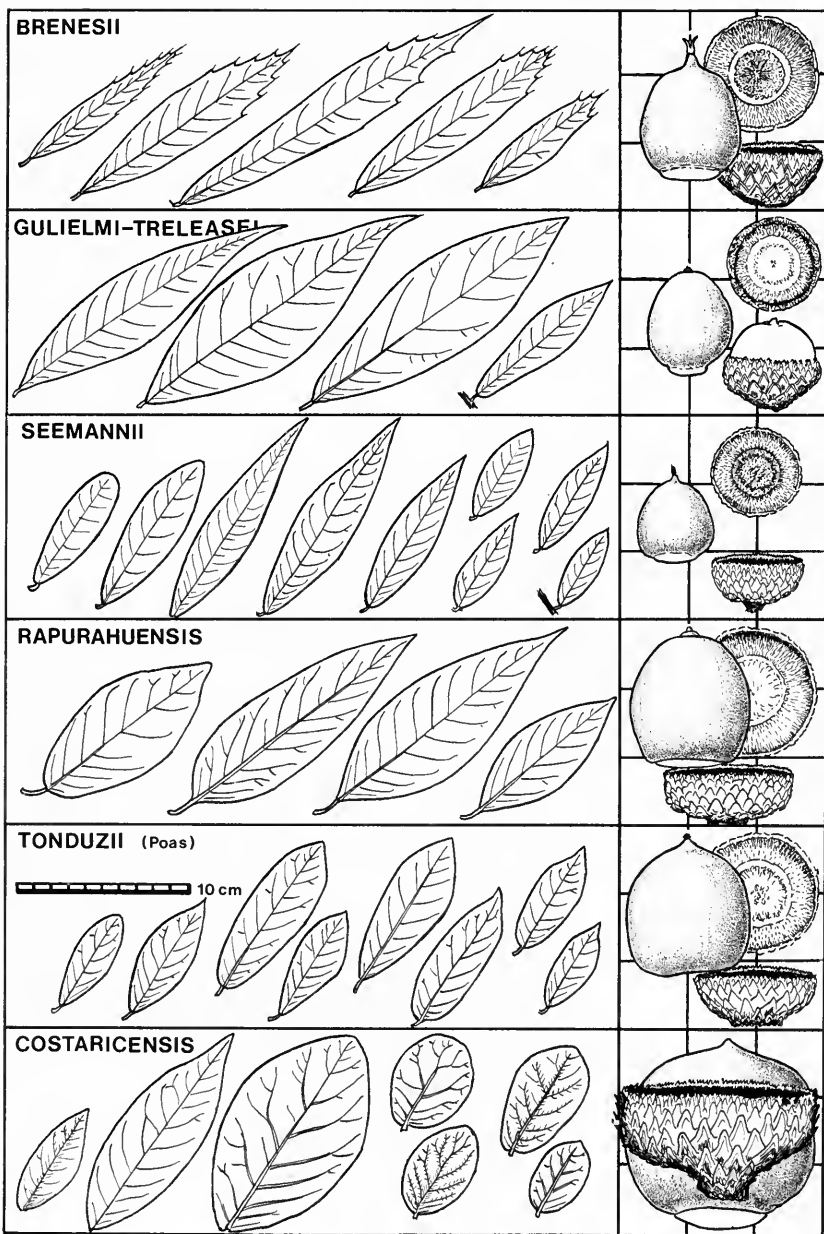


FIG. 11. Fagaceae: the Costa Rican species of *Quercus* subgenus *Erythrobalanus*, the black oaks.

theses that have to be revised as we learn more about the plants themselves and the populations of which they are a part.

## KEY TO THE SPECIES

- 1A. Trees of the lowland deciduous forest formations of Guanacaste Province between 50 and 500 m. elevation; the lower leaf-surface with minute (0.1 mm.) canescent hairs forming a dense covering between the veins . . . . . *Q. oleoides*.
- 1B. Trees of evergreen or semideciduous forest formations between 600 and 3400 m. elevation; the lower leaf-surfaces not covered by a dense tomentum of minute whitish hairs . . . . . 2A.
- 2A. Laminae narrowly elliptic to oblong with a conspicuously serrate margin of blunt or aristate teeth, becoming glabrous or very sparsely puberulent; trees not found above 2000 m. altitude . . . . . 3A.
- 2B. Laminae with entire margins or broadly elliptic to obovate when serrate; trees of 1000 to 3400 m. altitude . . . . . 5A.
- 3A. Serrations aristate with slender tips 1-5 mm. long, laminae 1-3 cm. broad, stipules caducous; year-old stems remaining dark and smooth (a black oak); acorns about 16 mm. long and 14 mm. thick; trees of the Pacific slope of west-central Costa Rica between 600 and 1500 m. elevation . . . . . *Q. brenesii*.
- 3B. Serrations blunt or with very short (1 mm.) rounded tips, laminae 2-6 cm. broad; stems becoming rough and grayish after a year (white oaks); acorns becoming more than 25 mm. thick at maturity; trees growing between 1000 and 2000 m. elevation . . . . . 4A.
- 4A. Petioles (4) 8-25 mm. long and the laminae usually drying stiffly chartaceous, stipules caducous; trees of apparently drier evergreen forest formation on the Pacific slope between 1200 and 1900 m. elevation . . . . . *Q. corrugata*.
- 4B. Petioles 1-6 (9) mm. long and the laminae often drying thin chartaceous, stipules often persisting; trees of the moister evergreen forest formations on both the Pacific and Caribbean slopes between 1000 and 1800 m. elevation . . . . . *Q. pilarius*.
- 5A. Laminae usually bluntly serrate and obovate in general form, commonly 10-25 cm. long; stipules usually persisting; acorns becoming more than 3 cm. thick at maturity; white oaks with the year-old stems usually pale gray . . . . . 6A.
- 5B. Laminae rarely serrate and not usually obovate; acorns more than 3 cm. thick only in *Q. costaricensis* with the year-old stems smooth and dark . . . . . 9A.
- 6A. Lower surface of the laminae with hairs persisting only along the midvein, petioles 1-6 (9) mm. long . . . . . 7A.
- 6B. Lower surface of the laminae with persisting stellate hairs or occasionally with the hairs persisting only in the axils of the secondary veins . . . . . 8A.
- 7A. Laminae drying stiffly chartaceous to subcoriaceous, with both stellate and simple hairs beneath or glabrous; acorns not more than 2.5 cm. thick; trees of higher montane forests (1800-3000 m.) . . . . . *Q. copeyensis*.
- 7B. Laminae often drying thin-chartaceous, with only a few simple ascending hairs persisting along the midvein beneath; acorns probably exceeding 3 cm. at maturity; trees of middle elevations (1000-1800 m.)

*Q. pilarius*.

- 8A. Petioles 1-6 (10) mm. long, and the laminae usually cuneate at the base, drying stiffly chartaceous; trees of wet forests between 1100 and 2300 m. altitude . . . . . *Q. oocarpa*.
- 8B. Petioles 5-25 mm. long and the laminae usually abruptly truncate to cordulate at the petiole, drying stiffly chartaceous to subcoriaceous; trees of wet forests between 1000 and 1800 m. elevation. . . . . *Q. insignis*.
- 9A. Stipules usually persisting, stems becoming rough and grayish after a year (a white oak); laminae variable but often cuneate at the base and bluntly acute or rounded apically, drying stiffly chartaceous to subcoriaceous; trees of high (1800-3000 m.) montane rain forests . . . . . *Q. copeyensis*.
- 9B. Stipules caducous, stems often remaining smooth and very dark in color after one year (black oaks). . . . . 10A.
- 10A. Laminae drying subcoriaceous to coriaceous and usually with the venation impressed above to give a somewhat bullate appearance, apex of the lamina blunt to rounded (rarely acute), densely puberulent to glabrous beneath, petioles 0-4 (8) mm. long; acorns becoming 20-35 mm. thick; trees of very high (2200-3300 m.) montane forest formations . . . . . *Q. costaricensis*.
- 10B. Laminae drying thin chartaceous to subcoriaceous and usually flat above, apex of the laminae acute to acuminate or rarely blunt and rounded . . . . 11A.
- 11A. Acorns becoming 14-22 mm. thick at maturity . . . . . 12A.
- 11B. Acorns becoming 10-14 mm. thick at maturity . . . . . 13A.
- 12A. Trees endemic to Volcán Poas above 2200 m. elevation; petioles 2-8 mm. long, laminae, generally 4-11 cm. long and 1.5-4 cm. broad, often drying subcoriaceous . . . . . *Q. tonduzii*.
- 12B. Uncommon trees between 1000 and 2500 m. elevation on the Pacific side of the Cordillera de Talamanca; petioles (4) 8-26 mm. long, laminae generally 9-18 cm. long and 3-7 cm. broad, usually drying stiff-chartaceous.  
*Q. rapurahuensis*.
- 13A. Laminae often drying stiff-chartaceous to subcoriaceous, gradually or abruptly narrowed to both base and apex, (2.5) 4-10 (16) cm. long and (1) 1.5-3 (4) cm. broad on petioles 1-6 (10) mm. long; trees of wet and very wet forests from 1100 to 3100 m. elevations . . . . . *Q. seemannii*.
- 13B. Laminae usually drying thin chartaceous, very gradually narrowed to both base and apex, (6) 9-18 (25) cm. long and (2) 3-6 (8) cm. broad, on petioles 0-5 mm. long; trees of very wet forests between 1500 and 2500 m. elevation.  
*Q. gulielmi-treleasei*.

**Quercus brenesii** Trel., Mem. Nat. Acad. Sci. 20:186, pl. 377. 1924. Figure 11.

Trees 8-25 m. tall, leafy internodes 1-20 (40) mm. long, (0.7) 1-3 mm. thick, glabrous or pale yellowish-brown tomentulose in early stages, twigs dark and smooth with small (0.5 mm.) but conspicuous lenticels, becoming grayish after 1 or 2 years; buds 2-5 mm. long, becoming narrowly ovoid, bud scales glabrous or puberulent and ciliolate along the edge. Leaves said to be deciduous, petioles 1-7 mm. long, 0.7-1.5 mm. thick, glabrous or puberulent, terete or slightly winged; laminae 5-17 cm. long, 1-3 cm. broad, very narrowly elliptic to lanceolate, linear-lanceolate, or occasionally

oblanceolate, tapering to the long-acuminate or acute apex, aristate at the tip, acute to attenuate at the base, margins entire along the basal half and usually with 2 to 5 diverging aristate teeth on each side distally, the aristae as much as 5 mm. long, the lamina drying stiffly chartaceous and grayish-green, smooth and slightly lustrous above and below, quickly becoming glabrous on both surfaces, the hairs on young parts yellowish-brown stellate tomentulose, about 0.1-0.2 mm. long, midvein slightly raised above with 5 to 11 pairs of major secondary veins, the secondary and tertiary veins often becoming slightly raised on drying; stipules ligulate and caducous. Male spikes to 8 cm. long, the flowers becoming 2-10 mm. distant on the glabrescent rachis, perianth densely and persistently tomentulose, filament equaling the anthers in length, anthers about 1.5 mm. long and 0.5 mm. thick, the connective produced beyond the thecae into a slender tip about 0.2 mm. long, glabrous; female flowers solitary or paired on short (3-12 mm.) thick (2 mm.) axillary peduncles, female flowers about 4 mm. long becoming thickened above the middle during development (10 mm.). Fruit produced in a year, solitary or paired on short peduncles, the cup about 10 mm. long and 16 mm. broad, saucer-shaped and abruptly narrowed to the base, puberulent within, the scales densely puberulent with minute grayish-brown hairs but with glabrescent brown margins, the nut (acorn) about 16 mm. long and 14 mm. thick, ovoid but abruptly narrowed at the base, densely puberulent with grayish-brown hairs but these rubbing off, the narrowed apex of the fruit to 4 mm. long (with the persisting styles), basal scar about 8 mm. in diameter (description of the fruit based on *Molina 22979* from Nicaragua).

This species is found in the seasonally dry evergreen (premontane and lower montane moist and wet) forest formations on the Pacific slope between 600 and 1500 m. elevation. Collections have been made from the area between Monteverde (Puntarenas) and San Ramon (Alajuela); flowering in January and fruiting in November. This species was thought to be endemic to Costa Rica but recent collections by Williams et al. (23936, 24728, & 27862) and Molina (20127 & 22979) from the Cordillera Central de Nicaragua appear to be this species.

*Quercus brenesii* is a species of the subgenus *Erythrobalanus*. The very narrow leaves with slender aristate teeth distally and the lower altitude habitat on the Pacific slope separate this oak from all the other Costa Rican species of the genus. The recent collections from Nicaragua and Costa Rica have given us a better idea of variation within the species. However, this expanded concept of *Q. brenesii* may prove to be conspecific with material from northern Central America that has been referred to *Q. anglohondurensis* Muller, *gracilior* Muller, *Q. tenuiaristata* Trel., and *Q. trichodonta* Trel. This group is in turn related to *Q. conspersa* Benth. and *Q. skinneri* Benth. with larger acorns and characteristically long petioles.

*Quercus copeyensis* C. H. Muller, U.S.D.A. Misc. Publ. 477:30, pls. 31 & 32. 1942. *Q. costaricensis* f. *kuntzei* Trel., Mem. Nat. Acad. Sci. 20:146, pl. 283 b. 1924. *Q. copeyensis* Muller emend E. L. Little, Carib. Forest. 9:348. 1948. *Q. aaata* auctores in herb. as to Costa Rica. Figure 10.

Trees 8-35 m. tall, trunk becoming more than 1 m. thick, leafy internodes 1-16 (30) mm. long, 2-4 (6) mm. thick, sparsely stellate puberulent or glabrous, pale brown becoming grayish in age; buds 3-5 mm. long, ovoid, bud-scales glabrous or puberulent distally. Leaves deciduous and often clustered at the ends of branchlets, petioles 1-6 (8) mm. long, 1-2.5 mm. thick, simple or stellate puberulent or glabrous, sulcate adaxially; laminae quite variable, 4-10 (15) cm. long, 2-5 (6.5) cm. broad, elliptic to oblong, obovate, or occasionally oblanceolate, bluntly acute to rounded at the apex, tapering to the obtuse, cuneate, or slightly rounded base, often truncate or cordulate at the petiole, margin entire or slightly undulate distally (rarely obscurely dentate), the lamina drying stiffly chartaceous to subcoriaceous, smooth and often lustrous above and becoming glabrous, persistently puberulent along the midvein beneath or occasionally glabrous, the hairs both simple and stellate, 0.2-0.8 mm. long, major veins often raised in slight depressions above, prominent beneath, the (4) 6 to 12 pairs of major secondary veins arising at angles of 35-55 degrees; stipules often persisting, 7-12 mm. long and 1-2 mm. broad, ligulate, sparsely puberulent. Male spikes (3) 4-8 (12) cm. long, flowers becoming distant on the glabrous or sparsely puberulent rachis, perianth 2-2.5 mm. long, ciliolate distally, filaments 1-2 mm. long, anthers 0.8-1.5 mm. long (dry); female spikes 2-6 cm. long and about 2 mm. thick, each spike with 4 to 10 flowers, flowers about 4-6 mm. long. Fruiting spikes 2-8 cm. long, cup about 10-16 mm. long and 20 mm. broad at the apex, tapering gradually to the base and thin at the edge, said to enclose one-third to one-half of the mature acorn, cup-scales densely puberulent on the basal umbo but glabrescent apically, nut (acorn) 22-28 mm. long and 18-22 mm. thick, ovoid, glabrous or persistently puberulent apically, basal scar about 10 mm. in diameter, area above the basal scar occasionally drying dark.

A dominant species of the wet evergreen montane (premontane and lower montane rain) forest formations between (1800) 2000 and 2800 (3000) m. altitude; flowering collections have been made between December and March, fruit have been collected in May (immature?), August, and November. The species, as here understood, ranges from Central Costa Rica to Chiriquí, Panama. In Costa Rica the species is found in the Cordillera Central from near Zarcero and Palmira (Alajuela) to Irazú and from the areas of Escazu and Tarbaca (San Jose) eastward along the central part of the Cordillera de Talamanca. The species is commonly collected along the Interamerican Highway but is not known from Sta. Maria de Dota and is apparently uncommon on Volcán Poás and Volcán Barba.

This species is recognized by its stiff, usually obovate and blunt leaves often lustrous above with few persistent hairs beneath, thick grayish twigs often retaining stipules and bud-scales, and the average-size acorns. The bark grayish and forming flat scales marks *Q. copeyensis* as a white oak (Subgenus *Quercus*) and distinguishes it from *Q. costaricensis*, a black oak with rather similar foliage. See the article concerning this species by E. L. Little in the *Caribbean Forester*, vol. 9:345-353. 1948.

As I understand it, *Q. copeyensis* is an extremely variable species often found in dominating stands. Little is known about the flowers and fruit; I have only seen three fruiting collections: *Burger & Burger 8181* (Fila Cedral, San Jose), *Little 20043* (Volcán Irazú, Cartago), and *Allen 3491* (Chiriquí, Panama). The species possesses considerable variety in leaf-form, leaf-texture, leaf-pubescence, and venation. These characters can vary on the same branch, or (more often) they may be quite uniform on an individual tree. Present collections give little evidence of correlations between these variable characters, and they are not correlated with geographic locale or habitat, except that the very small thick-leaved collections appear to come from exposed sites at high altitudes. The narrowly obovate and thinner laminae characterizing material previously referred to as *Q. aaata* Muller is, I believe, no more than an unusual form found in individual trees or groups of trees. There are all manner of intermediates between this form and the thick shorter and broader laminae with few secondary veins characteristic of other trees and groups of trees. The two forms appear to have much the same ecological range. In the absence of more fertile material, it is impossible to say whether *Q. aaata* in a restricted sense (Guatemala and Honduras) and with leaves of very thin texture is conspecific with the material placed here.

*Quercus corrugata* Hooker, *Icones Plant* 5: pl. 403-404, 1842. *Q. pilgeriana* Seemen, *Bull. Herb. Boissier*, 2 ser. 4:655. 1904. Figure 10.

Trees 6-20 m. tall, the trunk becoming 70 cm. thick with dark brown bark peeling off in large flat pieces, leafy internodes (1) 4-30 (50) mm. long, 2-5 mm. thick, glabrous or minutely stellate-tomentulose at the nodes, brown and soon becoming gray or yellowish-brown; buds 3-5 mm. long, globose to ovoid, bud-scales glabrous or minutely ciliate along the distal margin. Leaves said to be deciduous, petioles (4) 8-25 mm. long, 0.7-1.8 mm. thick, terete or slightly sulcate adaxially, glabrous or very minutely (0.2 mm.) puberulent with yellowish hairs simple or branched from the base; laminae (5) 8-18 (25) cm. long, 2-5.5 cm. broad, very narrowly obovate to

lanceolate or narrowly elliptic, usually tapering gradually to the acuminate or acute apex, abruptly obtuse or occasionally cordulate or truncate at the narrowed base, often unequal with the margins of the lamina 1-3 mm. distant on the petiole, margin entire below the basal third or fourth and with 4 to 12 blunt or serrate teeth on each side (rarely entire throughout), the lamina drying stiffly chartaceous, smooth and lustrous above, glabrous or with a few longer (0.5-1 mm.) hairs persisting basally or along the midvein, larger veins often raised within slight depressions on the upper surface, the 8 to 14 pairs of major secondary veins prominent below and arising at angles of 40-70 degrees; stipules immediately caducous. Male spikes not seen from Costa Rica, said to be 5-6 cm. long and loosely flowered with the anthers much exerted; female flowers not seen from Costa Rica, said to be solitary or paired on short (5 mm.) peduncles. Fruit produced in one year, solitary on a thick (4 mm.) peduncle 0.5-3 cm. long, cup about 15 mm. long and 3 cm. broad but said to become as much as 6 cm. broad, cup- or bowl-shaped (but not seen at maturity and completely mature fruit not seen from southern Central America), densely velutinous on the walls within, scales thickened basally and tightly appressed, densely puberulent with minutely, yellowish-white hairs, nuts (acorns) subglobose to ovoid or cylindrical, ours 2.5 cm. long and 1.5 cm. thick but said to become 3-5 cm. thick, longitudinally corrugated or smooth (dry), often puberulent distally, the basal scar (8) 12-16 mm. in diameter, area above the scar usually drying dark and contracting somewhat on drying.

Plants of evergreen montane (premontane wet) forest formations between 1200 and 1900 m. elevation and apparently confined to the somewhat drier Pacific slope in Costa Rica. Our collections range from the southern slopes of Volcán Poas (Alajuela) in the west to Boruca (Puntarenas) in the southeast, and though a number of collections have been made from the area of Santa María de Dota, none have been made from the somewhat moister areas along the Interamerican Highway on the Cerro de la Muerte. The species ranges from Chiapas, Mexico, to western Chiriquí in Panama.

The usually narrow leaves conspicuously bluntly serrate on relatively long slender petioles, generally glabrous parts, restricted habitat, and large acorns easily separate *Q. corrugata* from our other white oaks (Subgenus *Quercus*).

*Quercus costaricensis* Liebmann, Overs. Danske Vidensk. Selsk. Forhandl. 1854:184. 1854. *Q. irazuensis* Kuntze, Rev. Gen. Pl. 2:641. 1891. *Q. endresi* Trel., Mem. Nat. Acad. Sci. 20:145, pl. 280. 1924, ex char. Figure 11.

Trees 8-30 m. tall, the trunk becoming as much as 1 m. thick, the crown often dense and rounded, bark smooth, leafy internodes 1-30 mm. long, 2-8 mm. thick, very densely stellate-tomentose in early stages or glabrous, the pale brownish hairs about 0.5 mm. long and rubbing off, twigs becoming glabrescent and very dark brown changing to dark gray; buds about 6 mm. long and 4 mm. thick, ovoid, bud-scales puberulent apically. Leaves deciduous, petioles 0-4 (8) mm. long, 1-3 mm.

thick, densely puberulent to glabrous; laminae 3-10 (18) cm. long, 2-6 (9) cm. broad, broadly oblong to elliptic-oblong or obovate or rarely ovate, rounded at the apex or occasionally bluntly obtuse to acute, obtuse to rounded and cordulate at the base, the margin entire to undulate or slightly lobed distally and becoming revolute, the lamina drying coriaceous to subcoriaceous and pale grayish-green, smooth and lustrous above, glabrous or with hairs persisting along the midvein above, densely tomentulous beneath with pale brownish stellate hairs falling off in age (laminae almost completely glabrous in material formerly ascribed to *Q. irazuensis*), venation strongly impressed above with the larger veins prominent within the depressions, the 4 to 7 (8) pairs of major secondary veins often dividing distally and very prominent beneath, lower surface often becoming minutely bullate; stipules caducous. Male inflorescences becoming 4-9 cm. long, the flower crowded or 1-6 mm. distant on the densely stellate-tomentulose rachis, perianth campanulate and about 2.5 mm. long, puberulent, filaments becoming 2-3 mm. long, anthers 1.8-2.3 mm. long and 1 mm. broad, glabrous, female spike with (1) 3 to 10 flowers, to 5 cm. long, the flowers about 6 mm. long. Fruit produced in a year, solitary or paired and sessile or on a short (1-10 mm.) thick (3-4 mm.) peduncles near the apex of the stem, the shallow cup 10-15 mm. long and 15-35 mm. broad, abruptly constricted and flattened beneath, the scales sparsely puberulent and minutely ciliolate distally, usually lustrous brown and the apices becoming free, mature nut (acorn) enclosed less than one-fourth by the cup, 15-30 mm. long, 20-35 mm. thick, hemispheric to ovoid, glabrous or puberulent near the apex, pale brown, basal scar 10-15 mm. in diameter.

This species is restricted to high montane wet forest and rain forest formations between (2200) 2700 and 3300 m. elevation. Flowering collections have been made from November to August and fruit has been collected from January to June. The species is known only from a small area bounded on the west by the slopes of Volcán Irazú and extending eastward along the Cordillera de Talamanca as far as Cerro Chirripó.

*Quercus costaricensis* belongs to the subgenus *Erythrobalanus*, the red or black oaks. However, this species is most easily mistaken for a white oak, *Q. copeyensis*, among our species, and the two are often found together in high montane forests. The dark twigs and the very stiff, usually short sessile leaves rounded apically with impressed venation above and persistent tomentum beneath, that dry pale yellowish-brown or gray-green distinguish this species. Material previously placed under *Q. irazuensis* is distinguished by having glabrous leaves narrowed at both ends, but these have never been collected with flowers or fruit and represent, I believe, no more than an unusual form of this very well-defined and quite variable species.

*Quercus guglielmi-treleasei* C. H. Muller, U.S.D.A. Misc. Publ. 477:58, pl. 79, 80. 1942. Figure 11.



Trees 8-30 m. tall, trunk to over 1 m. in diameter, leafy internodes (0) 2-30 mm. long, 1.5-4 (5) mm. thick, usually only sparsely floccose in early stages and soon glabrous, very dark brown or grayish-black with conspicuous (0.5-1 mm.) lenticels; buds 3-4 mm. long, ovoid, bud-scales sparsely puberulent and slightly lustrous. Leaves probably deciduous, petioles 0-5 (12) mm. long, 1.5-3 mm. thick, densely stellate-floccose to glabrate, the winged margins prominent and flat or forming an adaxial groove, swollen at the base; laminae (6) 9-18 (25) cm. long, (2) 3-6 (8) cm. broad, narrowly elliptic-oblong to lanceolate or oblanceolate, often asymmetrical and curved to one side, tapering gradually to the long-acuminate or less often short-acuminate or acute apex, the tip only occasionally aristate, usually tapering gradually to the acute or attenuate base, the margin entire, becoming undulate and slightly revolute on drying, continuous with the wings of the petiole, the lamina drying chartaceous and usually dark gray-green or brownish above, slightly lustrous, glabrous and smooth above, glabrous beneath or persistently puberulent near the base and along the midvein, the 9 to 18 pairs of major secondary veins branching distally, impressed above but raised within the grooves, prominent beneath, the smallest reticulate veins usually raised on the upper surface (dry); the ligulate stipules early caducous. Male inflorescence and flowers unknown; female flowers unknown. Fruit probably formed in one year, solitary to several on a peduncle 1-4 cm. long and 1.5-3 mm. thick, the cups 5-10 mm. long and 13-18 mm. broad, saucer-shaped to goblet-shaped and abruptly narrowed at the base, scales sparsely puberulent and tightly appressed, umbonate at the base and often lustrous brown, nuts (acorns) 7-15 mm. long, 11-15 mm. thick, hemispheric to broadly ovoid, apex rounded or flat (? immature), minutely sericeous but becoming glabrous, enclosed one-third or less within the cup, basal scar 7-9 mm. in diameter.

Trees of wet montane (premontane and lower montane rain) forest formations between (1100) 1500 and 2600 m. altitude. The species as presently known ranges from the wet Caribbean slopes near Zarcero (Alajuela) to the Chiriquí highlands in Panama. The two fruiting collections from Chiriquí were made between April and July.

*Quercus gulielmi-treleasei* is a poorly understood species of the subgenus *Erythrobalanus* and appears to intergrade with the very closely related *Q. seemannii*. The relatively long and narrow leaves, which are tapered at both ends and often sessile, and which dry thin and dark in color, are important but very variable characteristics. This species is often very difficult to separate from *Q. seemannii* and may be no more than an ecotype form of that species commonly found in wetter montane forests. A collection by Alfonso Jimenez (1276E) from Monteverde in the Cordillera de Tilarán (Puntarenas) may be this species or an unusual juvenile form of *Q. brenesii*.

*Quercus insignis* Mart. & Gal., Bull. Acad. Brux. 10:219. 1843. *Q.*

*schippii* Standley, Carn. Inst. Wash. Publ. 461:53. 1936. *Q. seibertii* Muller, U.S.D.A. Misc. Publ. 477:19, pl. 6 & 7. 1942. Figure 10.

Trees 15-30 (40) m. tall, trunk exceeding 1 m. in diameter, bark dark brown to grayish brown and often peeling in strips to appear shaggy, leafy internodes 5-30 mm. long, 2-6 mm. thick, densely covered with yellowish or orange (fulvous to rufous) stellate hairs 0.3-0.9 mm. long, becoming glabrescent after 1 or 2 years and grayish or brown with conspicuous lenticels; buds 2-5 mm. long (expanding to 15), globose to ovoid, bud-scales distally glabrous. Leaves probably deciduous, petioles 5-25 mm. long, 1.5-3 mm. thick, densely stellate tomentose and terete; laminae 10-24 cm. long, 3.5-9 (12) cm. broad, quite variable in shape, most often oblong to obovate, tapering abruptly to the bluntly obtuse apex or occasionally acute or rounded, often gradually narrowed below the middle and then abruptly truncate or cordulate at the petiole (rarely subcordate), margins entire to undulate or bluntly short-serrate, revolute (dry) and the lamina stiffly chartaceous to subcoriaceous, smooth and lustrous above, persistently puberulent on the midvein above, densely to sparsely puberulent on all surfaces beneath, the orange or yellowish stellate hairs 0.2-0.6 mm. long, primary and secondary veins often raised within depressions on the upper surface, the 9 to 18 pairs of major secondary veins arising from the midvein at angles of 40-60 degrees, very prominent beneath, tertiary veins subparallel and occasionally impressed above; stipules often persisting, 8-12 mm. long, ligulate, densely appressed sericeous on the abaxial surface. Male inflorescences 3-8 cm. long, the flowers remaining crowded on the densely puberulent rachis, perianth about 2 mm. long, apically ciliolate, filaments very short (1 mm.), anthers 1-1.5 mm. long (based on *Shank 13954*); female spike 1-3 cm. long with 1 to 3 globose female flowers about 4 mm. long (based on *J. Leon 1165*). Fruit produced in 1 year and usually solitary, the cup becoming 2-3 cm. long and 4-8 cm. broad, broadly saucer-shaped and abruptly narrowed beneath or occasionally tapering to the base, cup-scales densely and minutely sericeous, the free apex 4-6 mm. long and about 2.5 mm. broad; nuts (acorns) said to become 3-5 cm. long and 3-7 cm. thick, ovoid to globose and flattened above, longitudinally striate, basal scar about 25 mm. in diameter, tissue above the scar-edge often contracting on drying.

This species is known only from lower montane (and premontane) wet forest formations between 1000 and 1800 m. elevation in Costa Rica; collected at Zarcero (*A. Smith 141, 177, & 2769*), Alajuela, south of Guatuso (*Lent 1165*), Cartago, Las Lajas above El General (*J. Leon 1165*), San Jose, and Agua Buena (*Shank 13954*), Puntarenas. In our area, flowering material has been collected in January and fruit in July. The species ranges from Veracruz, Mexico, to Chiriquí, Panama.

*Quercus insignis* is an unusual oak distinguished by its rather thick, persistently yellowish puberulent laminae, usually truncated at the base and borne on prominent petioles. The usual leaf-shape and very large acorns indicate that this species is very closely related to *Q. oocarpa*, and the species do not differ greatly in habitat, though they have not been collected at the same sites in Costa Rica. The type collection of *Q. seibertii* (*Seibert 225* from Chiriquí) has

unusually broad and entire leaves that are subcordate at the base. A review of our recent collections leads me to believe that this is only an unusual leaf-form and not specifically distinct. The type of *Q. davidsoniae* Standley (*Davidson 864* from Chiriquí) has characteristics of both *Q. insignis* and *Q. oocarpa*, and I believe that it is either a hybrid or a backcross between the two. Our present sampling of *Quercus* populations is so poor that we can not clearly define the parameters of these species, and assignment of unusual collections is no more than guesswork.

*Quercus oleoides* Schlecht. & Cham., *Linnaea* 5:79. 1830. *Q. retusa* Liebm., *Overs. Danske Vidensk. Selsk. Forhandl.* 1854:187. 1854. *Q. oleoides* var. *australis* Trel., *Mem. Nat. Acad. Sci.* 20:114, pl. 192 & 193. 1924. Figure 10.

Trees 5-15 m. tall, often much branched and with a dense crown, leafy internodes 2-15 (30) mm. long, 2-4.5 mm. thick, pale grayish-white with minute stellate hairs, remaining puberulent or becoming glabrous; axillary buds 2-3 mm. long, ovoid, sparsely puberulent and reddish-brown. Leaves persisting, petioles 4-8 (10) mm. long, 1-1.8 mm. thick, subterete, pale grayish with minute canescent stellate hairs; laminae 3-11 cm. long, 2-5 (6) cm. broad, oblong or elliptic to slightly obovate, obtuse to rounded and emarginate at the apex, abruptly obtuse to acute or cuneate at the base, the margin entire or rarely with a few blunt or mucronate lobes distally and becoming slightly revolute, the lamina drying stiffly chartaceous to subcoriaceous, dark green but drying pale gray-green or pale buff above and very pale gray beneath, smooth, lustrous, and becoming glabrous or remaining puberulent on the midvein above, becoming sparsely puberulent on the veins beneath but densely appressed puberulent between the veins with canescent stellate hairs about 0.1 mm. long, the 4 to 7 pairs of major secondary veins flat above, reticulum of the tertiary veins usually visible and slightly raised on the upper surface; stipules immediately caducous. Male spikes becoming 3-4 cm. long, the rachis puberulent and the flowers approximate, anthers about 1 mm. long on very short filaments, thecae with short (0.1 mm.) whitish hairs; female spikes 3-30 mm. long, with 1 to 6 (8) flowers, flower about 7 mm. long. Fruit produced in one year, solitary or several on a short (5-50 mm.) thick (1-3 mm.) peduncle, the cup 7-12 mm. long and 12-17 mm. broad, tapering gradually to the base and turbinate to hemispheric in shape, the scales relatively flat and covered with canescent hairs, the interior of the cup with similar hairs, mature nut (acorn) 15-28 mm. long and 10-14 (18) mm. thick, narrowly ovoid to ellipsoid, glabrous and drying light to dark brown, enclosed less than one-third by the cup, often elevated about 1 mm. on the base, basal scar about 5-7 mm. in diameter.

This species is restricted in Costa Rica to a small area in the northern part of Guanacaste province between 50 and 500 m. altitude in the deciduous (tropical dry and premontane moist) forest formations. Flowering material has been collected during the dry period, December to May, and mature fruit have been collected from

July to January. The species ranges northward in a series of disjunct populations to Tamaulipas, Mexico.

*Quercus oleoides* is a member of the subgenus *Quercus* and is easily separated from all our other oaks by the restricted low-altitude habitat and by the very pale-colored lower leaf-surfaces. This species is not closely related to other Central American white oaks; its relationships lie with species of the southern United States and northern Mexico. The type of *Q. retusa* Liebmann, not *Q. retusa* Rafinesque, (*Oersted* s.n. in C) has the locality as Volcán Barba 7000 ft. but I am sure that this is incorrect and the species is restricted in Costa Rica to Guanacaste. See the excellent discussion of the phytogeography of this species by J. M. Montoya Maquin in *Turrialba* 16:57-66, 1966.

*Quercus oocarpa* Liebm., Overs. Danske Vidensk. Selsk. Forhandl. 1854:184. 1854. Figure 10.

Trees 8-30 m. tall, trunks with dark brown bark coming off in strips, leafy internodes 0-2 (4) cm. long, 3-5 mm. thick, densely and usually persistently tomentulose for the year with yellowish or yellowish-brown hairs 0.5-1.5 mm. long, becoming pale gray or whitish gray after a year or two, the hairs stellate (often difficult to see); buds globose to ellipsoid, 4-8 mm. long and obscured by the stipules. Leaves deciduous, petioles 1-6 (10) mm. long, 2-3 mm. thick, densely yellowish tomentulose, apparently terete; laminae (8) 12-25 (30) cm. long, 4-9 (11) cm. broad, usually obovate but occasionally elliptic to oblong, tapering abruptly to the acute or short acuminate apex, tapering gradually below the middle to the cuneate base, occasionally acute or slightly rounded at the petiole, margin serrate above the basal half or third (rarely subentire or undulate), the 5 to 15 (18) teeth on each side quite variable from blunt to curved or with a tip 0.5 mm. long, the lamina drying stiffly chartaceous and the edge slightly revolute, smooth and often slightly lustrous above, usually densely and persistently stellate-puberulent on the major veins above and sparsely puberulent to glabrous between the veins, persistently puberulent beneath especially on the veins, major veins prominent above in slight depressions, the 12 to 18 pairs of major secondary veins arising from the midvein at angles of 40-70 degrees, secondary and tertiary veins prominent beneath; stipules usually persisting, 8-4 mm. long and ligulate, sericeous on the abaxial surface. Male spikes 3-7 cm. long, flowers remaining crowded distally on the densely tomentulose rachis, perianth about 2 mm. long with conspicuous pale yellowish hairs about 0.5 mm. long on the edge, anthers barely exerted on filaments less than 1 mm. long, thecae 1-1.5 mm. long, glabrous, the connective not usually prolonged; female flowers on a short (5-30 mm.) spike, about 5 mm. long. Fruit usually solitary, cup 2-3 cm. long and 3-4 cm. broad but probably becoming larger, gradually tapering and bowl-shaped but probably becoming saucer-shaped at full maturity, sericeous on the walls within, apices of the cup-scales about 4 mm. long and loosely appressed, persistently puberulent, nut (acorn) 3-4 cm. long and 2-3 cm. thick but said to become 5 cm. thick and 4-5 cm. long at full maturity, cylindrical to globose and depressed above (not fully mature?), remaining minutely puberulent at the apex, one-half to one-fourth

enclosed by the cup, basal scar 12-18 mm. in diameter, with a darkened and contracted ring just above the scar on drying.

Trees of wet evergreen montane (lower montane wet, lower montane rain, and premontane rain) forest formations between (700) 1100 and 2300 m. elevation in Costa Rica. Flowering material has been collected in January and March and fruiting material (immature ?) in July in our area. The species, as here understood, ranges from Vera Cruz, Mexico, to Chiriquí, Panama. It has been collected in Costa Rica from Monteverde (Puntarenas) in the Cordillera de Tilarán, along the Cordillera Central, near Escazú (San José), Muñeco (Cartago), and along the Cordillera de Talamanca. This species has not been collected along the Interamerican highway, though the highway crosses the Cordillera de Talamanca not far from some areas where the trees are common.

*Quercus oocarpa* is recognized by the yellowish or orange-brown pubescence on younger parts, very short petioles, larger obovate laminae usually cuneate at the base with distinct low serrations distally, numerous secondary veins, and the leaves usually clustered at the ends of branchlets. The male flowers are distinctive; the fruit are poorly known but apparently become very large. This species is part of a difficult complex of Central American white oaks (subgenus *Quercus*). *Quercus oocarpa* is very closely related to *Q. insignis* and the fact that they share much the same habitat in Costa Rica and much the same range may indicate that the two are not really different species; see the discussion under *Q. insignis*. *Quercus tomentocaulis* Muller from Honduras is probably synonymous with the concept of *Q. oocarpa* described here.

***Quercus pilarius*** Trel., Mem. Nat. Acad. Sci. 20:44, pl. 19. 1924. Figure 10.

Trees 8-25 m. tall, trunk becoming more than 1 m. thick, leafy internodes 2-20 mm. long, 1.2-3 (4) mm. thick, sparsely to densely puberulent but soon becoming glabrescent and grayish, the hairs simple or stellate, 0.5-1 mm. long; buds 2-4 mm. long, globose to ovoid and usually obscured by the stipules, glabrous abaxially and minutely ciliolate. Leaves deciduous or persisting during the new growth, petioles 1-6 (9) mm. long, 0.6-2 mm. thick, sparsely puberulent or glabrous, slightly winged at the lamina and terete basally; laminae (6) 10-26 cm. long, 2-6 (9) cm. broad, oblanceolate to very narrowly obovate or elliptic, gradually tapering to the acuminate or acute apex, very gradually narrowed below the middle to the cuneate or subcuneate base and acute or slightly rounded at the petiole, conspicuously serrate along the distal margins, the slightly mucronate serrations 4 to 11 on each side and curved forward, the lamina drying chartaceous or stiffly chartaceous with the edge slightly revolute, usually smooth and slightly lustrous on both surfaces, soon be-

coming glabrous or with a few persisting hairs on the midvein beneath, these hairs usually simple, straight, and ascending, 0.5-1 mm. long and whitish, secondary veins slightly raised above and prominent beneath, the 10 to 16 pairs of major secondaries arising at angles of 40-60 degrees; stipule 4-10 mm. long and often persisting, ligulate, short strigose on the abaxial surface; flowering material not seen. Fruit said to become about 5 cm. thick and 4 cm. long, subglobose, the cups unknown, nuts (acorns) and cups probably very similar to those of *Q. oocarpa*.

Plants of wet evergreen montane (premontane wet, premontane rain, and montane rain) forest formations between 1000 and 1800 m. elevation in Costa Rica and known from the following areas: near Monteverde (*Burger and Gentry 8585*), Cataratas de San Ramon (*Brenes 13437*) and near La Laguna (*Molina et al. 17528*) in Alajuela, east of Turrialba (*Barbour 1013*) and near Moravia (*Williams 16197*) in Cartago, and around Sta. Maria de Dota (*Standley 42425 & 42842*) in San José. The species ranges from Chiapas, Mexico, to Chiriquí, Panama.

*Quercus pilarius*, a member of subgenus *Quercus*, is closely related to *Q. oocarpa*, but the former is easily distinguished by the glabrescent parts and the thinner leaves that are much narrower with the midvein beneath retaining only a few simple ascending whitish hairs. The wood is said to be extremely hard and durable, and good for heavy construction. A collection from Boquete, Chiriquí (*Davidson 497*), appears to be a collection of *Q. oocarpa* with some of the characteristics of *Q. pilarius* and may indicate that these species hybridize.

***Quercus rapurahuensis* Pittier ex Trelease, Mem. Nat. Acad. Sci. 20:143, pl. 275. 1924. *Q. baruensis* Muller, Trop. Woods 108:75. 1958. Figure 11.**

Trees 10-30 m. tall, trunk becoming more than 1 m. thick, leafy internodes 2-20 (30) mm. long, 1.2-5 mm. thick, stellate tomentulose but quickly becoming glabrous, dark brown or reddish-brown with small (0.5 mm.) but conspicuous lenticels; buds 3-4 mm. long, ovoid, bud-scales glabrescent abaxially and ciliate. Leaves said to be deciduous, petioles (4) 8-26 mm. long, 0.8-1.8 mm. thick, terete or flattened and slightly winged adaxially, glabrescent or becoming so; laminae (6) 9-18 cm. long, 3-7 cm. broad, narrowly ovate or lanceolate to elliptic or oblong (rarely obovate), acute to short-acuminate at the apex, acute to abruptly obtuse and occasionally unequal at the base, margin entire or undulate and slightly revolute on drying, lamina drying stiffly chartaceous and often pale grayish above and yellowish-brown beneath, often slightly lustrous on both surfaces, becoming glabrous above, persistently tomentulose in the axils of the veins beneath, the stellate hairs pale or yellowish-brown and 0.2-0.4 mm. long, midvein prominent above, the (7) 9 to 12 pairs of major secondary veins prominent beneath and often forking distally, tertiary veins becoming slightly raised on the upper surface (dry) and the smallest veins usually

easily seen above ( $\times 10$ ); stipules immediately caducous. Male spikes probably becoming 4-5 cm. long with the flowers distant on the sparsely puberulent rachis, perianth 1-1.5 mm. long, free to near the base, minutely ciliolate, anthers on very short filaments and about 1.2 mm. long (before anthesis), glabrous; female spikes with 1 to 4 flowers on short (3-16 mm.) thick (1-2 mm.) peduncles, flowers about 4-6 mm. long, style-branches 2 mm. long and recurved. Fruit usually 2 or 3 on short (1-2 cm.) thick peduncles, the cup 8-13 mm. long, 16-20 mm. broad and abruptly narrowed beneath and saucer-shaped, bud-scales tightly appressed and often thickened basally, pale brown with minute appressed buff colored hairs, the nut (acorn) 15-20 mm. long and 14-20 mm. thick, ovoid to ellipsoid, densely pale brownish sericeous but becoming glabrous in age, the mature nut enclosed less than one-third by the cup, basal scar 10-14 mm. in diameter.

Trees of the wet evergreen montane (lower and premontane wet and lower and premontane rain) forest formations between 1000 and 2500 m. elevation. The species is known in Costa Rica from the areas of Sta. Maria de Dota, Copey, and in the Cordillera de Talamanca on the northern slopes of the General Valley; collected in flower from December to April and with fruit from May to July. The species ranges from Central Costa Rica to Chiriquí, Panama.

*Quercus rapurahuensis* is a black oak (subgenus *Erythrobalanus*) whose leaves usually dry pale-colored, are often long-petiolate, and with only 2 or 3 fruits on short thick peduncles. The acorns are considerably larger than those of the closely related *Q. seemannii* (see discussion under that species). There are two type sheets of *Tonduz 11795* at the U.S. National Herbarium, and I suspect that they represent a mixed collection. I take sheet 930372 to be the type, as illustrated by Trelease, and sheet 93067 to be a specimen of *Q. seemannii*. Outside of our flora, *Q. rapurahuensis* is most closely related to *Q. benthamii* A.DC. of Guatemala, which differs in the longer and narrower buds and the secondary veins arising more acutely from the midvein. The wood is said to be good for firewood but not for lumber.

*Quercus seemannii* Liebmann, Overs. Danske Vidensk. Selsk. Forhandl. 1854:188. 1854. *Q. eugeniaefolia* Liebm., l.c. 185. *Q. granulata* Liebm., l.c. 186, not *Q. granulata* Raf. *Q. citrifolia* Liebm., l.c. 187. *Q. bumelioides* Liebm., l.c. 188, fide Trelease. *Q. borucasana* Trel., Mem. Nat. Acad. Sci. 20:161, pl. 315. 1924. *Q. eugeniaefolia* f. *petiolata* Trel., l.c. 161, pl. 316b. *Q. boquetensis* Standl., Field Mus. Bot. 22:13. 1940. *Q. panamandinaea* Muller, U.S.D.A. Misc. Publ. 477:29, pls. 21 & 22. 1942, pro parte: as to stems and leaves only. *Q. sapotaefolia* auctores as to Costa Rica. Figure 11.

Trees 6-15 (25) m. tall, the trunk becoming over 1 m. thick with relatively smooth gray or brownish bark; leafy internodes 1-30 mm. long, 1.2-6 mm. thick, sparsely puberulent with yellowish stellate hairs about 0.3 mm. long but soon becoming glabrescent, often dark reddish brown and lustrous in the first year; buds narrowly ovoid 4-7 mm. long, bud-scales puberulent only on the edges. Leaves deciduous or persisting (for a short period?) after the new flush of growth, petioles 1-6 (10) mm. long, 0.8-2 mm. thick, sulcate above with adaxial ridges or wings continuous with the margins of the lamina, soon glabrescent; laminae (2.5) 4-10 (16) cm. long, (1) 1.5-3 (4) cm. broad, narrowly oblong to elliptic, lanceolate, or narrowly obovate, usually tapering gradually to the acute and aristate apex or occasionally blunt and rounded (on the same stem or on different trees), tapering to the acute base or rarely obtuse and contracted abruptly at the petiole, margin entire and usually becoming revolute, the lamina drying thick chartaceous to subcoriaceous, usually becoming glabrous and lustrous above, becoming glabrous beneath or with a few brownish stellate hairs persisting along the midvein, midvein prominent above with the secondaries flat or slightly impressed, the 5 to 13 pairs of major secondary veins arising from the midvein at angles of 45-80 degrees; stipules 6-12 mm. long, 0.5-1.5 mm. broad, translucent brown, caducous. Male inflorescences 3-10 cm. long, flowers usually separate on the minutely and sparsely puberulent rachis, male flowers sessile or very short (0.5 mm.) pedicellate, perianth parts 1-1.5 mm. long, filaments 1.5-2 mm. long, anthers 0.8-1.4 mm. long (dry); female flowers solitary or 2 to 4 on peduncles 1-5 mm. long, flowers narrowed at the base, 5-7 mm. long, bracts (scales) minutely brownish puberulent. Fruit maturing within a year, subsessile on very short (0-2 cm.) peduncles, solitary or 2 to 4, the cup 8-12 mm. broad and 6-8 mm. long, deeply cup- or goblet-shaped, larger cup-scales about 2 mm. broad at the base, narrowed to a rounded apex, becoming glabrescent on the upper abaxial surface, nut (acorn) 10-18 mm. long, (8) 10-12 (14) mm. thick, usually with an abruptly narrowed tip 1-2 mm. long and the persisting style-base 1-2 mm. long, broadly ovoid to hemispheric but often very narrowly ellipsoid in early stages, persistently minutely sericeous, the basal scar 6-8 mm. broad.

This species is commonly found in both premontane and montane wet forest and rain forest formations between 1400 and 2400 m. elevations, but occasional collections have been made as low as 1100 m. and as high as 3100 m. (on Cerro Chirripó). Male flowers have been collected in November and December with a single collection in April, while mature acorns have been collected between April and August. The species ranges in our area from San Ramon and Zarcero, Alajuela, in the west through the Central Highlands and along the Cordillera de Talamanca to the Chiriquí highlands in Panama.

*Quercus seemannii* is a species of considerable but not unusual variability. It is characterized by its small acorns, generally small lustrous leaves often acute at both apex and base, and its glabrescent parts. This species probably intergrades with *Q. guilmi-treleasei*, and it may hybridize with *Q. rapurahuensis* and *Q. tonduzii*. These species may be difficult to separate in the absence of



acorns and comparative material. *Quercus seemannii* and its close relatives in Costa Rica are, in turn, related to the entire-leaved black oaks (subgenus *Erythrobalanus*) of middle and northern Central America. These species together make up the most difficult complex in Central America's oaks. Though many names and distinctions have been proposed to separate them, I believe that no adequate treatment of these plants is presently available and that they are in need of careful study in the field. The following comments deal with a few names applicable to this group that have been in use in Costa Rica and Panama.

The name *Q. sapotaefolia* has been used for oaks of this species with small oblong leaves blunt at the apex. This type of leaf-form is very rare in Costa Rica (*Lems 630714, Opler 147, Pittier 2036*), and it can occasionally be found together with aristate leaf-tips on the same branchlet (*A. Jimenez 2782, Lent 774, Williams & Molina 13851*). These are merely variants in *Q. seemannii* of Costa Rica and I am sure that the name *sapotaefolia* does not apply. Liebmann describes the type (*Skinner* in herb. Hooker) as being from Guatemala, not Costa Rica (*Trelease 1924, Muller 1941*), and I am sure that he is correct. The holotype sheet of *Q. panamandinaea* (*Woodson & Schery 360* in MO) possesses foliated stems that match perfectly with some material that I have included under *Q. seemannii*. The acorns associated with the specimen, but detached, appear to be those of *Q. corrugata* though not quite mature. I believe this name is based on a mixed collection. Type material of *Q. citrifolia* (*Oersted 3461, 3 sheets* in C) has distinctly petiolate laminae abruptly narrowed at the base. I had at first thought that this was the same as *Q. rapurahuensis* but examination of the type material leads me to believe that it represents only an unusual form of *Q. seemannii*.

I prefer to use the name *Q. seemannii* because of the excellent illustration presented by Liebmann and Oersted in *Chenes de l'Amerique Tropicale* (plate 20) and presence of type material in the Hookerian herbarium at Kew (fide *Trelease 1924*). Type material of *Q. eugeniaefolia*, said to have been at Berlin, is probably destroyed.

*Quercus tonduzii* Seemen, Bull. Herb. Boissier, ser. 2, 4:656. 1904. *Q. wesmaeli* Trel., Mem. Nat. Acad. Sci. 20:172, fig. 344a. 1924, as to type only. Figure 11.

Trees (6) 10-30 m. tall, leafy internodes (0) 1-15 (25) mm. long, 1.5-4 mm. thick, densely stellate-floccose, the hairs 0.4-1 mm. long and rubbing off quickly, the older

twigs retaining only a few scattered yellowish hairs; buds narrowly ovoid, 3-8 mm. long, bud scales puberulent on the edges and apex but glabrous on the abaxial surface. Leaves usually deciduous before the new flush of growth, petioles 2-8 mm. long, 1-2 mm. thick, slightly sulcate above with narrow adaxial ridges (wings) continuous with the margins of the lamina, floccose at first but soon glabrescent; laminae (3) 4-10 (11) cm. long, 1.5-3.5 (4) cm. broad, elliptic to oblong or slightly obovate, acute and aristate to rounded and blunt at the apex (on different plants or on the same branch), tapering gradually or abruptly to the acute or obtuse base, often slightly rounded at the petiole, margin entire and drying revolute, the lamina drying stiffly chartaceous to subcoriaceous, upper surface becoming glabrous and lustrous in age, lower surface with a mat of soft stellate hairs sloughing off and persisting only along the midvein, secondary veins becoming slightly impressed in age and the midvein prominent above, the 4 to 8 pairs of major secondary veins arising at angles of 45-70 degrees; stipules 5-10 mm. long, 0.3-1 mm. broad, immediately caducous. Male inflorescences 3-7 cm. long, the flowers usually separate on the persistently puberulent rachis, male flowers sessile or short (1 mm.) pedicellate, perianth parts about 2 mm. long and 1 mm. broad, filaments 1.5-2.5 mm. long, anthers 1.3-2 mm. long; female inflorescences 0.5-2 cm. long with 2 to 5 flowers, the female flower about 4 mm. long and subtended by thin puberulent bracts. Fruit on very short (0-2 cm.) peduncles, solitary or 1 to 4, the cup becoming about 20 mm. broad and 10 mm. long, deeply saucer-shaped, bud-scales about 3 mm. broad at the base and with a long (2-3 mm.) narrow apex, persistently puberulent, nut (acorn) becoming about 20 mm. long and 20 mm. thick, broadly ovoid to subglobose, basal scar about 8 mm. broad.

*Quercus tonduzii* is endemic to the summit of Volcán Poas, Alajuela, above 2100 m. altitude in montane rain forest and associated vegetation; flowers have been collected in March and fruit in November.

This species is closely related to *Q. seemannii* sensu lato and differs in the relatively broader leaves more abruptly tapered at the apex and in the larger fruit and anthers. Only one collection of mature fruit is known (*Tonduz 10788*, the type), but other collections with immature acorn-cups have the same large cup-scales as the type and together differ in this regard from *Q. seemannii*. The leaves of this species are quite variable with those of the type resembling material of *Q. seemannii*. Collections with mature acorns are rare in this and the related species; because of this, the species concepts themselves are quite hypothetical.

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*QUERCUS* OF COSTA RICA AND PANAMA  
 Acronyms refer to species

Allen, P. H. 302 GUL; 303 OOC; 672 COS; 1595 RAP?; 1596 OOC; 3464 RAP;

3465 SEE; 3467 RAP; 3491 COP; 3496, 3523 RAP; 4683 OOC; 4722, 4731 SEE;  
16480 GUL.

Barbour, W. R. 1013 PIL.

Brenes, A. M. 5178 BRE; 5194 BRE?; 5566, 6010, 6224 BRE; 6704 SEE; 11602  
BRE; 13437 PIL; 14520 TYPE BRE; 15590 OLE; 16966 BRE.

Burger, W. C. et al. 5940 COP; 6001, 7385 COS; 7386 SEE; 7387, 7486 COS; 7911 A,  
B, C, D, E, F, 7967 COP; 8169 SEE; 8172, 8181 COP; 8236 A, B COS; 8380 A,  
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Cohn, G. G. 44 RAP?

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Davidson, M. E. 133 COP; 437 SEE; 497 OOC; 677, 721, 780 SEE; 864 TYPE *Q.*  
 *davidsoniae*, INS x OOC?; 909, s.n. SEE.

Dayton, W. A. 3084 COS.

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Ebinger, J. E. 814 COR.

Frostal 41 COR.

Gonzalez M., R. RGM-3 COS; RGM-18-X-3 SEE; RGM-19-X-4 COP; RGM-20-X-6  
COS; RGM-25-X-12, RGM-40-X-40 COP.

Hatheway, W. H. 1276 SEE; 1308 COS.

Hunter, J. R. 8 OLE.

Jiménez M., A. 194 TON; 292, 293 SEE; 296 COR; 462 TON; 478 OOC; 550, 585  
OLE; 602 SEE; 1276 A, B BRE; 1276 C OOC; 1276 D BRE; 1276 E GUL?;  
1276 G BRE; 1419 COP; 1430, 1488, 2610, 2782 SEE; 3359 OLE; 3986 COS;  
s.n. BRE.

Jiménez, O. 20 COS; 21 COP; s.n. OLE; s.n. RAP.

Kukachka, B. F. s.n. BRE.

Kuntze, O. 22826 TYPE COP in part, COS in part.

Lankester, C. H. 214 COR.

Lems, K. 63071302 COS; 630714, 63071401 SEE; 63071402 COR; 630726 TON?;  
64090604 GUL?; 640909 COP; s.n. SEE.

Lent, R. W. 390 COS; 774 TON; 1116 INS; 1756 BRE.

León, J. 847 COR; 1099, 1105, COP; 1165 INS?; 1178 SEE; 1271, 1294 COP.

Little, E. L., Jr. 6001, 6002, 6003, 6004, 6005, 6008 COP; 6009 SEE; 6010 COP; 6011  
SEE; 6035 COP; 6036 OOC; 6038, 6039 COP; 6045 SEE; 6054 RAP; 6055 PIL;  
20043 COP.

Madriz V., A. AMV-1 COS; AMV-15 COP; AMV-16, AMV-17 SEE; AMV-18 COP;  
AMV-21-X-2 COS; AMV-24 SEE.

Merker, C. A., Scholten, J. A., & Dayton, W. A. 3153 COP; 3154 COS.

Molina R., A. 15029 OLE; 17045, 17105 COP; 17113 OOC; 17528 PIL; 17809 GUL?;  
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- Opler, P. A. 120, 121 TON; 122 GUL; 126 TON; 127 COS; 128, 130 COP; 147, 148 SEE; 149 COP; 150 GUL.
- Pittier, H. 871 COS; 2036 TON; 2197 COR; 2262, 5305, 10553 SEE; 14120 COS; s.n. COR.
- Quinós, M. 187 BRE.
- Raven, P. H. 20952 COP; 20971 COS; 20976 COP.
- Rodriguez, R. L. 549 OOC.
- Rowlee, W. W., & Stork, H. E. 940 COS.
- Seibert, R. J. 225 INS?; 226 GUL; 317 OOC.
- Shank, P. 13954 INS; 13963 GUL?.
- Skutch, A. F. 3584 COP.
- Smith, A. A141 INS; A464, H370, P.C.198 SEE; 177 INS; 2742 COR; 2756 COP; 2769 INS; 2828, 2877 SEE; 2878 OOC; 2879 COP; 10082 SEE.
- Soels, K. KSW-1, KSW-2 COP.
- Solane J., I. ISJ 6 23 SEE.
- Standley, P. C. et al. 9550, 9584 SEE?; 9993 BRE; 10335, 10375, 10385 SEE?; 32619, 33869 OOC; 33875 GUL; 34181 SEE; 34186 OOC?; 34395 COP; 34561 COR; 35958, 39798, 41459 OOC; 41611 SEE; 41707 COR; 42220 SEE; 42425 PIL; 42558 SEE?; 42573, 42583, 42629 COP; 42834 COR; 42842 PIL; 42876, 42985, 42988, 43046 SEE; 43403 COR; 43564, 43671, 43752, 43789, 43972 COS; 43982, 50546 COP; 50588 SEE; 50651 COP; 50707 SEE; 50921 GUL; 51147 OOC; 51223 GUL; 51270 OOC; 51382 GUL; 52178, 52194 COP.
- Stern, W. L., & Chambers, K. L. 52 GUL; 76 RAP.
- Stern, W. L. et al. 1124 INS; 1998 SEE.
- Stork, H. E. 347 COS; 1042 GUL; 1129 OOC; 1130 SEE; 1365 COP; 1500 SEE; 1745 RAP; 2089 COS; 2420 RAP; 2591 BRE x SEE?; 3052 COS?; 3131 RAP.
- Taylor, B. W. 4533 OLE.
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- Tessene, M. F. 1568 TON.
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- Wilbur, R. L., & Stone, D. E. 8743 COS.
- Williams, L. O. et al. 13803 OOC; 13819 COS; 13845 COP; 13851 SEE; 13854, 13886 COP; 16008 COS; 16197 PIL?; 16268 COP; 16271 COS; 16308 OOC; 16623 COP; 16664 SEE; 20114 OOC; 23909 SEE?; 23936 BRE; 24455 COS; 24657 OOC; 24728, 24850 BRE; 26373 OLE; 27862 BRE; 28122, 28209, 28515 COP; 28637 GUL; 28848 COS; 28898 OOC.
- Woodson, R. E., Jr., & Schery, R. W. 206 OOC; 318 SEE; 360 SEE in part; 868 SEE.

## ULMACEAE

WILLIAM BURGER

REFERENCE: T. Elias, The genera of the Ulmaceae in the South-eastern United States. Journ. Arn. Arb. 51: 18-40. 1970.

Trees or shrubs (rarely climbers in *Celtis*), bisexual or unisexual, the wood usually hard, the sap transparent; stipules usually present. Leaves simple and alternate or rarely opposite (in *Lozanella*), usually distichous, laminae often inequilateral. Inflorescences basically cymose and often fasciculate or the female flowers solitary, axillary on growth of the same or previous year; flowers small and bisexual or unisexual, radially symmetrical or slightly bilaterally symmetrical, perianth of a single whorl with 4 to 6 (rarely 2 to 9) sepals (tepals) free or united below, stamens the same number as the sepals and opposite them or rarely twice as many (in *Ampelocera*), erect in bud, anthers 2-locous and dehiscent longitudinally, dorsifixed and often somewhat versatile, a pistillode usually present in male flowers; staminodes present or absent in female flowers, pistil solitary, ovary superior and sessile or stipitate, 1-locular or rarely 2-locular (in *Ulmus* spp.), ovule 1 and pendulous from near the apex of the locule, styles (style-branches) 2 and simple or bifurcate. Fruit drupaceous or dry and flattened, often winged when dry, seed usually lacking endosperm.

A family of about 15 genera and 150-200 species best represented in the north temperate zone. The Ulmaceae are very closely related to the Moraceae and Urticaceae, forming the natural order Urticales.

### KEY TO THE GENERA OF ULMACEAE

- 1a. Leaves opposite, stipules united and ligulate, leaving an interpetiolar line across the stem; fruit drupaceous, slightly flattened and ribbed along the edge, 2-3 mm. long (in ours); very wet montane forests between 1400 and 2300 m.  
*Lozanella*.
- 1b. Leaves alternate, stipules free, paired and lateral, not leaving an interpetiolar scar. . . . . 2a.
- 2a. Fruit very flat, ciliate edged and samara-like; laminae with 8 to 16 pairs of secondary veins; becoming very tall trees, between 1000 and 2000 m. . . *Ulmus*.
- 2b. Fruit drupaceous and fleshy, seed rounded; laminae with fewer than 7 pairs of major secondary veins . . . . . 3a.

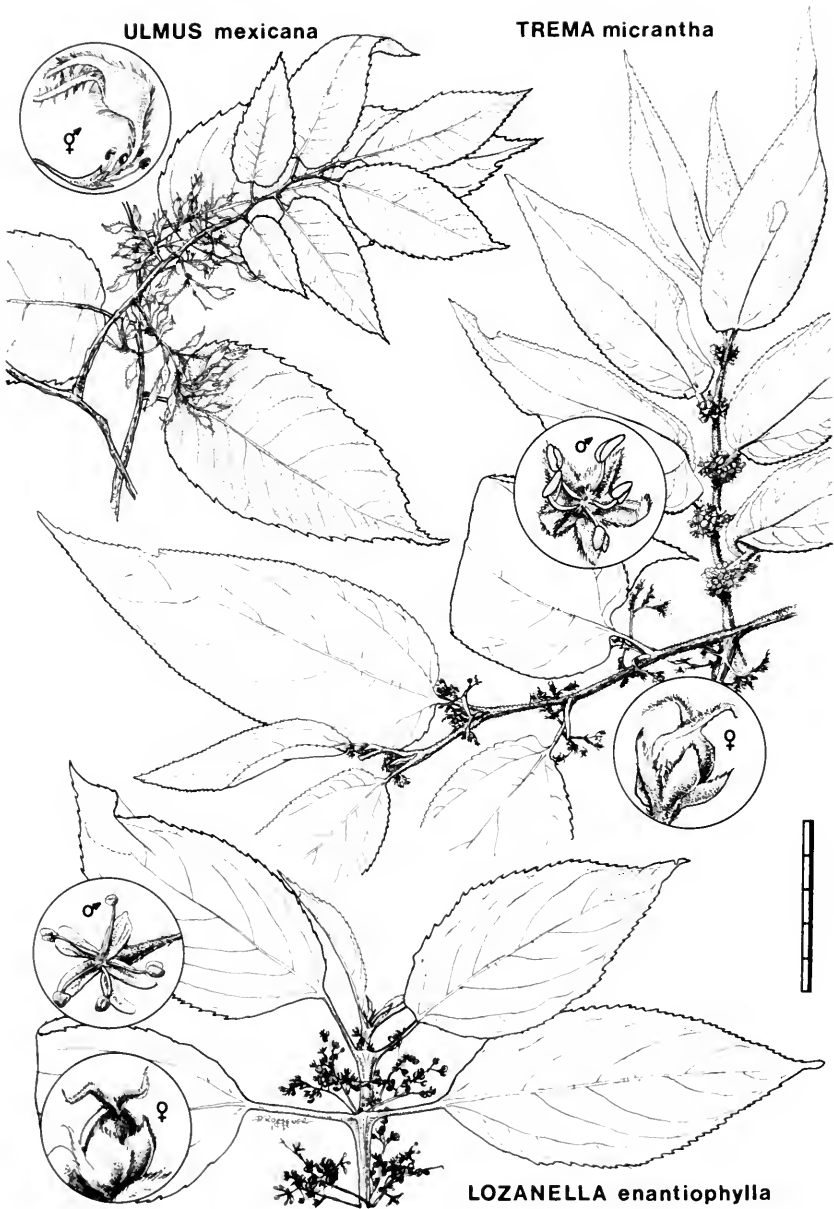


FIG 12. Ulmaceae: Central American species of *Ulmus* (or *Chaetoptelea*), *Trema*, and *Lozanella* (with opposite leaves).

**CELTIS iguanaea**

**C. schippii**



**AMPELOCERA hottlei**

FIG. 13. Ulmaceae: Costa Rican species of the genera *Ampelocera* and *Celtis*.

- 3a. Fruit less than 3 mm. long with narrow cotyledons; leaves and stems usually covered by grayish pubescence (in ours), common and wide ranging shrubs and trees from sea level to 2000 m. . . . . *Trema*.
- 3b. Fruit more than 5 mm. long with broad cotyledons; trees, shrubs, and climbers not found above 1200 m. . . . . 4a.
- 4a. Stamens equal in number to the sepals, the two styles (style-branches) deeply bifid; spines often present . . . . . *Celtis*.
- 4b. Stamens twice as many as the sepals, the two styles (style-branches) simple; spines absent . . . . . *Ampelocera*.

### AMPELOCERA Klotzsch

Bisexual trees, the stems lacking spines; stipules paired and lateral. Leaves alternate on short petioles, laminae slightly inequilateral, entire to distantly serrate, pinnately veined. Inflorescences fasciculate or solitary in the axils of the current year's growth, subtended by dry scales; flowers bisexual or functionally male, the bisexual flowers with 4 or 5 imbricate sepals, united near the base or for part of their length to form a short tube or cup, stamens usually twice as many as the sepals (rarely more or only 4 or 5), exserted; pistil sessile, ovary 1-locular, styles or style-branches 2 and united at the base, divaricate and persisting; male flowers with a pistillode. Fruit a small drupe or somewhat berry-like.

A genus of four or five species, one Central American and the others found in South America and the West Indies.

*Ampelocera hottlei* (Standl.) Standley, Trop. Woods 51:11. 1937.  
*Celtis hottlei* Standl., l.c. 20:20. 1929. Figure 13.

Bisexual trees 10-30 m. tall, the trunk becoming 70 cm. thick with a smooth pale colored bark, leafy internodes (1) 2-6 cm. long, 1.2-3.5 mm. thick, glabrous or sparsely and very minutely puberulent with grayish white hairs 0.1-0.2 mm. long; stipules 2-4 mm. long, triangular and 2 mm. broad at the base, minutely puberulent with appressed whitish hairs 0.1-0.2 mm. long. Leaves distichous, petioles 3-12 mm. long, 1-3 mm. thick, terete; laminae (6) 10-19 (26) cm. long, (3) 5-9 (12) cm. broad, elliptic to ovate or oblong, gradually or abruptly acute or acuminate at the apex, obtuse or subtruncate and slightly rounded at the subequal or unequal base, margin entire, revolute and sometimes dark on drying, lamina drying stiffly chartaceous to subcoriaceous, smooth, glabrous and often lustrous above, dull and usually glabrous below, the young laminae said to be bluish or purplish in color, primary and secondary veins slightly raised above, the 3 to 6 pairs of major secondary veins usually distant along the midvein and arising at angles of 30-50 degrees, the lowermost pair of secondaries often arising at the petiole and very prominent. Inflorescences axillary and only 1-2 cm. long, flowers crowded and sessile, bisexual, subtended by bracteoles; sepals 4- or 5-lobed, about 2 mm. long with the lobes about 1 mm. long, puberulent abaxially, stamens apparently 8 or 10, filaments 1-2 mm. long, anthers about 1.3 mm. long; pistil with the ovary about 2 mm. long, globose to ovoid, style-branches about 2.5 mm. long, simple and densely brownish-puberulent adaxially. Fruit ellipsoid to ovoid or globose, 8-10 mm. long, densely velutinous with short (0.1-0.2 mm.) stiff yellowish hairs.



A species of the wet forests between sea level and 300 m. altitude, and ranging from central Mexico and Belize along the Caribbean side of Central America to Panama and Colombia. This species is apparently common on the Caribbean side of Guatemala and Honduras and is known from a single collection in Panama (*Pittier 4319*). I have seen no collections from Nicaragua or Costa Rica, though the species undoubtedly grows in the wet forests of the Caribbean coastal plain.

The species is characterized by the stiff lustrous usually glabrous leaves, distichous and often in a single plane, the pale smooth bark, and the very small inflorescences. Common names used are *Achote de Monte* and *Aepito* in Colombia, and *Manteca* in Honduras.

### CELTIS Linnaeus

Trees, shrubs or rarely climbers, bisexual, the branches with or without spines; stipules paired and lateral. Leaves alternate and distichous, persistent or deciduous, pinnately or palmately veined, often inequilateral, entire or serrate. Inflorescences axillary, usually on the growth of the current year, male inflorescences cymose or fasciculate, female inflorescences solitary or fasciculate and few-flowered; flowers small and usually pedicellate, bisexual flowers with 4 or 5 imbricate sepals united at the base, stamens equal in number to the calyx lobes, exerted at maturity, anthers versatile, extrorse, a small disc present, pistil sessile and 1-locular, styles (or style-branches) 2 and simple or bifid, sometimes united at the base, reflexed in age; male flowers with a small pistillode; female flowers without staminodes. Fruit a drupe, ovoid to globose or ellipsoid, with a thin succulent exocarp and hard endocarp, embryo curved, cotyledons broad, conduplicate or rarely flat, variously folded.

A genus of temperate and tropical regions with about 100 species in both hemispheres. The species are quite variable and often difficult to segregate taxonomically.

Climbers, shrubs, or small trees of both evergreen and deciduous vegetation, stems usually armed with short spines; laminae usually drying thin-chartaceous, 3-13 cm. long; fruit puberulent . . . . . *C. iguanaea*.

Rare trees of the Caribbean lowlands, stems lacking spines; laminae usually drying stiff-chartaceous, 6-22 cm. long; fruit glabrous . . . . . *C. schippii*.

***Celtis iguanaea* (Jacq.) Sargent, Silva N. Amer. 7:64. 1895, as *iguaneus*. *Rhamnus iguaneus* Jacq., Enum. Pl. Carib. 16. 1762. Figure 13.**

Bisexual climbers, lianas, shrubs or occasionally small trees 2-6 (12) m. tall, usually armed with straight or recurved axillary spines, 4-10 mm. long, leafy stems straight or zig-zag, leafy internodes (0.5) 1-3 (5.5) cm. long, 1-3 (4) mm. thick, minutely (0.1-0.3 mm.) puberulent, becoming glabrous and lenticellate, brown to pale gray, lenticels ellipsoid and longitudinally 2-parted; stipules caducous, about 3

mm. long and 1 mm. broad at the base. Leaves distichous, apparently deciduous and growing in flushes, petioles 5-14 mm. long, 0.6-1.5 mm. thick, minutely strigose with whitish hairs 0.1-0.7 mm. long, terete; laminae (3) 5-13 cm. long, 2-6 cm. broad, ovate to elliptic or oblong, acute to short-acuminate at the apex, obtuse to rounded and subcordate at the equal or subequal base, margin bluntly to sharply serrate with teeth 3-6 mm. distant, lamina drying thin- to stiff-chartaceous, smooth or slightly rough to the touch on either surface, puberulent above and below in early stages with yellowish hairs 0.1-0.3 mm. long, becoming glabrous, primary and secondary veins becoming impressed above in age, venation palmate or pinnate with 2 or 3 pairs of major secondary veins prominent beneath, the basal pair often arising at the petiole. Inflorescences usually produced with the new leaves from the axils of new or fallen leaves, cymose and fasciculate but occasionally borne in alternate groups on a leafless rachis, 1-4 cm. long; male flowers sessile and in compact clusters, perianth about 1.2 mm. long, filaments about 1.5 mm. long, anthers 0.8 mm. long; bisexual flowers short-pedicellate or terminal, usually only 1 or 2 per inflorescence, perianth ciliate, about 1.5 mm. long and early deciduous, sepals usually 5, stamens 5, ovary about 2 mm. long and 1 mm. thick, puberulent, the 2 style branches becoming 4 mm. long and bifurcate, densely papillate-puberulent. Fruit 12-15 mm. long, about 8 mm. thick (dry), ellipsoid to ovoid, fleshy and puberulent.

Plants of wet or seasonally dry evergreen and deciduous forest formations of both the Caribbean and Pacific watersheds between sea level and 1200 m. elevation in Costa Rica; collected with flowers from February to June and with fruit from August to January. The species ranges from the southernmost parts of the eastern United States southward through the West Indies, Mexico, and Central America to southern South America.

*Celtis iguanaea* is noteworthy for its very wide geographical range and for the variety of its growth forms. The usual presence of spines, thin subpalmate distichous leaves, and small inflorescences with minute flowers helps to distinguish this species. The species is commonly called *cagalera* in Costa Rica and Nicaragua. See the discussion under *Celtis schippii*.

***Celtis schippii*** Standley, Field Mus. Bot. 12:409. 1936. Figure 13.

Trees 10-20 m. tall, spines absent, leafy internodes 0.8-4 cm. long, 1.5-3 mm. thick, glabrous and usually pale gray; stipules apparently minute and caducous. Leaves distichous, petioles 5-10 mm. long, 0.8-1.6 mm. thick, glabrous, sulcate adaxially; laminae 6.5-22 cm. long, 4-10 cm. broad, ovate to elliptical, tapering gradually to the acuminate apex, abruptly narrowed to the obtuse or somewhat rounded base, margin entire, lamina drying stiffly chartaceous, smooth or very slightly scabrous on either surface, glabrous above and below or very minutely (0.05-0.1 mm.) puberulent on the midvein beneath, primary and secondary veins raised above and prominent beneath, the 3 to 5 (6) pairs of major secondary veins usually quite distant on each side of the midvein and arising at angles of 30-50 degrees, the lowermost pair of secondaries arising at the petiole, very prominent, and strongly ascending. Inflorescences 4-8 mm. long, flowers few and sessile, perianth 5-parted, about 1.5 mm.

long and united only near the base, not seen at anthesis. Fruit about 15 mm. long and 8 mm. thick, ellipsoid, fleshy and drying dark, glabrous.

A species of the Caribbean lowlands, and known only from British Honduras and from a recent collection (*Molina et al. 17656*) near Los Angeles, Llanura de San Carlos, Alajuela, in Costa Rica. The species has been collected in fruit in February (Costa Rica), March, July, and September; probably flowering throughout the year.

This species is closely related to *Celtis iguanaea* but differs in having the glabrous fruit, larger and stiffer leaves with entire margin and somewhat different venation, and the larger consistent tree-form. Our knowledge of the trees of the Caribbean lowland is very poor; I doubt that the Costa Rican collection represents a true disjunction.

### LOZANELLA Greenman

Unisexual shrubs or trees, the branches often opposite; stipules united to form a single ligule-like structure on the petiole and united near the leaf-base with the ligulate stipule of the opposing leaf, deciduous and leaving an interpetiolar scar. Leaves opposite and decussate, the leaves of a pair often unequal, long petiolate, laminae pinnately veined but with prominent secondaries from near the base, sides of the laminae occasionally slightly unequal, serrate. Inflorescences cymose or with some of the flowers in terminal clusters on lateral branches of the inflorescence, axillary on growth of the current year or in the axils of fallen leaves, minute bracteoles present; flower unisexual, male flowers pedicellate with 5 (6) imbricate sepals united near the base, stamens as many as the sepals and arising below a pilose disc with a central pistillode; female flowers sessile and in clusters or separate, sepals 5 (6), imbricate and united near the base, staminodes absent, ovary sessile, 1-locular, terete, styles 2, spreading and persistent. Fruit a small drupe subtended by persistent sepals, with succulent exocarp and hard endocarp, embryo and cotyledons slightly curved.

A genus of two or three species, the others South American. The genus is unique in the family because of its opposite leaves and unusual stipules that have become ligule-like and are basally united to form an interpetiolar ridge.

*Lozanella enantiophylla* (Donn.Sm.) Killip & Morton, Journ. Wash. Acad. Sci. 21:339. 1931. *Trema enantiophylla* Donn. Smith, Bot. Gaz. 33:259. 1902. *Lozanella trematoides* Greenm., Proc. Amer. Acad. Sci. 41:236. 1905. Figure 12.

Unisexual trees or shrubs 3-10 (20) m. tall, leafy internodes 1-5 cm. long, 1-4 (6) mm. thick, densely strigulose with minute (0.1-0.4 mm.) grayish or pale-brown hairs, becoming glabrous and reddish brown, terete, an interpetiolar scar or ridge pro-

duced between the leaf-bases; stipules of the same leaf united above the petiole to form a ligulate structure about 3 mm. long, fused stipules (ligules) of opposing leaves united at the base and leaving an interpetiolar scar or ridge. Leaves opposite and usually decussate, both laminae and petioles of an opposing pair often unequal, petioles (6) 15-45 (65) mm. long, 0.7-1.8 mm. thick, minutely strigulose, deeply sulcate adaxially; laminae 5-18 cm. long, 1.5-7 (9) cm. broad, lanceolate (in small leaves) to broadly ovate, tapering gradually to the acute or acuminate apex, acute to obtuse or rounded at the equal to subequal base, margin serrulate with the teeth 2-6 mm. distant, lamina drying thin-chartaceous and scabrous on both surfaces, minutely (0.1-0.2 mm.) strigulose above and below, hairs of the upper surface broad-based, hairs narrower and less conspicuous on the lower surface, venation becoming impressed above only in age, the 3 to 5 pairs of major secondary veins arising at angles of 20-50 degrees, the lower pair of secondaries often very prominent and the venation subpalmate. Male inflorescences 2-3 cm. long, 2 per axil (4 per node), rachis slender (0.2-0.3 mm.) and minutely strigulose, male flowers sessile or short (0-2 mm.) pedicellate, subtended by small (0.7 mm.) bracteoles, perianth usually 5-parted and separate to near the base, about 2 mm. long, filaments 2-2.5 mm. long, anthers 1-1.5 mm. long, disc with conspicuous whitish hairs, pistillode about 1 mm. long; female inflorescences 3-5 cm. long, 2 per axil, flowers subsessile or short pedicellate, subtended by small (0.7 mm.) bracteoles and clustered or separate on the slender rachis, perianth 1.5-2.2 mm. long, ovary lenticular and green, 1.5 mm. long, style-branches 0.7-1.5 mm. long, densely brownish papillate-puberulent. Fruit lenticular, ellipsoid or subglobose, 2-3 mm. long, 2-keeled and often with prominent ribs on the edges, becoming yellow or orange.

Plants of the very wet (premontane rain and lower montane rain) forest formations along the Caribbean side of the Central Highlands and along the Cordillera de Talamanca to the highlands of Chiriquí at elevations from 1400 to 2300 m. The species has only been collected between the areas of Zarcero (Alajuela) in the west and above San Isidro del General (San Jose) toward the east within Costa Rica; flowering material has been collected from January to March, while the collections between June and September are largely fruit. This species ranges from Southern Mexico to Peru.

Plants of open or partly shaded sites often found along stream edges. The opposite leaves are very unusual and make separation from other Ulmaceae easy, but they give the plants the appearance of some Urticaceae. Leaf-form is quite variable, often on the same branch. The fused ligule-like stipules forming an interpetiolar ridge are distinctive.

### TREMA Loureiro

Bisexual trees or shrubs, lacking spines but often with stiff hairs; stipules paired and lateral. Leaves alternate and usually distichous, short-petiolate and pinnately or palmately veined, usually unequalateral, mostly serrate. Inflorescence cymose,

fasciculate or solitary in the axils of leaves or fallen leaves, flowers and inflorescences bisexual or unisexual, the bisexual flowers with 4 or 5 sepals connate at the base, stamens as many as the sepals and opposite them, anthers dorsifixed and introrse, pistil sessile, ovary 1-locular, styles 2 and united near the base; male flowers with a minute pistillode and the sepals usually induplicate valvate; female flowers without staminodes and the sepals usually slightly imbricate. Fruit a small ovoid to globose drupe with persisting styles, exocarp succulent and the endocarp hard, embryo curved with thick cotyledons.

A genus widely distributed in the tropics and subtropics. The 30 to 55 species are often quite variable and taxonomically difficult. A single species is found in Central America.

*Trema micrantha* (L.) Blume, Ann. Mus. Bot. Lugd. Bat. 2:58. 1853. *Rhamnus micranthus* L., Syst. Nat. ed. 10, 2:937. 1759. Figure 12.

Trees 4-12 (20) m. tall, trunk becoming 70 cm. thick with smooth gray or brown bark, usually with a single straight axis and distant horizontal branches spreading widely to form a broad open crown, leafy internodes 6-20 (40) mm. long, 1.2-4 mm. thick, densely strigulose with pale grayish hairs 0.3-0.9 mm. long or rarely glabrescent, often somewhat zig-zag and branching in a horizontal plane; stipules about 5 mm. long, lanceolate. Leaves distichous, petioles 3-10 mm. long, 0.8-2 mm. thick, densely strigulose, sulcate above; laminae 4-14 (17) cm. long, 1.4-5 (7) cm. broad, lanceolate to narrowly ovate or triangular, tapering gradually to the acute or acuminate apex, rounded at the unequally truncate or cordulate base, margin usually serrulate and revolute (dry), teeth about 1 mm. distant, lamina drying stiffly chartaceous, very scabrous and hirsutulous above, occasionally lustrous, densely to sparsely strigulose beneath with pale grayish hairs 0.2-0.7 mm. long, major veins becoming impressed above, the 2 to 4 pairs of major secondary veins arising at angles of 20-40 degrees with the lowermost pair often arising at the petiole, very prominent, and the venation subpalmate. Inflorescences bisexual or unisexual, male inflorescences 5-30 mm. long, with short branches, flowers sessile or very short pedicellate and often in crowded clusters, perianth usually puberulent and about 1.5 mm. long, valvate or slightly imbricate, anthers 0.6-1 mm. long, pistillode about 0.7 mm. long and 2-lobed; female inflorescences 5-35 mm. long, female flowers borne on pedicels 1-3 mm. long, perianth 0.7-1.5 mm. long and usually sparsely puberulent, ovary globose to ovoid, narrowed at the base, style branches (styles or stigmas) 1.5 mm. long and densely papillate-puberulent. Fruit globose or ellipsoid, becoming about 2 mm. thick and orange or yellowish, subtended by persisting but minute perianth.

A common species usually found in open or partly shaded sites and secondary growth on well drained soils in a wide variety of ecological zones, ranging from sea level to 2100 m. elevation and from the semi-deciduous forests of Guanacaste to the very wet highland forests of the Caribbean slope, but rare at lower elevations on the Caribbean side in Costa Rica; flowering throughout the year. The species is found on Cocos Island and ranges from Mexico to southern South America and the West Indies.

The scabrous leaves often with palmate venation and grayish pubescence, distichous foliage and branching, open crown, and minute flowers in small inflorescences distinguish this species. Young specimens may be mistaken for plants belonging to the Urticaceae, Euphorbiaceae, or Malvales. The bark has been used as a source of fibers, and the trees are known by a variety of common names, such as: *Bara blanca*, *Capulin blanco*, *Capaslan*, and *Jucó*. The plants are quite variable, both in pubescence and form of the inflorescence, but these variations do not seem to be correlated with each other or with the environment.

### ULMUS Linnaeus

Bisexual trees or shrubs; stipules paired and lateral, caducous. Leaves alternate and usually distichous, deciduous or persistent, pinnately veined and serrate, the laminae usually inequilateral and oblique at the bases. Inflorescence racemose or fasciculate, borne in the axils of the previous year's growth and at first covered with imbricate scales, the flowers numerous and bisexual or rarely unisexual, sepals 4 to 9, imbricate and united near the base, stamens as many as the sepals and opposite them, becoming exerted, pistil sessile or stipitate, 1 or rarely 2-locular and compressed longitudinally, styles 2, stigmatic on the inner face, recurved and usually persisting. Fruit a samara or dry drupe, lenticular or flattened and usually with thin winged lateral margins (but these lacking in our species), embryo straight with flat cotyledons, endosperm absent.

A genus of about 45 species of the Northern Hemisphere. Our species has been placed in the genus *Ulmus* by some authors and in its own genus, *Chaetoptelea*, by others. Sweitzer, who has recently studied the comparative anatomy of the Ulmaceae (Journ. Arn. Arb. 52:523-571. 1971), finds that the wood anatomy does support the segregation of *Chaetoptelea* as a distinct genus. I believe that these distinctions in wood anatomy and in the lack of winged fruit may be worthy of subgeneric rank but are not so unusual that they are worthy of separating this species as a distinct genus; in general aspect, this species is just another elm.

***Ulmus mexicana* (Liebm.) Planch. in DC., Prodr. 17:156. 1873.**  
*Chaetoptelea mexicana* Liebm., Kjoeb. Vidensk. Meddel. 77. 1850.  
 Figure 12.

Trees 10-40 m. tall, the crown becoming more than 20 m. high and up to 20 m. broad but usually narrower, trunk becoming more than 1 m. thick with scaly gray bark, leafy internodes 1-2 cm. long (to 6 cm. long on sprout shoots), 1-2 (4) mm. thick, glabrous or puberulent with thin whitish hairs 0.1-0.3 mm. long, often dark reddish-brown, buds 2-5 mm. long and enclosed in several bud-scales minutely ciliate along the edge; stipules 6-8 mm. long, narrowly triangular, occasionally

persisting. Leaves distichous and produced in flushes, petioles (2) 5-14 mm. long, 0.6-1.8 mm. thick, minutely canescent or less often glabrous, terete; laminae 4-12 (16) cm. long, 1.8-5 (7) cm. broad, lanceolate or narrowly ovate to ovate-oblong, tapering gradually to the usually acuminate apex, very unequal (oblique) at the base with one side often rounded and cordulate and the other attenuate, margin sharply serrate with teeth 2-5 mm. distant, lamina drying stiffly chartaceous, smooth or scabrous above, scabrous beneath, often slightly lustrous on both surfaces, glabrous or minutely puberulent only along the midvein above, glabrous or puberulent beneath with very thin whitish hairs 0.2-0.7 mm. long, major veins becoming impressed above, the 8 to 16 pairs of major secondary veins arising at angles of 30-60 degrees, and very prominent beneath. Inflorescences emerging from buds in the axils of fallen leaves, the 2 or 3 pairs of decussate bud-scales glabrous, rachis of the inflorescences usually unbranched, 2-6 cm. long; flowers borne in whorls of 3 or 4, pedicels 2-5 mm. long, perianth 1-2 mm. long, united more than half and usually campanulate, stamens 5, exserted, filaments 2-4 mm. long, very slender, anthers about 1 mm. long and equally broad; pistil with style-branches about 2 mm. long, minutely brownish puberulent. Fruit becoming 10 mm. long including stipe and style-branches, body of the fruit lenticular and ellipsoid to obovoid in outline, about 2 mm. broad, ciliate along the edges with whitish hairs 0.7-1.5 mm. long.

Trees of wet montane forest formations between 900 and 1900 m. elevation in Costa Rica; flowering material has been collected between February and April. I have only seen the following collections from Costa Rica: *Brenes 22687* along the Río Jesus de San Ramon (Alajuela), *Tonduz 11792* near El Copey (San Jose), *J. Leon 180* along the Río Reventazon (Cartago). The species ranges from Mexico to Chiriquí, Panama.

The great size attained by these trees probably accounts for the very few flowering collections found in herbaria. The small leaves with rough surfaces, toothed margin, asymmetric base, and many veins are produced from scale-covered buds and make vegetative material easy to identify (but leaves on sprout shoots can be as much as 16 cm. long). *Cenizo (-a)* is a common name reported from Panama.

## MORACEAE

WILLIAM BURGER

REFERENCES: E. J. H. Corner, The Classification of Moraceae. Gard. Bull. Singapore 19:187-252. 1962. C. C. Berg, Olmediae and Brosimeae. Flora Neotropica, Monog. 7:1-229. 1972.

Trees, shrubs, or rarely climbers (*Ficus* spp.) and herbs (*Dorstenia*) bisexual or unisexual, latex present and usually whitish; stipules present, paired at the node or solitary by connation. Leaves alternate and simple (in ours), distichous or in a spiral, usually petiolate, the lamina entire, serrate, or lobed to deeply incised (in *Artocarpus*, *Cecropia*, and *Pourouma*) capitate or subcapitate multicellular microscopic hairs ( $\times 150$ ) often present. Inflorescences axillary, often paired at the node, unisexual or bisexual, extremely variable in the family and ranging from cymose-paniculate or simple racemes and spikes to condensed heads, discoid structures or urceolate with the flowers enclosed (as in *Ficus*); flowers small and unisexual, perianth of a single whorl of usually 4 (0-8) free or united parts, imbricate or valvate, persistent; stamens as many as the perianth parts and opposite them or variously reduced and occasionally the male flowers not organized with the stamens and interspersed bracts arising directly from the rachis, filaments straight or bent inward in bud, anthers usually 2-theous, dehiscence longitudinal to circumscissile, pistillode present or more often absent; pistil often adnate to the perianth, ovary 1-locular (very rarely 2-locular), superior to inferior by adnation of the perianth-tube, or often imbedded within the receptacle, style and style-branches (or stigmatic arms) 2 or less often 1, stigmas usually linear, very rarely capitate or peltate, ovule 1, pendulous from near the apex of the locule and anatropous or campylotropous or basal and erect in *Cecropia*, *Coussapoa*, and *Pourouma*. Fruits usually fleshy, the tissue of the ovary, perianth, or receptacle becoming succulent, or the endocarp crustaceous to woody, often connate in fleshy syncarps, seeds small to large, cotyledons various and equal or unequal.

The Moraceae are commonly present in lowland evergreen tropical forests, but they are very poorly represented in herbaria. Short flowering-period, inconspicuous inflorescences, and the tree habit probably account for the paucity of collections. The family can often be recognized by the white sap, alternate leaves (distichous or in a spiral), stipules that are sometimes united and often surround the stem, small flowers often in capitate or discoid inflorescences, stamens opposite the perianth parts (when present), and the usually 2-branched style. Members of the family are easily mistaken for



species of Euphorbiaceae, Flacourtiaceae (including Lacistemaceae), and the closely related Ulmaceae and Urticaceae.

Corner (Gard. Bull. Singapore 19:187-252. 1962) has stated that the genera of the subfamily Conocephaloideae are more closely related to genera of the Urticaceae than to other genera of the Moraceae. The Conocephaloideae have erect basal ovules and they often lack whitish sap, as do most Urticaceae. However, an equally valid argument can be made for their inclusion in the Moraceae or for separation in a family of their own. Because this is a reference work, we are placing our genera of the Conocephaloideae (*Cecropia*, *Coussapoa*, and *Pourouma*) among other genera of the Moraceae where they have been placed traditionally and where most readers will look for them.

The genus *Maclura* is represented in Central America by *Maclura brasiliensis* (Martius) Endlicher (= *Chlorophora scandens* Standl. & L. Wms.), which is naturalized in small areas of the Dept. of Olancho, Honduras.

#### KEY TO THE GENERA OF MORACEAE

- 1a. Plants herbaceous, stems less than 0.4 m. tall and not woody, with whitish sap; inflorescences disc-like with a flattened apical surface, the minute flowers imbedded in the disc. . . . . *Dorstenia*.
- 1b. Trees or shrubs, stems becoming more than 2 m. tall and woody . . . . . 2a.
- 2a. Stipules only partly encircling the stem, stipule-scars not united around the stem (as seen on younger stems), the stipules always paired at the node . . . 3a.
- 2b. Stipules completely encircling the stem, stipule-scars forming a ring around the stem on younger stems, the stipules paired or united and solitary at each node 24a.
- 3a. Inflorescences spicate or racemose, long and narrow. . . . . 4a.
- 3b. Inflorescences capitate, discoid, or of a few closely crowded or solitary flowers . . . . . 13a.
- 4a. Inflorescences with anthers, the flowers male. . . . . 5a.
- 4b. Inflorescences with pistils or fruit, female . . . . . 10a.
- 5a. The flowers not definitely organized and the stamens apparently interspersed with bracts or with a minute perianth and a single stamen, anthers minute (0.5 mm.), flowering parts sessile on the slender spikes, tall trees. . . . . 6a.
- 5b. The flowers with a definite 4-parted perianth and each with usually 4 stamens, inflorescence spicate with sessile flowers or racemose with pedicellate flowers . . . . . 7a.
- 6a. Flowers not definitely organized, the spikes usually paired at a node *Clarisia*.

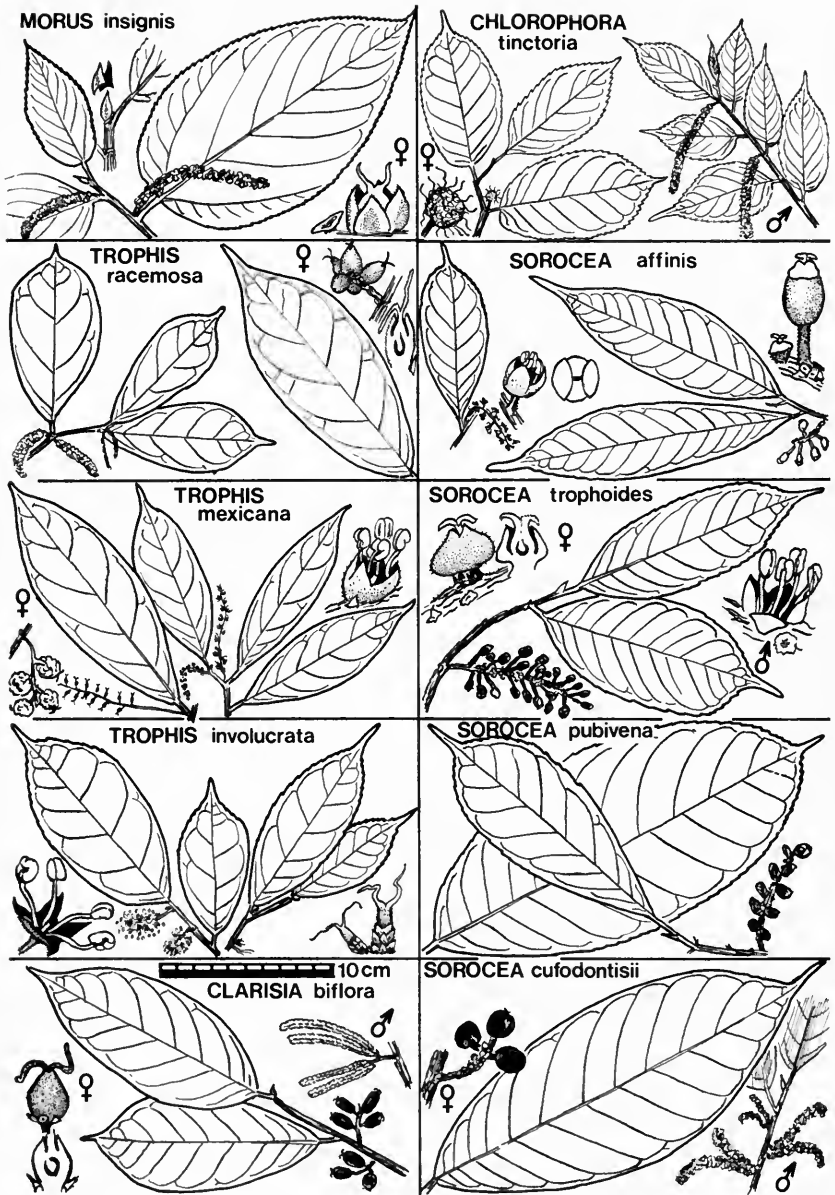


FIG. 14. Moraceae with the flowers often in spikes and racemes: *Chlorophora*, *Clarisia*, *Morus*, *Sorocea*, and *Trophis*.

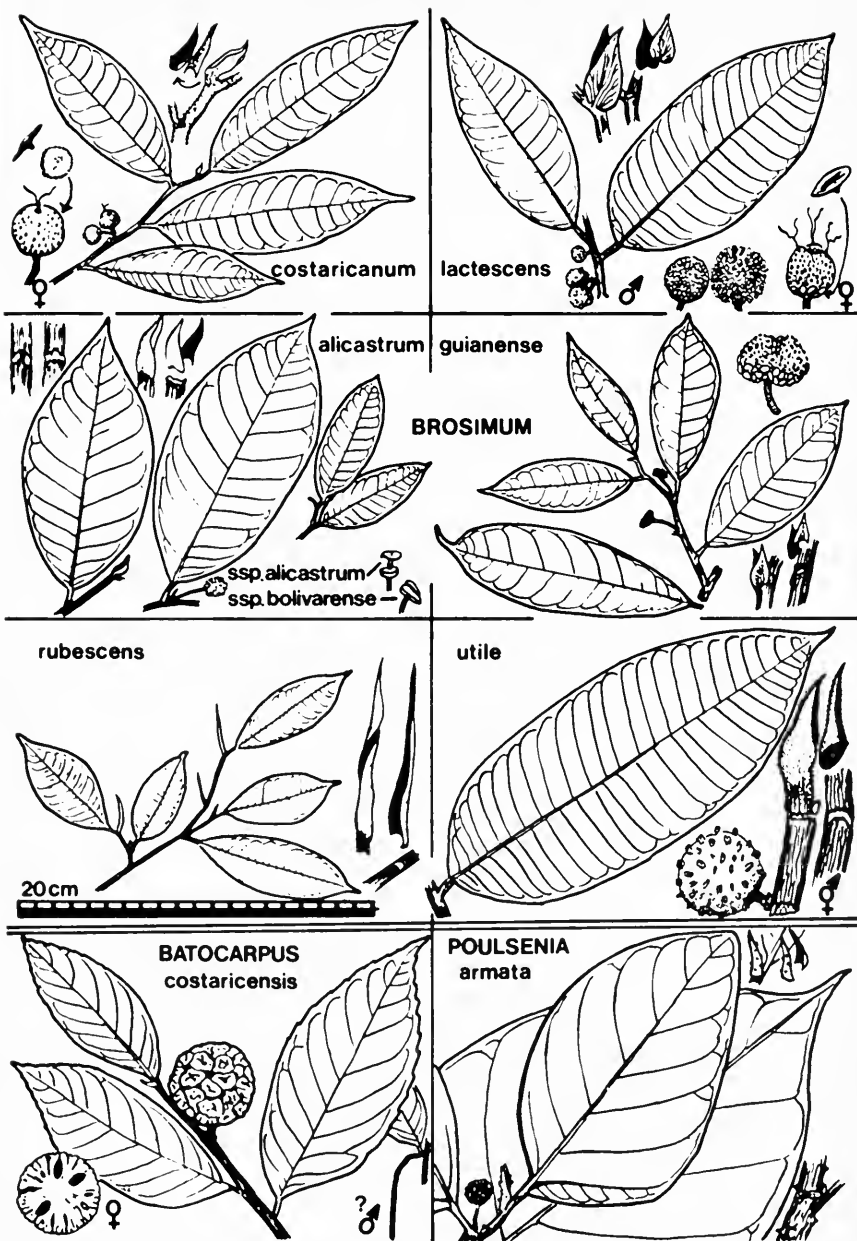


FIG. 15. Moraceae with the flowers usually in globose heads, lacking an involucre of bracts at the base: *Batocarpus*, *Brosimum*, and *Poulsenia*.

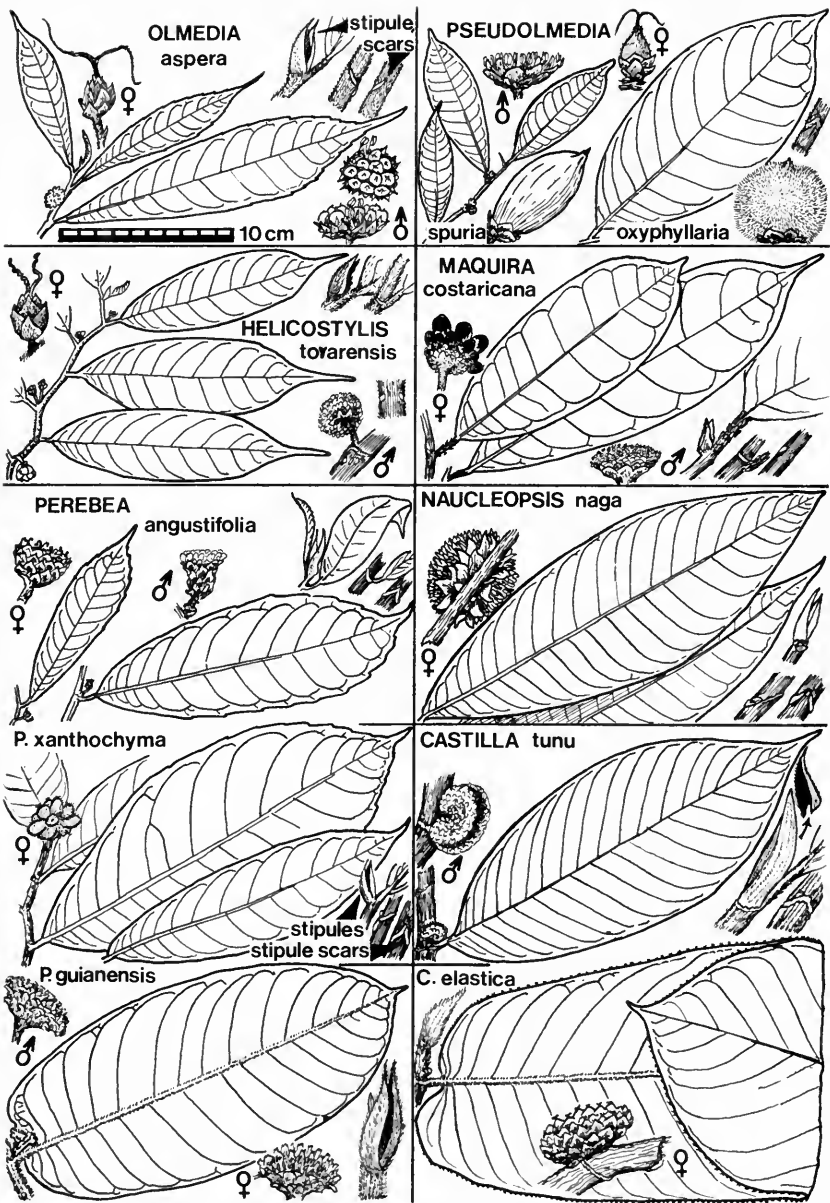


FIG. 16. Moraceae with usually disc-like inflorescences: *Castilla*, *Helicostylis*, *Maquira*, *Naucleopsis*, *Olmedia*, *Perebea*, and *Pseudolmedia*.

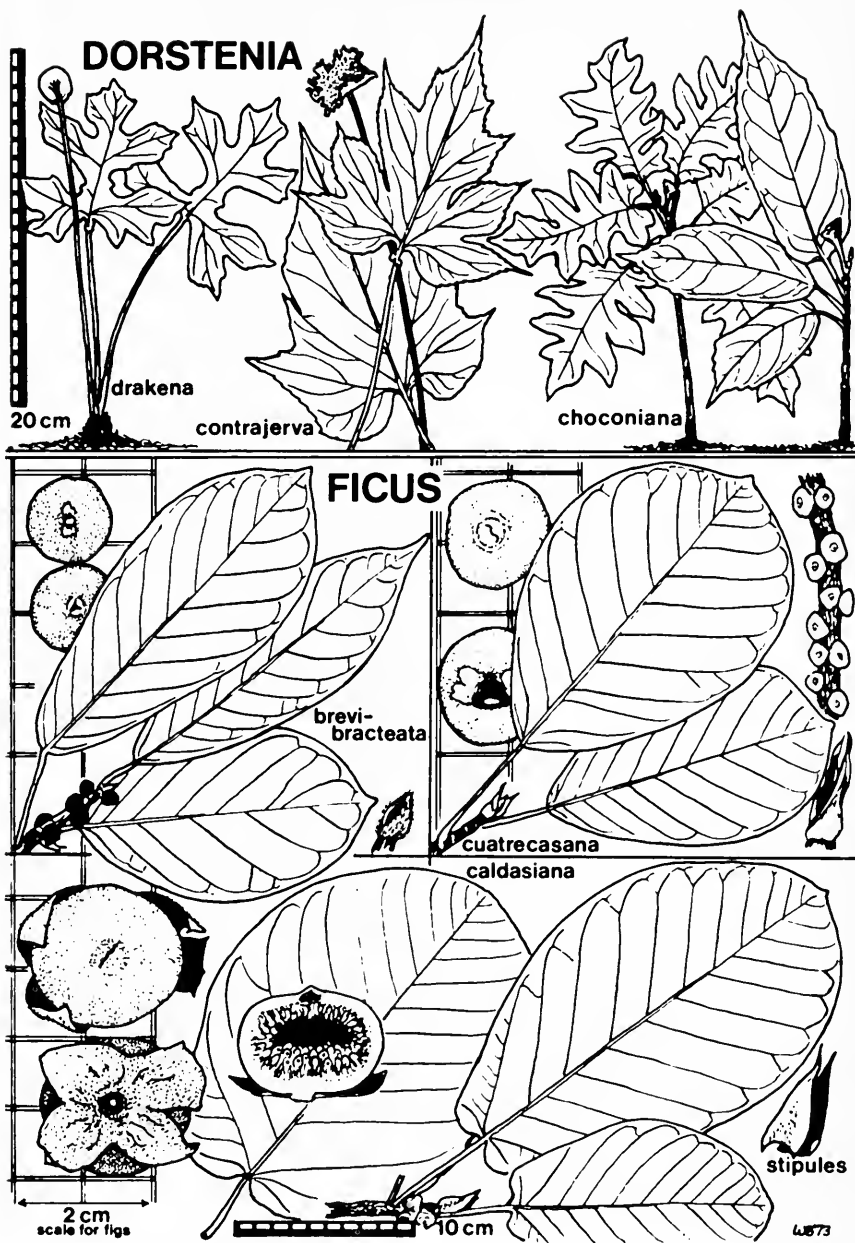


FIG. 17. Moraceae: *Dorstenia* and species of *Ficus*, subgenus *Urostigma* with larger, long-petiolate leaves, and sessile figs.

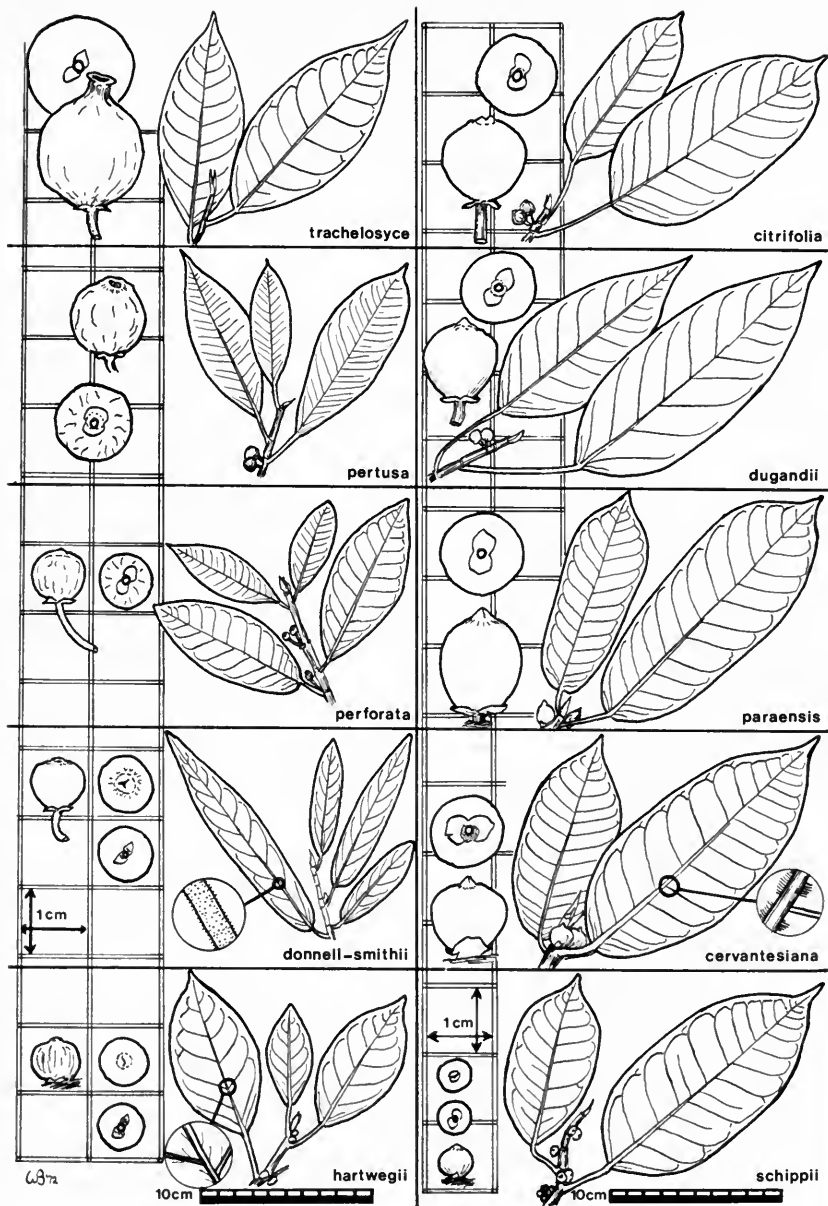


FIG. 18. Moraceae: *Ficus*, species of subgenus *Urostigma* with smaller leaves or acuminate leaf-tips, the figs mostly pedicellate.

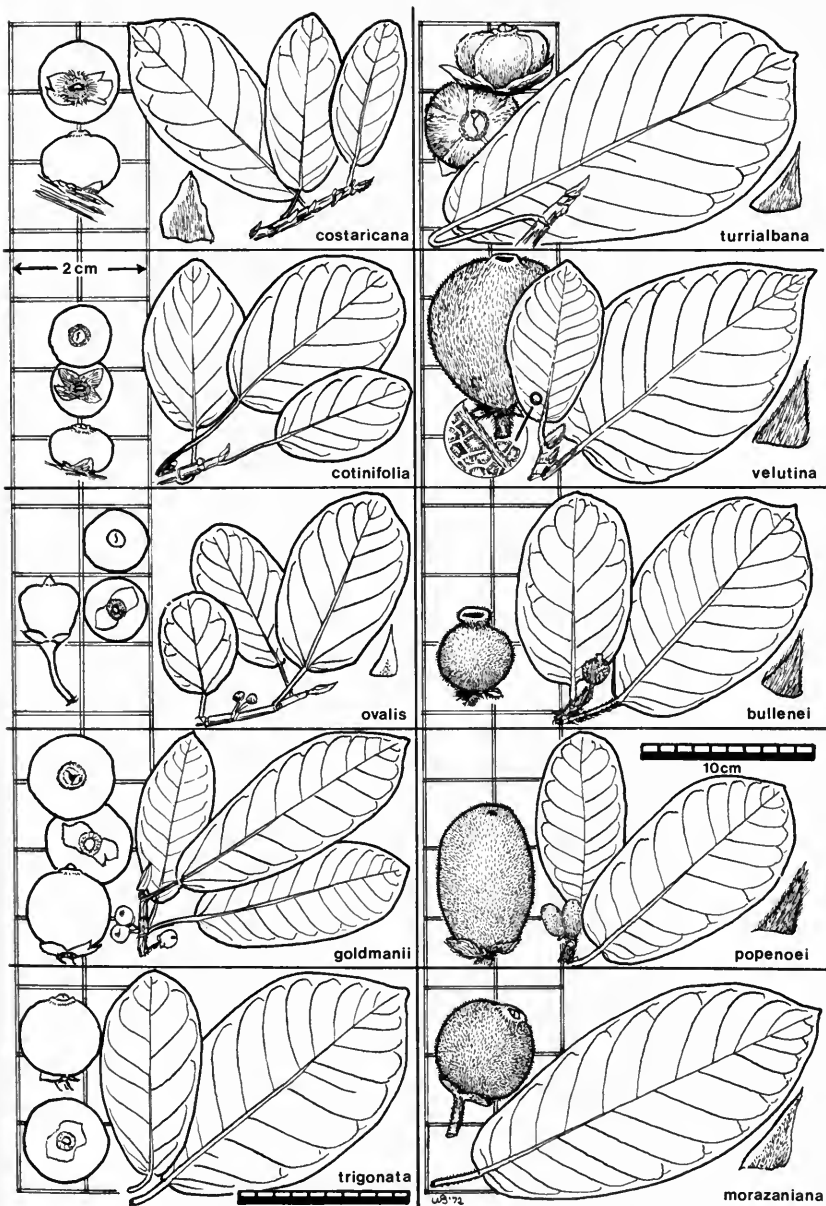


FIG. 19. Moraceae: *Ficus*, species of subgenus *Urostigma* with puberulent figs or blunt-tipped leaves.

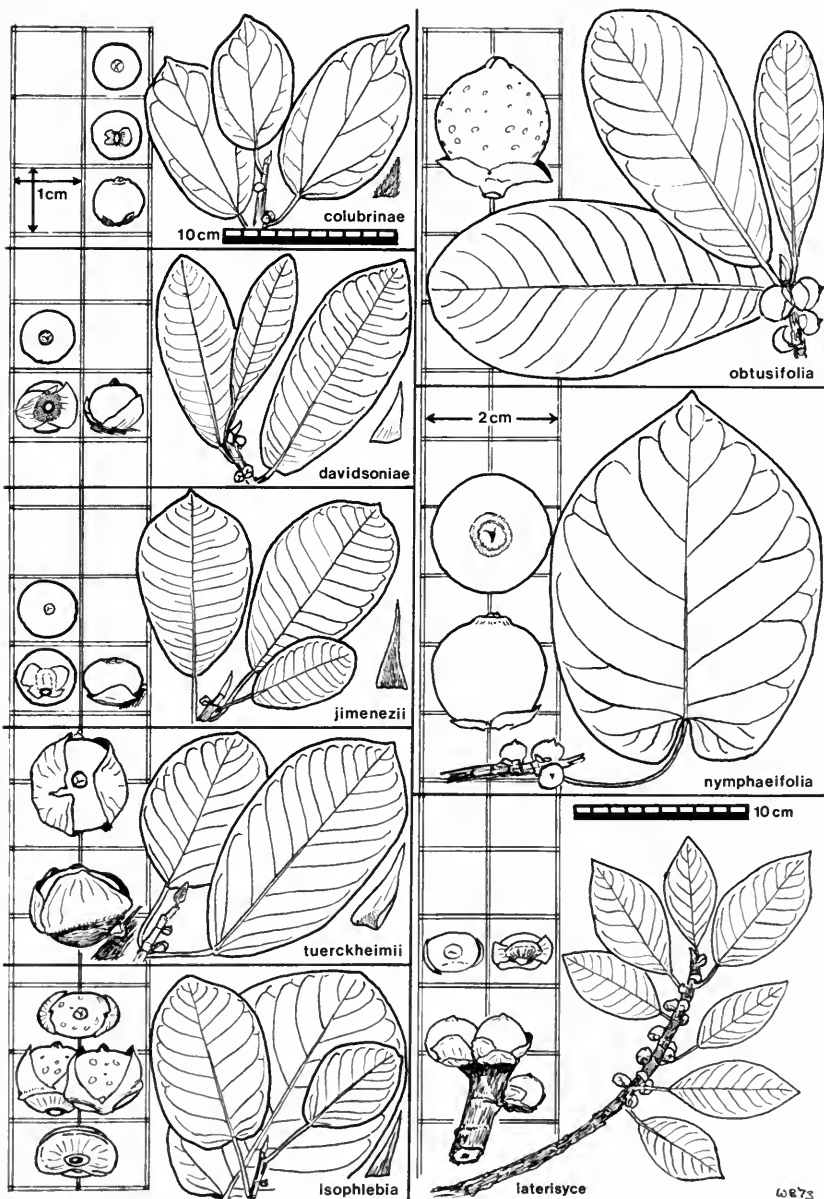


FIG. 20. Moraceae: *Ficus*, species of subgenus *Urostigma* with sessile figs and large bracts or with unusual leaves.



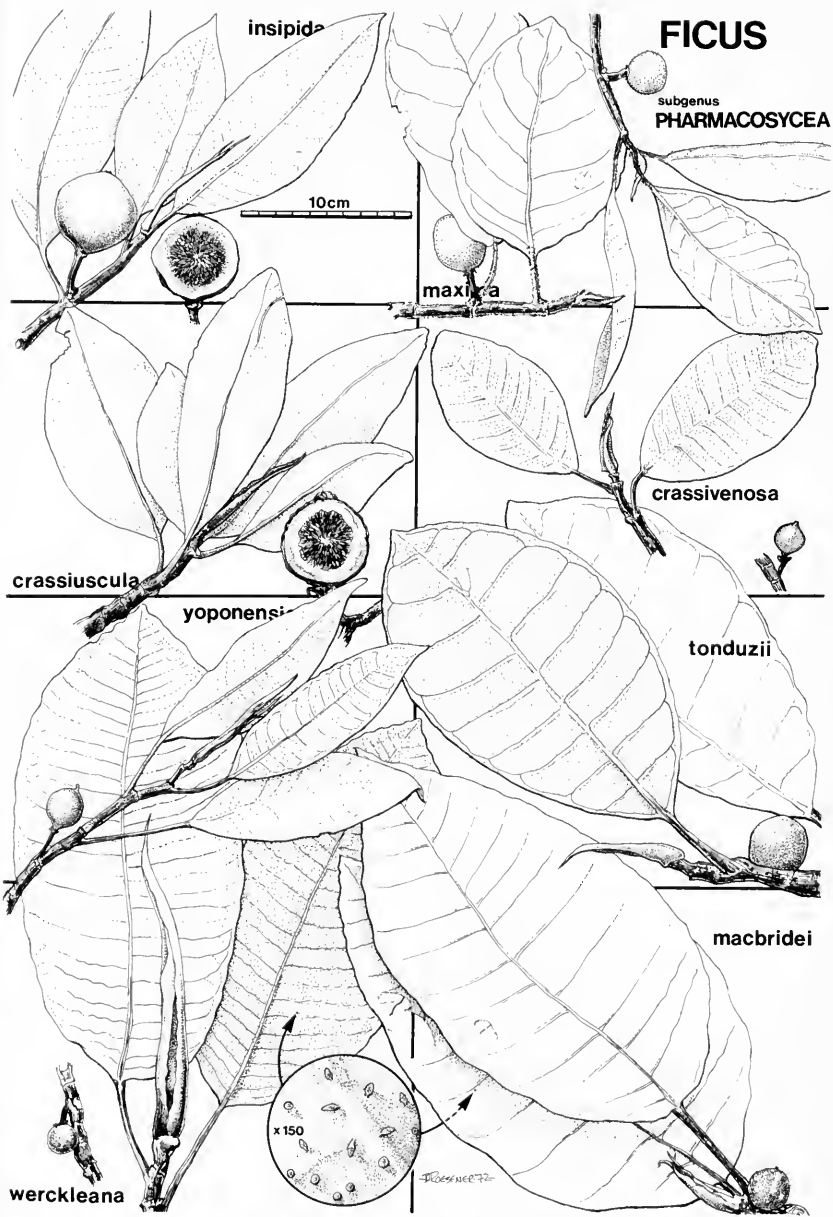


FIG. 21. Moraceae: *Ficus*, species of subgenus *Pharmacosycea* with only one fig at a node and usually three basal bracts.

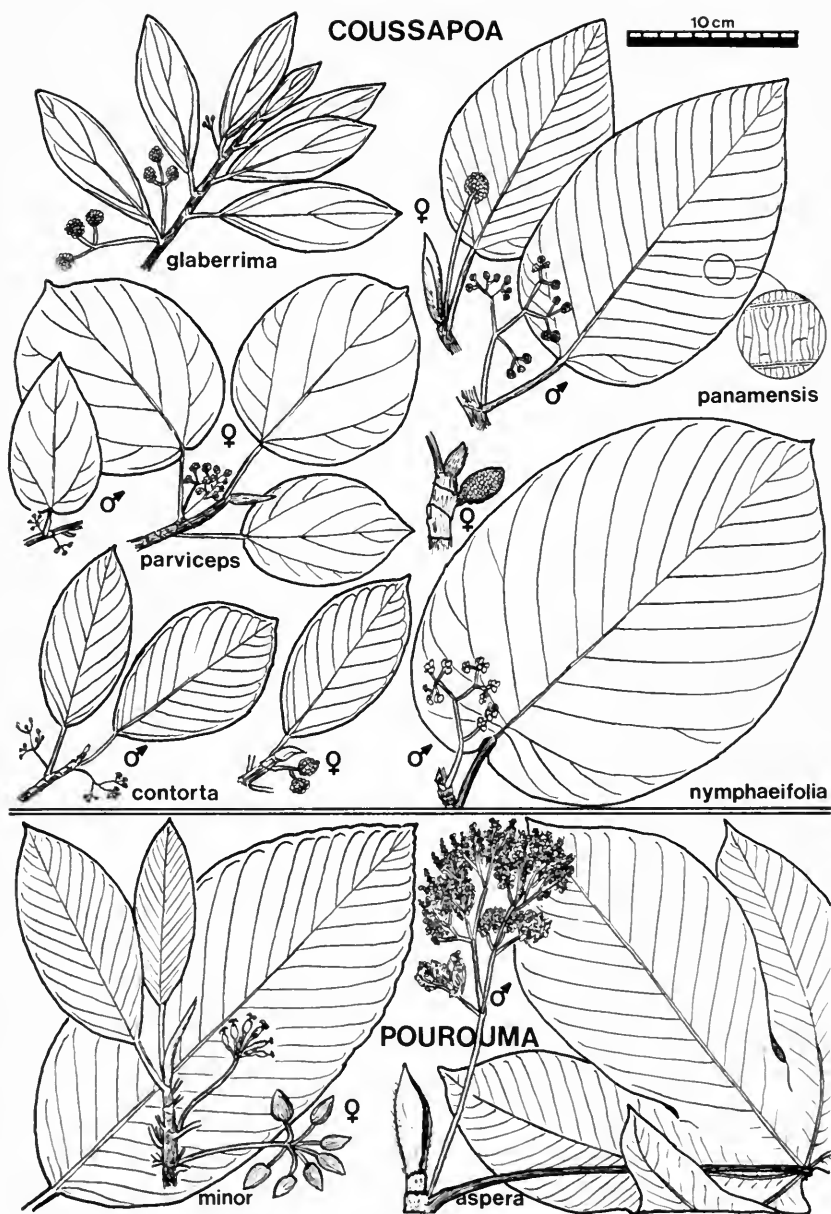


FIG. 22. Moraceae, subfamily Conocephaloideae: the Costa Rican species of *Pourouma* and the often epiphytic *Coussapoa*.

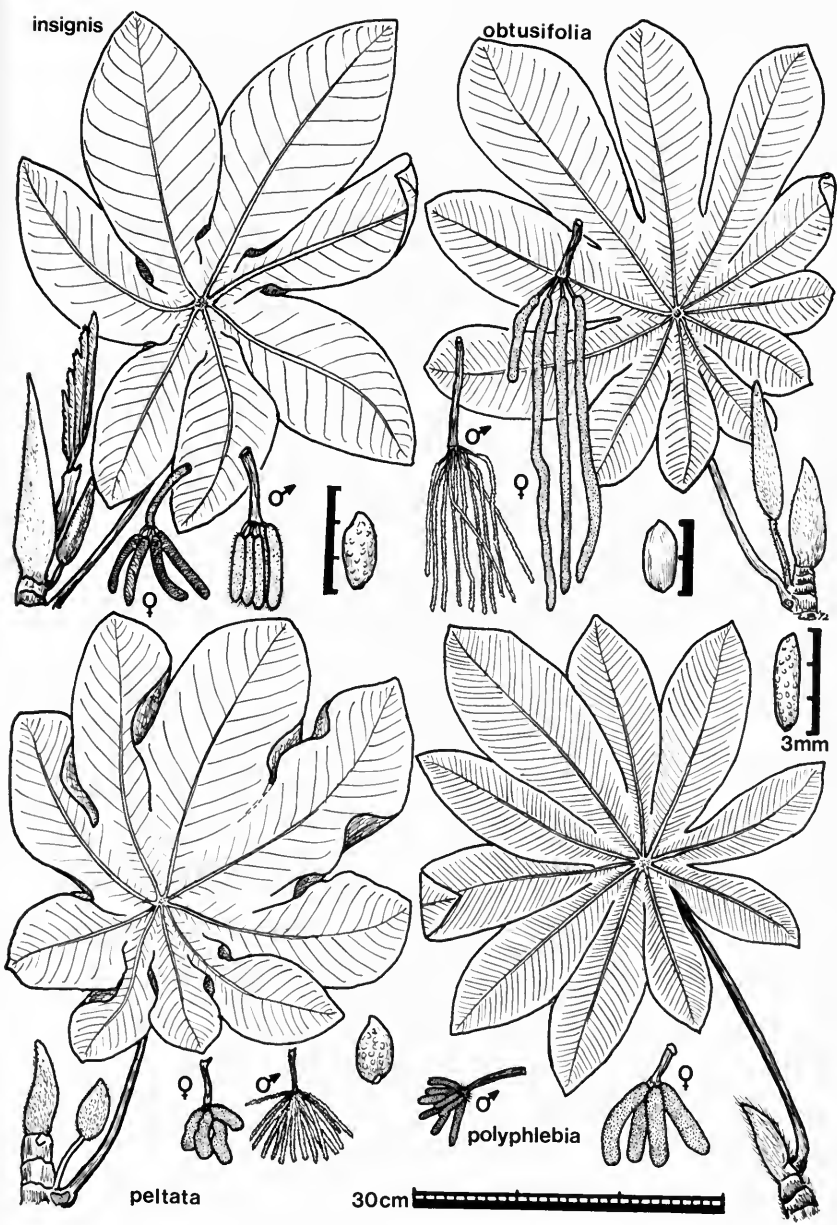


FIG. 23. Moraceae, subfamily Conocephaloideae; the continental Costa Rican species of *Cecropia*.

- 6b. Flowers with a minute 2- or 4-lobed perianth, spikes solitary at a node  
*Batocarpus*.
- 7a. Stamens with the filaments straight and the perianth decussate-imbricate in bud, perianth-parts often broadly sessile on the rachis. . . . *Sorocea*.
- 7b. Stamens with the filaments bent inward in bud, the filaments consequently usually longer than the perianth-parts . . . . . 8a.
- 8a. Inflorescences usually paired at a node; perianth-parts valvate in bud  
*Trophis*.
- 8b. Inflorescences solitary at the node; perianth-parts imbricate in bud  
9a.
- 9a. Lowland trees common in deciduous areas, wood yellowish; spikes without peltate bracts. . . . . *Chlorophora*.
- 9b. Trees from between 1500 and 2200 m. altitude; spikes with peltate bracts (in our species) . . . . . *Morus*.
- 10a. Pistil free, enclosed within 4 separate perianth-parts, the flowers sessile and closely crowded; inflorescences solitary at a node . . . . . *Morus*.
- 10b. Pistil free or united with the perianth, enclosed or subtended by a tubular (united) perianth, the perianth often very difficult to distinguish and often almost completely united with the pistil; inflorescences usually paired or of paired pedicellate flowers . . . . . 11a.
- 11a. Inflorescences of pistils in distichous pairs on leafless stems, peltate bracts present at the base of the pistil above the pedicel; tall lowland trees . . . . . *Clarisia*.
- 11b. Inflorescences spicate or racemose with few to many crowded or separate and sessile or pedicellate flowers, peltate bracts found only on the rachis of the inflorescence. . . . . 12a.
- 12a. Style-branches (or stigmas) slender; lower surface of the leaf lacking microscopic ( $\times 150$ ) capitate hairs . . . . . *Trophis*.
- 12b. Style-branches usually short and broad; lower leaf surface usually with microscopic capitate multicellular hairs . . . . . *Sorocea*.
- 13a. Inflorescences with anthers, male parts present . . . . . 14a.
- 13b. Inflorescences with pistil or fruit, female . . . . . 17a.
- 14a. Inflorescences usually globose, with thin flat round peltate bracts on the surface. . . . . *Brosimum*.
- 14b. Inflorescences discoid and with subtending imbricate bracts usually forming an involucre . . . . . 15a.
- 15a. Flowers with the filaments curved inward in bud and opening elastically, perianth-parts valvate in bud; laminae scabrous and denticulate; 0-600 m. elevation . . . . . *Olmedia*.
- 15b. Flowers with the filaments straight in bud and the perianth-parts decussate-imbricate; laminae smooth (in ours). . . . . 16a.
- 16a. Leaves sparsely to densely puberulent, usually drying dull above; 700-1500 m. . . . . *Helicostylis*.
- 16b. Leaves glabrous, usually drying lustrous above; 0-850 m. . . . . *Maquira*.
- 17a. Inflorescence usually globose and lacking an involucre of imbricate basally attached bracts . . . . . 18a.

- 17b. Inflorescence usually discoid to ovoid or occasionally with short lobes, subtended by imbricate basally attached bracts forming an involucre or the flowers borne in pairs from the leaf-axil or on short-shoots . . . . . 20a.
- 18a. Inflorescences with thin flat round peltate bracts on the surface or near the base . . . . . *Brosimum*.
- 18b. Inflorescences lacking thin round flat peltate bracts on the surface . . . 19a.
- 19a. Style branch or stigma 1 per pistil, fruiting inflorescence 1-2 cm. in diameter; trees of wet evergreen and seasonally dry deciduous areas . . . . . *Chlorophora*.
- 19b. Style branches (stigmas) 2 per pistil, fruiting inflorescence 4-5 cm. in diameter; trees of wet evergreen forests in the Golfo Dulce area . . . . . *Batocarpus*.
- 20a. Flowers distinctly pedicellate and paired in the axils of leaves or borne in alternate pairs on short (1-3 cm.) leafless stems, flat round peltate bracts borne at the base of the pistil above the pedicel; tall trees of the wet lowlands . . . . . *Clarisia*.
- 20b. Flowers sessile on the inflorescence, never pedicellate . . . . . 21a.
- 21a. Inflorescence discoid, with more than 10 flowers; leaves entire, usually drying lustrous; 0-850 m. . . . . *Maquira*.
- 21b. Inflorescence with fewer than 5 flowers, usually less than 10 mm. long; leaves usually serrulate . . . . . 22a.
- 22a. Inflorescence usually with 2 or 3 flowers; small treelets of lowland Caribbean wet forest formations . . . . . *Trophis*.
- 22b. Inflorescence usually with a single female flower . . . . . 23a.
- 23a. Leaves scabrous above, 0-600 m. . . . . *Olmedia*.
- 23b. Leaves smooth above, 700-1500 m. . . . . *Helicostylis*.
- 24a. Stipules paired, 2 at a node, enclosing the shoot-apex and overlapping (sometimes difficult to distinguish as two different parts) . . . . . 25a.
- 24b. Stipule solitary at the node, a single structure enclosing the shoot-apex (but lateral buds and inflorescences may be enclosed by more than one stipule-like structure) . . . . . 31a.
- 25a. Flowers borne within an enclosed cavity in a rounded fruit-like structure (the syconium or fig) that is closed to the outside except for a small spical ostiole with interleaved scales; the figs solitary or paired in the leaf-axils, with 2 or 3 bracts near the base; small to very large trees, often beginning as epiphytes and strangling the host . . . . . *Ficus*.
- 25b. Flowers not borne within an enclosed surface, the inflorescence not a globose fruit-like structure except in *Brosimum* and then with many peltate bracts on the surface. . . . . 26a.
- 26a. Inflorescences globose to ellipsoid or clavate, lacking a definite involucre of imbricate basally attached bracts at the base. . . . . 27a.
- 26b. Inflorescence discoid or of only 1 or a few flowers, subtended by an involucre of imbricate basally attached stiff bracts. . . . . 29a.
- 27a. Inflorescences usually globose with few to many flat thin round peltate bracts on the surface, 1-5 cm. in diameter; plants lacking spines, leaves entire. . . . . *Brosimum*.

- 27b. Inflorescences lacking thin flat round peltate bracts . . . . . 28a.
- 28a. Plants usually with short spines on younger stems, leaves entire; inflorescences globose, the male 1-1.5 cm. in diameter, fruiting heads 2-3 cm. in diameter . . . . . *Poulsenia*.
- 28b. Plants lacking spines, leaves entire or large and deeply pinnately lobed; inflorescences globose to long and irregularly ellipsoid or clavate, 3-50 cm. in diameter . . . . . *Artocarpus*.
- 29a. Female inflorescence with only a single flower (solitary pistil); stamens free among concentrically arranged bracts and not within definite 4-parted flowers; leaves with entire margins . . . . . *Pseudolmedia*.
- 29b. Female inflorescences with several to many flowers; stamens in flowers with 4-parted perianth . . . . . 30a.
- 30a. Leaves usually puberulent and denticulate; ovary mostly on the surface of the receptacle; male inflorescence open before anthesis, male flowers usually with 4 stamens . . . . . *Perebea*.
- 30b. Leaves glabrous and entire; base of the ovary immersed in the receptacle; male inflorescence closed before anthesis, male flowers usually with fewer than 4 stamens. . . . . *Naucleopsis*.
- 31a. Inflorescences globose with few to many thin flat round peltate bracts on the surface . . . . . *Brosimum*.
- 31b. Inflorescences lacking thin round peltate bracts . . . . . 32a.
- 32a. Inflorescences subtended by a conspicuous involucre of stiff imbricate basally attached bracts, flattened at the top and discoid or folded. . . . . *Castilla*.
- 32b. Inflorescences lacking an involucre of stiff imbricate bracts, varying from cymose and branched to umbellate, capitate, or digitate; pistil with a single short penicillate stigma and erect basal ovule; plants usually lacking milky sap (subfamily Conocephaloideae) . . . . . 33a.
- 33a. Leaves peltate with the petiole attached near the center of the lamina, palmately lobed; free standing trees with few major branches, biting ants often present in and on the stems; flowers in thick (4-14) spikes borne on a common peduncle and the inflorescence often digitate in form . . . . *Cecropia*.
- 33b. Leaves never peltate, the petiole attached at the lamina base, flowers in cymose groups or heads, never in digitate spikes; biting ants absent . . . . 34a.
- 34a. Trees, usually free-standing from early stages, fruit 10-30 mm. long; male flowers pedicellate, never in globose heads, with 4 stamens and 4 perianth-parts; leaves lobed or entire . . . . . *Pourouma*.
- 34b. Trees or shrubs, usually epiphytic in early stages; fruit 1-4 mm. long; male flowers sessile in globose heads, with 2 united stamens and 4 free or united perianth-parts; leaves entire . . . . . *Coussapoa*.

### ARTOCARPUS J. R. & G. Forster Nomen conservandum

Small to large trees with whitish milky sap; stipules paired, amplexicaul and leaving ring-like scars around the stem (subgenus *Artocarpus*) or smaller and lateral to interpetiolar, not leaving scars around the stem (subgenus *Pseudojaca*), caducous. Leaves alternate and in a spiral (subgenus *Artocarpus*) or distichous

(subgenus *Pseudojaca*), simple (in ours) or rarely pinnately compound, entire to deeply pinnatifid, mature leaves often differing from the juvenile. Inflorescences axillary or on old wood, paired or solitary, unisexual and capitate, globose, ellipsoid or cylindrical, usually pedunculate, flowers tightly compacted and numerous, the single pistil or stamen enclosed by perianth and often with interspersed stalked bracts. pale flowers reduced to a single stamen, perianth tubular with 2-4 imbricate lobes, filament straight, pistillode absent. Female flowers with the tubular perianth thickened above and with a small orifice for the style, perianth often connate with the perianth of adjacent flowers above and forming a syncarp, staminodes absent; pistil with an apical or lateral style, style simple or with 2 style-branches (stigmas). Fruit a syncarp formed by the enlargement of the entire female head, the individual fruit (achenes) included within the succulent tissue of the syncarp.

A genus of about 48 species, native to southern Asia and ranging from India to Southern China, the Philippines, Indonesia, New Guinea, and the Solomon Islands. The genus is now pantropical because of the distribution by man of two important food-plants: the Breadfruit and the Jack, or Jackfruit. These are the species commonly encountered in Central America and both belong to the subgenus *Artocarpus*.

Leaves deeply pinnately lobed; stipules 10-25 cm. long; inflorescences borne on the young branches, fruiting inflorescence usually globose . . . . . *A. communis*.

Leaves usually entire, stipules 1.5-5 cm. long; inflorescences borne on short shoots arising from thick branches and trunk, fruiting inflorescence ellipsoid or irregular . . . . . *A. heterophyllus*.

***Artocarpus communis*** J. R. & G. Forster, Char. Gen. 101. 1776.  
*Rademachia incisa* Thunb., Vet. Acad. Handl. Stockholm 37:253.  
 1776. *Artocarpus incisus* (Thunb.) L.f., Suppl. Pl. 411. 1781.

Trees to 20 (35) m. tall, leafy internodes 5-15 mm. thick, glabrous to sparsely puberulent at the stipule-scars; stipules 10-25 cm. long, sparsely to densely puberulent with slender ascending hairs about 2 mm. long. Leaves quite variable in size and lobing, petioles 2-4 cm. long; laminae of mature trees 30-100 cm. long, 25-65 cm. broad, rhomboid to elliptic in outline with 3 to 7 lobes on each side, acuminate at the apex, usually scabrous above, with 6 to 12 pairs of major secondary veins. Male inflorescences on peduncles 3-6 cm. long, head 7-30 cm. long, 1.5-4 cm. thick, long-cylindrical to clavate. Female inflorescences globose to ellipsoid, on peduncles 3-13 cm. long, becoming 20-30 cm. in diameter, globose to ellipsoid; some varieties lacking seeds. Fruiting syncarp green to yellow with acute pyramidal projections.

Introduced plants usually found only in hot lowlands with sufficient rainfall to support an evergreen vegetation. The species is not a commercially important fruit in Central America. See Standley's discussion in "Flora of Guatemala," Fieldiana Botany 24, 4:12. 1946. This species is called *palo de pan*, breadfruit, or sometimes the bread-nut when seeds are present.

**Artocarpus heterophyllus** Lamarck, *Encycl. Meth. Bot.* 3:209. 1789. *A. integrifolius* auctores non L.f.

Trees to about 10 to 15 m. tall, leafy internodes 2-10 mm. thick, sparsely puberulent and becoming glabrous; stipules 1.5-5 (8) cm. long, minutely puberulent or glabrous. Leaves not especially variable in mature plants, petioles 1-3 (4) cm. long; laminae 8-20 cm. long, 4-10 cm. broad, broadly elliptic to obovate, rounded to obtuse at the apex, unlobed on mature plants, drying coriaceous and smooth above, with 4 to 8 pairs of major secondary veins. Male inflorescence on peduncles 1-5 cm. long borne in axils of leaves more distal than those subtending the female or cauliflorous, heads 2-7 cm. long and 8-28 mm. thick. Female inflorescences solitary or paired in axils of the lowest leaves or cauliflorous, on peduncles 5-10 cm. long, becoming heads 30-90 cm. long, 25-50 cm. thick, cylindrical to ellipsoid or clavate. Fruiting syncarp yellow and often with a sharp sweet unpleasant odor, the surface with small papillae.

Introduced plants occasionally planted in areas of evergreen vegetation between sea level and 1200 m. This species is called the Jack-fruit and probably originated in India.

### BATOCARPUS Karsten

Trees, unisexual, without spines, sap yellow or white; stipules paired and free, lateral, caducous and leaving small scars that encircle less than half the stem. Laminae distichous, petiolate, the lower surface with few microscopic ( $\times 200$ ) globose-capitate hairs, very small hooked (uncinate) hairs and round transparent epidermal cells with sharp conical apex. Male inflorescences long slender spikes, solitary in the axils of leaves or several on leafless short-shoots, pedunculate, flowering portions of the spike usually long (5-12 cm.) and thin (1-4 mm.), male flower with a minute 2- to 4-lobed perianth and a single stamen, anthers minute (less than 0.5 mm.). Female inflorescences usually solitary and short-pedunculate, a globose to ellipsoid head of many compacted flowers and lacking an involucre; the female flowers with a tubular truncate fleshy perianth, the ovary free (superior) but enclosed within the perianth, style short, stigmas 2, short and reflexed. Fruit formed within the fleshy globose infructescence formed by the fleshy accrescent perianths closely crowded together on the fleshy receptacle, the perianths coherent but not grown together, seed with a thin coat.

A very poorly known genus of three species ranging from southwestern Costa Rica to Bolivia. The slender spikes of staminate flowers with single stamens tightly congested and the round heads of coherent female flowers are very distinctive. The male spikes resemble those of *Piper* and the infructescences resemble those of *Annona*. The genus is probably closely related to *Acanthinophyllum* of South America; the male spikes are similar to those of *Clarisia biflora*, among our species.

This circumscription of the genus follows that of Fosberg (*Proc. Biol. Soc. Wash.* 55:99-101. 1942), who synonymized *Anonocarpus*



of South America under *Batocarpus*. Woodson (Ann. Missouri Bot. Gard. 47:134-136. 1960) mistook a collection of *Maquira costaricana* (Cooper 601) for the male of *Batocarpus orinocensis* and concluded that *Batocarpus* and *Anonocarpus* differed in their male inflorescences. Our species of the genus is known from only two female collections. The genus has recently been revised by De Mello Filho in Bol. Mus. Nac. Rio de Janeiro Bot. 37:1-15. 1968.

***Batocarpus costaricensis* Standley & L. O. Williams, Ceiba, 3:25. 1952. Figure 15.**

Trees to 30 m. tall, the trunk slender (45 cm.) and without buttresses, sap from the trunk pale yellowish-white, sap from the branchlets and fruit dull orange, leafy internodes 0.5-3 cm. long, 1.5-5 mm. thick, very minutely (0.05-0.2 mm.) puberulent with thin usually ascending hairs, dark brown but becoming glabrous and grayish; stipules about 5 mm. long and 2 mm. thick near the base, covered with thin ascending brown or yellowish-brown minutely sericeous hairs, scars about 1-1.5 mm. broad, encircling less than half the stem. Leaves often asymmetric, petioles 4-8 mm. long, about 2 mm. thick, minutely and sparsely puberulent, the periderm flaking off in age; laminae 8-17 cm. long, 3-6.5 cm. broad, elliptic-oblong, often with one side broader than the other, gradually or more often abruptly narrowed to the short acuminate apex, obtuse to rounded or acute on one side at the usually unequal base, margin bluntly serrate to obscurely serrulate with 1 to 3 teeth per cm., the laminae drying stiffly chartaceous, smooth and glabrous above, glabrous or very sparsely and minutely puberulent beneath, the midvein flat or slightly impressed above, the 8 to 12 pairs of major secondary veins irregularly loop-connected near the margin, microscopic globose-capitate hairs few or absent beneath, very small ( $\times 150$ ) hooked hairs and round transparent epidermal cells with sharp conical apex present beneath, the stomates readily visible. Male inflorescences and flowers not known (see generic description). Female inflorescences subsessile globose, about 2 cm. thick, the many flowers tightly congested and only opening apically; female perianth parts brownish velutinous, the rounded apices little projecting from the surface of the head, style and stigmas projecting about 2 mm. above the head. Fruit borne within the fleshy subsessile globose syncarp 4-5 cm. in diameter, green becoming brownish (dry), perianth and ovary coherent but not becoming fused in fruit, perianth parts fleshy and remaining rounded apically (on the surface of the smoothly globose head), seed about  $10 \times 5$  mm.

Plants of the wet evergreen forest formation of the Golfo Dulce area in southwestern Costa Rica between 50 and 500 m. elevation; collected with early and mature fruit in February. This species is known from only two collections made by Paul Allen (5948 & 5971) near Palmar Norte, Puntarenas.

*Batocarpus costaricensis* is recognized by the serrulate often slightly asymmetric leaves, tall habit with slender trunk, small lateral stipules, globose heads of female flowers with thick perianth that remains separate in fruit, and (probably) the male flowers

tightly congested on slender spikes. Allen (Rain Forests of Golfo Dulce 136. 1956) states that the male flowers are in catkin-like spikes, but we have no collections of staminate material. The fruiting heads resemble those of *Maclura* (Moraceae) or *Annona* (Annonaceae).

### BROSIMUM Swartz

REFERENCE: C. C. Berg, Brosimeae, Fl. Neotrop. Monog. 7:161-208. 1972.

Bisexual or unisexual trees, without spines, usually with small uncinata hairs on the younger parts, the latex white or yellowish; stipules free and paired or united and solitary, fully encircling the stem or not, usually caducous. Leaves distichous, usually entire, the microscopic multicellular hairs of the lower leaf-surface globose-capitate or oblongoid-capitate. Inflorescences bisexual or unisexual, paired or solitary in the leaf-axils, pedunculate, the receptacle at first covered with round peltate bracts, capitate and globose to hemispheric, turbinate or convexly discoid; the male flowers several to many on an inflorescence, perianth 4-lobed or 4-parted (as in *B. costaricanum*) or variously reduced in number and size or lacking, the stamens 4 to 1, filaments straight in bud, anthers latrorse to extrorse (with circumscissile dehiscence in *B. alicastrum*), a pistillode absent; the female flowers usually 1 (several) in an inflorescence, the flower immersed in and fused with the receptacle beneath, perianth vestigial and united with the ovary beneath, stigmas 2. Fruit borne within the enlarged and pulpy, yellowish or red receptacle, seed large, cotyledons thick, equal or unequal.

A genus of 13 species ranging from Mexico and the Greater Antilles southward to southern Brazil. The globose to discoid head can be either unisexual or bisexual with one or a few female flowers imbedded centrally; the male flowers are usually found over a large part of the inflorescence surface. The peltate bracts, thin and flat distally and round in outline, cover the young inflorescence and probably indicate a relationship with other genera having similar bracts, such as *Clarisia* and *Sorocea*. Many species of *Brosimum* grow to be very tall (50 m.), have useful wood, potable sap, and edible fruit. These plants are very poorly represented in herbaria, perhaps because of their size. They are often called *ojoche*, *ramon*, and *breadnut* in Central America. These names also are applied occasionally to species of *Trophis* and *Sorocea*.

- 1a. Stipules of the same node completely united and thus solitary at a node, completely encircling the stem, the stipule scar completely encircling the stem; heads usually bisexual . . . . . 2a.
- 1b. Stipules of the same node free and paired, the stipule scars variable but not completely surrounding the stem; heads bisexual or unisexual. . . . . 3a.

- 2a. Laminae 15-30 (50) cm. long; heads becoming 3 cm. thick in fruit . . . . *B. utile*.
- 2b. Laminae 2-13 cm. long; heads becoming 2 cm. thick in fruit . . . . *B. rubescens*.
- 3a. Stipule scars of the same node encircling more than half the stem and almost joining on the leaf-opposed side of the stem; leaves usually glabrous; heads unisexual, stamens often with united anthers and circumscissile dehiscence  
*B. alicastrum*.
- 3b. Stipule scars of the same node encircling less than half the stem . . . . . 4a.
- 4a. Stipule 3-15 mm. long and broad above the base with prominent raised fan-like venation; lamina with the midvein often deeply impressed above, 3-12 cm. broad, usually glabrous, tertiary venation prominent beneath . . . *B. lactescens*.
- 4b. Stipule 2-7 mm. long but narrow and the venation not prominent; the midvein flat above, laminae rarely more than 5 cm. broad, usually puberulent beneath and the tertiary veins flat . . . . . 5a.
- 5a. Laminae with the midvein often minutely puberulent above, the lower surface usually with thin straight hairs and brownish in color; the heads usually globose, unisexual, anthers about 1 mm. long. . . . . *B. costaricanum*.
- 5b. Laminae with the midvein glabrous above, usually very lustrous above, the lower surface with minute (0.2 mm.) hooked hairs and with a grayish color and microscopic (150X) projections on the epidermis; the heads often lobed, hemispheric to discoid, usually bisexual, anthers about 0.2 mm. long. . *B. guianense*.

***Brosimum alicastrum*** Swartz, Prod. Veg. Ind. Occ. 12. 1788.  
*Helicostylis ojoche* Schumann ex Pittier, Pl. Usuales de Costa Rica 119. 1908. *Brosimum terrabanum* Pittier, Contr. U.S. Nat. Herb. 18:69. 1914. *B. bernadetteae* Woodson, Ann. Missouri Bot. Gard. 47:131. 1960. *B. gentlei* Lundell, Wrightia 3:167. 1966. Figure 15.

Trees to 45 m. tall, unisexual (rarely bisexual?), with buttresses, latex white to yellow, leafy internodes 0.5-5 cm. long, 1-4 mm. thick, glabrous or very sparsely puberulent; stipules paired, 3-15 mm. long, 1-2 mm. broad at the base, glabrous or very minutely (0.1 mm.) puberulent along the midrib. Leaves usually symmetrical, petioles (2) 4-14 mm. long, 1-2.5 mm. thick, narrowly sulcate above; laminae 4-20 cm. long, 2-8 cm. broad, elliptic or oblong to somewhat ovate or obovate, acute to caudate-acuminate at the apex, acute to obtuse or rarely rounded at the base, margin entire to slightly repand or drying undulate, laminae chartaceous to subcoriaceous, smooth and glabrous above, glabrous or very minutely (0.1 mm.) puberulent beneath, midvein usually flat or slightly raised above, the 10 to 20 pairs of major secondary veins usually loop-connected near the margin, the tertiary veins often forming a parallel intermediate vein between adjacent secondaries, microscopic oblongoid hairs and hooked (uncinate) hairs present on the veins beneath. Male inflorescences usually 1 or 2 per axil, borne on peduncles to 16 mm. long, heads globose to ellipsoid, 3-8 mm. in diameter, peltate bracts 0.2-2 mm. broad present and minutely puberulent, with usually 1 central non-functional female flower, male flowers not organized, the surface covered with many individual stamens; male perianth absent or minute, filaments 0.4-1.6 mm. long, anthers 0.4-0.5 mm. long, the thecae fused and with circumscissile dehiscence (in subspecies *alicastrum*) or the thecae free and dehiscing laterally (in subspecies *bolivarense*). Female inflorescences usually 1 or 2 per axil, borne on peduncles to 14 mm. long (rarely sessile),

globose to ellipsoid, 2-5 mm. in diameter, peltate minutely puberulent bracts 0.2-2 mm. broad present on the surface of the receptacle, bracts near the base often basally attached, usually with 1 (2) functional female flowers; style 1.5-8.5 mm. long, stigmas 0.2-8 mm. long, unequal. Fruit borne within the globose succulent infructescence 1.5-2 cm. in diameter.

Plants of deciduous, partly deciduous, or wet evergreen forest formations from sea level to about 700 m. altitude (in our area). The species is represented by subspecies *alicastrum* in the Pacific watershed of Costa Rica and by subspecies *bolivarensis* (Pittier) Berg on the Caribbean watershed of Costa Rica and on both watersheds in western Panama. The species ranges from Sonora, Mexico, to Venezuela and Guyana in eastern South America, and southward to Peru and the state of Acre in Brazil. The species is also found on Cuba, Jamaica, Trinidad, St. Vincent, and Carriacou islands.

*Brosimum alicastrum* is recognized by the paired stipules almost completely encircling the stems, the almost glabrous leaves with unusual tertiary venation, the small globose inflorescences with flat thin round peltate bracts, the lack of organized male flowers (on the male head) and the very unusual anthers in subsp. *alicastrum*. This tree is often called *ojoche*, *ojeche*, *berga*, *ramon*, and *breadnut*. The foliage is often used to feed cattle, especially in the dry season. Sap and fruit are edible.

***Brosimum costaricanum*** Liebmann, Danske Vidensk. Selsk. Skrift. ser. 5,2:334. 1851. *Helicostylis montana* Pittier, Contr. U.S. Nat. Herb. 20:96. 1918. *Brosimum sapiifolium* Standl. & L. Wms., Ceiba 3:40. 1952. Figure 15.

Trees to 30 m. tall, unisexual, latex white, leafy internodes 0.6-3 cm. long, 1-3 mm. thick, with thin straight or slightly crooked yellowish hairs 0.1-0.5 mm. long; stipules paired, 3-7 mm. long, with thin ascending hairs along the midrib, stipule scars small (1 mm.) and encircling less than half the stem. Leaves usually symmetrical, petioles 3-8 mm. long, 0.7-1.5 mm. thick, sparsely to densely puberulent with minute (0.1-0.3 mm.) often retrorse and hooked hairs, terete or very slightly sulcate above; laminae (4) 7-15 cm. long, 1.5-4.5 cm. broad, narrowly elliptic to elliptic-oblong or narrowly obovate, gradually narrowed to the acuminate apex, acute to obtuse and slightly rounded at the base, margin entire, the lamina drying stiffly chartaceous, smooth and essentially glabrous above except over the midvein, with thin whitish hairs about 0.2 mm. long beneath, midvein usually flat or slightly impressed above, the 7 to 19 pairs of major secondary veins loop-connected near the margin, microscopic globose-capitate hairs present beneath. Male inflorescences borne on peduncles 3-6 mm. long, globose, about 6 mm. in diameter, with many peltate or subpeltate bracts 0.5-1.5 mm. broad, with many flowers; male perianth 3 or 4 parted, stamens 2 to 4 per flower, anthers about 1 mm. long and 0.4-0.5 mm.

broad, connective narrow. Female inflorescences borne on peduncles and solitary or 2 per node; female flower solitary. Fruit borne within the globose succulent infructescence about 15 mm. in diameter, fruiting peduncles 5-18 mm. long.

Plants of evergreen or partly deciduous forest formations on the Pacific slope of central and southern Costa Rica and western Panama between sea level and about 1000 m. altitude; flowering material has been collected from December to March. The species is known only from the area between Central Costa Rica (Naranjo, Alajuela) and the eastern border of Chiriquí province.

*Brosimum costaricanum* is recognized by the paired stipules leaving only small scars, the narrow leaves with thin short hairs, the small globose unisexual inflorescences with thin round peltate bracts, and the large anthers.

*Brosimum guianense* (Aubl.) Huber, Bol. Mus. Emilio Goeldi 5:337. 1909. *Piratinera guianensis* Aublet, Pl. Guian. 2:888, t. 340. 1775. *P. panamensis* Pittier, Contr. U.S. Nat. Herb. 20:100. 1918. *Brosimum panamense* (Pittier) Standl. & Steyer., Field Mus. Bot. 23:40. 1944. Figure 15.

Shrubs or trees to 30 m. tall, bisexual, with or without buttresses, latex white to yellow, leafy internodes 0.1-3 (6) cm. long, 0.8-3.5 mm. thick, very sparsely to densely puberulent with minute (0.2 mm.) thin often retrorse uncinata hairs, becoming gray; stipules 2-5 mm. long, densely to very sparsely puberulent, scars encircling less than half the stem. Leaves often asymmetric at the base, petioles 2-6 mm. long, 0.5-1.5 mm. thick, with retrorse uncinata hairs about 0.2 mm. long; laminae (2) 4-10 (15) cm. long, (1) 2-4.5 (6) cm. broad, elliptic-oblong to obovate-oblong or less often narrowly ovate, abruptly narrowed at the acute or short-acuminate apex, acute to obtuse or somewhat rounded (often on only one side) at the base, margin entire, the lamina drying chartaceous to subcoriaceous, smooth, glabrous, and lustrous above, very sparsely to densely puberulent beneath with minute thin hairs, the midvein prominent above, the 6 to 14 pairs of secondary veins forming an arcuate submarginal vein, the lower surface often grayish with microscopic (150X) projections on the epidermis, thin transparent hairs, and few oblongoid-capitate hairs distally orange. Inflorescences usually bisexual usually solitary, sessile or more often on peduncles to 20 (30) mm. long, the head hemispheric to broadly turbinate or discoid, often lobed, 3-12 mm. in diameter, the peltate bracts many, 0.4-1 mm. broad; male flowers few to many, male perianth 3- or 4-lobed, stamen 1 (per flower), filaments 0.3-0.8 mm. long, anthers 0.1-0.3 mm. long and almost equally broad, connective broad and swollen; female flower 1 to several (per head), style 0.4-1 mm. long, stigmas 0.1-0.3 mm. long. Fruit borne within the succulent globose or subturbinate infructescence about 12 mm. in diameter or the infructescence lobed and up to 16 mm. in diameter when containing 2 or more fruits, reddish at maturity, seed about 8 by 5 mm.

Plants of seasonally dry semi-deciduous forest or wet evergreen forest formations between sea level and 1000 m. elevation in both

primary and secondary vegetation. This species has a very discontinuous distribution pattern and is known in Costa Rica only from the Osa peninsula (*A. Jimenez 3044*). It is known from southern Mexico and British Honduras and from southern Panama, northern Colombia, northwestern Venezuela and coastal Brazil in the state of Guanabara, but the main areas of distribution are the Amazon Basin, the Guiana Shield, and Trinidad.

*Brosimum guianense* is recognized by its small paired stipules encircling less than half the stem, the small leaves shiny above and with unusual surface beneath ( $\times 150$ ), hemispheric to discoid heads with thin round peltate bracts, and male flower reduced to a single stamen. The larger trees of the neotropics have not been well sampled, and it is possible that this species does occur rarely in areas where it is presently thought to be absent.

***Brosimum lactescens*** (Moore) Berg, *Acta Bot. Neerl.* 19:326. 1970 *Brosimopsis lactescens* S. Moore, *Trans. Linn. Soc. ser. 2*, 4:473, t. 30 & 31. 1895. *Brosimum ojoche* Woodson, *Ann. Missouri Bot. Gard.* 47:126. 1960. Figure 15.

Trees to 35 (50) m. tall, unisexual, with buttresses, latex white to yellowish or greenish, leafy internodes 5-35 mm. long, 1.8-4 mm. thick, minutely (0.1-0.5 mm.) and sparsely puberulent with thin whitish hairs, often with minutely hooked (uncinate) hairs; stipules 3-15 mm. long, broad near the base, minutely puberulent along the midrib, with prominent fan-like venation. Leaves usually symmetrical, petioles (3) 4-14 mm. long, 1.3-3 mm. thick, very minutely (0.05-0.2 mm.) puberulent or glabrescent; laminae (3) 6-20 (32) cm. long, (2) 3-8 (12) cm. broad, elliptic to oblong-elliptic or occasionally somewhat ovate or obovate, gradually or abruptly narrowed to the acute or acuminate apex, acute to abruptly narrowed and somewhat rounded at the obtuse base, margin entire with the edge often revolute, the lamina drying very stiffly chartaceous to subcoriaceous, smooth above and often slightly scabrous beneath, glabrous or glabrescent above and below, midvein impressed above the 9 to 20 pairs of major secondary veins usually weakly loop-connected near the margin, tertiary veins forming a slightly raised reticulum beneath, microscopic straight or hooked (uncinate) hairs on the veins beneath (150X). Male inflorescences usually 2 per node, borne on peduncles 1-8 mm. long, usually with peltate bracts and small hooked hairs, the globose head 3-10 mm. in diameter with many flowers; and many peltate bracts 0.2-0.9 mm. broad; male perianth usually 4- (3-) parted, 1.5-2.5 mm. high, stamens 2 to 4, filaments 2-5 mm. long, anthers 0.6-1.5 mm. long and 0.2-0.7 mm. broad, thecae often apiculate or hairy at the tip. Female inflorescences usually solitary at a node, borne on peduncles 1-8 mm. long, globose to ovoid, obovoid, or lobed, 2-6 mm. in diameter, receptacle often covered with minute uncinata hairs and few to many peltate bracts 0.2-0.5 mm. broad, with broader (1 mm.) bracts near the base, 1 to 5 (13) flowers per head; styles 1-3 mm. long, stigmas 2-9 mm. long, filiform. Fruit borne within a globose infructescence when solitary or within a lobed in-

fructescence when 2 or more, the infructescence 1-2 cm. in diameter, becoming yellow to reddish, seed 1 cm. long.

Tall trees of the wet evergreen forest formations below 600 m. elevation (in our area) on the Caribbean watershed and in the Golfo Dulce area of Costa Rica; collected with flowers or fruit from December to May (in our area). The species ranges from Central Mexico to Costa Rica and in South America from the eastern Andes of Venezuela and Colombia to southern Brazil.

*Brosimum lactescens* is recognized by the paired short but broad stipules with prominent fan-like venation, the midvein usually conspicuously impressed above, the tertiary veins drying pale yellowish-brown and forming a fine reticulum beneath, the minute unciniate hairs on many parts, and the small unisexual inflorescences with thin round peltate bracts.

***Brosimum rubescens*** Taubert, Bot. Jahrb. 12 (Beibl. 27):4. 1890. *B. caloxylon* Standl., Trop. Woods 17:11. 1929. Figure 15.

Trees to 40 m. tall, usually bisexual, apparently without buttresses, latex white, leafy internodes (0.2) 0.6-7 cm. long, 0.8-3 mm. thick, glabrous to sparsely puberulent (in ours); stipules completely united and apparently solitary at the node, 5-28 (40) mm. long, 1-2 mm. thick, very sparsely and minutely puberulent, drying dark reddish-brown. Leaves usually symmetrical, petioles 2-10 (13) mm. long, less than 1 mm. thick, narrowly sulcate above, minutely (0.1-0.4 mm.) puberulent; laminae (2) 4-13 cm. long, 1-3.5 (6) cm. broad, short-acuminate to abruptly long-acuminate, acute to obtuse at the base, margin entire, lamina drying stiffly chartaceous to subcoriaceous, smooth and glabrous above, nearly glabrous to sparsely puberulent beneath, the 10 to 22 pairs of secondary veins loop-connected near the margin, slender oblongoid-capitate hairs present or absent on the veins beneath. Inflorescences usually bisexual, solitary, subglobose to subturbinate, hemispheric, or somewhat irregular, 2-8 mm. in diameter, borne on peduncles 2-12 mm. long and 0.2-2 mm. thick, receptacle glabrous to puberulent; peltate bracts few to many, 0.2-1.2 mm. broad; male flowers few to numerous, perianth 3- to 5-parted, 0.1-0.5 mm. high, stamens 1 or 2 (3), filaments 0.2-1.5 mm. long, anthers 0.1-0.3 mm. long, connective narrow or broad; female flowers 1 to several, style about 1 mm. long, stigmas 0.1-0.8 mm. long. Fruit borne within the succulent globose infructescence to 2 cm. in diameter, reddish at maturity.

Plants of lowland wet evergreen forest formations and known in our area only from sterile material collected by Cooper (535 the type of *B. caloxylon* and 607) in the region of Almirante, province of Bocas del Toro, Panama; the species ranges disjunctly to the Guianas, the Amazon Basin, and near Rio de Janeiro, Brazil.

*Brosimum rubescens* is recognized by the very slender stipules completely united and therefore solitary at the node and completely

encircling the stem, the small almost glabrous leaves with many veins (in ours), and relatively small usually bisexual heads with thin round peltate bracts. The tree has been called *bloodwood cacique* in Panama. The fact that our material is sterile and disjunct from other members of the species makes the assignment to this species somewhat tentative.

***Brosimum utile*** (H. B. K.) Pittier, Contr. U.S. Nat. Herb. 20:102. 1918. *Galactodendrum utile* H.B.K., Nov. Gen. & Sp. 7:125 (or 163). 1825. *Brosimum allenii* Woodson, Ann. Missouri Bot. Gard. 47:128. 1960. Figure 15.

Trees to 50 m. tall, usually bisexual, latex white, leafy internodes 0.7-8 cm. long, 3-7 mm. thick, very minutely puberulent and with sparse longer hairs, longer (0.5 mm.) hairs usually present below the stipule-scar; stipules united and solitary at the node, 0.8-1.8 cm. long (in ours), usually with ascending thin hairs about 0.2 mm. long. Leaves usually symmetrical, petioles 6-12 (20) mm. long, 2-4 mm. thick, dark brown and deeply ridged on drying; laminae 15-30 (56) cm. long, 5-12 (18) cm. broad, narrowly ovate to oblong or elliptic, abruptly short-acuminate, obtuse to somewhat rounded and truncate or subcordate (rarely acute) at the base, margin entire to repand, the lamina drying very stiffly chartaceous to coriaceous, smooth and glabrous above or puberulent near the petiole, glabrous to very sparsely puberulent beneath, the 20 to 30 pairs of major secondary veins usually loop-connected near the margin, tertiary veins occasionally parallel with each other, microscopic oblongoid-capitate orange hairs present on the lower surface. Inflorescences bisexual (rarely unisexual) and solitary, borne on peduncles 2-10 mm. long, subglobose and 5-10 mm. in diameter, with peltate bracts often long-stipitate; male flowers many on the surface of the head, male perianth with 4 basally connate parts about 1 mm. high, stamens 2, filaments 1.5-2 mm. long, anthers 0.8-1 mm. long and about 0.5 mm. broad, connective narrow, sometimes apiculate; female flower usually solitary in the distal center of the head, style about 1.5-2 mm. long, stigmas 0.5-3 mm. long. Fruit borne within the globose succulent head, the infructescence about 3 cm. in diameter at maturity and becoming brown.

Very tall trees of the evergreen forest formations below 700 m. elevation and apparently restricted to the areas of the General Valley and Golfo Dulce region on the Pacific side of southern Costa Rica in our area; the species ranges from southwestern Costa Rica to northern South America, Peru, and the Amazon Basin in Brazil. The species is represented in Costa Rica by the endemic subspecies *allenii* (Woodson) Berg.

*Brosimum utile* is recognized by the completely united (and therefore solitary) stipules forming an unbroken scar around the young stems, the relatively large leaves with many secondary veins, bisexual globose heads with many stamens usually in twos, and thin round peltate bracts. The very great height of these trees may ac-



count for the small number of collections: *Allen 5813* (type of the subspecies), *Echeverria 981*, *Marsh s.n.*, *Williams et al. 24234*. This species, as defined by Berg (*Flora Neotropica*, Monog. 7:1-229. 1972), includes considerable variation in floral structure in the different subspecies. More and better collections of the species throughout its range may require a reassessment of the importance of floral variations.

### CASTILLA Sessé

REFERENCE: C. C. Berg, *Olmedieae*, *Fl. Neotrop. Monog.* 7:92-104. 1972.

Trees, unisexual or bisexual, often with buttresses and self-pruning twigs; stipules united and fully encircling the stem, with distinct parallel venation, large and caducous. Leaves distichous and often large, short-petiolate, chartaceous to subcoriaceous, the margin entire or undulate, puberulent and often with a number of short hairs around the base of the rigid unicellular hairs, microscopic multicellular hairs infrequent and globose-capitate or oblongoid-capitate. Male inflorescences of two kinds, the primary pedunculate, widening to a flabellate bivalvate disc with the receptacle covered with large imbricate bracts in the primary inflorescences, the secondary inflorescences (associated with female inflorescences) much smaller and infundibuliform to cyathiform, entire to 2-lobed, with few to many stamens; male flowers not definitely organized, the stamens solitary or pairs along radiating and branched ridges of the receptacle, interspersed with free or connate membranaceous interstaminal bracts, anthers basifixed or dorsifixed. Female inflorescences usually solitary but often accompanied by small male inflorescences, sessile, discoid to cupuliform or subglobose, the receptacle with broadly overlapping bracts, many-to several-flowered; female flowers free or basally united, perianth tubular and entire or 4- (5-) lobed, the ovary free, partly united with the perianth, or immersed in the receptacle, stigmas short. Fruit united near the base, the infructescence 1.5-4.5 cm. in diameter, seeds with thick equal cotyledons.

A genus of three species ranging from Central Mexico to Peru and Brazil below 900 m. elevation but absent in northeastern South America and the West Indies except as introduced. These are very striking trees with relatively few wide-spaced branches and large distichous leaves borne on very short petioles. The stipules have become completely united and are therefore solitary at each node, surrounding and enclosing the shoot-apex in its early stages. In our area members of the genus are usually called *hule* or *ule*. Indian names used for members of the genus in Costa Rica are said to be *gsi-kra* (Brunka), *quiri* (Guatuso), *seru* and *soro* (Terraba), and *tsini* (Bribri and Cabecara). *Castilla elastica* has been used as a source of rubber in Costa Rica.

Laminae usually abruptly rounded and subcordate at the symmetrical base, margin usually minutely denticulate, often abruptly narrowed to the short-acuminate apex; stipules with white tomentellous hairs along the edges; Nicoya Peninsula and the Caribbean lowlands . . . . . *C. elastica*.

Laminae usually obtuse on one side of the asymmetric base, margin entire to undulate, often tapering gradually to the acuminate apex; stipules lacking white tomentellous hairs along the edges; common in the Golfo Dulce area but apparently rare on the Caribbean lowlands . . . . . *C. tunu*.

**Castilla elastica** Sessé in Cervantes, Suppl. Gaz. Lit. Mexico, 1794. *C. costaricana* Liebm., Danske Vidensk. Selsk. Skrift. ser. 5, 2:319. 1851. *C. nicoyensis* Cook, Science 18:438. 1903. *C. panamensis* Cook, loc. cit. Figure 16.

Trees to 30 (40?) m. tall, with low buttresses, sap white and rubber-like, leafy internodes 1-8 (12) cm. long, 3-13 mm. thick, with slender ascending yellowish to brownish hairs 0.5-1.5 mm. long; stipules 2-11 cm. long, densely ascending strigose to sericeous, the yellowish hairs minutely stellate at the base. Leaves usually symmetrical and the laminae in a single horizontal plane, petioles 5-20 mm. long, 1.5-4 mm. thick, densely strigose; laminae (10) 18-38 (55) cm. long, (5) 7-18 (25) cm. broad, oblong to obovate-oblong or slightly pandurate, mostly broadest above the middle but occasionally broadest below the middle and ovate-oblong, caudate to abruptly short-acuminate, the slender tip about 1 cm. long, usually truncate to cordulate at the subequal base, occasionally deeply cordate with the lobes overlapping, margin obscurely to minutely denticulate with 5 to 12 teeth per cm. often marked by tufts of hairs, laminae drying stiffly chartaceous to subcoriaceous, scabrous or slightly scabrous above with scattered stiff hairs 0.2-0.6 mm. long between the veins and longer hairs more dense on the major veins, lower surface with strigose or hispid hairs grayish-white to yellowish-brown in color, the 14-22 pairs of major secondary veins not usually loop-connected near the margin, microscopic globose-capitate hairs present on the lower surface but often difficult to see, the larger hairs often echinate or stellate at the base ( $\times 100$ ). Male inflorescences associated with the female flowers variable, 5-20 mm. broad, independent male inflorescences often 4 per node, borne on peduncles 3-15 mm. long, conduplicate-reniform and 2-valved or 2-valved and folded with a U-shaped apex (a folded discoid structure with the stamens on the inner face), about 10-25 mm. broad and 7-25 mm. high, receptacle covered with 10 to 12 series (centrally) of many yellow strigose bracts often acuminate at the apex, interstaminal bracts irregular in shape, to 2.5 mm. long, puberulent; stamens numerous, solitary, filaments 0.5-3.5 mm. long, anthers mostly 0.5-1.2 mm. long, often irregular and unequal. Female inflorescences solitary (rarely paired) but often with small male inflorescences, sessile or subsessile, discoid to cupuliform, 1-2 cm. in diameter, receptacle covered with 5 to 10 series of many yellow strigose bracts acute to acuminate at the apex, with (10) 15 to 30 basally connate flowers; female perianth-tube 2-3 mm. high, 4-lobed, minutely velutinous, ovary partly united with the perianth, style short (to 1.5 mm.) with long (3-6 mm.) stigmas or the style longer (2-3 mm.) and with shorter stigmas, stigmas 2 (3). Fruit ellipsoid, 8-10 mm. long, borne within the velutinous accrescent perianth, united below and free (3-10 mm.) above, borne on the surface of the discoid infructescence 2.5-4.5 cm. broad, perianth ribbed and grooved.

Trees of wet evergreen forest formations between sea level and 850 m. elevation and also found in seasonally dry, partly deciduous forest formations; flowering throughout the year but collected most often between January and June. The species ranges from Mexico through Panama and the coastal regions of western Colombia to western Ecuador and is represented in our area by two subspecies (see below): *ssp. elastica* and *ssp. costaricana* (Liebm.) Berg.

*Castilla elastica* is recognized by the large distichous leaves often held in a horizontal plane, generally oblong laminae subcordate at the base and very abruptly narrowly acuminate at the apex, the yellowish strigose hairs on most parts (these often minutely echinate or stellate at the base), the 2-valved or doubly folded male inflorescences, the discoid female infructescence with fruiting perianth united basally, and the single large stipule enclosing the shoot apex. The species is represented in Costa Rica by two subspecies that are apparently geographically disjunct in our area. They can usually be separated in the following way:

Hairs usually spreading (patent) on the secondary veins beneath; free part of the fruiting perianth much longer than the basal united part; styles 0-1.5 mm. long, stigmas 3-6 mm. long; Nicoya peninsula . . . . . *ssp. elastica*.  
 Hairs usually appressed or ascending on the secondary veins beneath; free part of the fruiting perianth much longer to less than the length of the basal united part; styles 1.5-3 mm. long, stigmas 2-3 mm. long; Caribbean lowlands . . . . .  
*ssp. costaricana*.

**Castilla tunu** Hemsley, Hook. Ic. Pl. 27:2651. 1900. *C. fallax* Cook, Science 18:438. 1903. Figure 16.

Trees to 35 m. tall, with buttresses, latex yellow to dark brown and said to be gum-like not rubber-like, leafy internodes 1-7 cm. long, 4-12 mm. thick, densely covered with slender appressed-ascending yellowish hairs about 0.5 mm. long, often hollow; stipules 2-10 cm. long, densely strigose or sericeous with golden-brown hairs, completely united and apparently solitary at the node. Leaves distinctly asymmetric at the base, petioles 6-18 mm. long, usually 3-4 mm. thick, densely sericeous or strigose; laminae 16-40 cm. long, 6-16 cm. broad, oblong to elliptic-oblong or slightly obovate, narrowed to the short-acuminate apex, the base usually oblique with one side acute and the other rounded to obtuse, margin entire or repand, the lamina drying stiffly chartaceous to subcoriaceous, somewhat scabrous above with scattered slender appressed hairs 0.2-0.8 mm. long (denser on the veins), slightly scabrous and more densely strigose beneath, the 16 to 20 pairs of major secondary veins not usually loop-connected near the margins, microscopic globose-capitate or oblongoid-capitate hairs often orange and difficult to see among the larger hairs with unusual rough surfaces ( $\times 150$ ). Male inflorescences paired in the axils of leaves, subsessile, 2-valved conduplicate-reniform (a folded discoid structure with the stamens on the inner faces), 12-20 mm. broad, 6-15 mm. high, receptacle covered

with 10 to 18 series of bracts (in the central area), the bracts yellowish or golden-brown strigose to sericeous; interstaminal bracts triangular, acute, puberulent; stamens many, often paired, filaments 1-3 mm. long, anthers 0.5-1 mm. long and equally broad. Female inflorescences solitary and sessile, at leafy or leafless nodes, discoid, 1-1.5 cm. in diameter, receptacle covered with 6 to 8 series of yellowish strigose to sericeous bracts, flowers 15 to 30, usually free to the base; female perianth tubular, 2-3.5 mm. high, entire or dentate, densely puberulent, style 2-2.5 mm. long, stigmas 1-1.5 mm. long, twisted. Fruit ellipsoid, 7-9 mm. long, enclosed within the (free) 3- to 5-ribbed yellowish to orange sericeous perianth-tube, the 10 or more fruits borne on the discoid or oblate-globose infructescences 2.5-3.5 cm. in diameter.

Plants of lowland wet evergreen forest formations between sea level and 200 m. elevation, apparently common in the Golfo Dulce area but rare in the Caribbean lowlands of Costa Rica; probably flowering throughout the year, but collected primarily between December and March in our area. The species ranges from British Honduras to northwestern Colombia.

*Castilla tunu* is recognized by the large oblong, often drooping leaves asymmetric at the base, the yellowish-brown sericeous or strigose hairs on many parts, the 2-lobed male inflorescences and the discoid female infructescence with separate (basally congested) angled and ellipsoid fruiting perianth, and the single stipule enclosing the shoot-apex.

### CECROPIA Linnaeus

Unisexual trees, upper trunk and branches often hollow with transverse septa, primary branches usually few and often forming an open candelabra-like crown, bark smooth and usually very pale gray, most species often harbouring aggressive ants within the stems; stipules completely united and apparently solitary, fully enclosing the stem and leaving an encircling scar, usually large. Leaves borne in a spiral, simple, the first leaves unlobed and narrowly elliptic, often with a serrate margin, the subsequently formed leaves showing a gradual transition (first 3 lobes, then 5, etc.) to the typical adult foliage, peltate, petioles long and often enlarged beneath at the base (the pulvinus); laminae slightly to deeply lobed and usually eccentrically peltate in ours, tertiary veins usually subparallel. Inflorescences paired in the axils of leaves, each inflorescence of minute (ca. 1 mm. long) densely congested flowers in several to many spikes at first enclosed in a deciduous or caducous spathe at the apex of a common peduncle. Male flowers with a tubular perianth thickened and transversely split at the apex, anthers 2, usually exerted individually. Female flowers with a shredding tubular perianth, stigma one and minutely fimbriate, ovule basal in the locule. Fruit a minute achene, with glabrous surface.

*Cecropia*, containing perhaps as many as 60 species, is one of the most characteristic genera of the American tropics. Some species are common in secondary growth, and their tall, few-branched habit

with very large umbrella-like leaves produces a striking silhouette. Other species are found in mature forests and may reach 30 m. in height. The aggressive biting ants that are often present in these trees have apparently deterred botanical collectors, so that these common plants are poorly represented in herbaria and their species are very poorly understood. Knowledge of both male and female flowering parts is necessary for the effective delimitation of species. These plants are commonly called *guarumo* in Central America.

*Cecropia* belongs to the subfamily Conocephaloideae and, like the other genera of that subfamily, is probably more closely related to genera of the Urticaceae than to other Moraceae. The Conocephaloideae are retained in the Moraceae here for the sake of convenience, though their basal ovules and lack of milky sap in leaves and inflorescences indicate their proper placement in Urticaceae (Corner, Gard. Bull. Singapore 19:187-252. 1962). *Cecropia* is closely related to *Musanga* of Africa and more distantly to *Cousapoa* and *Pourouma*.

The ants housed by a single *Cecropia* tree can reach very large numbers. They feed on minute food-bodies (Mullerian bodies) produced among the short matted hairs of the pulvinus at the base of the petiole, as well as on the sugary exudate of associated coccid insects. Among our species, *C. polyphlebia* and *C. pittieri* have never been reported to be associated with ants.

- 1a. Laminae very shallowly lobed; plants endemic to Cocos Island. . . . . *C. pittieri*.
- 1b. Laminae with sinuses one-third as deep as the adjacent primary veins or deeper; plants not found on Cocos Island . . . . . 2a.
- 2a. Laminae smooth to the touch above, primary veins 7 to 11 in mature foliage; male and female spikes 5-12 cm. long, 7-12 mm. thick, wet evergreen formations 0-1500 m. elevation . . . . . *C. insignis*.
- 2b. Laminae scabrous above, male spikes usually more slender . . . . . 3a.
- 3a. Primary veins 11 to 13 (rarely 8 to 15) in mature foliage, longest primary vein with about 30 pairs of secondary veins, laminae very deeply lobed; female spikes 18-50 cm. long, male spikes 8-22 cm. long; wet evergreen formations, 0-1200 m. elevation . . . . . *C. obtusifolia*.
- 3b. Primary veins usually 7 to 11; spikes usually shorter . . . . . 4a.
- 4a. Longest vein of the leaf with 14 to 20 pairs of major secondary veins, sinuses about half the length of the adjacent primary veins; common plants of secondary growth in wet and seasonally dry formations, 0-1200 m . . . . . *C. peltata*.
- 4b. Longest vein of the leaf with 30 to 40 pairs of major secondary veins, sinuses about three-fourths the length of the adjacent primary veins; plants with conspicuous long whitish hairs and lacking ants, in very wet montane forests, 1400-2400 m. . . . . *C. polyphlebia*.

***Cecropia insignis*** Liebmann, Danske Vidensk. Selsk. Skrift., ser. 5, 2:318. 1851, e descr. *C. eximia* Cuatrecasas, Rev. Acad. Colomb. Cienc. 6:287. 1945, (female); descr. ampl. loc. cit. 9:326-327. 1956, (male). *C. sandersoniana (standleyana)* P. Allen, The Rain Forests of Golfo Dulce: 162 & 709. 1956. Figure 23.

Trees 10-40 m. tall, the trunk becoming 90 cm. thick above the buttresses, young trunks said to be dark in color and without rings, stilt-roots becoming buttresses; stipules (12) 18-34 cm. long, about 6 cm. thick unopened, pink or reddish (live), sparsely to densely strigose with whitish hairs about 1 mm. long and rough to the touch. Leaves simple, petioles 40-90 cm. long, 1-2.5 cm. thick, sparsely to densely puberulent with whitish arachnoid hairs closely appressed to the surface, longitudinally ribbed, basal thickening (pulvinus) with a dense covering of small brownish scabrous or velutinous hairs and longer thin interspersed whitish hairs; laminae eccentrically peltate, 40-120 cm. long and almost as broad, with (7) 8 to 10 (11) lobes, sinuses two-thirds to seven-eighths as long as the adjacent primary veins, the longer lobes tapering to a bluntly obtuse apex, the shorter lobes rounded apically, margins entire and undulate, the lamina drying stiffly chartaceous to subcoriaceous, smooth and glabrous or with slender stiff hairs above, glabrous or minutely puberulent on the veins beneath, areas between the veins greenish to densely whitish arachnoid-lanate, primary veins (7) 8 to 10 (11), longest primary vein with 18 to 30 pairs of major secondaries, central secondaries arising at angles of 40-60 degrees and 12-25 mm. distant, tertiary veins readily apparent. Male inflorescences with common peduncles about 10 cm. long and 12 mm. thick bearing 5 to 7 spikes, male spikes about 6 cm. long and 7-10 mm. thick, borne on individual peduncles 4-20 mm. long and 4-6 mm. thick, the enclosing spathe 10-15 cm. long and 2-4 cm. thick before anthesis. Female inflorescences with common peduncles 8-12 cm. long and 5-8 mm. thick, bearing 5 to 7 spikes, female spikes (6) 8-12 cm. long, 8-12 mm. thick, borne on individual peduncles 5-10 mm. long and about 6 mm. thick or occasionally subsessile. Fruiting spikes becoming 13 cm. long and 15 mm. thick, seeds 2-2.5 mm. long, about 0.8 mm. thick, longitudinally 2- or 3-angled, pointed at both base and apex, surface slightly muricate.

This species occurs in both secondary and primary vegetation from near sea level to 1500 m. elevation in wet evergreen forest formations on both the Pacific and Caribbean sides of Costa Rica; flowering from January to June and fruiting through September. The species ranges southward to Colombia.

*Cecropia insignis* is recognized by the deeply lobed leaves with relatively few primary and secondary veins and the very thick male spikes. The leaves vary from bright whitish to dull green beneath. *Cecropia insignis* is vegetatively very similar to *C. sylvicola*, a montane forest species of Nicaragua to Guatemala, but the male inflorescences are very different. The description of the male spikes of this species (under *C. eximia*) in the "Flora of Panama" (Woodson, Ann. Missouri Bot. Gard. 47:175. 1960) is incorrect and, I believe, was based on a mixed collection from Costa Rica (*United Fruit Co.*

390) in the U.S. National Herbarium. Liebmann listed two species of *Cecropia* from Costa Rica: *C. humboldtiana* Klotzsch, apparently a synonym of *C. peltata*, and *C. insignis*. Both were based on collections of Oersted along the Río San Juan. The description of *C. insignis*, though it lacks flowering or fruiting parts, clearly refers to this large-leaved species. I thank Dr. Leslie Holdridge for pointing this out.

*Cecropia obtusifolia* Bertoloni, Fl. Guatemal. 39. 1840. *C. mexicana* Hemsl., Biologia Cent. Amer. 3:151. 1883. *C. panamensis* Hemsl., loc. cit. 151. *C. mexicana* var. *macrostachya* Donn.-Smith., Bot. Gaz. 27:442. 1899. Figure 23.

Trees 5-15 (20) m. tall, trunk becoming 25-50 cm. thick, bark gray to whitish, major branches few, leafy internodes 1.5-4 cm. thick, very scabrous, usually inhabited by biting ants; stipules 5-12 cm. long, sparsely whitish sericeous. Leaves simple, said to be 4-ranked, petioles 25-60 (90) cm. long, 10-15 mm. thick, minutely (0.1-0.3 mm.) grayish-white puberulent, longitudinally ridged, pulvinus at the petiole-base beneath with a dense covering of brown velutinous hairs and very few longer whitish hairs; laminae eccentrically peltate and deeply lobed, 35-75 cm. long and almost as broad, with (8) 10-13 (15) lobes, sinuses one-third to four-fifths as long as the adjacent primary veins, longer lobes with rounded, obtuse, or occasionally very short-acuminate apices, margins entire and undulate, the lamina drying very stiffly chartaceous or subcoriaceous, dark, scabrous, and sparsely puberulent above, very minutely (0.05-0.1 mm.) puberulent on the veins beneath or the hairs longer (0.5 mm.) and sparse, areas between the veins pale greenish to grayish-white, primary veins (8) 10-13 (15), longest primary with about 30 pairs of major secondary veins, central secondaries arising at angles of 30-60°, an arcuate marginal vein and the tertiary veins usually readily visible. Male inflorescences with common peduncles (3) 5-25 cm. long and 3-6 mm. thick, glabrous or very minutely puberulent bearing 12 to 18 spikes emerging from a spathe 9-13 cm. long and 1.5-2 cm. thick; male spikes 8-22 cm. long, (2) 3-5 mm. thick, borne on individual peduncles 5-10 (25) mm. long, 0.5-1.3 mm. thick, often united above the spathe-scar. Female inflorescences with common peduncles 6-23 (32) cm. long, 6-8 mm. thick, sparsely puberulent with thin whitish hairs 0.5 mm. long, bearing usually 4 (3-5) spikes from within spathes 18-28 cm. long and about 2 cm. thick; female spikes 18-50 cm. long, 3-6 mm. thick, subsessile or on individual peduncles 1-10 mm. long and 3-5 mm. thick. Fruiting spikes becoming 10 mm. thick; fruit about 2 mm. long and 1.2 mm. broad, usually flattened, abruptly rounded at base and apex, the surfaces smooth.

Common plants of open secondary vegetation only rarely encountered as tall prop-rooted individuals in mature forest in areas of wet evergreen formations between sea level and 1200 m. altitude on both the Caribbean and Pacific slopes of Costa Rica; probably flowering throughout the year. This species appears to be absent in the seasonally very dry (tropical dry) formations of the Pacific slope. The species ranges from central Mexico to northern South America.

*Cecropia obtusifolia* is recognized by the deeply lobed leaves, very long female spikes, long slender male spikes, and apparent preference for areas of high rainfall or high soil moisture.

***Cecropia peltata* L.**, Syst. Nat. ed. 10, 2:1286. 1759. *C. arachnoidea* Pittier, Contr. U.S. Nat. Herb. 18:226. 1917. *C. asperrima* Pittier, loc. cit. 227. Figure 23.

Trees 8-15 (20) m. tall, trunk and stems pale in color with encircling rings, leafy internodes and stems hollow and often harbouring biting ants; stipules 5-9 cm. long, about 2 cm. thick unopened, sparsely to densely puberulent with short (1 mm.) stiff whitish hairs and scabrous. Leaves simple, petioles 15-50 cm. long, 5-12 mm. thick, densely to sparsely puberulent with crooked whitish hairs 0.1-0.5 mm. long, longitudinally ridged, the basal thickening (pulvinus) with a dense covering of brown velutinous hairs with usually few longer whitish hairs interspersed; laminae eccentrically peltate, 25-90 cm. long and almost as broad, with (8) 9 to 11 (12) lobes, distal lobes about twice the length of the basal lobes, largest lobes 6-12 cm. broad, sinuses one-third to two-thirds as long as the adjacent primary veins, the longer lobes tapering to an obtuse or rounded apex (rarely abruptly short-acuminate), margins entire and undulate, the lamina drying very stiffly chartaceous to subcoriaceous, minutely puberulent, scabrous and dark above, minutely (0.1-0.3 mm.) puberulent on the veins beneath, sparsely to densely whitish arachnoid-villous between the veins, primary veins (8) 9 to 11 (12), longest primary vein with 14 to 20 pairs of major secondary veins, central secondaries arising at angles of 30-60 degrees, tertiary veins often obscured by the tomentum. Male inflorescences with common peduncles 3-14 (16) cm. long, 2-4 mm. thick, bearing 12 to 32 (40) spikes, at first enclosed in a spathe 4-8 cm. long and 1.5-3 cm. thick; male spikes (1.5) 3-7 cm. long, 2-4 mm. thick, subsessile or borne on individual peduncles 1-8 mm. long and 1-2 mm. thick, male flowers tightly compressed. Female inflorescences with common peduncles 6-10 cm. long, 2-3 mm. thick, sparsely to densely puberulent and bearing (2) 3 to 4 (6) spikes, emerging from within a spathe 6-12 cm. long; female spikes (2.5) 4-10 cm. long, (4) 5-10 mm. thick, subsessile on the common peduncle, tomentum between the pistils whitish and evident in fruit. Fruiting spikes becoming 10-12 mm. thick, fruit about 2 mm. long and 0.8 mm. thick, longitudinally 2-or 3-angled, ellipsoid, the surfaces muricate.

Common plants of secondary growth ranging from sea level to 800 m. altitude or less commonly to 1200 m., collected most often on the seasonally dry Pacific side and only rarely in the Caribbean lowlands in Costa Rica, probably flowering throughout the year. The species ranges from Mexico to Colombia, Venezuela, and the West Indies.

*Cecropia peltata* is characterized by the leaves with lobes about half as long as the primary veins, the very short female spikes, the very large numbers of short male spikes on each common peduncle, and the tolerance of seasonally dry conditions. *Cecropia maxonii* Pittier from El Boquete, Chiriquí, is probably no more than an unusual specimen of *C. peltata* with rugose leaf-surfaces.



***Cecropia pittieri*** Robinson in Stewart, Proc. Calif. Acad. Sci. ser. 4, 1:389. 1912.

Trees 10-20 m. tall, leafy internodes 2-4 cm. thick, with short (0.5 mm.) stiff white hairs; stipules often persisting, 11-17 cm. long, 1.5-4 cm. thick unopened, whitish sericeous except along the margin abaxially. Leaves simple, petioles 20-40 cm. long, about 10 mm. thick, densely grayish-white puberulent with appressed arachnoid hairs, the basal pulvinus usually lacking short velutinous hairs and with scattered whitish hairs; laminae eccentrically peltate, 20-60 cm. long, with usually 9 or 10 short lobes, sinuses about one-fourth to one-third as long as the adjacent primary veins, lobes broadly rounded at the apex, distal portion of the lamina (petiole to apex) about twice as long as the basal (petiole to base) portion, drying very stiffly chartaceous to subcoriaceous, smooth or slightly scabrous and very sparsely puberulent above, with slender whitish hairs 1-2 mm. long on the veins beneath. areoles between the veins pale grayish with a very minute appressed tomentum, primary veins usually 9 or 10, longest primary vein with 18 to 22 prominent secondary veins, central secondaries arising at angles of 35-70 degrees. Male inflorescences with common peduncles about 8 cm. long and bearing about 19 sessile spikes emerging from a spathe 14-16 cm. long; male spikes about 10 cm. long and 3 mm. thick. Female inflorescences with common peduncles 6-10 cm. long, with usually 4 spikes; the female spikes 14-22 cm. long and 5-6 mm. thick, spikes usually subsessile. Fruiting spikes 6-10 mm. thick, fruit 1-1.5 mm. long, about 0.8 mm. broad, flattened on 2 sides and abruptly rounded at base and apex, surfaces smooth.

This species is endemic to Cocos Island and common on that island's eastern and northern coasts, especially on steep slopes near the beach, to 150 m. elevation.

*Cecropia pittieri* is characterized by its isolated island habitat and very shallowly lobed leaves. The species is not known to be associated with ants, and the pulvinus at the petiole-base lacks the unusual brownish velutinous hairs characteristic of our continental species.

***Cecropia polyphlebia*** Donnell-Smith, Bot. Gaz. 27:442. 1899. Figure 23.

Trees 8-25 m. tall, trunk becoming 40 cm. in diameter at breast height, leafy internodes 2-5 cm. thick, with translucent or white slender hairs 2-10 mm. long; stipules 9-30 cm. long, covered with long whitish hairs abaxially except along the margins. Leaves simple, petioles 25-55 cm. long, 6-14 mm. thick, longitudinally ridged, sparsely to densely tomentose or villous with whitish or translucent multicellular hairs 2-8 mm. long; base of the petiole beneath (pulvinus) with the very short velutinous brownish hairs obscured by the longer whitish hairs; laminae eccentrically peltate and deeply lobed, 30-80 cm. long, almost as broad, lobes 10 or 11, sinuses two-thirds to seven-eighths as long as the adjacent primary veins, lobes 6-12 cm. wide, the longer lobes obtuse to acute or short-acuminate at the apex, entire and somewhat undulate, drying very stiffly chartaceous to subcoriaceous, scabrous and with short (1 mm.) slender hairs on the veins above, very sparsely to moderately

strigulose between the veins, very sparsely to densely soft villous on the veins beneath with hairs 0.3-10 mm. long, aereoles between the veins whitish with a dense arachnoid tomentum, the primary veins 10 or 11, longest primary veins with 30 to 40 pairs of prominent secondaries, central secondaries arising at angles of 30-50 degrees, about 5-10 mm. distant, a loop-connected marginal vein often apparent, tertiary veins usually dark in contrast to the whitish surface. Male inflorescences solitary or paired, with common peduncles 4-7 cm. long and about 4 mm. thick, flattened and ridged on drying, glabrous except near base and apex, bearing 8 to 16 spikes emerging from a caducous spathe 4-8 cm. long; male spikes 2.5-4.5 cm. long, 5-8 mm. thick, borne on very short peduncles at the strigulose apex of the common peduncle. Female inflorescence with common peduncles 1-4 cm. long and 4-7 mm. thick, bearing (3) 4 to 6 spikes emerging from a small (4 cm.) caducous spathe; female spikes (1.5) 3.5-6 (9) cm. long, 7-16 mm. thick, sessile on the common peduncle. Fruiting spikes 10-20 mm. thick, fruit 2.5-3 mm. long, 0.5-0.9 mm. thick, ellipsoid, with a muricate surface.

*Cecropia polyphlebia* is known only from the very wet montane forest formations subject to the wet Caribbean weather between 1400 and 2400 m. elevation; probably flowering throughout the year. The species has been collected from the areas of Monteverde (Puntarenas), La Palma and the Río Para Blanco (San José), Cachi and Tapanti (Cartago), and near El Empalme on the Cerro de la Muerte (San José & Cartago) in Costa Rica and recently (*Blum & Dwyer 2600*) on Cerro Horqueta in Chiriquí, Panama.

This species is distinguished by the long whitish hairs on younger parts, leaves deeply lobed and white beneath with many secondary veins, short thick spikes, wet montane habitat, and the apparently consistent absence of resident ants. Only *C. insignis* shares some of the same wet highland habitats in Costa Rica. *Cecropia polyphlebia* appears to be closely related to *C. palmatisecta* Cuatr. of similar altitudes in Colombia and Venezuela.

### CHLOROPHORA Guadichaud

Unisexual trees, occasionally armed with axillary spines, the sap white; stipules paired, lateral, caducous, leaving a scar on half the stem. Leaves alternate and distichous, simple, entire to dentate. Inflorescences unisexual, solitary in the leaf axils, the male flowers crowded on long spikes, the female in globose capitular or on long spikes (in Africa); male flowers sessile, perianth segments 4, imbricate in bud, free, stamens 4, filaments inflexed in bud, anthers sub-basifixed, introrse, a pistillode often present; female flowers sessile and congested in the head, perianth 4-lobed or 4-parted, thickened near the apex and covering the ovary, style usually simple and slender, sublateral near the apex of the ovary. Fruit with the perianth becoming slightly fleshy, forming a loosely coherent globose or oblong syncarp (in ours), fruit an achene, ovate and compressed.

A genus of three species, with two others in western tropical

Africa. This genus has been united with *Maclura* by Corner (Gard. Bull. Singapore 19:187-252. 1962) and given the status of section within that genus. However, I believe it is better to retain the narrowly defined small genus until more intensive studies are done. See the recent study by R. C. Kaastra in *Acta Botanica Neerlandica* 21:657-670. 1973.

***Chlorophora tinctoria* (L.) Gaudichaud in Freycinet ex Bentham & Hooker, Gen. Pl. 3:363. 1880; Gaudichaud in Freycinet, Voyage Uran. Physic. 509. 1830. *Morus tinctoria* L., Sp. Pl. 986. 1753. Figure 14.**

Shrubs or trees 5-30 m. tall, the bark light brown, wood yellowish, branches occasionally armed with sharp spines, leafy internodes 5-25 mm. long, 1-3 thick, minutely (0.1-0.2 mm.) puberulent with ascending whitish hairs; stipules 2-10 mm. long, subulate, caducous. Leaves often deciduous, petioles 4-14 mm. long, 0.6-1.4 mm. thick, minutely puberulent or glabrescent, sulcate above; laminae often lobed on young branches, 4-13 cm. long, 1.5-5 cm. broad, narrowly ovate to ovate-elliptic or lanceolate, usually with a long-acuminate apex, obtuse to truncate (subcordate) at the usually inequilateral base, margin serrate to entire, drying chartaceous, smooth and glabrous above or with a few small hairs above the midvein, glabrous or sparsely and minutely puberulent on the veins beneath, the 4 to 8 pairs of major secondary veins often weakly loop-connected near the margin, central secondaries arising at angles of 45-65 degrees. Male spikes 4-12 cm. long, about 4 mm. thick, peduncles 4-10 mm. long, about 0.5 mm. thick, glabrous or very minutely (0.05 mm.) puberulent, perianth about 1 mm. long and minutely puberulent, filaments about 2 mm. long (dry) anther 0.7 mm. long. Female capitula (heads) 2-8 mm. in diameter, borne on short (2-4 mm.) slender (0.5 mm.) peduncles, female flowers densely crowded, styles about 6 mm. long and papillate-puberulent. Fruiting head becoming 1-2 cm. in diameter, globose.

Plants of the seasonally dry deciduous and semi-deciduous forest formations of the Pacific slopes between sea level and 1000 m. elevation in Costa Rica; flowering from the end of the dry season into the wet season, April to August. The species ranges from Central Mexico and the West Indies southward to Argentina.

*Chlorophora tinctoria* is recognized by its solitary inflorescences, male catkins, female capitula, yellowish wood, and the seasonally dry habitat. The species was important in commerce as a source of yellowish dye from the wood. The strong durable wood has had many uses in Central America (see Standley in *Fieldiana: Bot.* 24, 4:24. 1946, and Allen in *Rain Forests of Golfo Dulce*, 174. 1956). The common names *mora*, *mora de espina*, *morillo brasil*, *macano*, and *fustic* have been used for this species in our area. The sap is said to be used to ease the extraction of teeth.

**CLARISIA Ruiz & Pavon**

Unisexual trees with milky sap, lacking spines; stipules paired and lateral, usually caducous, encircling less than half the stem. Leaves alternate and distichous, simple and entire, petiole sulcate above, venation pinnate. Inflorescences paired in the leaf axils or cauliflorous on older branchlets; male inflorescences in densely crowded sessile flowering parts on a spicate axis with bracts and stamens often lacking along a narrow line on one or two sides of the spike; male flowers of solitary stamens interspersed with bracts and perianth parts arising directly from the rachis, anthers sub-basifixed; female flowers paired in the leaf axils (in ours) or on racemiform shoots, pedicellate with 3-7 suborbicular peltate bracts at the base of the receptacle (base of the ovary), the pedicel is probably the peduncle of a reduced inflorescence that now appears as a single pedicellate flower, ovary inferior by adnation of the tubular perianth, the perianth free only near the apex, ovary 1-locular with pendulous ovule, style branches 2, long and narrow. Fruit drupaceous, perianth accrescent and succulent.

A genus of two or three species of tall trees ranging from Mexico to the Amazonian Basin. In ours, the male spikes and individual female flowers are usually borne in axillary pairs, but in the Amazonian species these are borne on long racemiform leafless shoots. The male flowers have lost their organization, and stamens and perianth parts are not regularly arranged.

**Clarisia biflora** Ruiz & Pavon, Syst. Veg. Fl. Peruv. & Chil. 255. 1798. *C. panamensis* Woods., Ann. Missouri Bot. Gard. 47:123. 1960. Figure 14.

Trees to 35 m. tall, trunk becoming 1.2 m. in diameter with smooth brown bark, leafy internodes 2-4.5 mm. thick, sparsely appressed puberulent and soon becoming glabrous, lenticels inconspicuous; stipules 3-8 mm. long, narrowly to broadly cuneate, the scars inconspicuous. Leaves with petioles 6-22 mm. long, 1-2.5 mm. thick, minutely (0.1-0.2 mm.) and sparsely puberulent but becoming glabrous, periderm often breaking up into small flakes; laminae 8-25 cm. long, 2.5-9 cm. broad, narrowly oblong to elliptic-oblong or broadly elliptic, acuminate at the apex, acute to obtuse at the base, entire, drying thin to thickly chartaceous, smooth and glabrous above, glabrous or very sparsely and minutely (0.1 mm.) puberulent beneath, the (4) 6 to 12 pairs of major secondary veins not clearly loop-connected near the margin, central secondaries arising at angles of 40-70 degrees. Male inflorescences of paired axillary spikes or rarely the spikes on leafless racemiform shoots, spikes 2-10 cm. long and borne on peduncles 3-6 mm. long, sparsely puberulent, rachis with numerous spatulate to peltate bracts, stamens interspersed with the bracts (perianth in part?), filaments about 1 mm. long, anthers 0.4-0.8 mm. long, slightly apiculate in ours. Female inflorescences of two axillary flowers or occasionally in alternate pairs on a leafless shoot, pedicels 0.5-6 mm. long, densely and minutely puberulent with 3 to 7 peltate bracts 0.6-1.4 mm. broad at the base of the pistil, perianth-tube 2.5-5 mm. long, 1-5 mm. thick, narrowly ovoid to globose, glabrous except at the minutely lobed apex, style branches 2-6 mm. long. Fruit ovoid to ellipsoid, becoming 25 mm. long and globose, smooth and glabrous.

Trees of the very wet evergreen forest formations between sea level and 1000 m. elevation on both the Caribbean and Pacific slopes (near Golfo Dulce) in Costa Rica; probably flowering throughout the year, but fruiting material has been most often collected between September and December. The species ranges from Central Mexico to Bolivia and Brazil.

Large trees recognized by the unusual male spikes with intermixed bracts and stamens and the usually paired female flowers with peltate bracts at the apex of their pedicels. The vegetative parts are often glabrous or nearly so, and the larger roots are said to be reddish. The foliage of this species is very similar to that of species of *Brosimum*, *Sorocea*, and *Trophis*. In *Clarisia* the mid-vein is impressed above, and multicellular gland-tipped trichomes ( $\times 150$ ) are lacking on the lower surface of the leaves. These tall trees are poorly represented in herbaria, and there are no staminate collections from our area.

### COUSSAPOA Aublet

Unisexual trees or shrubs, usually epiphytic in early stages and sometimes strangling the host, the sap clear or colored but not milky; stipules completely united and apparently solitary, fully amplexicaul, enclosing the stem-apex and leaving a scar completely surrounding the stem, often large. Leaves simple, alternate in a spiral, often large and subcoriaceous, petiolate, the laminae basifixed, entire to undulate, tertiary veins subparallel. Inflorescences unisexual, usually paired in the axils of current foliage, the flowers minute and densely clustered in usually small heads (capitula), the heads solitary on a peduncle to many on a branched inflorescence, the flowers interspersed with bracts slender at the base and spatulate or somewhat peltate at the apex; male flowers with 3 or 4 usually separate perianth-parts (tepals or sepals), the stamens 2 (or apparently solitary, free with 2-theous anthers or completely fused and the anther apparently 4-theous by connation; female flowers with the perianth united and tubular or clavate, often thickened apically, usually with a minute aperture apically through which the penicillate stigma protrudes, ovary and style included but free, ovary superior with a single basal ovule. Fruiting inflorescence occasionally becoming somewhat succulent, fruit included in the persisting perianth, fruit a very small glabrous achene with crustaceous endocarp, a mucilaginous mesocarp and a membranaceous exocarp.

A genus of more than 30 species, largely South American where it exhibits considerable morphological diversity. With the exception of a few more common species, the genus is very poorly known, perhaps because of the difficulty in collecting large epiphytic plants. Many species are known from only a very few collections, and these seem to indicate that the genus flowers primarily from January to May in Costa Rica. The genus resembles *Ficus* in the epiphytic ger-

mination and strangling habit, but *Coussapoa* is apparently less aggressive than *Ficus* and strangled hosts are only rarely seen. This genus, like *Cecropia* and *Pourouma*, is a member of the subfamily Conocephaloideae, a subfamily that should be removed from the Moraceae and transferred to the Urticaceae, according to Corner (1962). It is retained in the Moraceae here to facilitate reference.

- 1a. Largest laminae (on mature plant-parts) more than 20 cm. long and 15 cm. wide, whitish or pale brown beneath with short slender hairs and long thin floccose hairs, with 9 to 16 pairs of major secondary veins, and prominent tertiary veins; wet evergreen formations, 0-1000 m. . . . . 2a.
- 1b. Largest laminae (on mature plant-parts) less than 20 cm. long and 15 cm. broad; plants rarely collected. . . . . 3a.
  - 2a. Large laminae abruptly truncate at the base; female capitula solitary or several on peduncles 1-8 cm. long; common and widespread. . . *C. panamensis*.
  - 2b. Large laminae cordate at the base with a sinus 2-3 cm. deep; female inflorescence solitary and subsessile; endemic and rare in collections.
 

*C. nymphaeifolia*.
- 3a. Laminae with 9 to 12 pairs of major secondary veins, drying chartaceous; short (0.2-1.5 mm.) slender hairs usually present on stipule-scars and stipules; wet evergreen formations of southwestern Costa Rica. . . . . *C. contorta*.
- 3b. Laminae with 2 to 6 pairs of major secondary veins, drying subcoriaceous or very stiffly chartaceous; glabrous or minutely (-0.2 mm.) puberulent. . . . . 4a.
- 4a. Laminae usually narrow (2-6 cm.), with only 2 or 3 pairs of major secondary veins; Caribbean lowlands, 0-500 m. . . . . *C. glaberrima*.
- 4b. Laminae usually relatively broad (8-13 cm.), with 3 to 6 pairs of major secondary veins; wet cloud forest formations, 500-1200 m. . . . . *C. parviceps*.

***Coussapoa contorta* Cuatrecasas, Caldasia 7:289. 1956. Figure 22.**

Trees 5 to 25 m. tall, beginning as epiphytes, the trunk becoming contorted, leafy internodes 3-26 mm. long, 2-4 mm. thick, glabrous, with minute hairs or with slender hairs 0.2-1.5 mm. long on the stipule scar (in ours); stipules 1-2.5 cm. long, 2.5-6 mm. thick, very minutely (0.05-0.2 mm.) sericeous and with scattered longer hairs (in ours) or glabrous. Leaves relatively uniform in size, petioles (1) 2-5.5 cm. long, 0.7-2 mm. thick, glabrous or minutely puberulent, (especially near the apex), narrowly sulcate above; laminae (5) 8-16 cm. long, (2) 4-7 cm. broad, elliptic to elliptic-oblong or slightly obovate, abruptly acuminate or very short-acuminate (in ours), cuneate to obtuse at the base, entire, drying chartaceous, smooth and glabrous above, glabrous or very sparsely puberulent beneath, the 9 to 12 pairs of major secondary veins loop-connected near the margin to form a thin submarginal vein, central secondaries arising at angles of 30-50 degrees, tertiary veins very slightly raised beneath. Male inflorescences of 8 to 20 capitula borne on a branched rachis (1) 2-8 cm. long, common peduncle 0.4-1 mm. thick, minutely puberulent, male capitula 2-6 mm. in diameter, globose, with about 10 to 30 flowers. Female inflorescence of one or 2 capitula on a rachis about 2 cm. long, female capitula 6-12 mm. in

diameter, globose, with more than 20 flowers, perianth pale brown and very minutely puberulent. Fruit about 2 mm. long, ellipsoid and flattened.

This species is known from only a single male collection in Costa Rica: *Paul Allen 5949*, from above Palmar Norte de Osa, Puntarenas, at 450 m. altitude, February 1951. Otherwise, the species is only known from the Pacific slope of northern Colombia (Choco, Valle) between sea level and 100 m. elevation.

*Coussapoa contorta* is an easily recognized species of the genus because of its relatively small thin leaves, often lustrous on both sides, with a relatively large number of secondary veins and the very small male capitula. The Costa Rican material differs from the South American collections in the even smaller male capitula, the thin petioles, and differences in pubescence. Our sampling of this species is still so small (four collections) that these differences may prove to be individual differences, and not differences in the populations. This species was referred to as *Coussapoa parviceps* in the Rain Forests of Golfo Dulce (Allen 1956).

*Coussapoa glaberrima* Burger, *Phytologia* 26:422. 1973. Figure 22.

Small trees, independent or epiphytic, with watery sap, leafy internodes 4-15 mm. long, 2-5 mm. thick, essentially glabrous; stipules 8-23 mm. long, 3-4 mm. thick at the base, glabrous and drying dark brown. Leaves rather uniform and not usually clustered at the ends of branches, petioles 6-15 (20) mm. long, 1-2.5 mm. thick, glabrous and drying dark, flattened or sulcate above, petiolar tissue often extending 1-4 mm. down the stem at the base; laminae 7-14 cm. long, 2.3-6 cm. broad, obovate to narrowly elliptic or oblanceolate, obtuse to acute at the apex, cuneate to obtuse at the base, entire, the laminae drying very stiffly chartaceous to subcoriaceous, smooth and glabrous on both surfaces, often dark above (dry), venation subpalmate, the 2 or 3 pairs of major secondary veins not loop-connected, basal secondaries arising from the petiole and parallel with the primary vein for 0-10 mm. viewed from above or apparently united when viewed from below, pockets sometimes present at the juncture of the basal secondaries with the primary vein, central secondaries arising at angles of 15-30 degrees, tertiary veins slightly raised beneath. Male inflorescences and flowers unknown. Female inflorescences of 2 or 3 capitula on a common peduncle 2-4 cm. long, about 1-1.4 mm. thick, glabrous, peduncles of the capitula 5-15 mm. long, female capitula 6-14 mm. in diameter, globose, each with about 14 to 40 flowers. Fruit 2-2.5 mm. long, about 1.3 mm. broad, abruptly rounded at both ends, slightly flattened longitudinally.

This species is known from only two collections, both from lowland rain-forest formations: *A. Jimenez 3016*, 8 km. south of Rincon, Peninsula de Osa (Puntarenas) in Costa Rica and the type from near Cerro San Isidro, Río Kama, Río Escondido (Bluefields) in Nicaragua, flowering on February 28 and March 10, respectively.

*Coussapoa glaberrima* is distinguished by its relatively small narrow leaves with few secondary veins and its glabrous parts. This species appears to be related to *C. parviceps* among our species but differs in the narrower leaves with fewer veins, more compact inflorescences, and lower altitude habitat. Because these plants are so rarely collected, the species of the genus and their interrelationships are very poorly understood.

***Coussapoa nymphaeifolia* Standley, Proc. Biol. Soc. Wash. 37:50. 1924. Figure 22.**

Trees or strangling epiphytes, 5-22 m. tall, trunk becoming 1 m. thick at the base, leafy internodes 2-40 mm. long, 4-14 mm. thick, glabrous or very minutely puberulent, the leaf-scars becoming as wide as the internodes; stipules 17-35 mm. long, 10-15 mm. thick at the base, densely ascending sericeous with pale brownish hairs 0.3-1 mm. long. Leaves in terminal clusters, petioles 8-14 cm. long, 3-5 mm. thick, longitudinally ridged, very minutely (0.01-0.05 mm.) brownish puberulent and with a few longer hairs, longitudinally striate, abruptly expanded at the base; laminae about 28 cm. long and 20 cm. broad, ovate to ovate-oblong, bluntly obtuse to broadly rounded at the apex, shallowly cordate at the base with the basal lobes extending 2-3 cm. below the petiole attachment, margin undulate, laminae drying stiffly chartaceous to subcoriaceous, smooth or slightly scabrous and glabrous or sparsely puberulent above, puberulent beneath with short (0.3 mm.) thin grayish hairs and soft spreading floccose hairs along the margins, the 9 to 12 pairs of major secondary veins weakly loop-connected near the margin, tertiary veins prominent beneath. Male inflorescence of (4) 10 to 30 capitula borne on a branching rachis 3-8 cm. long, common peduncle about 1.7 mm. thick, densely ferruginous puberulent, male capitula 5-8 mm. in diameter, with about 30 flowers, anthers about 0.5 mm. long. Female inflorescences of a single capitulum, subsessile or on a very short (1-4 mm.) peduncle, somewhat cylindrical or ellipsoid in form, about 2 cm. long and 1 cm. in diameter, with many densely crowded flowers. Fruit about 3 mm. long (immature?).

A species based on only two collections from the wet Caribbean slopes in the province of Alajuela: *Cook & Doyle 157* (the type, female) from Buena Vista, San Carlos valley, at 600 m. altitude and *Austin Smith H1632* (male) from Villa Quesada at 825 m. altitude; the male flowers were collected in February and the young fruiting material in April.

*Coussapoa nymphaeifolia* is a distinctive but very poorly known species. The above description is based on only four leaves. The subsessile female inflorescence is very unusual. The cordate leaves with arachnoid hairs along the edge and the very large leaf-scars help to distinguish this species from *C. panamensis* with somewhat similar leaves. The original description of this species included material (*Sutton Hayes 354*) from Panama, which is the type of the name *C. chagresiana* A. D. Hawkes and which was placed in synonymy



under *C. magnifolia* Trec. by Woodson (1960). This latter species ranges from Central Panama to Peru and is not closely related.

***Coussapoa panamensis*** Pittier, Contr. U.S. Nat. Herb. 18:226. 1917. *C. donnell-smithii* Mildbr., Notizbl. Bot. Gart. Berlin 10:414. 1928. Figure 22.

Tree, 5-30 m. tall, often epiphytic and strangling, sap yellowish, leafy internodes 3-20 mm. long, 3.5-8 mm. thick, glabrous or very minutely puberulent or occasionally with long (0.5-2 mm) slender hairs, often longitudinally ridged (dry) and reddish-brown; stipules (1.5) 3-14 (19) cm. long, about 1 cm. thick at the base, minutely (0.1-0.3 mm.) grayish-brown puberulent or occasionally with longer hairs. Leaves extremely variable in size on the same tree, petioles (2) 3-8 (11) cm. long, 1.5-5 mm. thick, glabrous, minutely puberulent or with hairs 1-3 mm. long, longitudinally deeply ridged, epidermis often coming off in small scales; laminae (8) 12-32 (40) cm. long, (4) 7-21 (28) cm. broad, narrowly ovate (rarely elliptic) to broadly ovate or ovate-oblong, tapering gradually to a usually obtuse apex, abruptly obtuse to rounded or truncate at the base (rarely subcordate), margin somewhat undulate, laminae drying subcoriaceous, smooth, glabrous and often slightly lustrous above, puberulent beneath with short straight hairs 0.1-0.4 mm. long (rarely longer) and thin yellowish or grayish arachnoid or floccose hairs, the (9) 11 to 14 (16) pairs of major secondary veins weakly loop-connected near the margin, central secondaries arising at 30-50 degrees, tertiary veins prominent beneath. Male inflorescences of (2) 4 to 12 capitula borne on a branched rachis 1.5-4 (10) cm. long, common peduncle densely and minutely (0.1-0.2 mm.) puberulent or with longer (1-2 mm.) hairs, male capitula about 4-8 mm. in diameter, globose, with more than 30 male flowers, anthers 0.2-0.4 mm. long. Female inflorescence of usually solitary capitula on peduncles (1.5) 3-8 cm. long, 1.3-3 mm. thick, glabrous or minutely puberulent, occasionally with the common peduncle branched and bearing 2 or 3 capitula (only in Costa Rica?), female capitula 8-18 mm. in diameter, globose, with usually more than 30 female flowers; fruit about 4 mm. long and 1.8 mm. broad, ellipsoid and flattened with pits on the broad surfaces.

Plants of very wet evergreen forest formations between sea level and 1000 m. elevation on both the Caribbean and Pacific slopes in Costa Rica; flowering throughout the year but collected most often between January and May. The species ranges from southern Mexico to Panama and probably into adjacent Colombia.

*Coussapoa panamensis* is recognized by its large leaves (not always present) truncated at the base of the lamina and yellowish-gray beneath with prominent tertiary veins. Several collections from the General Valley and the Golfo Dulce area possess more elliptic leaves and long slender hairs quite different from those commonly encountered elsewhere. These collections may represent a locally differentiated population. (Long hairs are occasionally seen in other areas of the range.) This species is by far the most common-

ly collected *Coussapoa* in Costa Rica. The name *Urostigma intramarginale* Liebmann (Danske Vidensk. Selsk. Skrivt. ser. 5, 2:320. 1851) was based, I believe, on the leaves of *Coussapoa panamensis* and the figs of *Ficus turrialbana* (Oersted 14317). Liebmann's name is based on discordant elements and should be excluded from considerations of priority.

***Coussapoa parviceps*** Standley, Proc. Biol. Soc. Wash. 37:51. 1924. *C. brenesii* Standl., Field Mus. Bot. 18:382. 1937. Figure 22.

Trees 6-10 (17) m. tall, epiphytic or independent, with a viscous yellowish sap, leafy internodes 4-15 mm. long, 4-8 mm. thick, essentially glabrous and drying reddish-brown; stipules 1-3 (4.2) cm. long, 3-8 mm. thick at the base, glabrous or very sparsely puberulent, drying dark. Leaves usually uniform in size and clustered near the ends of stems, petioles 15-45 mm. long, 1-2.8 mm. thick, glabrous or very minutely puberulent in early stages, sulcate above; laminae 7-20 cm. long, 8-14 cm. broad, broadly ovate to suborbicular or broadly obovate, obtuse to abruptly very short-acuminate at the apex or occasionally rounded, rounded to subtruncate at the base, margin entire, laminae drying stiffly chartaceous to subcoriaceous, smooth and glabrous above, usually drying lustrous and very dark, paler below, glabrous or very minutely (0.05-0.1 mm.) puberulent beneath, the 3 to 5 (6) pairs of major secondary veins not loop-connected near the margin, basal secondaries arising at the petiole and the venation subpalmate, central secondaries arising at angles of 30-50 degrees, tertiary veins usually obscure. Male inflorescences of 10 to 20 capitula on a branched common peduncle 3-8 cm. long, about 1 mm. thick, glabrous or very minutely puberulent, male capitula 2-5 mm. in diameter, globose, with 3 to 15 flowers each, anthers about 0.3 mm. long. Female inflorescences of 3 to 12 capitula borne on a branching peduncle 3-9 cm. long, about 1 mm. thick, essentially glabrous, female capitula 2-5 mm. in diameter, globose, with 12 to 30 flowers. Fruiting capitula about 6 mm. thick, fruit about 1.5 mm. long and 1 mm. thick, somewhat flattened and abruptly narrowed at both ends.

An endemic species of Costa Rica's wet cloud forests between 500 and 1200 m. altitude. Collections have been made from near San Ramon and above the San Carlos plain in Alajuela, near Orosi in Cartago, and Agua Buena (Cañas Gordas) in southernmost Puntarenas; flowering and fruiting collections have been made from February to April.

*Coussapoa parviceps* is distinguished by its very small inflorescences (both male and female), relatively broad leaves often lustrous and dark brown above (dry), and general lack of conspicuous hairs. The type of *C. brenesii* (Brenes 20542) has more rounded laminae with fewer secondary veins than the type of *C. parviceps* (Pittier 11166), but our other collections exhibit sufficient variation in these characters of the leaf to encompass both. The leaves of this species are smaller than, but similar to, those of *C. magnifolia*

Trecul (Panama to Peru), but the latter has very different female inflorescences.

## DORSTENIA Linneaus

Herbs, perennial from rhizomes with or without leaf-bearing stems (woody shrubs in Africa), sap whitish; stipules paired, free, lateral. Leaves alternate and simple, petiolate, laminae often very variable in different plants of the same species, entire to pinnately deeply lobed. Inflorescences usually solitary, axillary, often with long peduncles, the flowers sunken into the tissue of the flattened receptacle, the receptacle borne on and continuous with the apically expanded peduncle, variously shaped but often saucer-like with the flowers in the broad slightly concave distal surface, usually bisexual with flowers of both sexes intermixed or the male flowers surrounding solitary female flowers, bracts minute and inconspicuous, confined to the margin of the receptacle, perianth usually connate with the receptacle, male flowers with usually 2 (1 or 3) stamens, inflexed in bud and becoming exerted; female flower with the ovary included within the tubular perianth in the receptacle, style lateral or eccentric with 2 style branches. Fruit developing within the receptacle, protruding only at maturity and sometimes expelled with force (the exocarp remains in the receptacle), seeds small.

A genus of about 50 species; pantropical but with the greatest number of species in tropical America and Africa. A very unusual genus of the Moraceae because of its herbaceous habit (in ours) and the discoid inflorescences with imbedded flowers.

- 1a. Leaves borne on erect or ascending herbaceous stems and distant on the stem, elliptic-oblong and entire to apically toothed or deeply pinnately lobed with the narrow lobes about the same size, venation pinnate; receptacle rounded on edge; plants of very wet evergreen forest formations. . . . . *D. choconiana*.
- 1b. Leaves borne from the apex of the rhizome and arising close together on long petioles, usually deeply lobed or with large teeth and the basal lobes or teeth much larger than the distal, venation pinnate to palmate . . . . . 2.
- 2a. Receptacle more or less rectangular in outline and usually with conspicuous narrow lobes; plants of evergreen formation. . . . . *D. contrajerva*.
- 2b. Receptacle rounded on edge, orbicular to oval or ellipsoid; plants of the deciduous forest formations of Guanacaste. . . . . *D. drakena*.

*Dorstenia choconiana* Watson, Proc. Amer. Acad. Sci. 22:477. 1887. *D. choconiana* var. *integrifolia* Donn.-Smith, Bot. Gaz. 13:76. 1888. *D. cordato-acuminata* Cufod., Archivo Bot. Sist. Fitogeog. & Genet. 10:27. 1934. Figure 17.

Herbs to about 40 (90) cm. tall, leafy internodes 2-15 (22) mm. long, 1.2-4 (6) mm. thick (dry), somewhat succulent, puberulent with slender crooked hairs 0.2-1 mm. long; stipules 3-8 mm. long, 2 mm. broad at the base, subulate, often persisting. Leaves very variable on different plants (rarely lobed and unlobed on the same

plant), petioles 1-4.5 cm. long, 0.8-2 mm. thick, longitudinally ridged (dry), puberulent; laminae usually of two types, unlobed laminae oblong to obovate, acute to acuminate at the apex and attenuate to obtuse or rarely truncate at the base, occasionally with a few small (5 mm.) lobes in the distal third, the lobed laminae with (2) 3 to 5 (6) prominent pinnate lobes on each side, the lobes usually opposite and symmetrical, basal lobes often slightly smaller than the more distal, sinuses one-half to two-thirds the length of the associated secondary veins, truncate at the base, both kinds of laminae 6-25 cm. long and 3-10 cm. broad, drying thin-chartaceous, glabrous or very sparsely puberulent above, usually scabrous beneath and sparsely to densely puberulent on the veins with short (0.2-0.6 mm.) stiff hairs, the 3 to 8 pairs of major secondary veins weakly loop-connected near the margin or with a sub-marginal vein along the sinuses. Inflorescence solitary from the axils of current foliage, peduncles 1-3 cm. long, 1-2 mm. thick, expanding gradually to the circular or ellipsoid disc (as viewed from above), disc 10-25 mm. broad, slightly concave and often deep blue-green in color (live).

Plants often found in deep shade on the floor of very wet ever-green forests between sea level and 1600 m. (rare above 1100 m.) on both the Caribbean and Pacific slopes in Costa Rica; flowering throughout the year. The species ranges from the Caribbean side of Guatemala to within a few kilometers of the border with Panama in Costa Rica.

*Dorstenia choconiana* is easily recognized among our species because of its leaves borne at intervals along the elongated stem. This species is unusual in having two definite kinds of leaves that are never found on the same plant and with very few plants having intermediate kinds of leaves. Both forms (or varieties) can be found in a large population, but one usually greatly outnumbers the other. The plants with deeply pinnately lobed leaves can be referred to as variety *choconiana*, and those with almost entire oblong leaves, often with long acuminate apices, can be referred to as variety *integrifolia* Donn.-Smith. The plants with deeply lobed leaves are not as common as those with entire leaves in Costa Rica, on the basis of our present sampling of the species.

*Dorstenia contrajerva* L., Sp. Pl. 121. 1753. *D. houstoni* L., Sp. Pl. ed. 2, 176. 1762. *D. contrajerva* var. *houstoni* (L.) E. Bureau in DC., Prodr. 17:259. 1873. *D. contrajerva* ssp. *tenuiloba* S. F. Blake, Contr. U.S. Nat. Herb. 24:2. 1922. *D. contrajerva* var. *tenuiloba* (Blake) Standl. & Steyer., Field Mus. Bot. 23:40. 1944. Figure 17.

Herbs, acaulescent from a tuberous base or rarely from a short (3 cm.) stem with several internodes, becoming about 20-40 cm. tall, slightly succulent; stipules 2-6 mm. long, aculeate and often persisting. Leaves originating close together at the apex of the rhizome, petioles 8-26 cm. long, 1-2.5 mm. thick, longitudinally ribbed (dry), puberulent with minute (0.2-0.8 mm.) crooked whitish hairs; laminae quite

variable on different plants, variously lobed, 7-26 cm. long, 9-34 cm. broad, with 1 to 8 lobes or prominent teeth on each side, sinuses shallow to very deep, acute to acuminate at the apex, attenuate or obtuse to deeply cordate at the base, margins minutely dentate to entire, the laminae drying thin-chartaceous, smooth or scabrous above, sparsely puberulent with minute hairs or with a few stiff longer (0.5-2 mm.) hairs, sparsely to densely puberulent on the veins beneath, with minute (0.1-0.3 mm.) hairs, venation pinnate to subpalmate with 3 to 6 pairs of major secondary veins, the basal pair often bordering the basal sinuses of the laminae. Inflorescences apparently solitary in the axils of the current leaves, peduncles 10-34 cm. long, 0.8-3 mm. thick (dry), glabrous to densely and minutely puberulent, abruptly expanded below the centrally peltate receptacle, the receptacle approximately rectangular (viewed from above) but with a very irregular and often lobed margin, the lobes few to many, receptacle flat or slightly concave distally, 8-45 mm. broad, anthers about 0.2-0.3 mm. long.

Plants of shaded sites in evergreen forest formations from sea level to 1200 (1400) m. elevation on both the Caribbean and Pacific slopes in Costa Rica; probably flowering throughout the year, but with the greatest number of collections being made from June to August. The species ranges from Central Mexico through Central America and the West Indies to Peru and the Guianas in South America.

*Dorstenia contrajerva* is recognized by its unusual receptacle of roughly rectangular outline with irregularly lobed edges. It is found in areas that are very wet to those that are seasonally dry but where shade is present throughout the year. The common name, *contrayerba* or *contrahierba*, refers to its use to counteract fever. Several varieties have been proposed, but these seem to be no more than unusual leaf-forms that are usually consistent for an individual plant but not for a population. Variety *houstoni* has few-lobed laminae that are ovate to triangular with cordate bases and variety *tenuiloba* has very deeply lobed laminae.

*Dorstenia drakena* L., Sp. Pl. ed. 2, 176. 1762. *D. mexicana* Benth., Pl. Hartweg. 51. 1839. Figure 17.

Herbs, acaulescent from a tuberous base, becoming 20-40 cm. tall, slightly succulent; stipules 2-4 mm. long, obtuse to acute apically, persisting on the rhizome. Leaves originating close together at the apex of the rhizome, petioles 1.5-20 cm. long, 0.8-3 mm. thick, sparsely to densely puberulent with small irregular whitish hairs 0.1-0.8 mm. long; laminae very variable on different plants, 4-20 cm. long, 4-23 cm. broad, oval to triangular in outline, with 1 to 5 lobes or large teeth on each side, sinuses shallow to deep, acute to acuminate at the apex, truncate to deeply cordate at the base, margins entire to bluntly dentate, lamina drying thin-chartaceous, scabrous above with scattered stiff slender hairs 0.1-1 mm. long, minutely puberulent beneath but with larger hairs near the edges, venation pinnate to subpalmate with 2 to 5 pairs of major secondary veins. Inflorescences apparently solitary in the

axils of the current foliage at the apex of the rhizome, peduncles (3) 8-28 cm. long, 0.7-3 mm. thick, very minutely puberulent or apparently glabrous, abruptly expanded below the eccentrically peltate receptacle, the receptacle broadly elliptic to oval or somewhat oblong (viewed from above), 1-5 cm. long, distal surface essentially flat, anthers 0.2-0.3 mm. long.

Plants from the floor of the seasonally very dry deciduous forest formations of Guanacaste province between sea level and 300 m. elevation in Costa Rica; flowering in June, July, and August. The species ranges from Central Mexico to Costa Rica and occurs in South America.

*Dorstenia drakena* is recognized by its elliptic to oval receptacle attached near the edge with entire margin and the deciduous forest habitat with restricted flowering period. This species displays a pattern of leaf variation that is very similar to that found in *D. contrajerva*, varying from triangular-cordate to deeply pinnately lobed.

### FICUS Linnaeus

REFERENCES: P.C. Standley, The Mexican and Central American Species of *Ficus*, Contr. U.S. Nat. Herb. 20:1-35. 1917. G.P. DeWolf, Jr., *Ficus* in Flora of Panama, R.E. Woodson, Jr., & R.W. Schery, Ann. Missouri Bot. Gard. 47:146-165. 1960.

Trees or shrubs with milky or rarely clear (*F. citrifolia*) sap, rarely climbers (as in *F. meistosyce* and the cultivated *F. pumila*), often beginning as epiliths or epiphytes and the coalescing roots surrounding the host plant as a "strangler"; stipules 2 at a node and enclosing the shoot-apex, usually caducous and leaving scars that encircle the stem. Leaves alternate in a spiral and entire in native species, short to very long petiolate. Inflorescence a hollow usually round fruit-like structure called the fig (receptacle, syconium, *higo*) with a small apical opening, the ostiole, formed by overlapping scales, the base subtended (in ours) by a whorl of 2 or 3 bracts; the flowers borne on the inner wall of the fig, usually numerous and interspersed with bracts, the fig with both male and female flowers in native species and the plants bisexual (or the fig with flowers of one sex and the plants unisexual in subgenus *Ficus* of the Old World); the flowers are of three kinds and usually intermixed in American species, male flowers of American species generally have 2 to 6 perianth-parts and 1 or 2 stamens, female flowers with 2 to 4 perianth-parts, pistil 1 with a single style borne from the side of the ovary, stigma 1, sterile flowers usually called gall-flowers but formed without the intervention of an insect and serving as the food source for the larvae of the pollinators; fruit small achenes or drupes borne within the receptacle which usually becomes succulent at maturity; the usually juicy fruiting fig is eaten by many animals, especially birds.

A genus of several hundred species found throughout the tropics but especially diverse in southeast Asia. *Ficus* is a very distinctive genus with one of the most unusual inflorescences and

pollinating mechanisms in the plant world. The flowers and fruit enclosed by a fleshy receptacle require that pollen enter the ostiole through a barrier of overlapping scales. Only the small fig-wasps, chalcid wasps of the family Agaonidae, can effect pollination in *Ficus* and these wasps can only develop within the fig. The wasps have developed unusual morphology and behavior patterns to carry on pollination, and the different species of *Ficus* are pollinated by different and specific species of wasps (see Ramirez, Evolution, 24:680-691. 1970). The developmental phases of the fig (syconium) have been divided by Galil and Eiskowitch (in New Phytol. 67:745-758. 1968) as follows: Phase A, the *prefemale*, or the immature fig prior to opening of the ostiole. Phase B, the *female*, as the ostiolar scales loosen, female flowers ripen, wasps enter the fig and oviposit into the ovaries. Phase C, *interfloral*, as the wasp larvae and seed embryos develop within the fig and the ovaries occupied by larvae become galls. Phase D, the *male*, as male flowers mature and the wasps reach adulthood, mate, and the female wasps leave the fig. Phase E, *post-floral*, as the fig becomes more succulent and the seeds ripen to the point where they are ready for dispersal.

The genus is quite distinctive vegetatively with its entire (in native species) usually stiff leaves and stipules protecting the shoot-tip and leaving circular rings on the stem. These circular stipule-scars are useful in recognizing trees without figs as species of *Ficus*, but several other genera of the Moraceae have similar stipules, as do the Magnoliaceae and some Polygonaceae.

#### KEY TO THE SPECIES OF *FICUS*

- 1a. Plants growing wild in forests, pasture, or roadsides, not usually planted . . . 2a.
- 1b. Plants grown for ornament, shade, or fruit, usually found only in gardens, parks, or abandoned homesites . . . . . 55a.
- 2a. Figs solitary at a node (rarely 2 or more), the older leaf-scars never subtending 2 fig-scars but often subtending a single fig-scar and an axillary bud or bud-scar; bracts subtending the fig 3, ostiole of the fig often with more than 3 scales visible; laminae with unusual clear translucent clavate hairs on the lower surface ( $\times 150$ ); independent trees rarely beginning as epiphytes and often restricted to streamsides (subgenus *Pharmacosycea*) . . . . . 3a.
- 2b. Figs usually 2 at a node, older leaf-scars often subtending 2 fig-scars; bracts subtending the fig 2 (but often deeply split and appearing as 3 or 4), ostiole of the fig usually with only 2 or 3 exterior scales visible; laminae lacking clavate hairs ( $\times 150$ ) but slender hairs with somewhat enlarged distal cells translucent reddish-brown often present; plants often beginning as

- epiphytes and becoming independent or strangling, the trunks often deeply fluted or of grown-together stems (subgenus *Urostigma*) . . . . . 10a.
- 3a. Figs sessile; laminae medium to large in size (14-40 cm.) and relatively broad, the width usually exceeding half the length. . . . . 4a.
- 3b. Figs subsessile to pedunculate; laminae small to large, the width of the larger laminae generally less than half the length. . . . . 5a.
- 4a. A definite submarginal vein present near the edge of the lamina, laminae glabrous beneath; wet evergreen formations 0-1000 m. . . . . *F. tonduzii*.
- 4b. A definite submarginal vein absent or the secondaries weakly loop-connected near the margin, lamina usually scabrous beneath; very wet Caribbean slopes (500) 1000-1600 m. . . . . *F. macbridei*.
- 5a. Stipule 10-25 mm. long, petioles with reddish-brown epidermis usually peeling off in small flakes (in ours), laminae 7-20 cm. long with 5 to 13 pairs of secondary veins and slightly scabrous beneath; figs 14-20 mm. in diameter; widespread, 0-1000 m. . . . . *F. maxima*.
- 5b. Stipules 20-160 mm. long, petioles with the epidermis only rarely flaking off (in ours), laminae with 12 to 40 pairs of secondary veins, smooth to the touch beneath . . . . . 6a.
- 6a. Figs 25-60 mm. in diameter at maturity, with very thick walls. . . . . 7a.
- 6b. Figs 12-22 mm. in diameter (dry) or unknown . . . . . 8a.
- 7a. Laminae thin to moderately thick, acute to short acuminate at the apex; stipules usually drying yellowish-green, 3-8 cm. long; widespread, 0-500 m. . . . . *F. insipida*.
- 7b. Laminae very thick, obtuse to acute at the apex; stipules usually drying dark, 2-5 cm. long; montane forests 1200-2000 m. . . . . *F. crassiuscula*.
- 8a. Stipules 7-17 cm. long, laminae 14-32 cm. long with 16 to 24 pairs of major secondary veins; figs 15-22 mm. in diameter, with a conical ostiole; 0-800 m. . . . . *F. werckleana*.
- 8b. Stipules 2-9 cm. long, laminae 5-15 (20) cm. long, secondary veins often difficult to distinguish from the intermediate veins, 10 to 50 pairs . . . . . 9a.
- 9a. Laminae drying thin, acute to short-acuminate; mature figs 12-16 mm. in diameter, with a narrow apex supporting the ostiole; (0) 500-1200 (1600) m. . . . . *F. yoponensis*.
- 9b. Laminae drying very stiff, rounded to obtuse at the apex; figs about 15 mm. in diameter; wet Caribbean lowlands. . . . . *F. crassivenosa*.
- 10a. Laminae glabrous beneath when viewed with a  $\times 10$  hand lens . . . . . 11a.
- 10b. Laminae puberulent beneath, the hairs 0.1 mm. long or longer . . . . . 36a.
- 11a. Largest laminae rarely more than 12 cm. long (not measuring the petiole), usually less than 5 cm. broad; acute to acuminate or sharply obtuse at the apex . . . . . 12a.
- 11b. Largest laminae usually more than 13 cm. long (not including the petiole) or bluntly obtuse to rounded at the apex when shorter . . . . . 18a.
- 12a. Laminae with sub-palmate venation, 3 prominent primary veins usually arising from the apex of the petiole; figs sessile, 5-8 mm. in diameter, evergreen lowlands, 0-800 m. . . . . *F. colubrinae*.



- 12b. Laminae with pinnate venation, with 4 or more pairs of secondary veins ..... 13a.
- 13a. Laminae with 4 to 8 pairs of major secondary veins; figs sessile .... 14a.
- 13b. Laminae with 7 to 20 pairs of major secondary veins; figs usually pedunculate ..... 16a.
- 14a. Mature figs 4-6 mm. in diameter, the fig attached at the base; 900-1600 m. .... *F. hartwegii*.
- 14b. Mature figs 7-10 mm. in diameter ..... 15a.
- 15a. Figs attached on the side, sessile and leaving depressions in the stem; laminae acute to obtuse at the apex; wet Caribbean slope  
*F. laterisyce*.
- 15b. Figs usually borne on peduncles; laminae rounded at the apex; plants of the seasonally very dry deciduous formations. .... *F. ovalis*.
- 16a. Laminae mostly acute to obtuse; ostiole flat or slightly raised, mature figs 6-9 mm. in diameter; 0-1200 m. .... *F. perforata*.
- 16b. Laminae mostly acute to acuminate; ostiole enclosed by a crateriform ring or collar of elevated tissue ..... 17a.
- 17a. Mature figs 8-14 mm. in diameter, ostiole enclosed by a short (1-2 mm.) ring of elevated tissue; (0) 900-1600 (2000) m. .... *F. pertusa*.
- 17b. Mature figs 14-18 mm. in diameter, ostiole hidden within a deep (3-6 mm.) collar of elevated tissue; seasonally dry areas, 0-1000 m.  
..... *F. trachelosyce*.
- 18a. Laminae cordate to subcordate with basal lobes extending 1-7 cm. below the petiole attachment, petioles 5-18 cm. long, laminae 10-24 cm. broad; figs subsessile with a lustrous minutely velutinous surface; wet evergreen lowlands. .... *F. nymphaeifolia*.
- 18b. Laminae attenuate to subcordate, never deeply cordate, the basal lobes rarely more than 1 cm. long. .... 19a.
- 19a. Laminae often abruptly acuminate at the apex, usually short- to long-acuminate, often oblong in general outline; stipules glabrous or sparsely and very minutely puberulent; the figs glabrous ..... 20a.
- 19b. Laminae rounded to obtuse or acute at the apex, only rarely short-acuminate. .... 26a.
- 20a. Figs with an apical collar 3-6 mm. high surrounding the ostiole, pedunculate; laminae small (7-16 cm.) and thin; seasonally dry Pacific slope, 0-1000 m. .... *F. trachelosyce*.
- 20b. Figs without an apical collar, rare or absent on the seasonally dry Pacific slope ..... 21a.
- 21a. Figs only 4-5 mm. in diameter at maturity, sessile and often in clusters; plants often climbers in lowland rain forest ..... *F. schippii*.
- 21b. Figs becoming 8-16 mm. in diameter (dry) and never in clusters; plants often epiphytic but not climbers ..... 22a.
- 22a. Figs borne on peduncles to 10 mm. long or occasionally subsessile; leaves with petioles 15-120 mm. long ..... 23a.
- 22b. Figs sessile or occasionally borne on peduncles to 3 mm. long; leaves with petioles 8-36 mm. long ..... 24a.

- 23a. Figs on peduncles 5-10 mm. long; laminae oblong; twigs usually brownish to grayish, sap clear and thick; moist forests of the Caribbean slope and eastern Meseta Central, 0-1200 m. . . . . *F. citrifolia*.
- 23b. Figs sessile or on peduncles 1-4 mm. long; laminae ovate-oblong; twigs usually dark reddish-brown, sap whitish; moist forest formations, 0-1000 m. . . . . *F. dugandii*.
- 24a. Laminae with unusual hairs along the sides of the midvein beneath in the basal (proximal) half of the lamina, elliptic-oblong to oblong; figs sessile; moist montane formations 1200-1700 m. . . . . *F. cervantesiana*.
- 24b. Laminae lacking unusual flat hairs along the sides of the midvein beneath; plants of moist evergreen lowlands, 0-1000 m. . . . . 25a.
- 25a. Laminae usually oblong and abruptly acuminate; figs subsessile and usually longer than thick, the ostiole usually conical, basal bracts 2-4 mm. long. . . . . *F. paraensis*.
- 25b. Laminae usually obovate and gradually acuminate or very short-acuminate; figs sessile and shorter than thick, ostiole flat, basal bracts 1-2 mm. long. . . . . *F. brevibracteata*.
- 26a. Stipules usually persisting with the leaves, with sericeous hairs along the base and midrib abaxially; figs sessile, oblate, 10-14 mm. in diameter, leaving shelf-like depressions in the stems; petioles 7-40 mm. long, laminae usually abruptly narrowed at both base and apex; 300-1200 m. and common in the Central Highlands. . . . . *F. costaricana*.
- 26b. Stipules rarely persisting (in ours). . . . . 27a.
- 27a. Figs with the basal bracts small and inconspicuous, the figs sessile or pedunculate . . . . . 28a.
- 27b. Figs with the basal bracts large and conspicuous, covering the basal half or third of the fig, the figs usually sessile. . . . . 30a.
- 28a. Stipules glabrous or sparsely puberulent; figs borne on peduncles 4-14 mm. long; seasonally dry evergreen and deciduous formations of the Pacific slope. . . . . *F. goldmanii*.
- 28b. Stipules densely hairy; figs sessile or borne on peduncles 0-5 mm. long; wet evergreen formations . . . . . 29a.
- 29a. Figs sessile or pedunculate, basal bracts 4-7 mm. broad from a basal disc; stipules usually lacking hairs along the edges . . . . . *F. trigonata*.
- 29b. Figs sessile, basal bracts 1-2 mm. broad, a basal disc absent; stipules densely puberulent throughout . . . . . *F. brevibracteata*.
- 30a. Mature figs 16-22 mm. in diameter (dry); laminae often somewhat obovate and widest above the middle. . . . . 31a.
- 30b. Mature figs 5-16 mm. in diameter, sessile, often attached on the side . . 32a.
- 31a. Surface of the fig minutely velutinous ( $\times 20$ ), fig often on a short peduncle; laminae 11-22 cm. long by 5-10 cm. broad; widespread, 0-1000 m. . . . . *F. obtusifolia*.
- 31b. Surface of the fig glabrous, fig sessile; laminae 14-32 cm. long by 9-20 cm. broad; rare on the wet Caribbean slopes around 1000 m. . . . . *F. cuatrecasana*.

- 32a. Major secondary veins often difficult to distinguish from the intermediate veins (dry), (6) 10 to 20 pairs; evergreen formations, 800-1400 m. . . . . 33a.
- 32b. Major secondary veins usually easy to distinguish from the smaller intermediate veins, 6-11 pairs. . . . . 34a.
- 33a. Stipules glabrous or very minutely (0.05 mm.) puberulent; laminae bluntly acute to obtuse; figs 6-8 (10) mm. in diameter . . . *F. davidsoniae*.
- 33b. Stipules densely puberulent; laminae bluntly obtuse to rounded and emarginate; figs 8-10 mm. in diameter. . . . . *F. jimenezii*.
- 34a. Figs 12-15 mm. diameter at maturity, leaving deep shelf-like depressions in the stems; moist montane formations, 1000-1800 m. . . . *E. tuerckheimii*.
- 34b. Figs 8-12 mm. in diameter, leaving only slight depressions in the stems; wet or seasonally dry lowlands, 0-1000 m. . . . . 35a.
- 35a. Laminae usually rounded at the apex and base, often more than 12 cm. long; plants of both Caribbean and Pacific slopes 0-500 (800) m.  
*F. isophlebia*.
- 35b. Laminae acute to short-acuminate at the apex, acute to obtuse at the base, rarely more than 12 cm. long; known only from the wet Caribbean slopes around 750 m. altitude . . . . . *F. laterisycyca*.
- 36a. Laminae densely puberulent beneath, usually rounded or bluntly obtuse at the apex; figs often puberulent and often with a ring or collar around the ostiole. . . . . 37a.
- 36b. Laminae sparsely or very minutely (-0.5 mm.) puberulent beneath. . . . . 43a.
- 37a. Trees of montane forests, 1000-2000 m. elevation; leaves with the tertiary venation very prominent beneath, smooth above; figs globose, 18-22 mm. in diameter with a short (1-2 mm.) collar around the ostiole, puberulent, pedunculate. . . . . *F. velutina*.
- 37b. Trees of lowland and lower montane formations, 0-1200 m. elevation; leaves with the tertiary veins usually only slightly raised . . . . . 38a.
- 38a. Pubescence very dense, lower leaf-surface and young parts often dark brown; laminae often scabrous above; figs puberulent, with a distinct collar or longer than broad; plants of wet evergreen formations . . . . . 39a.
- 38b. Pubescence not usually so dense, lower leaf-surface and young parts not dark brown, laminae smooth above; figs globose to obovate, lacking a high collar around the ostiole . . . . . 40a.
- 39a. Fig ellipsoid to cylindrical, distinctly longer than broad, 9-16 mm. in diameter, ostiole not surrounded by a ring of elevated tissue; pubescence of young parts often yellowish-brown . . . . . *F. popenoei*.
- 39b. Fig globose, 10-14 mm. in diameter, ostiole surrounded by a collar 1-3 mm. high; pubescence of younger parts often very dark brown.  
*F. bullenei*.
- 40a. Figs pedunculate or subsessile and the basal bracts inconspicuous; petioles 1.2-4 (6) cm. long . . . . . 41a.
- 40b. Figs sessile and with conspicuous basal bracts 7-15 mm. long; petioles 2-9 cm. long; plants of the very wet Caribbean slopes . . . . . 42a.
- 41a. Figs minutely puberulent; laminae with 9 to 14 pairs of secondary veins; trees commonly found on the seasonally very dry Pacific slope.  
*F. morazaniana*.

- 41b. Figs glabrous, laminae with 6 to 11 pairs of major secondary veins; trees of evergreen vegetation (in our area) . . . . . *F. trigonata*.
- 42a. Laminae much narrower than broad, obtuse to subtruncate at the base; figs 12-16 mm. in diameter, densely puberulent. . . . . *F. turrialbana*.
- 42b. Laminae almost as broad as long, rounded and subcordate at the base; figs about 22 mm. in diameter, sparsely puberulent . . . . . *F. caldasiana*.
- 43a. Largest laminae rarely more than 12 cm. long (except *F. davidsoniae*); figs not exceeding 10 mm. in diameter at maturity (dry) . . . . . 44a.
- 43b. Largest laminae usually more than 12 cm. long (on mature plant parts); figs often more than 10 mm. in diameter at maturity . . . . . 48a.
- 44a. Laminae with sub-palmate venation, 3 prominent primary veins usually arising from the apex of the petiole; figs sessile, 5-8 mm. in diameter; wet lowlands, 0-800 m. . . . . *F. colubrinae*.
- 44b. Laminae with pinnate venation . . . . . 45a.
- 45a. Laminae narrowly lanceolate or very narrowly elliptic-oblong, rarely more than 2.5 cm. broad; figs borne on peduncles 4-9 mm. long, the figs 7-10 mm. in diameter (when dry); wet Caribbean areas below 500 m. elevation.  
*F. donnell-smithii*.
- 45b. Laminae never lanceolate, usually more than 2.5 cm. broad; figs sessile or subsessile; plants of the seasonally dry Pacific slope or in evergreen areas above 500 m. elevation . . . . . 46a.
- 46a. Stipules 12-35 mm. long, glabrous; laminae very stiff, brownish beneath; figs 6-9 mm. in diameter; wet forest formations, (0) 800-1200 m.  
*F. davidsoniae*.
- 46b. Stipules 5-12 mm. long, usually with conspicuous hairs . . . . . 47a.
- 47a. Figs 6-10 mm. in diameter; petioles 10-80 mm. long, laminae broadly elliptic to suborbicular; seasonally dry Pacific slope, 0-900 m. . . . . *F. cotinifolia*.
- 47b. Figs 4-6 mm. in diameter; petioles 8-35 mm. long, laminae broadly elliptic to obovate or ovate; wet evergreen forest formations on both Pacific and Caribbean slopes, 900-1600 m. . . . . *F. hartwegii*.
- 48a. Laminae glabrous except for unusual hairs in rows along the proximal half of the midvein beneath; figs sessile, about 10 mm. in diameter; very wet montane formations, 1300-1700 m. . . . . *F. cervantesiana*.
- 48b. Laminae puberulent over a larger area beneath . . . . . 49a.
- 49a. Laminae almost as broad as long, 8-20 cm. broad, rounded and often cordulate at the base; figs becoming 22 mm. in diameter, sessile; wet Caribbean slope, 800-1300 m. . . . . *F. caldasiana*.
- 49b. Laminae usually much narrower than broad and not rounded at the base (except *F. cotinifolia*); figs usually less than 20 mm. in diameter . . . . . 50a.
- 50a. Stipules densely puberulent, petioles 10-80 mm. long, laminae with 4-12 pairs of prominent secondary veins . . . . . 51a.
- 50b. Stipules sparsely puberulent, petioles 5-35 mm. long, laminae with 10-20 pairs of secondary veins; wet evergreen formations . . . . . 54a.
- 51a. Figs 6-10 mm. in diameter, sessile, basal bracts 2-4 mm. long; laminae usually very broad; seasonally dry Pacific slope, 0-900 m. . . . . *F. cotinifolia*.

- 51b. Figs 12-15 mm. in diameter; laminae usually about half as broad as long.  
52a.
- 52a. Figs sessile with conspicuous basal bracts 5-10 mm. long, surface of the fig densely puberulent; wet Caribbean slope 600-800 m. . . . . *F. turrialbana*.
- 52b. Figs sessile or pedunculate, the basal bracts inconspicuous, 1-3 mm. long; 0-1100 m. . . . . 53a.
- 53a. Figs glabrous (in ours), laminae with 6 to 11 pairs of major secondary veins; evergreen vegetation . . . . . *F. trigonata*.
- 53b. Figs minutely puberulent; laminae with 9 to 14 pairs of major secondary veins; commonly found in deciduous areas . . . . . *F. morazaniensis*.
- 54a. Petioles 4-18 mm. long, laminae bluntly acute to obtuse and often reddish-brown beneath; figs 6-10 mm. in diameter, globose; wet evergreen formations, (0) 800-1200 m. . . . . *F. davidsoniae*.
- 54b. Petioles 8-36 mm. long, laminae usually short-acuminate; figs 10-14 mm. in diameter, often longer than broad; 0-1000 m. . . . . *F. paraensis*.
- 55a. Introduced plants climbing on walls and flat surfaces with adventitious roots and small cordate leaves, fruiting branches shrub-like lacking roots, and with larger ovate leaves . . . . . *F. pumila*.
- 55b. Plants not climbers. . . . . 56a.
- 56a. Laminae with bluntly serrate margins and palmate venation; shrubs or small trees, rarely more than 6 m. tall. . . . . 57a.
- 56b. Laminae with entire margins and never deeply lobed, venation pinnate; trees often becoming more than 10 m. tall . . . . . 58a.
- 57a. Figs edible, 2-5 cm. in diameter; leaves usually 3-lobed. . . . . *F. carica*.
- 57b. Figs inedible, 1-2 cm. in diameter; leaves sometimes 3-lobed . . . . *F. palmata*.
- 58a. Laminae very short (3-12 cm.) and narrow (1-4 cm.), usually lanceolate to elliptic; commonly planted in parks and along avenues . . . . . 59a.
- 58b. Laminae larger, never lanceolate. . . . . 61a.
- 59a. Trees with many aerial roots, planted in wet lowland areas; figs 5-8 mm. in diameter . . . . . *F. retusa*.
- 59b. Trees with few or no aerial roots, planted at higher elevations and in lowland areas with a dry season; figs 8-14 mm. in diameter. . . . . 60a.
- 60a. Introduced trees often grown in parks and along walkways with widely spreading trunks; figs sessile. . . . . *F. benjamina*.
- 60b. Native trees often used in hedgerows as living fences; figs pedunculate.  
*F. pertusa*.
- 61a. Laminae broadly ovate and abruptly truncate at the base, with a very long slender apex, petioles 5-10 cm. long; often planted in parks . . . . . *F. religiosa*.
- 61b. Laminae lacking a long slender apex and borne on petioles much shorter than the laminae . . . . . 62a.
- 62a. Laminae becoming 40 cm. long, broadest above the middle and pandurate in shape; planted in gardens and also in pots as house plants. . . . . *F. lyrata*.
- 62b. Laminae not becoming so large, widest at or below the middle. . . . . 63a.
- 63a. Laminae with many (50) pairs of major secondary veins and very thick, the laminae often differing greatly in size on different trees; figs narrowly oblong;

introduced and planted in parks and gardens as well as in pots indoors.

*F. elastica.*

- 63b. Laminae with fewer pairs of secondary veins and stipules rarely exceeding 5 cm.; native trees found in parks and along streets. Compare *F. costaricana* (with persisting stipules), *F. jimenezii* (thick glabrous leaves), *F. goldmanii* (with pedunculate figs), and others in key under native species.

**Ficus benjamina** L., Mant. Pl. 129. 1767.

Trees 5-20 m. tall, branching from near the ground and with a very broad crown, the terminal branchlets often drooping, leafy internodes 5-30 mm. long, 1.2-3 mm. thick, glabrous; stipules about 1 cm. long. Leaves glabrous, petioles 5-16 mm. long, about 1 mm. thick; laminae 4-12 cm. long, 2-4.5 cm. broad, elliptic to elliptic-oblong or narrowly ovate, acute or short-acuminate at the apex with a blunt tip, abruptly rounded at the usually obtuse base, margin entire but somewhat undulate and the lamina stiff-chartaceous (dry), major secondary veins difficult to distinguish from the intermediate veins and numerous (more than 15). Figs usually paired at a node, sessile, 8-11 mm. in diameter, globose or slightly ovoid, bracts not evident, ostiole flat or slightly conical.

Handsome spreading trees planted in parks and along paths, originally from India. The small leaves with many secondary veins, short stipules, lack of pubescence, small sessile figs, and characteristic growth-form distinguish this species.

**Ficus brevibracteata** Burger, Phytologia 26:423. 1973. Figure 17.

Trees 8-18 m. tall, leafy internodes 0.5-2.5 cm. long, 5-12 mm. thick, sparsely puberulent with thin yellowish or grayish hairs about 1 mm. long, often becoming glabrous, smooth and gray, with few prominent angular ridges on drying; stipules 7-12 mm. long, about 6 mm. broad at the base, densely sericeous with thin pale grayish ascending hairs. Leaves often confined to the ends of twigs, petioles 1.4-8.2 cm. long, 1.5-4 mm. thick, with scattered thin hairs 0.8-1.5 mm. long or glabrous, periderm often peeling off in small flakes; laminae 12-28 cm. long, 5-12 cm. broad, elliptic-oblong to obovate, usually broadest at or above the middle, abruptly narrowed at the short-acuminate apex, obtuse or rounded and occasionally cordulate at the petiole, margin entire or occasionally slightly rounded-crenate distally, the laminae drying stiff-chartaceous to subcoriaceous, smooth and glabrous above, glabrous or with slender ascending hairs on the midvein beneath, the 6 to 9 pairs of major secondary veins arising at angles of 30-60 degrees, loop-connected and forming a submarginal vein only near the apex, the basal secondaries often differing from those above and arising at a smaller angle. Figs usually paired at a node, sessile, the basal bracts difficult to see, 1-2 mm. long and equally broad, pale grayish sericeous; the fig 10-15 mm. in diameter (dry), slightly flattened above and below, subglobose to oblate, glabrous or with a few thin hairs near the base, smooth and drying dark, often with a few pale spots, the ostiole within a slightly elevated circle of tissue 2.5-4 mm. broad; seeds and galls about 1 mm. long.

Plants of the very wet evergreen forest formations of the Caribbean slopes between 100 and 800 m. elevation; fertile collections

have been made in December, January, and April. This species is known only between the area of Volcán Arenal (Alajuela) and the basin of the Río Pacuare (Cartago) in Costa Rica.

*Ficus brevibracteata* is recognized by the unusual fluted leafy stems (when dry), the short stipules broad at the base and covered with long pale grayish hairs, laminae often on long petioles and broadest above the middle, the sessile figs subtended by very small bracts, and the ostiole only very slightly elevated. The paired figs and distally brown oblongoid-capitate microscopic hairs ( $\times 150$ ) on the lower leaf surface are characteristics of the subgenus *Urostigma*. This species is closely related to *F. trigonata* L. and *F. morazaniensis* Burger, but those usually have pedunculate figs and the leaves are quite different. This species is known from below Volcán Arenal (the type), near the Río Sarapiquí (*Hartshorn* 989 and *Walters* 32), near the Río Puerto Viejo (*Burger & Matta* 4205 and *Hartshorn* 1099), and near Turrialba (*GMV* 640, Museo Nacional 40467). A number of sterile collections with somewhat thicker leaves with the major veins broadly impressed to give the laminae a corrugated appearance are probably this species and were collected near Taus (*Lent* 2536 & 2752) and Valle Escondido (*Walter* 77) in the province of Cartago.

***Ficus bullenei* I. M. Johnston, Sargentia 8:113. 1946. Figure 19.**

Trees 5-20 m. tall, leafy internodes 3-15 (40) mm. long, 3.5-6 mm. thick, densely velutinous with stiff erect usually dark brown hairs 0.5-1.5 mm. long, longer internodes becoming longitudinally striate (dry); stipules 10-22 mm. long, 4-8 mm. thick at the base unopened, densely ascending sericeous. Leaves clustered or distant (? juvenile shoots), petioles 8-40 mm. long, 1.5-3 mm. thick, densely dark brown or orange-brown velutinous, not obviously sulcate above; laminae 7-26 cm. long, 4-13 cm. broad, ovate-oblong to slightly obovate or broadly elliptic, rounded or occasionally very short acuminate at the apex, rounded to truncate at the base and slightly cordulate at the petiole, drying very stiffly chartaceous and the margins strongly revolute, scabrous and puberulent above, puberulent beneath with mostly straight stiff yellowish-brown hairs 0.5-1.2 mm. long (but not scabrous), the 5 to 10 pairs of major secondary veins slightly impressed above and very prominent beneath, central secondaries arising at angles of 45-70 degrees, secondaries weakly loop-connected near the margin, tertiary veins usually prominent beneath. Figs usually paired at a node, subsessile or short-pedunculate, basal bracts 2, entire or cleft, about 2 mm. long from a small disc-like area formed by the apically flared peduncle, with dark brown hairs to 1 mm. long; fig 10-14 mm. in diameter, globose, the surface densely tomentulose with yellowish-brown or grayish hairs 0.2-0.5 mm. long, the ostiole hidden within an elevated collar of receptacular tissue 1-3 mm. high and 3-5 mm. in diameter; seeds and galls about 1.2 mm. long.

Trees of evergreen lowland wet forest formations from sea level to 200 m. (?) elevation and known in Costa Rica from only two collections (*Allen 6638* & *Croat 16622*) made near Palmer Sur, Puntarenas. The known range of this species extends from southernmost Costa Rica to Central Panama.

*Ficus bullenei* is recognized by the densely brown velutinous pubescence on many parts, laminae scabrous above, and the relatively small fig with unusually large apical collar surrounding the ostiole. The species is vegetatively very similar to *F. popenoei* with very different figs and is related to *F. velutina* of montane forests.

*Ficus caldasiana* Dugand, *Caldasia* 1, no. 4:33. 1942. Figure 17.

Trees to about 25 m. tall, becoming very large with trunks over 3 m. in diameter and a crown over 20 m. broad, leafy internodes 4-30 mm. long, 5-16 mm. thick, with thin whitish hairs 0.3-0.8 mm. long; stipules 12-34 mm. long, about 8 mm. thick near the base, narrowly acute, with thin whitish hairs about 0.5 mm. long except along the edges. Leaves clustered at the ends of stems in mature growth, petioles 3-9 cm. long, 2-4.5 mm. thick, densely pilose with thin white hairs; laminae (9) 15-27 cm. long, 8-19 (21) cm. broad, broadly elliptic or elliptic-oblong to broadly obovate, abruptly narrowed at the bluntly obtuse or round apex, abruptly rounded and usually subcordate at the base, margin entire, laminae drying stiffly chartaceous to subcoriaceous, smooth above and with minute hairs above the major veins, densely pilose or hirtellous on the veins beneath, the thin 0.3-0.8 mm. long hairs sparse between the veins, the 8 to 12 pairs of major secondary veins arising at angles of 50-70 degrees, only weakly loop-connected in the distal third of the lamina. Figs usually paired at a node, sessile and often producing shelf-like structures on old stems, the basal bracts 2 but usually deeply split and apparently 3 or 4, becoming 15 mm. long and 15 mm. broad at the broadest point, whitish sericeous, covering the fig in early stages; the fig becoming about 14 mm. long and 22 mm. in diameter, flattened at both ends and oblate, the surface with thin whitish hairs 0.3-1 mm. long, ostiole flat, 2-5 mm. broad and densely sericeous; seeds and galls about 1.5-2 mm. long.

Trees of the very wet Caribbean slopes and the area of the General Valley between 800 and 1300 m. elevation. The species has been collected in Costa Rica above Turrialba (*Holdridge 6809* & *6810*) near Juan Viñas (*O. Jimenez s. n.*. Museo Nacional 38280), along the Río Grande de Orosi near Tapanti (*Burger & Gentry 9206*), all in the province of Cartago, and northeast of San Isidro del General (*Luteyn 3283*) in the province of San Jose. Otherwise the species is only known from the province of Caldas, Colombia.

*Ficus caldasiana* is recognized by its broad leaves subcordate at the base with long petioles, large sessile figs subtended and at first enclosed by large basal bracts, and the thin whitish hairs on



both figs and vegetative parts. The paired figs, two bracts, and ostiole with only three exposed scales (in most stages) are characteristics of the subgenus *Urostigma*. This species resembles *F. cuatrecasana*, but the figs are larger with larger bracts and the plants are more puberulent in *F. caldasiana*. However, two recent collections from the road to Dominical west of San Isidro del General, lacking figs and tentatively placed here (*Burger & Baker 10101b & 10115*) may indicate that this species contains glabrous individuals. Placement of this Costa Rican material under the species originally described from Colombia is a tentative expedient; further study may show that the plants are not conspecific. *Ficus garcia-barrigae* Dugand and *F. jaramilloi* Dugand, both of Colombia, appear to be close relatives of *F. caldasiana*.

***Ficus carica* L., Sp. Pl. 1059. 1753.**

Small trees 3-10 m. tall, wood soft, leafy internodes 1-8 cm. long, 5-10 mm. thick, glabrous or sparsely puberulent; stipules 15-30 mm. long. Leaves usually sparsely puberulent, petioles 4-14 cm. long, about 2.5 mm. thick; laminae 12-24 cm. long, 10-22 cm. broad, broadly ovate to orbicular in general outline but usually deeply 3-lobed in the distal half with small lobes present or absent near the base, cordate at the base, the margin bluntly dentate, drying stiffly chartaceous and scabrous above, venation palmate with 3 (5) main veins arising at the apex of the petiole. Fig solitary at a node, sessile or subsessile below the small bracts, narrowed above the bracts and usually pyriform to obovoid, 2-5 cm. in diameter.

Widely cultivated for ornament as well as for the edible figs, which vary greatly in size and shape in different varieties. This species is readily recognized by the lobed leaves, small stature, and edible figs (*higos*). *Ficus carica* is not an economically important crop in Central America.

***Ficus cervantesiana* Standley & L. O. Williams, Ceiba 3:194. 1953. Figure 18.**

Trees 6-20 m. tall, leafy internodes 5-20 (32) mm. long, 2.8-4 mm. thick, glabrous, the periderm becoming longitudinally ridged and pale grayish on drying; stipules 16-36 mm. long, 2-5 mm. thick at the base unopened, glabrous or very minutely (0.05-0.1 mm.) puberulent, drying dark brown. Leaves not usually clustered at the ends of twigs, petioles 10-28 mm. long, 1.6-2.8 mm. thick, glabrous and narrowly sulcate above; laminae (6) 9-21 cm. long, (3) 4-8.5 cm. broad, oblong to elliptic-oblong, tapering abruptly to the acuminate apex, tapering abruptly and somewhat rounded at the obtuse base, laminae drying chartaceous to very stiffly chartaceous or subcoriaceous, smooth and glabrous above, smooth below with a few groups of pale colored strigulose hairs 0.5-1 mm. long on the sides of the midvein in the basal half of the lamina, the 12 to 18 pairs of major secondary veins raised above

and prominent below, central secondaries arising at angles of 60-80 degrees, loop-connected near the margin but not forming a definite submarginal vein, tertiary veins becoming raised on both surfaces. Figs usually 2 per node, sessile or subsessile, basal bracts 2 and entire or split 3-4 mm. long and about 4 mm. broad, glabrous, the fig about 10 mm. in diameter, subglobose with a flattened apex, surface smooth and glabrous or very minutely (-0.05 mm.) puberulent, drying dark, ostiole flat or slightly conical, about 2 mm. broad, exterior scales 2 (3); seeds and galls 1-1.5 mm. long.

Trees of the very wet montane (premontane wet) forest formations between 1000 and 1700 m. elevation and presently known from only four collections: *Reark 394*, the type, from near Cervantes (Cartago); *Standley 36149* from La Hondura; *Burger & Liesner 7098* from the upper Río Chirripó del Pacifico (San José); and *Lent 2613* from Quebrada Azul northwest of San Ramon (Alajuela); mature figs have been collected at the end of August and the end of December.

*Ficus cervantesiana* is recognized by the abruptly acuminate leaves with slightly raised venation on both surfaces, very unusual hairs along the side of the midvein beneath in the basal part of the lamina, the smaller sessile figs, and restricted wet montane habitat. This species is poorly known but appears to be related to *F. paraensis*.

***Ficus citrifolia* P. Miller, Gard. Dict. ed. 8, Ficus no. 10. 1768, fide DeWolf. Figure 18.**

Small to medium sized trees 5-12 (16) m. tall or rarely a shrub, often found originating as epiphytes, the sap usually clear and very viscous, leafy internodes 3-20 (35) mm. long, 3-7 mm. thick, glabrous, periderm often peeling off in small (0.5 mm.) flakes, older stems brown to pale gray; stipules 6-16 mm. long, 3-5 mm. thick at the base unopened, glabrous and drying brown. Leaves usually distant on the stem, petioles 1.4-6 (12) cm. long, 1-2.3 mm. thick, quite variable in length on the same tree, glabrous, slightly sulcate above; laminae 8-18 (22) cm. long, 4-8 (10) cm. broad, oblong to elliptic-oblong, gradually to abruptly narrowed to the acuminate apex, obtuse to rounded and subtruncate at the base, drying chartaceous to stiffly chartaceous and flat, smooth and glabrous on both surfaces, the 4 to 12 pairs of major secondary veins flat above and slightly raised beneath, central secondaries arising at angles of 50-70 degrees, secondaries loop-connected near the margin and often forming a weak submarginal vein, tertiary veins usually flat beneath. Figs usually paired at a node, borne on peduncles 5-10 mm. long, about 2 mm. thick, glabrous or very minutely (0.05 mm.) puberulent, slightly expanded at the apex, bracts 2, entire or divided, about 2 mm. long and 4 mm. broad, glabrous; figs 10-14 mm. in diameter, globose to obovoid and slightly narrowed at the base, surface smooth and glabrous, usually green ostiole slightly raised or slightly conical, the usual 3 outer scales surrounded by a slight ridge of receptacular tissue 3-5 mm. in diameter; seeds and galls 1-1.4 mm. long.

Plants of moist and wet evergreen forest formations from sea level to 1200 m. in Costa Rica on the Caribbean slopes and on the eastern side of the Meseta Central around San José; probably flowering throughout the year. This species, as interpreted by DeWolf, ranges from southern Florida and Mexico to Paraguay.

*Ficus citrifolia* is a striking species because of its oblong laminae abruptly narrowed at both ends and short-acuminate apically, long slender petioles, glabrous parts (in ours), and pedunculate figs often slightly narrowed at the base. The species is unusual because of its clear thick sap (fide Holdridge and Croat). This species is very closely related to *F. dugandii* (*F. turbinata*), which has milky sap, dark brown twigs, thinner leaves, and apparently grows to a larger size.

*Ficus colubrinae* Standley, Contr. U.S. Nat. Herb. 20:16. 1917. Figure 20.

Small to medium sized trees 4-12 (20) m. tall, epiphytic and strangling or occasionally independent, trunk smooth or several grown together, leafy internodes 2-15 (22) mm. long, 1.5-4 mm. thick, sparsely puberulent with slender crooked or straight hairs 0.8-3 mm. long, soon becoming glabrescent and gray on drying; stipules 4-8 mm. long, about 2-3 mm. thick at the base unopened, densely covered with long thin crooked hairs. Leaves often numerous and clustered on the ends of branchlets, petioles 8-20 (26) mm. long, 0.8-2.4 mm. thick, densely to sparsely puberulent with straight and crooked hairs 0.5-3 mm. long, ridged on drying and sulcate above, the epidermis often peeling off in small flakes; laminae (4) 6-12 cm. long, (2) 3-6 cm. broad, obovate to broadly elliptic, usually abruptly narrowed at the short acuminate (rarely rounded) apex, obtuse to rounded at the base, lamina drying stiffly chartaceous and the margin flat or slightly revolute, smooth and glabrous above, sparsely puberulent beneath with slender hairs, the 2 to 4 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 35-60 degrees, basal secondaries very prominent and the venation sub-palmate. Figs usually paired at the node, sessile, bracts 2, entire or split, about 2 mm. broad and 1-2 mm. long, with slender yellowish hairs 0.3-1 mm. long, often slightly (0.5 mm.) united to the receptacle basally and the peduncle somewhat acentric; figs 5-8 mm. in diameter, globose or flattened apically, surface smooth and glabrous pale pink but yellowish and wrinkled when dry, ostiole slightly raised of lustrous tissue drying dark, 2-3 mm. broad, the wall very thin; galls and seeds 0.7-1 mm. long.

Trees of wet evergreen forest formations from sea level to about 800 m. altitude in Costa Rica on both the Caribbean and Pacific slopes; flowering throughout the year. The species, as here defined, ranges from British Honduras and Guatemala to central Panama.

*Ficus colubrinae* is easily recognized by its small leaves with subpalmate venation with few prominent secondary veins, small

stipules, small figs, and lower elevation habitat. This species is very closely related to *F. hartwegii* but differs in habitat and leaf-venation; see the discussion under that species.

***Ficus costaricana*** (Liebm.) Miquel, Ann. Mus. Bot. Ludg.-Bat. 3:298. 1867. *Urostigma costaricanum* Liebm., Danske. Vidensk. Selsk. Skrivt. 5, ser. 2:322. 1851. Figure 19.

Small to large trees 8-20 (30) m. tall, independent or rarely seen as a strangler, trunk relatively smooth and usually short, leafy internodes 5-15 (50) mm. long, 3-8 mm. thick, with stiff straight or crooked hairs 0.3-1 mm. long in early stages, becoming gray and ridged, often with the persisting stipules and shelf-like formations above the leaf-scars where figs were attached; stipules 7-30 mm. long, 3-5 mm. broad at the base unopened, with slender whitish hairs 0.3-1 mm. long at the base and along the midrib. Leaves usually clustered at the ends of branchlets, petioles 7-30 (50) mm. long, 1.2-3.2 mm. thick, sparsely puberulent near the base, very narrowly sulcate above; laminae very variable (on different trees), 5-16 cm. long, 3-6.5 (8) cm. broad, obovate to broadly elliptic or oblong, gradually to abruptly narrowed to the obtuse or rounded apex (occasionally short-acuminate), narrowed gradually or abruptly at the base and cuneate to rounded, drying stiffly chartaceous, glabrous and smooth on both surfaces, the (3) 4 to 8 (10) pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of (35) 40-65 degrees, basal secondaries strongly ascending, secondaries not usually loop-connected near the margin, tertiary veins obscure. Figs usually paired at a node, sessile and the stem becoming shelf-like at the point of attachment, bracts 2 and usually split, about 4 mm. long and 4 mm. broad, with long (1 mm.) ascending yellowish hairs, united with the receptacle for about 1 mm. from the slightly acentric base, figs becoming oblate and distinctly flattened at both ends at maturity, 10-12 (14) mm. in diameter, surface smooth and glabrous, becoming pink marked by red spots, wall of the fig very thin, ostiole conical in early stages, very slightly raised and drying dark at maturity, 2-3 mm. broad, exterior scales 2 or 3; seeds and galls about 1.2 mm. long.

Trees of evergreen forest formations between sea level and 1200 m. elevation on both the Caribbean and Pacific slopes in Costa Rica. The species is common on the Meseta Central but is rarely collected below 300 m.; mature figs have been collected in all months but September and October. The species ranges from Guatemala to Panama.

*Ficus costaricana* is recognized by its relatively thick stems with broad brown stipules often persisting as long as the leaves and the sessile figs broader than long. The leaves vary greatly in the species but are often small to medium-sized and usually taper abruptly at both ends. This species is related to *F. hartwegii* among our species but is more likely to be confused with *F. turrialbana*. The illustration

in the "Flora of Panama" (Ann. Missouri Bot. Gard. 47:164. 1960) is very atypical.

Standley placed a large number of collections from northern Central America under this name, but these differ from ours in a number of ways and, I believe, are better placed under his *F. kellermanii*. The two are in turn related to a group of species that are often difficult to distinguish and appear to be closely related; these include *F. cotinifolia*, *F. hartwegii*, *F. hondurensis*, *F. inamoena*, *F. morazaniana*, and *F. trigonata*.

***Ficus cotinifolia* H.B.K., Nov. Gen. & Sp. 2:49. 1817. Figure 19.**

Small to large trees 6-20 (40) m. tall with broad spreading crown, trunks fluted and the branches with aerial roots, leafy internodes 2-30 mm. long, 2.5-6.5 mm. thick, dense soft grayish tomentulose hairs 0.1-1 mm. long, becoming prominently ridged and grayish on drying; stipules 5-12 mm. long, 3-4 mm. thick at the base unopened, densely grayish strigulose or tomentulose or glabrous apically. Leaves not usually clustered, petioles (6) 12-80 mm. long, 1.2-3.5 mm. thick, densely soft puberulent but becoming glabrous and the epidermis flaking off, narrowly sulcate above; laminae (5) 7-15 cm. long, (3) 4-8 cm. broad, very broadly oblong or elliptic to suborbicular or somewhat ovate or obovate, rounded to bluntly obtuse at the apex, obtuse to rounded or subtruncate at the base, drying stiffly chartaceous, smooth and glabrous above, sparsely puberulent with thin whitish hairs 0.1-0.7 mm. long beneath, the 4 to 7 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 35-70 degrees, secondaries weakly loop-connected near the margin, tertiary veins distinct beneath. Figs usually 2 at a node, sessile, bracts 2 and usually split, 2-4 mm. long, 3-5 mm. broad, densely puberulent on both surfaces with the inner hairs longer, united with the receptacle only near the base; figs 6-10 mm. in diameter, globose or slightly broader than long, surface smooth to the touch and very minutely (0.05 mm.) puberulent or apparently glabrous, ostiole slightly sunken within a ring of thickened tissue 1.5-2 mm. in diameter, entrance covered by 2 exterior scales, wall very thin; seeds and galls about 0.8 mm. long.

Trees of the seasonally very dry deciduous and evergreen formations of the Pacific slope in central and northwestern Costa Rica from sea level to about 900 m. elevation; apparently flowering throughout the year. The species ranges from Mexico along the drier western slopes of Central America to Central Costa Rica.

*Ficus cotinifolia* is recognized by the relatively broad leaves usually on long petioles and rounded at the apex, short stipules often covered with thin pale grayish hairs, small figs, and seasonally dry habitat. This species is related to *F. hartwegii* (with smaller leaves and figs at higher elevations), *F. costaricana* (with persisting stipules, larger figs, and wetter habitat), and perhaps most closely

with *F. trigonata* and its allies (q.v.). I am using this name as Standley applied it, not having seen the type. An unusual collection (*Burger & Gentry 9149*) from above the falls of the Río Potrero west of Bagaces is placed here. This tree has short-pedunculate figs and short-petiolate leaves very similar in shape and venation to leaves of *F. hartwegii*. I believe it represents no more than a very unusual combination of morphological characters in the species.

***Ficus crassiuscula*** Warburg ex Standley, Contr. U.S. Nat. Herb. 20:12. 1917. Figure 21.

Medium-size to large trees 7-25 m. tall, trunks smooth or slightly buttressed, leafy internodes 2-25 (45) mm. long, 3-6 mm. thick, glabrous or very sparsely puberulent with minute (0.1 mm.) straight whitish hairs, periderm smooth or slightly striate, drying very dark on new shoots or pale gray; stipules 2-5 cm. long, 3-6 cm. thick at the base unopened, glabrous and usually drying very dark. Leaves often crowded near the ends of branchlets, petioles 12-22 (30) mm. long, about 2 mm. thick, glabrous, deeply sulcate above, epidermis not usually flaking off; laminae (6) 8-16 cm. long, (2.5) 4.5-8 cm. broad, elliptic to narrowly obovate or oblong, abruptly narrowed to the obtuse to acute apex but rounded at the tip, obtuse to cuneate at the base, drying subcoriaceous and the margins usually revolute, smooth and glabrous on both surfaces, the 12 to 17 pairs of major secondary veins flat above and only slightly raised beneath, central secondaries arising at angles of 60-80 degrees, secondaries loop-connected near the margin and forming a slightly arcuate submarginal vein, the submarginal vein often joining a bifurcated midvein near the apex, tertiary veins often obscure. Fig solitary at a node, borne on a peduncle 5-15 mm. long, 2-4 mm. thick, glabrous, basal bracts 3, usually entire, 3-4 mm. long, 4-5 mm. broad; figs becoming 3-5 cm. in diameter with a very thick wall, globose and narrowed above the bracts to form a stalk-like continuation of the peduncle, surface smooth and glabrous, ostiole conspicuously raised in early stages and 5-10 mm. broad at maturity, exterior scales 3-6 mm. broad at the base, 3 with the apices of interior scales readily visible, wall very succulent, 3-6 mm. thick (dry); seeds and galls 2-2.8 mm. long.

Trees of wet evergreen cloud forests between 1200 and 2000 (? 2500) m. altitude and known in Costa Rica from Volcán Rincon de la Vieja (Guanacaste), La Palma de San Ramon and Fraijanes (Alajuela), Zurqui, Irazú, and Cerro de la Carpintera (San Jose) above Orosi (Cartago), and above San Vito de Java (Puntarenas). The species, as here understood, occurs from Guatemala southward to Chiriquí, Panama.

*Ficus crassiuscula* is distinguished by its thick blunt glabrous leaves, broad stipules drying dark, thick twigs, large figs with very thick walls, and cloud-forest habitat. The solitary figs and unusual trichomes on the lower leaf-surface ( $\times 150$ ) are characters of the subgenus *Pharmacosycea*. This species is closely related to *F. yopo-*

*nensis* and is part of a group of species that were considered conspecific with *F. insipida* (q.v.) in the "Flora of Panama." Unlike many other species of the subgenus *Pharmacosycea*, this species does not appear to grow near streams.

***Ficus crassivenosa* Burger, Phytologia 26:424. 1973. Figure 21.**

Trees to over 30 m. tall or occasionally epiphytic, leafy internodes 1-35 mm. long, 2-6 mm. thick, glabrous or sparsely and very minutely puberulent, the epidermis occasionally reddish-brown and flaking off in long (5 mm.) strips, the periderm becoming deeply ridged and striate when dry, twigs grayish in age; stipules 2-3 cm. long, about 2-4 mm. thick at the base unopened, glabrous. Leaves separate or clustered at the ends of branchlets, petioles 8-24 mm. long, 1-3 mm. thick, usually glabrous, sulcate above; laminae 5.5-13 cm. long, (2) 3-7 cm. broad, obovate to elliptic or elliptic-oblong, rounded to obtuse and with a blunt tip at the apex, obtuse at the base, drying subcoriaceous and the margins slightly revolute, smooth and glabrous (10×) above and below, often lustrous above, the 10 to 40 pairs of major secondary veins often difficult to distinguish from the intermediate veins, raised on both surfaces, appearing thickened above, the central secondaries arising at angles of 60-90 degrees, the secondaries connected by a submarginal vein 1-2 mm. from the margin, tertiary veins slightly raised on both surfaces. Figs solitary at a node, borne on peduncles 6-8 mm. long, 1-1.5 mm. thick, glabrous, basal bracts 1-2 mm. long and 2-3 mm. broad, sparsely and minutely puberulent, deciduous, the fig narrowed beneath to form a stalk-like portion 1-3 mm. long above the 3 bracts, expanded portion of the fig globose, about 15 mm. in diameter, surface smooth and glabrous or with a few minute (0.05 mm.) hairs, ostiole conical, wall of the fig about 1 mm. thick (dry), seeds and galls 1.5-2 mm. long.

Very tall trees or (?) epiphytes in the very wet forests of the Caribbean slopes and lowlands between about 60 and 600 m. elevation. The species is known from only three collections: the type, *Hartshorn 1238* from near La Selva on the Río Puerto Viejo; *Burger & Burger 8134* from Tirimbina near the Río Sarapiquí, Heredia; and *Walters 79* from Valle Escondida, Cartago.

The characteristic microscopic oblongoid-capitate trichomes (×150) on the lower leaf surfaces and the solitary figs with three bracts are characteristics of the subgenus *Pharmacosyce*. The thick leaves with many secondary veins and a submarginal vein near the edge are similar to the leaves of *F. crassiuscula*, but the tertiary veins are more pronounced and the laminae more blunt in this species. The lowland habitat and small stipules and figs are also very different from those of *F. crassiuscula*. The figs of this species are very similar to those of *F. yoponensis*, but that species has very different foliage. This species was only known from two sterile twigs until Gary Hartshorn collected material with figs on 29 May 1973.

**Ficus cuatrecasana** Dugand, *Caldasia* 1, no. 4:36. 1942. Figure 17.

Small trees about 8 m. tall (becoming very large?), Crown open, the branches wide-spreading, leafy internodes 1-12 (20) mm. long, 4-8 (12) mm. thick, glabrous or with slender hairs about 1 mm. long near the node, periderm becoming striate or somewhat ridged, grayish; stipules 14-30 (60) mm. long, 6-14 mm. thick at the base unopened, glabrous and deciduous in ours (densely reddish brown appressed puberulent and persisting in Colombia). Leaves usually clustered at the ends of shoots, petioles 3-8 (11) cm. long, 2-4 (5) mm. thick, glabrous or sparsely puberulent with slender whitish hairs, terete; laminae (10) 14-32 (40) cm. long, (8) 10-20 (24) cm. broad, elliptic-obovate to slightly pandurate, usually broadest above the middle, rounded or abruptly narrowed to a very short acute or obtuse apex, abruptly truncate to subcordate at the base (in larger leaves), drying stiffly chartaceous, smooth and glabrous on both surfaces, the 9 to 13 pairs of major secondary veins slightly raised above and prominent beneath, central secondaries arising at angles of 50-80 degrees, not strongly loop-connected near the margin, the basal pair of secondaries often very prominent and strongly ascending, tertiary veins flat beneath. Figs 2 at a node, maturing well behind the current foliage in ours (maturing both behind and among the leaves and persisting stipules in the type), sessile, bracts 2, variously split and 3-5 lobed, 3-5 mm. long, glabrous to puberulent with slender hairs about 0.5 mm. long, united near the base and occasionally forming a small disc-like area with the attachment acentric; figs 16-20 mm. in diameter, 10-12 mm. long, oblate to obovoid with the apex usually strongly flattened, surface smooth and glabrous, brown, ostiole flat or slightly raised forming a circular area 3-4 mm. broad, exterior scales 2 or 3; seeds and galls 1-1.5 mm. long.

Poorly known trees tentatively placed under this name and known from only two collections from the wet Caribbean slopes at 500 and 1000 m. elevation in Costa Rica: *Lent 3445* from the slopes of Volcán Arenal, Alajuela, and *Burger 4162* from the Río Claro (Río La Hondura-Río Zurqui drainage) below La Palma, San José; mature figs were collected in December and January. The species was originally described from Colombia (*Cuatrecasas 8218*).

*Ficus cuatrecasana* is recognized by the large laminae usually broadest above the middle and borne on long petioles and the mature oblate figs borne well behind the leaves (in ours). I have seen only two fertile collections, which may not be conspecific but which are very closely related. The type material differs from the Costa Rican collections in that the stipules are densely reddish-brown puberulent and larger and more persistent, and the figs are borne among as well as behind the leaves. The two collections are very similar in leaf-shape, microscopic hairs ( $\times 150$ ), venation, and form and size of the figs. It seems best to treat these collections as a single species until the populations concerned are better understood. This species is closely related to *F. richteri* Dugand of Colombia and to *F. caldasiana* and its allies.



***Ficus davidsoniae*** Standley, Field Mus. Bot. 22:15. 1940. Figure 20.

Small to large trees 10-30 m. tall, independent or epiphytic, leafy internodes 5-17 mm. long, 3-7 mm. thick, glabrous or sparsely puberulent, periderm becoming pale gray and longitudinally striate; stipules 12-30 mm. long, 3-5 mm. thick at the base unopened, glabrous or very minutely (0.05 mm.) puberulent. Leaves usually clustered at the ends of branchlets, petioles 4-18 mm. long, 1.3-4 mm. thick, glabrous near the base but with thin whitish hairs 0.5-1.5 mm. long distally, deeply sulcate above, laminae 6-14 (18) cm. long, 2-6 (9) cm. broad, narrowly obovate to elliptic or elliptic-oblong, bluntly acute to obtuse or occasionally rounded near the apex, cuneate to obtuse and somewhat rounded at the base, lamina drying subcoriaceous and the margins revolute, smooth, glabrous, and often glaucous above, usually pale brown beneath, glabrous or with crooked or straight whitish hairs 0.3-1.5 mm. long on the proximal half of the midvein, the 10 to 20 pairs of major secondary veins slightly raised on both surfaces and often difficult to distinguish from the intermediary veins, an arcuate submarginal vein present, tertiary veins forming a very slightly raised reticulum. Figs usually paired at a node, sessile and forming a small shelf-like depression on the stem, bracts 2, entire or split, 3-5 mm. long, about 8 mm. broad, united to the receptacle and forming a thickened basal area on one side, bracts conspicuous and glabrous; figs 6-8 (10) mm. in diameter, 4-6 mm. high, globose to obovate, surface smooth and glabrous, brown, ostiole about 1.5 mm. broad, conspicuously umbonate and drying dark, 1-1.5 mm. high, exterior scales 2 or 3, wall of the fig thin; seeds and galls about 1 mm. long.

Trees of wet evergreen forest formations between (600) 800 and 1200 m. elevation, known only from the Caribbean slopes between Turrialba and Moravia (Cartago) in Costa Rica. In Panama the species is known from Boquete (Chiriquí) and near El Valle de Anton (Coclé); figs have been collected in November, December, and May. The species is, I believe, endemic to this area in Central America.

*Ficus davidsoniae* is recognized by its very thick generally narrowly obovate leaves brownish beneath, glabrous stipules, small sessile figs with umbonate ostiole and conspicuous bracts, and high-land habitat. This species is probably related to *F. jimenezii* among our species.

***Ficus donnell-smithii*** Standley, Contr. U.S. Nat. Herb. 20:21. 1917. Figure 18.

Small to medium size trees 4-16 m. tall, epiphytes or independent, leafy internodes 2-10 (15) mm. long, 1.7-3.8 mm. thick, minutely puberulent with erect grayish hairs 0.1-0.3 mm. long, periderm becoming somewhat striate and dark gray; stipules (2) 3-9 mm. long, 1.5-2.5 mm. thick at the base unopened, drying dark brown with a uniform covering of minute (0.05 mm.) grayish hairs. Leaves clustered or distant, petioles 7-22 mm. long, 0.9-1.7 mm. thick, minutely (0.1 mm.) puberulent, narrowly sulcate above; laminae 5-15 cm. long, 1.4-3.2 cm. broad, narrowly lanceolate to very

narrowly elliptic, tapering gradually to the acute or obtuse apex and often rounded at the tip, acute to abruptly obtuse at the base, drying stiffly chartaceous and usually dark in color (above) with flat or slightly involute margins, smooth and very minutely puberulent on both surfaces with erect grayish hairs about 0.1 mm. long, the 6 to 12 pairs of major secondary veins flat above and slightly raised beneath, central secondaries arising at angles of 40-60 degrees, tertiary veins flat and often obscure. Figs usually paired at a node, borne on peduncles 4-9 mm. long, 0.5-1 mm. thick, slightly expanded at the apex, glabrous or very minutely (0.05 mm.) puberulent, bracts 2, usually entire and rounded, 1-2 mm. long, glabrous or very minutely puberulent; figs 7-10 mm. in diameter, globose or somewhat flattened at the top, surface smooth and glabrous, drying reddish brown or yellowish and not conspicuously wrinkled, ostiole flat and often surrounded by wrinkled tissue at the apex of the fig (dry), about 2 mm. broad, exterior scales 3, drying dark; seeds and galls 0.7-1 mm. long, enclosed within the conspicuous perianth.

Trees of the wet Caribbean Lowlands from sea level to about 500 m. elevation and known in Costa Rica from only two collections: near the mouth of the Río Colorado, Limón (*Walter 53*), and near the Río Puerto Viejo, Heredia (*Hartshorn 1068*). The species is otherwise known only from British Honduras and Guatemala, with mature figs having been collected in December in Costa Rica and in February, May, August, and November in northern Central America.

*Ficus donnell-smithii* is easily recognized by its small narrow leaves on prominent petioles, many parts drying dark in color and having a pubescence of very small (0.05-0.2 mm.) erect slender grayish hairs, and the small pedunculate figs. The species appears to be related to *F. perforata*.

**Ficus dugandii** Standley, *Trop. Woods* 32:20. 1932. *F. turbinata* Pittier, *Bol. Soc. Venez. Cienc. Nat.* 4(30):61. 1937 (non Willd. 1806), fide auctores in herb. Figure 18.

Medium to large size trees 10-25 m. tall, not seen as stranglers, leafy internodes 4-35 mm. long, 2.5-6 mm. thick, glabrous, periderm becoming irregularly ridged or smooth (dry) and reddish-brown; stipules 5-15 (40) mm. long, 2-5 mm. thick at the base unopened, glabrous or very minutely (0.05 mm.) puberulent, drying brown. Leaves usually distant on the twigs, petioles 2-9.5 cm. long, 1-2.4 mm. thick, glabrous, slightly sulcate above; laminae 11-22 cm. long, 4-8 cm. broad, ovate-oblong to elliptic-oblong, tapering gradually or abruptly to the short- or long-acuminate apex, abruptly obtuse to subtruncate at the base, drying chartaceous and flat, smooth and glabrous on both surfaces, the 6 to 13 pairs of major secondary veins flat above and slightly elevated beneath, central secondaries arising at angles of 45-65 degrees, weakly loop-connected near the margin and a submarginal vein absent, tertiary veins flat beneath. Figs paired or solitary at a node, subsessile or borne on peduncles 0-4 mm. long, 1-2 mm. thick, glabrous or very minutely puberulent, bracts 2, entire or split, 2-4 mm. long, 3-4 mm. broad, glabrous or very

minutely (0.05 mm.) puberulent; figs 9-13 mm. in diameter, subglobose to obovoid or turbinate in early stages, surface smooth and glabrous, drying pale yellowish in color, ostiole slightly conical, 1.5-3 mm. broad, exterior scales usually 3; seeds and galls 1-1.5 mm. long.

Trees of the moist evergreen forest formation from sea level to about 1000 m. elevation; probably flowering throughout the year. This species is known in Costa Rica from only two collections: *Lankester & O. Jimenez 1316* from La Hermosa, Perez Zeledon, in the General Valley and *Brenes 23013* from San Pedro de San Ramon. The species is also known from several collections in the Canal Zone (*Croat 8293, 12694, & 15242; Muenscher 12302*), and the type (*Dugand 27*) near Galapa, Colombia.

*Ficus dugandii* is recognized by its thin ovate-oblong laminae on long slender petioles, and short-pedunculate figs often turbinate in form. This species has been mistaken for *F. citrifolia* but differs in the white sap, dark brown branchlets, thinner laminae of slightly different form, somewhat different ostiole, and apparently larger habit.

***Ficus elastica* Roxb., Fl. Ind. ed. 2, 3:541. 1832.**

Large trees to over 20 m. tall but most often cultivated in a juvenile form (often as a potted plant in homes), leafy internodes 1-10 cm. long, 5-15 mm. thick; stipules (1.5) 5-20 cm. long. Leaves glabrous, petioles 2-7 cm. long; laminae (6) 12-30 cm. long, (4) 5-12 cm. broad, oblong to elliptic, sharply acute at the apex, drying subcoriaceous, major secondary veins very numerous (50+), united near the margin by a submarginal vein. Figs usually paired at a node, sessile but with a thick articulated base about 4 mm. long and 4 mm. thick (dry), figs 5-8 mm. in diameter and 10-12 mm. long, oblong, glabrous, ostiole slightly conical and surrounded by a ring of tissue 2-3 mm. broad.

Common small trees of homes and gardens occasionally growing to large size in gardens and parks (as in the Parque Nacional, San José). The large lustrous thick leaves, usually dark green above, and the very large, often pink, stipules make this a very striking species. However, some trees do not have these large stipules and large leaves. The variations in leaf-size in the trees of this species must be due to genetic differences in different cultivated forms. The large tree in the northwestern corner of Parque Nacional in San José with small (6-12 cm. long) leaves looks very different from the large-leaved plants of this species that one usually sees.

***Ficus goldmanii* Standley, Contr. U.S. Nat. Herb. 20:32. 1917.**  
*Urostigma verrucosum* Liebm., Danske Vidensk. Selsk. Skrivt. 5, 2:321. 1851. *Ficus verrucosa* Hemsl., Biol. Centr. Amer. Bot.

3:148. 1883, not *F. verrucosa* Miquel, 1867. *F. hemsleyana* Standl., l.c. 20:29. 1917, as to type only, not *F. hemsleyana* King, 1887. Figure 19.

Trees 6-15 m. tall, trunks often fluted and branching near the ground, aerial roots often present, leafy internodes 2-25 (55) mm. long 3-8 mm. thick, glabrous, periderm smooth but becoming ridged and pale brown (dry); stipules 8-14 mm. long, 3-4 mm. thick at the base unopened, glabrous to very minutely (-0.05 mm.) puberulent or with a few sericeous hairs 0.2-0.5 mm. long. Leaves clustered or distant, petiole 16-38 mm. long, 1.2-2.8 mm. thick, glabrous or very minutely (0.05 mm.) puberulent, slightly sulcate above; laminae 8-21 cm. long, 3-9 (11) cm. broad, oblong to elliptic-oblong, abruptly rounded to obtuse or with a very short acute tip at the apex, obtuse to rounded at the base, stiffly chartaceous to subcoriaceous, smooth and glabrous on both surfaces, the 7 to 12 pairs of major secondary veins flat above and slightly raised beneath, central secondaries arising at angles of 50-75 degrees, secondaries weakly loop-connected near the margin, tertiary veins often obscure. Figs usually paired at a node, borne on peduncles 4-14 mm. long, 1.2-3 mm. thick, glabrous or very minutely puberulent, slightly expanded at the apex but not forming a definite disc-like area, bracts 2, entire or split, about 3 mm. long and 3-4 mm. broad, essentially glabrous; figs globose, 9-14 mm. in diameter, surface smooth and glabrous or very minutely (-0.05 mm.) puberulent, ostiole raised and conical, 3-4 mm. in diameter, the outer scales usually 3 (4) and occasionally surrounded by a weakly developed ring of receptacular tissue 3-4 mm. in diameter; seeds and galls 1.3-1.7 mm. long.

Trees of seasonally dry deciduous and evergreen forest formations along the Pacific Coast in Costa Rica between sea level and 300 m. elevation (to 1000 m. in Honduras); fertile collections have been made in December-January and July-August. The species ranges from Western Mexico and British Honduras to Panama.

*Ficus goldmanii* is recognized by its glabrous or very minutely puberulent parts with pale colored hairs less than 0.05 mm. long (longer hairs on the stipules), usually oblong leaves, pedunculate figs, and seasonally dry lowland habitat. This species is said to be used for living fence posts in the Golfito area. This species is closely related to *F. morazaniana*, but that species has larger figs on shorter peduncles and is densely pubescent in many parts. A photograph of the type of *Urostigma verrucosum* (Oersted 14339 in C) appears to be this species. Standley proposed a new name for this species, *Ficus hemsleyana*, but did not see the type and placed material under his *F. hemsleyana* that is clearly referable to *F. citrifolia* Miller.

*Ficus hartwegii* (Miq.) Miquel, Ann. Mus. Bot. Lugd.-Bat. 3:299. 1867. *Urostigma hartwegii* Miq. in Hooker, London Journ. Bot. 6:545. 1847. *Ficus brenesii* Standl., Field Mus. Bot. 18:385. 1937. Figure 18.

Trees 6-15 m. tall, epiphytes and stranglers or independent, leafy internodes 3-20 mm. long, 2-5 mm. thick, sparsely puberulent or glabrous, periderm smooth but becoming longitudinally ridged on drying and pale brown; stipules (4) 6-11 mm. long, 2.5-3.5 mm thick at the base unopened, densely strigose with ascending straight or crooked hairs. Leaves often clustered near the ends of branchlets, petioles (8) 10-35 mm. long, 0.8-2.2 mm. thick, glabrous or with a few slender hairs 0.5-1.5 mm. long, epidermis often coming off in small (0.5 mm.) flakes, usually sulcate above; laminae 4-11 cm. long, 2.5-6 cm. broad, broadly elliptic to obovate or occasionally ovate, obtuse to acuminate or occasionally rounded at the apex, rounded or obtuse at the base, drying stiffly chartaceous, smooth and glabrous above, smooth below and usually with a few slender yellowish hairs along the midvein, the 4 to 8 pairs of major secondary veins slightly raised above and prominent beneath, central secondaries arising at angles of 40-70 degrees, basal secondaries prominent and strongly ascending, secondaries weakly loop-connected near the margin, tertiary veins slightly raised beneath. Figs usually paired at the nodes, sessile and leaving a slight shelf on the stem, basal bracts 2, entire or deeply split, about 3 mm. broad and 1.5 mm. long, often united to the receptacle to form a circular area 3 mm. broad with the peduncle attached acentrally, puberulent at the base; figs 4-6 mm. in diameter, subglobose and flattened at the apex, surface smooth and glabrous, ostioles slightly elevated and disc-like, 1.5-2 mm. broad, wall of the fig very thin; galls and seeds 0.7-1 mm. long.

Trees of the wet evergreen forest formations between 900 and 1600 m. elevation and known in Costa Rica from the areas of San Pedro de San Ramon (*Brenes 21931*), La Palma de San Ramon (*Brenes 5193*, the type of *F. brenesii*), and near San Carlos (*A. Smith 1668*) in Alajuela; Cedral de Montes de Oro (*Lankester & O. Jimenez 1344*) in San José; near Cervantes (*Walters 48*), Santa Cruz de Turrialba (*Valerio 1296*), and near Tapanti (*Lent 838*) in Cartago; collected with mature figs from December to April. The species, as here defined, ranges from Costa Rica to Colombia.

*Ficus hartwegii* is recognized by its small pinnately veined leaves with a few slender hairs along the midrib, small stipules and figs, and lower montane habitat. This species has been interpreted (De-Wolf 1960) to include the closely related *F. colubrinae*, which has, however, very different leaf-venation and lowland habitat. The lack of intermediates, both in morphology and altitudinal range, convinces me that these are distinct species. This species is more distantly related to *F. costaricana*.

***Ficus insipida* Willd., Sp. Pl. ed. 4, 4:1143. 1806. *F. glabrata* H.B.K., Nov. Gen. & Spec. 2:47. 1818. Figure 21.**

Small to very large buttressed trees 8-40 m. tall, leafy internodes 4-35 mm. long, 2-6 (8) mm. thick, glabrous, periderm smooth or slightly striate, often with the epidermis breaking off in small (0.5 mm.) flakes, grayish; stipules (2.5) 4-8 cm. long,

2-5 mm. thick at the base unopened, glabrous, drying yellowish-green. Leaves somewhat clustered or distant near the ends of branchlets, petioles 16-50 mm. long, 1-2.2 mm. thick, glabrous and narrowly sulcate above; laminae 8-22 cm. long, 3-8 cm. broad, oblong to elliptic or narrowly ovate, acute or short-acuminate at the apex, rounded to obtuse at the base, drying stiffly chartaceous and usually flat along the edge, glabrous and relatively smooth on both surfaces, the 12 to 24 pairs of major secondary veins slightly raised on both surfaces, central secondaries arising at angles of 60-90 degrees, secondaries weakly loop-connected near the margin and a submarginal vein present or absent, tertiary veins often obscure. Fig solitary at a node, borne (in ours) on a peduncle 5-10 mm. long, 2-4 mm. thick, glabrous, basal bracts 3, usually entire, about 3 mm. long and 3 mm. broad; figs 25-50 mm. in diameter at maturity (dry), globose to obovoid and distinctly narrowed above the basal bracts, sometimes stalked above the bracts, surface smooth and glabrous, green with paler colored spots but these drying darker, ostiole conical and 1-2 mm. high in early stages, remaining slightly raised in later stages, 2.5-5 mm. broad, exterior scales 3-5, the apices of the interior scales visible in later stages, wall of the figs. 3-6 mm. thick (dry), seeds and galls 1.5-3 mm. long.

Trees of the lowland areas of both the Caribbean and Pacific sides between sea level and 500 m. elevation in both wet evergreen forest formations and seasonally dry deciduous formations in Costa Rica; mature figs have been collected in December, March, and April. The species ranges from southern Mexico to southern Brazil (fide DeWolf).

*Ficus insipida* is recognized by its often long narrow leaves gradually tapering to the apex and with many secondary veins, glabrous parts, very large figs, and lowland habitat. The solitary figs, unusual trichomes on the lower leaf-surface, and frequent stream-side growth-site are characters of the subgenus *Pharmacosycea*. This species is more narrowly defined here than it was by DeWolf in the "Flora of Panama." Of the species recognized here and considered conspecific with *F. insipida* by DeWolf, *F. crassiuscula* is most easily separated by both its morphology and ecology. *Ficus werckleana* differs only slightly in its larger, more blunt leaves and larger stipules, but the mature fruit appear to be much smaller. *Ficus yoponensis* is also closely related but seems to be more common in wetter regions and at higher altitudes and the smaller leaves have more secondary veins. While the above are all closely related, it is interesting that no definite intermediates are known to me, but we do have several collections (*Burger & Ramirez 4119*, Guanacaste, and *Croat 12695*, Canal Zone) that appear to represent hybrids with *F. maxima*. *Ficus insipida* appears to be better isolated from its close allies than from the more distantly related *F. maxima*. The latex is said to be used to remove intestinal parasites.

**Ficus isophlebia** Standley, Contr. U.S. Nat. Herb. 20:14. 1917.  
Figure 20.

Small to large trees 5-20 (30) m. tall, often with broad crowns and fluted banyan-like trunks, leafy internodes 5-15 (25) mm. long, 4-7 mm. thick, glabrous, becoming somewhat striate and grayish, figs forming slight indentations on the stems; stipules 12-35 (70) mm. long, 3-6 mm. thick at the base unopened, essentially glabrous. Leaves often clustered near the ends of branchlets, petioles 1.5-4.5 (12) cm. long, 1.3-2.8 mm. thick, glabrous, narrowly sulcate above; laminae 5-12 (21) cm. long, 3-9 (16) cm. broad, oblong-orbicular to ovate or slightly obovate, usually rounded or more rarely bluntly obtuse at the apex, rounded at the base (rarely obtuse) and often cordulate at the petiole, lamina drying stiff-chartaceous to subcoriaceous and the margin flat, smooth and glabrous above and below, the 6 to 9 pairs of major secondary veins flat or slightly raised above and below, central secondaries arising at angles of 45-70 degrees, weakly loop-connected near the margin and sometimes forming an arcuate submarginal vein distally, tertiary veins flat beneath. Figs usually 2 at a node, sessile and forming depressions on the stem, basal bracts 2, borne on the edge of a disc-like area on the lower half or third of the fig and marked by a peripheral ring of tissue or the bracts apparently united to the receptacle to form the disc-like area (in dried material), bracts about 6 mm. long and 8 mm. broad (free portion), glabrous or minutely (0.05-0.1 mm.) puberulent, peduncle attached acentrically on the disc; figs 8-12 mm. in diameter, globose or becoming flattened apically and in the plane of attachment, covered about 50 per cent by the bracts, surface glabrous and smooth with dark spots, ostiole about 2 mm. broad, raised and conical, about 1.5 mm. high and drying dark, seeds and galls 1.2 mm. long.

Trees known only from near sea level (0-80 m.) in Costa Rica and Panama on both the Caribbean and the Pacific coasts. This species is also found in Nicaragua on the Pacific slopes to as high as 900 m. altitude on the Sierra de Managua and ranges to Tabasco, Mexico, along the Caribbean slope. Figs have been collected in May, July, and September.

*Ficus isophlebia* is recognized by the usually small rounded glabrous leaves, glabrous stipules, and very unusual figs. In living material the lower half or third of the fig appears quite different from the top and is not simply the area where the bracts are adnate to the receptacle. Rather, the bracts arise from the edge of this basal "disc." These differences are very difficult to see in dried material. This unusual base, with acentrically attached peduncle rimmed by a periphery of thickened tissue from which the bracts arise, is similar to that seen in *F. jimenezii*. The depressions formed by the figs on the stems are not as deep and shelf-like as those seen on *F. tuerckheimii*. *Ficus aurea* Nutt. of the West Indies is more distantly related to *F. isophlebia* and its Costa Rican allies.

***Ficus jimenezii* Standley, Contr. U.S. Nat. Herb. 20:13. 1917. Figure 20.**

Trees 10-25 m. tall, often with large spreading crowns, epiphytic stranglers or independent, trunks becoming 2 m. in diameter and fluted, grayish, leafy internodes 3-14 (20) mm. long, 3-6 mm. thick, glabrous, periderm striate and dark to pale gray, stems often with shelf-like depressions formed at the fig attachments; stipules (5) 16-42 mm. long, 3-5 mm. thick at the base unopened, densely puberulent (except along the margins) abaxially with grayish white ascending hairs 0.05-0.4 mm. long. Leaves usually clustered at the ends of twigs, petioles 12-25 (45) mm. long, 1.2-3 mm. thick, glabrous, narrowly sulcate adaxially; laminae 5-12 (15) cm. long, 3-79 cm. broad, broadly elliptic to oblong, obovate, or suborbicular, rounded or bluntly obtuse at the apex and occasionally emarginate, rounded to subtruncate or abruptly obtuse at the base, drying subcoriaceous and the margin flat or slightly revolute, glabrous and smooth on both surfaces, the 6 to 18 pairs of major secondary veins usually flat on both surfaces and difficult to distinguish from intermediate veins, central secondaries arising at angles of 50-80 (90) degrees, a slightly arcuate submarginal vein present but often difficult to see, tertiary veins flat but readily visible beneath. Figs usually 2 at a node, often crowded behind the leaves near the ends of branchlets, sessile and attached on its side (relative to the ostiole), bracts 2, arising from the edge of a basal disc-like area on the fig, entire or split, about 4 mm. long and 7 mm. broad, encircling half the fig, glabrous; figs 8-10 mm. in diameter, flattened longitudinally and oblate, round or slightly 3-cornered, surface glabrous and smooth, pale reddish to whitish, ostiole drying darker, slightly raised and conical, exterior scales usually 2; seeds and galls 0.7-1.2 mm. long.

Common large trees of the seasonally dry evergreen forest formations between about 800 and 1400 m. elevation in Costa Rica; probably flowering throughout the year. The species is known from near Tilarán (Guanacaste) in the west to the eastern edge of the Meseta Central near Santa Ana (San José) and Cartago (Cartago) in Costa Rica; it ranges northward to Guatemala.

*Ficus jimenezii* is recognized by the thick glabrous rounded leaves with venation somewhat obscure (dry), stipules with minute whitish hairs, small figs with conspicuous bracts borne from a large (3-6 mm. broad) basal "disc" and attached to the stem near the edge of this disc, and the very restricted distributions. This species is commonly planted in hedgerows and in parks. *Ficus isophlebia*, *F. jimenezii*, and *F. tuerckheimii* are a closely related trio and were considered conspecific in the "Flora of Panama"; see the discussion under *F. tuerckheimii*.

***Ficus laterisyce* Burger, Phytologia 26:426. 1973. Figure 20.**

Medium sized (10 m.) trees, often stranglers, leafy internodes 4-12 (16) mm. long, 2-6 mm. thick, essentially glabrous, becoming grayish and longitudinally striate with shelves formed beneath the sessile figs; stipules (5) 8-18 mm. long, about 4 mm.



broad at the base, glabrous or very minutely (0.05-0.1 mm.) puberulent throughout. Leaves often clustered near the ends of branches, petioles 1.2-3.6 cm. long, about 2 mm. thick, glabrous or very minutely puberulent, longitudinally striate when dry and sulcate above; laminae 4.5-11 cm. long, 2.5-6 cm. broad, elliptic to elliptic-oblong or slightly obovate, acute or very short acuminate at the apex, acute to obtuse (rarely rounded) at the base, entire, the laminae drying stiffly chartaceous, smooth and glabrous on both surfaces, the 5 to 9 pairs of major secondary veins arising at angles of 30-60 degrees, weakly loop-connected near the margin, flat on both surfaces and often somewhat obscure beneath. Figs usually paired at a node, sessile and leaving shelves on the branchlets, usually attached on the side with respect to the ostiole, basal bracts arising from the edge of a broad disc-like area about 5 mm. broad beneath, attachment of the fig at the edge of this often pustulate disc-like area, bracts about 3-4 mm. long (measured from the edge of the disc) and 5 mm. broad, glabrous or very minutely (0.05-0.1 mm.) puberulent; the fig 6-8 mm. in diameter (larger at maturity?), flattened above and below and occasionally on one side but usually oblate, the surface smooth and glabrous, ostioles 2-2.5 mm. broad, very slightly conical, lustrous brown, with usually only 2 exterior scales; seeds and galls about 0.7-1.3 mm. long.

The species is only known from the wet Caribbean slopes between Cariblanco and San Miguel de Sarapiquí, Alajuela, and near Taus, Cartago. All of these collections were made near an altitude of 750 m. with figs in pre-fruiting stages in October, April, and May.

*Ficus laterisyce* is distinguished by the glabrous or very minutely puberulent parts, small laminae on prominent petioles, sessile figs attached at the side and leaving prominent shelves in the branchlets, and the relatively large bracts arising from the edge of a disc-like area beneath the fig. The paired figs, strangling habit, and few exterior scales on the ostiole are characteristics of the subgenus *Urostigma*. The figs of this species are very similar to those of *F. isophlebia* in the development of the disc-like base and lateral attachment, but the leaves are quite different. This species also resembles *F. davidsoniae*, which has much more coriaceous leaves with many more secondary veins and the figs not usually laterally attached.

Dr. Leslie Holdridge has recently suggested that *F. laterisyce* is conspecific with *F. jimenezii*. The type of *F. laterisyce* (Lent 2972) differs from material of *F. jimenezii* in the leaves more acute at the base and apex, the venation more prominent above, the petioles shorter, the stipules only minutely puberulent, and somewhat smaller figs (see fig. 20). These differences, however, may be only extremes of variation centering around the more typical characters of *F. jimenezii*. More extensive sampling of these populations will be required to resolve these problems.

**Ficus lyrata** Warburg, Bot. Jahrb. 20:172. 1894. *F. pandurata* auctores in hort.

Trees to 20 m. tall, leafy internodes 1-5 cm. long, 6-12 mm. thick, glabrous or sparsely puberulent. Leaves usually glabrous, petioles 5-30 mm. long, 2-6 mm. thick, often shorter than the lamina-lobes; laminae 11-40 cm. long, 7-20 cm. broad, usually pandurate in shape with the distal half broader than the proximal half, abruptly rounded at the apex with a blunt rounded tip, narrowed below the middle and narrowly cordate at the base, margin entire but often somewhat undulate, drying subcoriaceous, the 4 to 6 pairs of major secondary veins prominent beneath, a submarginal vein absent. Figs usually paired at a node, sessile or subsessile, globose, becoming 3-5 cm. in diameter.

Grown in parks and gardens as trees and also in pots within homes. The large dull green leaves of unusual shape are very distinctive.

**Ficus macbridei** Standley, Field Mus. Bot. 13:305. 1937. *F. torresiana* Standl., l.c. 18:387. 1937. Figure 21.

Small or medium-size trees 6-15 m. tall with spreading branches and a broad crown, trunk relatively smooth, leafy internodes 2-30 (40) mm. long, 6-15 (20) mm. thick, glabrous or sparsely puberulent, periderm with small dark lenticels, often pale and peeling off in small flakes; stipules 4-6 (7) cm. long, 5-10 mm. thick at the base unopened, glabrous to very densely and minutely sericeous. Leaves borne near the ends of thick branchlets, petioles (2) 4-16 cm. long, 3.5-6 mm. thick, sparsely and minutely (0.3-0.6 mm.) puberulent, epidermis often breaking off in small (0.5 mm.) flakes, longitudinally striate or deeply ridged, terete; laminae 20-36 (42) cm. long, 10-23 (28) cm. broad, broadly elliptic or ovate, broadest at or just below the middle, tapering abruptly to the obtuse to short-acuminate apex, abruptly narrowed or rounded to the truncate or sub-cordate base, margins usually cordulate at the petiole, drying stiff-chartaceous and often pale grayish green, usually glabrous and smooth above, puberulent beneath with thin straight whitish hairs 0.1-0.5 mm. long and very sparse to moderately dense on the midvein, the 9 to 13 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 60-90 degrees, weakly loop-connected near the margins but not forming a submarginal vein, tertiary veins slightly raised beneath. Figs solitary at a node, sessile or subsessile on peduncles 0-4 mm. long and 2-3 mm. thick, bracts 3, usually entire, 4-8 mm. long and equally broad, glabrous; figs becoming 3 cm. in diameter and 2.5 cm. long, obovoid to slightly oblate, surface dark green with paler green spots but these drying dark on a paler background, minutely hispidulous between the spots and the surface somewhat scabrous, ostiole about 2 mm. broad, conical, with several exterior scales and the apices of interior scales evident, fig-wall 2.5-4.5 mm. thick (dry); seeds and galls 2-2.8 mm. long.

Plants of the very wet Caribbean slopes between (400) 1000 and 1600 m. elevation; known in Costa Rica only from the areas of Volcán Arenal, La Calera de San Ramon, and Zarcero in Alajuela, from the La Hondura area in San José, and from the upper Río

Reventazon drainage in Cartago. Mature figs have been collected in May and immature figs in April and September. The species ranges to Venezuela and Peru.

*Ficus macbridei* is distinguished by the large and relatively broad leaves scabrous beneath and lacking a definite submarginal vein. The figs solitary at a node and the unusual multicellular trichomes on the lower leaf-surface (150X) are characteristic of the subgenus *Pharmacosycea*. This species is very closely related to *F. tonduzii* but is of smaller stature, with rather different leaves, and usually found at higher elevations. An unusual collection from the lower slopes of Volcán Arenal (*Lent 3326*) has one, two, or three figs at a node.

The name *Ficus lapathifolia* (Liebm.) Miq. has been used incorrectly in Central America and Mexico, according to Gomez-Pompa (Estudios Botánicos en la región de Misantla, Vera Cruz, Mexico, D.F., 1966). It is, in fact, a species of *Pharmacosycea* similar to *F. macbridei*, but differs in the less puberulent laminae with a greater number of secondary veins. That species, like *F. macbridei*, differs from *F. tonduzii* in the laminae scabrous beneath and lacking a definite submarginal vein. The three species are closely related but appear to be unrepresented in the area between Veracruz and Honduras.

***Ficus maxima*** P. Miller, Gard. Dict. ed 8, Ficus no. 6. 1768. *F. radula* H. & B. ex Willd., Sp. Pl. ed. 4, 4:1144. 1806. Figure 21.

Small to large trees 7-25 m. tall, trunk usually smooth, often developing buttresses, leafy internodes 5-30 (45) mm. long, 2-5 mm. thick, glabrous, periderm dark brown or reddish brown, smooth or somewhat striate, epidermis often peeling off in small strips; stipules 10-25 (35) mm. long, 2-4 mm. thick at the base unopened, glabrous or puberulent near the base. Leaves usually distant near the ends of branchlets, petioles 8-30 (40) mm. long, 1.5-3 mm. thick, glabrous, epidermis usually cracking and peeling off in small (0.5 mm.) flakes and reddish-brown; laminae (7) 10-19 (23) cm. long, (3) 5-8 (12) cm. broad, elliptic to oblong or obovate, abruptly acute, or short-acuminate, obtuse at the apex but the tip usually rounded, obtuse to acute or occasionally cuneate at the base, drying stiff-chartaceous and the margins often revolute, usually smooth above and scabrous beneath, glabrous on both surfaces, the (5) 8 to 11 (13) pairs of major secondary veins usually flat above and prominent beneath, loop-connected near the margin but with a definite submarginal vein only in the proximal third of the lamina (or rarely throughout), central secondaries arising at angles of 60-80 degrees, basal secondaries strongly ascending and forming the submarginal vein, tertiary slightly raised beneath. Fig solitary at a node, usually borne on peduncles (2) 5-18 (25) mm. long, 1-2 mm. thick, glabrous or minutely puberulent, bracts 3, usually entire, about 1 mm. long and 2 mm. broad;

figs 14-20 (28) mm. in diameter, globose or slightly narrowed at the base and subglobose-obovoid, surface scabrous, glabrous ( $\times 10$ ) or very minutely (0.05 mm.) puberulent in ours, ostiole 1-2 mm. broad, flat, external scales several with the apices of interior scales evident, wall of the fig 0.5-2.5 mm. thick (dry); seeds and galls 1.5-2 mm. long.

A tree of lower (0-1000 m.) elevations on both the Caribbean and Pacific sides of Costa Rica, frequently growing along streams and more commonly collected in the seasonally dry areas; mature figs have been collected from January to August. The species ranges from southern Mexico into the Amazonian basin.

*Ficus maxima* is recognized by the brownish stems, exfoliating epidermis on the petioles, medium-size leaves scabrous beneath, and pedunculate figs with scabrous surface. The solitary figs and unusual trichomes on the lower leaf-surface ( $\times 150$ ) are characters of the subgenus *Pharmacosycea*. The species is related to *F. insipida* and there are collections (A. Jimenez 93 and Burger & Ramirez 4119) that appear to represent hybrids between the two species. Collections from the Caribbean lowland are distinguished in our area by leaves with a rather prominent submarginal vein throughout the length of the lamina.

***Ficus morazaniana*** W. Burger, *Phytologia* 26:427. 1973. *F. lapathifolia* auctores not *F. lapathifolia* (Liebm.) Miquel. Figure 19.

Trees 5-25 m. tall, trunk often fluted of grown-together stems, usually seen as independent trees but often beginning as epiphytes or stranglers, leafy internodes 8-65 mm. long, 4-12 mm. thick, sparsely to densely puberulent with erect slender hairs about 0.5 mm. long, periderm becoming glabrous, smooth and longitudinally deeply ridged (dry); stipules 12-30 mm. long, 5-9 mm. thick at the base unopened, with minute (0.05 mm.) or larger (0.5 mm.) ascending hairs. Leaves clustered or distant, petioles 12-40 mm. long, 2-4 mm. thick, densely hirsute with brownish hairs 0.3-1 mm. long, terete to narrowly sulcate above and longitudinally striate on drying; laminae 10-29 (33) cm. long, 5-13 (16.5) cm. broad, obovate to oblong or broadly elliptic, abruptly rounded or occasionally obtuse at the apex, obtuse to rounded at the base and often slightly cordulate at the petiole, drying very stiffly chartaceous and the margins slightly revolute, smooth but minutely hirsute above, densely hirsute beneath with slender pale brownish hairs 0.3-1 mm. long, the 9 to 14 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 50-80 degrees, secondaries weakly loop-connected near the margin and a submarginal vein usually absent, tertiary veins readily evident beneath. Figs usually paired at a node, borne on peduncles 4-8 mm. long, 1.5-3 mm. thick, hirsute with ascending yellowish hairs about 0.7 mm. long, bracts 2, usually entire, about 2-4 mm. long and 5 mm. broad, minutely puberulent, a disc-like thickening at the base of the bracts usually absent or poorly developed (sometimes present); figs 12-19 mm. in diameter, 16-20 mm. long, globose to somewhat obovoid, the surface densely pale tomentulous with hairs 0.05-0.5 mm. long, ostiole conical in early stages

but becoming surrounded by a ring of thickened tissue 2-3 mm. broad, often elevated above the surface of the fig; seeds and galls 1-1.5 mm. long.

Trees of the seasonally dry deciduous and evergreen forest formations from sea level to about 1100 m. elevation on the Pacific slopes of Costa Rica and more rarely on the wet Caribbean slopes; mature figs have been collected between November and March. This species ranges from southern Mexico to Central Costa Rica, mostly along the Pacific slopes.

*Ficus morazaniana* is recognized by its puberulent leaves and stems, pedicellate figs with densely puberulent surface and rather small bracts, and its apparent preference for seasonally dry habitats. This species is very closely related to *F. trigonata* L. but differs in the slightly larger and more puberulent figs, more puberulent laminae with a greater number of secondary veins, and different habitat and range. This species is a member of the subgenus *Urostigma* but the plants have been incorrectly placed under the name *F. lapathifolia* (Liebm.) Miq., which is a Mexican species belonging to the subgenus *Pharmacosyce*.

There are collections from the Yucatan peninsula and from a few areas of Central America that lack the dense pubescence typical of *F. morazaniana*, and these resemble *F. trigonata*. There are insufficient collections at present to determine whether these are local variants or whether they represent intermediates between what are here considered to be two different species. *Ficus morazaniana* can also be mistaken for *F. velutina* and *F. goldmanii*.

Dr. Leslie Holdridge has recently made a collection (6804) from Nosara on the Pacific coast of the Nicoya peninsula, which differs from typical material of this species by having figs 3.5 cm. in diameter that become about 2.8 cm. in diameter when dry with seeds and galls 1.5-2 mm. long. A rather similar collection (Lundell 1242) has been made from Monterey, Campeche, Mexico. These collections may be unusual representatives of this species or they may indicate that more than one species is represented by the material placed under this name. A study of these plants will have to include the closely related *F. perez-arbelaezii* Dugand and *F. sanguinosa* Dugand of Central Colombia.

***Ficus nymphaeifolia*** P. Miller, Gard. Dict. ed. 8, Ficus no. 9. 1768. *F. duquei* Dugand, Caldasia 1:42. 1942. Figure 20.

Small to very large trees 7-35 m. tall, epiphytes or independent, occasionally with buttress-like aerial roots, leafy internodes 2-25 (50) mm. long, 4-10 mm. thick, gla-

brous, periderm striate on drying, figs often forming shelf-like depressions in the stem; stipules 16-30 (40) mm. long, 4-9 mm. thick at the base unopened, glabrous and drying dark brown. Leaves usually clustered at the ends of branchlets, petioles 5-18 cm. long, 1.7-3 mm. thick, terete but longitudinally striate on drying; laminae (10) 14-35 cm. long, (9) 11-24 cm. broad, broadly ovate or ovate-elliptic, narrowed abruptly to the obtuse, acute, or short-acuminate apex, cordate at the base with the rounded lobes extending 1-7 cm. below the petiole attachment and slightly overlapping in larger leaves, drying chartaceous and flat, smooth and glabrous on both surfaces, the 4 to 8 pairs of major secondary veins flat or slightly raised above and below, central secondaries arising at angles of 40-80 degrees, tertiary veins forming a fine flat reticulum beneath. Figs usually paired at a node, sessile or subsessile on a peduncle 1-4 mm. long and about 3 mm. thick, basal bracts 2, usually entire and quite variable, 6-20 mm. long, about 6 mm. broad at the base, united with the receptacle near the base, glabrous or minutely (0.03-0.1 mm.) puberulent; figs 17-20 (25) mm. in diameter, globose or oblate, surface smooth to the touch with very minutely (0.01 mm.) velutinous hairs, drying pale in color, ostiole usually raised on a ring of tissue 5-7 mm. in diameter, exterior scales usually 3, wall of the fig very thin (dry); seeds and galls 1.6-2 mm. long.

Trees of the lowland wet evergreen forest formations along the Caribbean coast and in the Golfo Dulce areas of Costa Rica between sea level and 500 m. elevation; probably flowering throughout the year. The species ranges from Costa Rica southward to Colombia and northern Brazil.

*Ficus nymphaeifolia* is one of our most easily recognized species with its long-petiolate broadly cordate leaves, subsessile figs with satin-like surface, and wet lowland habitat. The species is apparently common but, perhaps because of its size, only rarely collected.

***Ficus obtusifolia*** H.B.K., Nov. Gen. & Sp. 2:49. 1817. *Urostigma involutum* Liebm., Danske Vidensk. Selsk. Skrivt. 5, ser. 2:320. 1851. *Ficus involuta* (Liebm.) Miq., Ann. Mus. Bot. Lugd. Bat. 3:298. 1867. *F. proctor-cooperi* Standl., Field Mus. Bot. 4:201. 1929. Figure 20.

Small to very large trees 8-25 (45) m. tall, stranglers or independent, the trunks often fluted and with narrow buttresses, leafy internodes 2-25 mm. long, 5-10 (14) mm. thick, glabrous, periderm becoming deeply ridged longitudinally and often grayish, figs producing shelf-like depressions in the branchlets; stipules 10-40 mm. long, 7-11 mm. thick at the base unopened, glabrous, occasionally persisting with the leaves. Leaves usually clustered at the ends of twigs, petioles 8-25 (45) mm. long, 1.5-5 mm. thick, glabrous, deeply sulcate above; laminae 11-22 cm. long, 5-10 cm. broad, obovate, abruptly rounded at the apex or occasionally bluntly obtuse, attenuate at the base, drying stiffly chartaceous to subcoriaceous and the margin slightly revolute, smooth and glabrous on both surfaces, the 5 to 10 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 45-70 de-

grees, secondaries usually loop-connected only near the apex of the lamina, tertiary veins slightly raised or flat beneath. Figs usually paired at a node, often clustered at the ends of stems, borne on short (2-5 mm.) thick (3-6 mm.) peduncles, peduncles slightly expanded apically, glabrous, bracts 2, entire or split, 6-14 mm. long, about 12 mm. broad, united basally with the receptacle over an area about 10 mm broad, glabrous or very minutely (0.05 mm.) puberulent; figs 16-20 mm. in diameter, globose or becoming flattened at both ends, 12-16 mm. long, surface very minutely (0.05 mm.) velutinous and soft to the touch, often lustrous, ostioles 3-5 mm. broad, flat or slightly raised to form an elevated disc, exterior scales usually 2 (3); seeds and galls 1.5-2.5 mm. long.

Trees of the lowland forest formation between sea level and 1000 m. elevation on both the very wet Caribbean slopes and in the seasonally very dry areas of Guanacaste in Costa Rica; mature figs have been collected in February, March, and September. The species ranges from southern Mexico to northern Peru.

*Ficus obtusifolia* is readily recognized by the obovate leaves rounded at the apex attenuate at the base and crowded at the ends of branchlets, essentially glabrous parts, and large sessile figs with very conspicuous basal bracts. This species does not appear to be closely related to other Costa Rican species but compare *F. nymphaeifolia*. This species possesses a wider ecological amplitude as regards rainfall than most of our species of *Ficus*, but its altitudinal range is not unusual.

***Ficus ovalis* (Liebm.) Miq., Ann. Mus. Bot. Lugd. Bat. 3:299. 1867. *Urostigma ovale* Liebm., Danske Vidensk. Selsk. Skrivt. 5, 2:324. 1851. Figure 19.**

Shrubs or small trees 4-10 m. tall or occasionally becoming large with spreading branches, leafy internodes 1-10 (25) mm. long, 2-5 mm. thick, glabrous or puberulent with slender hairs 0.2-0.5 mm. long, becoming grayish and smooth or ridged; stipules 6-14 (18) mm. long, 2-4 mm. thick at the base unopened, glabrous or sparsely and very minutely puberulent near the base. Leaves clustered or occasionally distant, petioles 6-20 (40) mm. long, glabrous or puberulent, narrowly sulcate above; laminae (4) 5-11 cm. long, (2) 3-7 cm. broad, broadly oblong to obovate or rarely ovate, rounded to bluntly obtuse at the apex, narrowed to truncate or rounded at the base and often emarginate at the petiole, drying very stiffly chartaceous, smooth and glabrous above, glabrous to densely puberulent beneath with slender erect hairs 0.2-0.7 mm. long, the 3 to 5 (6) pairs of major secondary veins raised above and prominent beneath, central secondaries arising at angles of 30-60 degrees, tertiary venation slightly raised beneath. Figs usually paired at a node, borne on peduncles 2-12 (17) mm. long, 0.8-1.5 mm. thick, expanded at the base of the bracts, glabrous or very minutely puberulent, bracts 2, about 3 mm. long and 4 mm. broad, glabrous; mature figs 8-10 mm. in diameter, globose or slightly obovoid, surface smooth and glabrous, often yellowish, ostiole 2-3 mm.

broad and usually conspicuously umbonate, 1-2 mm. high, only 2 exterior scales usually visible; seeds and galls 0.7-1 mm. long.

A species of the seasonally very dry deciduous formations of the Pacific slope in southern Central America and ranging from sea level to 1200 m. elevation; mature fruit have been collected from November to July but the majority of collections are from June. The species ranges from southern Mexico and British Honduras southward to Nicaragua and northwestern Costa Rica. The type (*Oersted 14326*) from Sta. Rosa, Guanacaste, is the only collection reported from Costa Rica.

*Ficus ovalis* is distinguished by its small pedunculate figs with prominent ostiole, small rounded leaves, and seasonally very dry habitat. Nicaraguan and Costa Rican material is glabrous but collections from Honduras vary from glabrous to densely puberulent on the leaves beneath; the figs are always glabrous. This species is apparently related to *F. perforata*, *F. hartwegii*, and *F. goldmanii* among our species.

***Ficus palmata* Forsk., Fl. Aegypt. Arab. 179. 1775.**

Shrubs or small trees 2-6 m. tall, leafy internodes 5-30 mm. long, 4-7 mm. thick, densely puberulent; stipules 5-10 mm. long. Leaves quite variable and sometimes 3-lobed, petioles 2-7 cm. long, 1.5-3 mm. thick, densely hispidulous; laminae 8-18 cm. long, 6-16 cm. broad, usually ovate, obtuse at the apex or occasionally 3-lobed, rounded at the truncate to subcordate base (occasionally with 2 side lobes at the base), the margin bluntly dentate, drying stiffly chartaceous and very scabrous above, venation somewhat palmate with 3 main veins from the base, midvein with 3 to 5 pairs of secondaries, densely puberulent beneath. Fig solitary at a node, borne on a peduncle about 1 cm. long, 1.5 mm. thick and densely hispidulous, bracts 3; fig stalked above the bracts, obovoid to pyriform, 12-18 mm. in diameter, ostiole slightly elevated and conical.

Occasionally planted in the gardens of San José and called *higueron de Kabul*. This species can be mistaken for *F. carica* and is unusual in that the male flowers have three to six stamens; it is native to northern Africa and Arabia.

***Ficus paraensis* (Miq.) Miquel, Ann. Mus. Bot. Lugd. Bat. 3:298 1867. *Urostigma paraensis* Miq., Hook. London Journ. Bot. 6:534. 1847. *F. panamensis* Standl., Contr. U.S. Nat. Herb. 20:15. 1917. Figure 18.**

Shrubs or small to large trees 5-20 m. tall, often seen as epiphytes and associated with the aerial carton nests of ants, leafy internodes 6-18 (30) mm. long, 2.3-6 mm. thick, glabrous (in ours), periderm weakly ridged or striate and gray or pale brown, the figs often leaving shallow shelf-like depressions in the stems; stipules 12-28 mm.



long, 3-5 mm. thick at the base unopened, glabrous or very minutely (0.05 mm.) puberulent, drying dark brown. Leaves usually distant along the stem, petioles 8-36 mm. long, 1.3-2.3 mm. thick, glabrous or very minutely (0.05 mm.) puberulent, deeply sulcate above; laminae 8-20 (25) cm. long, 3.5-7 cm. broad, narrowly oblong to elliptic-oblong or narrowly obovate, tapering abruptly to the short-or long-acuminate apex, the narrowed tip 5-15 mm. long, gradually narrowed below the middle but abruptly narrowed and rounded or subtruncate to cordulate at the petiole, drying stiffly to very stiffly chartaceous, smooth and glabrous on both surfaces or very minutely (0.05 mm.) puberulent on the midvein beneath, the (6) 10-17 (20) pairs of major secondary veins usually flat above and prominulous beneath, central secondaries arising at angles of 60-75 (80) degrees, secondaries weakly loop-connected near the margin and sometimes forming a weak submarginal vein. Figs usually paired at a node, sessile, subsessile or borne on a peduncle to 3 mm. long, 2-3 mm. thick, bracts 2, usually entire, 2-4 mm. long, 3-4 mm. broad, glabrous or very minutely puberulent, occasionally with the apex of the peduncle forming a disc-like ring 3 mm. in diameter at the base of the bracts; figs 10-14 mm. in diameter, globose to slightly ellipsoid or sub-pyriform, surface smooth, glabrous and often pale in color with darker longitudinal streaks, ostiole prominently raised and cone-like or umbonate, 1-3 mm. high and 2-4 mm. broad, usually with 2 large outer scales and a third smaller scale apparent, usually drying dark; seeds and galls 1-1.5 mm. long.

Trees of wet evergreen forest formations between sea level and 1000 (1600) m. elevation and known in Costa Rica from only the General Valley, San Jose (*Skutch 5423*), and Pejivalle, Cartago, (*Skutch 4623*). The species ranges from southern Mexico and British Honduras to Peru and Northern Brazil.

*Ficus paraensis* is recognized by its usually abruptly acuminate oblong-obovate leaves, essentially glabrous parts, and sessile or short-pedunculate figs often longer than thick and with a very prominently umbonate ostiole. The species is often associated with the aerial nests of ants, either as an epiphyte growing on or with the nest and as independent trees. This species appears to be closely related to *F. citrifolia* and *F. cervantesiana* among our species.

***Ficus perforata* L.**, Pl. Surinam. 17. 1775. *Urostigma eugeniaefolium* Liebm., Danske Vidensk. Selsk. Skrivt. 5, ser. 2:329. 1851. *U. oerstedianum* Miq. in Seem., Bot. Voy. Herald 196, t. 36. 1854. *Ficus oerstediana* (Miq.) Miq., Ann. Mus. Bot. Lugd. Bat. 3:299. 1867. *F. eugeniaefolia* (Liebm.) Hemsl., Biol. Centr. Amer. Bot. 3:144. 1883. *F. georgii* Standl. & L.O. Williams, Ceiba, 1:236. 1951. Figure 18.

Small to large trees (4-20 (30) m. tall, often branching near the ground, only occasionally seen as epiphytes, leafy internodes 1-12 (25) mm. long, 1.4-3.5 (5) mm. thick, glabrous, periderm becoming striate and often peeling in small (0.5 mm.) flakes, grayish brown; stipules 4-16 mm. long, 2-4 mm. thick at the base unopened, mi-

nately (0.05-0.1 mm.) puberulent or glabrous. Leaves distant or clustered, petioles 4-18 mm. long, 1-1.5 mm. thick, glabrous or very minutely (0.05 mm.) puberulent, sulcate above; laminae (2.5) 4-12 cm. long, (1.5) 2-5.5 cm. broad, elliptic to obovate or oblanceolate, obtuse to acute or short-acuminate (rarely rounded) at the apex but often blunt at the tip, cuneate to obtuse at the base, drying very stiffly chartaceous to subcoriaceous, smooth and glabrous above and below, the 7 to 14 pairs of major secondary veins slightly raised on both surfaces and often difficult to distinguish from the intermediate veins, central secondaries arising at angles of 60-80 degrees, secondaries loop-connected near the margins and an arcuate submarginal vein usually present, tertiary veins slightly raised on both surfaces. Figs usually paired at a node, borne on peduncles 4-12 mm. long, 0.5-1 mm. thick, flared at the apex, glabrous, bracts 2, usually entire, 1-2 mm. long, about 2 mm. broad, glabrous or very minutely (-0.05 mm.) puberulent; figs (4) 6-9 mm. in diameter, globose to somewhat obovoid or turbinate, with narrowed base and flattened apex, surface glabrous and smooth, pale in color with darker spots, ostiole 2-3 mm. broad, flat or slightly raised, drying dark, sometimes with a thickened ring of tissue around the periphery, exterior scales 2 or 3; seeds and galls 0.7-1 mm. long.

Plants of the very wet evergreen forest formations between sea level and 1200 m. elevation and probably flowering throughout the year. Most commonly collected between 400 and 1000 m. on the Caribbean slope in Costa Rica and planted on the Meseta Central. The species ranges from Guatemala and British Honduras southward to Colombia and is found in the Bahamas and Greater Antilles.

*Ficus perforata* is recognized by the usually very small, stiff glabrous leaves and small pedunculate figs with flat or slightly raised ostiole. This species is similar to *F. pertusa* in leaf-size and shape but differs in the fig.

***Ficus pertusa* L.F., Suppl. Plant. 442. 1781. *F. padifolia* H.B.K., Nov. Gen. & Sp. 2:47. 1817. Figure 18.**

Usually small trees 5-12 (30) m. tall, often seen as epiphytes or stranglers, leafy internodes 3-20 (30) mm. long, 1.2-3.5 mm. thick, glabrous or less often puberulent with small whitish hairs 0.1-0.3 mm. long, periderm becoming irregularly striate and grayish; stipules (3) 5-10 mm. long, 1.2-3 mm. thick at the base unopened, glabrous or very minutely (0.05 mm.) puberulent. Leaves distant or congested, petioles 6-25 (32) mm. long, 0.6-1.6 mm. thick, glabrous, deeply sulcate; laminae 5-11 cm. long, 1.8-4 cm. broad, narrowly elliptic to elliptic-oblong, acute or acuminate at the apex, obtuse to acute at the base, lamina drying chartaceous to very stiffly chartaceous and the margin flat or slightly revolute, smooth and glabrous on both surfaces, the (4) 7 to 12 (20) pairs of major secondary veins very slightly raised above and below, often difficult to distinguish from the intermediate veins, central secondaries arising at angles of 60-80 degrees, secondaries loop-connected near the margin and a weak arcuate submarginal vein usually present, tertiary veins slightly raised above and below, upper surface usually distinctly punctate. Figs usually paired at a node,

borne on peduncles 2-6 mm. long, about 1 mm. thick, slightly expanded at the apex, usually glabrous, bracts 2, usually entire, about 2 mm. long, 2-3 mm. broad, glabrous or very minutely (0.05 mm.) puberulent; figs 8-14 mm. in diameter, globose, surface smooth and glabrous but often drying prominently wrinkled, pale colored with darker spots, ostiole surrounded by a flat or slightly raised collar of receptacular tissue 0-2 mm. high and 1-3 mm. in diameter, external scales usually 3, below the level of the collar; seeds and galls 0.7-1 mm. long.

Trees of wet evergreen forest formations from sea level to 2000 m. elevation, but usually found between 900 and 1600 m. in Costa Rica, and common in the wetter parts of the Meseta Central; flowering throughout the year. The species ranges from southern Mexico and Jamaica to Paraguay (fide DeWolf).

*Ficus pertusa* is recognized by its small, often acuminate leaves, glabrous parts, and small pedunculate figs with a crateriform apex formed by a collar of tissue around and above the ostiole. Lowland collections from our area are rare and often puberulent, while the highland collections are usually glabrous. This species is very similar vegetatively to *F. perforata* with somewhat smaller figs lacking the crateriform apex.

***Ficus popenoei* Standley, Field Mus. Bot. 4:301. 1929. *F. tolimensis* Standl., l.c. 17:177. 1937. Figure 19.**

Trees 10-25 m. tall, often found as stranglers, leafy internodes 3-12 (40) mm. long, 4-8 mm. thick, densely hirsute with stiff yellowish-brown or dark brown hairs 0.3-0.8 mm. long, periderm becoming dark gray and not strongly ridged; stipules 6-10 (14) mm. long, 3-5 mm. thick at the base unopened, ascending sericeous with golden-brown hairs about 1 mm. long. Leaves clustered or distant, petioles 2-15 (23) mm. long, 1.3-4 mm. thick, obscurely sulcate above, densely hirsutulous with yellowish-brown hairs 0.3-1 mm. long; laminae (6) 7-18 cm. long, (3) 4-8 cm. broad, oblong to broadly obovate, abruptly rounded at the apex or occasionally obtuse, narrowed to the base and abruptly truncate to cordulate at the petiole, laminae drying very stiffly chartaceous to subcoriaceous with the margins often strongly revolute, usually scabrous and minutely hispid above, hirsutulous beneath with yellowish-brown hairs 0.2-0.7 mm. long, the 6 to 9 pairs of major secondary veins slightly raised above and prominent beneath, central secondaries arising at angles of 45-65 degrees, the secondaries loop-connected near the margin but a definite submarginal vein absent, tertiary veins raised beneath. Figs usually paired at a node, sessile or borne on peduncles to 3 mm. long, 1-2 mm. thick, not expanded at the apex, densely yellowish hirsute, basal bracts 2, usually entire, about 2-4 mm. long and 3-4 mm. broad, appressed hirsute basally and along the midrib abaxially; figs distinctly longer than thick 15-24 mm. long, 9-16 mm. in diameter, surface of the fig densely yellowish hirsutulous, ostiole often obscure, flat or slightly conical, 1.5-3 mm. broad; seeds and galls 1.3-1.7 mm. long.

Trees of wet evergreen forest formations between sea level and (?) 1000 m. elevation; fertile collections have been made in August,

October, and November. The species ranges from British Honduras to Colombia but is known in Costa Rica from only a single collection: *Holm & Iltis 806* near the Rio Frio, Alajuela.

*Ficus popenoei* is recognized by the unusual shape of its figs, densely hirsute pubescence on many parts, and the usually obovate laminae rounded at the apex. This species is vegetatively similar to *F. bullenei* with very different figs.

***Ficus pumila* L., Sp. Pl. 1060. 1753.**

Plants climbing on surfaces or becoming small shrubs 1-2.5 m. tall, stems with slender adventitious roots and with small (2-3 cm.) leaves, fruiting stems thicker (2-5 mm.) and with larger leaves, puberulent; stipules 8-16 mm. long, densely sericeous. Leaves on fruiting stems with petioles 4-18 mm. long, about 1.5 mm. thick; laminae on fruiting stems 3-9 cm. long, 2-4 cm. broad, oblong to narrowly ovate, obtuse and often rounded at the apex, rounded to shallowly cordate at the base, drying subcoriaceous, the 3 to 5 pairs of major secondary veins strongly ascending, tertiary veins prominent beneath and forming a reticulum, puberulent beneath, laminae of the rooting stems 12-25 mm. long and sessile. Fig solitary at a node, borne on a short (3-7 mm.) puberulent peduncle, narrowed above the bracts and pyriform or obovoid, 2-4 cm. in diameter and 5-7 cm. long, abruptly narrowed distally but with the ostiole borne on a conical apex.

Widely planted in gardens to cover walls and other surfaces and requiring relatively little care. The stiff distichous leaves, large figs of unusual shape, and unusual habit distinguish this species. Native of Japan and China, the plants are referred to as *hiedra* in Costa Rica.

***Ficus religiosa* L., Sp. Pl. 1059. 1753.**

Trees 8-20 m. tall, often planted for shade, leafy internodes 5-25 mm. long, 2-5 mm. thick, glabrous; stipules 4-30 mm. long. Leaves glabrous, petioles 5-10 cm. long, 0.8-2 mm. thick; laminae 7-15 cm. long, 3-9 cm. broad, ovate but with a very long (15-40 mm.) narrow (1-3 mm.) acuminate tip, abruptly truncate at the base, drying stiffly chartaceous, the 6 to 11 pairs of major secondary veins slightly raised on both surfaces. Figs usually paired at a node or occasionally several, sessile, 5-8 mm. in diameter, globose, subtended by conspicuous puberulent bracts, surface of the fig glabrous, ostiole slightly conical.

Trees planted in parks and large gardens and along streets. The unusual laminae broadly ovate, but with a very long tip and borne on long slender petioles, distinguish this species.

***Ficus retusa* L., Mant. Pl. 129. 1767. *F. nitida* Thunb., Diss. Fic. 10.**

Becoming large trees more than 20 m. tall, producing many aerial roots, leafy internodes 3-15 mm. long, about 4 mm. thick, glabrous; stipules 5-10 mm. long.

Leaves glabrous, petioles 5-10 mm. long, about 1 mm. thick; laminae 3-8 cm. long, 1-3 cm. broad, elliptic, acute to acuminate at the apex, cuneate at the base, drying stiffly chartaceous, major secondary veins difficult to distinguish, 6-12 pairs. Figs usually paired at a node, sessile, about 5-8 mm. in diameter, globose, subtended by 3 very small (1.5 mm.) bracts, ostiole flat.

Trees from the wet tropical lowlands of southeastern Asia; called the "malayan banyan" or referred to as *laurel de la India* in Costa Rica. These are the trees that dominate the parks of Limon. The aerial roots, small leaves, very small figs, and glabrous parts are distinguishing characteristics.

*Ficus schippii* Standley, Field Mus. Bot. 8:7. 1930. *Ficus meisto-syce* Standl. & L. O. Wms., Ceiba 3:195. 1953. Figure 18.

Woody climbers or trees 6-20 m. tall, leafy internodes 3-24 mm. long, 2.5-5 mm. thick, glabrous, periderm often becoming strongly ridged and pale gray or brown; stipules 12-22 mm. long, 2-4 mm. broad at the base unopened, glabrous, drying pale brown to dark brown. Leaves clustered or distant on the stems, petioles 14-44 (58) mm. long, 1.2-2.6 mm. thick, essentially glabrous with the epidermis often flaking off in small (0.5 mm.) flakes, narrowly sulcate above; laminae 7-18 (20) cm. long, 3-7.5 (9) cm. broad, oblong to elliptic-oblong or occasionally slightly ovate or obovate, abruptly short-acuminate to caudate-acuminate at the apex, rounded to the obtuse base, lamina drying stiffly chartaceous, smooth and glabrous on both surfaces, (rarely with hairs along the sides of the midvein beneath), the 6 to 12 pairs of major secondary veins slightly raised above and prominent beneath, central secondaries arising at angles of 60-80 degrees, joined near the edge by a distinct and arcuate submarginal vein, tertiary veins slightly raised beneath. Figs usually paired at a node but also found in clusters of 3 to 9 on very short (?) short-shoots, subsessile or borne on very short (0-2 mm.) peduncles, basal bracts 2, usually entire, about 2 mm. broad and 1.5 mm. long, glabrous; figs 4-5 mm. in diameter, subglobose and slightly flattened at the apex, surface smooth and glabrous, often drying orange-brown, ostiole flat or slightly raised, 1.4-1.8 mm. broad, galls and seeds about 0.5 mm. long.

Plants of the lowland Caribbean wet forest formations between sea level and about 500 m. elevation; probably flowering throughout the year. The species ranges from British Honduras southward along the Caribbean to Central Panama and perhaps south-central Colombia.

*Ficus schippii* is one of our most unusual species of *Ficus* because of the climbing habit seen in many individuals and the very small figs often found in clusters of three to nine at a node. Some plants have the figs often borne in these clusters while other plants exhibit this clustering only rarely. The species is known in Costa Rica from only two fertile collections: *Hartshorn 1055* from near the Río Puerto Viejo (Heredia) and *Shank & Molina 4208*, type of *F.*

*meistosyce*, from the drainage of the Río Parismina and Río Reventazon (Limon). *Ficus microclada* Dugand of south-central Colombia is a liana with very small clustered figs probably conspecific with Central American material placed here.

*Ficus tonduzii* Standley, Contr. U.S. Nat. Herb. 20:8. 1917. Figure 21.

Small or medium-size trees (5) 10-20 m. tall, trunks simple and usually smooth, leafy internodes 5-20 (40) mm. long, 5-11 mm. thick, essentially glabrous, periderm becoming deeply striate and pale gray (dry) often with the epidermis flaking off; stipules 2-4 (6) cm. long, 5-10 mm. thick at the base unopened, glabrous. Leaves usually distant but near the ends of branchlets, petioles (2) 3-8.5 cm. long, 3-6 mm. thick, glabrous, epidermis often cracking and coming off in small (0.5 mm.) flakes, longitudinally striate and terete or slightly sulcate above; laminae (12) 16-32 cm. long, 7-15 cm. broad, broadly elliptic or slightly obovate to elliptic-oblong, abruptly narrowed or rounded at the bluntly acute or obtuse apex, narrowed or slightly rounded at the obtuse base (never cordulate at the petiole), lamina drying stiffly chartaceous and the margin slightly revolute, glabrous and relatively smooth on both surfaces, the 7 to 11 (14) pairs of major secondary veins slightly raised above and prominent beneath, central secondaries arising at angles of 55-90 degrees, secondaries loop-connected near the margin and forming a definite submarginal vein, tertiary veins slightly raised beneath. Fig solitary at a node, sessile (in ours), or on a peduncle 1-10 mm. long and 3-4 mm. thick, bracts 3, entire or more often variously split, 2-3 mm. long 3-4 mm. broad, glabrous, united with the receptacle near the base; figs becoming 20-35 mm. in diameter, globose or somewhat obovoid and narrowed above the basal bracts, green with pale round markings, glabrous or very minutely (0.1 mm.) hispidulous and slightly rough to the touch, wall of the fig 2-3 mm. thick (dry), ostiole flat or slightly raised, about 2 mm. broad, exterior scales several and the apices of the interior scales evident; seeds and galls 1.5-3 mm. long.

Trees of the very wet evergreen forest formations between sea level and 1000 (? 1400) m. elevation on the Caribbean side of the Central Highlands, on the Caribbean slope and lowlands, and in the General Valley and Golfo Dulce region in Costa Rica; probably flowering throughout the year. The species ranges from Honduras to Ecuador.

*Ficus tonduzii* is distinguished by its relatively broad leaves glabrous and smooth on both surfaces with a prominent submarginal vein. The figs solitary at a node, unusual trichomes on the lower leaf-surface ( $\times 150$ ), and frequent streamside habitat are characters of the subgenus *Pharmacosycea*. This species is very closely related to *F. macbridei* but differs in possessing a distinct submarginal vein, smaller figs, and growing at lower elevations.

*Ficus trachelosyce* Dugand, Caldasia 4:69, fig. 14. 1942. Figure 18.

Medium to large trees 10-25 m. tall, stranglers or independent, trunk to over 1 m. diameter and often of intertwined parts, leafy internodes (4) 8-30 mm. long, 1.5-3 mm. thick, glabrous, periderm becoming striate and often pale grayish brown; stipules (3) 5-16 mm. long, 1.3-2.7 mm. thick at the base unopened. Leaves usually distant, petioles 8-20 mm. long, 0.8-2 mm. thick, glabrous and deeply sulcate above; laminae 7-16 cm. long, 2.5-6 cm. broad, elliptic to elliptic-oblong, usually tapering gradually to the acuminate apex, acute to obtuse at the base, drying stiff-chartaceous and the margin often involute, smooth and glabrous on both surfaces with small raised dots above, the 6 to 15 pairs of major secondary veins very slightly raised above and below, often difficult to distinguish from the intermediate veins, central secondaries arising at angles of 60-75 degrees, loop-connected near the margin to form an arcuate submarginal vein, tertiary veins often obscure. Figs usually paired at a node, borne on a peduncle 2-6 mm. long, 1-1.5 mm. thick, glabrous, slightly expanded at the apex and occasionally forming a disc-like area at the base of the bracts, bracts 2, usually entire, 1-2 mm. long, 1-2 mm. broad, glabrous; figs 14-18 mm. in diameter, globose but with a conspicuous apical collar, surface smooth and glabrous, often wrinkled and yellowish on drying, ostiole deeply hidden within the 3-6 mm. high and 2-4 mm. broad urceolate collar; seeds and galls 1.2-1.5 mm. long.

Trees of the seasonally dry Pacific Slope in Costa Rica between sea level and 1000 m. elevation and known only from San Miguel de San Ramon, Alajuela, (*Brenes 14953 & 21909*) and near Sta. Cruz, Nicoya Peninsula, (*Burger & Ramirez 4104*). The only other collection seen from our area is from Puerto Armuelles, Chiriquí (*Allen 6295*). Mature figs have been collected in January, August, and December. The species ranges to Colombia.

*Ficus trachelosyce* is distinguished by its small glabrous thin leaves and its very unusual figs with apically developed collar. This species is very closely related to *F. pertusa* but differs in the development of the collar, larger fig size, and the very different habitat. Collections lose their leaves within 24 hr. if not quickly killed. The species is called *tinajita* near San Ramon.

### ***Ficus trigonata* L., Pl. Surinam. 17. 1775. Figure 19.**

Trees 10-25 m. tall, often large, leafy internodes 5-30 mm. long, 2.5-6 (8) mm. thick, glabrous or puberulent at the nodes with yellowish hairs 0.5-1 mm. long, periderm smooth and drying with prominent longitudinal ridges and pale brown; stipules 8-20 (27) mm. long, 2.4-4 mm. thick at the base unopened, with ascending whitish strigose hairs basally and along the midrib. Leaves clustered or distant, petioles (7) 12-40 (60) mm. long, 1.2-3.5 mm. thick, glabrous or very sparsely puberulent, very narrowly sulcate above; laminae (5) 8-25 cm. long, 3-13 cm. wide, obovate to elliptic or oblong, usually rounded at the apex but occasionally acute to short-acuminate, obtuse to rounded at the base and often slightly cordulate at the petiole, drying very stiffly chartaceous, smooth and glabrous above, glabrous or puberulent beneath with hairs 0.05-0.7 mm. long, often slightly rough to the touch beneath, the 6 to 11 pairs of major secondary veins flat above and prominent beneath, central secondaries arising at angles of 45-80 degrees, basal pair of secondaries usually

prominent and strongly ascending, secondaries usually loop-connected near the margin but a definite submarginal vein absent, tertiary veins usually evident beneath. Figs usually paired at a node, sessile or short pedunculate, peduncles 0-5 mm. long, 1-2.4 mm. thick, very minutely puberulent, a basal disc usually present about 3-5 mm. broad with thickened edges from which the bracts arise, peduncle acentric near the edge of the disc, bracts 2 and entire or split, often semicircular, 1-3 mm. long and 4-7 mm. broad, strigose or occasionally glabrous; figs becoming red at maturity, 10-15 mm. in diameter, globose or broader than long, the surface smooth and glabrous, ostiole conical in early stages but becoming surrounded by a ring of thickened tissue 2-4 mm. in diameter; seeds and galls 1-1.5 mm. long.

Plants of the moist or wet evergreen forest formations from sea level to 700 m. elevation on both the Caribbean and Pacific slopes of Costa Rica; probably flowering throughout the year. The species ranges from the Yucatan peninsula through Central America mostly along the Caribbean coast to Colombia and the West Indies.

*Ficus trigonata* is recognized by the subsessile or short-pedunculate figs with a small basal "disc" from which the short bracts arise and by the ostiole within a ring of tissue. This species is very closely related to *F. morazaniana* and the two may be conspecific. They are maintained separately here to focus attention on their differences and because they appear to live in somewhat different habitats. Also closely related is *F. brevibracteata* with stipules densely sericeous throughout, similar stems, and sessile figs with very small basal bracts.

***Ficus tuerckheimii* Standley, Contr. U.S. Nat. Herb. 20:13. 1917. Figure 20.**

Small to very large and massive trees, 5-25 (35) m. tall, epiphytic or independent, trunk often banyan-like and fluted, leafy internodes 3-15 mm. long, 3.5-8 mm. thick, glabrous, becoming irregularly ridged or wrinkled and grayish, stems with shelf-like depressions where figs were borne; stipules (6) 14-24 (32) mm. long, 4-8 mm. thick at the base unopened, glabrous or very minutely (0.05 mm.) puberulent at the base. Leaves usually clustered at the ends of twigs, petioles 15-40 (65) mm. long, 1.6-3 mm. thick, glabrous, slightly sulcate above; laminae quite variable in size and shape, 7-18 cm. long, 5-12 cm. broad, broadly ovate to oblong or suborbicular, obtuse to rounded or very short and bluntly acuminate at the apex, obtuse to rounded, truncate, or occasionally shallowly cordate at the base, lamina drying stiff-chartaceous to subcoriaceous and the margins flat, glabrous and smooth on both surfaces, often somewhat glaucous above (dry), the 6 to 11 pairs of major secondary veins usually flat on both surfaces, central secondaries arising at angles of 45-70 degrees, the basal pair of secondaries often prominent and strongly ascending, secondaries weakly loop-connected near the margin, tertiary veins often obscure. Figs usually 2 at a node, often clustered near the ends of branchlets, sessile and leaving a prominent shelf on the stem, attachment of the fig somewhat lateral (in respect to the ostiole) near the edge of a disc-like basal area from which the 2 entire



or split bracts arise, bracts almost half the circumference (12 mm.) of the fig, broad at the base, 4-8 mm. long and covering the sides of the fig, glabrous; figs 12-15 mm. thick, globose or somewhat flattened in the plane of attachment, surface smooth and glabrous, ostiole about 2-3 mm. broad, slightly conical, or elevated and ringed, hidden by the bracts in early stages, exterior scales 2 or 3; seeds and galls about 1.2 mm. long.

Trees of wet evergreen forest formations between (1000) 1200 and 1800 m. elevation known only from the area of the Montes de Aquacate and Zarcero (Alajuela), eastward to La Palma (San José), Irazú and Cartago (Cartago); probably flowering throughout the year. This species, as here interpreted, is endemic to Costa Rica and adjacent Panama.

*Ficus tuerckheimii* is recognized by the stems with "shelves" formed by the figs, glabrous broad leaves often rounded at the base, figs laterally attached on the edge of a disc-like area from which the bracts arise, bracts glabrous and covering much of the upper surface of the fig, and the restricted highland distribution. This species is closely related to *F. jimenezii*, but that species has smaller figs, thicker leaves, densely puberulent stipules, and stems in which the depressions left by the figs are not as prominent. *Ficus tuerckheimii* is even more closely related to *F. isophlebia*, but that species differs in the smaller figs with more prominent ostiole, figs forming only slight depressions in the stems, smaller bracts, and lowland habitat. All three species were considered as one in the "Flora of Panama"; however, I prefer to consider them distinct, as there is virtually no evidence of intergradation, though sterile collections are difficult to place. The unusual basal disc-like area (see under *F. isophlebia*) is a significant character in distinguishing this group and is comparable to a similar structure in *F. trigonata*.

### ***Ficus turrialbana* Burger, Phytologia 26:429. 1973. Figure 19.**

Medium-size trees 15-20 m. tall, leafy internodes 2-28 mm. long, 4-12 mm. thick, sparsely puberulent with slender white or brown hairs 0.3-1 mm. long, periderm becoming pale gray and striate; stipules 8-12 mm. long, 4-7 mm. broad at the base unopened, densely ascending sericeous with brownish or whitish hairs but the hairs usually absent along the margins abaxially. Leaves not closely crowded, petioles 2-7 cm. long, 1.8-4 mm. thick, minutely puberulent, deeply striate on drying but not usually sulcate above; laminae 12-24 cm. long, 6-12 cm. broad, elliptic-oblong to somewhat obovate, tapering abruptly to the bluntly obtuse apex or sometimes with a very short acute tip, obtuse to sub-truncate at the base but often rounded at the petiole, margin entire or very shallowly indented distally, drying stiffly chartaceous to subcoriaceous with the margin slightly revolute, smooth and glabrous or very minutely (0.05 mm.) puberulent above, densely to sparsely puberulent on the veins

and veinlets beneath with slender straight hairs 0.1-0.9 mm. long, the 9 to 12 pairs of major secondary veins usually flat above and prominent below, central secondaries arising at angles of 35-55 degrees, secondaries weakly loop-connected near the margin and a submarginal vein absent, tertiary veins often prominent beneath. Figs usually 2 at a node, sessile and often leaving shelf-like impressions on the stems basal bracts 2 but often deeply split and 2- to 5-lobed, 6-8 mm. long (measured from the area of attachment), densely puberulent with brownish hairs to 1 mm. long near the base, united with the receptacle for 1 or 2 mm. around the base; figs 12-16 mm. in diameter, (globose) oblate and about 1 cm. high (dry), surface densely puberulent and often longitudinally 3- to 5-ribbed, ostiole conical and surrounded by a small ring of tissue 3-4 mm. in diameter, external scales 2 or 3; seeds and galls 0.9-1.2 mm. long.

Plants of the very wet Caribbean slopes and lowlands (premontane wet forest formations) around 700 m. elevation in Costa Rica: *Burger 4004*, *Ramirez s.n.* (Museo Nacional 41515), and *Leon 2463*, all from near Turrialba, Cartago; fruiting collections have only been made in December.

*Ficus turrialbana* is distinguished by its blunt or shortly acute leaves puberulent beneath, prominent petioles, densely pubescent stipules with glabrous edges, thick stems with depressions formed by the sessile puberulent figs with large bracts and conspicuously umbonate ostiole surrounded by a thickened ring of tissue. This species can be mistaken for *F. costaricana* (persistent stipules and glabrous leaves and figs), *F. morazaniensis* (pedunculate figs and small bracts), and *F. velutina* (larger pedunculate figs and montane habitat). I have seen figs similar to the type only in *F. tequendamae* Dugand, a high-altitude species of Colombia. The species mentioned above are part of a complex of species that include *F. trigonata* L. and are well represented in northern South America and Central America.

*Ficus turrialbana* appears to be a wide ranging species of the Caribbean slopes of Central America and Mexico but fertile collections are rare. A collection from Veracruz, Mexico (*Llewelyn Williams 8766*) is conspecific and very similar to the type, both in its leaves and its figs. The figs of this species were described under *Urostigma intramarginale* by Liebmann (1851); however, the figs were associated with the leaves of *Coussapoa panamensis*. These discordant elements are a sufficient basis for rejecting Liebmann's name.

***Ficus velutina* H. & B. ex Willd., Sp. Pl. 4: 1141. 1806. Figure 19.**

Small to medium sized trees 7-15 (20) m. tall, trunks often fluted or several grown together, leafy internodes 8-50 mm. long, 4-12 mm. thick, densely to sparsely tomentose.

tulose with brownish hairs 0.5-1 mm. long, periderm becoming prominently ridged on drying; stipules 12-20 mm. long, 4-10 mm. thick at the base unopened, densely brownish tomentulose to sericeous. Leaves distant or clustered and often relatively few per twig, petioles 14-34 mm. long, 2-5 mm. thick, densely brownish tomentulose, sulcate above; laminae 10-26 cm. long, 6-17 cm. broad, ovate to broadly elliptic, tapering to an obtuse apex or abruptly rounded, usually tapering slightly to a rounded obtuse to truncate base (occasionally cordulate), laminae drying very stiffly chartaceous to subcoriaceous with the margins revolute, smooth and sparsely puberulent above, densely brownish tomentulose beneath with soft crooked hairs 0.3-1.5 mm. long, the 6 to 12 pairs of major secondary veins slightly impressed above and very prominent beneath, central secondaries arising at angles of 30-70 degrees, weakly loop-connected near the margin, tertiary veins prominent beneath and forming a conspicuous reticulum. Figs usually paired at a node, borne on very short (2-6 mm.) thick (2 mm.) puberulent peduncles, apex of the peduncle sometimes expanded and forming a disc-like area, bracts 2 but often deeply split, 2-4 mm. long, about 4 mm. broad, usually with smaller hairs than the peduncle; figs 18-22 mm. in diameter (dry), narrowed at the base and obovoid or globose, surface densely puberulent with hairs 0.1-0.6 mm. long, ostiole within an elevated ring of tissue 3-5 mm. broad forming a short (1-2 mm.) collar; seeds and galls 1.4-1.8 mm. long.

Trees of moist and wet evergreen forest formations between 1000 and 2000 m. elevation and known only from the northeastern side of the Meseta Central and along the Cordillera de Talamanca as far east as the Río Chirripó del Pacifico in Costa Rica; mature figs have been collected in July and from November to February. The species ranges from Guatemala southward to Colombia and Venezuela.

*Ficus velutina* is readily recognized by the presence of usually orange-brown hairs on younger parts, stiff leaves with the tertiary veins forming a prominent reticulation beneath, short-pedunculate figs with the ostiole within a short collar, and the montane habitat. This species is easily distinguished by these attributes from all our other figs but is closely related to *F. trigonata* and the lowland *F. bullenei*.

***Ficus werckleana* Rossberg, Repert. Sp. Nov. 42:60. 1937. Figure 21.**

Trees to 35 m. tall, trunks usually straight and pale colored, leafy internodes 6-20 (30) mm. long, 4-9 mm. thick, glabrous or puberulent with slender whitish hairs 0.3-1 mm. long, periderm smooth or slightly striate, occasionally with the epidermis flaking off; stipules (6) 9-16.5 cm. long, 4-11 mm. thick at the base unopened, glabrous. Leaves at the ends of branchlets but not crowded, petioles (18) 25-80 mm. long, 2-5 mm. thick, glabrous, slightly sulcate adaxially, often striate (dry); laminae (11) 14-32 cm. long, (5) 6-16 cm. broad, oblong to elliptic or less often slightly ovate or obovate, tapering abruptly to the obtuse or rarely short-acute apex, often rounded at the tip, rounded to obtuse at the base, laminae drying stiff-chartaceous to subcoriaceous, glabrous and smooth on both surfaces, the 16 to 24 pairs of major sec-

ondary veins slightly raised above and below, central secondaries arising at angles of 60-80 degrees, secondaries usually loop-connected near the margin and a submarginal vein often present, 1-3 mm. from the edge, tertiary veins often obscure. Fig solitary at a node, borne on peduncles 5-12 mm. long and about 2 mm. thick, glabrous, bracts 3, entire or slightly split, about 2 mm. long and 3 mm. broad, glabrous; figs (14) 18-22 mm. in diameter, globose or obovoid and narrowed above the basal bracts, surface glabrous and smooth, ostiole about 2.5 mm. broad, conical, exterior bracts several with apices of the interior bracts visible, wall of the fig 1-3 mm. thick (dry); seeds and galls 1.5-2.2 mm. long.

Plants of river edges and bottomlands (or areas with a high water table) in wet evergreen forest formations on both the Pacific and Caribbean slopes below 800 m. altitude in Costa Rica; mature figs have been collected in January and March. The species probably ranges from British Honduras southward to northern South America.

*Ficus werckleana* is recognized by the often larger leaves bluntly obtuse or rounded at the apex, very large stipules, and figs about 2 cm. in diameter (dry) at maturity and with a prominent (2 mm.) ostiole. The figs solitary at a node, unusual trichomes on the lower leaf-surface ( $\times 150$ ), and frequent streamside habitat are characters of the subgenus *Pharmacosycea*. This species has usually been considered conspecific with *F. insipida* but Dr. Leslie Holdridge, who knows these plants in the field, states that they are very different. Our collections with mature figs are very few (*A. Jimenez 94, Cooper 444, and Tonduz 17435*), but these appear to be much smaller than those of *F. insipida*.

***Ficus yoponensis* Desv., Ann. Sci. Nat. Ser. 2, 18:310. 1842, fide DeWolf. *Ficus multinervis* Pittier, in herb. (? nom. nud). Figure 21.**

Medium-size to large trees 8-50 m. tall, trunk usually straight and smooth, leafy internodes 5-30 mm. long, 2-5 mm. thick, glabrous, periderm smooth to somewhat striate (dry) and light brown, the epidermis not usually flaking off; stipules (2) 3-6 (9) cm. long, 1.5-6 mm. thick at the base unopened, usually drying yellowish green or yellowish brown, glabrous. Leaves usually distant near the ends of branchlets, petioles 10-28 (40) mm. long, 1.2-2 (3) mm. thick, glabrous, shallow or deeply sulcate above; laminae (5) 6-14 (26) cm. long, 2-5 (6.5) cm. broad, elliptic to narrowly oblong or narrowly obovate, acute to short-acuminate at the apex, obtuse to acute at the base, drying stiff-chartaceous and the margins slightly revolute, smooth and glabrous on both surfaces, the 16-28 (52) pairs of major secondary veins slightly raised on both surfaces and often difficult to distinguish from the intermediate veins, central secondaries arising at angles of 60-80 degrees, secondaries joined 0.5-1 mm. from the margin by a slightly arcuate submarginal vein, tertiary veins usually obscure. Fig solitary at a node, usually borne on a peduncle 6-16 mm. long and 1-1.5

mm. thick, glabrous, bracts 3, usually entire, about 1 mm. long and 2 mm. broad, glabrous; figs 12-16 mm. in diameter, globose but narrowed abruptly at the base and borne on a stalk above the bracts 1-6 mm. long and as thick as the peduncle, surface smooth and glabrous, ostiole borne on a narrowed column at the apex of the receptacle 1-4 mm. long and about 2 mm. thick, ostiole about 1.5 mm. broad at the apex of the column, exterior scales several, wall of the fig 0.5-1 mm. thick (dry); seeds and galls 1-1.5 mm. long.

Trees of moist ravines, river edges, and wet forests from sea level to 1600 m. elevation, but most commonly collected between 500 and 1200 m. in our area on both the Caribbean and Pacific slopes. The species is known in Costa Rica from near Tilarán (Guanacaste), near San Ramon (Alajuela), near San Francisco de Guadalupe (San José), and along the Río Pacuare near Tuis (Cartago). The species is known from Barro Colorado Island (Canal Zone) and the Boquete area (Chiriquí) in Panama. The species ranges from Chiapas, Mexico, and British Honduras to Colombia and Venezuela.

*Ficus yoponensis* is recognized by its relatively narrow glabrous leaves with many secondary veins and definite submarginal vein, long stipules drying pale in color, and small figs stalked above the bracts and with a distinct apical "column." The solitary figs and unusual trichomes on the lower leaf-surface ( $\times 150$ ) are characters of the subgenus *Pharmacosycea*. The species is closely related to *F. crassiuscula* and *F. insipida* and has often been mistaken for the latter, and they are difficult to distinguish in the absence of mature figs.

### HELICOSTYLIS Trecul

REFERENCE: C.C. Berg, *Olmedieae. Fl. Neotrop. Monog.* 7:75-92. 1972.

Unisexual or bisexual trees, without spines; stipules not completely encircling the stem, free, small and caducous. Leaves distichous, petiolate, margin entire to denticulate apically, chartaceous to coriaceous, usually brownish when dry and dull above, usually puberulent, the microscopic multicellular hairs globose-capitate or oblongoid-capitate. Male inflorescences solitary, paired or more numerous on short shoots, often together with female inflorescences, receptacle discoid and pedunculate, covered with imbricate bracts usually incurved in early stages, flowers mostly free and numerous; male flower with (2-) 4-lobed or (2-) 4-parted perianth, the 2 whorls of perianth-parts and the 2 whorls of (2-) 4 stamens usually different in form, filaments straight in bud, anthers basifixed or dorsifixed, connective narrow or broad. Female inflorescences solitary or with 1 or more male inflorescences (or the female inflorescences paired and uniflorous in *H. towarensis*), sessile or pedunculate, the receptacle covered with imbricate bracts, each inflorescence with about 5 (1 in *H. towarensis*, many in *H. pedunculata*) flowers; female flowers with 4 free or

united perianth-parts, the tepals of the 2 whorls are often different in form, the inner cohering by thin hairs, ovary almost free, stigmas slender, straight or twisted. Fruit with succulent perianth becoming yellow, free or somewhat adnate to the perianth, cotyledons thick and equal.

A genus of seven species best represented in the Western Amazon Basin and ranging from Costa Rica to Peru and Brazil. Our species differs from others in the genus and resembles *Olmedia aspera* in general aspect.

A recent collection of *Helicostylis* (*W. H. Lewis et al.* 2188) from about 300 m. altitude in Bocas del Toro province, Panama, is probably *H. tomentosa* (Poeppig & Endlicher) Rusby (C.C. Berg, pers. comm.). That species differs from *H. towarensis* in the leaves usually being scabrous above. Both species may occur in Costa Rica.

***Helicostylis towarensis*** (Klotz. & Karst.) C.C. Berg, *Acta Bot. Neerl.* 18:464. 1969. *Olmedia towarensis* Klotzsch & Karsten, *Linnaea* 20:526. 1847. *Helicostylis urophylla* Standley, *Field Mus. Bot.* 18:389. 1937. Figure 16.

Trees to 25 m. tall, unisexual, sap yellowish, leafy internodes 1-3 cm. long, 1.3-4 mm. thick, with thin yellowish brown hairs 0.3-0.9 mm. long; stipules 2-10 mm. long, densely velutinous to sericeous, narrow. Leaves often very slightly inequilateral, petioles 3-10 mm. long, 0.7-2 mm. thick, densely puberulent; laminae (3) 5-15 (17) cm. long, 1.5-4.5 cm. broad, narrowly oblong to narrowly obovate, acuminate to caudate-acuminate at the apex, the narrow tip 5-25 mm. long, margin entire or serrulate near the apex, thin to stiffly chartaceous, upper surface smooth and glabrous but minutely puberulent above the major veins, sparsely to densely puberulent on the veins beneath with thin ascending straight or curved hairs 0.3-0.8 mm. long, the major veins slightly prominent to impressed above and prominent beneath, with 6 to 12 pairs of major secondary veins, the lower surface with numerous microscopic oblongoid-capitate hairs, the narrow distal part orange on a short transparent base ( $\times 150$ ). Male inflorescences 1 or 2 in the axils of leaves or fallen leaves, hemispherical in form and 9-12 mm. in diameter, borne on peduncles 2-8 (25) mm. long, the receptacle with 3 or 4 series of bracts forming an involucre at the base of the more than 20 flowers; male flowers free or united at the base, perianth 1.5-2.7 mm. high, 4-lobed or 4-parted, minutely puberulent, filaments 2.5-4 mm. long, anthers 0.8-1.4 mm. long, apiculate or not, a pistillode occasionally present. Female inflorescences 1 or 2 in the axils of leaves or fallen leaves, borne on peduncles 1-8 (25) mm. long, receptacle with 3 or 4 series of broadly triangular, acute to obtuse, puberulous bracts forming an involucre 2-6 mm. thick, ovoid and enclosing the solitary female flower; perianth about 3 mm. high, style subterminal and 1-2.5 mm. long, stigmas 5-10 mm. long. Fruit 7-10 mm. long, 5-8 mm. thick.

In wet forest formations of the Caribbean slope and adjacent areas between 700 and 1500 m. elevation in Costa Rica: probably flowering throughout the year but collected at anthesis only in Feb-

ruary and March in our area. The species is known from Costa Rica and ranges from the coastal ranges of Venezuela through Colombia along the Andes to Peru. The species is known from the Caribbean slopes above the San Carlos River (*Holdridge 6780 & A. Smith 1695*) and near San Ramon (*Brenes 5536 & 13578*) in the province of Alajuela and from Cerro Doán, east of Cachi (*Lent 2340*) in the province of Cartago.

*Helicostylis tovarensis* is recognized by the puberulent leaves with narrow tip and often serrulate near the apex, the hemispheric little male inflorescences with puberulent bracts covering the receptacle, or the small ovoid female inflorescences with broadly overlapping puberulent bracts including a single flower with two slender stigmas. The upper leaf-surfaces, glabrous except above the major veins, help to distinguish this species from plants with similar leaves such as *Olmedia aspera*, *Sorocea trophoides*, and others.

### MAQUIRA Aublet

REFERENCE: C. C. Berg, *Olmedieae*. Fl. Neotrop. Monog. 7:62-75. 1972.

Trees, usually unisexual, without spines, periderm of the twigs peeling off easily; stipules small and free, not completely encircling the stem, caducous. Leaves distichous, petiolate, subcoriaceous to coriaceous, the margins entire, glabrous or sparsely puberulent, usually greenish when dry and lustrous above, the microscopic multicellular hairs oblongoid-capitate. Male inflorescences pedunculate, on short shoots, discoid to globose, the flowers numerous and free or basally connate; male flowers with 4-lobed or 4-parted perianth, stamens 4 (rarely 3 or 2), filaments straight or slightly curved in bud, anthers basifixed, connective broad or narrow. Female inflorescence mostly solitary, subsessile or pedunculate, with imbricate bracts covering the receptacle, with many free flowers, a few connate flowers, or one flower; female flower with the perianth (2-) 4-lobed or (2-) 4-parted, ovary almost entirely united with the perianth or free above, stigmas short and disciform to long and filiform. Fruit with perianth becoming succulent, the seed large with a large terminal hilum, cotyledons thick and equal.

A genus of five species ranging from the Caribbean side of Nicaragua southwards to Peru and Brazil. The genus is rather similar in its flowering parts to *Perebea* but differs in the stipules, the more glabrous leaves with entire margins, and the periderm of the twigs.

*Maquira costaricana* (Standl.) C.C. Berg, *Acta Bot. Neerl.* 18:463. 1969. *Perebea costaricana* Standley, *Field Mus. Bot.* 18:390. 1937. *P. trophophylla* Standl. & L.O. Williams, *Ceiba* 3:196. 1953. Figure 16.

Shrubs or trees 2-10 (20) m. tall, unisexual, leafy internodes 1-4 cm. long, 1-5 mm. thick, glabrous or very minutely puberulent, brownish and often becoming ridged on drying; stipules 3-8 mm. long, minutely puberulent. Leaves often inequilateral at the base, petioles 6-13 mm. long, ridged on drying and the cuticle often peeling off in small reddish-brown flakes; laminae 9-22 (30) cm. long, 3.5-8 (9.5) cm. broad, oblong to elliptic-oblong or slightly obovate, abruptly acuminate at the apex with the narrowed tip 5-20 mm. long, obtuse to acute or occasionally rounded at the often oblique base, margin entire or slightly undulate, the lamina drying stiffly chartaceous to subcoriaceous, glabrous and lustrous above, essentially glabrous beneath, smooth on both surfaces, major veins prominent on both surfaces, the 7 to 15 pairs of major secondary veins loop-connected near the margin, microscopic aculeate hairs with a perimeter of small cells around the base present on the lower surface, epidermal cells and stomates readily visible (dry). Male inflorescences 1 to 3 in the axils of leaves, borne on peduncles 2-8 mm. long, discoid in form and 5-10 mm. in diameter, receptacle with about 5 series of deltoid to ovoid puberulent bracts 1-2 mm. broad basally, the flat disc with more than 20 flowers; male flowers free, perianth 4-parted, 0.6-1 mm. high, stamens 4, filaments 0.8-1.2 mm. long, straight or slightly incurved before anthesis, anthers 0.4-0.5 mm. long. Female inflorescence solitary in the leaf axils, subsessile or with a peduncle to 6 mm. long, discoid and 6-10 mm. in diameter, receptacle with 3 to 6 series of often broad (1-3 mm.) puberulent acute or obtuse bracts, with usually 15 to 35 flowers; female perianth 2-2.5 mm. high, 4-lobed, minutely brownish puberulent, ovary basally adnate to the perianth, style 0.5-1 mm. long, stigmas very broad and 0.5-1.5 mm. long, recurved. Fruit united with the succulent perianth (except near the top), drupaceous and ellipsoid, about 1.5 cm. long, glabrescent, reddish, the infructescence with few ellipsoid drupes separate or with more numerous fruit clustered and 3-4 cm. in diameter, seed 9-10 mm. long.

Plants of the wet evergreen forest formations on both the Caribbean and Pacific sides of Costa Rica; flowering from February to June. The species ranges from the Caribbean lowlands of Nicaragua to Peru at altitudes to 850 m. It has been collected near Ciudad Quesada (*Burger & Stolze 4951* and *A. Smith (H) 1733*), Alajuela, near Guapiles (*Standley 37027*, the type), Limon, and near Golfito (*Allen 6348*), Puntarenas.

*Maquira costaricana* is usually found as a shrub or small tree but occasionally reaches 20 m. in height (*Allen 6348*). The essentially glabrous, entire, oblong leaves with abruptly acuminate apices and loop-connected venation, and flat discoid inflorescences with overlapping brownish and minutely puberulent bracts covering the lower part distinguish this species. The cuticle of the petioles and peduncles often cracks and flakes off in small (1 mm.) pieces.

### MORUS Linnaeus

Trees or shrubs, bisexual or unisexual, sap white, without spines; stipules paired and free, lateral, caducous. Leaves alternate and distichous, petiolate, usually den-



tate or serrate, with or without prominent lobes, pinnately veined or palmately 3-veined, microscopic ( $\times 150$ ) globose-capitate hairs usually present, hooked (uncinate) hairs occasionally present, transparent aculeate hairs or epidermal cells with sharp conic tips often present. Male inflorescences axillary and solitary, pedunculate, elongate narrow spikes (catkins); male flowers sessile or subsessile, with usually 4 imbricate perianth-parts, usually puberulent and ovate, stamens 4, filaments bent inward in bud, springing back suddenly and elastically at anthesis, the anther becoming exerted, basifixed or dorsifixed. Female inflorescences axillary and solitary, pedunculate, short or long spikes with sessile closely crowded flowers; female perianth with 4 free ovate decussate-imbricate perianth-parts, ovary superior but included within the perianth, globose to ovoid, style apical and short, stigmas 2, equal. Fruit included within the accrescent succulent perianth, the outer part of the ovary (fruit) also succulent, seed with membranous testa and equal cotyledons.

A genus of about a dozen species in the temperate and tropical regions of both hemispheres. The genus is recognized by the small lateral stipules, serrate leaves, male spikes with sessile four-parted flowers with stamens incurved in bud, and the female spikes with crowded flowers with four perianth-parts that become succulent in fruit. The genus may also be represented in Costa Rica by the widely cultivated *Morus alba* L., native of China, with long petiolate leaves often cordate at the base. *Morus celtidifolia* H.B.K. with much smaller leaves and spikes has an unusual disjunct distribution: Mexico and Guatemala, Colombia to Bolivia.

### ***Morus insignis* Bureau in DC., Prodr. 17:247. 1873. Figure 14.**

Shrubs or medium sized trees to about 15 m. tall, the trunk and branches often thick, sap whitish, leafy internodes 0.5-5 cm. long, 1.5-4.5 mm. thick, sparsely to densely puberulent with thin ascending hairs 0.1-0.3 mm. long; stipules 7-12 mm. long, sparsely to densely minutely puberulent, scars about 3 mm. long, encircling about half the stem. Leaves often slightly asymmetric, petioles 8-22 mm. long, 1.3-2.7 mm. thick, with thin whitish ascending hairs 0.1-0.4 mm. long, narrowly sulcate apically; laminae (6) 9-25 cm. long, (3) 5-13 cm. broad, ovate to elliptic-ovate, narrowed to the acuminate apex, obtuse to rounded and truncate or subcordate at the base, the margin conspicuously serrate with 2 to 6 teeth per cm. the teeth usually with a small (0.5 mm.) tip terminating a tertiary vein, the laminae drying thinly to stiffly chartaceous, smooth to scabrous above but essentially glabrous, sparsely puberulent beneath with very thin whitish hairs to 0.5 mm. long, the midvein impressed above, the 7 to 9 pairs of major secondary veins weakly loop-connected near the margin, microscopic globose-capitate hairs with orange coloring present beneath and with broad-based transparent aculeate hairs on the veins ( $\times 100$ ). Male inflorescences 3-11 cm. long, short-pedunculate, with flat round or irregularly shaped peltate bracts covering the flowers in early stages; male perianth about 1.5 mm. long, with thin whitish hairs abaxially, filaments 2-3 mm. long, anthers about 1.2 mm. long, broader than long. Female inflorescence borne on peduncles 5-10 mm. long, puberulent and with a few flat peltate bracts 1-2 mm. broad, spikes becoming 12 cm. long,

with numerous peltate bracts among the closely contiguous flowers; female perianth and bracts dark centrally with pale brownish edges, perianth-parts about 1.5 mm. long, sparsely puberulent, stigmas 1-2 mm. long, minutely puberulent. Fruit drying angular, often separate on the rachis, loosely enclosed within the slightly succulent perianth, 2-3 mm. high, the reddish stigmas persisting, seed lenticular-ovoid, about 2 mm. long.

Trees of the evergreen montane forest formations between 1500 and 2200 m. elevation on the Caribbean and Eastern sides of the Meseta Central and near Copey in the Cordillera de Talamanca in Costa Rica; collected in fruit in March and May. The species is found in Guatemala, Costa Rica, Venezuela, and from Colombia southward to Peru.

*Morus insignis* is recognized by its rather broad serrate leaves usually rough to the touch, paired stipules leaving conspicuous scars, sessile male flowers congested on narrow spikes sessile female flowers with distinct perianth parts, and the presence of broad flat-topped peltate bracts on both male and female inflorescences. The trees can have trunks to 2 m. in diameter and are said to have a low spreading crown with very thick branches (probably in highland pastures). The species is known from only a few collections and may have been common in the moister forests in the eastern half of the Meseta Central (on the Pacific watershed) that have now been largely destroyed. This species appears to be quite different from other species in the genus; the long inflorescences and peltate bracts are uncommon in this genus.

### NAUCLEOPSIS Miquel

REFERENCE: C. C. Berg, *Olmedieae*. Fl. Neotrop. Monog. 7:104-144. 1972

Trees, unisexual or rarely bisexual, without spines; stipules free, completely encircling the stem, caducuous or tardily deciduous. Leaves distichous, petiolate, often coriaceous to subcoriaceous, margins always entire, mostly glabrous, microscopic multicellular hairs not frequent, oblongoid-capitate. Male inflorescence 1 to 4 per axil, mostly pedunculate, disc-like to cup-shaped, receptacle covered with imbricate bracts, the inner bracts often perianth-like and covering the flowers before anthesis, male flowers free or basally connate, perianth with usually 4 (0-8) parts, free or basally connate, often cucullate to subpeltate, stamens 1-4, filaments straight in bud, connectives mostly broad. Female inflorescences solitary, sessile or short-pedunculate, discoid to hemispherical, with many to few (rarely 1) flowers; female flowers with usually 4 to 6 (3-10) perianth-parts, the perianth parts free to completely united, often similar to the pseudobracts, ovary completely immersed within the receptacle, stigmas filiform to short-linguiform; pseudobracts present or absent, very variable in form. Fruit borne within hemispheric to subglobose infruc-

tescences, perianth-parts and pseudobracts becoming enlarged, hard and often angular, seeds imbedded in the pulpy receptacle, cotyledons thick and equal.

A genus of 18 species ranging from the Caribbean side of Honduras southward to Peru and to the state of Rio de Janeiro in Brazil.

*Naucleopsis naga* Pittier, Contr. U.S. Nat. Herb. 13:440. 1912. *Ogcodeia naga* (Pittier) Mildb., Notizbl. Bot. Gart. Berlin 11:420. 1932. Figure 16.

Trees to 15 m. tall, unisexual, the sap brownish, leafy internodes 5-40 mm. long, 3-7 mm. thick, essentially glabrous, dark brown to pale gray, longitudinally striate when dry; stipules 10-19 mm. long, very narrow in the distal half, dark brown, minutely (0.2 mm.) puberulent along the midrib and basally (abaxially). Leaves usually slightly asymmetric, petioles 7-22 mm. long, 2-4 mm. thick, narrowly sulcate distally; laminae 14-30 (40) cm. long, 5-11 cm. broad, oblanceolate to narrowly obovate or elliptic-oblong, gradually to abruptly short-acuminate at the apex, obtuse or slightly rounded at the base, the margins usually forming a slit in the distal part of the petiole above, margins entire or slightly undulate, the lamina drying very stiffly chartaceous or subcoriaceous, smooth and lustrous above, glabrous on both surfaces, the midvein prominent above, the 15 to 26 pairs of major secondary veins flat or slightly raised above, very weakly loop-connected near the margin, microscopic capitate hairs absent or few on the lower surface. Male inflorescence and flowers unknown. Female inflorescences solitary in the axils of leaves or fallen leaves, hemispherical with a flat or curved sessile base, receptacle subtended by 3 to 5 series of thick woody deltoid to lanceolate bracts with minute (0.1 mm.) appressed hairs, bracts numbering about 24-32, dark brown, the larger 5 mm. broad at the base, the flowers more than 40 per inflorescence; female perianth-parts free, similar to the pseudobracts, subulate to clavate, acute, minutely brownish puberulent, ovary immersed in the receptacle, style about 4 mm. long, stigmas about 3 mm. long. Fruit borne within the receptacle of the infructescence, the infructescence becoming woody, 3-5 mm. in diameter, the perianth-parts and pseudobracts becoming spine-like and woody, 7-22 mm. long.

Small trees of the wet evergreen forest formations below 600 m. elevation on the Caribbean slopes and lowlands; collections with developing fruit have been made in June and August. The species ranges along the Caribbean from northern Honduras to Central Costa Rica. Only a single fertile (fruiting) collection has been made in Costa Rica: *Pittier 13444* from the Llanura de Santa Clara.

*Naucleopsis naga* is distinguished by the unusually long and narrow glabrous and lustrous leaves that are usually widest above the middle, the stipules encircling the stem, the petiole narrowly sulcate apically, and the very unusual infructescence with short spinelike structures covering much of the surface. The species is apparently rare and the male flowers probably have a very short flowering period. The names *majao de indio* and *concha de indio* have been used for this species in Honduras.

## OLMEDIA Ruiz &amp; Pavon

REFERENCE: C.C. Berg, *Olmedieae*. Fl. Neotrop. Monog. 7:13-17. 1972.

Trees or shrubs, unisexual, spines absent; stipules free, partly encircling the stems, caducous. Leaves distichous, petiolate, chartaceous to subcoriaceous, scabrous or slightly scabrous, usually dentate or denticulate. Male inflorescences axillary, usually solitary or paired, subsessile to pedunculate, discoid in form, with 3 to 4 series of imbricate bracts covering the outer surface of the receptacle, many- to several-flowered; male flowers free or basally connate, perianth-parts coherent and 2-, 3-, or 4-parted on opening, valvate; stamens 4, bent inward in bud and snapping open elastically at anthesis, anthers basifixed or dorsifixed, latrorse to introrse. Female inflorescences, axillary, subsessile to pedunculate, usually solitary or paired, surface of the receptacle with a few series of imbricate bracts, nearly always with a single flower; female flower with a tubular 4-dentate perianth, ovary free, stigmas filiform. Fruit enclosed in the fleshy perianth, cotyledons thick and equal, radicle short and apical.

The genus is composed of a single species ranging from Costa Rica southward along the Andes to Bolivia.

***Olmedia aspera*** Ruiz & Pavon, Fl. Peruv. & Chil. 1:257. 1798.  
*O. falcifolia* Pittier, Contr. U.S. Nat. Herb. 13:435. 1912. Figure 16.

Shrubs or trees to 15 (20) m. tall, unisexual, leafy internodes 5-45 mm. long, 1-4 mm. thick, glabrous to hispidulous, the sap white or yellow; stipules 5-12 mm. long, very minutely puberulent and slightly scabrous. Leaves often asymmetric and somewhat curved, petioles 3-8 (15) mm. long, 0.7-1.5 mm. thick, usually minutely hispidulous and with transverse cracks in the cuticle; laminae 6-26 (40) cm. long, 1.5-7 (12) cm. broad, oblanceolate to narrowly obovate, oblong or elliptic, usually somewhat asymmetric and subfalciform, narrowly acuminate to caudate-acuminate, the narrow tip 1-3 cm. long, gradually narrowed to the acute base, margin bluntly serrulate in the distal half of the lamina (rarely entire), the lamina drying thin- to thick-chartaceous and often grayish above, glabrous and scabrous to very slightly scabrous above, usually scabrous beneath with hispid hairs 0.1-0.5 mm. long, the major veins prominent beneath but flat above, with 6 to 18 pairs of prominent secondary veins, the lower surface with microscopic ( $\times 150$ ) narrowly aculeate transparent hairs. Male inflorescences 1 or 2 (rarely to 6) in the axils of current leaves, subsessile or borne on peduncles to 6 mm. long, receptacle with 3 or 4 series of ovate to lanceolate bracts forming an involucre around the edge of the disc, the larger bracts 2 mm. broad near the base, minutely strigose, the flat top of the inflorescence 4-10 mm. in diameter with 10 to 30 flowers; male perianth 2-3 mm. high, 2- to 4-parted at anthesis, minutely strigulose apically, filaments 3.5-5 mm. long, anthers 1.3-1.8 mm. long and 0.5-0.9 mm. broad. Female inflorescences 1 or 2 (rarely to 5) in the axils of current or fallen leaves, subsessile or borne on peduncles to 6 mm. long, receptacle covered with 5 to 7 series of ovate to deltoid bracts about 2-4 mm. broad, with minute (0.1-0.2 mm.) stiff appressed hairs, inflorescence ovate in form, 3-6 mm. thick, with 1 (very rarely 2) flowers, female perianth 3-3.5 mm. high, minutely strigulose, ovary free, often with minute stiff appressed hairs apically, style 1.2-4 mm. long, the stig-

mas 5-11 mm. long, very slender. Fruit borne within the orange to red fleshy perianth, about 4-5 mm. thick, subglobose.

Small trees of moist and wet evergreen forest formations between sea level and 66 m. elevation on both the Caribbean and Pacific slopes in Costa Rica; flowering throughout the year but collected most often between October and March. The species has not been collected north of the General Valley on the Pacific slope and is rarely encountered north of the Río Reventazon on the Caribbean side of Costa Rica; it ranges southward through the Andes to Bolivia.

*Olmedia aspera* is recognized by the narrow, often curved and slightly scabrous leaves that are bluntly serrulate distally and have a long narrow tip, the bracteate ovoid little female inflorescence with single flower and two long stigmas, and the male flowers on small flat-topped receptacles. Often the trees arch over brooks and small streams. The bent anthers can be released by touch; this quick motion may be an adaptation for pollen dispersal by small insects. However, the stream-side habitat may be one in which wind-pollination is possible and anthers may be released by desiccation.

### PEREBEA Aublet

REFERENCE: C.C. Berg, *Olmediaeae*. Fl. Neotrop. Monog. no. 7:38-61. 1972.

Trees or shrubs, unisexual or bisexual, without spines; stipules free, encircling the stem completely, caducous. Leaves distichous, petiolate, chartaceous to coriaceous, often dentate to denticulate, usually drying brownish and often gray above, the microscopic multicellular hairs either globose-capitate or oblongoid-capitate and mostly abundant. Male inflorescences borne on well developed short-shoots or axillary and pedunculate, 1 to several per axil or many on the short-shoots, mostly discoid in form, with many to few (1) flowers; male flowers with (2-3) 4 free or connate perianth-parts, each with usually 4 (2-6) stamens, filaments straight or slightly incurved before anthesis, free or united near the base, anthers small, basifixed or dorsifixed, connective broad. Female inflorescences axillary and solitary or accompanied by males, sessile or pedunculate, receptacle covered with imbricate bracts forming an involucre, with 1 to many flowers; female flowers mostly free, perianth 3-4 lobed or parted or completely united and forming a tube with entire margin, ovary free or partly united with the perianth, stigmas filiform to short and thick. Fruiting perianth fleshy, the fruit free or variously united to the perianth; seed with a large orbicular to reniform hilum, cotyledons thick and equal.

A genus of eight species, all represented in the western part of the Amazon Basin, with three species reaching their northwestern limits in our area. The involucre of thin imbricate bracts covering the

receptacle of the rather small inflorescences, the fruit usually borne about the surface of the receptacle, and the distally narrowly sulcate petioles are useful in recognizing the genus.

- 1a. Stipules 30-60 mm. long; laminae 20-50 cm. long, 8-18 cm. broad, slightly rounded to cordate at the base, with 16 to 26 pairs of major secondary veins, densely hirsute beneath; Western Panama . . . . . *P. guianensis*.
- 1b. Stipules 4-25 mm. long; laminae usually narrowed and acute to obtuse at the base, sparsely puberulent or glabrescent beneath . . . . . 2a.
- 2a. Laminae 12-34 (48) cm. long, 4-12 (20) cm. broad, with 12 to 18 pairs of major secondary veins; male inflorescence with more than 20 flowers; Caribbean and Pacific slopes . . . . . *P. xanthochyma*.
- 2b. Laminae 5-17 (22) cm. long, 1-7 cm. broad with 8-12 pairs of major secondary veins; male inflorescence usually with fewer than 20 flowers; Caribbean lowlands . . . . . *P. angustifolia*.

***Perebea angustifolia*** (Poep. & Endl.) C.C. Berg, Acta Bot. Neerl. 18:463. 1969. *Olmedia angustifolia* Poeppig & Endlicher, Nov. Gen. 2:30 t. 143. 1838. Figure 16.

Shrubs or slender trees 3-10 (20) m. tall, unisexual, latex white, leafy internodes 5-50 mm. long, 1-3 mm. thick, with thin appressed white or yellowish hairs; stipules 4-10 mm. long, with slender ascending pale yellowish or whitish hairs on the base and midrib. Leaves usually symmetrical, petioles 2-10 mm. long, 0.5-1.1 mm. thick, appressed sericeous with straight thin hairs 0.2-0.5 mm. long; laminae 5-17 (22) cm. long, (1) 2-7 cm. broad, narrowly oblong to elliptic-oblong or narrowly obovate, abruptly acuminate or caudate-acuminate at the apex, the slender tip 1-2 cm. long, obtuse to acute at the base and slightly rounded at the petiole, margin entire to bluntly serrulate distally, lamina drying chartaceous, smooth on both surfaces, essentially glabrous and the midvein prominent above, sparsely and minutely strigose on the veins beneath, the 8 to 12 pairs of major secondary veins weakly loop-connected near the margin, microscopic oblongoid-capitate hairs usually present beneath. Male inflorescences usually 1 or 2 in axils of leaves or fallen leaves, goblet-shaped at anthesis (abruptly narrowed beneath), 3-5 mm. in diameter, borne on bracteate peduncles 1-3 mm. long, the receptacle covered by 4 to 5 series of 15 to 25 thin ovate bracts obtuse at the apex and sparsely puberulent abaxially, flowers 5 to 20; male perianth 1-2 mm. high, 4-lobed or 4-parted, not thickened distally, filaments free, anthers 0.2-0.5 mm. long. Female inflorescences solitary, 1-5 mm. in diameter, borne on peduncles 1-3.5 mm. long and bracteate distally, receptacle covered with 3 to 5 series of 6 to 23 thin suborbicular to ovate bracts, minutely puberulent, flowers 1 to 12; female perianth urceolate, 2-2.5 mm. high, 4-lobed, minutely appressed puberulent, ovary almost free or partly united with the perianth, nearly glabrous, stigmas 0.6-1 mm. long, slender. Fruit enclosed within the fleshy sparsely appressed puberulent perianth.

Small trees and slender treelets in the understory of wet evergreen forest formations between sea level and 200 m. on the Caribbean side of Costa Rica (to 600 m. elsewhere); probably flowering

throughout the year. The species ranges from Central Costa Rica southward to the upper Amazon Basin of Brazil and Peru.

*Perebea angustifolia* is usually found as a slender treelet with thin (1-3 cm.) stems on the dark forest floor. The thin, narrow almost glabrous leaves, often abruptly acuminate and with a few blunt teeth distally, stipules surrounding the stem, white sap, and minute inflorescences with thin imbricate bracts distinguish this species. The plants resemble juvenile specimens of *Sorocea*. The small few-flowered inflorescences are very difficult to see and may account for the very few collections in herbaria. This species is known in Costa Rica from near Puerto Viejo de Sarapiquí (*Burger et al.* 4325, 9281, & 9286 and *Hartshorn* 821) Heredia, and from near El Carmen (*Lent* 2473) in the province of Limón.

*Perebea guianensis* Aublet, Pl. Guian. 2:953, t. 361. 1775. *P. castilloides* Pittier, Contr. U.S. Nat. Herb. 13:438. 1912. Figure 16.

Usually small trees, 3-20 m. tall, unisexual, latex white to yellowish, leafy internodes 3-7 (13) mm. thick, subsericeous to substrigose or hirsute with slender yellowish hairs; stipules 3-6 cm. long, occasionally persisting, yellowish subsericeous to hirsute. Leaves usually slightly asymmetric, petioles 3-16 mm. long, 2-6 mm. thick, with thin ascending yellowish hairs 0.8-2 mm. long; laminae 20-50 cm. long, 8-18 cm. broad, oblong to ovate-oblong or obovate-oblong, widest in the distal or proximal part, abruptly acuminate or caudate at the apex with the narrowed tip 1-2 cm. long, truncate and rounded to cordulate at the base with the small basal lobes sometimes overlapping, margin entire to repand, the laminae drying stiffly chartaceous to subcoriaceous, smooth and puberulent on the major veins above, hirsute on the veins beneath with yellowish hairs 1-1.5 mm. long, the 16 to 26 pairs of major secondary veins usually weakly loop-connected near the margin, narrowly oblongoid-capitate microscopic hairs present on the veins beneath. Male inflorescences often in groups on short-shoots in the leaf axils, discoid, 10-15 mm. in diameter, on peduncles as much as 30 mm. long, receptacle covered with 5 or 6 series of about 50 to 90 thin bracts narrowed apically, flowers more than 15; male perianth 1-1.5 mm. high, filaments 1-1.6 mm. long, anthers 0.4-0.5 mm. long, apiculate. Female inflorescences solitary or rarely together with the males, discoid, 10-15 mm. in diameter, receptacle covered with 3 to 5 (9) series of 30 or more thin bracts narrowed apically and subsericeous to hirtellous, flowers 8 to 27; female perianth 4-6 mm. high, the perianth-tube 4-lobed with the free lobes 0.5-2 mm. long, style 2-5 mm. long, stigmas 1.2-1.7 mm. long, plane and 0.6-2 mm. broad or revolute to 4 mm. broad. Fruit borne within the succulent ellipsoid perianth 10-22 mm. high on the discoid infructescence 2-5 cm. broad.

Plants of wet evergreen forest formations between sea level and about 1000 m. altitude in our area. This species has not been collected in Costa Rica but is known from Bocas del Toro and Chiriquí Provinces in Panama and ranges southward to the Amazon Basin and the Guianas.

*Perebea guianensis* is represented in our area by subspecies *castillodes* (Pittier) Berg. The plants are distinctive because of the large, usually oblong leaves slightly cordate at the base, short petioles, slender silky yellowish hairs on many parts, and discoid pedunculate inflorescences with an involucre of thin imbricate puberulent bracts. The plants are very similar to *Castilla elastica*, but that species has the two stipules at each node fused and the leaves are minutely denticulate whereas our material of *Perebea guianensis* has separate stipules and entire leaf-margins.

***Perebea xanthochyma*** Karsten, Fl. Colomb. 2:23. t. 112, 1862. *P. hispidula* Standl., Ann. Missouri Bot. Gard. 29:350. 1942. *P. molliflora* Standl. & Wms., Ceiba 3:41. 1952. Figure 16.

Shrubs or trees to 35 m. tall, unisexual or bisexual, latex yellowish but turning brown or reddish, leafy internodes 5-50 mm. long, 1.6-6 (8) mm. thick, variable in pubescence with minute (0.1-0.3 mm.) appressed ascending hairs or longer (0.5-1.5 mm.) spreading straight hairs or both, often becoming glabrescent; stipules 5-15 (25) mm. long, yellowish to pale grayish sericeous with lustrous thin ascending hairs. Leaves often slightly asymmetric, petioles 2-10 (20) mm. long, about 1.8 mm. thick, narrowly sulcate distally, often hirsute; laminae 12-34 (48) cm. long, 4-12 (20) cm. broad, abruptly acuminate at the apex, the narrow tip 1-3 cm. long, acute to obtuse and slightly rounded at the usually unequal base, margin entire to repand or distinctly serrate, laminae drying thinly to stiffly chartaceous, smooth on both surfaces, glabrescent and the midvein prominent above, almost glabrous to conspicuously puberulent on the veins beneath with slender stiff hairs to 1 mm. long, the 12 to 18 pairs of major secondary veins weakly loop-connected near the margin or not, microscopic narrowly oblongoid-capitate hairs present on the lower surface. Male inflorescences 3-6 (10) mm. in diameter, borne on peduncles 1-3 (6) mm. long, receptacle covered with 4 to 8 series of about 25 to 60 broad thin subsericeous bracts, flowers 10 or more; male perianth 0.8-1.1 mm. high, perianth-parts free and yellowish puberulent, filaments 0.6-1.1 mm. long, free, anthers 0.3-0.5 mm. long. Female inflorescences solitary or with male inflorescences in the axils of leaves, discoid to subglobose, 4-15 mm. in diameter, subsessile or borne on a bracteate peduncle to 3 mm. long, receptacle covered by 4 to 10 series of 20 to 90 thin subsericeous bracts, flowers (5) 10 or more; female perianth about 2 (rarely, 3.5) mm. high, perianth-tube entire or minutely 4-lobed, yellowish to whitish puberulent, ovary partly united to the perianth, style 0.5-2 mm. long, stigmas 0.5-1.5 mm. long, 0.2-0.7 mm. broad. Fruit borne within the succulent perianth on infructescences 1-2 cm. in diameter, fruiting perianth ellipsoid, 10-13 mm. long and 8-10 mm. thick (dry), sparsely to densely hirsute with long (1 mm.) yellowish hairs, becoming red.

Plants of the lowland wet evergreen forest formations from sea level to 850 m. elevation; on both the Caribbean and Pacific slopes of Costa Rica; probably flowering throughout the year. The species ranges from Costa Rica to Peru.

*Perebea xanthochyma* is recognized by the yellowish sap, stipules



encircling the stem, thin and occasionally long leaves abruptly acuminate and sparsely puberulent beneath, small inflorescences with thin overlapping bracts forming an involucre, and the usually hirsute ellipsoid drupe-like fruit borne on the infructescence. The margins of the lamina form a narrow slit at the apex of the petiole, and this is useful in placing material with immature flowering parts, but compare *Naucleopsis*.

### POULSENIA Eggers

Trees, bisexual, the younger branches usually with short broad-based spines; stipules paired and free at a node, completely enclosing the shoot-apex, caducous and leaving a scar encircling the stems. Leaves distichous, petiolate, laminae often large, epidermal cells often with sinuate outlines, very narrow oblongoid-capitate hairs present on the lower surface (150X), the lower surface with microscopic transparent cells round in outline and apparently flat. Male inflorescences usually solitary in the axils of leaves, pedunculate, globose or subglobose heads with many flowers; male flower with 4 perianth-parts and 4 stamens, compressed and angular in early stages, with the perianth united basally and 4-lobed, stamens 4, apparently straight in bud, anthers basifixed. Female inflorescences a capitate sessile cluster of flowers, solitary in the leaf-axil, the (3) 5 to 15 flowers united in the lower half; female flower with the free upper portion of the perianth tubular and conic, shortly 4-dentate, ovary free of the perianth but within the united part of the flower and becoming immersed in fruit, style exerted, stigmas 2. Fruit formed within the fleshy head (syncarp).

A genus with a single species ranging from Veracruz, Mexico, to Ecuador. There is great variation in leaf-size, venation, and symmetry in different collections but the small spines, often found on petioles and stipules as well as stems, distinguish these plants from other Moraceae in our flora.

*Poulsenia armata* (Miq.) Standley, Trop. Woods 33:4. 1933.  
*Olmedia armata* Miquel in Seem., Bot. Voy. Herald 196, 1854.  
Figure 15.

Trees, 5-25 m. tall, bisexual, sap white, leafy internodes (0.8) 1.5-6 (10) cm. long, 3-8 mm. thick, glabrous or with very minute (0.5 mm.) appressed brownish hairs, usually with scattered spines 2-4 mm. long, broad (1.3 mm.) at the base with a thickened brownish central portion and abruptly narrower translucent sharp tip; stipules 1-6 cm. long, 5-10 mm. thick near the base, glabrous or with brown multicellular hairs, often with short spines. Leaves symmetric or often very asymmetric near the base on flowering branchlets; petioles 1-4.5 cm. long, 2.5-4.5 mm. thick, glabrous or with very minute (0.05-0.1 mm.) appressed hairs, a few spines usually present, narrowly sulcate above; laminae (8) 12-45 cm. long, (4) 8-22 cm. broad, ovate to ovate-oblong, acute to acuminate or occasionally obtuse at the apex, obtuse to rounded and truncate or cordate at the equal to very unequal base, margin entire or slightly

sinuate, the laminae drying very stiffly chartaceous to subcoriaceous, smooth and the major veins prominent above, essentially glabrous on both surfaces, the 4 to 12 pairs of major secondary veins weakly loop-connected near the margin (an arcuate submarginal vein absent), microscopic hairs very narrowly oblongoid beneath. Male inflorescences borne on peduncles 1-2 cm. long, the globose head about 1-1.5 cm. in diameter (dry), lacking an obvious involucre of bracts, the young flowers variously angled by compression, about 0.8 mm. in diameter; perianth-lobes about 0.5 mm. wide, minutely puberulent, stamens slightly exerted above the perianth, anthers about 0.5 mm. long and 0.8 mm. broad, with a broad connective. Female inflorescence a loose head of apically separate flowers sessile in the leaf axil, subglobose to obovoid or ovoid in general form, 1.5-2 cm. in diameter; free portion of the female flowers 3-5 mm. high, perianth-lobes 1-2 mm. long, sparsely and very minutely puberulent. Fruit borne within the fleshy syncarp about 2-3 cm. in diameter, apices of the individual fruiting perianths about 3 mm. high with the larger part of the seed beneath the surface of the syncarp, seed about 8 mm. long and 4 mm. thick.

Plants of evergreen wet forest formations between sea level and about 400 (?) m. elevation; flowering material has been collected in April and September (in Panama). The species ranges from Central Mexico to Bolivia.

*Poulsenia armata* is recognized by the aculeate spines, milky sap, stipules encircling the stem, large leaves, and capitate inflorescences that are globose and pedunculate in the male and a sessile cluster united basally in the female. The inflorescences of both sexes lack an involucre and have no peltate bracts but the peduncle is often dilated at the apex and may resemble an involucre. The whorled arrangement of bracts may give the impression of an involucre in the female inflorescence. The species is very poorly represented in collections. The larger trees appear to have smaller leaves that are often very asymmetric.

### POUROUMA Aublet

Unisexual trees, often tall with relatively slender smooth trunks, independent or (?) rarely epiphytic; the sap clear but quickly becoming dark in color, not milky; stipules connate and (consequently) solitary, enclosing the stem-apex and leaving a scar encircling the stem, usually large. Leaves simple and alternate in a spiral, petiolate and basifixed, the lamina entire to deeply lobed (entire and narrowly elliptic in juvenile stages), pinnately or palmately veined, tertiary veins subparallel, often pale-grayish tomentose beneath. Inflorescences unisexual, usually paired in the axils of the current leaves, peduncle usually branched with the flowers in cymose clusters or rarely unbranched and the flowers umbellate. Male flowers usually in congested clusters or capitate, sessile on the branches of the inflorescence; perianth of 3 or 4 parts or lobes, stamens 3 or 4, filaments erect, free or connate at the base. Female flowers sessile or more often pedicellate, perianth tubular with a small opening at the apex, enclosing ovary and style and persisting in fruit, stigma simple, papillate-puberulent, peltate-discoid, ovule borne on the wall of the locule near the

base by adnation of the funicle. Fruit moderately large (1-3 cm.), tightly enclosed within the persisting slightly succulent perianth.

A poorly understood genus of probably fewer than 30 species, represented in Central America by only the following two species. Unlike its close relative, *Coussapoa*, the epiphytic-strangling habit is apparently never encountered in *Pourouma*. Like *Coussapoa* and *Cecropia*, also members of the subfamily Conocephaloideae, these plants are probably more closely related to the Urticaceae than to the other genera of the Moraceae (Corner, 1962).

Laminae of mature trees usually deeply lobed and scabrous above; female inflorescences distally much-branched with the flowers in cymose groups; common and widespread in wet evergreen formations, 0-1000 m. . . . . *P. aspera*.

Laminae of mature trees entire and elliptic, smooth above; female inflorescence umbellate with 5 to 9 flowers on each peduncle; rare (?) and known only from the low hills (200 m.) at the edge of the Caribbean escarpment in Costa Rica . . . . . *P. minor*.

***Pourouma aspera*** Trecul, Ann. Sci. Nat. ser. 3, 8:102. 1847. sensu lato. *P. scobina* Benoist, Bull. Mus. Hist. Nat. Paris 28:320. 1922. *P. johnstonii* Woodson, Ann. Missouri Bot. Gard. 47:166-167. 1960. Figure 22.

Trees (5) 10-30 m. tall, trunk smooth and mottled with shades of gray and brown, the cut trunk producing clear sap but the branchlets producing a sap that quickly becomes dark brown or black, leafy internodes 8-20 mm. thick, sparsely to densely puberulent with minute or long (3 mm.) hairs; brown circular lenticels often present; stipules 5-12 cm. long, 5-20 mm. thick, densely pale yellowish gray sericeous with hairs 0.5-3 mm. long, caducous. Leaves very variable (on different trees and occasionally on the same tree) in mature plants, petioles 12-30 cm. long, 3-7 mm. thick, minutely (0.1-0.5 mm.) appressed sericeous, smooth or weakly striate; laminae on mature plants 12-50 cm. long, 10-40 cm. broad, with 3 to 5 (7) usually deep or occasionally shallow lobes, distal lobes acute to acuminate at the apex or less often obtuse, cordate to truncated at the base, margins usually undulate, the laminae drying stiffly chartaceous to subcoriaceous, scabrous and sparsely puberulent above, puberulent beneath with slender ascending hairs about 1 mm. long and thin minutely floccose or arachnoid hairs giving the under-surface a pale grayish color, venation palmate with 3 to 5 (7) primary veins, the central primary with 16 to 24 pairs of major secondary veins, central secondaries arising at angles of 30-60 degrees, tertiary veins slightly raised beneath. Male inflorescences 10-28 cm. long, common peduncle 3-12 cm. long, 1-3 mm. thick, densely ascending sericeous, distally much branched and the flowers in dense clusters; anthers about 0.4 mm. long. Female inflorescences 10-22 cm. long, common peduncle 5-11 cm. long, 2-4 mm. thick, distally much branched and the flowers in cymose groups, female flowers borne on short (1-10 mm.) thick (1-2 mm.), densely reddish puberulent pedicels expanded apically and somewhat cupulate, the female flowers 3-7 mm. long, (above the cupule), 1.5-3 mm. thick, narrowly ovoid, densely reddish-brown puberulent, stigma 1-2 mm. broad, minutely puberulent. Fruit becoming 15 mm. long and 10

mm. thick, ovoid, abruptly truncate or rounded at the base narrowed to the persisting stigma, the surface puberulent and scabrous.

Large trees of rain forest formations from sea level to 900 m. altitude on both the Caribbean and Pacific slopes but not collected below 150 m. in Costa Rica; flowering and fruiting collections have been made between January and August. The species ranges from British Honduras southward to Venezuela and the Guianas.

*Pourouma aspera* is recognized by the usually deeply lobed leaves scabrous above, complex inflorescences much branched distally, and the female flowers covered with minute reddish-brown hairs. This is the only species of the genus ranging into northern Central America. I believe that most of the material referred to under *Pourouma* in the "Flora of Panama" (Woodson, 1960) is synonymous with *P. aspera* as interpreted here. This species is called *Yahal*, *Pacica*, *guarumo de montaña*, and *guarumo macho* in Nicaragua and Costa Rica. The leaves are used for scouring, and the fruits were said to be eaten.

***Pourouma minor*** Benoist, Bull. Mus. Hist. Nat. Paris 30:103. 1924, sensu lato fide C.C. Berg in litt. *P. umbellifera* Burger, Phytologia 26: 430. 1973. Figure 22.

Trees 10-25 m. tall, leafy internodes 2-10 (30) cm. long, 2.5-7 (15) mm. thick, densely to sparsely puberulent with slender ascending hairs 0.5-2 mm. long, periderm becoming wrinkled (dry); stipules 5-15 cm. long, 4-14 mm. thick, densely sericeous with lustrous pale silvery hairs about 1 mm. long. Leaves often clustered near the ends of branchlets, quite variable in size (on the same tree), petioles 2-6 cm. long, 1.5-4 (5) mm. thick, longitudinally ridged, puberulent with mostly ascending appressed hairs about 1 mm. long; laminae (6) 10-28 (34) cm. long, (3) 4-12 (16) cm. broad, narrowly elliptic to elliptic-oblong, abruptly acute at the apex, obtuse or slightly rounded at the base, paired gland-like thickenings often present at the base of the blade above the petiole (adaxially), margin slightly rounded-undulate distally, laminae drying stiffly chartaceous to subcoriaceous, smooth above and puberulent only on the midvein, densely pale yellowish or whitish sericeous on the veins beneath, minutely whitish floccose between the veins, venation pinnate, the (8) 15 to 22 pairs of major secondary veins weakly loop-connected near the margin, central secondaries arising at angles of 30-50 degrees, tertiary veins slightly raised beneath. Male inflorescences about 6 cm. long, paniculate, peduncles about 3-4 cm. long and 1 mm. thick, appressed sericeous, secondary and tertiary branches with the lustrous hairs not closely appressed; male flowers pedicellate or sessile, usually in clusters about 4 mm. broad, perianth about 1.5 mm. long, brownish with pale hairs along the midrib abaxially, anthers about 0.4 mm. broad. Female inflorescences umbellate, peduncle (2) 4-8 cm. long, about 2 mm. thick, sparsely or densely puberulent, with 5 to 9 flowers per umbel, pedicels (2) 5-15 mm. long (lengthening in fruit), very slightly expanded at the apex; female flowers 4-8 mm. long, 1.5-3 mm. thick, narrowly ellipsoid or ovoid, densely yellowish or grayish velutinous, stigma peltate, thick and

undulate, densely and minutely reddish velutinous. Fruiting inflorescence with fruit borne on pedicels 1-3 cm. long, about 1.5 mm. thick, sparsely puberulent, the perianth-tube becoming 15-22 mm. long, 10-15 mm. thick, ovoid, abruptly narrowed at the base, gradually narrowed at the apex, sparsely puberulent with slender ascending hairs about 0.3 mm. long, fruit only slightly smaller than the enclosing perianth, ovoid and somewhat flattened with suture-like lines on the flattened surfaces, glabrous and lustrous.

A species of the Caribbean coastal plain and adjacent slopes between 50 and 300 m. elevation in Costa Rica; flowering collections have been made in October, January, and May. Fertile collections have been made near Tirimbina (*Lent 2327*) and Las Horquetas (*Hartshorn 1224*) in Heredia and above Siquerres (*Holdridge 6818*) in Limon. The species ranges southward to the Amazon basin.

*Pourouma minor* is distinguished by the long-petiolate elliptic leaves with many parallel secondary and tertiary veins, whitish undersurfaces, and umbellate female inflorescence. Vegetatively these plants resemble some species of *Coussapoa*, but those usually begin as epiphytes. I am following Dr. C.C. Berg's interpretation (pers. comm. ) that *P. minor* is a variable species of wide range.

### PSEUDOLMEDIA Trecul

REFERENCE: C.C. Berg, *Olmedieae*. Fl. Neotropica. Monog. 7:17-38. 1972.

Unisexual trees, branches without spines; stipules free, encircling the stem completely, caducous. Leaves distichous, petiolate, mostly entire, microscopic multicellular oblongoid-capitate or globose-capitate hairs often abundant. Male inflorescences 1 to 4 (rarely more) in each axil, sessile, discoid in form, receptacle covered with imbricate bracts, forming an involucre that covers the stamens until anthesis; male flowers not recognizable, the many free stamens intermixed with concentrically arranged interstaminal bracts, the interstaminal bracts variable in size and shape, filaments straight in bud, anthers basifixed, often apiculate and with or without apical hairs, the thecae opening laterally. Female inflorescences 1 or 2 (rarely more) in the leaf-axils, sessile, receptacle covered with imbricate bracts forming an involucre, flower solitary in each inflorescence; female flower with a tubular 4-dentate perianth, ovary completely united with the perianth-tube, stigmas filiform. Fruit relatively large within the reddish and fleshy perianth, cotyledons thick and equal.

A genus of nine species ranging from southern Mexico and the West Indies to Brazil and Bolivia.

Fruit pale yellowish sericeous to velutinous, subglobose to ellipsoid; laminae usually 6-17 cm. long and 2-7 cm. broad; between 500 and 1000 m. elevation in our area

*P. oxyphyllaria*.

Fruit sparsely puberulent near the tip and glabrous over most of its surface, oblongoid to obovoid or ellipsoid; laminae usually 4-14 cm. long and 1.5-4.5 cm. broad; rarely found above 500 m. elevation in Costa Rica. . . . . *P. spuria*.

***Pseudolmedia oxyphyllaria*** Donnell-Smith, Bot. Gaz. 20:294. 1895. *P. mollis* Standl., Journ. Wash. Acad. Sci. 13:30. 1923. *Brosimum ramonense* Standl., Field Mus. Bot. 18:379. 1937. *Pseudolmedia simiarum* Standl. & Steyer., loc. cit. 23:154. 1944. *P. malacocarpa* Standl. & Wms., Ceiba 3:42. 1952. Figure 16.

Trees to 20 (30) m. tall, latex whitish, leafy internodes 5-40 mm. long, 0.7-3.5 mm. thick, essentially glabrous or sparsely puberulent with thin yellowish hairs 0.2-0.8 mm. long, bark of the twigs usually smooth (dry); stipules 4-10 mm. long, minutely puberulent abaxially (rarely sericeous or hirsute). Leaves generally symmetrical, petioles 2-9 mm. long, 1-2.5 mm. thick, glabrous to sparsely puberulent; laminae 6-17 (28) cm. long, 2-7 (10) cm. broad, lanceolate to narrowly oblong or elliptic-oblong, abruptly and narrowly acuminate, obtuse to acute at the base, margin entire, the lamina drying stiffly chartaceous to subcoriaceous, smooth on both surfaces, essentially glabrous and the midvein prominent above, glabrous to sparsely puberulent beneath, the 8 to 18 pairs of major secondary veins prominent beneath and usually loop-connected near the margin, microscopic globose-capitate or oblongoid-capitate hairs usually present on the lower surface, clear or orange distally. Male inflorescences 1 to 4 in the axils of leaves or fallen leaves, sessile, 5-10 mm. in diameter, bracts 14 to 22 in 3 to 7 series, 1.5-4 mm. broad and acute to broadly obtuse, minutely sericeous, stamens more than 20 per inflorescence; interstaminal bracts 2-4.5 mm. long, spatulate to oblanceolate, filaments 0.3-1.5 mm. long, anthers about 2 mm. long, narrow. Female inflorescence 1 or 2 in the axils of leaves or fallen leaves, ovoid, 2-4 mm. in diameter, the 10 to 18 broad bracts in 3 to 6 series, acute to obtuse and minutely sericeous, with slender pale yellowish hairs, flower solitary; female perianth 2-2.5 mm. high, densely velutinous with ascending straight yellowish hairs about 0.5 mm. long, style 0.8-1 mm. long, stigmas 5-7 mm. long, slender. Fruit formed within the subglobose to ovoid or ellipsoid perianth, 20-23 mm. long, 17-20 mm. thick, pale yellowish sericeous to velutinous.

Rare plants of moist evergreen forest formations between 500 and 1000 m. elevation in Costa Rica (0-1800 m. elsewhere); flowering from February to May, fruiting from March to June. This species ranges from the State of Veracruz, Mexico, to central Costa Rica.

*Pseudolmedia oxyphyllaria* is recognized by the stipules encircling the stem, the medium sized leaves with entire margins, glabrous or very sparsely puberulent beneath, and the small sessile inflorescences enclosed in an involucre of thin broad sericeous bracts. This species is very similar to *Pseudolmedia spuria* with essentially glabrous fruit and less puberulent floral bracts. Fruiting collections from Costa Rica have larger, more puberulent leaves that dry much darker in color than the leaves of the male collections. It may be that the former represent a distinct entity to which the type of *Bros-*

*imum ramonense* would belong. This species is very poorly represented in collections, and decisions at this time must be considered no more than tentative.

***Pseudolmedia spuria*** (Sw.) Grisebach, Fl. Brit. W. Ind. 152. 1859. *Brosimum spurium* Swartz, Prodr. Veg. Ind. Occ. 12. 1788. Figure 16.

Trees 5-30 m. tall, sap white, leafy internodes 0.5-5 cm. long, 1.5-2.5 mm. thick, glabrous or sparsely and very minutely puberulent, usually smooth and brown; stipules 2-12 mm. long, about 1 mm. broad at the base, very slender apically, minutely puberulent along the midrib and basally (abaxially) or glabrous, dark brown. Leaves usually symmetrical, petioles 3-8 mm. long, 0.5-1.5 mm. thick, smooth, dark brown and essentially glabrous; laminae 4-14 (17) cm. long, 1.5-4.5 (6) cm. broad, narrowly elliptic to narrowly oblong or ovate-lanceolate, usually short-acuminate at the apex, acute to obtuse and usually equal at the base, margins entire, the lamina drying stiffly chartaceous, smooth and essentially glabrous on both surfaces, mid-vein prominent and the smaller veins usually slightly raised above, the 10 to 18 pairs of major secondary veins loop-connected near the margin, lower surface with very few narrow (oblongoid-capitate) microscopic hairs and the stomates usually readily apparent. Male inflorescences 1 to 4 in the axils of leaves or fallen leaves, subsessile or sessile, ovoid before anthesis, receptacle covered by an involucre of 2 to 4 series of 15 to 25 mostly ovate to lanceolate bracts, brown and minutely puberulent along the midrib, interstaminal bracts 2-4 mm. long, narrow and often broadened apically, stamens about 15 per inflorescence; filaments 0.5-1 mm. long, anthers 1.2-2 mm. long, apiculate. Female inflorescences usually 1 or 2 in the axils of leaves or fallen leaves, ovoid, 1.5-2 mm. in diameter, receptacle hidden within an involucre of 3 to 6 series of deltoid to ovate bracts 1-3 mm. broad, minutely puberulent centrally (abaxially) and brown, thin, the flower solitary; female perianth-tube 2-2.5 mm. high, minutely puberulent, style 1-1.5 mm. long, stigmas 2-6 mm. long. Fruit enclosed within the fleshy perianth-tube and drupaceous, 9-15 mm. long and 5-9 mm. thick, oblongoid to obovoid or ellipsoid, sparsely puberulent near the tip, the involucre of bracts remaining small but persisting at the base.

Apparently rare plants of the wet evergreen forest formations with a short but definite dry season between sea level and about 400 (900) m. elevation; flowering from February to June (September). The species ranges from Chiapas, Mexico, to Panama and in the Greater Antilles but has only been collected from along the Rio Grand de Tarcoles, near Capulin (*Standley 40109 & 40145*), Alajuela, and from Palmar Norte (*Allen 5961*), Puntarenas, in Costa Rica.

*Pseudolmedia spuria* is recognized by the relatively small, essentially glabrous leaves on slender branchlets with stipule encircling the stem, and the small sessile inflorescences enclosed in an involucre of thin broad bracts, the drupe-like fruit subtended by the small imbricate bracts, and lack of organized male flowers. The smaller leaves, more sparse pubescence, and lowland habitat (in

ours?) distinguish this species from the rather similar *Pseudolmedia oxyphyllaria*.

### SOROCEA St. Hilaire

REFERENCE: W. Burger, J. Lanjouw, and J. G. Wessels Boer, The genus *Sorocea*, Acta Bot. Neerl. 11:428-477. 1962.

Shrubs or trees, unisexual, without spines, sap whitish; stipules paired and lateral, caducous or rarely persistent, their scars encircling less than half the stem. Leaves simple, alternate and distichous, petioles sulcate above, venation pinnate, margins entire to sharply serrate. Inflorescences paired or solitary in the axils of present or fallen leaves, racemose or spicate (capitate in South America), with numerous suborbicular, usually peltate bracts along the rachis; flowers often lacking along one side of the rachis. Male flowers sessile or pedicellate, perianth 4-parted with equal or unequal tepals, decussate-imbricate in bud, stamens 4 and opposite the tepals, filaments straight in bud, glabrous, anthers usually dorsifixed and opening outwards (extrorse), a pistillode usually absent. Female flowers sessile or pedicellate, perianth tubular or rarely 4-parted and accrescent in fruit, irregularly or minutely 4-lobed at the apex, ovary inferior to superior by adnation of the perianth-tube, style bifid with the style branches usually short and thick. Fruit drupaceous, perianth accrescent and succulent, the stone globose or ellipsoid, lacking endosperm, the cotyledons thick, the pedicels often elongating and thickening in fruit.

A genus of about 22 species ranging from Guatemala to Paraguay, southern Brazil, and northernmost Argentina, but with centers of diversity in Costa Rica and Panama, the upper Amazon Basin, and in eastern Brazil near Rio de Janeiro. This genus is very similar to *Trophis* and *Clarisia* as regards the female flowers, but the male flowers are very different. Sterile material is also difficult to separate from *Brosimum* and other small genera of the Moraceae. The plants resemble some Euphorbiaceae and some Flacourtiaceae such as *Lozania*.

The species of *Sorocea* are quite variable and often difficult to separate from each other. There are a few collections that may be intermediate between what are here described as species. This is especially the case with collections between 300 and 1000 m. elevation, many of which are sterile. These may represent hybrids between *S. trophoides* and *S. affinis* or *S. pubivena*, or they may only be unusual individuals on the periphery of one of these populations. These same kinds of problems are found in the Amazon Basin where the greatest number of species of *Sorocea* are found.

- 1a. Plants rarely found below 800 m. elevation; male flowers with filaments 1.8-2.6 mm. long and anthers 0.7-1.1 mm. long; female flowers with an urceolate perianth-tube. . . . . *S. trophoides*.



- 1b. Plants rarely found above 500 m. elevation; filaments 1.1-2 mm. long, anthers 0.4-0.8 mm. long; female flowers with an urceolate to ovoid or globose perianth-tube ..... 2a.
- 2a. Male flowers pedicellate or rarely subsessile; fruiting pedicels 0.7-1.7 mm. thick (dry); leaves glabrous and usually entire, rarely more than 16 cm. long and 6 cm. broad ..... *S. affinis*.
- 2b. Male flowers broadly sessile on the rachis; fruiting pedicels 1.5-3 mm. thick; leaves often more than 16 cm. long and 6 cm. broad ..... 3a.
- 3a. Plants of the Caribbean slopes and lowlands; leaves usually bluntly serrate distally and usually puberulent beneath; fruit usually ellipsoid, about 8 mm. thick, and borne on an elongated rachis 4-14 cm. long. .... *S. pubivena*.
- 3b. Plants of Golfo Dulce and adjacent areas in the Pacific lowlands; leaves entire and usually glabrous; fruit globose, about 1 cm. in diameter and borne on a short (2-3 cm.) rachis ..... *S. cufodontisii*.

**Sorocea affinis** Hemsley, Biol. Centr. Amer. 3:150.1883. Figure 14.

Shrubs or trees, 3 to 15 m. tall, leafy internodes 3-25 mm. long, 0.9-2.8 mm. thick, puberulent but often becoming glabrous, lenticels often conspicuous; stipules 2-5 mm. long, narrowly cuneate, puberulent, caducous, the scars inconspicuous. Leaves in 2 ranks, petiole 3-11 mm. long, 0.6-1.8 mm. thick, sparsely puberulent and soon glabrescent; laminae 8-18 (23) cm. long, 2.5-7.2 cm. broad, narrowly elliptic to elliptic-oblong or narrowly obovate, acuminate to abruptly caudate-acuminate at the apex, acute or occasionally obtuse at the base, margin entire or occasionally bluntly serrate, the laminae drying thin chartaceous, smooth and glabrous on both surfaces, midvein slightly impressed above, the 5 to 10 pairs of major secondary veins loop-connected near the margin and forming an arcuate submarginal vein. Male inflorescences paired or solitary, racemose or occasionally spicate, peduncles 1.2-4.8 mm. long, minutely puberulent, bracts 0.6-1.9 mm. broad on stipes 0.5 mm. long, flowers numerous and distant; male flowers usually pedicellate, pedicels (0) 0.3-1.7 mm. long, perianth-parts subequal, about 2 mm. long and 1.5 mm. wide, sparsely and minutely puberulent, filaments about 1.5 mm. long, anthers 0.5-0.8 mm. long, connective forming a gland-like projection. Female inflorescences paired or solitary, racemose, 1.3-5.8 cm. long, peduncles 1.2-3.8 mm. long, minutely puberulent, bracts 0.5-1.4 mm. broad on prominent stipes, flowers 10 to many and usually distant; female flowers on pedicels 0.4-2 mm. long, perianth-tube ovoid to globose and later becoming thickened above, about 2 mm. in diameter, sparsely and very minutely (-0.05 mm.) papillate-puberulent on the basal half, ovary adnate to the perianth-tube, style-branches 0.6-1.2 mm. long and recurved. Fruit about 8 mm. in diameter, globose, becoming red, glabrous or very minutely puberulent, fruiting pedicels 2-10 mm. long and 0.7-2 mm. thick.

Plants of the lowland wet evergreen forest formations of both the Caribbean coastal plain and the Golfo Dulce region between sea level and 300 m. elevation in Costa Rica; probably flowering throughout the year but collected mostly between November and

April. The species ranges from the Caribbean coast of Guatemala to the Darien region of Panama.

*Sorocea affinis* is recognized by its generally glabrous parts, thin abruptly acuminate leaves, usually pedicellate male flowers, short female inflorescences with very minutely puberulent fruit, and lowland habitat. Very few fertile collections are known from Costa Rica (*Allen 5492 & Lent 2243*), but the species is common in Central Panama. These trees are usually found on well-drained sites.

*Sorocea cufodontisii* W. Burger, *Acta Bot. Neerl.* 11:447. 1962, as *cufodonti*. Figure 14.

Trees, leafy internodes 5-40 mm. long, about 1.5-3.5 mm. thick, glabrescent, lenticels becoming conspicuous; stipules about 5 mm. long, cuneate. Leaves in 2 ranks, petioles 9-20 mm. long, 1.4-3 mm. thick, glabrous; laminae 13-30 cm. long, 8-11 cm. broad, narrowly elliptic to narrowly obovate or elliptic-oblong, abruptly acuminate at the apex, the narrow tip 8-30 mm. long, acute to obtuse at the usually oblique base, margin entire, drying stiffly chartaceous, smooth and glabrous above, glabrous or very minutely (0.01 mm.) puberulent below, midvein slightly impressed above, the 8 to 14 pairs of major secondary veins loop-connected near the margin and forming a marginal vein in the distal half of the lamina. Male inflorescences usually paired, spicate, 2-10 cm. long, peduncles about 4 mm. long, sparsely minutely puberulent, bracts 0.9-1.5 mm. broad, flowers numerous and usually not closely crowded; male flowers sessile, 1.8-3.5 mm. wide, perianth-parts broadly oval, about 2 mm. long, obtuse at the apex, minutely puberulent, filaments 0.7-2 mm. long, anthers 0.7-1 mm. long, the connective slightly prolonged beyond the thecae, a prominent pistillode broad at the base and with a slender twisted style very rarely present in the center of the flower. Female inflorescences about 2 cm. long, female flowers about 3 mm. high on pedicels 0-1.5 mm. high, perianth-tube broadly urceolate, about 2.5 mm. in diameter. Fruit borne on a short (2 cm.) unexpanded rachis, the pedicels becoming 3-9 mm. long and 1.5-3.5 mm. thick, drupes globose or slightly ellipsoid about 1 cm. in diameter, the surface apparently glabrous with trichomes less than 0.03 mm. long.

Plants of the lowland evergreen rain (tropical wet) forests around the area of Golfo Dulce between sea level and perhaps 200 m. elevation in Costa Rica and adjacent Panama; male flowers have been collected between March and June and fruit in August. The species as presently known is endemic to the area between Palmar Sur, Costa Rica, and Progreso, Panama.

*Sorocea cufodontisii* is very closely related to *S. pubivena* but geographically isolated and poorly known. This species differs from *S. pubivena* in the entire, more glabrous leaves tapering more gradually to a usually longer acuminate tip, the less arcuate submarginal vein, the female inflorescences remaining short in fruit, and

the larger more globose fruit on short thick pedicels. The male flowers appear to be very similar to those of *S. pubivena*; the pistillode that was used to separate this species in the original description is apparently very rare. This redefinition of *S. cufodontisii* includes the following collections: *Brenes 12207*, *Burger & Stolze 5500* (♂), *Cooper & Slater 174* (♀), *Cufodontis 200* (♂) the type, *Raven 21558* (♀), and *Tonduz 6751* (♂). The tree is called *lechosa* in Panama.

*Sorocea pubivena* Hemsley, Biol. Centr. Amer. 3:150. 1883. *Trophis macrostachya* Donn.-Sm., Bot. Gaz. 40:10 1905. *Clarisia mollis* Standl., Ann. Missouri Bot. Gard. 30:85. 1943. Figure 14.

Shrubs or trees to 20 m. tall, leafy internodes 1-6 cm. long, 1.5-5 mm. thick, densely to sparsely hirtellous with hairs 0.1-0.5 mm. long, becoming glabrous, lenticels usually conspicuous; stipule 4-8 mm. long, cuneate, puberulent, caducous, scars often conspicuous. Leaves in 2 ranks, petioles 7-23 mm. long, 1.2-4.5 mm. thick, minutely puberulent in early stages; laminae 10-28 cm. long, 4.2-11 (14) cm. broad, narrowly to broadly elliptic to oblong or obovate, abruptly acuminate or caudate-acuminate at the apex, acute to obtuse at the base, margin bluntly serrate distally, the lamina drying chartaceous, smooth and glabrous above, puberulent with slender straight hairs 0.2-0.5 mm. long or glabrescent beneath, midvein slightly impressed above, the 7 to 12 pairs of major secondary veins loop-connected near the margin and forming a submarginal vein in the distal half of the lamina. Male inflorescences paired or solitary, spicate, 4-11 cm. long, peduncle 2-5.5 mm. long, densely hirtellous, bracts 0.7-1.4 mm. broad, flowers numerous but not congested, male flowers broadly sessile, 1.8-3.5 mm. broad, perianth-parts about 1.8 mm. long, obtuse at the apex, minutely puberulent, filaments 1.1-1.6 mm. long, anthers 0.6-0.8 mm. long, connective often forming a gland-like projection at the apex. Female inflorescences solitary or paired, spicate, 1.3-6.5 cm. long, elongating in fruit, peduncle 1.2-4.3 mm. long, densely hirtellous, bracts 0.7-1.5 mm. broad, flowers numerous but becoming distant in fruit; female flowers at first subsessile or on very short (0.5 mm.) pedicels, the pedicels elongating in fruit, perianth-tube about 2 mm. in diameter, ovoid or cylindrical, very minutely (0.05 mm.) papillate-puberulent, ovary partly adnate to the perianth or free, style-branches 0.6-1 mm. long. Fruit usually ellipsoid, about 8 mm. in diameter, glabrescent or very minutely puberulent, occasionally subsessile but usually borne on stout pedicels to 13 mm. long, and 3 mm. thick, the fruiting raceme becoming as much as 14 cm. long.

Plants of the very wet evergreen forest formations between sea level and 800 m. on the Caribbean side of Costa Rica; flowering throughout the year. The species is known only from Costa Rica and western Panama.

*Sorocea pubivena* is recognized by the broadly sessile male flowers, the female inflorescences elongating in fruit, and the usually puberulent leaves slightly rough to the touch beneath and often caudate-acuminate at the apex. The trees usually exude abundant sap when cut. These plants are often found near streams or on poor-

ly drained soils but not in swampy locations. Occasional specimens are encountered that can be interpreted as intermediate with the other species; see the discussion under the genus and under the very closely related *S. cufodontisii*.

***Sorocea trophoides* W. Burger, Acta Bot. Neerl. 11:450. 1962. Figure 14.**

Trees to 15 m. tall, trunk becoming 1 m. thick, leafy internodes 8-40 mm. long, 0.8-2.5 mm. thick, sparsely and very minutely (0.1 mm.) appressed puberulent in early stages but soon glabrous; stipules 3-7 mm. long, narrowly cuneate, essentially glabrous, caducous, the scars inconspicuous. Leaves in 2 ranks, petioles 5-14 (22) mm. long, about 1.4 mm. thick, laminae 7-17 (28) cm. long, 2-6 (9) cm. broad, elliptic to elliptic-oblong, long-acuminate at the apex with the acumen 1-3 (4) cm. long, acute to obtuse at the base, the margin bluntly serrate, drying chartaceous, smooth and glabrous above, glabrous or minutely puberulent beneath, the 6 to 10 pairs of major secondary veins weakly loop-connected near the margin, central secondaries arising at angles of 50-80 degrees. Male inflorescences paired or solitary, spicate, 2.5-6.5 cm. long, peduncles about 2-3 mm. long, bracts 0.7-1.8 mm. broad, flowers numerous and crowded; male flowers sessile, perianth-parts about 2 mm. long, glabrous, obtuse at the apex, filaments 1.8-2.6 mm. long, anthers 0.7-1.1 mm. long, connective forming a small projection. Female inflorescences solitary or paired, racemose, 2-4 cm. long but elongating to 10 cm. in fruit, peduncle 3-8 mm. long, puberulent, with 12 to many flowers; female flowers pedicellate, pedicels enlarging in fruit, the urceolate perianth-tube about 2 mm. in diameter, glabrous, ovary free within the tube, style-branches 0.5-1.2 mm. long. Fruit borne on pedicels 4-20 mm. long, 1-1.8 mm. thick, globose or ellipsoid, 4-8 mm. in diameter, the surface sparsely and very minutely (0.02 mm.) puberulent, becoming reddish and turning black.

Plants of wet evergreen (premontane and lower montane rain) forest formations between 750 and 2000 m. elevations on both the Caribbean and Pacific slopes in Costa Rica; flowering from May to July and collected with fruit from July to October. The species has been collected from near San Ramon (Alajuela) in the west to near San Vito (Puntarenas) near the border with Panama, but it is apparently now very rare around the Meseta Central.

*Sorocea trophoides* is recognized by the thin leaves with abruptly long-acuminate tips, short spikes of male flowers, female inflorescence with the fruit becoming raised on elongated pedicels, and the wet montane forest habitat. Specimens from lower altitudes may be difficult to distinguish from *S. affinis* or *S. pubivena* and may represent some intergradation with those species, but there is very little material presently available from these altitudes (300-800 m.).

**TROPHIS P. Browne****Nomen conservandum**

Unisexual shrubs and trees, without spines, sap whitish; stipules paired, lateral, stipule-scars encircling less than half the stem. Leaves alternate and distichous, simple, entire or serrate, pinnately veined. Inflorescences paired or solitary in the axils of leaves or of fallen leaves, racemose or spicate, with triangular or suborbicular peltate or basally attached bracts along the rachis, flowers usually lacking along one side of the inflorescence; male flowers sessile or pedicellate, perianth 4-parted or 4-lobed, valvate in bud, stamens 4 and arising at the base of the perianth parts (opposite the tepals) and incurved in bud, erect at anthesis, anthers subcentrally dorsifixed, dehiscent laterally and introrse, 2-theous; female flowers sessile or pedicellate, perianth tubular and irregularly or obscurely 4-lobed at the apex, ovary superior to inferior by adnation of the perianth-tube, style deeply bifid with the style-branches slender and minutely papillate-puberulent on the inner surface. Fruit drupaceous, the perianth-tube accrescent and succulent, stone globose.

A genus of four neotropical species with perhaps a few additional species in the western Pacific. Vegetatively these plants are very similar to several other genera of the Moraceae (*Brosimum*, *Clarisia*, *Sorocea*, etc.) as well as some Euphorbiaceae and Flacourtiaceae. The female flowers of this genus are very similar to those of *Clarisia* and *Sorocea*, but the male flowers are quite different. The recently discovered *Trophis involucrata* has very unusual female flowers, but the male flowers are very similar to those of *T. mexicana*.

- 1a. Leaves usually rough to the touch on one or both surfaces, with a short or broad acuminate apex; female flowers broadly sessile on short spikes, lacking a basal involucre of bracts; male flowers sessile; trees rarely found above 800 m. elevation. . . . . *T. racemosa*.
- 1b. Leaves smooth to the touch on both surfaces, usually with a long slender acuminate apex; male flowers sessile or pedicellate . . . . . 2a.
- 2a. Female flowers sessile and subtended by a basal involucre of bracts; inflorescences 1-4 cm. long; small treelets of the wet Caribbean forest floor 0-200 m. . . . . *T. involucrata*.
- 2b. Female flowers pedicellate; inflorescences 4-10 cm. long; trees usually found in montane forests, 600 to 1800 m. . . . . *T. mexicana*.

***Trophis involucrata* Burger, Phytologia 26:432. 1973. Figure 14.**

Small treelets 3-5 m. tall, unisexual, leafy internodes 5-35 mm. long, 0.7-1.6 mm. thick, densely puberulent on new growth with minute (0.1-0.2 mm.) stiff erect hairs; stipules paired, about 2 mm. long and 1 mm. broad at the base, minutely puberulent, occasionally persisting, scars encircling less than half the stem. Leaves usually symmetrical, often few at the ends of slender twigs, petioles 2-5 mm. long, about 1 mm. thick, minutely puberulent; laminae 6-15 cm. long, 2-6

cm. broad, broadly elliptic-oblong to slightly obovate, abruptly narrowed at the long-acuminate apex, obtuse or slightly rounded at the base, margin bluntly serrulate with 2 to 4 teeth per cm., laminae drying chartaceous, smooth and glabrous above, minutely (0.1-0.2 mm.) puberulent near the base or glabrous beneath, the midvein flat above, the 6 to 10 pairs of major secondary veins weakly loop-connected near the margin, microscopic globose-capitate hairs present on the lower surface and with clear round apically acute cells in the epidermis and epidermal cells with sinuate outlines ( $\times 100$ ). Male inflorescences usually paired at a node, 1-3 (4) cm. long, racemose, peduncle and rachis densely puberulent with minute (0.1 mm.) erect hairs, rachis with triangular bracts about 0.5 mm. long, and basally attached; male flowers borne on pedicels 1-2.3 mm. long and 0.2-0.4 mm. thick, perianth-parts about 2 mm. long, acute at the apex, sparsely and minutely puberulent, united near the base, filaments 2-3 mm. long, anthers about 1 mm. long (dry), a minute puberulent pistillode present. Female inflorescences usually paired in leaf axils but small (5-10 mm.) and branched near the base (or on short-shoots?), the rachis densely puberulent with minute (0.1 mm.) erect hairs, with spine-tipped bracts about 1.5 mm. long subtending the inflorescence-branches, the rachis and bases of the flowers with smaller triangular basally-attached bracts 0.5-1 mm. long; female flower about 3-4 mm. high, the lower half or two-thirds enclosed within an involucre of small puberulent bracts in 2 or 3 series; perianth bract-like, 4-lobed, about 1 mm. high, ovary 1.5-2 mm. high (to the stigmas or style-branches) about 1 mm. thick, minutely puberulent, stigmas about 3 mm. long, arising from the apex of the ovary. Fruit not known.

Small trees in the dark understory of the tropical wet forest formation in the Caribbean lowlands of Costa Rica; collected in flower in mid-January, 1973. The species is known only from the La Selva field station of the Organization for Tropical Studies along the Río Puerto Viejo above the confluence with the Río Sarapiquí (*Hartshorn 1091 & 1094* and *Opler 1657*).

*Trophis involucrata* is recognized by the relatively short leaves with abruptly acuminate apex and serrulate edges, small lateral stipules, short male racemes with pedicellate 4-parted flowers and stamens incurved in bud, and the very small axillary female inflorescences with few flowers subtended by an inconspicuous perianth and several series of imbricate bracts. The slender minutely puberulent stigmas arising from the apex of the narrowed ovary are also distinctive. The male flowers and inflorescences are very similar to those of *T. mexicana* and *T. chiapensis* Brandeg. The female flowers and inflorescences, however, are very different from other neotropical representatives of *Trophis*.

***Trophis mexicana*** (Liebm.) Bureau in DC., Prodr. 17:253. 1873. *Sorocea mexicana* Liebm., Danske. Vidensk. Selsk. Skrivt. ser. 5, 2:335. 1851. *Skutchia caudata* Pax & Hoffm., Journ. Wash. Acad. Sci. 27:307. 1937. Figure 14.

Shrubs or trees to 20 m. tall, leafy internodes 4-25 mm. long, 1.5-3.2 mm. thick, minutely puberulent or more often glabrous; stipules 2-3.6 mm. long, occasionally persistent, lanceolate, minutely puberulent, stipule scars very small. Leaves in 2 ranks, petioles 3-15 mm. long, 0.7-1.5 mm. thick, glabrescent; laminae 6-16 (20) cm. long, 2-6.5 cm. broad, narrowly elliptic to oblong or occasionally obovate, usually long-acuminate at the apex, acute to obtuse at the base, entire or bluntly serrulate distally, the laminae drying chartaceous and smooth on both surfaces, glabrous above and below or rarely sparsely and very minutely (0.05 mm.) puberulent beneath, midvein plane above, the 4 to 9 pairs of major secondary veins usually loop-connected and forming a submarginal vein in the distal half of the lamina, microscopic globose-capitate hairs usually absent on the lower surface but with round transparent apically acute cells in the epidermis. Male inflorescences solitary or less often paired, spicate, 4-11 cm. long, peduncle 3-12 mm. long, minutely puberulent, bracts 0.4-0.8 mm. broad, the 13 to many flowers loosely crowded, male flowers sessile or rarely subsessile, perianth-parts 1.5-2.6 mm. long, 0.5-1.3 mm. broad, acute at the apex and connate at the base, very minutely puberulent, filaments 2-3.2 mm. long, anthers 0.6-1.2 mm. long, pistillode about 0.6 mm. long. Female inflorescences solitary or occasionally paired, racemose, (2) 4-10 cm. long, peduncles (to the first flowers) 4-25 mm. long, densely puberulent, bracts 0.5-1.1 mm. broad, rarely peltate; female flowers distant, 6-22 mm. long, pedicels (0) 0.5-2.3 mm. long and often elongating in fruit, perianth-tube 1.8-5 mm. long, 1.2-2.8 mm. thick, ovoid, sparsely puberulent, ovary half-inferior, style-branches 2.8-4.5 mm. long. Fruit globose, about 5-7 mm. in diameter, sparsely puberulent to glabrescent, becoming red, fruiting pedicels 2-6 (13) mm. long, or occasionally subsessile.

Uncommon trees of the seasonally dry cloud forests on the Pacific slopes between 600 and 1800 m. elevation or occasionally found at low elevations (Golfo Dulce) or in very wet montane (premontane rain) forests (near Zarcero, Alajuela) in Costa Rica; flowering collections have been made from January to March. The species ranges from Central Mexico to within a few kilometers of the border with Panama in Costa Rica.

*Trophis mexicana* is recognized by its long spikes, sessile male flowers with stamens incurved in the bud, pedicellate female flowers with two slender style-branches, and thin leaves often long-acuminate. The species is quite common in the cloud forests of the Cordillera Central de Nicaragua and it is probably common on the Cordillera de Guanacaste and Cordillera de Tilarán in Costa Rica, but it appears to be rare in other parts of Costa Rica. This species was mistaken to be a plant of the Euphorbiaceae by Pax and Hoffmann and was described as a new genus, *Skutchia*, honoring Dr. Alexander Skutch. Female inflorescences look like those of *Alchornea costaricensis* (Euphorbiaceae).

***Trophis racemosa*** (L.) Urban, Symb. Ant. 4:195. 1905. *Bucephalon racemosum* L., Syst. Nat. ed. 10, 1289. 1759. *Trophis ramon* Schlecht. & Cham., Linnaea 6:357. 1831. *Sahagunia urophylla* Donn.-Sm., Bot. Gaz. 40:11. 1905. *Clarisia urophylla* (Donn.-Sm.) Lanj., Rec. Trav. Bot. Veerl. 33:263. 1936. Figure 14.

Shrubs or trees to 18 m. tall, trunk becoming 50 cm. thick, leafy internodes 1.5 cm. long, 2.5 mm. thick, sparsely and minutely puberulent, glabrescent, becoming lenticellate; stipules 2-4 mm. long, caducous or persisting, scars small. Leaves in 2 ranks, petioles 4-16 mm. long, 0.7-2 mm. thick, minutely (0.05-0.1 mm.) puberulent and becoming glabrous, sulcate above; laminae 5-23 cm. long, 2.4-10 cm. broad, obovate to oblong or elliptic, acuminate to subcaudate-acuminate at the apex, acute to obtuse and often slightly oblique at the base, entire or bluntly serrate distally, drying chartaceous to subcoriaceous, usually scabrous above and below, glabrous above, glabrous or very minutely (0.05 mm.) puberulent beneath, midvein plane or impressed above (dry), the 3 to 8 pairs of major secondary veins loop-connected in the distal half and a submarginal vein sometimes present, microscopic globose-capitate hairs sometimes present on the lower surface and with clear round apically acute cells in the epidermis (100 $\times$ ). Male inflorescences paired or solitary, 1.5-7.5 cm. long, peduncles 2-11 mm. long, minutely velutinous, bracts 0.5-1.1 mm. broad, with 15 to many densely crowded flowers; male flowers sessile or rarely subsessile, perianth-parts 1.6-2.2 mm. long, 1-1.5 mm. broad, free or basally connate, minutely (0.1 mm.) puberulent, filaments 2-2.6 mm. long, anthers 0.8-1.2 mm. long, pistillode 0.3-0.6 mm. long. Female inflorescences paired or solitary, 1-3 cm. long, (in ours), peduncles 2-14 mm. long, bracts 0.5-1.2 mm. broad, with 4 to 15 crowded flowers rarely more than 1 mm. distant; female flowers broadly sessile, ovoid or conic, perianth-tube 2-4.5 mm. long, 1.4-2.5 mm. in diameter, densely velutinous with hairs about 0.1 mm. long, ovary inferior or half-inferior, style-branches 2-5.5 mm. long, slender. Fruit globose or ovoid, often with a narrow collar at the apex, smooth or ridged, becoming rose-red.

Shrubs and medium-sized trees of both wet and seasonally dry evergreen and semideciduous forest formations between sea level and 1000 m. elevation on the Caribbean and, less commonly, on the Pacific watersheds in Costa Rica; apparently flowering throughout the year but with the fruit collected most often between January and June. The species, comprising three subspecies, ranges from northern Mexico through Central America and the West Indies to Venezuela and Peru.

*Trophis racemosa* is recognized by the short female inflorescences with minutely velutinous flowers and fruit, male spikes with the anthers inflexed in bud, and the leaves usually abruptly acuminate and often scabrous on both surfaces. The species is apparently less common in Costa Rica than in other parts of Central America and Panama, where it is sometimes used for animal fodder. Common names used in our area are *ramon*, *ramoon*, *ojo-*



*chillo colorado*, and *breadnut*. Our plants belong to subspecies *ramon* (Schlecht. & Cham.) W. Burger, which ranges from Mexico to Panama.

## CANNABACEAE

(Cannabinaceae)

WILLIAM BURGER

Herbs, annual or perennial from a rhizome, unisexual or rarely bisexual, stems erect or scandent, usually ridged and scabrous; stipules paired, free or united, persisting. Leaves simple or palmately compound, alternate or opposite, petiolate, lamina margin lobed or serrate (rarely entire), lower surface puberulent and punctate, upper surfaces usually with cystoliths and short scabrous hairs. Male inflorescences axillary, bracteate, erect or pendant, cymose paniculate; the male flowers pedicellate, perianth of 5 tepals, regular, soft-puberulent, stamens 5 and opposite the tepals, erect in bud, filaments short, anthers dehiscent longitudinally, a pistillode absent. Female inflorescences axillary, basically cymose but forming spikes, glandular hairs usually present, subsessile, often two and subtended or covered by a bract or bracteole, perianth united to form a tube almost completely enclosing the ovary, staminodes absent, ovary free from the perianth, 1-locular with a solitary ovule pendulous from near the apex of the locule, style short but with 2 long stigmatic branches (style-branches), the latter caducous. Fruit an achene within the persisting perianth-tube, seed with little endosperm and a curved or coiled embryo.

A family of only two genera and perhaps three or four species, two of which are of great economic importance. *Cannabis sativa* L. (in a wide sense) is the source of hemp fibers and of the narcotic extracts *marijuana* and *hashish*. The stipular bracts of the fruiting inflorescence of *Humulus lupulus* L. produce lupulin, which is used to impart flavor and aroma to beer and also aids in the fermentation of beer. Both are now widely distributed over the world, but *Humulus* originated in temperate eastern Asia and *Cannabis* probably originated near the Caspian sea in western Asia. These plants have not been reported as naturalized in Central America, but they may be expected in horticultural areas.

The following key to the genera and the previous information have been adapted from Norton G. Miller. The genera of the Cannabaceae in the southeastern United States, in the Journal of the Arnold Arboretum, vol. 51: 185-203, 1970 (q.v.). These plants have also been placed in the Moraceae family.

Plants erect herbs; leaves palmately divided into long lanceolate serrate leaflets; 2-parted hairs absent on stems and petioles; female inflorescences erect

*Cannabis.*

Plants scandent herbs; leaves simple, palmately lobed or without lobes, 2-parted hairs present on stems and petioles; female inflorescences pendant . . . *Humulus.*

## URTICACEAE

WILLIAM BURGER

REFERENCE: N.G. Miller, The Genera of the Urticaceae in the Southeastern United States, Journ. Arnold Arbor. 52:40-68. 1971.

Herbs, shrubs, or small weak-stemmed trees, bisexual or unisexual, sap usually transparent, stems usually puberulent and often provided with stinging hairs (containing irritating liquid); stipules usually present, paired and free or variously united, caducous or persisting. Leaves alternate or opposite, the leaves at the same or adjacent nodes similar in size and shape or very different (as in some spp. of *Boehmeria*), petiolate; laminae mostly ovate to lanceolate with serrate or dentate margins, venation often palmate, punctate to linear or curved cystoliths often visible on the upper and/or lower surfaces. Flowers small and unisexual (in ours), often borne in dense fascicles or clusters, or on open cymose panicles, racemes, and spikes, sessile or pedicellate; male flowers greenish or whitish, the perianth-parts (tepals) in a single whorl of 3, 4, or 5, equal and valvate in bud, free or united, often with appendages, stamens as many as the perianth-parts and opposite them, filaments thin and inflexed in bud, anthers 2-theous, dehiscing laterally, a pistillode often present; female flowers usually very small, perianth 3- or 4-parted or united to form a tube or the perianth absent (as in *Phenax*), staminodia rarely present, pistil 1, ovary superior with a single locule and single basal ovule (but see the species of uncertain position included here), stigma long and linear or short-sessile, minutely glandular-puberulent or penicellate. Fruit a hard achene, usually flattened laterally and lenticular, ovoid to ellipsoid, usually enclosed in the persisting dry or succulent perianth parts or bracts.

A very natural family closely related to the Ulmaceae, Moraceae, and Cannabaceae, together forming the order Urticales. Like other members of the order, this family has only a single perianth-whorl with the stamens opposite the perianth-parts and a unilocular pistil with solitary ovule. The family is further characterized by the herbaceous or woody but weak-stemmed habit, the unisexual flowers, pistils with solitary stigma, and the usually serrate leaves with cystoliths. Many species are found along stream and brook edges and in protected wet sites. The palmately veined serrate leaves often resemble those of the Malvales, but the Urticaceae lack stellate hairs and the flowers are very different.

An unusual species that appears to be related to *Boehmeria* and having opposite leaves is placed at the end of the family without

generic designation because of its unique female flowers. These pistillate flowers have 2- or 3-locular ovaries, a condition otherwise unknown in the family. However, the female flowers are very few in the lower leaf-axils and the difficulty of finding stages in anthesis suggests that the flowers may be abnormal in their development.

*Gyrotaenia microcarpa* (Wedd.) Fawcett & Rendle has been collected once in the Changuinola Valley, Bocas del Toro, Panama (Dunlap 174). This record is probably of an isolated introduced plant, as this species is endemic to Jamaica and the genus is endemic to the West Indies. They are unisexual trees or shrubs with serrate pinnately veined alternate leaves, small spicate or paniculate inflorescences with sessile flowers, the female flowers with 2-lobed perianth and capitate stigma, and the male perianth 4-lobed.

Two genera with discontinuous distributions are found in Central America and in northern South America but have not been collected from Costa Rica or Panama. These are *Hemistylis*, shrubs and small trees, and *Rousselia*, puberulent herbs; both have alternate entire leaves and female flowers subtended by conspicuous greenish bracts. *Discocnide* is an endemic genus ranging from Mexico to Nicaragua that resembles *Urera* but has thin disc-like achenes with a hyaline pericarp.

Species of *Boehmeria* and *Phenax* with densely crowded flowers may be difficult to separate on the basis of the female flowers possessing or lacking a perianth-tube. The simplest way to determine this difference is by gently crushing an inflorescence between the fingers and allowing the parts to fall on a flat surface. If small naked pistils are found, the perianth-tube is probably lacking (*Phenax*). The perianth-tube of *Boehmeria* is quite strong and will not separate from the pistil unless considerable pressure is applied.

- 1a. Leaves opposite or whorled, two or more at each node (the leaves occasionally very unequal in size and apparently alternate) . . . . . 2a.
- 1b. Leaves alternate, always solitary at a node, never with even a very small sessile stipule-like opposing leaf . . . . . 5a.
- 2a. Plants with stinging hairs . . . . . *Urtea*.
- 2b. Plants without stinging hairs; leaves often unequal . . . . . 3a.
- 3a. Female perianth parts separate, not enclosing the fruit; stigma tufted, short; herbs or subshrubs . . . . . *Pilea*.
- 3b. Female perianth tubular and tightly enclosing the fruit; mostly small shrubs . . . . . 4a.

- 4a. Stigma filiform, easily seen, female flowers several to numerous, usually in sessile clusters at leafless nodes or on a branched inflorescence; ovary with a single locule . . . . . *Boehmeria*.
- 4b. Stigmas short, inconspicuous, female flowers very few among male flowers at lower leafy nodes; ovary with 2 or 3 locules, fruit often 3-angled. Species of uncertain position, placed at the end of the family.
- 5a. Some stinging hairs usually present, thin, translucent, straight and narrow, 0.5-3 mm. long; inflorescence complex and branched . . . . . 6a.
- 5b. Stinging hairs absent . . . . . 7a.
- 6a. Shrubs or trees, perennial, usually unisexual; stigma terminal and erect  
*Urera*.
- 6b. Herbs or subshrubs with succulent stems, annuals, usually bisexual; stigma becoming curved or subterminal. . . . . *Laportea*.
- 7a. Female flower and fruit borne within a persisting perianth tube, this tightly enclosing the fruit and open only at the apex (often difficult to see), perianth tube thin and dry in fruit (never fleshy), stigma or style linear-filiform  
8a.
- 7b. Female flower and fruit not enclosed by a tubular perianth; the perianth parts sometimes fleshy and accrescent in *Urera* . . . . . 9a.
- 8a. Female perianth tube without definite longitudinal ribs or prominent veins, surface of the achene dull, stigma persisting; leaves always dentate or serrate . . . . . *Boehmeria*.
- 8b. Female perianth tube with definite longitudinal ribs, surface of the achene lustrous, stigma deciduous; leaves usually entire . . . . . *Pouzolzia*.
- 9a. Flowers in small axillary glomerules or fasciculate; herbs or shrubs . . . . . 10a.
- 9b. Flowers on open paniculate or spicate inflorescences; stigma short penicellate; shrubs or trees. . . . . 11a.
- 10a. Shrubby plants; leaves crenate to serrate; stigma filiform; female perianth absent, many brownish, acute bracts subtending the flowers. . . . . *Phenax*.
- 10b. Herbs or small subshrubs; leaves entire (in ours); stigma short penicellate; female perianth present but difficult to see; bracts present, few, greenish, and exceeding the flowers in length. . . . . *Parietaria*.
- 11a. Female flowers without perianth but subtended by bractlets and the pistil with a puberulent surface; flowers on panicles with long pendulous spicate branches (in ours) . . . . . *Myriocarpa*.
- 11b. Female flowers with perianth segments often becoming fleshy orange and enclosing the fruit; flowers on short-branched panicles . . . . . *Urera*.

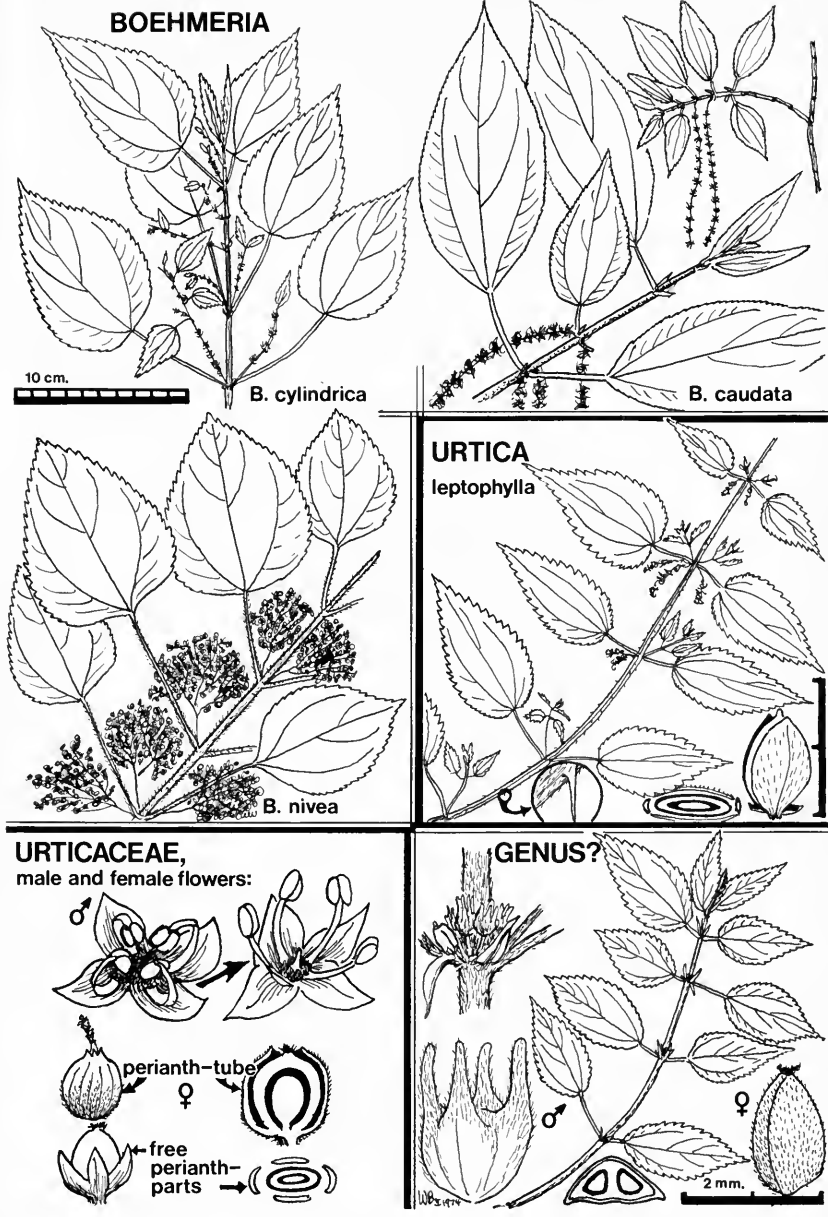


FIG. 24. Urticaceae with opposite leaves: species of *Boehmeria*, *Urtica*, and a species of uncertain position.

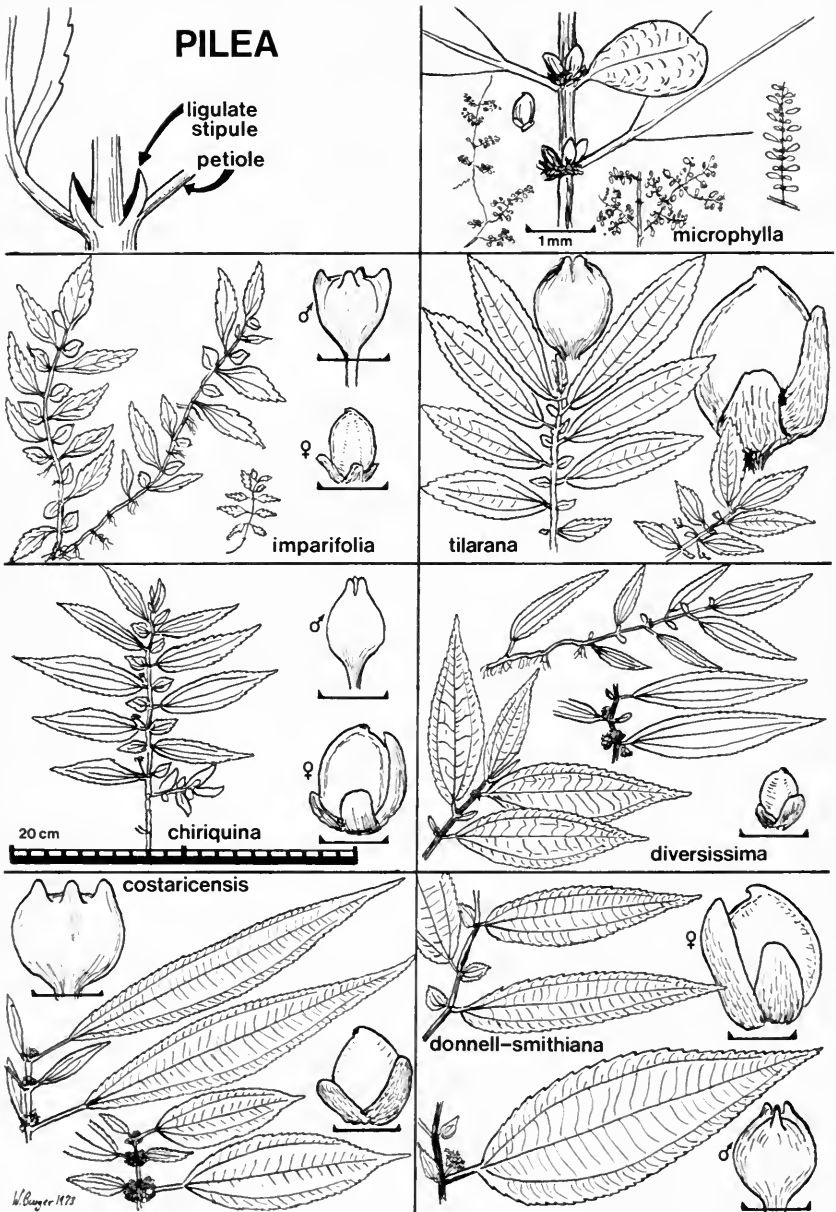


FIG. 25. Urticaceae with opposite leaves: species of *Pilea* with very unequal leaves at each node.



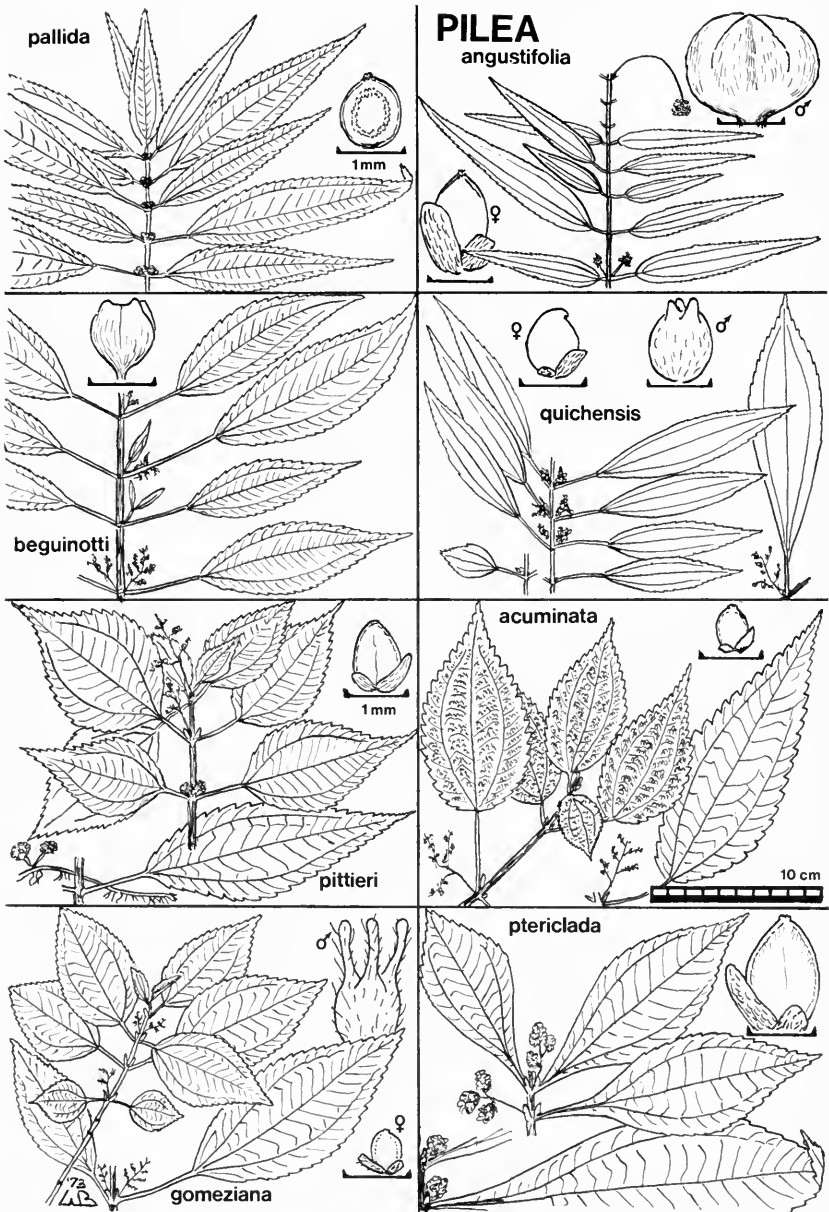


FIG. 26. Urticaceae with opposite leaves: species of *Pilea* with equal or subequal larger leaves at each node.

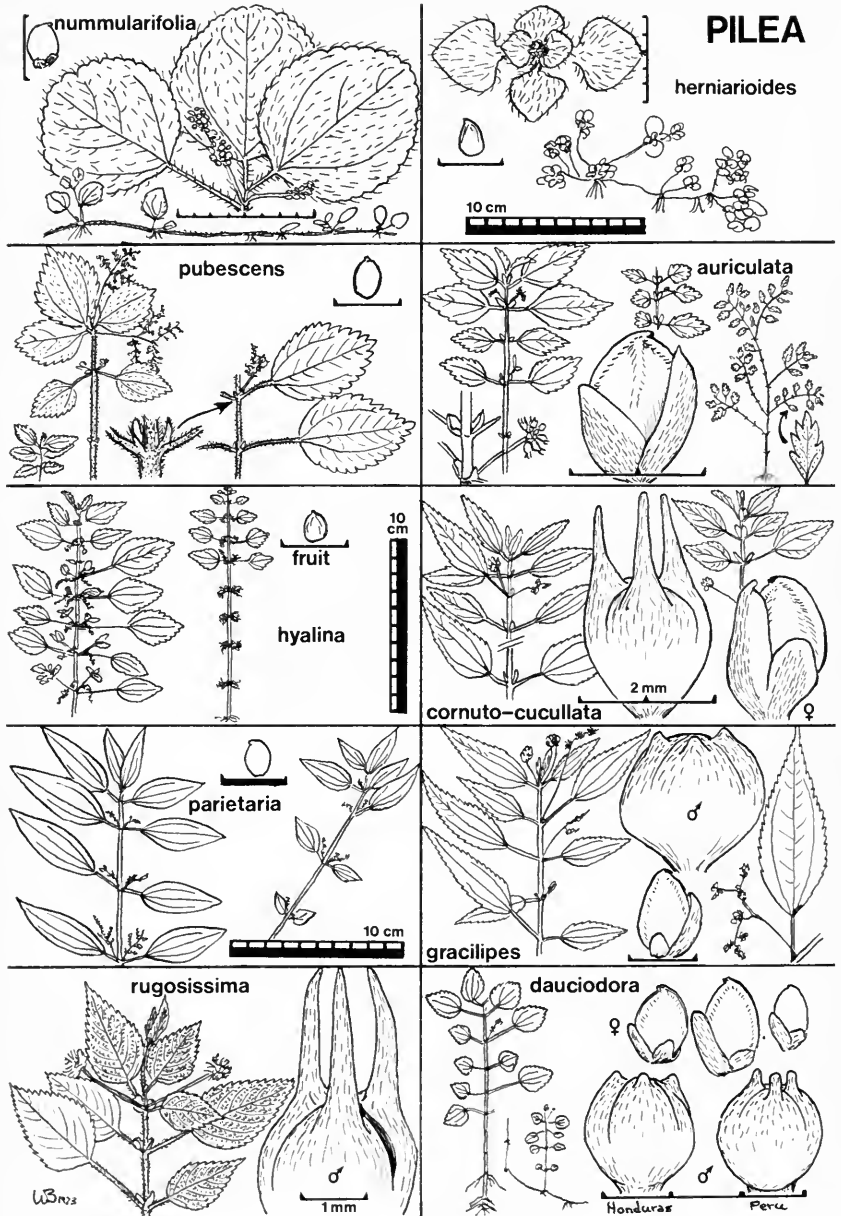


FIG. 27. Urticaceae with opposite leaves: species of *Pilea* with equal or subequal smaller leaves at each node.

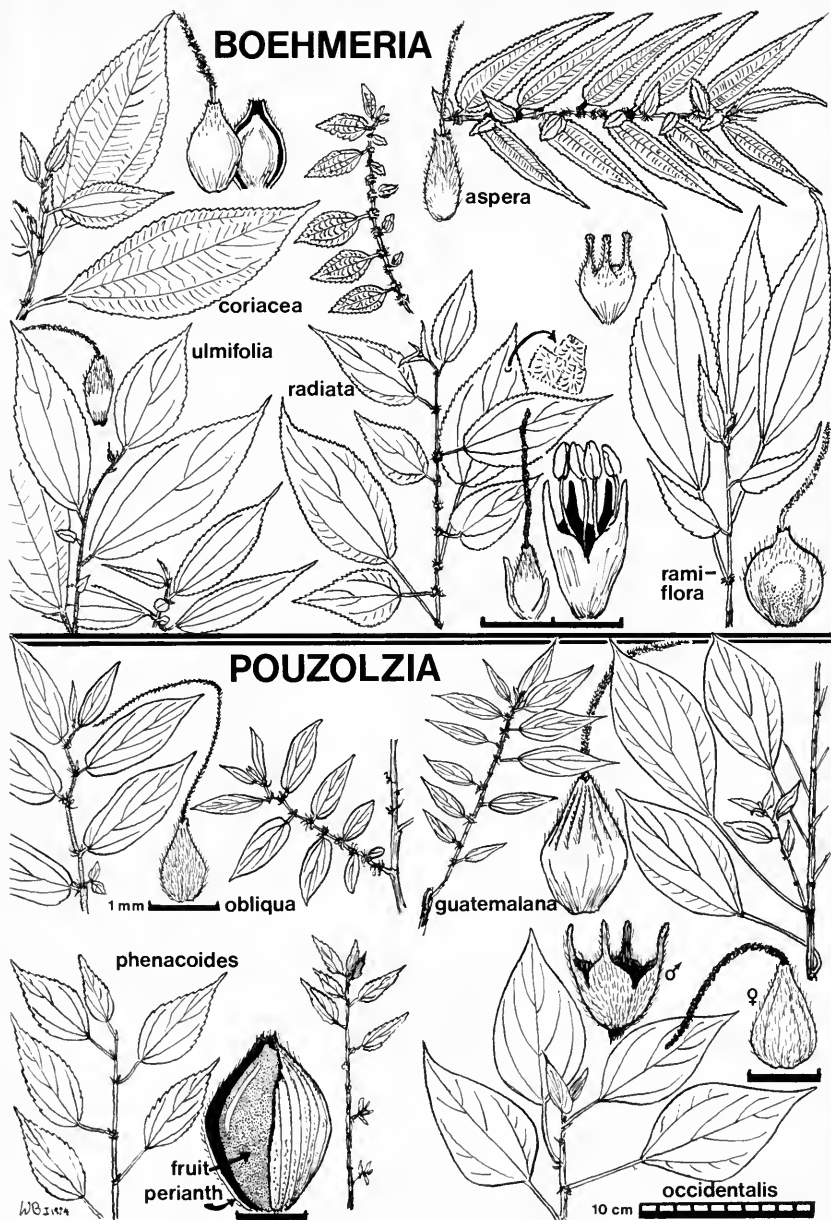


FIG. 28. Urticaceae with alternate leaves and the pistil and fruit enclosed in a perianth-tube: species of *Boehmeria* and *Pouzolzia*.

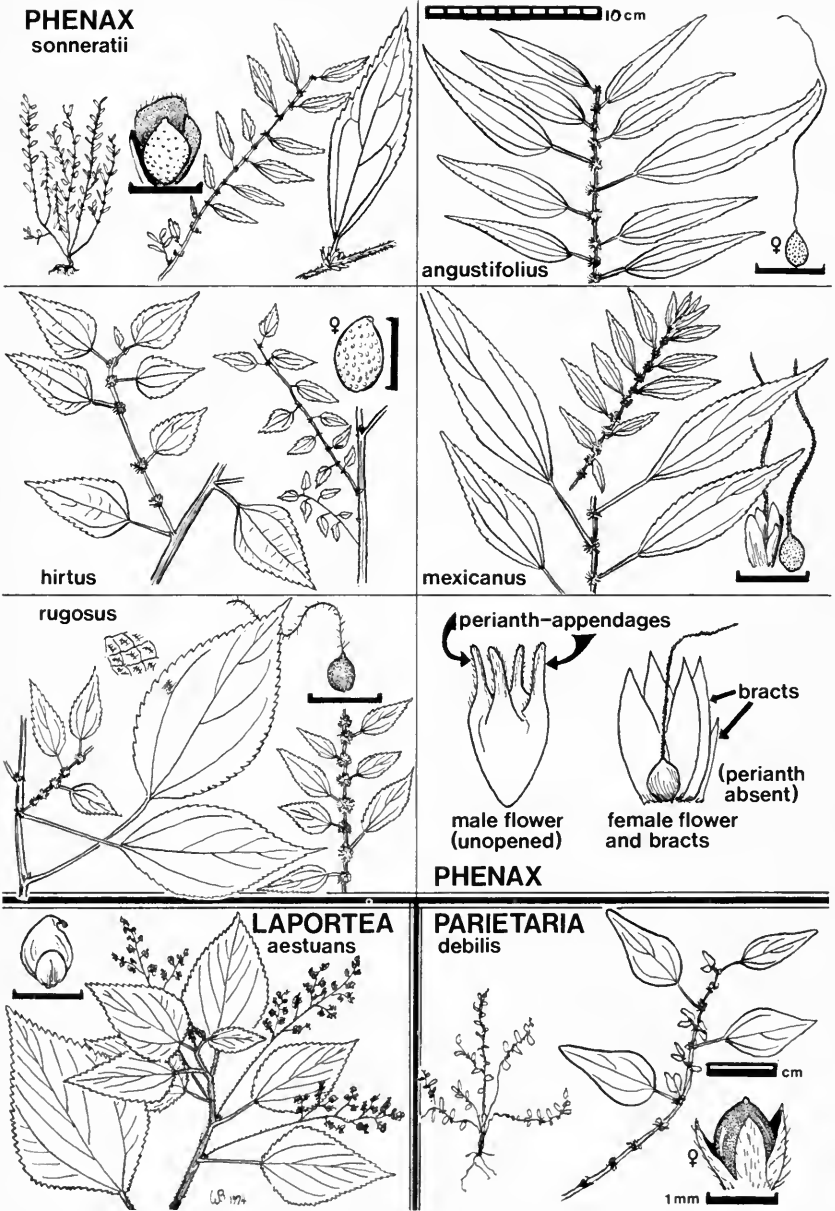


FIG. 29. Urticaceae with alternate leaves and the perianth-parts free or absent: *Laportea*, *Parietaria*, and *Phenax*.

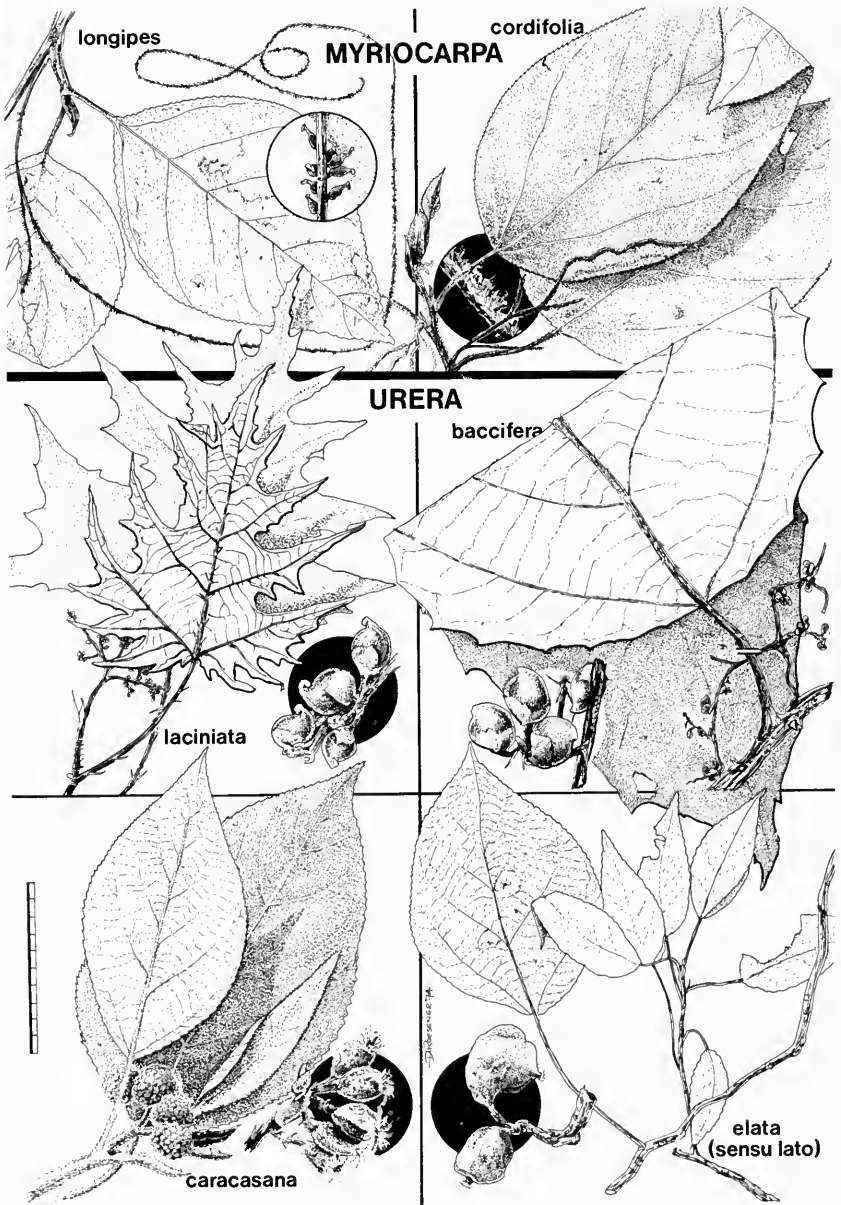


FIG. 30. Urticaceae with alternate leaves and long or much-branched inflorescences: species of *Myriocarpa* and *Ureia*.

## BOEHMERIA Jacquin

Shrubs, small trees, or perennial herbs, unisexual or bisexual, lacking stinging hairs; stipules paired and lanceolate (in ours), puberulent along the midrib abaxially and drying brown. Leaves alternate or opposite, those of adjacent nodes often very unequal in size in alternate-leaved species, petiolate; laminae usually palmately 3-veined, margins serrate to dentate, minutely punctate cystoliths usually present on the upper epidermis. Inflorescences cymose-paniculate, racemose, or fasciculate glomerules, solitary and axillary or in the axils of undeveloped leaves, bisexual or unisexual, the flowers in fasciculate globose clusters (glomerules) separate or congested on the inflorescence-rachis; male flowers sessile or short-pedicellate, perianth-parts 4 or rarely 3, valvate in bud, stamens 4 (3), a pistillode usually present; female flowers sessile, perianth united to form a tube completely enclosing the ovary and minutely toothed at the apex, minute straight and uncinata (hooked) hairs usually present on the perianth-tube, style and stigma linear. Fruit enclosed within the strongly persistent perianth-tube, the perianth-tube becoming inflated in a few species, the fruit a hard-walled achene, often slightly compressed laterally.

A genus of about 80 species best represented in the American and Asian tropics, but extending into the temperate zone in eastern Asia and eastern North America. Our species fall into two groups; those with opposite leaves and complex inflorescences and those with alternate leaves and sessile flower-clusters on leafy stems. The latter plants are very easy to confuse with species of *Phenax* and *Pouzolzia*. Some of these *Boehmeria* species are easy to recognize, however, because leaves at adjacent nodes differ so greatly in size. Those with isomorphic leaves must be carefully examined to distinguish them from *Phenax* and *Pouzolzia*.

- 1a. Leaves all or mostly opposite along the main stems; inflorescences complex or of sessile clusters along a leafless rachis; plants rarely found above 1200 m. 2a.
- 1b. Leaves alternate; flowers in small sessile globose clusters, usually in the axils of leaves or fallen leaves . . . . . 4a.
  - 2a. Leaves whitish beneath and with long petioles, plants cultivated for fiber, forage, or ornament; inflorescence complex and much branched. . . . *B. nivea*.
  - 2b. Leaves not whitish beneath; plants not cultivated; inflorescences usually spicate and unbranched. . . . . 3a.
  - 3a. Stipules 2-6 mm. long; inflorescences erect and often terminated by small leaves; margins of the fruiting perianth-tube slightly inflated. . *B. cylindrica*.
  - 3b. Stipules 8-18 mm. long; inflorescences long-pendulous and not terminating with small leaves, often densely flowered; margins of the fruiting perianth-tube thin and wing-like . . . . . *B. caudata*.
- 4a. Leaves becoming deeply rugose in age with major veins deeply impressed above and glabrous or very sparsely puberulent above; male flowers 4-parted, perianth-tube not becoming conspicuously flattened in fruit . . . . . 5a.

- 4b. Leaves rarely becoming deeply rugose, only the major veins becoming impressed above, puberulent above ..... 6a.
- 5a. Shrubs or small trees, leaves of adjacent nodes differing greatly in size and shape, the larger leaves lanceolate; perianth-tube pubescent near the apex; wet evergreen areas 0-1500 m. .... *B. aspera*.
- 5b. Herbs or subshrubs, leaves of adjacent nodes differing only slightly in size, larger leaves ovate to narrowly elliptic-ovate; perianth tube with very few hairs; very wet forests, 1400-1900 m. .... *B. coriacea*.
- 6a. Leaves differing greatly in size and shape at adjacent nodes but occasionally with the alternate leaf undeveloped and the leaves then apparently isomorphic (leafless nodes can be identified by the presence of flower clusters), petioles usually less than 10 mm. long, thin hairs or thicker strongly appressed hairs (resembling cystoliths) on the upper lamina-surface; male flowers 4-parted; fruiting perianth-tube slender ellipsoid and minutely puberulent; very wet evergreen formations 1000-2000 (2800) m. .... *B. ulmifolia*.
- 6b. Leaves differing by about 50 per cent or less in size at adjacent nodes and usually similar in shape, petioles thin, 3-90 mm. long; seasonally dry evergreen formations on the Pacific watershed (in Costa Rica) ..... 7a.
- 7a. Male flowers 4-parted; fruiting perianth-tube narrowly ellipsoid and densely brownish hirsutulous; hairs of the upper leaf-surface thick appressed and often radiating from the centers of areoles (resembling cystoliths) .....  
*B. radiata*.
- 7b. Male flowers 3-parted; fruiting perianth-tube strongly flattened with thin wing-like margins; hairs on the upper leaf-surface thin and not strongly appressed. .... *B. ramiflora*.

***Boehmeria aspera* Weddell, Arch. Mus. Paris 9:349. 1856. Figure 28.**

Shrubs or rarely small trees to 6 m. tall, leafy internodes 3-20 (40) mm. long, 0.8-4 mm. thick, densely sericeous with appressed ascending whitish hairs 0.2-0.2-0.7 mm. long; stipules 4-10 mm. long, 1-2 mm. broad at the base, sparsely puberulent, often persisting at the base of the inflorescences. Leaves alternate and usually very different in size and shape at adjacent nodes, petioles 1-23 mm. long, 0.5-1.5 mm. thick, minutely (0.1-0.5 mm.) hirsutulous; laminae usually of 2 different sizes at adjacent nodes, the smaller 1-3 cm. long and ovate in outline, the larger 4-18 cm. long, 1-3.5 cm. broad, lanceolate to very narrowly elliptic in form, tapering gradually to a long-acuminate apex, obtuse to rounded at the slightly unequal base, margin coarsely dentate-serrate with 4 to 7 teeth per cm., lamina drying stiffly chartaceous, slightly scabrous and strongly rugose with the veins deeply impressed above, lower surface densely puberulent with stiff slender whitish hairs 0.2-0.8 mm. long, venation palmate with 3 primary veins, midvein with many small secondaries or with 1 or 2 pairs of more prominent secondary veins in the distal half. Inflorescences usually unisexual, the flowers numerous and clustered in dense glomerules 4-10 mm. in diameter in the axils of leaves or at leafless nodes; male flowers more than 20 per glomerule and densely crowded, sessile or pedicellate, perianth 4-parted, stamens 4, anthers about 0.5 mm. long (dry); female flowers densely crowded and more than 20 per in-

florescence, bracts not usually visible between the flowers, pistil about 2 mm. long, style often with a slender glabrous portion below the long puberulent stigmatic part. Fruit enclosed within the persisting perianth-tube, perianth-tube about 1 mm. long and with erect hairs distally.

Plants of wet evergreen forest formations and locally common in open secondary vegetation between sea level and 1500 m. elevation on the Caribbean slopes and the moister sites above 500 m. on the Pacific slope in Costa Rica; flowering throughout the year. The species ranges from Costa Rica to Peru.

*Boehmeria aspera* is a very distinctive species with the leaves usually of very different size at adjacent nodes, the larger leaves usually lanceolate, and all the laminae becoming deeply rugose. The flowers are found in small clusters on the leaf-bearing stems. Our specimens give the impression of being dioecious; all the material of each collection is of the same sex.

***Boehmeria caudata* Swartz, Nov. Gen. & Sp. Pl. 34. 1788. *B. flagelliformis* Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:310. 1851. Figure 24.**

Unisexual shrubs or small trees (1) 2-6 (9) m. tall, leafy internodes 3-50 mm. long, 1.5-5 mm. thick, densely strigulose with ascending or appressed hairs 0.2-1 mm. long; stipules 8-18 mm. long, 1.5 mm. broad at the base, puberulent along the midrib, stipule scars almost united to form interpetiolar lines. Leaves opposite and usually similar in size and shape at adjacent nodes, petioles (3) 15-30 mm. long, 0.7-1.5 mm. thick, puberulent; laminae 4-22 cm. long, 2-11 cm. broad, ovate to elliptic in outline, acuminate at the apex, obtuse to rounded at the equal or subequal base, margin serrulate with 3 to 6 teeth per cm. laminae drying thin- to stiffly-chartaceous and often dark above, slightly scabrous with short (0.5 mm.) stiff hairs above and usually becoming rugose with both major and minor veins impressed, sparsely to densely puberulent beneath with slender hairs 0.1-0.5 mm. long, venation palmate or subpalmate with 3 primary veins, the midvein with 1 to 3 pairs of major secondary veins arising from the distal half, the minutely punctate cystoliths often obscure above. Inflorescences spicate and axillary (rarely branched near the base), the spikes pendulous and 5-25 (40) cm. long, flowers closely crowded in globose glomerules and these separate or adjacent on the slender (0.3-0.8 mm.) rachis; male flowers in small (4-8 mm.) glomerules, with about 10 to 20 flowers, buds 1-1.5 mm. in diameter, perianth-parts and stamens 4; female flowers in glomerules 4-10 mm. in diameter, with usually 10 to 20 flowers, female flowers 2-3 mm. long, sessile and congested at the base, style usually glabrous beneath the puberulent stigmatic tip. Fruit enclosed within the persisting perianth-tube, perianth-tube 1.5-2 mm. long, narrowed at the base and abruptly narrowed below the style, strongly flattened and with thin wing-like margins, sparsely puberulent.

Plants of stream sides and moist ravines from (0) 500 to 1500 m. altitude in areas of evergreen and partly deciduous formations on



both the Caribbean and Pacific slopes in Costa Rica; probably flowering throughout the year. The species ranges from Mexico to Argentina and the West Indies.

*Boehmeria caudata* is recognized by its opposite leaves, long pendulous spikes with flowers borne along the rachis in round clusters, unusual fruit, and stipule-scars often forming interpetiolar lines. The species is called *rabo de gato* in Honduras.

***Boehmeria coriacea* Killip, Journ. Wash. Acad. Sci. 13:359. 1923. Figure 28.**

Herbs or subshrubs to 1 m. tall, leafy internodes 2-38 mm. long, 1-2.3 mm. thick, strigulose with whitish ascending hairs 0.2-0.8 mm. long, becoming glabrate; stipules about 4 mm. long, 1 mm. broad at the base, glabrous except along the midrib. Leaves alternate and usually differing in size at adjacent nodes, very variable in size on the same plant or on different plants, often very different in size at adjacent nodes, petioles 2-40 mm. long, 0.8-1.3 mm. thick, ascending strigulose, laminae 1.2-12 cm. long, 0.8-4 cm. broad, ovate to elliptic-ovate, acute to acuminate at the apex, obtuse or slightly rounded at the base, margin coarsely serrate with 4 to 6 teeth per cm., drying stiffly chartaceous, smooth to the touch above with the veins usually becoming deeply impressed and the surface rugose-bullate, glabrous or very sparsely puberulent above, with stiff appressed hairs 0.2-0.4 mm. long, on the veins beneath, venation palmate with 3 primary veins, the midvein with numerous minor secondary veins, the secondary and tertiary veins often prominent beneath. Flowers in dense sessile glomerules in the axils of leaves or fallen leaves, unisexual or occasionally bisexual, the plants probably unisexual or bisexual; male flowers with usually 4 perianth-parts with whitish hairs distally and with a small projection just below the apex, stamens 4, anthers about 0.6 mm. long; female flowers numerous and densely crowded with small bracts between the flowers, perianth-tube smooth and glabrous or sparsely puberulent, style about 1.5 mm. long, and minutely puberulent. Fruit enclosed within the persistent perianth-tube, perianth-tube 1-1.4 mm. long and to 1 mm. broad, only slightly flattened, ovoid, glabrescent.

Plants of the very wet (premontane rain) forest formations of the Caribbean slopes between 1400 and 1900 m. elevation and usually found growing along or above shaded brooks and streams in Costa Rica; probably flowering throughout the year. The species is only known from Costa Rica and Colombia.

*Boehmeria coriaceae* is recognized by the herbaceous habit, restricted habitat, laminae that tend to become deeply bullate and are often glabrous above, and female perianth-tube with inconspicuous hairs. The leaves vary greatly in different plants; some have the largest leaves only 3 or 4 cm. long while others have laminae to 12 cm. Texture varies greatly also, occasionally on the same plant. The leaves possess translucent dots. Collections placed here are:

*Burger et al.* 5718, 6824, 6861, *Lent* 2251 (all of these are from the Río Grande de Orosi above Tapanti), and *Standley & Torres* 47721 (Viento Fresco, Alajuela). There is some question whether these collections should be placed in Killip's poorly known Colombian species, but I am sure that the two are very closely related if not, in fact, conspecific. It is not unusual for Costa Rican plants to be found at lower elevations than plants of the same species in Colombia. This is probably a result of the cooler maritime climate in Costa Rica.

***Boehmeria cylindrica* (L.) Swartz, Nov. Gen. & Sp. Pl. 34. 1788.**  
*Urtica cylindrica* L., Sp. Pl. 984. 1753. Figure 24.

Herbs or woody stemmed subshrubs 0.5-1 m. tall, leafy internodes 1-5 (9) cm. long, 1.2-6 mm. thick, puberulent with slender hairs 0.1-0.5 mm. long but becoming glabrescent; stipules 2-6 mm. long, about 1 mm. broad at the base, deciduous. Leaves opposite or subopposite, very variable in form on different plants but similar at adjacent nodes, petioles 2-70 mm. long, 0.7-1.5 mm. thick, appressed puberulent; laminae 4-18 cm. long, 2.5-8 cm. broad, lanceolate to broadly ovate, acuminate at the apex, obtuse to truncate at the base, margin coarsely dentate with 1 to 4 teeth per cm., laminae drying membranaceous to thin-chartaceous, smooth or slightly scabrous above with scattered short (0.2-0.5 mm.) hairs, very sparsely to moderately puberulent beneath, venation palmate or subpalmate with 3 primary veins, the midvein with 2 to 4 pairs of major secondary veins, minutely punctate cystoliths usually visible above. Inflorescences axillary, solitary and 3-7 (14) cm. long, spicate with the flowers in separate globose glomerules along the length of the unbranched rachis, the rachis often terminated by small leaves, the flower clusters or glomerules 2-6 mm. in diameter; male flowers in groups of 5 to 10, perianth-parts 4; female flowers about 1 mm. long in early stages, styles about 0.5 mm. long and puberulent at the apex. Fruit enclosed within the persisting perianth-tube, perianth-tube becoming about 1.5 mm. long and equally broad, somewhat flattened longitudinally, central area around the seed delineated by a groove from the peripheral and slightly inflated margins, puberulent apically.

Plants of alluvial sandy or gravelly soils in wet evergreen formations and growing along water courses and in wet situations in seasonally dry areas between sea level and 500 m. on both the Caribbean and Pacific slopes in Central America; probably flowering throughout the year in wet regions. A species of very wide range, from eastern Canada and the eastern and southern United States through Central America and the West Indies to southeastern Brazil.

*Boehmeria cylindrica* is distinguished by its opposite or subopposite leaves, small stipules, unusual spicate inflorescences often terminated by small leaves, small flowers, and unusual fruit. This species is apparently quite rare in Costa Rica and represented in

herbaria by a single collection from Zent, Limon (*United Fruit Co. 391*).

***Boehmeria nivea* (L.) Gaud.** in Freyc., *Voy. Bot.* 499. 1826. *Urtica nivea* L., *Sp. Pl.* 985. 1753. Figure 24.

Herbs or subshrubs 0.5-2 m. tall, leafy internodes 5-50 mm. long, 2-5 mm. thick, with stiff whitish hairs 0.5-1.5 mm. long; stipules 5-15 mm. long. Leaves alternate and usually of similar size at adjacent nodes, petioles 3-14 cm. long, hirsute; laminae 7-20 cm. long, 5-16 cm. broad, broadly ovate to elliptic-ovate, abruptly narrowed at the acuminate apex, obtuse to subcordate at the base, margin coarsely serrate with 1 to 3 teeth per cm., lamina drying thin chartaceous and usually very dark above, scabrous above, pale grayish-white beneath with a dense arachnoid tomentum between the veins, venation pinnate or subpalmate with the basal secondaries very prominent, the midvein with 2 or 3 pairs of major secondary veins above the basal pair, minutely punctate cystoliths usually visible above. Inflorescence axillary, complex in structure with small glomerules of flowers borne on a branched or unbranched rachis; male flowers usually 5 to 10 per glomerule, perianth-parts 4; female flowers in glomerules about 5 mm. in diameter, bracts inconspicuous, perianth-tube about 1 mm. long, puberulent, style and stigma about 1 mm. long and puberulent throughout.

A cultivated species planted from sea level to 1500 m. elevation in both the wet and seasonally dry areas of Central America. This species probably originated in China but is now widely planted.

*Boehmeria nivea* is recognized by its long petiolate opposite leaves whitish beneath and its complex unisexual inflorescences. The plants are occasionally grown for ornament as well as fiber and forage. They are the source of ramie fiber and are called *ramio* and *ramié* in Central America.

***Boehmeria radiata* W.** *Burger, Phytologia* 31: 267. 1975. Figure 28.

Shrubs 1-3 m. tall, bisexual or unisexual, leafy internodes 3-50 mm. long, 1-4.5 mm. thick, with appressed or curved thin whitish hairs 0.2-1 mm. long; stipules 3-5 mm. long, deciduous. Leaves differing in size at adjacent nodes but similar in shape, petioles 3-60 (90) mm. long, 0.3-1.8 mm. thick, puberulent with thin whitish hairs; laminae 2-13 (18) cm. long, 1-7 (10) cm. broad, ovate to elliptic-ovate, acute to acuminate at the apex, obtuse to abruptly rounded at the somewhat unequal base, margin crenate-serrate with 2 to 5 teeth per cm., laminae drying thin- to stiff-chartaceous, slightly rough to the touch above with whitish strongly appressed hairs 0.2-0.8 (1) mm. long, the lower surface with thin whitish hairs along the veins, venation palmate or subpalmate with 3 primary veins, midvein with 1 to 3 pairs of major secondary veins or often with the major secondaries on only one side or not readily distinguished from the smaller secondaries, minutely punctate cystoliths visible on the upper surface. Inflorescences small (4-10 mm.) globose sessile clusters in the axils of leaves or at leafless nodes, sometimes with 2 to 6 glomerules in a row at leafless

nodes 3-10 mm. distant along the stem; male flowers about 1.5 mm. broad, usually sessile, perianth-parts 4, apex of the perianth with a slender projection abaxially; female flowers very numerous and closely congested, styles and stigmas about 3 mm. long, minutely puberulent. Fruit small and enclosed within the persisting slender perianth-tube 1-1.5 mm. long, narrowly ellipsoid (narrowed at both base and apex), densely hirsutulous with minute brownish hairs.

Plants of the seasonally dry evergreen forest formations of the Pacific slope and Meseta Central between 500 and 1200 m. elevation in Costa Rica; collected with flower and fruit from October to March. The species ranges from Guatemala to Central Costa Rica.

*Boehmeria radiata* possesses unusual appressed hairs on the upper leaf-surfaces resembling linear cystoliths, and these are often arranged in circular patterns within the aereoles demarked by larger tertiary veins. The seasonally dry habitat, shrubby habit, long and thin petioles, male perianth-parts with unusual apices, and very small fruit within a slender brown-hirsutulous perianth-tube further distinguish this species. Despite these features *Boehmeria radiata* is often difficult to separate from *B. ulmifolia*, with its shorter petioles, wetter habitat, and adjacent leaves differing more in shape, or from *B. ramiflora*, with the male flowers 3-parted, fruit inflated and winged, and upper leaf-surfaces without cystolith-like appressed hairs. This species has often been mistaken for *Phenax mexicanus*.

***Boehmeria ramiflora*** Jacq., Enum. Syst. Pl. Carib. 31. 1760. *B. cuspidata* Weddell, Arch. Mus. Paris 9:345. 1856. *B. ramiflora* var. *cuspidata* Wedd. in DC., Prodr. 16, pt. 1:197. 1869. Figure 28.

Shrubs 1-3 (4) m. tall, bisexual or unisexual, leafy internodes 5-45 mm. long, 1-4 mm. thick, puberulent with usually thin appressed whitish hairs 0.1-0.4 mm. long; stipules 5-15 mm. long, puberulent along the midrib, deciduous, and not commonly subtending the flower clusters. Leaves of adjacent nodes usually differing in size but usually similar in shape, alternate, petiole 4-70 mm. long, about 1 mm. thick, appressed puberulent (in ours), laminae (2) 4-17 cm. long, 1-7 cm. broad, elliptic to elliptic-ovate or rhomboid-ovate, tapering gradually in larger leaves to the usually long-acuminate apex, narrowed or rounded on one side at the oblique base, coarsely serrate with 3 or 4 teeth per cm., lamina drying membranaceous to thin chartaceous and dark above, slightly rough to the touch with thin whitish appressed hairs about 0.5 mm. long above, more densely puberulent beneath, venation palmate with 3 primary veins, the midvein with 2 or 3 major secondary veins on only one side and the lamina asymmetric in area, minute punctate cystoliths present above. Inflorescences of small (4-8 mm.) glomerules of congested sessile or subsessile flowers in the axils of leaves or fallen leaves, flower clusters unisexual or bisexual; male flowers with 3-parted perianth, puberulent distally with some minute uncinata hairs, stamens 3; female flowers tightly clustered and narrowed at the base, laterally flattened, perianth tube puberulent, about 1.5 mm. long. Fruit borne within the persisting perianth-tube, the perianth-tube becoming 2 mm. long and 1 mm. broad,

very much flattened beyond the seed to produce wing-like margins, abruptly narrowed at the apex.

Apparently rare plants of the seasonally dry evergreen forest formations of the Pacific slope between 800 and 1300 m. elevation in Costa Rica; flowering from November to February. The species ranges from Veracruz, Mexico to Colombia, Venezuela and the West Indies.

*Boehmeria ramiflora* is distinguished by its 3-parted male flowers, fruit borne within a persisting perianth-tube with thin wing-like margins, and long petiolate asymmetric laminae with secondary veins often on only one side of the midvein. Superficially these plants look very much like *Boehmeria radiata* and *Phenax mexicanus*, and resemblance to these common plants may explain why this species is so rarely collected. Our Costa Rican collections come from San Pedro de Poás and San Miguel de San Ramon in Alajuela (*Brenes 17358* and *20299*) and above San Isidro del General in San José province (*Skutch 2562*).

***Boehmeria ulmifolia*** Weddell, Ann. Sci. Nat. ser. 4, 1:202. 1854, (sensu Killip in Ann. Missouri Bot. Gard. 47:188. 1960). Figure 28.

Shrubs or small trees 1-3 (5) m. tall, bisexual or unisexual, stems often brittle, leafy internodes 3-50 mm. long, 0.3-4 mm. thick, strigulose with stiff appressed hairs 0.2-0.7 mm. long; stipules (3) 4-7 mm. long, 1-1.5 mm. broad at the base, deciduous. Leaves alternate and usually very different in size at adjacent nodes or the alternate leaf failing to develop and adjacent leaves apparently of similar size, petioles 2-8 (16) mm. long, 0.8-1.4 mm. thick, puberulent; smaller laminae often reniform or orbicular and 2-5 mm. long, larger laminae 4-17 (22) cm. long, 1.5-7 cm. broad, elliptic to narrowly ovate or lanceolate and often asymmetric or curved, short- to long-acuminate at the apex, obtuse or slightly rounded at the asymmetric base, crenate-serrate with 1 to 6 teeth per cm., lamina drying membranaceous to thin-chartaceous and usually dark above with the veins often becoming impressed, slightly scabrous above with thin or stiff appressed hairs about 0.5-1 mm. long, sparsely to densely puberulent above, venation palmate with 3 major primary veins, the midvein with 2 to 4 major secondary veins often on only one side, punctate cystoliths usually visible above. Inflorescences usually unisexual, small (3-8 mm.) globose clusters in the axils of leaves or at leafless nodes, often 2 inflorescences close together with 1 in the axil of a leaf and the other in the axil of a minute or undeveloped leaf, persisting on leafless stems; male flowers with perianth about 1 mm. long, obtuse at the apex, anthers about 0.5 mm. long; female flowers about 2 mm. long, sessile, style and stigma puberulent. Fruit enclosed within a perianth-tube about 1.5 mm. long and 0.5 mm. thick, narrowed at both apex and base, very minutely puberulent, a few of the hairs uncinata, ellipsoid, and not noticeably flattened or winged.

Plants of very wet montane (premontane and lower montane rain) forest formations mostly along or near the Caribbean slope between

1000 and 2000 (2800) m. elevation in Costa Rica; flowering throughout the year but collected primarily between November and April. The species ranges from Guatemala to Western Panama.

*Boehmeria ulmifolia* is recognized by alternating leaves being very small or undeveloped (as evidenced by an inflorescence lacking the subtending leaf), asymmetric laminae, small sessile inflorescences, small slender fruit, and very wet montane habitat. Plants with unusual strongly appressed hairs (resembling linear cystoliths) are placed here with plants having much thinner hairs on the upper lamina-surface. There are other kinds of variation among the plants placed under this name but these do not seem to be correlated with characters of flower or fruit. The species is very difficult to distinguish from *B. radiata* or *B. ramiflora* in the absence of flowers or fruit.

## LAPORTEA Gaudichaud

### Nomen conservandum

REFERENCE: W.-L. Chew, A Monograph of *Laportea*. Gard. Bull. Singapore 25: 111-177. 1969.

Bisexual or rarely unisexual herbs or shrubs with stinging or irritating hairs; stipules paired, partly connate across the petiole and usually deeply bifid at the apex. Leaves alternate and simple, petiolate, drying thin, usually with a toothed margin. Inflorescences axillary, pedunculate and generally paniculate with the unisexual flowers in loose glomerules; male flowers with 4 or 5 perianth parts and the same number of stamens, a small pistillode present; female flowers with 4 very unequal perianth-parts, staminodes absent, pistil ovoid. Fruit a small achene, ovoid to semi-circular and usually compressed laterally, sessile or stipitate, usually becoming reflexed on winged pedicels.

A genus of 22 species best represented in Africa and Madagascar but with several very widely distributed species and ranging into the north temperate zone. Our species was formerly placed in the genus *Fleurya*, which has been changed to the status of a subgenus within *Laportea*.

***Laportea aestuans* (L.) Chew, Gard. Bull. Singapore 21:200. 1965.**  
*Urtica aestuans* L., Sp. Pl. ed. 2, 1397. 1763. *Fleurya aestuans* (L.) Miq. in Martius, Fl. Braz. 4, pt. 1:196. 1853. Figure 29.

Bisexual annual herbs, 0.3-1.5 (2) m. tall, slightly woody at the base, leafy internodes 5-60 mm. long, 0.6-5 mm. thick (dry), glabrescent to densely covered with slender gland-tipped hairs 0.3-3 mm. long, and simple sharp irritating hairs; stipules 4-10 mm. long, united in the lower half with linear-lanceolate apices. Leaves alternate in a spiral, petioles (1) 2-12 (20) cm. long, 0.3-1 mm. thick (dry), usually

glandular puberulent; laminae (2) 3-15 (30) cm. long, (1) 2-10 (22) cm. broad, ovate to very broadly ovate or triangular, acute to short-acuminate at the apex, obtuse or slightly rounded and truncate to subcordate at the base, margin coarsely serrate-dentate with about 2 to 5 teeth per cm. and 2-4 mm. high, the lamina drying membranaceous to very thin-chartaceous, upper surface with slender sharp hairs 0.3-1.5 mm. long, lower surface with somewhat shorter hairs and cystoliths occasionally visible ( $\times 10$ ), the 3 to 6 pairs of major secondary veins arising at angles of 20-60 degrees, the basal pair of secondaries prominent and the venation often subpalmate. Inflorescences bisexual or unisexual, 3-20 cm. long, usually solitary at a node, the lower often entirely male, paniculate with the flowers in distal clusters, the male flowers often distal within a cluster of male and female flowers; male flowers sessile or short pedicellate, about 1-1.5 mm. broad before anthesis, perianth-parts 4 or 5, puberulent only near the apex, 0.7-1.5 mm. long, anthers with very thin whitish walls; female flowers sessile or becoming pedicellate, perianth parts free and of 2 lateral tepals about 0.5 mm. long, a dorsal tepal about 0.3 mm. long with 3 to 5 glandular hairs, and a very minute ventral tepal, pistil about 0.5 mm. long. Fruit 1-2 mm. long, becoming reflexed on the pedicel, asymmetrically ovoid and glabrous, narrowed at the base, the edges somewhat ribbed and forming an enclosed warty area on the flattened sides of the achene, pedicel and perianth usually persisting and falling away together with the fruit.

Herbaceous weeds of semi-shaded areas in wet evergreen formations on both the Caribbean and Pacific slopes of Costa Rica between sea level and 700 (1200) m. elevation in Costa Rica; flowering throughout the year but collected most often between October and March. This species occurs on Cocos and the Galapagos Islands and ranges from Mexico and the West Indies to Peru and Brazil in this hemisphere, across tropical Africa, Arabia, Madagascar, and India to Java and the lesser Sunda Islands.

*Laportea aestuans* is recognized by the presence (usually) of stinging hairs and glandular hairs, the conspicuously toothed alternate leaves, long erect inflorescences with many clusters of flowers on racemose branches and the preference for lowland habitats.

### MYRIOCARPA Bentham

Shrubs or small to medium-size trees, unisexual or rarely bisexual, lacking stinging hairs; stipules apparently solitary, completely united across the base of the petiole and ligulate, usually enclosing the shoot-apex. Leaves alternate and simple, laminae and petioles very variable in size, margins serrate, dentate, or entire, pinnately or subpalmately veined, cystoliths usually visible on the upper leaf-surface ( $\times 10$ ). Inflorescences paniculate or of very long spikes from a branched base (in ours); male flowers clustered or separate, usually sessile, perianth 4-parted, stamens 4, pistillode usually absent; female flowers sessile, subsessile, or pedicellate, lacking a perianth but subtended by 2 small bracteoles, style and stigma 1 or the stigma rarely 2-lobed. Fruit flattened, the bracteoles and style usually persisting, dry and indehiscent (an achene).

A genus of five to ten species ranging from northern Mexico to Brazil and Bolivia. Several other species are known from Central America and Mexico. One of these differs from ours in the paniculate female inflorescences and in smaller entire leaves with relatively few secondary veins (*M. obovata* Donn.-Smith).

Pistil and fruit glabrous to puberulent but lacking definite cilia along the edges, bracteoles usually appressed to the base of the pistil or fruit; plants rarely found above 1100 m. altitude . . . . . *M. longipes*.

Pistil and fruit puberulent with definite small cilia along the edges, bracteoles usually divergent; plants rarely found below 1100 m. elevation (in Costa Rica) . . . . .  
*M. cordifolia*.

**Myriocarpa cordifolia** Liebmann, Danske Vidensk. Selsk. Skrirt. ser 5, 2:306. 1851. *M. longipes* sensu auctores non Liebmann. Figure 30.

Shrubs or small trees 2.5-8 m. tall, leafy internodes 1-5 cm. long, 4-10 mm. thick, sparsely to densely grayish hirsutulous with slender ascending or retrorse hairs 0.3-1 mm. long; stipules united and ligulate, 10-26 mm. long, densely sericeous. Leaves alternate in a spiral, petioles 1.4-18 cm. long, 1.5-3.5 mm. thick, usually densely puberulent with soft grayish hairs about 0.5 mm. long; laminae 8-22 (30) cm. long, 4-8 (15) cm. broad, ovate to broadly elliptic-ovate or elliptic, acute or short-acuminate at the apex, obtuse to rounded and subtruncate or subcordate at the base, margin with 4 to 7 teeth per cm., lamina drying thin-chartaceous, upper surface slightly scabrous and sparsely puberulent with slender hairs about 1 mm. long borne on raised areas from which small (0.3 mm.) narrow cystoliths radiate (but these not always visible), lower surfaces usually grayish puberulent with soft hairs 0.3-1 mm. long, the 4 to 7 pairs of major secondary veins arising at angles of 30-45 degrees, the basal pair of secondary veins often very prominent and the venation subpalmate. Male inflorescences 10-22 cm. long with 2 or 3 branches near (1-3 cm.) the base, rachis 0.3-0.7 mm. thick (dry) with slender whitish hairs 0.2-0.5 mm. long; male flowers sessile, 1.2-1.8 mm. broad, perianth-parts about 1 mm. long, minutely puberulent, filaments 0.2 mm. thick, anthers about 0.9 mm. long. Female inflorescences 20-40 cm. long, with several branches arising 1-3 cm. from the base, rachis about 0.7 mm. thick with whitish hairs 0.3-0.7 mm. long, pistil about 1 mm. long, subsessile or pedicellate, subtended by 2 minute (0.5 mm.) bracteoles. Fruit minute achenes about 2 mm. long with persisting divergent bracteoles and style, minutely puberulent and with the 2 edges distinctly ciliolate, flattened laterally and narrowed at the base.

Plants of the wet and very wet evergreen forest formations between 1100 and 1800 m. elevation on the Caribbean slopes and the adjacent areas of the Central Highlands in Costa Rica; flowering and fruiting collections have been made between November and May. The species, as presently understood, ranges from Central Costa Rica (near San Ramon, Alajuela, to near Capellades, Cartago) northward to Veracruz, Mexico.



*Myriocarpa cordifolia* is recognized by the long pendulous inflorescences with minute unisexual flowers, laminae somewhat bullate above with the cystoliths usually apparent ( $\times 10$ ), and the pistil and fruit with ciliolate edges. Material of this species has been referred to as *M. longipes*, but a close examination of Oersted material from Aguacate shows that this name is properly applied to the more common species of *Myriocarpa* in Costa Rica, which usually grows at lower elevations. Costa Rican material of *M. cordifolia* differs from Mexican collections in the narrower rarely cordate leaves and the restricted highland habitat.

***Myriocarpa longipes*** Liebmann, Danske Vidensk. Selsk. Skrivt. ser. 5, 2:306. 1851. *M. inaequilateris* Liebm., loc. cit. 307. *M. longipes* var. *yzabalensis* Donn.-Sm., Bot. Gaz. 16:13. 1891. *M. yzabalensis* (Donn.-Sm.) Killip, Proc. Biol. Soc. Wash. 40:29. 1927. Figure 30.

Unisexual or bisexual shrubs or small trees with slender trunks 2-6 (10) m. tall, leafy internodes 1-8 cm. long, 3-10 mm. thick, sparsely to densely puberulent with slender straight or crooked grayish hairs 0.5-1.5 mm. long, the longer hairs often reflexed; stipules connate and ligulate, (10) 15-25 mm. long, densely sericeous. Leaves variable in size and petiole-length, petioles 2-18 (35) cm. long, 2-4 mm. thick (dry), puberulent, ridged on drying; laminae 12-30 (46) cm. long, 8-14 (26) cm. broad, ovate to broadly elliptic or rarely narrowly elliptic, obtuse to acute or short-acuminate at the apex, obtuse to truncate or rounded at the base, margin serrate with about 3 teeth per cm., lamina drying chartaceous, upper surface smooth or slightly scabrous, usually glabrous with the linear or slightly arcuate cystoliths visible and radiating from central areoles above, cystoliths 0.2-0.5 mm. long, lower surface glabrescent or with slender grayish hairs, the (5) 6 to 11 pairs of major secondary veins arising at angles of 30-50 degrees. Male inflorescences whitish, pendant, to about 12 cm. long, branched in the basal fourth, the rachis 0.2-0.5 mm. thick and minutely puberulent, anthers about 0.7 mm. long (dry). Female inflorescence branched only near the base with long (20-60 cm.) pendulous spikes, bracts lanceolate, 1-4 mm. long near the base of the spikes, rachis 0.2-0.5 mm. thick and very sparsely puberulent; female flowers crowded or distant, short-pedicellate or subsessile, about 1.5 mm. long, bractlets subtending the flowers about 0.5 mm. long and appressed, pistil glabrous or very sparsely puberulent. Fruit with the basal bracteoles and style persisting, about 1.5 mm. long and 1 mm. broad, flattened, glabrous or sparsely puberulent but without definite cilia along the edge.

Plants of evergreen forest formations on both the Caribbean and Pacific slopes in Costa Rica between sea level and 1100 (1500) m. elevation; flowering and fruiting collections have been made from December to March. The species ranges from Veracruz, Mexico, southward to Central Panama.

*Myriocarpa longipes* is recognized by the long pendulous spikes of unisexual flowers, minute fruit lacking ciliolate edges, leaves with serrate-crenate edges, obvious cystoliths, and variable size and petiole-length, and usual lowland habitat. Members of this species may be difficult to separate from *M. cordifolia* (*M. longipes* of previous authors, not of Liebmann) in the absence of female flowers or fruit though the two appear to be ecologically isolated in Costa Rica. Our material of *M. cordifolia* is more often bullate and more densely puberulent than our material of *M. longipes*. Oersted collections that appear to be isotypes of *M. longipes* are conspecific with collections placed under the name *M. yzabalensis* by Killip. The plants are commonly called *ortiga* but they do not sting.

The name *Myriocarpa longipes* has been misapplied for some time; it is not the taxon of higher altitudes (in Costa Rica), which, I believe, is conspecific with *M. cordifolia*.

## PARIETARIA Linnaeus

Annual or perennial herbs, bisexual, usually much branched, puberulent and often with minutely hooked (uncinate) hairs; stipules not developed. Leaves alternate and simple, petiolate, the laminae entire, usually small and palmately 3-veined. Inflorescences usually bisexual, of sessile or subsessile flowers axillary in small dense cymes or fascicles (glomerules or clusters), subtended by bracts connate near the base or free; bisexual flowers and male flowers with 4-parted perianth and 4 stamens; female flowers free with the perianth equally 4-parted and persisting in fruit, pistil with a linear stigma or with a narrow style below the stigma, ovary sessile or short-stipitate. Fruit an achene, usually ovoid and laterally compressed to become somewhat lenticular, stigma terminal, pericarp smooth, perianth loosely enclosing the maturing fruit.

A genus of about eight species in the temperate and tropical regions of both hemispheres. Only one species is occasionally found in our area, though it is quite common in parts of Guatemala.

*Parietaria debilis* Forst., Fl. Ins. Austr. Prodr. 73. 1786. Figure 29.

Herbs, erect stems 10-60 cm. tall, older stems occasionally becoming woody, bisexual, leafy internodes 2-20 (30) mm. long, 0.5-1.5 mm. thick, sparsely to densely puberulent with very small (0.2 mm.) thin hairs; stipules absent but with stipule-like bracts subtending the inflorescences. Leaves alternate, petioles 3-35 mm. long, 0.2-0.5 mm. thick (dry), puberulent; laminae 3-45 mm. long, 3-20 mm. broad, ovate to ovate-lanceolate, tapering to the acuminate apex, abruptly obtuse to rounded at the base, margin entire, laminae drying membranaceous, sparsely puberulent on

both surfaces with thin whitish hairs about 0.5 mm. long, venation subpalmate but obscure, punctate cystoliths visible above. Inflorescences axillary, the flowers in short subsessile clusters with interspersed green linear bracts about 3 mm. long, flowers usually fewer than 8 and the inflorescence less than 5 mm. long. Fruit about 1 mm. long, ovoid and slightly flattened, the surface smooth and very lustrous.

Weedy plants introduced in Costa Rica and occasionally in cultivated land above 1000 m. elevation. The paucity of herbarium material may indicate that populations do not persist. This species is widely distributed in the tropics and temperate zones of both hemispheres.

### PHENAX Weddell

Shrubs, herbs, or occasionally small trees, bisexual or unisexual, lacking stinging hairs; stipules paired and free, lanceolate. Leaves alternate, petiolate, the lamina crenate or serrate (in ours), venation usually palmate, the cystoliths usually minutely punctate in the upper epidermis. Inflorescences of dense fasciculate clusters (glomerules) of sessile or short-pedicellate flowers in the axils of leaves or fallen leaves, bisexual or unisexual, floral bracts thin and brownish, often broad and perianth-like; male flowers with 4-lobed perianth united below the middle, the lobes valvate or subimbricate in bud and rounded or acuminate at the apex of the bud, stamens usually 4; female flowers without perianth, enclosed within thin bracts, ovary sessile or short-stipitate, laterally compressed; style and stigma linear and persistent. Fruit protected within the perianth-like bracts, a minute achene with glabrous surface, surface smooth to pusticulate.

A genus of about 12 species of tropical America with some having become naturalized in the Asian tropics (see discussion under *P. sonneratii*). Members of this genus are often confused with species of *Boehmeria* and *Pouzolzia* but differ in lacking a perianth-tube enclosing the pistil and fruit. The male flowers of *Phenax* are often narrowed to a minutely lobed apex or have projections on the back of the perianth-lobes that make these unopened or partly opened flowers resemble the female flowers of *Boehmeria* and *Pouzolzia*. The flower-clusters must be dissected to separate the floral bracts and expose the naked female flower to distinguish *Phenax* with certainty. Additionally, *Phenax* has usually many floral bracts and flowers in each inflorescence, and the leaves are never conspicuously alternating in size at adjacent nodes.

- 1a. Laminae very narrowly elliptic to lanceolate. . . . . 2a.  
 1b. Laminae narrowly to broadly ovate; plants usually bisexual . . . . . 4a.  
 2a. Plants unisexual; laminae usually narrowly lanceolate, inconspicuously serrulate (sub-entire), stipules 4-9 mm. long; fruit about 0.5 mm. long; uncommon shrubs, 0-1000 m. . . . . *P. angustifolius*.

- 2b. Plants usually bisexual; laminae narrowly elliptic to lanceolate, obviously serrulate. . . . . 3a.
- 3a. Shrubs or small trees, stipules becoming 4-7 mm. long; fruit about 0.7 mm. long; common, 1000-2500 m. . . . . *P. mexicanus*.
- 3b. Herbs or subshrubs to 1 m. tall, stipules 1-3 mm. long; fruit about 1 mm. long; weeds of very wet evergreen lowlands . . . . . *P. sonneratii*.
- 4a. Fruit about 0.6 mm. long; laminae often becoming rugose with both major and minor veins deeply impressed above, stipules about 4 mm. long; common shrubs, 500-2500 m. . . . . *P. rugosus*.
- 4b. Fruit about 1 mm. long; laminae drying thin chartaceous, only the larger veins becoming impressed . . . . . 5a.
- 5a. Herbs or subshrubs with spreading branches to 2 m. tall, laminae abruptly narrowed at the base, stipules usually 3-8 mm. long; 1200-2000 m. elevation  
*P. hirtus*.
- 5b. Herbs or subshrubs to 1 m. tall, laminae usually gradually narrowed to the base, stipules 1-3 mm. long; 0-300 (800) m. in areas of high rainfall. . . . .  
*P. sonneratii*.

**Phenax angustifolius** (H.B.K.) Weddell, Ann. Sci. Nat. ser. 4, pt. 1:193. 1854. *Boehmeria angustifolia* H.B.K. Nov. Gen. & Sp. 2:34. 1817. Figure 29.

Shrubs 1-2 (3) m. tall, unisexual, leafy internodes 1.5-15 (30) mm. long, 0.7-3 mm. thick, sparsely to densely puberulent with minute (0.1-0.4 mm.) ascending whitish hairs; stipules 4-9 mm. long, about 1 mm. broad at the base, persisting as long as the leaves. Leaves clustered at the ends of branches and resembling *Salix*, petioles 3-20 mm. long, 0.3-0.8 mm. thick, appressed puberulent; laminae 4-14 cm. long, 1-3 cm. broad, lanceolate, gradually tapering to an acute or acuminate apex, obtuse to slightly rounded at the base, margin minutely serrulate with 3 to 5 teeth per cm., laminae drying membranaceous to thin-chartaceous, and dark above, smooth and often glabrous above with the primary veins impressed above, appressed puberulent with thin whitish hairs about 0.3 mm. long on the veins beneath, venation palmate with 3 primary veins, midvein with many small secondary veins, minutely punctate cystoliths visible above. Inflorescences and the plants unisexual, globose glomerules in the axils of leaves and persisting on leafless nodes; male flowers not seen; female flowers usually more than 20 per inflorescence and the inflorescence about 1 cm. in diameter, bracts 1-1.5 mm. long, styles glabrous or very minutely puberulent, 3-5 mm. long. Fruit 0.4-0.6 mm. long, about 0.3 mm. broad, only slightly flattened laterally, ellipsoid, very minutely pusticulate.

A poorly known species of wet evergreen formations or in wet sites in seasonally dry evergreen formations between sea level and 1000 m. elevation in Costa Rica; collected with flowers or fruit from December to February. The species ranges from Costa Rica to Peru and Bolivia.

*Phenax angustifolius* is characterized by the lanceolate leaves

often at the ends of long slender branchlets, sessile unisexual inflorescences, and very small fruit.

**Phenax hirtus** (Sw.) Weddell in DC., Prodr. 16, pt. 1:235(38). 1869. *Urtica hirta* Swartz, Fl. Ind. Occ. 1:285. 1797. Figure 29.

Herbs woody at the base or small shrubs to 1.5 m. tall, but often with creeping or clambering lateral stems to 2 m. long, bisexual, leafy internodes 6-50 mm. long, 0.7-4 mm. thick, densely to sparsely puberulent with minute (0.3 mm.) curved yellowish hairs, the older stems glabrescent, brown or reddish-brown; stipules (1) 3-8 mm. long, 2 mm. broad at the base, persisting and often subtending the inflorescences. Leaves generally uniform in size and shape on a plant, petioles (4) 8-25 (50) mm. long, 0.3-0.7 mm. thick, minutely puberulent; laminae (2) 3-7 (12) cm. long, 1.5-4 (6) cm. broad, ovate, acuminate at the apex, rounded and truncate to subcordate at the base, margin coarsely crenate to serrate with 3 to 5 teeth per cm., laminae drying thin chartaceous and dark above, smooth above with few scattered hairs about 0.7 mm. long and the major veins occasionally becoming deeply impressed, minutely (0.1-0.5 mm.) puberulent on the veins beneath, venation palmate with 3 primary veins, the midvein with weak secondaries arising throughout the length of the blade, minutely black-punctate cystoliths usually visible above. Inflorescences bisexual, usually only in the axils of new and persisting leaves, each flower cluster with many thin brownish bracts; male flowers with an abruptly narrowed apex in bud, perianth-parts with an acuminate and thickened apex, anthers about 1 mm. long; female flowers enclosed in numerous thin bracts, style and stigma 3-5 mm. long. Fruit loosely enclosed in the broad bracts, about 1 mm. long and 0.7 mm. broad, slightly flattened laterally, drying dark, the surface minutely pustulate.

Plants of the very wet montane (premontane and lower montane rain) forest formations on the Caribbean slopes between 1200 and 2000 m. elevation in Costa Rica; probably flowering throughout the year but collected primarily from January through March. The species ranges from Mexico to Bolivia and to Jamaica and Hispaniola in the West Indies.

*Phenax hirtus* is recognized by the short or sprawling habit, isomorphic coarsely dentate leaves thin in texture and abruptly narrowed at the base, male perianth-parts with unusual apices, and relatively large fruit. This species resembles *Pouzolzia phenacoides* and species of *Boehmeria*.

**Phenax mexicanus** Weddell, Ann. Sci. Nat. ser. 4, pt. 1:193. 1854. Figure 29.

Shrubs or small trees 2-6 (10) m. tall, bisexual, leafy internodes 3-25 mm. long, 0.8-3.5 mm. thick, sparsely to densely puberulent with slender hairs 0.1-0.5 mm. long, drying reddish-brown and longitudinally ridged; stipules 4-7 mm. long, 1 mm. broad at the base, lanceolate, deciduous or persistent. Leaves quite variable in size and petiole-length on the same or different plants, petioles 3-18 (50) mm. long, 0.3-0.8

(1.1) mm. thick, minutely appressed puberulent; laminae 1.5-13 (19) cm. long, 0.6-3 (4) cm. broad, very narrowly elliptic to lanceolate, broadest at or below the middle, tapering gradually to the short- or long-acuminate apex, acute to obtuse at the equal or subequal base, margin crenate to serrate with 3 to 6 teeth per cm., lamina drying thin- to stiff-chartaceous, smooth above and glabrous or with minute (0.2 mm.) scattered hairs, very rarely rugose in age, sparsely puberulent on the veins beneath, venation palmate or subpalmate with 3 primary veins, the outer primary veins united above the petiole to the midvein and occasionally forming small pockets, midvein usually with 2 pairs of secondary veins in the distal half, minutely punctate cystoliths usually visible above. Inflorescence small (4-10 mm.) globose axillary clusters or glomerules often persisting at leafless nodes; male flowers 2 mm. broad before anthesis, perianth parts acute or obtuse at the apex, anther about 1 mm. long; female flowers enclosed in perianth-like bracts 2 mm. long, ovary about 0.5 mm. long, style 3-4 mm. long, minutely puberulent. Fruit about 0.7 mm. long and 0.6 mm. broad, slightly flattened, ovoid, smooth.

Plants of very wet montane (premontane and lower montane rain) forest formations between (800) 1000 and 2500 m. elevation primarily on the Caribbean slope in Costa Rica; collected with flowers and fruit throughout the year excepting October and November. The species ranges from southern Mexico to western Panama.

*Phenax mexicanus* is recognized by its globose bisexual inflorescences, small smooth-surfaced fruit, closely spaced narrow leaves with very variable petioles, and restricted montane habitat.

**Phenax rugosus** (Poir.) Weddell in DC., Prodr. 16, pt. 1:235. 1869.  
*Procris rugosa* Poiret in Lam., Encycl. 5:628. 1804. Figure 29.

Shrubs 1-3 m. tall, bisexual, leafy internodes 3-30 (50) mm. long, 0.7-3.5 mm. thick, densely hirsutulous with ascending or appressed hairs 0.2-1 mm. long; stipules about 4 mm. long, lanceolate, deciduous or occasionally persisting. Leaves and petioles differing greatly in size on different plants, petioles (2) 5-35 (60) mm. long, 0.6-1 mm. thick, densely hirsutulous; laminae 2-13 cm. long, 1-7 cm. broad, usually narrowly to broadly ovate in outline, acute to acuminate at the apex, obtuse to rounded at the base, margin dentate to serrate with 3 to 7 teeth per cm., laminae drying stiffly chartaceous, smooth or slightly rough to the touch and usually becoming rugose with all the veins deeply impressed above, hirsutulous or tomentulose with slender whitish hairs 0.2-1 mm. long on the veins beneath, venation palmate or subpalmate with 3 primary veins or 1 primary vein and 2 strongly ascending secondaries, midvein with 1 or 2 pairs of major secondary veins above the basal veins, minute punctate cystoliths usually visible above. Inflorescences small (5-12 mm.) globose glomerules in leaf-axils and persisting at leafless nodes; male flowers with the perianth parts acuminate at the apex, flower buds about 2 mm. broad; anthers about 1 mm. long; female flowers enclosed by thin brown perianth-like bracts 1-2 mm. long, styles 1-3 mm. long, very minutely puberulent. Fruit about 0.6 mm. long and 0.4 mm. broad, ellipsoid, very slightly flattened, smooth, and drying pale brownish.

Plants of moist and wet evergreen (premontane wet and rain, and lower montane wet and rain) forest formations between (500) 1000 and 2000 (2500) m. elevation on both the Caribbean and Pacific slopes in Costa Rica; probably flowering throughout the year but collected with flower and fruit primarily between November and April. The species ranges from Mexico to Venezuela and Bolivia.

*Phenax rugosus* is recognized by the shrubby habit, globose bisexual inflorescences, minute fruit, and usually rugose leaves more or less ovate in outline. The unopened male flowers are narrowed, acuminate, and often bilobed at the apex, resembling quite closely the female perianth-tube in the genus *Boehmeria*. This may explain why collections are so often placed in the wrong genus.

*Phenax sonneratii* (Poir.) Weddell in DC., Prodr. 16, pt. 1:235. 1869. *Parietaria sonneratii* Poiret in Lam., Encyc. 5:15. 1804. *Phenax vulgaris* Wedd., Ann. Sci. Nat. ser. 4, pt. 1:192. 1854. Figure 29.

Herbs or diffusely branched subshrubs 0.3-1 m. tall, bisexual, leafy internodes 2-50 mm. long, 0.3-1.5 mm. thick, very sparsely puberulent with minute (0.1-0.4 mm.) whitish hairs, becoming pale in color and longitudinally ridged when dry; stipules 1-3 mm. long, usually persisting beneath the flower-clusters. Leaves relatively uniform in size and shape, petioles 4-16 (35) mm. long, 0.3-0.8 mm. thick, sparsely and minutely puberulent; laminae 1.5-6 cm. long, 0.8-2.5 cm. broad, ovate to elliptic or lanceolate, acute to acuminate at the apex, obtuse, acute or attenuate at the base, serrate along the margin with 3 to 9 teeth per cm., laminae drying membranaceous to thin-chartaceous, smooth or slightly scabrous above with appressed hairs about 0.7 mm. long, with thin whitish hairs about 0.4 mm. long on the veins beneath, venation palmate to subpalmate with 3 primary veins, midvein usually with a pair of major secondary veins arising near the center, minute black-punctate cystoliths often visible above. Inflorescences dense small axillary glomerules occasionally persisting at leafless nodes, with about 10 to 20 flowers each, outer bracts relatively broad, drying dark, and with a conspicuously ciliolate apical edge; male flowers about 1 mm. long before anthesis; female flowers with slender very minutely puberulent styles 1-2 mm. long. Fruit about 1 mm. long and 0.7 mm. broad, ovoid, acute apically, minutely pusticulate.

Weedy plants of open and shaded sites in areas of very wet evergreen forest formations between sea level and 800 (1200) m. elevation along the Caribbean slopes and coastal plain in Costa Rica; flowering throughout the year. This species appears to have been introduced and is now widely naturalized in the Caribbean area (see below).

*Phenax sonneratii* is recognized by its short-lived habit, preference for disturbed and early secondary habitats, small stipules, unusual floral bracts, and relatively large fruit. It is often seen as a

weed on banana plantations and road sides. The type, which I have not seen, is said to have been collected by Sonnerat in India. However, later floras of India do not list the species and suggest that it was introduced to India; it is not listed as occurring in other Asian countries. Thus, the origin of this species is likely to be in the New World, where all the other species of the genus are found.

### PILEA Lindley

Herbs or rarely subshrubs, annual or perennial, erect to repent or climbing, occasionally epiphytic, unisexual or bisexual, stems lacking stinging hairs, often succulent, rooting from the nodes in some spp.; stipules connate across the base of the petiole to form a ligule-like structure, caducous or persistent. Leaves opposite and petiolate, similar in size and shape at a node or differing greatly; laminae entire or more often with serrate margins, mostly palmately 3-veined, glabrous or puberulent, linear to curved (less often punctiform) cystoliths usually visible. Inflorescences axillary or from older leafless nodes, bracteate, basically cymose but varying from open paniculate to capitate or spicate, flowers of different sexes born on different branches of the same inflorescences, on different inflorescences of the same plant, or on different plants; male flowers usually pedicellate, with 3 or 4 perianth-parts united near the base and often bearing prolonged vertical appendages on their abaxial surface just below the apex, stamens 3 or 4, pistillode very small and conical; female flowers sessile or pedicellate, perianth-parts usually 3 and equal or more often with 1 perianth-part much larger and somewhat hooded distally, staminodes 3 or not apparent (said to eject the fruit at maturity), pistil ovoid to ellipsoid with a short sessile penicellate stigma. Fruit laterally compressed and somewhat lenticular, ovate to orbicular or elliptic in outline, surface smooth to muricate, the apex sometimes becoming curved and subapical, the stigma usually deciduous, perianth persisting and tightly surrounding the fruit at its base.

*Pilea* is the largest genus of the Urticaceae with more than 600 species. These are mostly tropical with a few temperate representatives but the genus is absent in Europe, Australia, and New Zealand. The neotropics are rich in species and some areas especially so; the island of Jamaica has 49 species with about 35 endemic to the island. Our own species of *Pilea* are concentrated mostly in the wet evergreen montane forests between 1000 and 2500 m. elevation; they are uncommon above and below this range. While a few species are common as weeds or found in the cracks of city pavement (*P. microphylla*), most species are confined to the shaded floor of moist forests or to the proximity of streams and brooks.

The genus is usually easy to recognize because of its opposite leaves with unusual ligulate stipules. Some species have leaves very similar to those of the Melastomaceae family with the three or five primary veins subparallel and reaching the upper part of the lamina.



Some of the smaller species of *Pilea* lend themselves to cultivation under glass and in terraria. The "aluminum plant," *Pilea cadierei* Gagnep. & Guill., is often grown in gardens and parks in Central America.

- 1a. Laminae with entire margins . . . . . 2a.
- 1b. Laminae with crenate, serrate, or dentate margins, the teeth sometimes very small and confined to the distal part of the lamina . . . . . 5a.
- 2a. Laminae 1-6 cm. long, on long or short petioles; plants 10-100 cm. tall . . . 3a.
- 2b. Laminae 0.1-1 cm. long, petioles usually very short; plants 2-25 cm. tall  
4a.
- 3a. Laminae broadest below the middle, ovate to ovate-lanceolate, obtuse to acuminate, with short slender hairs; above 1000 m. . . . . *P. parietaria*.
- 3b. Laminae broadest near the middle, very narrowly elliptic to elliptic-lanceolate, long acuminate, glabrous . . . . . *P. quichensis*.
- 4a. Flowers in small axillary groups along the stems; leaves of a node usually different in size, usually longer than broad, glabrous . . . . . *P. microphylla*.
- 4b. Flowers in dense terminal clusters subtended by a "whorl" of closely spaced leaves; laminae usually similar in size at the same node, usually broader than long, glabrous or with thin hairs . . . . . *P. herniariodes*.
- 5a. Laminae of the same node differing greatly in size, the smaller lamina half the size of the larger or less than half as large, always glabrous; stipules 0.2-2 mm. long; inflorescences usually less than 2.5 cm. long; fruit 0.7-3 mm. long . . . 6a.
- 5b. Laminae of the same node of similar size but the petioles often very different in length, sometimes one lamina of a pair 20-40 per cent smaller than the other, glabrous or puberulent; stipules 0.3-20 mm. long; fruit 0.3-2 mm. long . . . 12a.
- 6a. Plants usually found as epiphytes, growing on tree-trunks, or growing on moss-covered rocks . . . . . 7a.
- 6b. Plants usually found growing on the soil . . . . . 8a.
- 7a. Larger laminae 2-7 cm. long, narrowly elliptic to elliptic-ovate, oblique at the base, venation pinnate or subpalmate, smaller laminae broad; inflorescences 2-5 mm. long, fruit about 1 mm. long; 0-1600 m. . . *P. imparifolia*.
- 7b. Larger laminae 2-12 cm. long, lanceolate to very narrowly elliptic, subequal at the base, venation palmate, smaller laminae very narrow; inflorescences 5-23 mm. long, fruit about 0.8 mm. long; (0) 500-1600 m. . . *P. diversissima*.
- 8a. Plants of the Cordillera de Tilaran and adjacent areas between 600 and 900 m., becoming 40 cm. tall; larger laminae 2-8 (12) cm. long and with small rounded teeth; inflorescences 1-2 cm. long, fruit very large (3 mm.) and drying dark brown . . . . . *P. tilarana*.
- 8b. Plants found along the Caribbean slopes and Central Highlands to western Panama, becoming 1 m. tall; fruit 0.8-2 mm. long . . . . . 9a.
- 9a. Stipules short or reduced to a ligulate ridge, 0.3-1 mm. high; larger laminae 2-10 (13) cm. long . . . . . 10a.

- 9b. Stipules 1-2 mm. high; larger laminae 4-18 cm. long, often long-acuminate  
11a.
- 10a. Inflorescence capitate on short peduncles, fruit about 1.7 mm. long; laminae acute to short acuminate; 1400-2300 m. in the highlands of Chiriqui, Panama . . . . . *P. chiriquina*.
- 10b. Inflorescence of open or compact cymes; fruit about 0.8 mm. long; laminae often long-acuminate; 0-1600 m., from eastern Nicaragua to central Costa Rica. . . . . *P. diversissima*.
- 11a. Laminae with small inconspicuous teeth, the secondary veins not very prominent, 10 to 20 pairs; male inflorescences forming globose clusters around the stem 1-4 cm. in diameter; fruit 1-1.5 mm. long . . . *P. costaricensis*.
- 11b. Laminae with large conspicuous teeth and the 7 to 30 pairs of secondary veins prominent below; inflorescences pedunculate and few-branched, never encircling the stem; fruit becoming 2 mm. long . . . . . *P. donnell-smithiana*.
- 12a. Stipules more than 4 mm. long (ligule-like above the petiole-base, present only on the younger leaves when deciduous) . . . . . 13a.
- 12b. Stipules less than 4 mm. long . . . . . 19a.
- 13a. Plants of Cocos Island; fruit less than 1 mm. long . . . . . *P. gomeziana*.
- 13b. Plants of mainland central America. . . . . 14a.
- 14a. Leaves with pinnate venation and very rugose; known only from western Panama . . . . . *P. rugosissima*.
- 14b. Leaves palmately 3-veined or with fewer than 3 pairs of prominent secondary veins. . . . . 15a.
- 15a. Leaves attenuate at the base with the petiole often winged, 5-20 cm. long; 0-1800 m. elevation. . . . . *P. ptericlada*.
- 15b. Leaves lacking a winged petiole, the lamina ending abruptly at the apex of the petiole where the major veins arise . . . . . 16a.
- 16a. Fruit 1.2 mm. long or less; laminae 4-19 cm. long, with prominent serrations; 500-2300 m. . . . . 17a.
- 16b. Fruit about 2 mm. long; laminae rarely more than 6 cm. long, bluntly serrate or less than 4 cm. long if prominently serrate; to 3000 m. . . . . 18a.
- 17a. Fruit 0.6-1 mm. long; stipules (4) 7-18 mm. long; laminae often bullate  
*P. acuminata*.
- 17b. Fruit about 1.2 mm. long; stipules 4-8 mm. long; leaves rarely bullate  
*P. pittieri*.
- 18a. Laminae drying thick, 1.5-6 (8) cm. long, with a few appressed hairs beneath, narrowly ovate to lanceolate; plants usually found above 2500 m. elevation. . . . . *P. cornuto-cucullata*.
- 18b. Laminae drying thin, 0.6-4 cm. long, glabrous beneath, ovate and prominently serrate; plants rarely found above 2500 m. elevation . . *P. auriculata*.
- 19a. Laminae usually becoming 10 cm. long, lanceolate to very narrowly elliptic or elliptic . . . . . 20a.

- 19b. Laminae rarely becoming more than 7 cm. long, narrowly to broadly ovate, usually broadest near the base . . . . . 23a.
- 20a. Laminae lanceolate to linear-lanceolate, male flowers in globose heads on long (2-7 cm.) pendant filiform peduncles; 1000-2300 m. . . . . *P. angustifolia*.
- 20b. Laminae narrowly ovate-lanceolate to very narrowly elliptic; peduncles never filiform . . . . . 21a.
- 21a. Leaves minutely and inconspicuously serrate, glabrous; wet Caribbean slopes 500-1000 m . . . . . *P. quichensis*.
- 21b. Leaves prominently serrate, glabrous or sparsely puberulent . . . . . 22a.
- 22a. Petioles generally short but occasionally 50 mm. long; male inflorescences axillary clusters, female to 15 mm. long; common on the Osa peninsula, rarely to 1700 m. . . . . *P. pallida*.
- 22b. Petioles to 8 cm. long; male flowers in open paniculate inflorescences 2-4 cm. long; only known from Volcan Irazú, 1500-2500 m. . . . . *P. beguinotii*.
- 23a. Small creeping plants with roots at most nodes, stems repent; laminae 3-15 mm. long, very broadly ovate to suborbicular . . . . . *P. nummularifolia*.
- 23b. Erect plants or having creeping stems with erect flowering shoots; laminae 7-80 mm. long, ovate to lanceolate . . . . . 24a.
- 24a. Fruit about 2 mm. long; male perianth-parts with prominent appendages 0.5-2 mm. long. . . . . 25a.
- 24b. Fruit 0.5-1.5 mm. long; male perianth-parts with appendages less than 0.5 mm. long or none. . . . . 26a.
- 25a. Laminae drying thick, 1.5-6 (8) cm. long, with a few appressed hairs beneath, narrowly ovate to lanceolate and serrulate; plants usually found above 2500 m. elevation. . . . . *P. cornuto-cucullata*.
- 25b. Laminae drying thin, 0.6-4 cm. long, usually ovate with prominent serrations; glabrous beneath; plants rarely found above 2500 m. elevation  
*P. auriculata*.
- 26a. Fruit more than 1 mm. long; plants glabrous; inflorescences usually few branched on prominent peduncles, unisexual; 1500-3000 m. . . . . 27a.
- 26b. Fruit less than 1 mm. long; plants usually puberulent or with a few hairs; inflorescences much branched and bisexual (male flowers often deciduous); 0-1600 m. . . . . 28a.
- 27a. Laminae 7-80 mm. long, usually narrowly ovate . . . . . *P. gracilipes*.
- 27b. Laminae 4-15 (30) mm. long, broadly ovate . . . . . *P. dauciodora*.
- 28a. Laminae with thin long (0.5-4 mm.) hairs on the upper surface, the margin conspicuously serrate, the upper leaves clustered close together; inflorescences 3-8 cm. long; 600-1600 m. . . . . *P. pubescens*.
- 28b. Laminae glabrous above or with a few scattered hairs about 0.5 mm. long, the margins bluntly or minutely serrate; inflorescences to 3 cm. long . . . . . 29a.
- 29a. Leaves not usually clustered at the ends of stems, laminae ovate to rhombic, to 4 cm. long; common native plants . . . . . *P. hyalina*.

- 29b. Leaves usually clustered at the ends of stems, obovate to oblong, to 6 cm. long; escaped from cultivation but native in Panama . . . . . *P. involucrata*.

***Pilea acuminata* Liebmann, Danske Vidensk. Selsk. Skrivt. ser. 5, 2:302. 1851. Figure 26.**

Herbs, stems often repent at the base, 0.2-1 m. tall, usually unisexual, the erect stems with few or no lateral branches, leafy internodes (1) 2-10 (12) cm. long, 1-4 mm. thick, glabrous or with curved or crooked hairs 0.4-1 mm. long but soon becoming glabrous, often drying deep green; stipules (4) 7-18 mm. long, rounded apically, with a few slender hairs along the edge, often with many linear cystoliths arranged longitudinally near the base, usually persisting. Leaves of the same node of similar size or occasionally with 1 twice the size of the opposing leaf or the petioles very different in length, petioles 0.6-6 (8) cm. long, 0.6-1.6 mm. thick, glabrous or sparsely puberulent; laminae (2) 4-19 cm. long, 1.5-6 cm. broad, narrowly ovate to lanceolate or ovate, long-acuminate and serrate along the tip, obtuse or slightly rounded at the base, prominently serrate with 1 to 3 (5) sharply acute teeth per cm., the laminae drying membranaceous to thin chartaceous and dark above, smooth above and glabrous or with a few long (0.5-2 mm.) transparent hairs in groups between the veins, sparsely puberulent with short (0.3-1 mm.) hairs on the veins beneath, venation palmate with 3 primary veins, midvein with 7 to 15 pairs of secondary veins, the veins often impressed above and the surface bullate, cystoliths often long (0.5-1 mm.) and prominent above. Inflorescences unisexual, borne in the axils of leaves near the ends of stems, pedunculate, male inflorescences 1-5 cm. long with the flowers in 3 to many dense clusters on a simple or few-branched rachis (rarely many-branched), female inflorescence (1) 3-7 cm. long, usually with 3 or more branches and the flowers separate; male flowers 1.2-2 mm. long before anthesis, perianth-parts with subapical dorsal appendages 0.2-0.5 mm. long, apically dark green and whitish near the base of the flower; female flowers 0.7-1 mm. long. Fruit 0.6-1 mm. long and 0.3-0.7 mm. broad, lenticular, ovoid to ellipsoid in outline with the central areas convex and the margin distinctly narrowed, drying brown.

Plants of the very wet evergreen forests of the Caribbean slopes between 500 and 1700 m. elevation in Costa Rica; flowering from January to June. The species ranges from Mexico to Colombia.

*Pilea acuminata* is recognized by the large stipules, relatively large and conspicuously serrate leaves often on petioles of different lengths and with the laminae of a node differing or similar in size and form and with long serrate tips, the peduncled relatively open inflorescences, appendaged male perianth-parts, and the small fruit. This species can be found on the moist forest floor but occurs more often on rocks near running water. The leaves are usually somewhat bullate with impressed secondary and tertiary veins, but this characteristic may be lost in pressed specimens.

Material of this species is extremely variable, both in collections from diverse areas and within populations. Individual plants grow-

ing together may differ in color, and those growing in sites of differing exposure may differ greatly in size and the texture of leaves. In addition, Costa Rican material is much more robust than Mexican collections of this species. Specimens of *P. acuminata* may be difficult to distinguish from *P. pittieri* (q.v.).

***Pilea angustifolia* Killip, Journ. Wash. Acad. Sci. 15:295. 1925. Figure 26.**

Herbs, bisexual or unisexual, 0.5-1.5 m. tall, stems erect and usually few-branched, leafy internodes 0.5-6 cm. long, 0.7-3 mm. thick, glabrous, usually striate on drying, minutely punctate cystoliths present or absent; stipules 0.1-1.3 mm. long, 1 mm. broad at the base, acute, deciduous. Leaves equal or subequal at a node, the smaller usually more than half as long as the larger, the petiole usually differing in size at a node, 2-11 mm. long, 0.3-0.7 mm. thick (dry); laminae (2) 3-14 cm. long, 0.5-2 cm. broad, linear-lanceolate to narrowly lanceolate or narrowly elliptic, acute to very long-acuminate, acute to slightly rounded at the base, minutely serrulate along the margin with 3 to 5 teeth per cm., the teeth more prominent distally, the laminae smooth and glabrous on both surfaces, drying thin chartaceous and green, venation palmate with the 3 primary veins separate or united near the base, secondary veins numerous, cystoliths minutely punctate or very short-linear. Male inflorescences globose heads on long (2-7 cm.) filiform peduncles, the heads about 1 cm. in diameter; male flowers pedicellate, buds about 2 mm. long, perianth without appendages, the free tips about 0.4 mm. long. Female inflorescences of dense cymose clusters on very slender peduncles 4-10 mm. long, the clusters 3-8 mm. thick; female flowers with the larger perianth-part 1-1.2 mm. long, linear-oblong. Fruit 0.8-1.2 mm. long, ovate in outline, lenticular, smooth and brown, with a definite darker edge.

Uncommon plants of open situations and also in shaded sites of wet montane forest formations between 1000 and 2300 m. elevation; probably flowering throughout the year. This species ranges from the Cordillera de Tilarán southward to Cerro Chirripó in the Cordillera de Talamanca in Costa Rica.

*Pilea angustifolia* is recognized by the long narrow leaves similar in shape and usually subequal in size at a node, their bright green color, the globose male heads on long thin peduncles, and the small clusters of female flowers on shorter peduncles that are also very thin.

***Pilea auriculata* Liebmann, Danske Vidensk. Selsk. Skrivt. ser. 5, 2:299. 1851. *Pilea cormanæ* Killip, Journ. Wash. Acad. Sci. 15:292. 1925. Figure 27.**

Herbs, erect or with stems procumbent near the base, 5-40 cm. tall, erect stems with few lateral branches or occasionally with many and shrub-like in form, usually unisexual, leafy internodes (0) 2-20 mm. long, 0.7-1.5 mm. thick, glabrous or with

minute (0.1-0.5 mm.) appressed hairs, often reddish; stipules 1.5-5 mm. long, about 2 mm. broad, slightly auriculate at the base, rounded at the apex, conspicuous and persisting, pale brownish translucent. Leaves of the same node of similar size or rarely one leaf about half the size of the other, petioles 2-30 (40) mm. long, 0.2-0.5 mm. thick (dry), glabrous or rarely sparsely puberulent; laminae 6-40 mm. long, 4-35 mm. broad, ovate to rhombic or triangular, apex formed by the terminal tooth of the coarsely crenate-serrate margin, abruptly narrowed at the base but slightly cuneate at the petiole, margin with 3 to 6 teeth per cm., the laminae drying membranaceous and often translucent, darker and with scattered transparent hairs 0.5-1 mm. long above, essentially glabrous beneath, venation subpalmate with 3 primary veins, the midvein with 1 to 3 pairs of major secondary veins above the prominent basal lateral veins, linear cystoliths very prominent on both surfaces (dry). Inflorescences usually solitary in the leaf-axils with peduncles (2) 5-30 mm. long, with 5 to 20 flowers in short-branched or subcapitate clusters; male flowers pedicellate, perianth-parts about 3 (4) mm. long with subapical appendages 0.5-1 (1.5) mm. long, glabrous; female flowers 1-2 mm. long, the perianth-parts of 2 sizes. Fruit about 2 mm. long and 1.5 mm. broad, very flat (lenticular), and ovate in outline, thickened along the edge, smooth and yellowish.

Plants of the wet evergreen formations of the Caribbean slopes and Central Highlands between 1200 and 2700 m. in Costa Rica; flowering throughout the year. The species ranges from Southern Mexico to Western Panama.

*Pilea auriculata* is recognized by the thin coarsely serrate and almost glabrous isomorphic leaves, conspicuous blunt intrapetiolar stipules auriculate at the base, small inflorescences on conspicuous peduncles, male perianth with appendages, and relatively large flattened fruit. The leaves are often dark green with the areas above the veins silvery-white or very pale green in life. A few plants have rather small (1-2 cm.) leaves with very prominent teeth (*Lent 1852*), but these are probably no more than an unusual form. *Pilea cornumanae* was distinguished on the basis of the leaves being rather different in size at each node and the staminate perianth with longer caudate appendages, but I believe that these represent a combination of unusual extremes within the range of variation of *P. auriculata*. Two collections that exemplify this form of variation (*Burger & Gomez 8356* and *Corman [Killip] 3543*, the type) are from the western part of the species range and are intermediate with *P. cornuto-cucullata* in some respects.

*Pilea beguinotti* Cufodontis, *Archivio Bot. Fitogeog. & Genet.* 10:29. 1934, photo. Figure 26.

Herbs, bisexual, 0.3-1 m. tall, stems erect and few-branched, leafy internodes 1-7 cm. long, 2-5 mm. thick (dry), glabrous; stipules about 2 mm. long, acute, persisting. Leaves of the same node equal or subequal and similar in form but the petioles

often differing in size, petioles 1.5-8 cm. long, 0.7-1.7 mm. thick (dry), glabrous, sulcate above; laminae 6-18 cm. long, 2-6 cm. broad, narrowly elliptic and widest at the center, short- to long-acuminate at the apex, acute and often unequal at the base, the margin bluntly serrate with 1 or 2 teeth per cm., the lamina drying very thin chartaceous and dark, glabrous, venation palmate with the 3 primary veins usually united above the lamina-base and separating from the midvein at different points, secondary veins ascending and often somewhat S-shaped, the cystoliths short linear and variously arranged, sometimes absent on the upper surface. Inflorescences bisexual or unisexual, 2-4 cm. long, those in lower leaf-axils mostly female, the distal mostly male, the clusters of 3 to 10 flowers separate along the thin glabrous branches of the inflorescence; male flowers borne on pedicels becoming 1 mm. long, flower buds about 1 mm. long, perianth parts with very short subapical mucronate appendages; female flowers sessile or short-pedicellate, about 1 mm. long, perianth-parts about 0.6 mm. long, Fruit about 1 mm. long, with an oblique apex (not

Rarely collected plants of the wet montane forests along the western and south-western slopes of Volcán Irazú between 1500 and 2500 m. elevation. This species is known from only two collections: *Cufodontis* 351 (the type) from near Guayabillos and *Standley* 38819 from near Las Nubes, flowering in March and May.

*Pilea beguinotii* is recognized by the large subequal leaves at each node, often on long slender petioles, the small stipules, glabrous parts, and flowers in small distant clusters on relatively short but open inflorescences. This species resembles *Pilea myriantha* Killip of northern South America, but that species has much larger inflorescences. Vegetatively this species resembles *P. quichensis* with smaller less distinctly serrulate laminae and *P. pittieri* with more distinctly serrate leaves that are usually broadest near the base.

*Pilea centradenioides* Seem. has been reported from Costa Rica (Standley, Field Mus. Bot. 18:394. 1937), but I have not seen material referable to this species collected in Costa Rica. I believe this record was based on the misidentification of a collection of *P. ptericlada*.

*Pilea chiriquina* Killip, Journ. Wash. Acad. Sci. 15:291. 1925. Figure 25.

Herbs to 1 m. tall, unisexual, stems becoming woody near the base, unbranched or rarely with a few lateral branches, leafy internodes 3-30 mm. long, 0.8-4 mm. thick, glabrous, longitudinally grooved and reddish brown when dry, semisucculent in life; stipules reduced to a ligulate ridge about 0.3 mm. high. Leaves of the same node very different in size, smaller leaves sessile, petioles of the larger leaves 1-4 mm. long; smaller laminae 1-2 (3) cm. long, ovate to ovate-lanceolate and usually very asymmetric, subauriculate on one side basally, larger laminae 2.5-9 cm. long, 0.7-2 (2.8) cm. broad, very narrowly elliptic to lanceolate or oblanceolate, tapering gradu-

ally to an acute or acuminate apex, narrowed gradually to the base but abruptly rounded and unequal at the petiole, margin crenate-serrate with 3 to 5 shallow teeth per cm., lamina drying very thin chartaceous and dark above, smooth and glabrous on both surfaces, venation palmately 3-veined or subpalmate with a pair of lateral veins arising from near the base, the 3 to 8 pairs of major secondary veins often obscure, linear cystoliths very conspicuous above. Inflorescences 1 or 2 in the axils of leaves, unisexual, male flowers in densely clustered cymes of 10-30 flowers on simple peduncles about 1 cm. long; male flowers not seen at maturity, probably 1.5 mm. long before anthesis and the perianth with minute (-0.5 mm.) subapical appendages; female flowers in dense capitate cymes on simple peduncles about 1 cm. long, the 8 to 20 flowers very short pedicellate; female flowers often diseased (?) with black knob-like structures at the apex of the pistil. Fruit 1.5-1.8 mm. long, about 1.5 mm. broad, thin and lenticular with the edges somewhat thickened, broadly ovate or suborbicular in outline, drying dark brown.

A species known only from the moist montane evergreen forest formations of the Chiriqui Highlands between 1400 and 2300 m. altitude in Western Panama; probably flowering throughout the year. Endemic to Western Panama but to be expected from the poorly known areas above 1400 m. in adjacent Costa Rica.

*Pilea chiriquina* is recognized by the relatively small leaves very unequal at each node with shallow teeth along the margin, glabrous parts, small (5-10 mm.) capitate inflorescences on short slender peduncles, and restricted range at higher altitudes. This species is closely related to *P. donnell-smithiana*, which seems to have the same kind of disease (?) afflicting its female flowers.

***Pilea cornuto-cucullata*** Cufodontis, Archivio Bot. Sist. Fitogeog. 10:29. 1934, photo. Figure 27.

Herbs with erect or procumbent stems, 10-50 cm. tall, usually bisexual, leafy internodes (0.5) 1-5 cm. long, 1-3 mm. thick, glabrous or with crooked ascending hairs about 0.5 mm. long; stipules 2-6 mm. long, 1-6 mm. broad, obtuse or rounded at the apex, brown, persisting. Leaves similar in size or with the smaller half the size of the larger at the same node, often differing in petiole-length, petioles 4-35 (40) mm. long, glabrous or with ascending crooked hairs; lamina 1.5-6 (8) cm. long, 1-3.5 cm. broad, ovate to ovate-lanceolate or elliptic, obtuse to acute at the apex, obtuse or slightly rounded at the base, margin crenate-serrate with 3 to 5 shallow teeth per cm., the lamina drying thin to stiff chartaceous and dark above, glabrous above and with a few appressed hairs on the veins beneath, venation palmate or occasionally almost pinnate (with the basal secondaries quite prominent), the 3 to 5 pairs of major secondary veins (above the lateral veins or basal secondaries) usually prominent beneath, linear cystoliths prominent above and below. Inflorescences solitary or paired in the upper leaf-axils, the 10 to 40 flowers in capitate or globose clusters 1 to 2 cm. in diameter or the female branched, peduncles 1-4 cm. long, 0.2-0.8 mm. thick (dry); male flowers pedicellate, buds about 4 mm. long before anthesis, the perianth usually 3-parted and with subapical appendages 1-2 mm. long, glabrous,



darker apically; female flowers with perianth of 2 lengths (1 hooded). Fruit about 2 mm. long, and 1.5 mm. broad, much flattened and thin-lenticular, broadly ellipsoid in outline, smooth, thickened along the edge and longitudinally in the center, drying pale greenish.

Plants often found in the deep shade of the forest floor and along brooks in montane forest formations between 2500 and 3200 m. elevation; flowering material has been collected in August and November. This species is endemic to the Cordillera de Talamanca and Volcán Irazú in Costa Rica.

*Pilea cornuto-cucullata* is recognized by the usually long-pedunculate inflorescences, male perianth-parts with long appendages, large flat fruit, blunt often broad stipules, and the very high altitude habitat. This species is closely related to *P. fallax* Weddell of Western Venezuela, Colombia, and Ecuador, which grows at similarly high elevations. Among Costa Rican species, *P. auriculata* is most closely related, and the material ascribed to *P. cornmanae* Killip (here placed into synonymy under *P. auriculata*) is in some ways intermediate between *P. auriculata* and *P. cornuto-cucullata*.

The proper delimitation of this species will require more intensive study. The type photograph appears quite atypical of the larger and thicker leaved specimens of higher altitudes that the present description is, in large part, based upon. Plants that in some ways appear to be intermediate between *P. cornuto-cucullata* (as here defined), *P. auriculata* (including *P. cornmanae*), and *P. gracilipes* have been collected both in Costa Rica and in western Panama. It may be that there is occasional hybridization between these three species or that they are not reproductively isolated and intermediate populations have not been sufficiently sampled.

Two collections from rocks bordering small streams at lower elevations of the wet Caribbean slope are tentatively placed here, though they may represent a new and closely related species: *Godfrey 66371* from near the Río Toro Amarillo (Limon) at about 200 m. and *Lent 3250* above Laguna Ule (Alajuela) at about 900 m.. These specimens have thinner and narrower leaves, shorter stipules, and male flowers with somewhat shorter appendages.

*Pilea costaricensis* Donn.-Smith, Bot. Gaz. 20:294. 1896. Figure 25.

Erect herbs to 1 m. tall, apparently unisexual, stems becoming somewhat woody, leafy internodes 5-40 mm. long, 1-4 mm. thick, glabrous, the cystoliths usually apparent; stipules 1-2 (4) mm. high, persisting. Leaves of the same node differing

greatly in size, smaller leaves about  $\frac{1}{4}$  the size of the larger and short-petiolate, petioles of the larger leaves 5-40 mm. long, about 2 mm. thick, slightly decurrent on the stem; smaller laminae 2-4 cm. long, very narrowly elliptic or elliptic-oblong, larger laminae 4-18 (21) cm. long, 1-6.5 cm. broad, narrowly elliptic-ovate to very narrowly elliptic or lanceolate, gradually tapering to the long-acuminate apex, gradually narrowed to the acute or attenuate and equal or subequal base, margin obscurely crenate-serrate with 2 to 4 very shallow teeth per cm., the laminae drying chartaceous and not usually conspicuously darker above than below, glabrous on both surfaces, venation palmate with 3 primary veins, the midvein with more than 10 pairs of major secondary veins joining the lateral veins, cystoliths linear, variously oriented and visible on both surfaces. Inflorescences axillary, much-branched cymose and globose, 0.5-4 cm. in diameter and often surrounding the stem at each flowering node, very short pedunculate or subsessile; male flower buds about 2 mm. long before anthesis, perianth-parts with subapical projections 0.2-0.5 mm. long, perianth dark green above and pale green beneath; female flowers about 1 mm. long, perianth-parts unequal. Fruit 1-1.5 mm. long and equally broad, broadly elliptic to suborbicular, the stigma subapical, flattened and lenticular with smooth pale brown surface.

Plants of the very wet forest formations of the Caribbean slopes and adjacent areas between 1200 and 1800 m. elevation in Costa Rica; flowering material has been collected between February and August. This species is known only from Central Costa Rica (see below).

*Pilea costaricensis* is recognized by the erect habit, long narrow leaves very different in size at a node, thick stems and petioles, glabrous parts, large round male inflorescences that often encircle the stem, and round smoothly lenticular fruit. While this species is very distinctive in full flower, vegetative material is very similar to a group of species (all with long narrow leaves very different in size at a node) that include *P. donnell-smithiana* and *P. ecbolophylla* Donn.-Smith of Guatemala. A series of collections by Davidson (56, 267, & 717) from Bajo Chorro, Chiriqui Province, Panama, are very similar to material placed here but differ in the smaller more congested inflorescences and greater development of the small leaf of each node. These collections also appear to have smaller flowers but they are probably immature. This Bajo Chorro material may represent a southern population of *P. costaricensis* or a closely related and undescribed species.

*Pilea dauciodora* (R. & P.) Weddell, Ann. Sci. Nat. ser. 3, Bot. 18: 223. 1852. *Urtica dauciodora* Ruiz & Pavon, name cited as synonym in Weddell, loc. cit. Figure 27.

Herbs, bisexual or unisexual, leafy stems erect, 10-30 cm. tall, leafy internodes 1-50 mm. long, 0.4-1.5 mm. thick, glabrous; stipules 0.5-1 (2) mm. long, persisting.

Leaves of the same node of similar size and shape or differing occasionally by about 25 per cent, petioles 1-20 mm. long, 0.1-1 mm. thick, sulcate above; laminae 4-15 (30) mm. long, 3-18 (25) mm. broad, broadly ovate to elliptic-ovate, obtuse or occasionally acute at the apex, rounded and truncate to obtuse at the base, margin serrate with 5 to 10 strongly ascending and slightly rounded teeth per cm. (often appearing to be rounded crenate), laminae drying chartaceous, glabrous on both surfaces, venation palmate with 3 primary veins, midvein with 2 to 4 pairs of prominent secondary veins, linear cystoliths apparent or obscure above. Male inflorescences 2-6 cm. long with peduncles 1-5.5 cm. long, with 1 to 3 separate clusters of flowers; male flower buds about 1.5 mm. in diameter, perianth parts with subapical appendages 0.1-0.3 mm. long. Female inflorescences 1-3 cm. long, with peduncles 8-25 mm. long, flower clusters separate on the simple rachis or on 1 to 3 short branches. Fruit 0.8-1.4 mm. long, 0.6-0.8 mm. broad, narrowly ovate in outline, the center rounded and thickened (lenticular) with a broadly or a narrowly flattened edge, surface smooth and pale brown.

Small plants of the shaded forest floor (or, rarely, epiphytes) in evergreen montane forest formations between 1500 and 3000 m. elevation. The species ranges from southern Mexico to Venezuela and Bolivia but is very rare in Costa Rica (see below).

*Pilea dauciodora* is recognized by the small broad leaves usually similar at a node (in our area), very small stipules, glabrous parts, long-pedunculate male inflorescences, shortly appendaged male perianth, and medium sized fruit with well defined margins. The proper circumscription of this species is not clear. Plants from Guatemala and Colombia are very similar but differ in details, while the plants commonly placed in this species from the cloud forests of Honduras are somewhat smaller in all respects. This species is unrecorded for Panama and Nicaragua and the few Costa Rican collections placed here (*Burger & Stolze 6077*, *A. Jimenez 1975 & 3246*, and *Williams et al. 24400*) may be no more than very small specimens of material otherwise placed under the name *P. gracilipes*. These two species, *P. dauciodora* and *P. gracilipes*, are very closely related and differ primarily in habit and the fact that *P. gracilipes* appears to be confined to Costa Rica and westernmost Panama. The disjunct range of *P. dauciodora*, the morphological variation in different parts of its wide range, and the relationships with closely allied (and perhaps conspecific) species, such as *P. gracilipes*, are worthy of more intensive study than a floristic review of the Costa Rican material can provide.

*Pilea diversissima* Killip, Field Mus. Bot. 18:394. 1937. Figure 25.

Herbs or climbers growing on tree trunks, also epiphytes and epiliths, apparently unisexual, 0.3-1 m. tall or creeping, leafy internodes 3-30 mm. long, 0.7-4 mm. thick,

becoming woody basally, glabrous, with prominent linear cystoliths; stipules forming a minute intrapetiolar (ligulate) ridge to 1 mm. high. Leaves of the same node very different in size and shape, small leaves often sessile, petioles of the larger leaves 2-8 (15) mm. long, 0.3-1.5 mm. thick, sulcate above and decurrent on the stem; small laminae 4-12 mm. long, narrowly elliptic to oblanceolate, often with inrolled margins, larger laminae 2-10 (13) cm. long, 5-20 (35) mm. broad, oblong-lanceolate to very narrowly elliptic or linear-lanceolate, tapering gradually to the long-acuminate apex, narrowed to the acute or obtuse and slightly unequal base, margin crenate-serrate with 2 to 4 blunt teeth per cm., the lamina drying thin chartaceous and usually dark above, smooth and glabrous on both surfaces, venation palmate with a single pair of lateral veins, secondary veins numerous, interconnecting the primary veins, cystoliths punctiform above and below but linear and fusiform near the edge above. Inflorescences 0.3-2.3 cm. long, axillary, male open and much branched, the female of compact cymes on short peduncles; male flowers borne on pedicels 1-4 mm. long, buds about 1.5 mm. long, before anthesis, perianth-parts minutely (0.1 mm.) mucronate; female flowers with perianth 0.5-0.7 mm. long. Fruit 0.7-0.9 (1) mm. long, 0.6-0.8 (1) mm. broad, broadly ellipsoid in outline, flattened but with the central axis raised, drying pale grayish-brown.

Plants of evergreen forests subject to the very wet Caribbean winds between (0) 500 and 1600 m. elevation in Costa Rica; apparently flowering throughout the year. This species ranges from Eastern Nicaragua to Central Costa Rica.

*Pilea diversissima* is recognized by the leaves differing greatly in size at the same node, the larger leaves narrow and trinerved, glabrous parts, small inflorescences, fruit with centrally thickened longitudinal ridge, and the plants often growing on tree trunks or rocks. This is a very distinctive species closely related to *P. pansamalana* Donn.-Smith of Guatemala with the smaller leaves of a node larger and petiolate and the larger laminae more prominently serrate. The plants vary greatly and it is with the larger erect plants that difficulties of delimitation arise. It may not be possible to distinguish these larger plants from *P. ecbolophylla* Donn.-Smith (Bot. Gaz. 46:115, the type not seen). The plants included here range from slender-stemmed creeping epiphytes with very narrow thin leaves in which the secondary veins dry dark in color on the lower surface (as in the type, *Brenes 4851*) to thicker-stemmed erect plants reaching almost 1 m. in height in wet sites and having thicker leaves that dry paler in color with obscure secondary venation. As these populations are better sampled, however, it may become apparent that the larger plants do represent a distinct species, perhaps closely related to *P. riparia* Donn.-Smith of Guatemala.

*Pilea donnell-smithiana* Killip, Journ. Wash. Acad. Sci. 15:292. 1925. Figure 25.

Erect herbs to 1 m. tall, apparently unisexual, stems often unbranched, leafy internodes 8-40 mm. long, 1-4.5 mm. thick, glabrous; stipules 1-2 mm. high, persisting or tearing off to leave a ligulate ridge. Leaves of the same node very different in size, smaller leaves subsessile and less than  $\frac{1}{4}$  the length of the larger, petioles of the larger leaves (0.5) 1-3 cm. long, 1-2 mm. thick, glabrous, slightly decurrent and forming an inter-petiolar line; smaller laminae 1-3 cm. long, ovate to elliptic, very asymmetric and slightly auriculate on one side basally, the larger laminae 7-18 cm. long, 3-9 cm. broad, elliptic to ovate-lanceolate, gradually tapering to the acuminate apex, obtuse to rounded at the asymmetric or oblique base, margins distinctly serrate with 2 to 4 teeth per cm., lamina drying very thin chartaceous, smooth and glabrous above and below, serration palmate with 3 primary veins, secondary veins variable in number (7-30 pairs) and spacing but usually at right angles to the primary veins and interconnecting them, linear cystoliths visible above and below. Inflorescences solitary or 2 in the leaf-axils, unisexual, the flowers in dense clusters on a single unbranched peduncle or in clusters on a few-branched axis, peduncles 2-20 (50) mm. long; male flowers 1-1.5 mm. long in bud, perianth apparently without subapical appendages; female flowers usually in clusters of 5-15 flowers, borne on short (0.5-2 mm.) pedicels, perianth of 2 sizes, the larger 2 mm. long. Fruit becoming 2 mm. long and 1.5 mm. broad, lenticular and broadly ovate in outline, smooth with thin edges, drying dull brown.

Plants of the very wet evergreen forests of the Caribbean slope and adjacent areas between 1200 and 1800 m. in Costa Rica; probably flowering throughout the year with fertile collections having been made from January through September. The species is known only from Central Costa Rica and the Boquete area of Chiriqui, Panama.

*Pilea donnell-smithiana* is recognized by the distinctly serrulate leaves very different in size at each node, with many secondary veins and asymmetric lamina-base, glabrous parts, small often subcapitate inflorescences, and very wet forest habitat. This species is very closely related to *P. purulensis* Donn.-Smith of Guatemala, but that species has the male flowers in more globose long-pedunculate heads and the fruit is smaller (1.5 mm.).

***Pilea gomeziana* W. Burger, Phytologia 31:269. 1975. Figure 26.**

Herbs, bisexual (unisexual in early stages) leafy stems erect and unbranched, 20-50 cm. tall, leafy internodes (2) 7-50 mm. long, 1-4 mm. thick, puberulent with thin curved or crooked whitish hairs 0.3-1 mm. long; stipules 4-8 mm. long, broad and rounded at the apex, persisting with the leaves. Leaves usually subequal and similar in form at each node, usually differing by about one-fourth in size but occasionally with the smaller leaf one-half the size of the larger (at the same node), petioles 1-5 cm. long, 0.4-2 mm. thick, sparsely puberulent, usually sulcate above; laminae 3-15 cm. long, 2.5-7 cm. broad, broadly ovate to elliptic-ovate or elliptic, usually broadest below the middle, short-acuminate at the apex, obtuse to truncate at the base, margins serrate with 2 to 4 prominent teeth per cm., laminae drying very thin chartaceous or membranaceous, upper surface with evenly spaced slender

and transparent hairs about 1 mm. long, lower surface with smaller hairs along the veins, venation palmate with 3 (5) primary veins, the 5 to 10 pairs of secondary veins ascending, very short linear cystoliths scattered or in groups above. Male inflorescences usually in the uppermost leaf-axils, 1-2 cm. long, usually of several small clusters of flowers on an unbranched rachis; male flowers sessile, the buds about 1 mm. in diameter with clavate subapical appendages 1 mm. long, perianth usually with a few thin hairs. Female inflorescence in lower leaf-axils or at lower leafless nodes, 2-5 cm. long, the primary rachis with 1 to 4 branches, flower-clusters very small and distant along the rachis; female flowers pedicellate, less than 0.5 mm. long. Fruit about 0.6 mm. long, oblong in outline with convex surfaces, pale brown, margins outlined by a submarginal ridge or dark-punctate lines.

Plants of stream sides and shaded forest on Cocos Island; collected with female flowers in August and with fruit and unopened male flowers in March. I have seen only three collections of this species: *Dressler 4469*, *Gomez 3304* the type, and *Pittier 16238*.

*Pilea gomeziana* is distinguished by its very small flowers and fruit, subequal leaves at each node, large stipules, pubescence of slender hairs, and isolated habitat. This species appears to be related to *P. pittieri* and *P. pubescens* among Costa Rican species. Closer relationships are to be expected with South American species, but I have not been able to find any thus far.

*Pilea gracilipes* Killip, Journ. Wash. Acad. Sci. 15:294. 1925.  
*P. standleyi* Killip, loc. cit. 298. Figure 27.

Herbs, stems often repent or climbing but the leafy flowering parts erect and usually few-branched, 10-40 cm. tall, bisexual or unisexual, leafy internodes 1-5 cm. long, 0.8-3 mm. thick, glabrous and succulent in life; stipules 0.8-4 mm. long, 1-2 mm. broad at the base, obtuse at the apex, persisting. Leaves of the same node similar in size and shape or the smaller occasionally one-half the length of the larger, petioles 3-30 (40) mm. long, 0.2-1.3 mm. thick, glabrous or rarely with a few hairs near the apex; laminae 0.7-8 cm. long, 7-30 mm. broad, elliptic-ovate to narrowly ovate or ovate-lanceolate, acute to acuminate at the apex or with the smaller leaves obtuse, obtuse to rounded at the base, bluntly to sharply serrate with 3 to 6 teeth per cm., lamina drying membranaceous to chartaceous, smooth and essentially glabrous on both surfaces or with a few hairs at the base, venation palmate with 3 primary veins, the lateral veins often united with the midvein 1-3 mm. above the midvein, midvein with 4 to many pairs of obscure secondary veins, linear cystoliths conspicuous above. Inflorescences 1 or 2 in the axils of upper leaves, unisexual but occasionally with both sexes from a single axil, often with a long (2-5 cm.) peduncle and 0 to 5 major branches, the flowers in sessile or short-stalked clusters with the male often in capitate groups 5-10 mm. in diameter and the female usually separate along the branches of the inflorescence; male flowers 1.5-2 mm. long before anthesis, perianth-parts 4 with subapical appendages 0.1-1.5 mm. long; female flowers often diseased (?) with black rounded structures at the apex of the pistil. Fruit 1.2-1.6 mm. long, 0.8-1 mm. broad, narrowly ovate in outline, lenticular but thickened in the middle and the margin narrowed and distinct, drying pale brown or yellow-brown, smooth.

Plants of wet evergreen montane forest formations between (1300) 1800 and 2800 (3300) m. elevation; probably flowering throughout the year. The species ranges from central Costa Rica to western Panama.

*Pilea gracilipes* is recognized by the medium-sized narrow leaves on thin petioles often differing slightly (25 per cent) in size at each node, the small stipules, the usual lack of pubescence, male flowers usually on long-stalked capitulae, male perianth-parts with very short (0.2 mm.) subapical appendages, female flowers in separate clusters along a simple or few-branched rachis, and the fruit a little more than 1 mm. long with definitely outlined margin. Plants of the Cordillera de Talamanca often have leaves that dry thicker and darker than those from the Central Volcanic Highlands while plants of the very moist slopes along the upper Río Grande de Orosi tend to have larger (1.5 mm.) fruit. In addition, there are plants from high altitudes that may represent intermediates with *P. cornuto-cucullata* and possess much more conspicuous appendages on the male perianth. The smaller plants of this species with more ovate leaves may be indistinguishable from plants placed in *P. dauciodora*: see the discussion under that species.

*Pilea herniarioides* (Sw.) Weddell, Ann. Sci. Nat. ser. 3, 18:207. 1852. *Urtica herniarioides* Swartz, Vet. Akad. Handl. Stockh. 8:64. 1787. *P. deltoidea* Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:298. 1851. Figure 27.

Very small herbs, erect or prostrate, 2-10 cm. tall, much branched, leafy internodes 0-10 (15) mm. long, about 0.3 mm. thick (dry), glabrous or with slender whitish hairs at the nodes; stipules about 0.3 mm. long, glabrous. Leaves of the same node similar in size, opposite along the stems but the upper with very short internodes and forming terminal rosettes, petioles (0) 0.2-6 mm. long, 0.2 mm. thick (dry), glabrous or with a few thin whitish hairs; laminae 1-8 mm. long, 2-8 mm. broad, deltoid to rhombic-orbicular or very broadly ovate, rounded to bluntly obtuse at the apex, abruptly narrowed and attenuate at the base, margins entire, the laminae drying membranaceous to thin chartaceous, glabrous or with very slender whitish hairs 0.1-0.7 mm. long on the upper surface and along the edge, venation palmate but obscure, linear cystoliths visible on the upper surface, variously oriented but the majority transverse (at right angles to the midvein). Inflorescences clustered within the axils of the terminal leaf-rosettes, about 3-4 mm. long, the flowers minute. Fruit about 0.5 mm. long and 0.2-0.3 mm. broad, ellipsoid and slightly lenticular, surfaces smooth and pale brown.

Small plants of wet evergreen areas or of wet sites in seasonally dry areas from 0-1200 m. elevation in Costa Rica; collected with flowers and fruit from July through December. This species ranges

from Southern Mexico to Western Panama, and from Florida in the United States through the West Indies.

*Pilea herniarioides* is recognized by the very small plant-size, small isomorphic leaves with entire margins, and rosette-like terminal leaves with the flowers restricted to the axils of these rosettes. This species appears to be uncommon in Costa Rica.

***Pilea hyalina*** Fenzl, Denkschr. Akad. Wiss. Math. Naturw. (Wien) 1:256. 1850. Figure 27.

Small erect herbs 10-30 cm. tall, bisexual, unbranched or more often with several lateral branches and bush-like form, leafy internodes 4-40 mm. long, 0.4-2.5 mm. thick, glabrous, succulent but drying yellowish and often translucent; stipules rudimentary and less than 1 mm. long, usually obscure. Leaves of the same node of similar size and shape, petioles 4-40 mm. long, 0.2-0.8 mm. thick (dry), glabrous; laminae 0.7-4 (6) cm. long, 0.6-3 (4) cm. broad, ovate to elliptic-ovate or rhombic, acute at the apex, obtuse to abruptly rounded at the base, crenate-serrate or serrate (except near the base) with 3 to 6 teeth per cm., laminae drying membranaceous, upper surface with a few scattered transparent hairs about 0.5 mm. long, the lower surface essentially glabrous, venation palmate with 3 primary veins, midvein with 3 to 7 pairs of obscure secondary veins, short-linear cystoliths usually visible above. Inflorescences in the axils of many nodes and solitary or paired, 3-20 (30) mm. long, short-peduncled but usually much-branched and cymose-paniculate, bisexual but the male flowers soon lost, flowers in congested clusters 1-3 mm. long; male and female flowers about 0.5 mm. long. Fruit 0.3-0.5 mm. long, ovoid to broadly ellipsoid in outline, thick-lenticular with narrowed margins, drying yellowish brown or pale brown.

Plants of seasonally dry or wet evergreen forest formations between (0) 500 and 1800 m. and collected most often around the Meseta Central and the General Valley in Costa Rica (apparently rare on the Caribbean slope and not recorded from the deciduous areas of Guanacaste), collected in flower and fruit from June to March. The species ranges from Mexico and the Lesser Antilles to Chile and Argentina.

*Pilea hyalina* is recognized by the small short-lived habit, thin isomorphic leaves at a node, few hairs on the upper lamina-surface, minute fruit, and lack of developed stipules. A succulent-stemmed plant of moist sites and along water courses; completing its life cycle in the wet season. This species resembles *P. dauciodora* with larger flowers and fruit.

***Pilea imparifolia*** Weddell, Ann. Sci. Nat. ser. 3, 18:212. 1852. Figure 25.

Herbs, scandent or rarely terrestrial and erect, usually rooting in the ground and



climbing up tree trunks with adventitious roots, occasionally epiphytic, apparently unisexual, leafy internodes 5-20 mm. long, 0.5-3 mm. thick, glabrous; stipules 0.2-1 mm. high, broad and rounded at the apex, usually persisting as an obscure ligulate ridge. Leaves of the same node differing greatly in size, the smaller leaves sessile or subsessile, larger leaves with petioles 2-10 mm. long, glabrous, decurrent on the stem; smaller laminae 5-15 mm. long, about equally broad and asymmetric, ovate to orbicular-reniform, larger laminae 2-7 cm. long, 1-3 cm. broad, elliptic to elliptic-ovate, oblong or rarely obovate, with a rounded or acute terminal tooth at the apex, acute to obtuse or attenuate at the oblique and asymmetric base, sides of the lamina often 1-2 mm. distant on the petiole, margin usually coarsely crenate-serrate with 2 to 4 teeth per cm., drying membranaceous to very thin chartaceous and dark above, glabrous, venation pinnate but with the basal secondaries often prominent and arising separately from the midvein and with 2 or 3 additional pairs of major secondary veins, cystoliths usually short-linear above and punctiform beneath. Inflorescences unisexual and very small (2-5 mm.), cymose of few (4-8) flowers sessile or on a peduncle 1-2 mm. long; male flowers borne on pedicels 1-3 mm. long, from a fasciculate base in leaf-axils or on lower leafless stems, perianth 1-2 mm. long before anthesis, minutely mucronate with subapical appendages 0.2-0.4 mm. long, glabrous; female flowers about 0.5 mm. long. Fruit about 1 mm. long, and 0.7 mm. broad, much flattened and ovoid-elliptic in outline, the edge and longitudinal central axis thickened, very pale in color (dry).

Plants of wet evergreen forest formations from near sea level to 1600 m. elevation on both the Caribbean and Pacific slopes of Costa Rica; probably flowering throughout the year. The species ranges from Costa Rica to Northern Peru and Amazonian Brazil.

*Pilea imparifolia* is recognized by the climbing habit, leaves of a node very different in size, unequal oblique base of the large laminae, pinnate or subpalmate venation, glabrous parts, and very small inflorescences. The very small size of flowers and inflorescences has resulted in very few fertile collections (*Lent 434, 1590, & 2811*). This species is closely related to *P. pansamalana* Donn.-Smith of Guatemala, but that species has longer and narrower large leaves with distinctly palmate (triplinerved) venation. *Pilea tilarana* of the Sierra de Tilaran and adjacent areas is a terrestrial with very different fruit but rather similar aspect vegetatively. Our material of *P. imparifolia* differs from South American material in the shorter appendages on the male perianth-parts (0.2 mm.) and somewhat different lamina-form. However, the form of the leaves varies greatly in this and related species, even on the same plant.

***Pilea involucrata*** (Sims) Urban, *Symb. Antill.* 1:298. 1899. *Urtica involucrata* Sims, *Bot. Mag.* 51: pl. 2481. 1824.

Herbs, lower stems often repent, erect stems 5-30 cm. tall, bisexual or unisexual, leafy internodes 0-5 (40) mm. long, about 1.5 mm. thick, with appressed ascending

often curved hairs 0.2-0.5 mm. long; stipules 3-4 mm. long equally broad, rounded at the apex, persisting. Leaves of the same node usually similar in size and shape, the leaves often clustered near or at the ends of erect stems, petioles 3-7 mm. long, about 1 mm. thick, puberulent; laminae 2-6 cm. long, 1.3-3.8 cm. wide, bluntly obtuse to rounded at the apex, narrowed below the middle to the obtuse or slightly rounded base, obovate to elliptic-obovate or oblong, margin very finely crenate-serrate in the distal half with 4 to 6 obscure teeth, laminae drying membranaceous or very thin chartaceous and dark above, ciliolate along the edge, puberulent on the veins beneath, venation palmate with 3 primary veins, cystoliths linear to fusiform and usually confined to the margin above. Inflorescences usually unisexual, subsessile in the axils of the distal leaves near the stem apex, 5-30 mm. long, much branched. Fruit about 0.5 mm. long and 0.4 mm. thick, ovoid or very slightly flattened, drying yellowish or pale brown, stigma becoming curved and subterminal.

Apparently an escape from cultivation near the Lankester gardens in the province of Cartago at 1300 m. elevation. The species ranges naturally from Central Panama to Colombia, Venezuela, and the West Indies.

*Pilea microphylla* (L.) Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:296. 1851. *Parietaria microphylla* L., Syst. ed. 10. 1308. 1759. *Pilea portula* Liebm., loc. cit. 297. 1851, (photo). Figure 25.

Herbs, erect or procumbent, usually much branched and often forming flat mats, 2-25 cm. tall, usually bisexual, stems succulent, leafy internodes (0) 1-20 mm. long, 0.3-3 mm. thick and longitudinally ridged when dry, glabrous; stipules minute or undeveloped. Leaves usually differing greatly in size at the same node, petioles 0.3-8 mm. long, glabrous; laminae 0.5-10 (14) mm. long, 0.5-4 (5) mm. broad, broadly elliptic to ovate or obovate, rounded to bluntly obtuse at the apex, usually cuneate at the base, margins entire, laminae drying thin to stiffly chartaceous (succulent in life), smooth and glabrous on both surfaces, venation pinnate, the 3 or 4 pairs of secondary veins obscure, linear cystoliths 0.2-0.4 mm. long usually visible on the upper surface and mostly transverse (at right angles to the midvein). Inflorescences of small axillary clusters 0.5-4 mm. long with 3 to 8 flowers, sessile or subsessile; male and female flowers about 0.5 mm. long. Fruit 0.3-0.5 mm. long and about 0.3 mm. broad, ovoid and somewhat flattened, smooth and lustrous brown.

Plants of open sites in wet evergreen areas or wet situations or periods in seasonally dry areas between sea level and 1500 m. elevation in Costa Rica but not collected from below 800 m. on the Pacific slopes; flowering throughout the year but collected most often from July to January. The species ranges throughout the American Tropics to altitudes as high as 2500 m. (fide Killip).

*Pilea microphylla* is recognized by its very small opposite and unequal leaves, small dense growth-form, and flowers in small axillary clusters. This species is often found in the moist crevices of walls and pavements in the towns of the Meseta Central during the

wet season. It is common in the Caribbean lowlands, but the species is not found in the deep shade of dark forest. The species varies greatly in size and aspect, from dense moss-like little plants to more diffuse forms with long (12 mm.) narrow leaves on slender internodes to 20 mm. long ( as in the type of *P. portula*).

***Pilea nummularifolia*** (Sw.) Weddell, Ann. Sci. Nat. ser. 3, 18:255. 1852. *Urtica nummularifolia* Swartz, Svensk. Vet. Akad. 8:63. 1787. Figure 27.

Herbs, usually unisexual, repent with adventitious roots at many nodes, leafy internodes 5-30 mm. long, puberulent with very thin hairs about 0.5 mm. long; stipules 2-3 mm. long, equally broad, translucent and ciliolate, rounded at the apex, persistent. Leaves usually of similar size at each node, petioles 3-12 mm. long; laminae 3-15 mm. long and equally broad, very broadly ovate to suborbicular, rounded or bluntly obtuse at the apex, rounded and subtruncate to subcordate at the base, margin minutely crenulate, the lamina drying opaque and membranaceous, upper surface with slender transparent hairs about 1.5 mm. long and with shorter hairs beneath, venation palmate with the 3 primary veins often obscure, cystoliths often obscure. Inflorescences axillary or terminal, about 1 cm. long, with few very short lateral branches. Fruit about 0.5 mm. long and 0.4 mm. broad, ovate in outline, slightly flattened and lenticular, surfaces smooth and pale brown.

Plants apparently escaped from cultivation and known only from the cities of San José and Limon in Costa Rica. The species ranges naturally from the West Indies to northern South America and Amazonian Peru. The very small round leaves crenate, puberulent, and of similar size at the same node on slender trailing stems make these plants especially attractive when grown in hanging baskets.

***Pilea pallida*** Killip, Journ. Wash. Acad. Sci. 15:295. 1925. Figure 26.

Herbs, unisexual, 0.3-0.8 m. tall, stems usually unbranched, often thickened between the nodes, leafy internodes 1-6 cm. long, 1-3.5 mm. thick (dry), minutely puberulent with appressed hairs 0.1-0.3 mm. long; stipules 2.5-4 mm. long, triangular, acute or blunt at the apex, persisting or deciduous. Leaves equal or subequal at a node (rarely differing greatly in size at the lower nodes), similar in shape, the petioles often differing in length at the same node, 4-50 mm. long, 0.6-1.7 mm. thick, glabrous or minutely puberulent, sulcate above; laminae 5-19 cm. long, 1.4-6 cm. broad, lanceolate to very narrowly elliptic or very narrowly ovate, long-acuminate at the apex, acute at the base, margin with 3 to 5 obtuse serrations per cm., lamina drying thin chartaceous, smooth and glabrous above, minutely puberulent or glabrous below, palmately 3-veined, the midvein with 10 to 16 secondary veins, minute punctate and short (0.4 mm.) linear cystoliths prominent on the darker upper surface. Male inflorescences tightly congested globose clusters in the axils of leaves, 5-10 mm. in diameter, branches of the cymes and pedicels not visible; male flower

buds about 2 mm. long including prominent (0.4 mm.) subapical appendages. Female inflorescences short-branched cymose clusters 3-15 mm. long and equally broad, the flowers closely approximate but not congested, female flower with the larger perianth-part 0.6-1 mm. long. Fruit 0.7-0.9 mm. long, broadly ovate in outline, lenticular, dark reddish brown to black and minutely papillose when dry, with raised circular areas on the 2 flat faces.

Plants of shaded sites in wet forest formations and common on the Osa peninsula but rarely found in montane forests to as high as 1700 m. elevation; flowering collections have been made from March through August. This species is known only from the areas between the Río Sardinal (Heredia) in Costa Rica and El Valle de Anton (Cocle) in Panama.

*Pilea pallida* is recognized by the large narrow and prominently serrate leaves usually subequal at a node that dry pale greenish-gray beneath, the dense axillary clusters of male flowers, and the small female inflorescences with unusual fruit.

*Pilea parietaria* (L.) Blume, Mus. Bot. Lugd. Bat. 2:48. 1856.  
*Urtica parietaria* L., Sp. Pl. 985. 1753. Figure 27.

Herbs, erect or procumbent, (10) 20-80 (100) cm. tall, bisexual, leafy internodes (5) 10-60 mm. long, 0.7-4 mm. thick, glabrous and succulent, becoming reddish; stipules 1-3 mm. long, with prominent linear cystoliths, persisting. Leaves of the same node usually of similar size but often differing in petiole-length, petioles 3-40 mm. long, 0.5-1 mm. thick, glabrous or with slender hairs, sulcate above; laminae (0.6) 1-6 (8) cm. long, (4) 6-28 mm. broad, elliptic to elliptic-ovate or ovate-lanceolate, the smaller laminae often ovate or broadly elliptic, acute or short-acuminate at the apex, obtuse or slightly rounded at the unequal base, margins entire, the laminae drying membranaceous or very thin chartaceous, smooth above with sparse slender transparent hairs 0.5-1.5 mm. long, with similar hairs along the margin and shorter hairs on the veins beneath, venation palmate with 3 primary veins, lateral veins occasionally forming cavities at the junction with the midvein, secondary veins thin and obscure, linear or slender curved cystoliths usually visible on both surfaces. Inflorescences solitary or paired in the leaf-axils, bisexual or unisexual, 1-4 cm. long, pedunculate and branched or unbranched, the flowers in clusters of 5 to 30 on a glabrous succulent rachis drying 0.2-0.6 mm. thick; male flowers usually borne on the distal inflorescences, perianth parts with very short (0.2 mm.) subapical appendages; female flowers about 1 mm. long, short-stipitate. Fruit 0.5-0.7 mm. long, 0.4-0.5 mm. broad, lenticular and ovoid to ellipsoid, pale brown and smooth, margin slightly thickened.

Plants of wet evergreen montane (premontane and lower montane wet and rain forest) formations between 1100 and 2200 m. elevation along the Caribbean slopes and in the central highlands of Costa Rica; flowering throughout the year but collected most often between January and August. The species ranges from Guatemala to Western Panama and the West Indies.

*Pilea parietaria* is recognized by the isomorphic opposite leaves with entire margins often on petioles of differing lengths, the thin laminae with slender hairs, the short persisting ligulate stipules, and the small fruit. This species is common in many areas, but it is not usually found in primary habitats. However, these primary areas do have relatively open, partly shaded sites similar to those favored by this species, and this may indicate that the species is not native to Costa Rica.

*Pilea pittieri* Killip, Journ. Wash. Acad. Sci. 15:298. 1925. *P. phenacoides* Killip in Standl., Field Mus. Bot. 18:1548. 1938. Figure 26.

Herbs, stems erect, procumbent, or climbing with adventitious roots, bisexual or unisexual, leafy internodes 1-8 (14) cm. long, 0.8-2.5 mm. thick, minutely puberulent with crooked hairs 0.1-0.5 mm. long or glabrescent; stipules 4-8 mm. long, about 2 mm. broad, blunt at the apex, oblong or obovate, glabrous, usually persisting with the leaves. Leaves of the same node of similar size or rarely one 75 per cent the length of the larger, petioles 6-50 mm. long, 0.7-1.5 mm. thick, minutely puberulent; laminae (1.5) 4-14 cm. long, 1.3-7 cm. broad, narrowly to broadly ovate or rarely elliptic-lanceolate, acuminate at the apex, obtuse to abruptly rounded at the base, margin conspicuously serrate to bluntly crenate-serrate with 1 to 4 teeth per cm., the laminae usually drying thin-chartaceous and dark above, glabrous and smooth above, puberulent on the veins beneath with very minute (0.1 mm.) curved hairs, venation palmate with 3 primary veins, midvein with 7 to 10 pairs of secondary veins, linear cystoliths 0.2-0.5 mm. long and apparent on the upper surface. Inflorescences unisexual, the male and female very different, male flowers in globose clusters 1-2 cm. in diameter on short (1-20 mm.) peduncles in the axils of older or fallen leaves, female inflorescence (2) 3-10 cm. long in the axils of distal leaves, paniculate in form with several major branches and the flowers in small open clusters; male flowers about 2 mm. long before anthesis with minutely puberulent clavate appendages about 1 mm. long subapically attached to the perianth-parts; female flowers narrowly tubular, about 1 mm. long, 1 perianth segment longer than the others and hooded. Fruit about 1.2 mm. long and 0.8 mm. broad, flattened and lenticular but often with a longitudinal central rib, ovate to elliptic in outline, drying reddish-brown.

Plants of the shade of very wet forest formations subject to the wet Caribbean winds between (500) 700 and 2300 m. elevation in Costa Rica; flowering material has been collected between February and August. This species is known only from the Caribbean slopes and adjacent highlands of Central Costa Rica, from above the San Carlos plain (Alajuela) eastward to the western edge of the General Valley (Cartago and San José).

*Pilea pittieri* is recognized by the generally isomorphic leaves often with petioles of different lengths, coarsely serrate laminae,

glabrous above and minutely puberulent on the veins beneath, large stipules, the male flowers in short-pedunculate subsessile heads and with unusual perianth-appendages, and the female flower on open branched inflorescences near the apex of the erect shoots. The plants often climb on the bases of tree trunks. The appendages on the male perianth-parts are quite variable. They may become 2 mm. long and clavate, but this may be a very unusual occurrence (*Burger & Gentry 8697*). The leaves vary from coarsely serrate to inconspicuously crenate. *Pilea pittieri* is closely related to, and may be difficult to distinguish from, *P. acuminata*.

***Pilea ptericlada*** Donn.-Smith, Bot. Gaz. 31:121. 1901. Figure 26.

Herbs, lower stems often decumbent, erect shoots 15-40 cm. tall, usually unbranched, bisexual or unisexual, leafy internodes (2) 5-35 mm. long, 1.5-4 mm. thick, at first with ascending brownish hairs 0.3-0.8 mm. long but becoming glabrescent; stipules (2) 5-8 mm. long, 3-5 mm. broad, blunt at the apex, thick and opaque, usually glabrous. Leaves of the same node usually of similar size and shape, petioles 5-18 mm. long, 0.7-1.5 mm. thick, glabrous or with ascending curved hairs 0.1-0.5 mm. long, sulcate above; laminae (3) 6-20 cm. long, 3-8.5 cm. broad, narrowly to broadly elliptic, elliptic-oblong, or narrowly obovate, usually acuminate at the apex, acute to attenuate at the base and often long decurrent, margin bluntly serrate with 1 to 4 prominent teeth per cm., laminae drying membranaceous to very thin chartaceous and dark above, glabrous above and with short (0.1-0.5 mm.) usually curved ascending yellowish-brown hairs on the veins beneath, venation palmate with 3 primary veins united for 5-20 mm. near the base, midvein with about 8 to 12 pairs of major secondary veins joining with the lateral veins, cystoliths punctate or short-linear and often obscure above. Inflorescences usually solitary in the upper leaf-axils, unisexual, 2-6 cm. long, pedunculate, with secondary and tertiary branching, paniculate with flowers in relatively open clusters; male flowers pedicellate, flower-buds narrow in early stages, about 1.5 mm. long before anthesis, perianth with subapical appendages about 0.3 mm. long; female flowers subsessile or borne on slender pedicels, pistil about 0.7 mm. long. Fruit 1.5-1.8 mm. long, 0.8-1 mm. broad, ovate to elliptic in outline, quite flat, edges and a central circular area outlined by very small brown spots on a pale yellowish background, slightly narrowed beneath the terminal stigma.

Plants of wet situations in shaded swamp forest and stream sides in evergreen lowland formations and on the forest floor in very wet evergreen forest formations from near sea level to 1800 m. elevation; flowering and fruiting collections have usually been made between March and June. The species is restricted to the Caribbean slopes and adjacent areas of Costa Rica and Panama.

*Pilea ptericlada* is recognized by the isomorphic leaves at each node that are serrate and resemble the leaves of Melastomaceae,

the laminae usually long-decurrent on the petiole with the lateral veins arising from the midvein well above the petiole, complex inflorescences, and unusual flat fruit with an ellipsoid area outlined by a narrow line of minute brown marks (dry). The decurrent lamina-base is unusual among our species but similar to *P. irrorata* Donn.-Smith of Guatemala.

*Pilea pubescens* Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:302. 1851. Figure 27.

Herbs 10-50 cm. tall, usually bisexual, lower stems often repent and rooting at the nodes, the erect stems with 1 or several branches, terminal internodes often very short with a rosette of leaves, leafy internodes (0) 7-80 mm. long, 1-3 mm. thick, puberulent with curved or crooked thin hairs 0.2-0.8 mm. long; stipules 1-4 mm. long, 1-2 mm. broad, rounded or obtuse at the apex, translucent, sparsely puberulent, persistent. Leaves of the same node similar in size, petioles 4-30 mm. long, 0.3-0.8 mm. thick, puberulent; laminae 1-6 (7) cm. long, 0.8-4 cm. broad, broadly ovate to triangular, acute to obtuse at the apex, obtuse to abruptly truncate at the base, margin coarsely serrate with 2 to 4 (6) teeth per cm., the laminae drying membranaceous to very thin chartaceous and dark above, smooth above but with translucent hairs 0.5-4 mm. long, with shorter thinner hairs on the veins beneath, venation palmate with 3 primary veins, the midvein with 3 to 6 pairs of secondaries, short linear cystoliths apparent above. Inflorescences usually restricted to the distal leafy nodes, axillary, often bisexual, 3-8 cm. long, with several divergent branches from a primary peduncle 1-6 cm. long, the secondary branches often with tertiary branches and the inflorescence a complex panicle, flowers in small (2-3 mm.) clusters along the branches of the panicle; male flowers in the lower parts of the panicle, about 2 mm. long before anthesis, perianth-parts with apical appendages about 0.3 mm. long; female flowers much more numerous than the male. Fruit 0.5-0.6 mm. long and 0.3 mm. broad, thick-lenticular, ovoid to ellipsoid in outline, smooth and reddish brown.

Plants of wet and seasonally dry evergreen forest formations between 600 and 1600 m. elevation in the Sierra de Tilaran and around the Meseta Central in Costa Rica; flowering throughout the year but collected most often between May and September. The species ranges from Mexico to Southeastern Brazil.

*Pilea pubescens* is recognized by its short stature, the leaves similar in size at a node and the upper ones closely clustered, presence of hairs on many parts, strongly serrate laminae with long hairs on the upper surface, complex often bisexual inflorescences with a few male flowers in lower parts, and the small fruit. This species is related to *P. acuminata* of larger size and the very much smaller *P. herniariodes*.

***Pilea quichensis* Donn.-Smith, Bot. Gaz. 19:12. 1894. Figure 26.**

Herbs, unisexual or bisexual, 0.5-1 m. tall, stems erect and usually unbranched above the base, leafy internodes 0.6-6 cm. long, glabrous or rarely very sparsely puberulent; stipules 0.5-3 mm. long or apparently absent in ours (caducous?), deciduous. Leaves equal or subequal at a node, similar in form, the petioles similar or very different at a node, 1-6 cm. long, 0.3-1.2 mm. thick (dry), sulcate above; laminae 6-15 cm. long, 1.3-3.5 cm. broad, very narrowly elliptic to narrowly elliptic-oblong or lanceolate, acuminate at the apex, acute at the base, the margin minutely serrulate with about 3 teeth per cm., often entire along the proximal half of the lamina, drying thin chartaceous and dark, smooth and glabrous on both surfaces, venation palmate with the 3 primary veins separate or united just above the base, secondary veins numerous, the pale colored linear cystoliths prominent on the dark upper surface. Male inflorescences (not seen from Costa Rica) 1-3 cm. long, paniculate, male flowers pedicellate, buds 1.8 mm. long, perianth with short (0.2 mm.) subapical appendages. Female inflorescences 1-3 cm. long, short-branched panicles with clustered flowers. Fruit about 0.8 mm. long, broadly ovate in outline, lenticular, surface brown and smooth or very minutely punctulate, the edge abruptly narrowed.

A species of wet evergreen cloud forests (premontane wet forest formations) between 500 and 700 m. elevation in our area and collected in January and from June to August. The species is known only from near Tilarán (Guanacaste) and Turrialba (Cartago) in Costa Rica; it ranges northward to Guatemala.

*Pilea quichensis* is recognized by the long narrow leaves similar in shape and subequal in size at a node, lack of prominent serrations, distinct cystoliths, glabrous parts, small short-branched open inflorescences, and restricted area (in Costa Rica).

***Pilea rugosissima* Killip, Proc. Biol. Soc. Wash., 52:28. 1939. Figure 27.**

Herbs with erect stems 30-100 cm. tall, usually with few or no lateral branches, apparently unisexual, leafy internodes (1) 2-7 cm. long, 2-3 mm. thick, with pale yellowish ascending strigose hairs 0.5-1.5 mm. long; stipules 6-9 mm. long, 3-4 mm. wide, rounded at the apex, auriculate at the base, translucent, slightly puberulent along the midrib abaxially, persistent. Leaves of the same node differing by about 25 per cent in lamina size and often differing greatly in petiole-length, petioles 8-50 mm. long, 0.7-1.5 mm. thick, strigose; laminae (1.5) 3-12 cm. long, (1.5) 3-6 cm. broad, ovate to narrowly ovate, acute to acuminate at the apex, abruptly rounded at the obtuse to truncate base, margin sharply serrate with 3 to 6 curved teeth per cm., laminae drying thin chartaceous and dark above, strongly rugose above with groups of hairs to 2 mm. long on the projections between the veins, much paler beneath with dense pale yellowish hairs 0.5-1 mm. on the veins and veinlets, venation pinnate or occasionally subpalmate with the basal secondaries only slightly more prominent than the distal, the 5 to 8 pairs of major secondary veins arising at angles of 30-60 degrees, minute punctate cystoliths present on the upper surface. Inflorescences unisexual and 1



or 2 in the upper leaf-axils, the male flowers in a capitate cluster about 1-2 cm. in diameter borne on an unbranched glabrous peduncle 2-4 cm. long and 0.7 mm. thick, the male flowers subsessile or short-pedicellate, flower buds about 5 mm. long (before anthesis) including the narrowly subulate distal perianth-appendages 2-3 mm. long; female flowers and inflorescences not known. Fruit unknown.

A species known only from a single collection (*Davidson 335*) from Bajo Chorro, Boquete District, Chiriquí, Panama. This collection was made in late February at an elevation of 1800 m.

*Pilea rugosissima* is recognized by the deeply rugose leaves with pinnate venation and groups of hairs on the raised projections of the upper leaf-surface, male capitula on well developed peduncles, and subsessile male flowers with very long subapical projections on the perianth-parts. While unrecorded for Costa Rica, this species may occur in the eastern parts of the Cordillera de Talamanca.

***Pilea tilarana* W. Burger, Phytologia 31:270. 1975. Figure 25.**

Herbs, usually terrestrial and erect, 10-40 cm. tall, unisexual or bisexual, leafy internodes (2) 5-20 mm. long, 1-3 mm. thick, glabrous, cystoliths apparent; stipules reduced to a ligulate ridge about 0.2 mm. high. Leaves of the same node very different in size and form but the small leaves on creeping (repent) stems sometimes isomorphic, the small leaves of a pair sessile or subsessile, petioles of the larger leaves 0.5-5 mm. long, decurrent on the stem; smaller laminae 5-20 mm. long, usually ovate to broadly elliptic, larger laminae 2-8 (12) cm. long, 0.7-2.5 (3.3) cm. broad, narrowly elliptic to elliptic-oblong or elliptic-lanceolate, obtuse at the apex, acute at the asymmetric and oblique base or slightly rounded on one side, crenate-serrate with 2 to 4 slightly raised teeth per cm., laminae drying thin chartaceous and dark above, smooth and glabrous on both surfaces, venation subpalmate with the 2 lateral veins arising near the base of the midvein, secondary veins 3 to 12 pairs and often obscure, cystoliths mostly linear, apparent on both surfaces. Inflorescences unisexual, 1-2 cm. long, male inflorescences probably borne on the leafless lower portions of the stem, cymose (?), female flowers in cymose clusters of 4 to 20 flowers on a peduncle 1-10 mm. long; male flowers not seen; female flowers with perianth parts of 2 lengths, the longer 2 mm. long, pistil 1-2 mm. long with prominent (0.4 mm.) fimbriate stigma. Fruit about 3 mm. long and 2 mm. broad, flattened and lenticular, suborbicular to ovate in outline and narrowed at the apex, stigma often persisting, drying dark brown.

This species is known only from the evergreen cloud forest (premontane wet forest) formations between 600 and 1000 m. elevation near Tilarán (Guanacaste) and near San Ramon (Alajuela) in Costa Rica; probably flowering throughout the year. The species occurs only along the Pacific side of northern Costa Rica.

*Pilea tilarana* is recognized by the leaves very different in size at the same node, the larger leaves relatively narrow and with very shallow teeth, small inflorescences, large fruit narrowed at the apex,

terrestrial habit, and the restricted range. This species is closely related to *P. chiriquina* Killip of western Panama and *P. seemanii* Killip of northern South America. *Pilea tilarana* is generally of smaller stature than either of those species and possesses much larger fruit. Collections of this species were previously identified as *P. pansamalana* Donn.-Smith of Guatemala but that species has smaller fruit, leaves that are more prominently serrate, and an epiphytic life-style. The latter resembles *P. diversissima* Killip among Costa Rican species.

Collections by Standley and Valerio (44742, 44753 the type, & 44758) from near Tilarán are generally larger and more robust than the collections from near San Ramon (*Brenes* 4527 & 20520 and *Lent* 2590), I expect that the species ranged across the Cordillera de Tilarán as far east as the area near San Ramon in a narrow altitudinal zone of forest that is now largely destroyed.

### POUZOLZIA Gaudichaud

Shrubs, subshrubs, or rarely small trees or climbers, usually bisexual; stipules paired at the nodes and free, often persistent, distally ciliolate in ours. Leaves alternate (in American species) and simple, petiolate, usually entire, venation subpalmate or pinnate with 2 prominent basal secondary veins, often trinerved, punctiform cystoliths usually visible above. Flowers borne in small axillary clusters or glomerules (in ours), male flowers with usually 4 (3-5) perianth parts and stamens, the tepals narrowed at the apex and forming a narrowed tip in the unopened bud (in ours); female flowers with a perianth-tube toothed at the narrowed apex, the perianth-tube with prominent longitudinal ribs or veins, completely enclosing the ovary, stigma long and slender. Fruit a nutlet or achene, usually smooth and glabrous, enclosed in the persisting perianth.

A pantropical genus of about 50 species. Our species may be difficult to distinguish from species of *Phenax* and *Boehmeria*. They appear to be relatively rare in our flora and are poorly represented in the collections. Like many other members of the family, these plants are often found along stream edges.

- 1a. Leaves crenate-serrate, plants of evergreen montane forest formations between 1500 and 1800 m. altitude . . . . . *P. phenacoides*.
- 1b. Leaves entire, plants not known from above 1000 m. altitude . . . . . 2.
- 2a. Petioles usually less than 1 cm. long, base of the lamina asymmetric and often emarginate (cordulate) at the petiole . . . . . *P. obliqua*.
- 2b. Petioles often much more than 1 cm. long, base of the lamina usually symmetrical. . . . . 3.
- 3a. Laminae, with a minutely tomentulose grayish or whitish surface between the

veins beneath, narrowed to an acute or obtuse base and usually narrow in outline ..... *P. guatemalana*.

- 3b. Laminae, lacking a whitish or grayish tomentum between the veins beneath, abruptly narrowed to a rounded or obtuse base, relatively broad. ....  
*P. occidentalis*.

***Pouzolzia guatemalana*** (Bl.) Weddell in DC., Prodr. 16, pt. 1:233. 1869. *Boehmeria guatemalana* Blume, Mus. Bot. Lugd. Bat. 2:206. 1856. Figure 28.

Shrubs or subshrubs 1-2 (3)m. tall, leafy internodes 8-30 mm. long, 1-4 mm. thick, sparsely to densely hirsutulous with thin whitish hairs 0.2-1 mm long; stipules about 6 mm. long and 1-2 mm. broad at the base, ciliolate along the edges and mid-vein distally. Leaves usually of similar size at adjacent nodes, petioles (0.5) 1-9 cm. long, 0.4-1 mm. thick, minutely hirsutulous; laminae (3) 6-14 cm. long, (1) 2-7 cm. broad, very narrowly ovate to lanceolate or elliptic, tapering gradually to the acuminate apex, tapering to the acute or obtuse and equal base, the margins entire, lamina membranaceous to very thin chartaceous, usually somewhat scabrous above with slender appressed hairs 0.5-1 mm. long, soft-puberulent with thin whitish hairs and a whitish or grayish tomentum covering the surfaces between the veins beneath, the 2 to 4 pairs of major secondary veins arising at angles of 30-50 degrees and strongly ascending, minute (0.05 mm.) cystoliths usually visible on the upper surface. Male flowers borne in dense axillary clusters usually below the female flowers in the same cluster, male flowers sessile or subsessile, perianth parts about 1 mm. long; with female flowers in dense axillary clusters, perianth-tube 1-1.5 mm. long, with 12-20 longitudinal ribs, densely appressed puberulent, stigma 2-3 mm. long, minutely brownish puberulent. Fruit enclosed within the persisting perianth-tube, nutlet 1-1.5 mm. long, about 1 mm. broad, broadest below the middle and ovoid, slightly flattened laterally, the surface smooth and very lustrous, drying very pale yellowish.

Plants of both evergreen and seasonally very dry and semideciduous forest formations on the Caribbean and Pacific watersheds of Costa Rica between sea level and 1000 m. altitude; probably flowering from August to December in the seasonally very dry areas and throughout the year in evergreen areas. The species occurs in Costa Rica, Panama, and Ecuador; the type was collected from Aguacate, Costa Rica, and not from Guatemala.

*Pouzolzia guatemalana* is distinguished by its alternate leaves usually pale grayish beneath and borne on long thin petioles. The isomorphic entire leaves, ribbed female perianth-tube, and ciliolate stipules help distinguish this species from rather similar looking plants in the genera *Boehmeria* and *Phenax*.

***Pouzolzia obliqua*** (Poepp.) Weddell, Archiv. Mus. Paris 9:405. 1857. *Margarocarpus obliquus* Poepp. ex Wedd., Ann. Sci. Nat. Paris ser. 4, 1:204. 1854. Figure 28.

Scandent or shrub-like plants 1-3 (5) m. tall, leafy internodes 5-50 mm. long, 0.5-3 mm. thick, usually densely puberulent with slender stiff whitish hairs 0.3-1 mm. long; stipules 3-8 (12) mm. long, narrowly triangular, puberulent along the edges and midrib abaxially. Leaves of approximately the same size at adjacent nodes, petioles (1) 2-7 (12) mm. long, 0.5-1.2 mm. thick, densely puberulent; laminae 2-12 cm. long, 0.8-5 cm. broad, very narrowly ovate or oblong to lanceolate, tapering gradually to the sharply acuminate apex, obtuse to slightly rounded at the unequal and asymmetric base, often slightly cordulate at the petiole in larger leaves, margin entire or slightly undulate, drying thin-chartaceous, smooth or slightly scabrous and with slender ascending hairs 0.5-1 mm. long above and below, the 2 to 4 pairs of major secondary veins strongly arcuate ascending, minute (0.05-0.1 mm.) round cystoliths visible above. Male flowers borne in axillary clusters of 5 to 15 flowers, perianth about 1.5 mm. long, united near the base, anthers about 0.7 mm. long (dry); female flowers borne in axillary clusters, sessile or subsessile, female perianth about 1 mm. long, styles and stigmas about 5 mm. long, minutely pale brownish papillate-puberulent. Fruit included within the persisting perianth-tube, perianth-tube about 2 mm. long, minutely puberulent and with prominent longitudinal ribs, fruit smooth and lustrous, about 1.5 mm. long, ovoid and very slightly flattened laterally.

Plants of lowland wet evergreen formations between sea level and 1000 m. on both the Caribbean and Pacific slopes of Costa Rica; flowering throughout the year. The species ranges from Guatemala to Venezuela and Peru.

*Pouzolzia obliqua* is recognized by the isomorphic entire short-petioled leaves asymmetric at the base, sessile flowers in axillary groups, female flowers with ribbed perianth-tube, and scandent or shrubby habit. This species is poorly represented in collections and appears to be rare but can be locally common; like other members of the family the plants are often found along streams.

***Pouzolzia occidentalis*** (Liebm.) Weddell, *Archiv. Mus. Paris* 9: 410. 1857. *Leucococcus occidentalis* Liebmann, *Danske Vidensk. Selsk. Skrivt. ser. 5*, 2:311. 1851. Figure 28.

Shrubs or small trees 2-5 m. tall, leafy internodes 8-40 mm. long, 1.5-3 mm. thick, minutely (0.3-0.9 mm.) hirsutulous with whitish slender hairs; stipules about 6 mm. long, 1-2 mm. broad at the base, ciliolate along the edges and midvein distally. Leaves about the same size at adjacent nodes, petioles 1.5-8 cm. long, about 1 mm. thick and longitudinally ridged when dry, minutely hirsutulous; laminae (7) 8-13 (15) cm. long, 3-7 (9) cm. broad, ovate to broadly elliptic-ovate, tapering gradually to the acuminate apex, abruptly narrowed at the obtuse or rounded and equal base, margins entire, laminae drying membranaceous or very thin chartaceous, smooth or slightly scabrous above with short (0.5 mm.) appressed hairs, soft-puberulent below with thin whitish hairs, lower surfaces between the veins drying dark and without a grayish or whitish tomentum, the usually 3 pairs of major secondary veins arising at angles of 30-50 degrees and strongly ascending, minute (0.05 mm.)

round cystoliths usually visible above. Male flowers in dense axillary clusters usually together with female flowers, the male flowers sessile or subsessile, perianth parts 1-1.5 mm. long; female flowers with a perianth-tube about 1 mm. long, stigma 2-3 mm. long. Fruit enclosed within the persisting and strongly 10-16 ribbed perianth-tube 1.5-2 mm. long, nutlet about 1.5 mm. long and 1 mm. broad, slightly lenticular, smooth, and very lustrous.

Rare plants of the wet evergreen formations of the Caribbean lowlands. I have seen only two collections from our area: *Oersted 14257* (the type) from the Río San Juan and *Woodson, Allen, & Seibert 1528* from the Isla Taboga, Panama. These were collected in June and July, respectively. The species ranges from Honduras to Colombia and Venezuela and is found in Puerto Rico (fide Killip).

*Pouzolzia occidentalis* is recognized by its relatively broad leaves on long slender petioles and lacking a whitish or grayish tomentum beneath. In other respects it is very similar to *P. guatemalana*.

***Pouzolzia phenacoides*** Killip, Journ. Wash. Acad. Sci. 15:299. 1925. Figure 28.

Herbs or subshrubs 1-2 m. tall, leafy internodes 3-30 mm. long, 0.6-2 mm. thick, puberulent with short (0.1-0.5 mm.) slender curved whitish hairs; stipules 3-8 mm. long, 1-2 mm. broad at the base, ciliate along the margins and midrib abaxially, drying pale brown. Leaves approximately the same size at adjacent nodes, petioles, (4) 8-40 mm. long, 0.3-0.6 mm. thick (dry), sparsely puberulent; laminae 1-7 cm. long, 0.6-3.5 mm. broad, ovate to narrowly ovate, acuminate at the apex, obtuse or slightly rounded at the equal and symmetrical base, margin with 3 to 6 conspicuous serrations per cm., the laminae drying membranaceous, smooth or somewhat scabrous with stiff slender hairs 0.5-1 mm. long on both surfaces, the 2 or 3 pairs of major secondary veins strongly ascending, minute cystoliths apparent on both surfaces. Male flowers 1 to 10 and sessile or with short (1 mm.) pedicels in the axils of leaves, perianth about 1.5 mm. long, anthers about 0.7 mm. long; female flowers subsessile or very short-pedicellate in axillary clusters (often beneath the male flowers), perianth-tube weakly 10-20 ribbed. Fruit finally breaking through the persisting perianth tube, 2-3 mm. long, ellipsoid and somewhat lenticular, smooth and very lustrous.

This species is apparently confined to shaded sites within lower montane moist forest formations between 1500 and 1800 m. elevations and is known from the collections of Paul Standley on the slope of Volcán Poas (Alajuela), above Escazu and Sta. Maria de Dota (San Jose), and the Cerro de la Carpintera (Cartago), made between December and February. The species is known only from Costa Rica and Guatemala.

*Pouzolzia phenacoides* is recognized by the thin isomorphic leaves with conspicuous teeth, ciliate stipules, weakly ribbed perianth-tube, and the small number of very lustrous fruit. This species looks

very much like species of *Phenax* or *Boehmeria*, but those differ in the secondary veins not strongly ascending, larger numbers of flowers per cluster, and lack of a perianth-tube (in *Phenax*).

### URERA Gaudichaud

Large herbs, shrubs or small trees, usually unisexual but occasionally bisexual, sharp stinging spines often present; stipules paired and free or more often connate across the base of the petiole and ligulate. Leaves alternate in a spiral, simple, petiolate, the laminae entire, serrate, or deeply lobed, usually pinnately veined, cystoliths often visible on the upper surface of older leaves. Inflorescences axillary or cauliflorous, dichotomously or irregularly branched and cymose or paniculate, occasionally simple with only a few clustered flowers. Male flowers with 4 or 5 imbricate perianth-parts, stamens 4 or 5, a pistillode present. Female flowers subtended or loosely enclosed or subtended by 4 equal or very unequal (in ours) perianth-parts, stigma minutely fimbriate and persisting in fruit. Fruit enclosed in the accrescent perianth or the perianth remaining thin and bract-like, achene usually lenticular with an apical or subapical stigma and glabrous surfaces.

The genus is found in tropical America, Africa, and Asia. The neotropical species are in need of a careful monographic study. Among our species, those with large spines that give a very painful sting (*U. baccifera* and *U. laciniata*) are poorly represented in collections, while those species that do not sting so fiercely (*U. caracasana* and *U. elata* s.l.) display a wide and complex pattern of variation.

- 1a. Leafy stems with many sharp stinging spines 1-10 mm. long; laminae deeply lobed or with conspicuous teeth 1-4 cm. apart; perianth remaining thin and bract-like in fruit . . . . . 2a.
- 1b. Leafy stems usually lacking large sharp stinging spines except in juvenile plants; laminae entire to closely serrate or dentate; stipules united across the petiole-base and ligule-like; perianth enclosing the ovary and becoming succulent in fruit, usually orange or red . . . . . 3a.
  - 2a. Leaves pinnately deeply lobed; stipules united only near the base. . . . .  
*U. laciniata*.
  - 2b. Leaves unlobed but distantly serrate or dentate; stipule usually united but with 2 separate apices . . . . . *U. baccifera*.
- 3a. Laminae usually broad and cordate or subcordate at the base, usually soft puberulent beneath, often bullate above, becoming as much as 40 cm. broad; stipules 12-18 mm. long and usually densely puberulent; fruiting inflorescence reddish to orange . . . . . *U. caracasana*.
- 3b. Laminae narrow to broad and usually acute to truncate at the base, glabrescent to sparsely puberulent beneath; stipules 5-14 mm. long and sparsely puberulent; fruiting inflorescence bright orange. . . . . *U. elata*.

*Urtica baccifera* (L.) Gaudichaud, Voy. Uran. Bot. 497. 1826. *Urtica baccifera* L., Sp. Pl. ed. 2, 1398. 1762. *Urtica grandidentata* Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:296. 1851. Figure 30.

Erect herbs, shrubs or few-branched trees 1-4 (6) m. tall, leafy internodes 1-20 cm. long, 6-20 mm. thick, hollow, minutely puberulent with slender hairs 0.2-0.5 mm. long and with short (1-4 mm.) broad-based stinging spines; stipules united for much of their length but usually with 2 separate apices and sometimes split in two, 10-16 mm. long, sparsely to densely puberulent. Leaves quite variable in size and form on different plants, petioles 3-30 cm. long, 2-6 mm. thick (dry), minutely puberulent and usually with a few stinging spines; laminae (10) 20-40 cm. long, (6) 18-40 cm. broad, ovate to very broadly ovate (rarely narrowly ovate to elliptic), short-acuminate at the apex, rounded to truncate or cordate (rarely obtuse) at the base, margin with prominent short (2-6 mm.) teeth 1-4 cm. distant, laminae drying membranaceous to thin-chartaceous, scabrous above with scattered distant minute (0.1-0.4 mm.) spines or these absent, usually with slender soft hairs 0.2-0.7 mm. long (in ours) and with sharp stinging spines 0.5-3 mm. long on the major veins beneath, the 6 to 8 pairs of major secondary veins arising from the midvein at angles of 50-70 degrees, cystoliths not conspicuous above. Male inflorescences separate or (rarely ?) the male flowers borne at the base of the large, essentially female inflorescence, the male flower 2-3 mm. broad before anthesis. Female inflorescences 4-12 cm. long, paniculate and much branched, female flowers separate or clustered, usually borne on a slender pedicel, pistil 1 mm. long in early anthesis, stigma about 0.3 mm. long and equally thick. Fruit often subtended by 2 thin broad bract-like perianth parts 1-2 mm. long, achene 3 mm. long and 2 mm. broad, lenticular, glabrous, with a thickened rim around the periphery, stigma terminal or subterminal.

Plants of evergreen or partly deciduous formations between sea level and 1200 m. elevation on both the Caribbean and Pacific slopes of Costa Rica and probably flowering throughout the year. The species ranges from southern Mexico to tropical South America and the West Indies.

*Urtica baccifera* is readily recognized by the stinging spines and unlobed leaves with prominent teeth. These plants are poorly represented in herbaria and probably for good reason: this is said to be one of the most severely stinging plants in Central America (see Standley in Fieldiana: Bot. 24, pt. 3:426. 1952). The plant is often used for hedgerows, and much of its present distribution may be attributable to man's use of the species for this purpose.

*Urtica caracasana* (Jacq.) Grisebach, Fl. Brit. W. Ind. 154. 1859. *Urtica caracasana* Jacq., Hort. Schoenbr. 3:71, pl. 396. 1798. *Urtica verrucosa* Liebm., Danske Vidensk. Selsk. Skrivt., ser. 5, 2:295. 1851. Figure 30.

Shrubs or small trees 2-8 (?15) m. tall, leafy internodes, 5-60 mm. long, 2-10 mm.

thick, at first densely puberulent with short (0.1-0.5 mm.) grayish hairs; stipules united and 2-ribbed, 12-18 mm. long, usually densely puberulent with hairs 0.5-1 mm. long. Leaves varied in different plants, petioles 3-15 (25) cm. long, 1-5 mm. thick, usually densely puberulent; laminae 10-32 (44) cm. long, 7-26 (40) cm. broad, broadly ovate or ovate (rarely broadly elliptic), acute to acuminate at the apex, rounded to the base and cordate to subcordate (rarely obtuse), margin serrate with 2 to 4 teeth per cm., lamina drying thin-chartaceous, scabrous to smooth above with scattered small (0.5-1.5 mm.) hairs, the hairs often elevated and the surface bullate, soft or slightly scabrous to the touch beneath with grayish-white hairs 0.5-1.5 mm. long on the veins beneath, the 7 to 11 pairs of major secondary veins arising at angles of 40-60 degrees, cystoliths usually small (0.05-0.1 mm.) and round, rarely long and narrow. Male inflorescence occasionally borne above the female when found on the same twig (?rare), 3-12 cm. long and variously branched, the branches with short thin hairs, male flower 1-2 mm. broad before anthesis, often clustered in small (3-6 mm) glomerules and pink in color. Female inflorescences 2-10 cm. long and enlarging in fruit, the flowers separate or occasionally in glomerules, female flowers sessile or pedicellate, pistil about 0.7 mm. long in early stages of anthesis. Fruiting inflorescence becoming as much as 30 cm. long and often with sharp stinging spines about 1 mm. long, fruit enclosed in the succulent perianth, drying irregularly, about 1.5 mm. long, orange when ripe, achene about 1 mm. long and equally broad, lenticular, glabrous, or slightly pusticulate.

Plants of evergreen or partly deciduous forest formations between sea level and 2500 (?2800) m. elevation in Costa Rica; flowering throughout the year but collected most often between January and July. The species ranges from Mexico to northern South America and the West Indies.

*Urera caracasana* is recognized by its generally broad laminae often cordate at the base and soft-puberulent beneath and the bright orange fruit. The members of this species vary less than those of the closely related *U. elata*, but there is sufficient variation among these plants so that about 10 per cent of the material seen cannot be identified with confidence. The patterns of variation of the two species overlap, but it is not possible to say whether the plants possessing intermediate characteristics are hybrids or whether they are simply unusual individuals of one or the other species. Whoever chooses to revise the neotropical species of this genus will encounter some of the most perplexing patterns of variation that the neotropical flora has to offer. These plants, like those of *U. elata*, are referred to as *ortiga*, *ortiga blanca*, and *tabaquillo* in Costa Rica.

*Urera elata* (Sw.) Grisebach, Fl. Brit. W. Ind. 154. 1860. sensu lato. *Urtica elata* Sw., Prodr. 37. 1788. *Urera killipiana* Standl. & Steyerl., Fieldiana: Bot. 24, pt. 3:427-428. 1952. Figure 30.



Shrubs, trees or occasionally scandent, 3-8 m. tall, leafy internodes 3-50 mm. long, 2-5 (7) mm. thick, minutely puberulent with grayish slender hairs 0.1-1 mm. long; stipules united and 2-ribbed, 5-14 mm. long, sparsely puberulent with short (0.1-0.5 mm.) hairs. Leaves extremely variable in size and shape (often on the same tree), petioles 2-10 (22) cm. long, 1-3 mm. thick, minutely puberulent and lacking spines; laminae 8-18 (28) cm. long, (3) 4-18 cm. broad, narrowly to broadly ovate, elliptic-ovate or narrowly elliptic to slightly obovate, short- to long-acuminate at the apex, obtuse to abruptly rounded (rarely subcordate) at the base, entire or with shallow (1-3 mm.) serrations with 2 to 4 teeth per cm., lamina drying membranaceous to thin-chartaceous smooth or somewhat scabrous above and glabrous or with scattered short (0.5 mm.) hairs, smooth or slightly scabrous beneath with slender hairs 0.1-1 mm. long or more often glabrescent, the 4 to 7 pairs of major secondary veins arising at angles of 20-60 degrees, cystoliths usually visible above on the older leaves, small (0.05-0.1 mm.) and round or longer (0.5 mm.) and narrow and radiating outward from small areoles. Male inflorescences 1-5 cm. long, of 1 to many glomerules or the flowers separate on a simple, few-branched, or many-branched (paniculate) rachis, the rachis minutely puberulent and often with small (1 mm.) stinging spines; male flower about 2 mm. broad before anthesis, sometimes becoming exserted on slender peduncles to 4 mm. long and the pedicels persisting. Female inflorescence 2-5 (9) cm. long, usually much branched, minutely puberulent and often with a few stinging spines, female flowers about 1 mm. long in early anthesis, stigma about 0.3 mm. long and equally thick. Fruit enclosed by 2 broad imbricate and accrescent perianth parts with a minutely verrucose surface, 1-2 mm. long, seed about 1 mm. long (? immature), lenticular, and with smooth glabrous surfaces.

Widespread plants of evergreen or partly deciduous formations from near sea level to 2200 m. elevation in Costa Rica and flowering throughout the year. The species ranges from Mexico and the West Indies to South America (but see below).

*Urera elata* is recognized by the bright orange fruit, quite variable leaves that are usually narrowed to the base and only sparsely puberulent beneath, and the small united stipules. Plants differ in the presence of stinging hairs on mature parts; often the stinging hairs are only found in the female inflorescences. The species, here interpreted in a very wide sense, encompasses a great deal of variation. In some collections the narrow radiating cystoliths on the upper leaf-surface is correlated with a consistently narrow leaf-form. These specimens have often been referred to as *U. alceifolia* (Poir.) Gaud., which, according to Killip (1960), is synonymous with *U. caracasana*. The present interpretation and circumscription of *U. elata* is very tentative, and the name may not apply to our material. This species was originally described from Jamaican material, and C.D. Adams (Flowering Plants of Jamaica 237. 1972) states that the species is endemic to Jamaica. He is probably correct (in a strict sense), but I prefer continuing to use this old name in a very broad

sense until the genus is given intensive monographic study; see the discussion under *U. caracasana*.

*Urera laciniata* (Goudot) Weddell, Annal. Sci. Nat. Paris ser. 3, 18:203. 1852. *Urtica lacinata* Goudot ex Wedd., loc. cit., as synonym. *Urera girardinoides* Seem., Bot. Voy. Herald 194. 1854. Figure 30.

Erect herbs or few branched shrubs or little trees 1-5 m. tall, leafy internodes 0.5-10 (20) cm. long, 5-20 mm. thick (dry), hollow, sparsely puberulent with minute (0.1-0.4 mm.) slender hairs and with numerous sharp stinging spines 2-9 mm. long; stipules apparently paired or partly fused near the base, 5-15 mm. long, sparsely puberulent. Leaves quite variable in size on the same plant, petioles 6-30 cm. long, 2-7 mm. thick, very minutely puberulent and armed with sharp stinging spines; laminae 15-40 cm. long, 10-45 cm. broad, broadly ovate or triangular in general outline but deeply pinnately lobed with the lobes diminishing in size toward the apex, acuminate apically, truncate to cordate at the base, margins of the lobes entire or with a few distinct teeth, laminae drying membranaceous to thin-chartaceous, upper surface slightly rough to the touch and with a few isolated spines, lower surface with spines 1-6 mm. long on the major veins and with very minute (0.05-0.2 mm.) hairs on all the veins, the 4 to 7 pairs of major secondary veins arising at angles of 50-80 degrees, cystoliths not apparent or minute on the upper surface. Male flowers said to be borne in glomerules (not seen). Female inflorescences 4-20 cm. long, paniculate and usually much-branched, the female flowers separate or occasionally clustered in small glomerules, sessile or subsessile, pistil 1-2 mm. long, the stigma long (1 mm.) and narrow. Fruit subtended by usually 2 thin bract-like perianth parts about 1 mm. long, achene 1.5-2 mm. long, about 1.6 mm. broad, thin and lenticular, essentially glabrous, stigma subapical on the fruit and curved.

An uncommon species of apparently evergreen formations and often found along streams and rivers between sea level and 800 m. elevation on both the Caribbean and Pacific sides of Costa Rica. The species ranges from Costa Rica southward to Venezuela and Peru.

*Urera laciniata* is easily recognized by its stinging spines, deeply lobed leaves with the basal lobes much larger than the distal, and few-branched habit. The stinging hairs may explain, in part, the scarcity of material in herbaria.

## URTICA Linnaeus

Annual or perennial herbs with stinging hairs, unisexual or bisexual, stems simple or branched; stipules paired and free or united across the stem (interpetiolar). Leaves opposite and simple, petiolate, the laminae serrate, dentate, or incised, usually thin, punctate cystoliths usually present. Inflorescences bisexual or uni-

sexual, the flowers in clusters in sessile groups, branched panicles, or spikes; male flower with 4 perianth-parts, the perianth-parts equal and without appendages; female flowers with 2 minute and 2 larger perianth parts, the larger erect and opposite, enclosing the pistil, persisting in fruit. Fruit ovate to elliptic in outline, compressed laterally and lenticular, enclosed by the larger inner perianth-parts, stigma terminal.

A genus of about 30 species found primarily in temperate regions and on high mountains in the tropics. The genus is represented by a single species in Costa Rica, but other species have been introduced and will continue to be introduced as weeds. However, these have apparently not persisted or spread extensively. The stinging hairs facilitate recognition of the genus. The common Spanish name "ortiga" or "hortiga" is a direct derivative of the Latin *urtica*.

*Urtica leptophylla* H.B.K. Nov. Gen. & Sp. 2:39. 1815. *U. nicaraguaensis* Liebm., Danske Vidensk. Selsk. Skrivt. ser. 5, 2:292. 1851. *U. copeyana* Killip in Standl., Field Mus. Bot. 18:398. 1937. Figure 24.

Herbs or subshrubs 0.4-1.5 m. tall with stinging hairs on stems, leaves, and inflorescences, usually bisexual, erect stems usually with branches, basal stems becoming woody, leafy internodes (1) 2-6 (10) cm. long, 0.7-3 mm. thick, with small (0.2 mm.) appressed hairs and sharp translucent stinging hairs 1-2 mm. long; stipules united across the stem for at least half their length, 2-5 mm. long, 1-3 mm. broad, bifurcate apically, sparsely puberulent, persistent. Leaves of the same node usually similar in size and shape, petioles 0.5-6 cm. long, 0.3-1.5 mm. thick (dry); laminae (1.5) 3-12 cm. long, 1-5 (8) cm. broad, narrowly ovate to triangular, tapering gradually to the acute or acuminate apex, usually abruptly narrowed at the truncate to subcordate base, margin prominently serrate with 2 to 4 teeth per cm., laminae drying thin chartaceous and usually dark on both surfaces, with isolated stinging hairs above and smaller (0.1-0.5 mm.) hairs on both surfaces, venation subpalmate with a pair of lateral secondary veins from the base, with 2 or 3 pairs of major secondary veins from the distal part of the midvein, minute punctate cystoliths present above. Inflorescences usually bisexual, usually paired in the axils of leaves throughout the length of the stem, 1-4 cm. long, spicate with flower clusters along the length of the unbranched rachis or rarely branched near the base, male flowers usually present at the base of the spikes, about 1.5 mm. long before anthesis, perianth-parts without appendages; female flowers densely or loosely clustered, the 2 larger perianth-parts becoming about 1 mm. long. Fruit about 1.2 mm. long and 1.1 mm. broad, ovate in outline and thick-lenticular, smooth and pale brown, narrowed slightly below the terminal stigma, loosely enclosed in the persisting perianth-parts.

Plants of partly open secondary vegetation in the wet evergreen montane forest formations between (500) 2000 and 3200 m. elevation in Costa Rica; flowering collections have been made in August and from December to March. The species is found in Costa Rica, Colombia, and Ecuador.

*Urtica leptophylla* is recognized by the stinging hairs, opposite conspicuously serrate leaves, spike-like inflorescences, and unusual stipules united (interpetiolar) for more than half their length and often quite broad. This species is closely related to *U. magellanica* Juss. ex Poir., but the latter has larger fruit and ranges no further north than Peru. This species resembles *U. mexicana* Liebm. but that species has separate stipules. Despite the name of one of the synonyms, this species has never been recorded from Nicaragua; the name referred to a small town on Volcán Irazú.

#### A SPECIES OF UNCERTAIN POSITION. Figure 24.

Herbs or subshrubs, erect to 50 cm. tall or scandent, usually with slender roots at most nodes, apparently bisexual, leafy internodes (1) 2-9 cm. long, 0.7-3.5 mm. thick, puberulent with short (0.1-1.3 mm.) thin whitish hairs, becoming sparsely puberulent and dark reddish in color; stipules 5-10 mm. long, 1.5 mm. broad at the base, aculeate and persisting, glabrescent. Leaves opposite, isomorphic or differing slightly in size or petiole-length at the same node, petioles (2) 4-30 (50) mm. long, 0.5-1.3 mm. thick, puberulent; laminae 2-11 cm. long, 1-7 cm. broad, ovate, acuminate at the apex, abruptly narrowed at the obtuse to subtruncate base, coarsely serrate with 2 to 6 teeth per cm., laminae drying membranaceous to thin chartaceous and dark in color, becoming slightly rugose in age, sparsely puberulent with thin lustrous hairs 0.7-2 mm. long, more densely puberulent with shorter hairs on the veins beneath, venation palmate with 3 primary veins, midvein with 2 to 4 pairs of prominent secondary veins, minute dark-punctate cystoliths visible above. Inflorescences fasciculate in the leaf axils, flower clusters about 8 mm. long and usually subtended by the 4 persisting stipules; male flowers sessile or pedicellate, perianth about 2.5 mm. long, including a narrow subapical projection 1-1.5 mm. long, filaments about 2 mm. long, anther 1 mm. long; female flowers about 1 mm. long with a central longitudinal groove and 2 short stigmas. Fruit sessile in the axils of lower leaves, 1-2 mm. long, 2- or 3-angled, stigmas apparently persisting, locules usually 2 (3), the fruit very tightly enclosed within the (apparent) perianth-tube.

Plants of the very wet Caribbean slopes of Central Costa Rica between 1000 and 1500 m. elevation; apparently flowering throughout the year. This species is known only from the Río Claro (Río Honduras drainage) below La Palma (*Burger et al.* 4137, 6270, & 7651) in the province of San José and above Cachi (*Lent 1607*) in Cartago Province.

This species is recognized by the opposite leaves subtending small clusters of flowers, the usually four persisting stipules at each leafy node, the 4-parted male flowers with projections on the perianth-parts, the 2- or 3-angled fruit tightly enclosed within a perianth-tube that is unlobed apically and the presence of usually two locules, each with a seed. The latter condition violates a basic char-

acter of the Urticaceae: an ovary with a single locule containing a single ovule. I believe the present situation may be attributable to the growing together of two female flowers. The longitudinal groove favors this interpretation. Because the stigmatic areas of these flowers are so small, it may be that the fruit develop without pollination.

The unusual fruit and opposite leaves make it difficult to place these plants. Because they have the four separate stipules and sessile clusters of flowers, I believe that these plants are closely allied to the genus *Boehmeria*.



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  *parietaria* 266  
  *verrucosa* 277  
Urticaceae 218-220, 221-227, 282-283
- Yahal* 202









Families of seed plants known or expected to occur in Costa Rica and adjacent areas numbered according to the sequence of Engler's *Syllabus der Pflanzenfamilien*, edition 11, reworked by L. Diels (1936).

1	Cycadaceae	79	Monimiaceae	154	Cactaceae
2	Taxaceae	80	Lauraceae	155	Thymelaeaceae
3	Podocarpaceae	81	Hernandiaceae	156	Elaeagnaceae
4	Araucariaceae	82	Papaveraceae,	157	Lythraceae
5	Pinaceae		incl. Fumariaceae	158	Punicaceae
6	Cupressaceae	83	Capparidaceae	159	Lecythidaceae
7	Gnetaceae	84	Cruciferae	160	Rhizophoraceae
8	Typhaceae	85	Tovariaceae	161	Combretaceae
9	Potamogetonaceae	86	Resedaceae	162	Myrtaceae
10	Najadaceae	87	Moringaceae	163	Melastomataceae
11	Alismataceae	88	Droseraceae	164	Onagraceae
12	Butomaceae	89	Crassulaceae	165	Halorrhagaceae
13	Hydrocharitaceae	90	Saxifragaceae	166	Araliaceae
14	Triuridaceae	91	Brunelliaceae	167	Umbelliferae
15	Gramineae	92	Cunoniaceae	168	Cornaceae
16	Cyperaceae	93	Hamamelidaceae	169	Clethraceae
17	Palmae	94	Rosaceae	170	Monotropaceae
18	Cyclanthaceae	95	Connaraceae	171	Pyrolaceae
19	Araceae	96	Leguminosae	172	Ericaceae
20	Lemnaceae	97	Krameriaceae	173	Theophrastaceae
21	Mayacaceae	98	Oxalidaceae	174	Myrsinaceae
22	Xyridaceae	99	Geraniaceae	175	Primulaceae
23	Eriocaulaceae	100	Tropaeolaceae	176	Plumbaginaceae
24	Bromeliaceae	101	Linaceae,	177	Sapotaceae
25	Commelinaceae		incl. Humiriaceae	178	Ebenaceae
26	Pontederiaceae	102	Erythroxylaceae	179	Symplocaceae
27	Juncaceae	103	Zygophyllaceae	180	Styracaceae
28	Liliaceae	104	Rutaceae	181	Oleaceae
29	Haemodioraceae	105	Simarubaceae	182	Loganiaceae
30	Amarylidiaceae	106	Burseraceae	183	Gentianaceae
31	Velloziaceae	107	Meliaceae	184	Apocynaceae
32	Dioscoreaceae	108	Malpighiaceae	185	Asclepiadaceae
33	Iridaceae	109	Trigonaceae	186	Convolvulaceae
34	Musaceae	110	Vochysiaceae	187	Polemoniaceae
35	Zingiberaceae	111	Polygalaceae	188	Hydrophyllaceae
36	Cannaceae	112	Dichapetalaceae	189	Boraginaceae
37	Marantaceae	113	Euphorbiaceae	190	Verbenaceae
38	Burmanniaceae	114	Callitrichaceae	191	Labiatae
39	Orchidaceae	115	Buxaceae	192	Solanaceae
40	Casuarinaceae	116	Coriariaceae	193	Scrophulariaceae
41	Piperaceae	117	Anacardiaceae	194	Bignoniaceae
42	Chloranthaceae	118	Cyrillaceae	195	Pedaliaceae
43	Lacistemaceae	119	Aquifoliaceae	196	Martyniaceae
44	Salicaceae	120	Celastraceae	197	Orobanchaceae
45	Garryaceae	121	Hippocrateaceae	198	Gesneriaceae
46	Myricaceae	122	Staphyleaceae	199	Lentibulariaceae
47	Juglandaceae	123	Icacinaceae	200	Acanthaceae
48	Batidaceae	124	Hippocastanaceae	201	Plantaginaceae
49	Betulaceae	125	Sapindaceae	202	Rubiaceae
50	Fagaceae	126	Sabiaceae	203	Caprifoliaceae
51	Ulmaceae	127	Balsaminaceae	204	Valerianaceae
52	Moraceae	128	Rhamnaceae	205	Dipsacaceae
53	Urticaceae	129	Vitaceae	206	Cucurbitaceae
54	Podostemonaceae	130	Elaeocarpaceae	207	Campanulaceae
55	Proteaceae	131	Tiliaceae	208	Compositae
56	Olaceae	132	Malvaceae		
57	Opiliaceae	133	Bombacaceae		
58	Loranthaceae	134	Sterculiaceae		
59	Aristolochiaceae	135	Dilleniaceae		
60	Rafflesiaceae	136	Actinidiaceae		
61	Balanophoraceae	137	Ochnaceae		
62	Polygonaceae	138	Caryocaraceae		
63	Chenopodiaceae	139	Marcgraviaceae		
64	Amaranthaceae	140	Quinaceae		
65	Nyctaginaceae	141	Theaceae		
66	Phytolaccaceae	142	Guttiferae		
67	Aizoaceae		incl. Hypericaceae		
68	Portulacaceae	143	Elatinaceae		
69	Basellaceae	144	Cistaceae		
70	Caryophyllaceae	145	Bixaceae		
71	Nymphaeaceae	146	Cochlospermaceae		
72	Ceratophyllaceae	147	Violaceae		
73	Ranunculaceae	148	Flacourtiaceae		
74	Berberidaceae	149	Turneraceae		
75	Menispermaceae	150	Passifloraceae		
76	Magnoliaceae	151	Caricaceae		
77	Anonaceae	152	Loasaceae		
78	Myristicaceae	153	Begoniaceae		













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