

A revision of *Helietta* and *Balfourodendron* (Rutaceae–Pteleinae)

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Pirani, J. R. (Universidade de São Paulo, Caixa Postal 11461, 05422-970, São Paulo, SP, Brazil). A revision of *Helietta* and *Balfourodendron* (Rutaceae–Pteleinae). *Brittonia* 50: 348–380. 1998.—A taxonomic revision of two of the four genera in the rutaceous subtribe Pteleinae is presented. *Helietta* and *Balfourodendron* are neotropical taxa that share trifoliolate leaves, terminal thyrses, small isostemonous flowers, syncarpous 4–5-carpellate ovaries, winged fruits, and seeds with endosperm. They differ mainly in that *Balfourodendron* has leaf domatia and a samara with broad verticillate wings, while *Helietta* lacks domatia and has a fruit that separates into free samaroid mericarps, each with a dorsal wing. Two species are recognized in *Balfourodendron*, *B. riedelianum* and *B. molle*, the latter being a new combination. *Helietta* comprises 8 species, including a new combination, *H. glaziovii*. Keys to the species, descriptions, synonyms, illustrations, and comments on the geographic distribution and ecology of each taxon are presented.

Key words: *Balfourodendron*, *Helietta*, Pteleinae, Rutaceae, South America, West Indies, Central America, United States, Mexico, taxonomic revision.

The subtribe Pteleinae Engl. (tribe Toddalioideae, subfamily Toddalioideae) is defined chiefly by trifoliolate, glandular-punctate leaves, small isostemonous flowers with a syncarpous, 2–5-carpellate ovary, winged fruits (most taxa), and seeds with endosperm. According to Engler (1931), it comprises four genera: *Ptelea* L., *Taravalia* Greene, *Helietta* Tul., and *Balfourodendron* Mello ex Oliver. The former consists of a single species, *P. trifoliata* L. (or of three species according to some authors), widely distributed in temperate to subtropical United States and in Mexico (Sonora to Tamaulipas and Oaxaca). Another monotypic genus, *Taravalia aptera* (Parry) Greene, is confined to Baja California, Mexico.

The other two genera have neotropical distributions. *Helietta* occurs in Mexico and adjacent United States (Texas), Cuba, Venezuela, Colombia, Peru, Brazil, Paraguay, and northern Argentina, while *Balfourodendron* is restricted to the latter three countries. This paper presents a taxonomic revision of these two closely related genera.

Taxonomic History

Helietta and its type, *H. plaeana* Tul., were described in 1847, on the basis of an A. Plée collection from Maracaibo, Venezuela. The generic name commemorates Dr. Louis Theodore Hélie, a French physician who wrote about the medicinal properties of *Ruta* (Tulasne, 1847).

Balfourodendron was described by Oliver in 1877, on the basis of a specimen collected by Correa de Mello in São Paulo State, Brazil, and sent by him to the Royal Botanic Gardens, Kew, along with a letter in which he suggested the generic name (dedicated to the British botanist J. H. Balfour) and specific epithet (*B. eburneum*, which alludes both to the resemblance of its wood to ivory and to one common name of the species). The same species, however, had been described previously as *Esenbeckia riedeliana* by Engler in 1874 and later transferred by Engler in 1896 to *Balfourodendron riedelianum* (Engl.) Engl.

The fruit is the main distinguishing char-

acter at the generic level in the Pteleinae, so flowering specimens can easily be misidentified to genus in this subtribe or mistakenly identified as *Esenbeckia* (Pilocarpinae, Cusparieae, Rutoideae), which has flowers somewhat similar to those of *Helietta* and *Balfourodendron*.

The type of *Esenbeckia mollis* Miq. bears flowers and only very young fruits, so Kaastra (1977) transferred it to *Helietta*. Recent collections, however, bear mature samaras, indicating that it is better placed in *Balfourodendron*, a genus heretofore considered monotypic. Likewise, *Esenbeckia glaziovii* Engl. and *E. cuspidata* Engl., described in 1896, and *Esenbeckia attata* Pittier, described in 1921, belong in *Helietta*.

Ptelea parvifolia A. Gray ex Hemsl., described in 1879, was based on two syntypes, both from Mexico: a fruiting specimen collected by Gregg that represents *Ptelea baldwinii* Torr. & A. Gray (? = *P. trifoliata* L.), as pointed out by Gray (1897), and a flowering specimen collected by Berlandier. The latter specimen is here designated as the lectotype of *Helietta parvifolia* (A. Gray ex Hemsl.) Benth., a combination which, when published in 1882, added a second species to this genus.

In the same publication, Bentham (1882) also described *Helietta apiculata* Benth., based on a specimen from Paraguay. This name was overlooked by most botanists for almost eight decades; *H. longifoliata* Britton was the name most commonly applied to this remarkable South American plant. From 1907 to 1984, six more species were described in *Helietta*, of which four are maintained in the present treatment.

Since the original descriptions, *Helietta* and *Balfourodendron* have always been associated with the other genera that Engler (1896, 1931) assigned to the subtribe Pteleinae. This subtribe was maintained with the same circumscription and in the same subfamily Toddalioideae in the various editions of *Engler's Syllabus der Pflanzenfamilien* (Scholz, 1964). In a recent proposal for a "more natural taxonomic grouping" of genera of the Rutaceae based on phytochemistry, Silva et al. (1988) did not recognize the Toddalioideae, but they kept *He-*

lietta, *Balfourodendron*, and *Ptelea* in a "Ptelea-tribe" (informal grouping) in the Rutoideae.

Morphology

HABIT

Most species of *Helietta* and *Balfourodendron* are branched, perennial shrubs or treelets, although some of them (*B. riedelianum* and *H. apiculata*) become medium- to large-sized trees. A general description of the wood anatomy of both genera is provided by Record and Hess (1940).

LEAVES

The leaves of both genera are trifoliolate and opposite; very rarely, some leaves in some species appear to be subopposite. The leaflets are mostly sessile in *Helietta* and short-petiolulate to petiolulate in *Balfourodendron*, but in both genera they are conspicuously articulate at the apex of the petiole, which bears a small adaxial prominence persistently pubescent even in the glabrescent species (see Fig. 5C). Characteristically, *Balfourodendron* bears evident domatia on the abaxial surface, in the axils of most of the secondary nerves. These domatia are usually evident also as emergences on the adaxial surface. Each consists of 1–4 cavities (Fig. 1A, B), their margins with many curved trichomes. These domatia were erroneously described by Cowan and Smith (1973: 4) as "large swollen glands," but Engler (1874) in his original description of this species noted that such "foveolis majusculis" in the axils of leaf veins were like those found in some Lauraceae, and usually used by arthropods as nests. I have been unable to find mites in these domatia. The domatia constitute an important vegetative character that can be used to consistently distinguish *Balfourodendron* from *Helietta*.

INDUMENTUM

Trichomes in these two genera are basically of two types: 1) simple, unicellular, thick-walled, straight to curved, cylindrical with a tapering apex and verruculous surface (Fig. 1A–E); or 2) multicellular, glan-

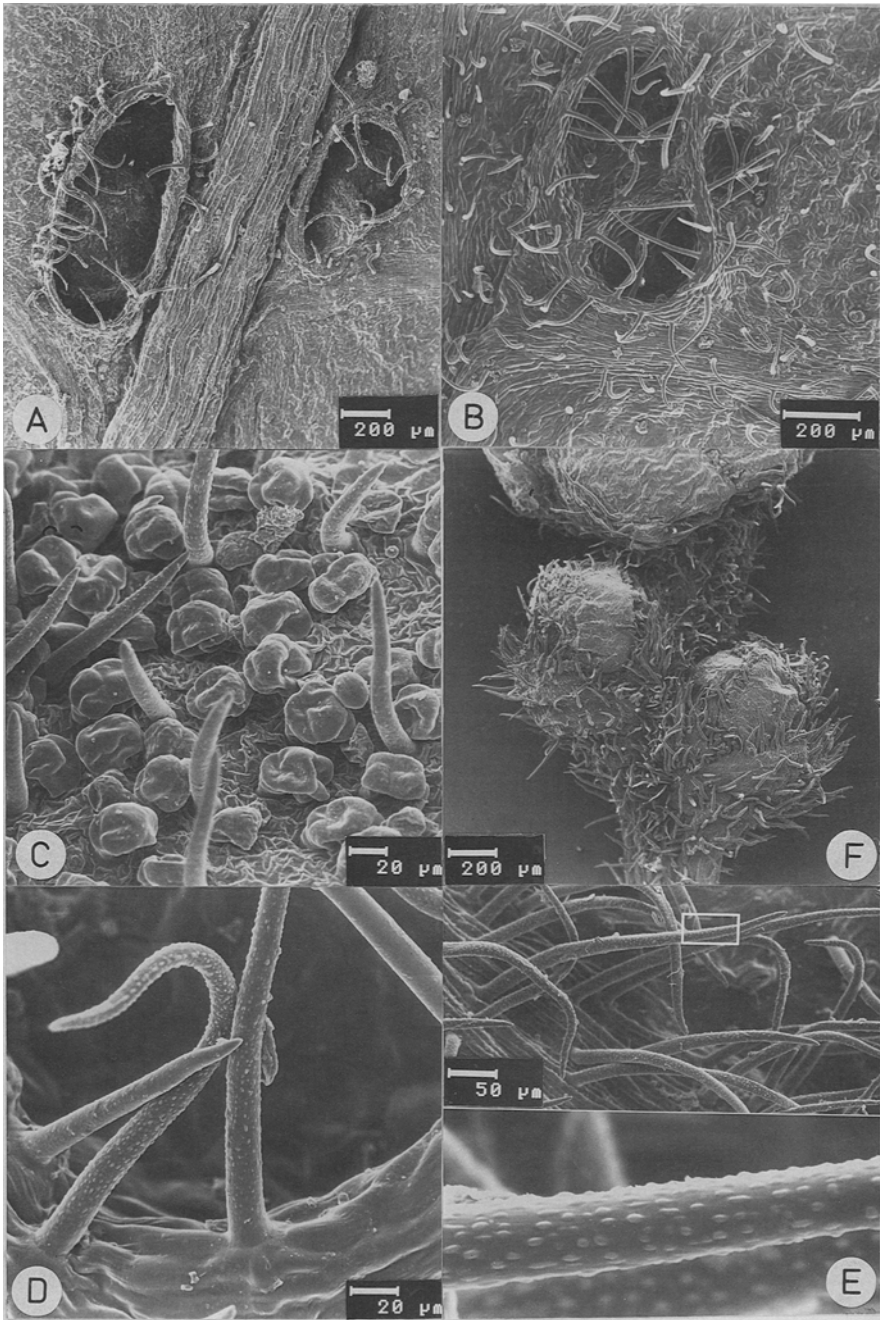


FIG. 1. Scanning electron micrographs of leaves and inflorescences. **A.** *Balfourodendron riedelianum*. Abaxial surface of leaflet showing midvein and 2 domatia, each consisting of a single cavity, in the axils of the secondary veins. **B–D.** *B. molle*. **B.** Abaxial surface of leaflet showing a domatium with 3 cavities. **C.** Adaxial surface of leaflet with erect, simple trichomes, and several glandular trichomes. **D.** Simple trichomes on the border of a leaflet domatium. **E, F.** *Helietta puberula*. **E.** Trichomes on abaxial surface of leaflet (top, 200 \times), with verruculous surface (lower right, 1600 \times). **F.** Cymule, showing base of apical flower and young buds subtended by 2 prophylls. (A, Pirani 472; B, C, Giulietti et al. CFCR 6950; D, Harley et al. 16374; E, F, Malme 2711.)

dular, club-shaped, and with a head of 6–8 cells and a short stipe. These trichomes are very small and can barely be noticed, but the microscope shows them in great number and density on the surface of leaflets and young fruits (Fig. 1C).

Although trichomes do not provide very useful taxonomic characters, the relative length and the persistence or absence of simple trichomes in fully mature structures can help distinguish some species in both genera.

INFLORESCENCE

The inflorescence of both genera is basically a terminal polytelic thyrses, in the sense of Weberling (1989). *Helietta parvifolia* has simple thyrses or monothyrses, i.e., an inflorescence whose lateral branches are all dichasial cymules, but the remaining species of *Helietta* and *Balfourodendron* have diplothyrses, i.e., synflorescences in which the terminal portion constitutes a principal florescence in the form of a simple thyrses and below which are 2–8(–16) coflorescences, each constructed as simple thyrses (Fig. 2D).

All branches of the inflorescences are basically opposite, but some subopposite branching is frequent in *Balfourodendron riedelianum* and *Helietta lottiae*, occasional in *Helietta apiculata*, and much rarer in the remaining taxa.

The thyrses are usually loosely branched and many-flowered, with spreading branches. They are typically terminal, very rarely subterminal.

The inflorescences can be short-pedunculate or sessile—i.e., their proximal branches or their proximal coflorescences are produced directly from the very base of the whole synflorescence. Both conditions can be observed in a single species.

Bracts are present at all points of branching, and the two prophylls (or bractlets) subtending each flower in the middle of the pedicel are mostly opposite and scale-like. Toward the base of the inflorescence, sometimes one or two bracts are foliose, i.e., expanded, leaf-like, and bearing three small leaflets.

The inflorescence axes are usually slen-

der and become lignified as the fruits develop, but soon after dispersal they break off from the stem.

FLOWERS

Perianth.—Like all Pteleinae, the flowers of *Balfourodendron* and *Helietta* are small, actinomorphic, dichlamydeous, 4–5-merous, white or cream-colored, and conspicuously glandular-dotted. In his original description of *Helietta*, Tulasne (1847) noted the occurrence of some trimerous flowers in *H. plaeana*, a notion that is repeated in the literature but that I have not been able to confirm; even after studying the type specimens of *H. plaeana* Tul. and additional material, I found only tetramerous and sometimes pentamerous flowers, as did Kaastra (1982: 114).

The flowers of *Balfourodendron* are always tetramerous. *Helietta* has species that are exclusively tetramerous or pentamerous, but most species of *Helietta* show some variation in the number of flower parts. As a rule, in basically pentamerous species such as *H. apiculata* and *H. glaziovii*, all flowers in most individuals are pentamerous, while in some individuals there will be scattered tetramerous flowers. The only exception seems to be *H. plaeana*, in which most specimens bear mostly tetramerous flowers, while many specimens bear mostly pentamerous flowers but also some tetramerous flowers.

In both genera the calyx is cupuliform with nearly free sepals, concave, persistent in fruit, usually green, and puberulent to glabrous; the sepals are imbricate in *Balfourodendron* and in tetramerous flowers of *Helietta* but are quincuncial in pentamerous *Helietta* (observable even after full anthesis).

Most flowers in these two genera are perfect, as most authors have described (Gray, 1897; Sargent, 1905; Britton, 1908; Spichiger & Stutz de Ortega, 1987; Simpson, 1988). Cowan and Smith (1973) simply stated that the flowers in both genera are polygamous. Tulasne (1847), in his detailed description of the genus and of the type species, *H. plaeana*, refers to the occurrence of trimerous flowers that are unisex-

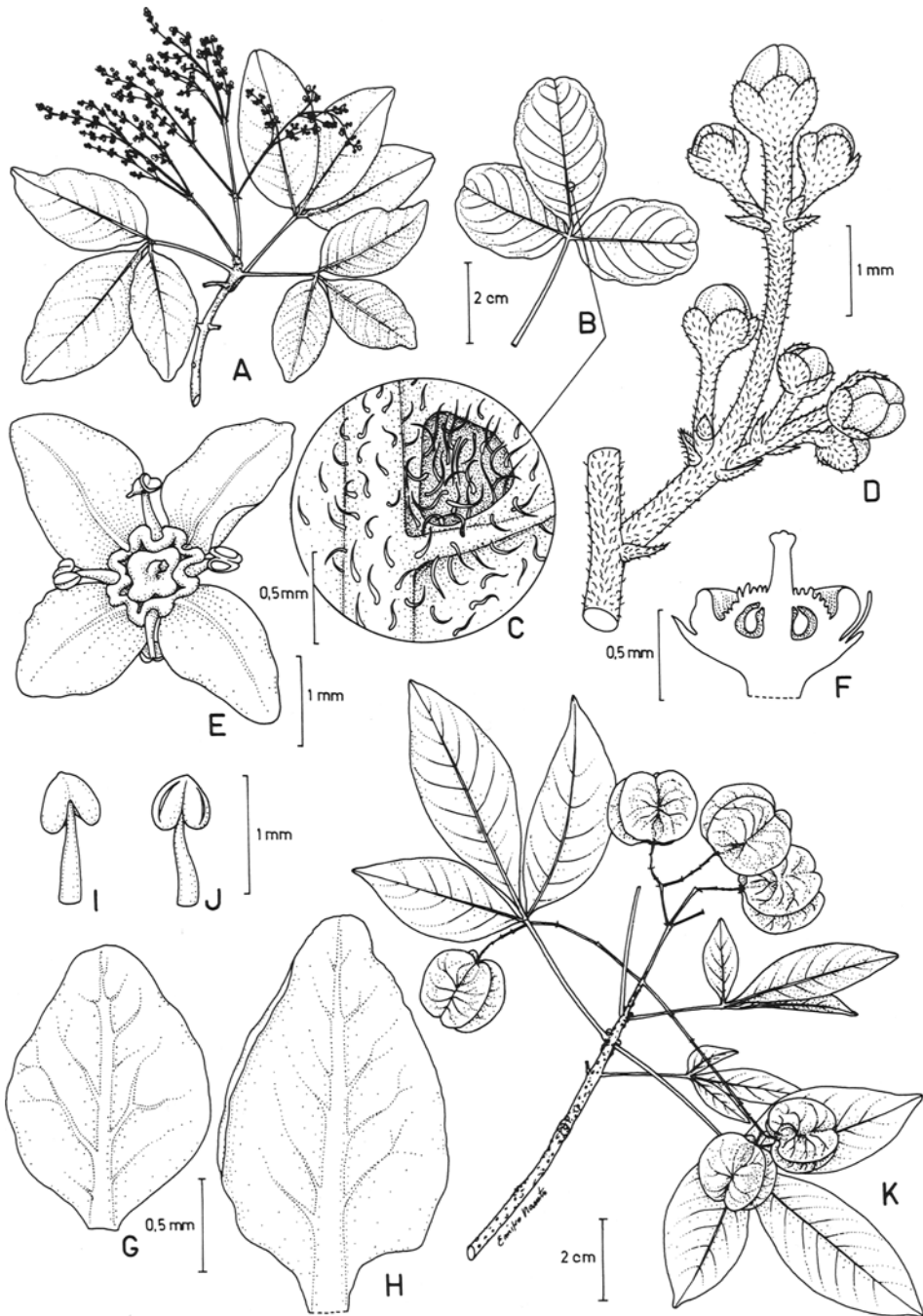


FIG. 2. A–G, K. *Balfourodendron molle*. A. Flowering shoot. B. Leaf. C. Detail of a domatium. D. Lateral branch (coflorescence) of the thyrses, showing the cymose arrangement of floral buds. E. Flower, frontal view. F. Longisection of flower, showing cupular disk surrounding the gynoeceum and pendulous ovule. G. Petal. K. Fruiting shoot. H–J. *Balfourodendron riedelianum*. H. Petal. I, J. Stamens, dorsal and ventral views. (A–F, Furlan et al. CFCR 349; G, Kallunki & Pirani 406; H, Itoman 67; I, J, Hatschbach et al. 25522; K, Hatschbach et al. 56546.)

ual by abortion of either the ovary or the stamens. However, I have not been able to confirm the occurrence of unisexual flowers in any specimen of *Helietta*. Even if sporadic occurrence of unisexual flowers is demonstrated, the predominantly bisexual flowers of these two genera will still contrast sharply with the consistently unisexual flowers of the closest relative, *Ptelea* (see Sargent, 1905; Britton, 1908).

Androecium.—The androecium is composed of free stamens equal in number to the petals. The anthers are introrse, but at anthesis the filaments recurve outward and the versatile anthers turn upside down with the slits facing outward, giving the impression that they are extrorse (see Fig. 8A, E). The anthers usually have a subacute apex, except in *H. lottiae* and *H. apiculata*, where they are apiculate.

Disk.—Like most of the Rutaceae, *Helietta* and *Balfourodendron* have an intrastaminal, cupular disk that looks like an erect, undulate rim (Figs. 2E, 8E). The undulation of the erect edge of the disk surrounds and follows the shape of the ovary and alternately accommodates the bases of the filaments.

The disk is likely nectariferous. In fresh flowers of *B. riedelianum*, *B. molle*, *H. apiculata*, and *H. glaziovii* I have examined, the disk was yellow and somewhat lustrous (like a wet secretory structure) and was, in fact, the most vividly colored part in the otherwise pale-cream to greenish flowers. Moreover, flowers of these four species as well as of some others (according to specimen labels) produce a fragrant scent during the day. These characters suggest the flowers are entomophilous.

The disk is a reliable taxonomic character for separating *Helietta* and *Balfourodendron* from the other genera in the Pteleinae (*Ptelea* and *Taravalia*), which in contrast have a stipitate, gynophoroid disk.

Gynoecium.—All Pteleinae have a syncarpic gynoecium. The ovary is completely surrounded by the disk. Each locule bears two pendulous, collateral ovules.

The dorsal lobes of the carpels expand very early after fertilization to form the wings of the fruit. Flowering collections of these two genera are often misidentified as

Esenbeckia (a genus in the Cusparieae–Pilocarpinae of which about half of the species bear trifoliolate leaves and superficially similar flowers), but such mistakes often can be avoided by careful examination of the ovary in old flowers, which will show already the wings typical of *Helietta* and *Balfourodendron*.

FRUIT AND SEED

The fruit is the most important reproductive feature distinguishing *Helietta* from *Balfourodendron* and separating them from the other genera in the Pteleinac. *Balfourodendron* produces a compound samara with an ellipsoid, more or less woody seed-locule surrounded by four (rarely three) thin-coriaceous, prominently radiately nerved, semicircular, vertical wings (Fig. 3A). The samara usually has four one-seeded locules. The epicarp is thin but coriaceous and forms the wings. The mesocarp is relatively thicker, soft, and densely glandular-dotted. The endocarp forms a hard, lignified, and ellipsoid stone. The seeds are oblong, and free from the endocarp; the testa is rough and brownish. Most of the seeds examined were abortive, a condition that seems to be common in this species and already noted in the original description of *B. eburneum* (= *B. riedelianum*). Recently, Lorenzi (1992) also called attention to the low percentage of germination in this species.

The fruit of *Helietta* is a samarium according to Spjut's (1994) classification of fruit types, in which four to five (rarely three) samaroid mericarps separate at maturity but remain apically attached to the receptacle by the long and somewhat lignified vascular bundles of the central axis, and later each will act as a diaspore (Figs. 3E–G, 7F). Each mericarp has an ellipsoid-trigonal seed-bearing body with two flat, smooth ventral faces and a convex, rugose to reticulate dorsal face bearing a dorsal pericarpial wing. The wings are ascending and usually with a thickened dorsal margin.

The epicarp of the fruit of *Helietta* is coriaceous and seems to be the only layer to constitute the wing; the mesocarp is very thin and soft and the endocarp is hard and

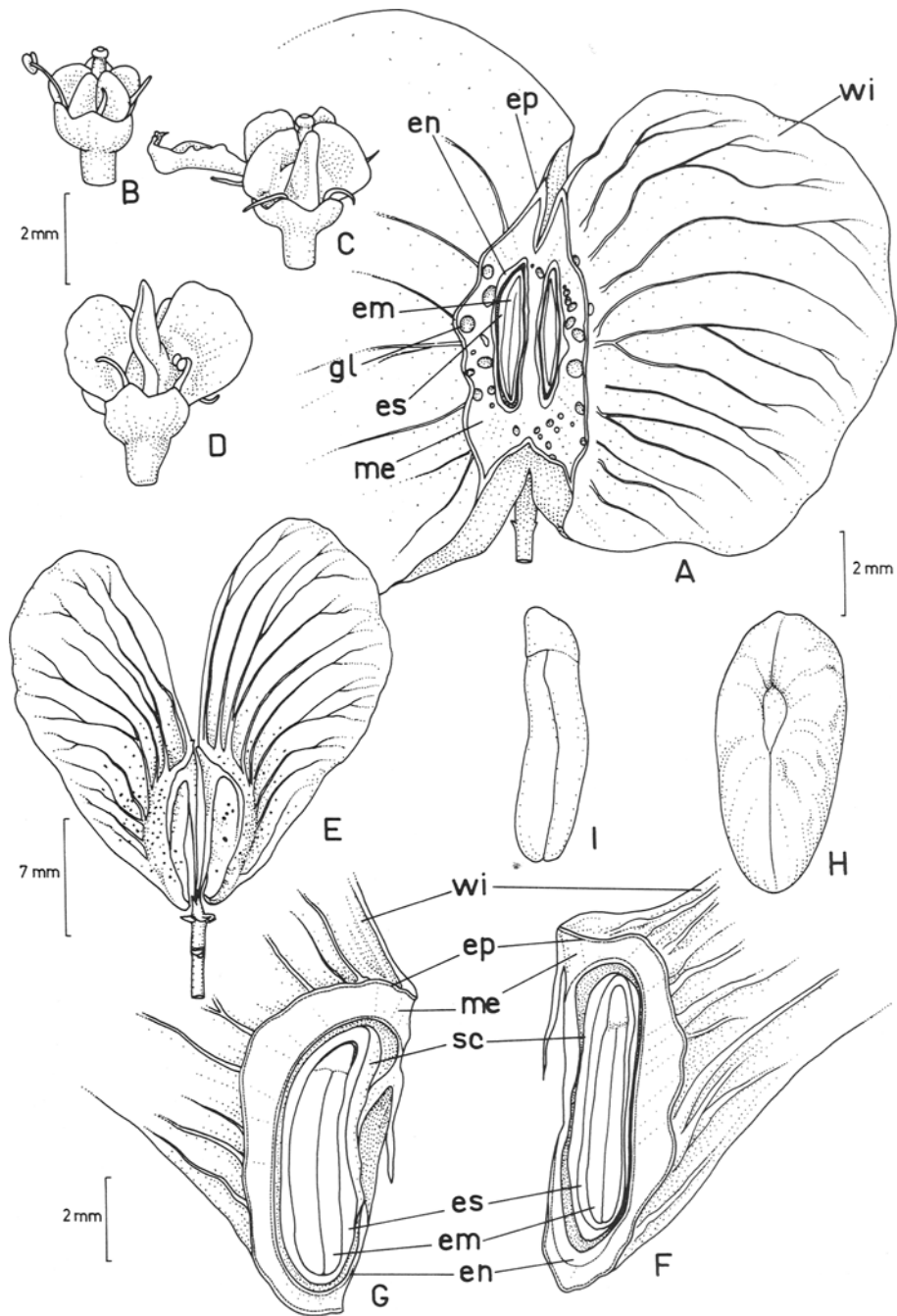


FIG. 3. A. *Balfourodendron riedelianum*. Fruit in longisection. B-D. *Helietta glaziovii*. Stages of formation of a fruit from a fertilized gynoecium. E. *Helietta plaearna*. Mature samarium in which only 2 mericarps are still attached. F. *Helietta apiculata*. Proximal part of a mericarp, the seed locule in longisection. G-I. *Helietta parvifolia*. G. Proximal part of a mericarp, the seed locule in longisection. H. Seed, ventral view. I. Embryo, with superior radicle. (wi, wing; ep, epicarp; me, mesocarp; en, endocarp; em, embryo; sc, seed coat; es, endosperm; gl, gland.) (A, Pirani 6-80; B-D, Pirani et al. CFCR 8878; E, Pittier 13298; F, Pirani 1-80; G-I, Palmer 142.)

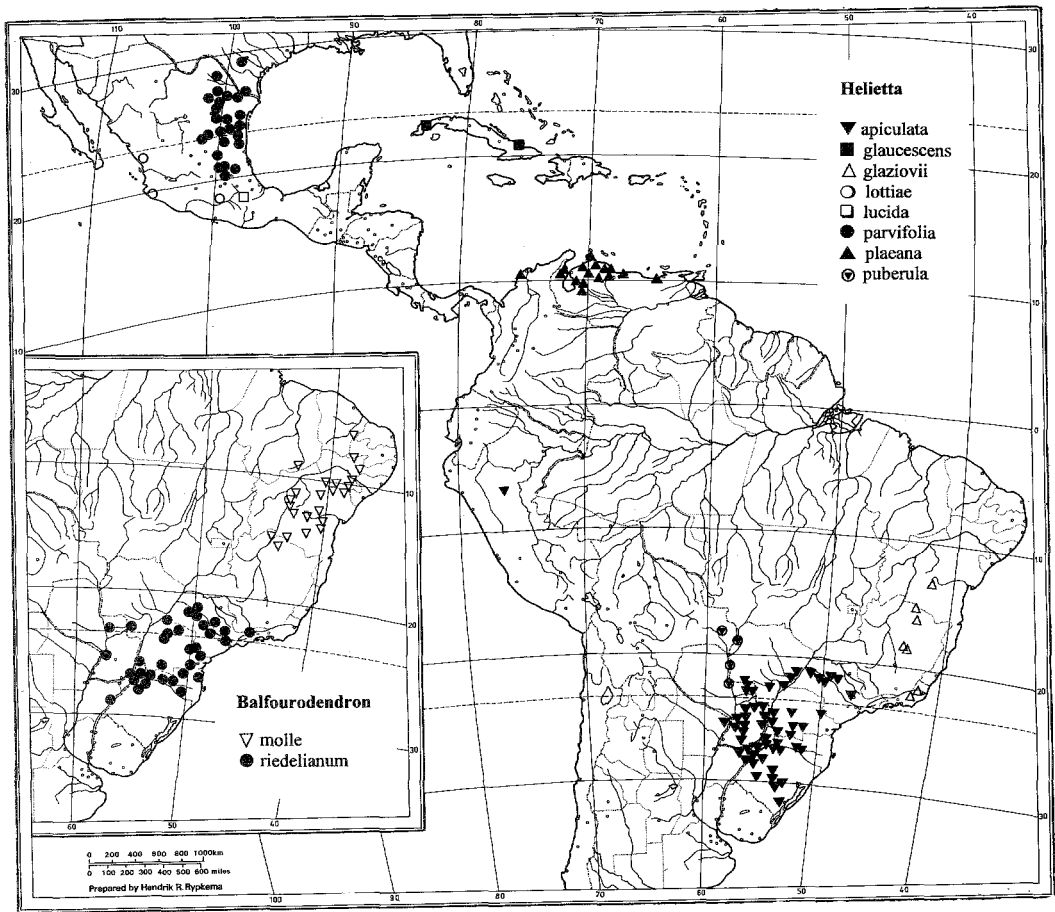


FIG. 4. Distribution of species of *Balfourodendron* (A) and *Helietta* (B) in the Americas.

lignified. There is a single oblong seed per carpel that is free from the endocarp. The testa is thin, dark-brown to black, coarse without, and smooth within. The soft, fleshy, cream-colored endosperm forms a thin layer around the embryo, which is linear-complanate, with a short, superior radicle, and two relatively long, flat-convex, obtuse cotyledons (Fig. 3G).

Biogeographical Background

Figure 4 depicts the known geographic distributions of the species of *Helietta* and *Balfourodendron*. Both are neotropical genera with a remarkable preference for sub-humid, mesic, or dry habitats; most species are absent from humid habitats like the for-

ests of the Amazon basin, the moist Andes, and the Atlantic coast of Brazil. They seem to fit well among the “dry-area-centered taxa” proposed by Gentry (1982) as one of the neotropical floristic distribution patterns. According to Gentry (1982), dry-area-centered taxa “tend to be largely shrubs and herbs,” and are well represented in Mexico (as are three species of *Helietta*), in the northern Venezuelan–Colombian region (as is *H. plaeana*), and the dry cerrado–chaco–caatinga region of the Brazilian shield (as are *B. molle* and two species of *Helietta*).

No species is truly widespread; all are rather restricted in their distributions, including endemic taxa like *H. lottiae*, *H. lu-*

TABLE I
COMPARISON OF THE GENERA IN SUBTRIBE PTELEINAE

	<i>Helietta</i>	<i>Balfourodendron</i>	<i>Ptelea</i>	<i>Taravalia</i>
Leaves	Opposite	Opposite	Alternate	Alternate
Domatia	Absent	Present	Absent	Absent
Inflorescence	(Mono)diplothyse	Diplothyse	Panicle (Tröll, 1969: 512)	Panicle
Flower	4-5-merous, perfect	4-merous, perfect	4-5(-6)-merous, imperfect	(4-5)-merous, imperfect
Filaments	Glabrous	Glabrous	Pubescent	Glabrous
Disk	Cupular, lobed	Cupular, lobed	Gynophoroid	Gynophoroid
Ovary	4-5-celled, globose, lobed	4-celled, globose, lobed	2(-3)-celled, complanate	2(-3)-celled, conical
Fruit	Samarium with (3-4)-5 mericarps, each with a dorsal, ascending, reticulate wing	Samara (3-4)-seeded, with (3-4) broad, verticillate, reticulate wings	Samara 2-seeded, with a broad reticulate wing completely surrounding the central body	Nut-like capsule, ± distinctly margined, tardily dehiscent in 2 valves, tuberculate
Plant	Hermaphrodite	Hermaphrodite	Subdioecious	Subdioecious?
Distribution	Texas (U.S.A.) to Mexico, Cuba, N and S South America	NE to S Brazil, E Paraguay and NE Argentina	U.S.A. (widespread) to N Mexico	Mexico (lower California)

cida, *H. glaucescens*, and *H. puberula*. The disjunct occurrence of *H. apiculata* in dry forest in northeastern Peru, far from the main area of the species further south, may represent some evidence of a wider distribution of this species in the past. The allopatric distribution patterns and the disjunct ranges of the species could be the result of fragmentation of a once wider range of an ancestor, during periods of Quaternary glaciations, when drier climates prevailed, as suggested by many authors such as Prance (1982) and Whitmore and Prance (1989).

Generic Relationships

The subtribe Pteleinae departs from the rest of the subfamily Toddalioidae (in which a single tribe, the Toddalieae, was recognized by Engler, 1931) by the following characters: trifoliolate leaves; more than one (usually 2-5) carpel; seeds with endosperm; and a dry winged fruit (or a nut-like capsule bearing a narrow margin that may represent a vestigial wing in the monospecific *Taravalia*).

The close affinity of these genera and their systematic status as a distinct taxon is supported by chemical data (Silva et al., 1988).

The four genera of the Pteleinae—*Ptelea*, *Taravalia*, *Helietta*, and *Balfourodendron*—are well delimited by the characters presented in Table I. While the fruit is the best character to define each genus, a combination of other features such as phyllotaxis, type of inflorescence, form of the disk, and number of carpels can be used to separate *Balfourodendron* and *Helietta* from *Ptelea* and *Taravalia*.

Taxonomic Treatment

Terms used in the following descriptions for shapes of leaflets and other organs, venation, and indumentum types follow the definitions of Hickey (1979) and Radford et al. (1974).

Key to the genera in subtribe Pteleinae

1. Leaves (sub-)opposite; disk cupular, undulate, surrounding the ovary; carpels 4 or 5; inflorescence a thyrsse.
 2. Fruit a samara with a single (3-)4-seeded body completely surrounded by (3-)4 broad wings; flowers 4-merous; leaflets with domatia in the axil of secondary veins (South America). *Balfourodendron*
 2. Fruit a samarium with (3-)4-5 mericarps, each bearing a dorsal ascending wing; flowers 4-5-merous; leaflets without domatia (North America, Cuba, South America). *Helietta*
1. Leaves alternate; disk gynophoroid, supporting the ovary; carpels 2(-3); inflorescence a panicle.
 3. Filaments pubescent; fruit a samara with a broad circular wing completely surrounding the 2-seeded, complanate seed locule (U.S.A., N Mexico). *Ptelea*
 3. Filaments glabrous; fruit a nut-like, tardily dehiscent capsule, \pm distinctly keeled but not winged, lenticular (NW Mexico). *Taravalia*

1. **BALFOURODENDRON** Mello ex Oliv., Hooker's Icon. Pl. 13: t. 1203-1204. 1877. TYPE: *Balfourodendron eburneum* Mello ex Oliv. (= *Esenbeckia riedeliana* Engl.).

Trees or *treelets* 2-30 m tall, with punctate glands usually visible on all unglanified parts; buds densely sericeous; young shoots appressed-pubescent. *Leaves* opposite, digitately 3-foliolate, densely glandular-punctate, pubescent to glabrescent; petiole semiterete to canaliculate, with a small, hairy appendage or a tuft of longer trichomes on the adaxial surface proximal to the base of the terminal leaflet; leaflets sessile to petiolulate, conspicuously articulate at the grooved petiole apex, chartaceous to subcoriaceous, the margin entire to seldom slightly crenulate; terminal leaflet symmetric and larger than the lateral ones, which are asymmetric at base; venation brochidodromous, the midvein usually raised on both surfaces; domatia (small, hairy, 1-4-celled cavities) in the axils of most secondary nerves. *Inflorescence* a terminal, polytelic diplothyrsse, usually longer than the leaves, pubescent, loose to dense; branches (sub-)opposite, patent; peduncle present or absent; bracts and prophylls (bractlets) linear-lanceolate, usually paired. *Flowers* tetramerous, perfect, actinomorphic, pedicellate, cream-colored. *Sepals* imbricate, pubescent or glabrous, persistent in fruit, scarious, ciliolate. *Petals* free, imbricate in bud, pellucid-punctate, glabrous, hyaline except for the midvein, margin entire to erose, at base attenuate to subunguiculate. *Stamens* 4, alternipetalous, free, glabrous; filaments subulate, translucent, inserted below the

disk, reflexed after anthesis; anthers ovoid, dorsifixed below the middle, versatile, introrse, 2-celled, the cells somewhat divergent at base. *Disk* intrastaminal, cupular, forming an erect, undulate rim, 4-lobed, each lobe 2-lobulate, glabrous, surrounding the ovary and about level with it. *Ovary* of 4 connate carpels conspicuously 4-lobed, depressed-globose, minutely glandular-tuberculate, glabrous; ovules 2 per locule, collateral, pendulous; style 1, terete, glabrous; stigma capitate and minutely 4-lobed. *Fruit* a (3-)4-locular samara with 4 expanded, vertical, rounded to rounded-truncate, subcoriaceous, prominently veined wings, glabrescent or glabrous; seed 1 per carpel, free from the endocarp, oblong, with a thin testa and fleshy endosperm, glabrous; embryo fleshy, with straight, oblong cotyledons and a superior radicle.

This is a neotropical genus of two species, ranging from northeastern to southern Brazil and adjacent eastern Paraguay and northeastern Argentina (Misiones); deciduous dry forests (caatingas) in northeastern Brazil, subtropical moist forest and mesic semideciduous tropical forests in southern Brazil and adjacent areas; 200-800 m elevation.

Key to the species of *Balfourodendron*

1. Tree (6-)9-25(-32) m; leaflets punctate only on abaxial surface, distinctly petiolulate, apex acuminate (seldom acute), lateral leaflets with attenuate, asymmetric base, blade pubescent only on the main nerve or completely glabrescent; petals ca. 2.5 mm long, subunguiculate at base; wings of samara (2.5-)3-5 cm long. 1. *B. riedelianum*
1. Treelet 3-4(-9) m; leaflets conspicuously punctate on both surfaces, sessile to short-

petiolulate, apex obtuse and often emarginate, seldom acute, lateral leaflets with obtuse asymmetric base, blade densely pubescent and partially persistently so; petals ca. 2 mm long, attenuate at base; wings of samara 1.8–2.4 cm long. 2. *B. molle*

1. **BALFOURODENDRON RIEDELIANUM** (Engl.) Engl. in Engler & Prantl, *Natur. Pflanzenf.* 3(4): 174. 1896. *Esenbeckia riedeliana* Engl. in C. Martius, *Fl. Bras.* 12(2): 142. 1874. TYPE: BRAZIL. São Paulo: Ypanema, s.d. (fl), *Sello 2174* (LECTOTYPE: SP; ISOLECTOTYPE: K).

Helietta multiflora Engl. in C. Martius, *Fl. bras.* 12(2): 185. 1874. TYPE: BRAZIL. Rio de Janeiro: Santa Gallo, s.d. (fl), *Peckolt 578* (HOLOTYPE: B—probably destroyed; ISOTYPE: probably BR-n.v.).
Balfourodendron eburneum Mello ex Oliver, Hooker's *Icon. Pl.* 13: t. 1203–1204. 1877. TYPE: BRAZIL. São Paulo: Campinas, s.d. (fl, fr), *J. C. Mello s.n.* (LECTOTYPE, here designated: K, photo at NY; ISOLECTOTYPE: NY).

Tree (6–)9–25(–32) m; trunk erect, 25–80(–100) cm diam. Bark pale gray, smooth. *Leaves* initially pubescent but soon (sub-)glabrous; petiole (2–)3–8 cm long, semiterete, articulated at apex; petiolules 2–13 mm long; leaflets obovate-oblong to narrowly elliptic, punctate only on the abaxial surface, both surfaces with trichomes persistent only on the main nerve, abaxial domatia densely hairy to subglabrous, margin entire and flat to slightly revolute, apex acuminate to acute, rarely obtuse, base attenuate to cuneate on the terminal leaflet, strongly attenuate-asymmetric on the lateral ones, terminal leaflet 7–13(–15) × 2–5 cm, lateral leaflets 5.5–11.5 × 1.6–5 cm. *Inflorescence* generally loose, many-branched, (7–)14–19 cm long; peduncle 1–2 cm long, densely appressed-pubescent with short, white, curved trichomes or glabrescent; first-order branches (paraclades) (3–)8–10, usually subopposite to sometimes opposite, patent, (5–)9–14 cm long; bracts and prophylls linear-lanceolate, short-pubescent, ca. 0.8 mm long. *Pedicel* 1.6–2.3 mm long, pubescent. *Sepals* green, suborbicular to broadly ovate, ca. 0.8 mm long, pubescent without. *Petals* white to cream, oblong, obtuse at apex, subunguiculate at base, ca. 2.5 × ca. 1.5 mm, pellucid-punctate, entire. *Stamens* ca. 1 mm long, filaments white,

anthers yellow, ovoid. *Samara* (2.5–)4.5–6 cm diam., the wings (2.5–)3–5 cm long.

Distribution (Fig. 4A), *habitat, and phenology*.—*Balfourodendron riedelianum* occurs in southern Brazil (São Paulo, Mato Grosso do Sul, and southern Minas Gerais to Rio Grande do Sul) and in adjacent eastern Paraguay and northeastern Argentina (Misiones, Corrientes). It is usually a large tree and characteristic of the mesic, seasonal, semi-deciduous forests of the Paraná River basin, (Klein in Cowan & Smith, 1973), less common in the Iguazu and Upper Uruguay basins. It is very rare in the moister Atlantic Forest in Santa Catarina, where it occurs mainly in disturbed areas. Flowering extends from August to February (being more pronounced from October to December), although there is one flowering collection made in June (*Little & Rombold 40168*, from Paraguay). Fruiting collections have been made from January to September.

Common Names.—**Brazil**: pau-marfim, marfim (many herbarium specimens and published references, e.g., Cowan & Smith, 1973; Lorenzi, 1992), embira (*Bicudo s.n.*, São Paulo), guamixinga (*Dusén 16782*, Paraná), pequiá-mamona (*Reitz & Klein 16978*, Santa Catarina), guatambu (*Reitz & Klein 16978*, Santa Catarina and Rio Grande do Sul), farinha-seca (São Paulo, Lorenzi, 1992), gramixinga, pau-liso, pau-cetim, guataia, guarataia, guamuxinga (Lorenzi, 1992); **Argentina**: guatambu blanco (Misiones, *Montes 27478*), guatambu morotí, ibirá-ñeté (Record & Hess, 1940); **Paraguay**: guatambu, yvyrá ñetí (*Bernardi 18587*, Spichiger & Stutz de Ortega, 1987).

Uses.—The white wood of this species is of “excellent quality and is highly esteemed . . . for turnery, tool handles, oars, agricultural implements, interior construction, and furniture,” according to Record and Hess (1940), who also provided a description of the anatomical features of the wood.

Illustrations.—Flora brasiliensis (Martius ed.) 12(2): t. 39. 1874 (as *Helietta multiflora*); Hooker's *Icon. Pl.* 13: t. 1203–1204. 1877. Color photographs: Lorenzi, 1992: 304.

Representative specimens examined. BRAZIL. **Mato Grosso do Sul**: Antônio João, descida para Campestre, 16 Mar 1985 (fr), *Hatschbach & Silva 49105* (MBM, SPF). **Minas Gerais**: Caldas, 30 Oct

1867 (fl), *Regnell III-397* (R). **Paraná:** Itararé-Sengés, 11 Dec 1910 (fl), *Dusen 11330* (NY, S); Maringá, Horto Florestal, 12 Oct 1965 (fl), *Hatschbach 12947* (MBM, NY, US); Terra Boa, Fazenda Mururê, 15 May 1969 (fr), *Hatschbach 21509* (MBM, NY); Coronel Vivida, Rod. BR 373, 26 May 1972 (fr), *Hatschbach 29613* (MBM, NY); Lapa, Johannisdorf, 12 Dec 1972 (fl), *Hatschbach 30958* (MBM, NY, UEC); Cerro Azul, Cabeceira do Ribeirão do Tigre, 23 Nov 1979 (fl), *Hatschbach 42586* (MBM, NY); Londrina, Parque Estadual Mata do Godoy, 21 Oct 1988 (fl), *Soares e Silva & Chagas e Silva 135* (NY, UPCB). **Rio Grande do Sul:** Tenente Portela, Reserva do Turvo, 10 Dec 1973 (fl), *L. M. Baptista et al. s.n.* (ICN-27634); Arroio do Tigre, Barragem de Itaúna, 19 Apr 1978 (fr), *A. Lise s.n.* (HAS-5862, UEC); Vicente Dutra, 18 Jan 1983 (fr), *Pirani et al. 472* (SP, SPF). **Santa Catarina:** Lacerdópolis, 30 Oct 1963 (fl), *Klein 4258* (HBR, NY, US); Itapiranga, 3 Mar 1964 (fr), *Klein 5233* (HBR, PACA); Mun. Joaçaba, 12 km S of Joaçaba, on W bank of Rio do Peixe, 27 Feb 1957 (fr), *Smith & Klein 11905* (HBR, NY, US); Mun. São Miguel d'Oeste, 2 km NW of São Miguel d'Oeste, 26°42'S, 53°32'W, 20 Oct 1964 (fl), *Smith & Reitz 12750* (HBR, NY, US). **São Paulo:** Teodoro Sampaio, Reserva Estadual do Morro do Diabo, 25 Sep 1985 (fl), *Baitello & Aguiar 155* (SPF, SPSF); Botucatu, Bairro Faxinal, 9 Aug 1978 (fl), *Bicudo s.n.* (SP 154505); São Paulo, Parque do Estado, 15 Mar 1944 (fr), *W. Hoehne s.n.* (SPF-11170); Bauru, Estação Experimental, 22 Oct 1991 (fl), *Itoman 67* (SPF, SPSF); Queluz, Linha Sorocabana, 22 Jun 1899 (fl), *Loefgren Comm. Geogr. Geol. São Paulo 5973* (NY, SP); Penápolis, Fazenda São Sebastião, Bairro Bonito, 31 Jul 1980 (fr), *Pirani 6-80* (NY, SPF); Promissão, Jul 1994 (fr), *Pirani et al. 3222* (SP, SPF, UEC); Brotas Rio Jacaré, Fazenda Santa Elisa, 31 Jul 1987 (fr), *Salis & Aidar 39* (UEC).

PARAGUAY. Alto Paraná: Centre Forestier Puerto Stroessner, Jul 1982 (fl), *Stutz 491* (G). **Amambay:** Sierra de Amambay, Oct 1907/1908 (fl), *Hassler 10659* (G, NY). **Caaguazú:** Caaguazú, Mar 1876 (fr), *Balansa 2517* (G). **Canendiyú:** 20 km al Sur de Cauteté siguiendo la supercarretera, 17 Dec 1982 (fl), *Fernandez Casas et al. 7636* (G, MO, NY). **Central:** E de Asunción, 10 Feb 1984 (fr) *Little Jr. & Rombold 40168* (NY, US). **Concepción:** Concepción, Sep 1902 (fl), *Hassler 7516* (G, NY). **Itapúa:** Inter Colonia Itapúa et Catupyry, 14 Nov 1978 (fl), *Bernardi 18587* (G, MO, NY); Itapúa, cerca de la Colonia Naranjal, 19 Sep 1980 (fr), *Fernandez Casas & Molero 3744* (G, NY).

ARGENTINA. Corrientes: Dep. Alvear, Ruta 40, 11 Mar 1982 (fr), *Tressens et al. 1994* (CTES, ICN). **Misiones:** Vic. de Puerto León, 12-21 Jul 1914 (fr), *Curran 679* (NY, US); Dep. San Pedro, El Soberbio, 20 Jul 1957 (fr), *Montes 27478* (NY); Salto Iguazú, 28 Sep 1910 (fl), *Rodriguez 458* (LIL, NY); Camino a La Plantadora, Jul 1927 (fr), *Scala 204* (LP, NY); Dep. Cainguás, Ruta 7, 5 km N del acceso a Aristóbulo del Valle, 30 Jul 1987 (fr), *Vanni et al. 891* (CTES, NY).

2. *Balfourodendron molle* (Miq.) Pirani, comb. nov. (Fig. 2A–G, K)

Esenbeckia mollis Miq., *Linnaea* 22: 796. 1850. *Helietta mollis* (Miq.) Kaastra, *Acta Bot. Neerl.* 26:

487. 1977. TYPE: BRAZIL. Bahia: Catingas, marais de Tapira, 1840 (fl), *J. S. Blanchet 3090* (HOLOTYPE: U–n.v.; ISOTYPES: BM, BR, C, G, K, NY, P, W–n.v.; photos of destroyed B isotype at F, MO, NY, SPF).

Treelet 3–4(–9) m tall; trunk slender, smooth, gray. *Leaves* densely pubescent with white, short, curved trichomes, partially glabrescent but persistently pubescent on midribs and petiole; petiole 1.5–3(–4) cm long, semiterete, slightly canaliculate adaxially, usually more densely pubescent adaxially at distal end; leaflets sessile to short petiolulate, obovate to elliptic, conspicuously black-punctate on both surfaces, the adaxial surface densely short-pubescent but (sub-)glabrescent, abaxial surface persistently pubescent to glabrescent, domatia densely hairy, margin entire to irregularly and slightly crenulate, flat to slightly revolute, apex obtuse and often emarginate, seldom acute, base attenuate in the terminal leaflet, obtuse and strongly asymmetric in the lateral ones; terminal leaflet 3.5–5.5(–8) × 1.4–2.5 cm, lateral leaflets 2.5–4(–7) × 1.5–2.5 cm. *Inflorescence* densely and many-flowered, 5–10 cm long; peduncle 2–5 mm long or absent; first-order branches (paraclades) ca. 12, opposite, 4–9 cm broad, densely short-villous with white, curved trichomes; bracts and prophylls linear-lanceolate, short-villous. *Pedicel* 1–2 mm long, glandular-punctate, pubescent. *Sepals* green, suborbiculate to broadly ovate, 0.5 mm long, pubescent to glabrous abaxially. *Petals* white to cream-colored, oblong, obtuse at apex, attenuate at base, ca. 2 × 1 mm, pellucid-punctate, entire to slightly erose. *Stamens* ca. 1 mm long, filaments white, anthers yellow, ovoid. *Samaras* 1.8–2.4 cm diam., the wings 1–2.4 cm long.

Distribution (Fig. 4A), *habitat*, and *phenology*.—This species is found in the caatingas, the xeric, deciduous forests that are dominant in the northeast of Brazil, i.e., from Piauí, Ceará, and Pernambuco to Bahia and northern Minas Gerais, where the southern limits of the caatingas are found. Flowering is November–June with a peak in December; fruiting is February–May.

While all fruiting specimens of this taxon in various herbaria were identified as *Bal-*

fourodendron riedelianum, the flowering ones, which happen to have younger, more densely pubescent leaves and inflorescences than the fruiting specimens, were invariably ascribed to *Helietta mollis* (Engl.) Kaastra. This species cannot belong in *Helietta* because of its fruits and its domatia, which are characteristic of *Balfourodendron*. Some collections of *B. riedelianum* show smaller leaflets and inflorescences and on first glance can be confused with *B. molle*, but the differences between these two species are consistent. Moreover, although their geographic ranges (Fig. 4A) may not be separated by a great distance, they occupy remarkably different habitats: *B. molle* is restricted to the dry caatingas, while *B. riedelianum* is fairly common in the southern mesophyllous to moist, inland forests from São Paulo to Argentina, and is not found in central or southern Minas Gerais. This fact obviously was overlooked by Pinto and Bautista (1990), Prado and Gibbs (1993), and others when citing the occurrence of this latter species in the caatingas.

Kaastra (1977) placed *Helietta puberula* R. E. Fr. in synonymy with *B. molle* [as *H. mollis* (Miq.) Kaastra]; Spichiger and Stutz de Ortega (1987) accepted this proposition in their treatment of the Rutaceae for the *Flora del Paraguay*. Nevertheless, the two allopatric species belong in two different genera and are distinguished by the characters stated in the generic key.

Common names.—**Brazil:** folha-miúda (Silva 699), mucambo (Pinto & Bautista, 1990), pereiro-preto (Salgado & Bautista 270) (Bahia); pau-marfim (Andrade-Lima 52-1025) (Pernambuco).

Representative specimens examined. **BRAZIL. Bahia:** Itiuba, 10°43'S, 39°50'W, Fazenda Experimental da EPABA, 27 May 1983 (fr), *Bautista & Pinto* 786 (HRB, NY); Jacobina, montagne de la Jacobina, 1837 (fl), *Blanchet* 2679 (F, G-2 sheets, MO, NY-2 sheets, P); Serra Açurua, 1838 (fl), *Blanchet* 2836 (F, G, NY); Jacobina, Pouço d'Areia, 1845 (fl), *Blanchet* 3901 (F, G, P); Aracatu, 20 km na Rod. Brumado-Vitória da Conquista, 29 Dec 1989 (fl), *Carvalho et al.* 2706 (CEPEC, SPF); Tucano, ca. 7 km na estrada Tucano para Araci, 20 Feb 1992 (fr), *Carvalho & Hind* 3838 (CEPEC, NY, SPF); Brejo de Cima, ca. 56 km de Mucujê, na estrada para Jussiapé, 15 Dec 1984 (fl), *Giulietti et al.* CFCR 6950 (K, NY, SPF); 49 km of Senhor do Bonfim on the BA-130 hwy. to Juazeiro, 10°05'S, 40°13'W, 26 Feb 1974 (fl), *Harley et al.* 16366 (CE-

PEC, K, SPF), *Harley et al.* 16374 (CEPEC, K, NY, RB, SPF); 10 km NE of Cansanção on the Monte Santo rd., 10°35'S, 39°26'W, 21 Feb 1974 (fl), *Harley et al.* 16449 (CEPEC, K, NY, RB); Urandi, Rod. BR-122, próximo à divisa com Ouro Branco, 4 Apr 1992 (fr), *G. & M. Haisbach* 56546 (MBM, SPF); Paulo Afonso, Estação Ecológica SEMA, 09°39'S, 38°35'W, 19 Mar 1985 (fr), *Jordy Filho & Orlandi* 198 (CEPEC, HRB); Itaberaba, ca. 15 km from Rui Barbosa on right side of old rd., ca. 12°22'S, 40°22'W, 29 Jan 1993 (fl), *Kallunki & Pirani* 406 (NY, SPF); Brejo das Almas, Brejo das Almas-Caetetu, 9 Nov 1938 (fl), *Markgraf et al.* 12119 (BHMH, F, R); Boa Nova, Rod. BR 116, ramal para Penachinho, a 23 km N de Poções, 7 Apr 1988 (fr), *Mattos Silva et al.* 2350 (CEPEC); Cícero Dantas, 10°36'S, 38°25'W, 28 May 1981 (fl), *Orlandi* 413 (RB); Jeremoabo, Raso da Catarina, 15 May 1981 (fr), *Pinto 107/81* (CEPEC, HRB, HUEFS, ICN); Oliveira dos Brejinhos, 24 Mar 1981 (fr), *Pinto 243/81* (CEPEC, HRB); Gentio do Ouro, 2 Dec 1980 (fl), *Pirani et al.* CFCR 349 (K, NY, SPF); Estação Ecológica do Raso da Catarina, 09°20'-55'S, 38°29'-43'W, 26 Jun 1982 (fl, fr), *Queiroz* 389 (HUEFS); Boquira, Fazenda Umburana, 12°43'S, 42°35'W, 20 Mar 1984 (fr), *Salgado & Bautista* 270 (CEPEC, HRB); Jequié, entrada do ramal localizado ao SW do km 38 da Rod. Jequié-Contendas do Sincorá, 15 Feb 1979 (fl), *T. S. Santos et al.* 3487 (CEPEC, NY, RB); Catinga de Moura, 1890 (fl), *Schreiner s.n.* (R 71059); Jeremoabo, 27 May 1982 (fl), *J. S. Silva* 699 (SP, SPF). **Ceará:** Pereiro, Serra do Pereiro, Fazenda Campos, 6 Aug 1988 (sterile), *Fernandes & Figueiredo s.n.* (EAC). **Minas Gerais:** Jaíba, Gleba B, Parcela 24, 4 Dec 1990 (fl), *M. B. Horta et al. s.n.* (BHCB-22135, SPF); Manga, Reserva Florestal, DIJ, May 1991 (fr), *M. B. Horta et al. s.n.* (BHCB-21755, SPF). **Pernambuco:** Ibimirim, entre Riacho Seco e Ibimirim, 7 Jun 1952 (fl), *Andrade-Lima* 52-1025 (IPA, PEUFR, R, SPF); Triunfo, 24 Mar 1970 (fl), *Andrade-Lima* 70-5864 (IPA, SPF). **Piauí:** São Raimundo Nonato, Bom Jardim, 15 Dec 1978 (fl), *A. Fernandes s.n.* (EAC).

2. HELIETTA Tul., Ann. Sci. Nat. ser. 3. 7: 280. 1847. TYPE: *Helietta plaeana* Tul.

Shrubs or *trees* with punctate glands usually visible on all unglanified parts; buds densely sericeous; young shoots pubescent, usually early glabrescent. *Leaves* (sub-)opposite, digitately 3-foliolate, densely glandular-punctate, velutinous to pubescent to glabrous; petiole semiterete, flat to canaliculate adaxially or sometimes acutely winged, with a reduced, hairy appendage or a tuft of long trichomes adaxially at apex; leaflets sessile or rarely short-petiollulate, conspicuously articulate at junction with the grooved petiole apex, membranous to chartaceous or subcoriaceous, margin entire (seldom irregularly crenulate), terminal leaflet symmetric and

larger than the lateral ones, the latter usually asymmetric at base; venation brochidodromous, the midvein usually raised on both surfaces. *Inflorescence* a terminal polytelic diplothyrsse or (in *H. parvifolia*) monothyrsse, longer or shorter than the leaves, lax, the branches (sub-)opposite, patent, peduncle short or absent; bracts and prophylls (bractlets) scale-like, usually paired. *Flowers* perfect, actinomorphic, 4–5-merous. *Sepals* united at base, quincuncial, persistent in fruit, scarious, usually slightly erose or ciliolate. *Petals* free, imbricate in bud, pellucid-punctate, glabrous, hyaline and erose or ciliolate or entire at margin, spreading at anthesis. *Stamens* as many as the petals, alternipetalous, free, glabrous; filaments complanate, translucent, inserted below the disk, reflexed after anthesis; anthers ovoid or heart-shaped, dorsifixed below the middle, versatile, introrse, 2-locular, the locules somewhat divergent at base. *Disk* intrastaminal, cupular, forming an erect, undulate rim, 4–5-lobed, each lobe 2-lobulate, surrounding and of about the same height as the ovary,

glabrous. *Ovary* depressed-globose, of 4–5 connate carpels but conspicuously 4–5-lobed, 4–5-loculed, minutely glandular-tuberculate, glabrous or pubescent; ovules 2 per cell, collateral, pendulous; style 1, terete, glabrous; stigma discoid to capitate, slightly 4–5-lobed. *Fruit* a samarium of (3–) 4–5 samaroid mericarps, velutinous to glabrous, separating at maturity acropetally, each with an ellipsoid-trigonal seeded body and a dorsal ascending, obtuse, chartaceous to subcoriaceous wing, velutinous to glabrous; seed 1 per carpel, free from the endocarp, oblong, with a thin testa and fleshy endosperm, glabrous; embryo fleshy, with straight, oblong cotyledons and a superior radicle, surrounded by a thin layer of a soft endosperm.

A neotropical genus of eight species, with disjunct ranges in North America (Mexico and adjacent Texas); Cuba; northern South America (Venezuela and Colombia); Peru; and eastern Paraguay, northern Argentina, and southeastern Brazil; mostly mesic to dry habitats; 20–2500 m elevation.

Key to the species of *Helietta*

1. All flowers 4-merous.
 2. Terminal leaflet usually twice as long as the lateral ones; petiole 0.5–1.8 cm long; inflorescence a monothyrsse 1–3.5 cm long; ovary densely pilose (NE Mexico, S Texas). 1. *H. parvifolia*
 2. Terminal leaflet slightly longer than the lateral ones; petiole (1–)2–6 cm long; inflorescence a diplothyrsse (2–)3–11.5 cm long; ovary glabrous.
 3. Leaflets drying glaucous, retuse to truncate at apex; midvein sunken adaxially; shoots with no evident lenticels (Cuba). 2. *H. glaucescens*
 3. Leaflets drying greenish to olive-brownish, not glaucous, apex obtuse or retuse to emarginate; midvein raised on both surfaces; shoots with many conspicuous white lenticels (N Venezuela, N Colombia). 3. *H. plaearana*
1. Most flowers 5-merous, occasionally some 4-merous flowers found in an inflorescence.
 4. Apex of leaflets apiculate via involute margin of blade (S Brazil, W Paraguay, NE Argentina). 8. *H. apiculata*
 4. Apex of leaflets not apiculate or involute.
 5. Leaves velutinous all over (W Paraguay, SW Brazil). 7. *H. puberula*
 5. Leaves (sub-)glabrous.
 6. Leaflets with prominent lateral veins; fruit with seed locule densely pubescent, the wings coriaceous and veins prominent (Central Mexico). 5. *H. lucida*
 6. Leaflets with lateral veins inconspicuous to slightly raised; fruit glabrous, the wings chartaceous to membranous and veins prominulous.
 7. Anthers apiculate; ovary pilose; main lateral coflorescences subopposite; leaflets dull above (W Mexico). 4. *H. lottiae*
 7. Anthers not apiculate; ovary glabrous; main lateral coflorescences opposite; leaflets shiny above.
 8. Inflorescence 2–6 cm long, shorter than the leaves; petals glabrous; wings of fruit 10–14 mm long; petiole (1–)2–3 cm long (N Venezuela, N Colombia). 3. *H. plaearana*
 8. Inflorescence 8–12 cm long, longer than the leaves; petals ciliolate; wings of fruit 15–19 mm long; petiole 0.5–2(–3) cm long (SE Brazil). 6. *H. glaziovii*

1. *HELIIETTA PARVIFOLIA* (A. Gray ex Hemsl.) Benth., Hooker's Icon. Pl. 14: 66, t. 1385. 1882. *Ptelea parvifolia* A. Gray ex Hemsl., Biol. Centr. Amer. Bot. 1: 170. 1879, TYPE: MEXICO. Nuevo Leon: Near Monterey, s.d. (fl), *Berlandier 1404* (LECTOTYPE, here designated: K; ISOLECTOTYPES: G, P) [excl. specim. *Gregg s.n.* (Mexico, Buenavista, syntypes: K, NY = *Ptelea baldwinii* (Torr.) A. Gray]. (Fig. 5A-F)

Helietta parviflora Benth. ex Small, Fl. S.E. U.S. 676. 1903 (wrong spelling).

Shrub or *tree(-let)* 1.5–12 m; shoots pale gray to pale brown, sparsely pubescent to glabrous, striate, with many cream-colored lenticels. *Leaves* densely white-pubescent when young, soon glabrescent or sparsely and minutely puberulous mainly on the petiole apex; petiole 0.5–1.5(–1.8) cm long, semiterete, subwinged or slightly to deeply canaliculate adaxially, minutely puberulous at apex; leaflets conspicuously black-punctate on both surfaces or only abaxially, chartaceous to subcoriaceous, greenish to olivaceous, shiny above, dull and paler beneath, sessile, oblanceolate to narrow-obovate (the lateral ones sometimes wide-obovate), the margin entire, seldom irregularly and sparsely crenulate, flat or revolute, apex obtuse to retuse or emarginate, sometimes subacute, base decurrent or cuneate or in lateral leaflets sometimes acute and subsymmetric; terminal leaflet 2.5–4(–5.5) × 1–1.7 cm; lateral leaflets 1.6–2.7(–3.2) × 0.7–1.4 cm; midvein slightly raised on proximal part of the blade, secondary veins mostly obscure to sometimes imperceptible. *Inflorescence* a sessile monothyrse 1–3.5 cm long, usually much shorter than the leaves, densely and minutely pubescent with white, appressed trichomes, sometimes subglabrous; bracts triangular, acute, ca. 1 mm long, pubescent abaxially. *Flowers* 4-merous; pedicel pubescent to subglabrous, ca. 1.5–2 mm long; bractlets ovate, pubescent. *Sepals* ovate, acute, pubescent to puberulous, ciliolate, ca. 1 mm long, greenish. *Petals* cream-colored, oblong, 3.2–3.5 mm long, glabrous, obtuse, margin entire or erose. *Stamens* ca. 1.5 mm long; anthers ovoid, short-apiculate. *Disk* 4-lobed, slight-

ly shorter than the ovary. *Ovary* 4-lobed, densely white-pilose with short trichomes; style glandular-punctate, ca. 0.8 mm long; stigma subcapitate, slightly 4-lobed. *Fruit* of (3–)4 mericarps, glabrous; seed locule ellipsoid, 5–10 mm long; wing ovate to oblong or rounded, 6–15 × 8–10 mm, chartaceous, with slightly prominent veins.

Distribution (Fig. 4B), *habitat*, and *phenology*.—This species occurs in northeastern Mexico and Texas, U.S.A., at (50–) 300–1600(–2500) m. According to Simpson (1988), it occurs in Texas on limestone soils in the Rio Grande Valley, where “it is confined to several small gravelly hills just east of Rio Grande City in Starr County and the chaparral for quite a few miles north of Rio Grande City.” Nevertheless, there is one collection from about 300 km further north (*Atha* 387, NY). In northeastern Mexico, the species is widespread, ranging from Coahuila, Nuevo León, and Tamaulipas to San Luís Potosí, Querétaro, and Hidalgo, mostly on the limestone ridges of the Sierra Madre Oriental. Rzedowski (1981: 256) stated that *H. parvifolia* is one of the most frequent species in the matorral submontano (also called “piedmont scrub”), a sclerophyllous evergreen vegetation that is dense, unarmed, and about 3–5 m tall, occurring in regions with 450–900 mm annual precipitation and rarely above 2000 m elevation. This formation is distributed mainly on the Sierra Madre Oriental, though extending also to the Altiplano and to the coastal lowlands. In Nuevo León and San Luís Potosí, the dominance of this species is so remarkable that botanists have called the local formations “matorral de *Helietta*” (e.g., Rzedowski, 1981).

Most (43 of 52) available flowering collections are from May to September, but others are from October, November, January, and April. Fruits have been collected between July and March. Simpson (1988) referred to a flowering period between March and May and to the presence of mature fruits in September and October, in Texas.

This species is easily distinguished from its congeners by its very small leaves, of which the lateral leaflets are usually half the size of the terminal one. Furthermore, it is

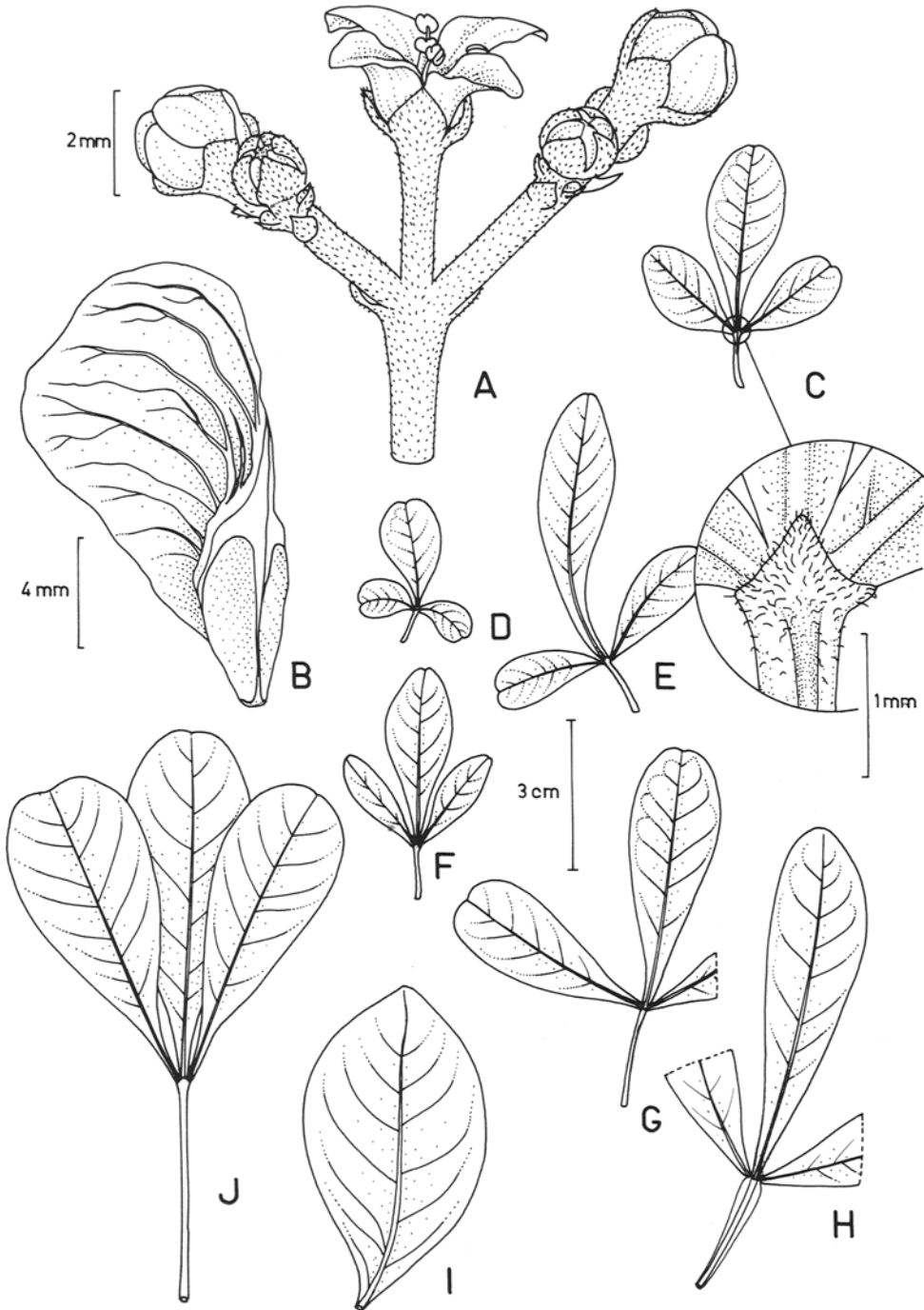


FIG. 5. A–F *Helietta parvifolia*. A. Dichasial part of an inflorescence. B. Mericarp. C–F. Leaves, showing variation in shapes and relative sizes of leaflets and a detail of the articulation of the leaflets and petiole. G–J. *Helietta glaucescens*. G, H, J. Leaves, showing variation in shapes and relative sizes of leaflets. I. Lateral leaflet. (A, Medrano 4501; B, Medrano et al. 2023; C, Palmer 142; D, Palmer 494; E, Atha 387; F, Seigler et al. 13140; G, Ekman 15889; H, Ekman 15269; I, Roig & Azcuy 2910; J, Clement & Clement 3971.)

the only species to have monothyrse instead of diplothyrses, and they are few-flowered and shorter than the subadjacent leaves. Its flowers are consistently tetramerous, a condition to be found elsewhere only in *Helietta glaucescens*; *H. plaeana*, though basically tetramerous, can be entirely pentamerous in some specimens.

Helietta parvifolia was originally described in *Ptelea*. Hemsley based its diagnosis on two syntypes from Mexico: the first, *Berlandier 1404*, is a flowering specimen here designated as the lectotype, while the second, *Gregg s.n.*, from Buenavista, represents a fruiting specimen of *Ptelea baldwinii* Torr. & A. Gray (= ? *P. trifoliata* L.). The latter was removed from *Helietta* by Gray (1897), but to date no formal lectotypification has been proposed.

Although in the protologue Hemsley cited *Berlandier 1404* as collected "near Carrizal," the locality on the original specimen at K, as well as on the isolectotypes at G and P, say "Near Monterey," as correctly published by Bentham when transferring this species to *Helietta*.

Common names.—**Mexico and Texas:** baretta, barreta, baretta (on labels of many herbarium specimens and citations by Britton, 1908; Standley, 1923; Martínez, 1937; Pesman, 1962; Simpson, 1988).

Uses.—According to Britton (1908), the wood of *H. parvifolia* is hard, close-grained, orange to brown, and used for fuel.

Representative specimens examined. UNITED STATES. **Texas:** HIDALGO CO.: E of San Fordija, 4 Feb 1941 (fr), *Lundell & Lundell 9907* (US); E of Sullivan City, 4 May 1941 (fl), *Lundell & Lundell 9980* (F, MO, US); Brownsville, vic. of Rio Grande, 13 Apr 1941 (fl), *Runyon 2555* (F). STARR CO.: Roma, Los Saenz, Ebony Ave. 0.8 km N of US Hwy. 83, 29°25'N, 99°00'W, 24 Dec 1993 (fr), *Atha 387* (NY); 6 mi E of Rio Grande City on S side of Hwy. 83, Jan 1953 (fl), *Nogle 11* (F).

MEXICO. **Coahuila:** Monclova, Gloria Mtns., 6 Aug 1939 (fl), *Marsh 1009* (F); Monclova, mtns., 1–6 Sep 1880 (fl, fr), *Palmer 144* (F, NY, US); 2 km NW de Núñez, km 84 carretera San Luis-A. Morelos, 2 Apr 1955 (fl), *Rzedowski 5800* (F, US). **Hidalgo:** Jacala, 8 Nov 1937 (fl, fr), *Edwards 737* (F, MO); 6 km N de Tasquillo, ladera de roca ignea, 7 Sep 1965 (fl), *González-Quintero 3092* (BM, F); Cañada El Salitre, Barranca de Metztilán, 5 May 1976 (fl), *González et al. 8989* (MEXU). **Nuevo León:** N of Vallecillo, 9 Jun 1935 (fl), *Clark 6656* (MO); km 18 Brecha Matehuala-La Culebrilla, Matehuala, 8 Jan 1973 (fr), *Díaz Luna*

3730 (MEXU); Rancho Resendez, Lampazos, 26 Jun 1937 (fl), *Edwards 367* (MO); Sierra del Fraile, near García Caves, 25°53'N, 100°30'W, 17 Jun 1979 (fl), *Hess & Byrne 4737* (F); mtns. near Monterey, Diante Canyon, Jul 1933 (fl), *Mueller & Mueller 97* (F, G); xeric W wall of Cañon de Potrero Redondo, Mun. de Villa Santiago, 4 Jul 1935 (fl), *Mueller 2084* (F, MO, NY, P); Galeana, ca. 4 km NW of village of Río San José, steep-walled canyon (Canyon Tomates) at bottom of riverbed, 24°37'N, 99°54'W, 18 Sep 1993 (fl), *Nesom et al. 7607* (NY); 20 mi W of Linares, near km 35 and Los Pinos, 14 Sep 1967 (fl), *Oliver et al. 1117* (MO); Sierra de la Silla, limestone ledges, 27 May 1889 (fl), *Pringle 2528* (BM, F, G, MO, NY, P, US). **Querétaro:** Landa, 200 m al N del Río Moctezuma, al S de Matzacintla, 7 Feb 1989 (fr), *Carranza 1444* (MEXU); between Vizarrón and Higuierillas, 23 Aug 1905 (fl), *Rose et al. 9772* (NY, US). **San Luis Potosí:** Rioverde, 11.5 mi N of San Francisco, 27 May 1981 (fl), *Fryxell & Anderson 3634* (F, MO, NY, US); Minas de San Rafael, Jul 1911 (fl, fr), *Purpus 5046* (MO, US); steep rocky hillside, 50 mi NE of San Luis Potosí toward Matchuala, 21 Nov 1958 (fl), *Rollins & Tryon 58201* (GH, NY). **Tamaulipas:** La Marita, vic. of Marmolejo, 11 Aug 1930 (fr), *Bartlett 10893* (F, US); Palmillas, 6 km al San Pedro al noroeste de Palmillas, 13 Jul 1984 (fr), *González-Medrano et al. 241* (MEXU, NY); 20–25 km al S de Méndez en el camino a Burgos (fr), *González-Medrano et al. 2023* (MEXU, MO); Tula, 4 km al N de San Rafael, entre San Rafael y El Salitrillo, 11 Aug 1972 (fl), *González-Medrano et al. 4501* (MEXU); González, entre Torrecillos y Pénjamo, 30 May 1974 (fl), *González-Medrano et al. 7294* (MEXU, NY); Miquihuana, 3 km al Noroeste de San José del Llano, S de Las Vacas, 12 Apr 1976 (fl), *González-Medrano et al. 8520* (MEXU, MO); Tula, 5 km al Oeste del Ejido El Saltillo, 3 Jul 1985 (fl), *Hiriart et al. 800* (MEXU); vic. of Victoria, 13 Jun 1907 (fl), *Palmer 494* (F, K, MO, NY, US).

2. *HELIETTA GLAUDESCENS* Urb., Symb. Antill. 9: 179. 1924. TYPE: CUBA. Prov. Oriente: Papayo in colli Mandinga, ca. 850 m, 5 Aug 1918 (fl), *E. L. Ekman 9456* (HOLOTYPE: S; ISOTYPES: BM, G, GH-n.v., MO, NY). (Fig. 5G–J)

Helietta cubensis Monach. & Moldenke, Phytologia 2(7): 223. 1947. TYPE: CUBA. Oriente, Mina Cayoguán, Pta. Gorda, 21 Jul 1944 (fl), *C. Clement & A. Clement 3971* (HOLOTYPE: NY).

Tree(-let); shoots pale brown, glabrous, suberose, longitudinally fissured and ridged, with no evident lenticels, when young conspicuously brown-punctate (when dry). *Leaves* pubescent when very young, soon glabrescent or the petiole minutely puberulent; petiole (1.4–)2–4(–6) cm long, semiterete to canaliculate and sometimes narrowly winged (*Ekman 15269*), pale cream with many brown glan-

dular dots; leaflets glaucous and conspicuously brown-punctate on both surfaces, chartaceous to subcoriaceous, shiny above, dull beneath, sessile, oblanceolate to narrow-obovate, margin flat to revolute, the apex obtuse to rounded, or sometimes truncate to emarginate, base decurrent to sometimes cuneate, in lateral leaflets slightly asymmetric; terminal leaflet (3-)5-8(-11) × (1.2-)1.8-3.8 cm; lateral leaflets 2.8-6.5(-8) × (0.9-)1.4-3.5 cm; midvein flat adaxially (may be slightly raised only on the proximal portion), slightly raised and pale cream on abaxial surface, fading distally, secondary veins 5-7 per side, inconspicuous on both surfaces or sometimes slightly prominent abaxially. *Inflorescence* a diplothyse 3-11.5 cm long, shorter or sometimes longer than the subjacent leaves, sparsely and minutely puberulous to generally glabrous, brown-punctate; peduncle 1-2 cm long; coflorescences 2-10, opposite, the proximal ones 1-8 cm long; bracts deltate, ca. 0.7 mm long, puberulous to ciliate abaxially. *Flowers* 4-merous; pedicel minutely puberulous to glabrous, 1-2 mm long; bractlets deltoid, puberulous to ciliate. *Sepals* suborbicular, puberulous, ca. 0.8 mm long, conspicuously punctate. *Petals* cream-colored, oblong, obtuse, ca. 2-2.3 × 1.2 mm, glandular-punctate, entire. *Stamens* ca. 1.3 mm long; anthers ovoid. *Disk* 4-lobed. *Ovary* 4-lobed, glandular-tuberculate; style punctate, ca. 0.4 mm long; stigma subcapitate, 4-lobed. *Fruit* of 4 samaroid mericarps, glabrous; seed locule ellipsoid, ca. 0.9 mm long; wing obovate, to 15 × 0.9 mm, chartaceous, with raised veins and black punctations.

Distribution (Fig. 4B), *habitat*, and *phenology*.—*Helietta glaucescens* is endemic to Cuba, occurring in Provincia Oriente (eastern extreme of the island) and in Provincia Pinar del Río (western extreme), in dry thickets known locally as "charrascales," at 300-850 m. It has been collected on serpentine soil (*Ekman 15269*) and on limestone at Sierra de Vinales. Flowering material has been collected in April-September; the two fruiting collections available were made in September (very young fruits) and December.

It is easily distinguished from the other

species in the genus by its whitish petiole and glaucous, conspicuously punctate leaflets with sunken (not raised) nerves.

The holotype of *Helietta cubensis* Monach. & Moldenke shows larger leaves and inflorescences than the other specimens examined, but besides the size of these structures there is no consistent difference in any other character. Nevertheless, the two taxa were kept apart by León and Alain (1951) in the *Flora de Cuba*.

Representative specimens examined: CUBA. **Oriente:** Sierra de Nipe, on path from Woodfred to Piedra Gorda, 24 Sep 1922 (fl, fr), *Ekman 15269* (F, G, NY, US); Sierra de Cristal, 9-10 Dec 1922 (fr), *Ekman 15889* (NY); Guantánamo, Maisí, orillas del arroyo del Pino entre Guajimero y Alto del Pino, 23 Apr 1986 (fl), *Gutiérrez et al. 59173* (HAJB, SPF). **Pinar del Río:** Pluviosilva a orillas del Arroyo Jaragua, 5 Aug 1975 (fl), *Bisse et al. 26972* (HAJB, SPF); Viñales, summit of Sierra de Viñales, 6 Jun 1923 (fl), *Ekman 16566* (G, K, P); top of Mogote de la Bandera, Sierra de Viñales, 9 Dec 1929 (sterile), *Roig & Azcuy 2910* (NY).

3. *HELIIETTA PLAEANA* Tul., Ann. Sci. Nat., ser. 3, 7: 281. 1847. TYPE: VENEZUELA [Nouvelle Grenade]. Maracaibo, 1826 (fl), *Plée s.n.* (HOLOTYPE: P; ISOTYPES: F, P-3 sheets, photos of holotype at F, MO, SPF). (Fig. 6A-D)

Esenbeckia atata Pittier, Arb. arbust. nuev. Venez. década 1: 7. 1921. TYPE: VENEZUELA. Distrito Federal: Hacienda Panarigua, Valle de Puerto La Cruz, 9 Sep 1917 (fl), *A. Jahn 492* (HOLOTYPE: US).

Shrub or *treelet* 2-7 m tall, rarely a tree to 12 m (*Pittier 9207*); shoots pale gray to pale brownish, with many white lenticels. *Leaves* pubescent only when very young, soon completely glabrous or with scattered trichomes remaining on the distal portion of petiole; petiole (1-)2-3 cm long, deeply canaliculate adaxially; leaflets dark-punctate on both surfaces, chartaceous, sessile to seldom short-petiolate, greenish to olive-brownish, shiny above, dull beneath, narrow-elliptic to narrow-obovate, margin slightly revolute, apex obtuse and often retuse to emarginate, seldom subacute, base cuneate to decurrent in the terminal leaflet, strongly asymmetric and acute to obtuse in the lateral leaflets; terminal leaflet 5-8(-9) × 2-3(-3.5) cm, lateral leaflets 3.5-7.2(-8) × 1.6-2.5(-3.2) cm; midvein raised on the

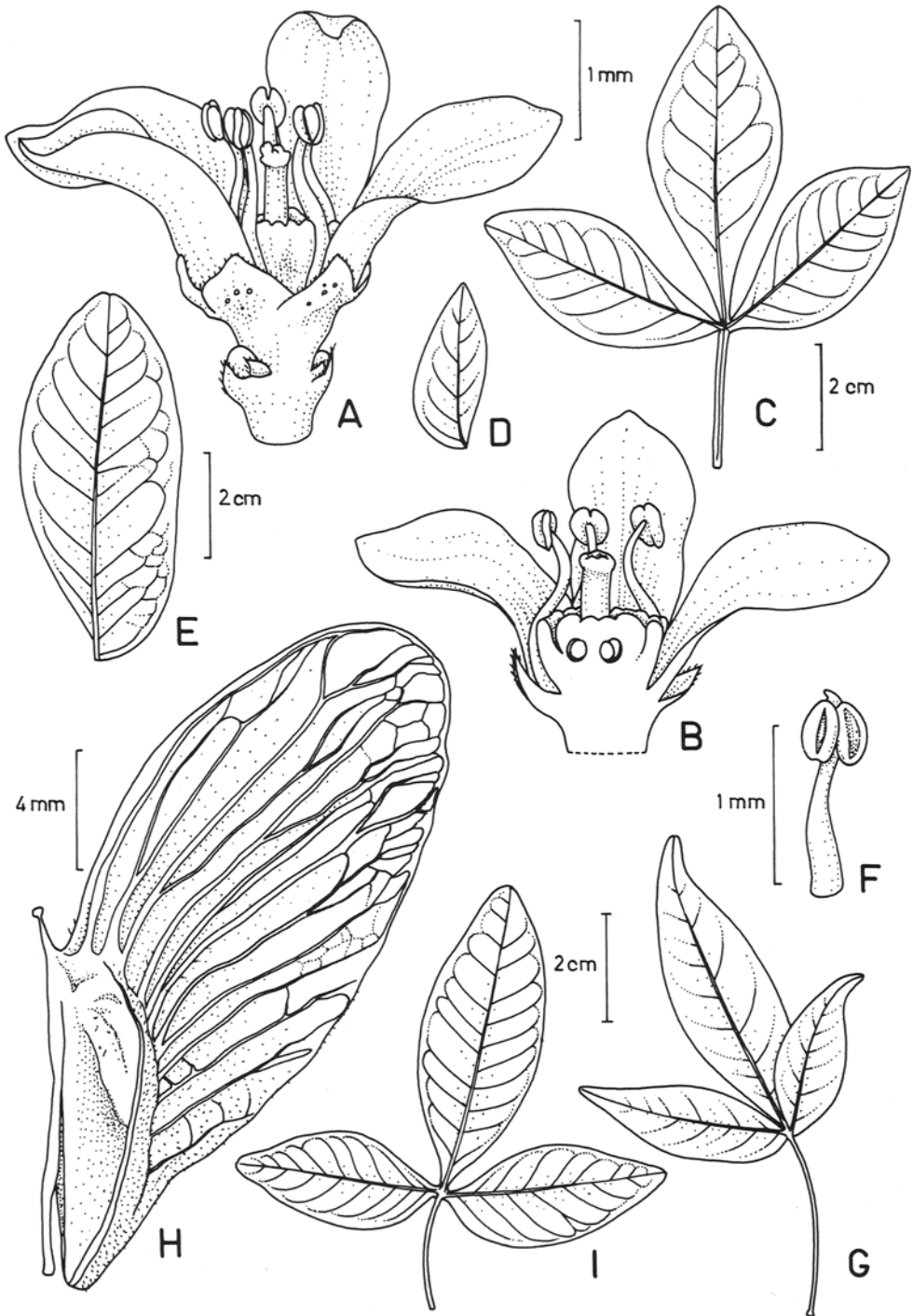


FIG. 6. A-D. *Helietta plaeana*. A. Flower (5-merous, one petal removed) with 2 buds in the axil of the bracteoles. B. Longisection of flower. C, E. Leaf. D. Lateral leaflet. F, G. *Helietta lottiae*. F. Stamen, ventral view. G. Leaf. H, I. *Helietta lucida*. H. Mericarp. I. Leaf. (A, B, *Breteler 4389*; C, *Bunting et al. 11804*; D, *Trujillo 6558*; E, *Pittier 10894*; F, *Magallanes 3630*; G, *Koch & Fryxell 8248*; H, *Lott & Wendt P-56*; I, *González-Medrano et al. 12752*.)

proximal $\frac{3}{4}$ of the blade on both surfaces, the secondary veins 5–8 per side, inconspicuous. *Inflorescence* a diplothyrs (2–) 4–6 cm long, shorter than the subjacent leaves, glabrous or sometimes with a few, scattered, small trichomes; peduncle 0–5 mm long; cymes 2–6, opposite, the proximal ones (1–)2.5–6 cm long; bracts ovate, acute, ca. 0.7 mm long, ciliate. *Flowers* 4(–5)-merous; pedicel glabrous, ca. 1.5 mm long; bractlets deltoid, ciliate. *Sepals* ovate, acute, glabrous with ciliate margin, ca. 1 mm long, greenish. *Petals* cream-colored or whitish, oblong, obtuse to subacute, ca. 2.6–3 × 1.2 mm, glabrous, entire. *Stamens* ca. 1.2 mm long; anthers ovoid, yellow, obtuse. *Disk* 4(–5)-lobed, yellow. *Ovary* 4(–5)-lobed, glabrous; style brown-punctate, ca. 0.8 mm long; stigma subcapitate, 4(–5)-lobed. *Fruit* of (3–)4(–5) mericarps, glabrous; seed locule ellipsoid, 5–10 mm long; wing oblong, 10–14 × 9–11 mm, chartaceous, with slightly prominent veins, glandular-punctate.

Distribution (Fig. 4B), *habitat*, and *phenology*.—This species seems to be restricted to the dry, semi-deciduous formations of northern Venezuela and adjacent Colombia, at 20–600 m. In Venezuela, it grows in very dry tropical forest and its transition to the dry tropical forest (Ewel & Madriz, 1968) or in dry chaparral (*Steyermark* 56802). I have seen only three collections from Colombia, of which only one has an exact location (Cartagena), where the vegetation is also very dry tropical forest (Espinal, 1990). In these dry communities, average temperature is higher than 24°C, the annual rainfall is about 500–1000 mm, and there is a predominance of deciduous plants (Espinal, 1990; Ewel & Madriz, 1968), though *Helietta plaecana* is evergreen. Flowers are present in February, May–July, October, and November; and fruits in December and February.

Flowers of this species are basically tetramerous, but some pentamerous flowers can be found in some specimens; only four collections have consistently pentamerous flowers: *Holst et al.* 2294, *Breteler* 4389, *Steyermark & Aristeguieta* 114, and *Jahn* 492. The latter is the holotype of *Esenbeckia atata* Pittier, a name already synon-

ymized under *Helietta plaecana* by Kaastra (1982). The paratypes of *E. atata* (Pittier 9207 at G, NY, and US) have mostly tetramerous flowers and even some young fruits with wings typical of *Helietta*.

The closest relative of *H. plaecana* seems to be *H. glaziovii*; their relationship is discussed under the latter.

Common names.—**Venezuela**: caritívá, caritivar, caritivano (Schnee, 1960), caritibal (*Aristeguieta et al.* 6742) (Zulia); marfil (Pittier et al., 1947) (Trujillo).

Other specimens examined. COLOMBIA. **Bolívar**: Cartagena, 1866 (fl), *Triana s.n.* (G, P). **Without specific locality**: S.d. (fl), *Dugand* 164 (F); s.d. (fl), *Dugand* 500 (F).

VENEZUELA. **Anzoátegui**: Hacienda Panarigua, valley of Puerto La Cruz, Feb 1921 (fl), *Pittier* 9207 (paratype of *Esenbeckia atata* Pittier; G, NY, US). **Aragua**: 8–9 km from redoma at Cata Beach, SW toward Cuyaga, 10°29'N, 68°42'W; on very steep slope, directly facing sea, 29 Nov 1985 (fl), *Holst et al.* 2294 (MO, NY). **Distrito Federal**: Faldas costaneras frente al mar, entre Punta Picure y Oricao, 1 Jul 1966 (fl), *Steyermark & Aristeguieta* 114 (NY–2 sheets, VEN); Depto. Libertador, dry slopes bordering Mar Caribe between Chichiriviche and Oricao, 11 Oct 1976 (sterile), *Steyermark & Espinoza* 112764 (NY, VEN). **Falcón**: Sierra de San Luís hacia Curimagua, 22–24 Oct 1977 (fl), *Aristeguieta* 12485 (NY); Península Paraguaná, La Ciénaga, between Pueblo Nuevo and Santa Ana, 20 Dec 1964 (fl, fr), *Breteler* 4389 (F, G); Buchivacoa, carretera Dabajuro–Represa Mamito–Fundo “El Peruano,” al sur de Dabajuro, 17 Jun 1978 (fl), *Bunting et al.* 6429 (NY); Paraguaná, s.d. (fl, fr), *Lasser & Aristeguieta* 3338 (F, VEN). **Lara**: Urdaveta, Cumbe de Baragua, 7 Oct 1927 (fl), *Christ* 32 (NY); between Trujillo–Lara boundary line and Carora, 28 May 1944 (fl), *Steyermark* 56802 (F, NY); Paso de Tacarigua, carretera Barquisimeto–Duaca, 18 Jul 1964 (fl, fr), *Trujillo* 6558 (NY, VEN). **Trujillo**: Vic. of Valera, on rd. to Escuque, 24 Nov 1922 (fl), *Pittier* 10791 (G, NY, P); Dividive, 28 Nov 1922 (fl), *Pittier* 10849 (G, NY, P); between Quebrada Seca bridge and Río Motatán, 1 Feb 1929 (fr), *Pittier* 13298 (F, G, NY). **Zulia**: Carretera Maracaibo–Perijá, entrada Centro Inseminación del MAC, s.d. (fr), *Aristeguieta et al.* 6742 (NY, VEN); Mara, entre Puerto Mara y Los Mayales, 18 Oct 1982 (fl), *Bunting et al.* 11804 (NY); Veras Altas, rd. Machiques–Maracaibo, 15 Oct 1922 (fl), *Pittier* 10509 (G, NY).

4. HELIETTA LOTTIAE F. Chiang, *Brittonia* 36: 455, fig. 1. 1984. TYPE: MEXICO. Jalisco: Municipio de La Huerta, Estación de Biología Chamela UNAM, al SE de la casa de investigadores, 3 Oct 1977 (fl), *L. A. Pérez J.* 1685 (HOLOTYPE: MEXU–n.v.; ISOTYPES: ENCB–n.v., FCME–n.v., NY). (Fig. 6F, G)

Treelet or *tree* 3–10(–15) m tall; shoots reddish-brown to grayish, sparsely pubescent to glabrous, suberose, longitudinally fissured and ridged, with many white lenticels. *Leaves* densely short-pubescent with white, appressed, curved trichomes when young, soon glabrescent or sparsely and minutely puberulous on main veins and on the petiole apex; petiole 1.8–5 cm long, slender, semiterete, flat adaxially to sometimes slightly canaliculate, pale cream-colored; leaflets conspicuously black-punctate on both surfaces, membranous to chartaceous, pale green to pale olivaceous, dull on both surfaces, sessile to sometimes short-petiolulate, narrow-elliptic to elliptic or seldom subobovate, margin entire, flat to slightly revolute, apex obtuse to short-acuminate with a rounded to retuse tip, base acute to cuneate in the terminal leaflet, acute to obtuse and mostly asymmetric in the lateral ones; terminal leaflet (3–)4.5–8(–12) × 1.4–3(–5) cm; lateral leaflets 2.8–7.5(–11) × 1.3–2 cm; midvein raised on abaxial surface, pale cream-colored, somewhat raised on adaxial surface, secondary veins 5–7 per side, mostly inconspicuous. *Inflorescence* a diplothyse 7–15 cm long, longer than the leaves, punctate, glabrous or sparsely short-pubescent with white, curved trichomes; peduncle 0–1.2 cm long; cofillorescences 4–6, mostly subopposite, the proximal ones 1.5–6.5 cm long; bracts triangular to ovate, ca. 0.5 mm long, puberulous. *Flowers* 5-merous; pedicel pubescent with white, short trichomes, 1–1.5 mm long; bractlets triangular, pubescent. *Sepals* ovate to oblong, apex acute, sparsely pubescent, ciliolate, ca. 0.7 mm long, greenish. *Petals* cream-colored to yellowish (or reddish-brown *vide* Chiang, 1984, in dried specimen?), elliptic, obtuse to subacute, 2–2.5 × ca. 1 mm, margin slightly erose. *Stamens* ca. 1.5 mm long; anthers heart-shaped, apiculate. *Disk* 5-lobed, slightly shorter than the ovary. *Ovary* 5-lobed, minutely white-villous; style glandular-punctate, ca. 0.3 mm long; stigma slightly 5-lobed. *Fruit* of 4 or 5 mericarps, villous to glabrescent; seed locule ellipsoid, 8–9 mm long; wing oblong to wide-ovate, 13–15 × 10–12 mm, chartaceous, with raised veins.

Distribution (Fig. 4B), *habitat*, and *pheno-*

nology.—This species is known only from tropical deciduous forests in Guerrero and Jalisco, southeastern Mexico, at 200–600 m. The few collections available have flowers in March and August–October and fruits in August and October. According to Lott (1993), in Chamela it flowers from March to August.

Helietta lottiae is distinguished from its congeners by its mostly elliptic, sometimes almost rhombic, acuminate, membranous to chartaceous, greenish leaflets; its slender petiole that can reach 4.8 cm; and its inflorescence that is longer than the leaves and bears subalternate lateral branches (cofillorescences). It is also unique in having apiculate anthers. The species was named after Emily Jane Lott, an active plant collector along the western coast of Mexico and author of checklist of the flora of the Estación Biológica de Chamela (Lott, 1993), the type locality of *H. lottiae*.

Representative specimens examined. MEXICO. **Guerrero:** Cañada del Zopilote, 10 Aug 1945 (fr), *Alexander & Hernandez X. s.n.* (NY); Tepecoacuilco, 33 km al Sur de Iguala, 15 Oct 1982 (fl), *Koch & Fryxell 8248* (BM, NY). **Jalisco:** La Huerta, Estación de Biología Chamela (UNAM), 21 Apr 1984 (fl), *Bullock 1507* (MEXU); Chamela, field station near dormitory, 19°30'N, 105°03'W, 21 Aug 1991 (fl), *Gentry & Woodruff 74496* (MO, NY); La Huerta, Estación Biológica Chamela (UNAM), 19°30'N, 105°03'W, 27 Oct 1982 (fr), *Lott 1520* (MEXU, NY); La Huerta, Estación Biológica Chamela, Vereda Chachalaca, 19 Aug 1981 (fl), *Magallanes 3083* (BM, MEXU, SPF); La Huerta, UNAM, Estación de Investigación Chamela, 2 Sep 1981 (fl), *Magallanes 3097* (K); Estación de Biología de Chamela, 30 Mar 1975 (fl), *Magallanes 3630* (MEXU, NY).

5. *HELIETTA LUCIDA* Brandegee, Univ. Calif. Publ. Bot. 4(11): 182. 1911. TYPE: MEXICO. Puebla: Vic. of San Luis Tultitlanapa, 1908 (fr), *C. A. Purpus 4451* (HOLOTYPE: UC). (Fig. 6H, I)

Shrub or *treelet* 2–3 m tall; shoots dark-brown to dark-grayish, longitudinally fissured, with many white lenticels. *Leaves* short-pubescent with cream-colored, erect to curved trichomes, soon glabrescent except persistently pubescent to sparsely so on main veins and on the petiole; petiole 1.5–4.2 cm long, cream-colored to yellowish, semiterete, flat adaxially to slightly canaliculate; leaflets punctate on both surfaces

(brown dots), chartaceous to subcoriaceous, olivaceous, shiny above, dull beneath, short-petiolulate or sessile, narrow-elliptic to narrow-oblong to lanceolate, margin flat to slightly revolute, apex obtuse to retuse, base cuneate to acute in the terminal leaflet, acute and strongly asymmetric in the lateral leaflets; terminal leaflet 5.2–11.5 × 1.8–5.5 cm; lateral leaflets 3.5–9 × 1–3.8 cm; midvein raised on both surfaces, yellowish, the secondary veins 7–11 per side, prominent on both surfaces. *Inflorescence* a diplothyse (?), only infructescences seen, 4–7 cm long, densely velutinous; cofiloflorescences ca. 2–4(–?), opposite. *Flowers* not known. *Fruit* of 4 or 5 mericarps, pubescent to glabrescent; seed locule ellipsoid, 9–12 mm long, pubescent; wing 11–18 × 8–11 mm, coriaceous, prominently nerved and glandular-punctate.

Distribution (Fig. 4B), *habitat*, and *phenology*.—*H. lucida* is known only from a few collections from Puebla, Mexico, where it occurs around 1900 m, in dry submontane scrub formation (“matorral submontano,” following the classification by Rzedowski, 1981) on limestone soil. This formation was also called “low deciduous forest” or “dry scrub” (“matorral seco”) by the collectors of the specimens examined. Fruiting specimens were collected in June and September.

It can be distinguished from the other species mainly by its yellowish, raised veins of the leaflets and by the pubescent mericarps with a coriaceous and reticulate wing.

Other specimens examined. MEXICO. **Puebla:** 11 km S de San Juan Ixcoquixtla, 29 Jun 1982 (fr), González-Medrano et al. 12747, 12752 (MEXU); Zapotitlán Salinas, 12.3 mi sudoeste de Tehuacán, sobre la carr. Tehuacán–Huajuapán, 0.7 mi sudoeste de Las Ventas, 18°19'N, 97°29'W, 14 Sep 1980 (fr), Lott & Wendt P-56 (MO).

6. *Helietta glaziovii* (Engl.) Pirani, comb. nov. (Fig. 7)

Esenbeckia glaziovii Engl., Bot. Jahrb. Syst. 21. Beibl. 54: 27. 1896. TYPE: BRAZIL. Rio de Janeiro: Alto Macahé [Macaé], 2 Jun 1891 (fl), A. Glaziou 18171 (LECTOTYPE, here designated: P; ISOLECTOTYPE: F; photos of destroyed B holotype at F, MO, NY, SPF).

Treelet 1.5–4(–7) m; shoots pale gray to

pale brown, glabrous, suberose, longitudinally fissured and rough, with many white lenticels. *Leaves* pubescent when very young, soon glabrescent or sparsely and minutely puberulous mainly on the petiole; petiole 0.5–2(–3) cm long, semiterete, slightly to deeply canaliculate adaxially; leaflets conspicuously punctate on both surfaces, chartaceous to subcoriaceous, greenish to olivaceous and shiny above, dull-green beneath, short-petiolulate to sessile, narrow-obovate to oblanceolate, margin flat to slightly revolute, apex obtuse and retuse to emarginate, base decurrent in the terminal leaflet, acute to decurrent but always asymmetric in the lateral leaflets; terminal leaflet 3.8–8(–9) × 1.8–3.4(–4.2) cm; lateral leaflets 3–7.8 × 1.4–2.5(–3.2) cm; midvein raised on both surfaces except distally, secondary veins 6–8 per side, prominent to prominent on both surfaces. *Inflorescence* a diplothyse 8–12 cm long, longer than the leaves, minutely pubescent to glabrous; peduncle 0–1.2 cm long; cofiloflorescences ca. 6, opposite, the proximal ones 5–8 cm long; bracts ovate, acute, ca. 1 mm long, abaxially pubescent to ciliolate. *Flowers* (4–)5-merous; pedicel puberulous to glabrous, 1–2 mm long; bractlets ovate, puberulous to ciliolate. *Sepals* suborbicular, glabrous with ciliolate margin, 0.9 mm long, greenish. *Petals* white to cream-colored, oblong, obtuse, ca. 3.2 × 1.8 mm, ciliolate. *Stamens* ca. 1.8 mm long; anthers ovoid, rounded at apex, yellow. *Disk* (4–)5-lobed, shorter than the ovary, yellow. *Ovary* (4–)5-lobed, greenish, glabrous; style punctate, ca. 0.7 mm long; stigma slightly (4–)5-lobed. *Fruit* of 4 or 5 mericarps, glabrous; seed locule ellipsoid, ca. 10 mm long; wing oblong, 15–17 × 9–11 mm, chartaceous, veiny, glandular-punctate.

Distribution (Fig. 4B), *habitat*, and *phenology*.—Although the type and three other 19th-century collections were made in the state of Rio de Janeiro, 13 more recent collections come from Planalto de Diamantina, Monte Azul, Grão-Mogol, and Abaíra, all in the Espinhaço Range, inland in the states of Minas Gerais and Bahia, southeastern Brazil. In these serras, the species occurs mainly in riparian forest or in the locally called “carrasco,” a dense scrub among

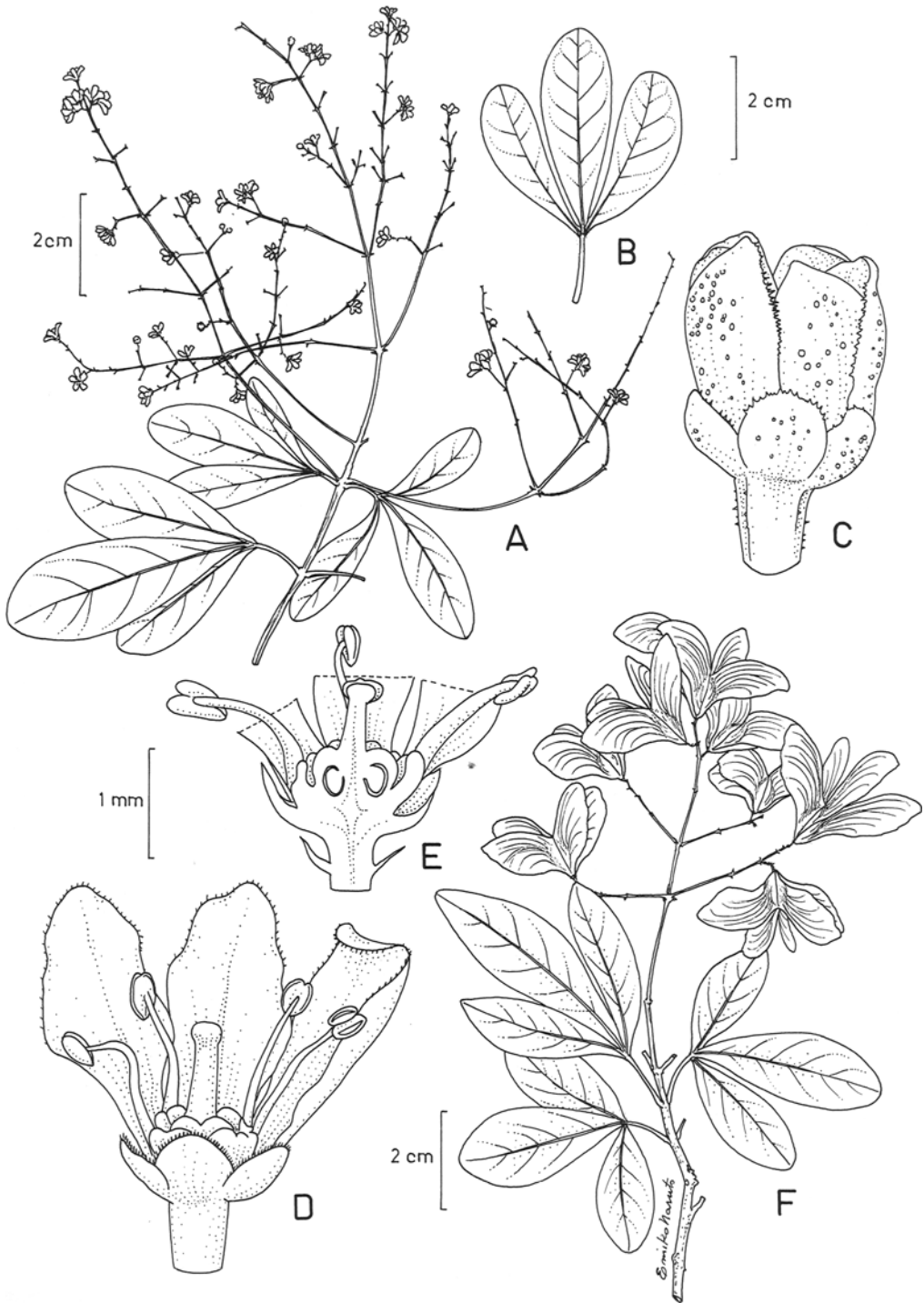


FIG. 7. *Helietta glaziovii*. A. Flowering shoot. B. Leaf. C. Bud. D. Flower (5-merous, two petals and one stamen removed). E. Longisection of flower. F. Fruiting shoot. (A, E, Pirani et al. CFCR 8878; B, Irwin et al. 27730; C, D, Glaziou 18171 (lectotype); F, Mello-Silva et al. CFCR 9679.)

TABLE II
CHARACTERS THAT DISTINGUISH *Helietta plaeana* FROM *H. glaziovii*

	<i>H. plaeana</i>	<i>H. glaziovii</i>
Sepals	Ovate, acute	Suborbicular
Petals	Glabrous	Ciliolate
Flowers	4(–5)-merous	(4–)5-merous
Ovary	Exceeded by disk	Exceeding disk
Inflorescence	Shorter than leaves (2–6 cm)	Longer than leaves (8–10 cm)
Petiole	(1–)2–3 cm long	0.5–2(–3) cm long
Wings of mericarp	10–14 mm long	15–19 mm long
Leaflets	Chartaceous, narrow-obovate to oblanceolate	Subcoriaceous, narrow-obovate to narrow-elliptic
Range	N Venezuela, N Colombia	SE Brazil

rock outcrops adjacent to cerrado or caatinga, 700–1150 m.

It is puzzling that after 1891 no further collections have been made in Rio de Janeiro. Given that Glaziou—sometimes guilty of pirating the collections of others—was concerned with the ones coming from this state, it may be that the species is actually endemic to serras in Minas Gerais, as it seems today. A similar problem occurs with specimens of *Metrodorea mollis* Taub. (Rutaceae, Pilocarpinae), a species well known from dry to rocky slopes from inland areas in Ceará, Pernambuco, and Bahia, but known also from two Glaziou specimens said to be collected in Minas Gerais, Rio de Janeiro, and Espírito Santo. According to Kaastra (1982), these two specimens are probably collections made by Freire Alemão in Ceará and pirated by Glaziou.

Kaastra (1982) treated *Esenbeckia glaziovii* as a synonym of *Helietta plaeana* Tul., but they are recognized here as two distinct allopatric species, separated mainly by the characters listed in Table II.

Common names.—**Brazil:** grumari, gumarim (Galvão 387 and 565), and três folhas (Glaziou 18177).

Representative specimens examined. BRAZIL. **Bahia:** Abaíra, Mendonça de Daniel Abreu, 18 Jan 1994 (fl), *Ganev* 2806 (HUEFS, K, SPF); Abaíra, Jambreiro, 31 Jan 1994 (fl), *Ganev* 2912 (HUEFS, K, SPF); Abaíra, caminho Catolés—Guarda Mor, 2 Jun 1994 (fr), *Ganev* 3277 (HUEFS, K, SPF); Abaíra, Estrada Catolés—Inúbia, 9 Jul 1994 (fr), *Ganev* 3481 (HUEFS, K, SPF). **Minas Gerais:** 3.5 km by rd. SW of Rio Jequití and Mendanha, 14 Apr 1973 (fr), *Anderson et al.* 8908 (F, K, MO, NY, R, UB, US); Diamantina, entre Conselheiro Mata e Rodeador, 27 Feb 1947 (fr), *Egler & Romariz s.n.* (RB-59997); Monte Azul, Serra do Es-

pinhaço, 14 Mar 1995 (fl), *Hatschbach et al.* 61855 (MBM, SPF); sandstone precipices and adjacent cerrado, ca. 18 km W of Grão-Mogol, 21 Feb 1969 (fr, fr), *Irwin et al.* 23664 (F, K, MO, NY, R); ca. 23 km E of Diamantina, 17 Mar 1970 (fr), *Irwin et al.* 27730 (F, K, MO, NY, R, UB, US); Grão-Mogol, entre a Fazenda Jambreiro e estrada para Cristália, 26 Feb 1986 (fr), *Mello-Silva et al.* CFCR 9679 (SPF); Grão-Mogol, vale do Rio Itacambiruçu, 4 Sep 1985 (fr), *Pirani et al.* CFCR 8403 (SPF); Grão-Mogol, margens do rio Itacambiruçu, Fazenda Jambreiro, 5 Jan 1986 (fl, fr), *Pirani et al.* CFCR 8878 (F, K, NY, RB, SP, SPF); Itambé do Mato Dentro, Estrada Canta Galo a Serra da Cabeça de Boi, 8 Aug 1992 (fl), *Stehmann & Sobral* 1117 (SPF). **Rio de Janeiro:** Alto Macahé de Nova Friburgo, 2 Jun 1891 (fl), *Glaziou* 18177 (R); São Fidelis, Apr 1880 (sterile), *Ramiz Galvão* 387 (P); São Fidelis, s.d. (sterile), *Ramiz Galvão* 565 (R).

7. HELIETTA PUBERULA R. E. Fr., *Bull. Herb. Boissier*, ser. 2, 7(12): 1001. 1907. TYPE: PARAGUAY. Fuerte Olympo cerrito, Oct 1895 (fl), *J. D. Anisits* 2049 (LECTOTYPE, here designated: S; ISOLECTOTYPE: P). (Fig. 8A–D)

Shrub to treelet 1–6 m; shoots pale brown and densely velutinous with white, slender, soft, straight, erect trichomes, glabrescent, turning grayish or brownish, longitudinally striate, with pale lenticels. *Leaves* velutinous mainly on the veins and petiole on both surfaces and more densely so on abaxial surface with white, soft, straight trichomes; petiole 1.2–2.5 cm long, semiterete, flat to slightly concave adaxially at its distal end, persistently velutinous; leaflets brown-punctate on both surfaces but more conspicuously adaxially, membranous, pale olive to pale brownish, dull on both surfaces, sessile, narrow-obovate to oblanceolate, margin slightly revolute and densely ciliate, apex rounded and emargin-

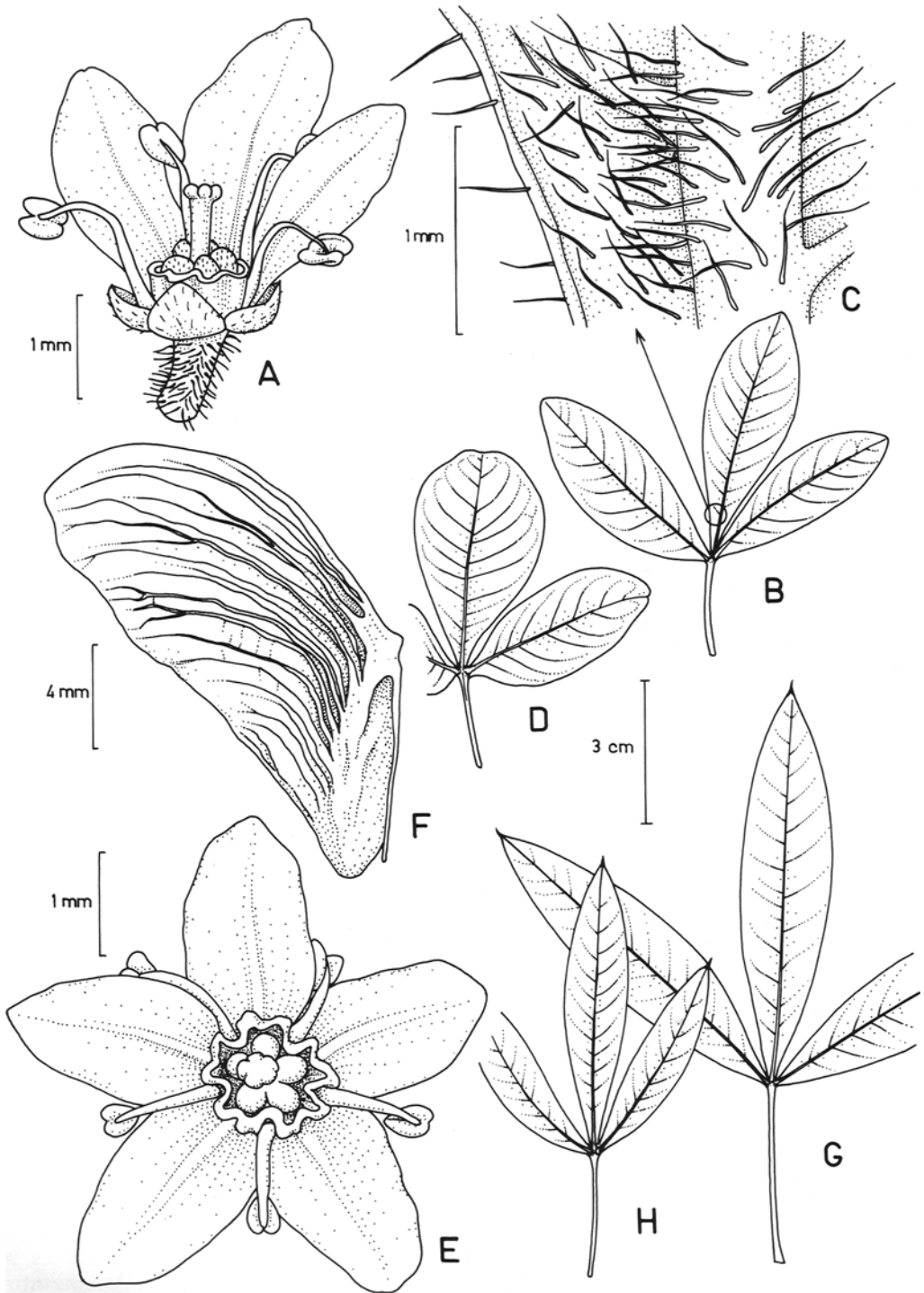


FIG. 8. A-D. *Helietta puberula*. A. Flower, two petals and one stamen removed. B-D. Leaves, in C a detail of indumentum on abaxial surface of the blade. E-H. *Helietta apiculata*. E. Flower in frontal view. F. Mericarp. G, H. Leaves. (A-C, Rojas 13633; D, Hatschbach et al. 60772; E, F, Pirani 1-80; G, Hartshorn 2469; H, Bertoni 443.)

ate, the base cuneate to decurrent on the terminal leaflet, acute and strongly asymmetric on the lateral ones; terminal leaflet 3.7–7.7(–9.5) × 1.6–2.7(–3.2) cm; lateral leaflets 2.8–5.5(–7.7) × 1.2–2.5 cm; mid-vein prominent on both surfaces except distally; secondary veins 5–8 per side, prominent on both surfaces. *Inflorescence* a diplothyse 5–9.5 cm long, shorter than the leaves, densely velutinous with white, soft, straight trichomes; peduncle 0–7 mm long; cymes 2–4, opposite, the proximal ones 4.5–8 cm long; bracts lanceolate, acute, 2–3 mm long, puberulous. *Flowers* 5-merous; pedicel velutinous, ca. 1 mm long; bractlets ovate, pubescent. *Sepals* suborbicular, ciliolate, 0.7 mm long. *Petals* cream-colored, oblong, obtuse, ca. 2.2 × 1 mm, margin ciliolate. *Stamens* ca. 1 mm long; anthers ovoid, rounded at apex, yellow. *Disk* 5-lobed, shorter than the ovary, yellow. *Ovary* 5-lobed, glandular-tuberculate, puberulous; style ca. 0.8 mm long; stigma slightly 5-lobed. *Fruit* of 5 mericarps, puberulous; seed locule ellipsoid, ca. 9 mm long; wing oblong-rounded, obtuse, 8–10 × 5–6 mm.

Distribution (Fig. 4B), *habitat*, and *phenology*.—This species is restricted to the eastern Chaco in Paraguay, eastern Bolivia, and adjacent Mato Grosso do Sul, Brazil (Corumbá). It occurs in seasonal forests (including secondary ones), on small hills with limestone outcrops or in sandy to gravelly soil. Flowering collections have been made January–October and fruits in June and September.

Helietta puberula is easily distinguished from its congeners by the dense, whitish, soft, velutinous indumentum that covers its leaves and inflorescences; moreover, the trichomes are comparatively long (Figs. 1E, 8C).

When Kaastra (1977, 1982) made the combination *Helietta mollis* (Miq.) Kaastra, he proposed *H. puberula* as a synonym of *H. mollis*. Nevertheless, the present study shows that the latter species, in fact, has to be transferred to *Balfourodendron*, because its fruit is a samara and its leaflets have domatia. *Helietta puberula* is a well-defined species bearing fruits typical of *Helietta* and no domatia, and it is completely allopatric

to *Balfourodendron molle* (cf. Figs. 4A, B). Spichiger and Stutz de Ortega (1987), following the proposition made by Kaastra, referred erroneously to this species in *Flora del Paraguay* as *H. mollis* and, consequently, described its flowers as both tetramerous and pentamerous. Nevertheless, I have seen only pentamerous flowers in *H. puberula*.

Illustrations.—Spichiger & Stutz de Ortega, 1987: fig. 14 (incorrectly labeled as *Helietta mollis*).

Representative specimens examined. BRAZIL. **Mato Grosso do Sul**: Jan 1940 (fl), Fróes 11692 (F, NY); Corumbá, MS-262, 5–10 km O do rio Paraguai, 7 Jun 1994 (fl, fr), Hatschbach et al. 60772 (MBM, SPF); Corumbá, 4 Apr 1903 (fl), Malme 2711 (syn-type: S); próximo de Corumbá, 19°06'S, 57°38'W, 15 Oct 1980 (fl), Paschoal 26 (HRB, RB); 24 May 1989 (fl, fr), A. Pott et al. 4870 (R); 1903 (fl), A. Robert 752 (K).

BOLIVIA. **Santa Cruz**: Chiquitos, Valle de Tucavaca, 18°10'26"S, 59°26'29"W, 30 Jan 1995 (fl, fr), B. Mostacedo et al. 2698 (SPF).

PARAGUAY. **Alto Paraguay**: Fuerte Olimpo, 26 Mar 1980 (fl), Bernardi 20314 (G); San Carlos, 18 Sep 1986 (fl, fr), Molas & Vera 1119 (G); Fuerte Olimpo, Chaco Paraguayo, 20 Oct 1946 (fl), Rojas 13633 (G, LIL, MO—2 sheets).

8. *HELIETTA APICULATA* Benth., Hooker's Icon. Pl. 14: 67. 1882. TYPE: PARAGUAY. Caaguazú, 7 Nov 1874 (fl), B. Balansa 2515 (HOLOTYPE: K—n.v.; ISOTYPES: G, P—2 sheets). (Figs. 8E–H, 9)

Helietta longifoliata Britton, Ann. New York Acad. Sci. 7: 69. 1892, nom. illeg. ex Art. 52, ICBN. TYPE: PARAGUAY. Caballero, 30 Jan 1889 (fl, fr), T. Morong 457 (LECTOTYPE, here designated: NY; ISOLECTOTYPES: F, GH—n.v.).

Esenbeckia cuspidata Engl. in Engler & Prantl, Natur. Pflanzenfam. 3(4): 159. [Mar] 1896, nom. nud. *Esenbeckia ? cuspidata* Engl., Bot. Jahrb. Syst. 21 Beibl. 54: 28. [12 May] 1896. *Helietta cuspidata* (Engl.) Chodat & Hassl., Bull. Herb. Boissier ser. 2, 4: 1285. 1904, nom. illeg. TYPE: BRAZIL. Brasília meridionalis (Rio Grande do Sul?), Sello 3714 (n.v.).

Helietta cuspidata f. *gracilis* Chodat & Hassl., l.c. TYPE: PARAGUAY. Cordillera de Altos, 1914 (fl), Chodat s.n. (G).

Helietta cuspidata f. *latifolia* Chodat & Hassl., l.c. TYPE: PARAGUAY. Igitimi iter ad Yerbales, montium Sierra de Maracayú, Oct 1899 (fl), Hassler 4857 (HOLOTYPE: G; ISOTYPES: NY, UC—n.v.).

Helietta cuspidata f. *subobtusata* Chodat & Hassl., l.c. TYPE: PARAGUAY. Cordillera de Altos, Jun 1895 (fl), Hassler 411 (G).

Treelet or *tree* 2–15(–22) m; shoots red-

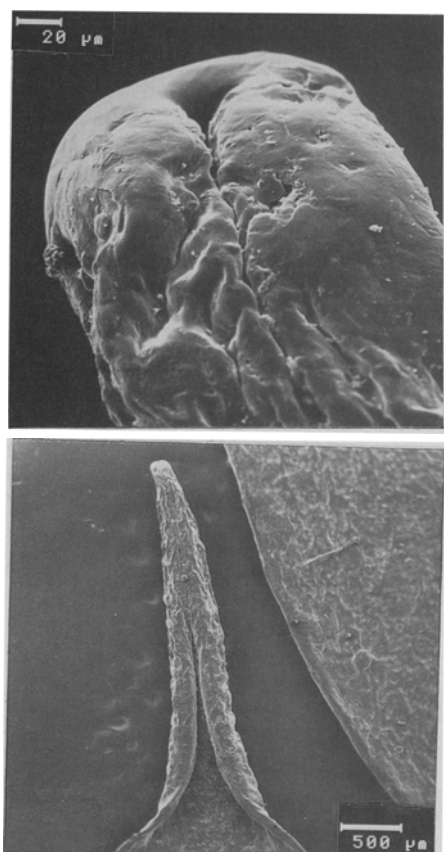


FIG. 9. Scanning electron micrographs of the apex of a *Helietta apiculata* leaflet, showing the involution of the margin forming an apiculum (Ivanauskas 68).

dish-brown to grayish, sparsely puberulent to glabrous, somewhat smooth to longitudinally striate, with numerous pale lenticels. *Leaves* initially puberulent with short, white, appressed trichomes, but soon glabrescent or some trichomes persisting on petiole apex and leaflet bases; petiole (1–) 1.5–3.5(–4) cm long, slender, semiterete, adaxially flat to slightly or deeply canaliculate; leaflets brown-punctate on both surfaces, more conspicuously so abaxially, membranous to chartaceous, pale green to pale olive to pale brown, dull on both surfaces, sessile, lorate to narrow-oblong to narrow-elliptic or sometimes oblanceolate, margin slightly revolute, the apex apiculate by the involution of margin (the apiculum 1–4 mm long, straight to curled, somewhat rigid), base attenuate to cuneate and sym-

metric, sometimes obtuse or slightly asymmetric on lateral leaflets, seldom the whole blade asymmetric; terminal leaflet (3.5–)6–8.5(–9.5) × 1–1.7(–2.5) cm; lateral leaflets (3–)5–8.3(–9.5) × 0.5–1.5(–2.5) cm; mid-vein prominent on both surfaces (except distally); secondary veins (5–)8–11 per side, inconspicuous to prominulous abaxially. *Inflorescence* a diplothyse 7–11(–14) cm long, much longer than the leaves, sparsely puberulent to subglabrous; peduncle 0–3 cm long; coflorescences 6–8(–16), opposite, proximal ones 5–8(–14) cm long and sometimes subopposite; bracts deltoid, acute, ca. 0.8 mm long, puberulent. *Flowers* (4–)5-merous; pedicel puberulent to subglabrous, 1–3 mm long; bractlets deltoid, puberulent. *Sepals* semiorbicular, rounded to obtuse, subglabrous and ciliolate, ca. 1 mm long, greenish. *Petals* cream-colored, oblong to elliptic, obtuse, 2–3 × ca. 1 mm, glabrous but adaxially minutely papillose, entire. *Stamens* ca. 2 mm long; anthers ovoid, yellow. *Disk* (4–)5-lobed, slightly shorter than the ovary, yellow. *Ovary* (4–)5-lobed, conspicuously glandular-verrucose, glabrous; style ca. 0.7 mm long; stigma (4–)5-lobed. *Fruit* of 4–5 mericarps, glabrous; seed locule ellipsoid, 5–9 mm long; wing oblong, 8–12 × 5–9 mm, membranous, veiny.

Distribution (Fig. 4B), *habitat*, and *phenology*.—*Helietta apiculata* occurs in eastern Paraguay, in southern Brazil (Mato Grosso do Sul and western São Paulo, Paraná, Santa Catarina, and Rio Grande do Sul), and in northeastern Argentina (Misiones). Its occurrence in Peru is based on one collection that, though sterile, bears the apiculate leaflets typical of this species. I believe this constitutes a real disjunction, rather than a gap of collections in the intervening area (Bolivia and northern Paraguay). For the same patch of dry forest around Tarapoto, Peru, Gentry (1993: 221) reported a species of *Schinopsis* (Anacardiaceae), disjunct from its main area of distribution in the Chaco region of Paraguay.

In its core area, *H. apiculata* is commonly found as a treelet in the semideciduous forests of the basins of the Paraná, Paraguay, and upper Uruguay Rivers. According to Klein (in Cowan & Smith, 1973: 59),

H. apiculata is a selective hygrophyte and heliophyte, particularly frequent in woods on wet to rocky (dry) soils, in lowlands near rivers and often in clearings, becoming rare to absent on deeper and drier soils. In Paraguay, it has been reported from riparian forests, margins of forests, and formations transitional between campos cerrados and forests (Spichiger & Stutz de Ortega, 1987). In northwestern São Paulo State, Brazil, it is fairly common also in secondary formations.

The species flowers and fruits throughout the year, and many collections bear both. From my own observations of populations in southern Brazil, the most expressive flowering period extends from October to March, or sometimes to May. Only 8 of 103 flowering collections were made from June to September. The peak fruiting period is December to May (38 out of a total of 47 fruiting collections seen). These periods coincide with those described by Spichiger and Stutz de Ortega (1987) for Paraguay and by Cowan and Smith (1973) for Santa Catarina. According to Lorenzi (1992), the flowering period occurs in November and December, and fruits are mature in March to May.

Helietta apiculata is the most easily recognizable species in the genus, because of its usually very narrow leaflets with a conspicuous apiculum produced by the involute margins of the blade (Fig. 9) and its relatively long, loose, many-flowered thyrse.

The name *Helietta apiculata* was published under Plate 1385 of *H. parvifolia* in *Hooker's Icones Plantarum*, therefore this name has been mostly overlooked. *Helietta longifoliata* Britton was the name most commonly used for the species until Tour-sarkissian (1957) showed clearly the priority of *H. apiculata*. The former is also an illegitimate name, as one of its syntypes (*Balansa 2515*) is the type of *H. apiculata*! Bentham undoubtedly intended to publish this last name as a distinct species, as appears from the text, and the diagnosis he presented, although short, is clear and precise. I agree with Kaastra's observation that Bentham published *H. apiculata* "under the

allied species *H. parvifolia* only by lack of a suitable plate" (Kaastra, 1982: 115).

Data on the wood anatomy of *H. apiculata* are presented by Mainieri and Steigleder (1968). The germination of the seeds is abundant, according to Lorenzi (1992).

Common names.—**Brazil:** amarelinho, osso-de-burro, canela-de-veado (Lorenzi, 1992) (São Paulo); cun-cun, canela-de-veado (Cowan & Smith, 1973; Lorenzi, 1992) (Santa Catarina, Rio Grande do Sul). **Argentina:** hiraoby (Corrêa, 1926). **Paraguay:** yvirá ovi, yvirá ovi guasú (Spichiger & Stutz de Ortega, 1987).

Uses.—Despite the suitable characters of its wood, which is compact and pale yellow, it has limited use because of its small diameter (20 cm average, seldom 50 cm).

Illustrations.—Spichiger & Stutz de Ortega, 1987: fig. 13. Color pictures: Lorenzi, 1992: 308.

Representative specimens examined. **PERU. San Martín:** Valley of Río Huallaga, 29 km S of Tarapoto, near El Abra, 06°40'S, 76°20'W, 6 Feb 1984 (sterile), *Gentry & Smith 45084* (MO).

BRAZIL. Mato Grosso do Sul: Brasilândia, estrada Porto João André-Brasilândia, 26 Nov 1992 (fl), *Catharino et al. 1830* (SP, SPF); 36 km S de Dourados, 13 Nov 1977 (fl, fr), *Costa 121* (HRB, RB); Antonio João, descida para Campestre, 16 Mar 1985 (fr), *Hatschbach & Silva 49091* (MBM, MG, SPF); Iguatemi, 21 Oct 1987 (fl), *Hatschbach & Silva 51519* (BM, MBM, NY). **Paraná:** Guaíra, Rio Piquiri, ca. 2 km da barra, 9 Apr 1061 (fl), *Hatschbach 7868* (MBM, NY, RB); Cândido Rondon, Pato Bragado, 13 Nov 1963 (fl), *Hatschbach & Pereira 10464* (K, MBM, RB); Clevelândia, Petry, 22 Nov 1972 (fl), *Hatschbach 30822* (MBM, NY); near Cantagalo, 30 km E of Laranjeiras do Sul, 4 Nov 1966 (fl), *Lindeman & Haas 2813* (F, K, NY, P, US); Pérola d'Oeste, Rio Feliciano, 15 Jan 1983 (fl), *Pirani et al. 441* (SP, SPF). **Rio Grande do Sul:** Capão do Leão, Horto Botânico, 6 Jan 1987 (fl, fr), *Jarenkow 600* (ICN, PACA); Santa Maria, 19 Jan 1936 (fr), *Ran 30* (RB); São Borja, Garunchos, 22 Nov 1957 (fl), *Schultz 3039* (ICN); Caçapava do Sul, BR 290, km 223, May 1985 (fl), *Sobral 3908* (ICN, MG, NY, SPF); Tupanciretá-Jari, Passo das Vassouras, 11 Nov 1991 (fl), *Wasum & Bastos* (NY, US). **Santa Catarina:** Perto de Marcelino Ramos, 26 Oct 1929 (fl), *Kuhlmann 283* (RB); Itapiranga, Conceição, 27°05'S, 53°47'W, 12 Nov 1964 (fl), *Smith & Klein 13208* (HBR, MO, NY, P, R, US). **São Paulo:** Teodoro Sampaio, Parque Estadual do Morro do Diabo, 26 Feb 1986 (fl), *Baitello 179* (SPF, SPSF); Marabá Paulista, 22°05'S, 52°08'W, 7 May 1982 (fl, fr), *Dambrós 273* (HRB, RB); Pindorama, 2 Oct 1937 (fl), *Mendes 2146* (RB); Penápolis, estrada para o Rio Lajeado, 21 Apr 1980 (fl fr), *Pirani 1-80* (HUFU, NY, SPF).

PARAGUAY. **Alto Paraná:** Cerca de Hernandarias, 31 Jan 1982 (fr), *Fernández Casas & Molero 5728* (G, MO, NY). **Amambay:** Bella Vista, dry deciduous forest along Río Apa, 22 Mar 1983 (fl), *Simonis et al. 164* (NY, SPF, U, US); Parque Nacional Cerro Corá, vic. of Cerro Muralla, 22°39'S, 56°03'W, Feb 1982 (fr), *Solomon et al. 6789* (MO, NY). **Caazapá:** Tavai, 28 Oct 1988 (fl), *Degen 856* (G). **Canendiyú:** Sierra de Maracayú, in regione vicine Igatimí, Oct 1899 (fl), *Hassler 4857* (G, K, P). **Central:** Sapucay, Mar 1913 (fl), *Hassler 12160* (BM, G, K, NY). **Cordillera:** Caacupé. Bairro Buena Vista, 2 Feb 1987 (fl, fr), *Bordas 4148* (K, NY); Tobatí, Cerro Tobatí, 23 Oct 1987 (fl), *Degen & Zardini 370* (MO, SP); Cerro de Tobatí, ca. 4.5 km al S de Tobatí, 12.2 km de Rta. 2 en Caacupé, 9 Feb 1987 (fl, fr), *Ginzberg et al. 440* (NY, TEX). **Guairá:** Cordillera de Villa Rica, Jan 1905 (fr), *Hassler 8733* (BM, G, K, NY, P); Colonia Independencia, 25°45'S, 56°13'W, 21 Dec 1986 (fl), *Schinini & Bordas 25072* (CTES, NY, SPF); Tororo, Arroyo Polilla, 25°55'S, 56°15'W, 14 Dec 1988 (fl), *Soria 2819* (G). **Itapúa:** Arroyo San Rafael, SE de General Delgado, 16 Nov 1978 (fl), *Arbo et al. 2012* (CTES, F). **Misiones:** Santiago, Estancia "La Soledad," 15 Nov 1956 (fl), *Pedersen 4304* (CTES, K, P, US). **Paraguari:** Cerro Acabay, Compañía Virgen de Fátima, 25°54'S, 57°09'W, 30 May 1985 (fl, fr), *Brunner 1109* (NY); Parque Nacional Ybicuí, 56°50'W, 26°03'S, Mar 1983 (fl), *Hahn 1157* (MO, NY), Mar 1980 (fl, fr), *Hartshorn 2485* (G, MO, NY); Cordillera de Altos, Jun 1897 (fl, fr), *Hassler 3047* (G, MO, NY, US). **San Pedro:** Distr. San Estanislao, 2 Nov 1969 (fl), *Pedersen 9350* (CTES, K); Alto Paraguay, Primavera, 17 Sep 1957 (fl), *Woolston 877* (K, NY, P, SP).

ARGENTINA. **Corrientes:** San Tomé, Garruchos, 1 Aug 1979 (sterile), *Medan et al. 144* (MO); Ituzaingó, desembocadura del Arroyo Garapé en el Río Paraná, 45 km E de Ituzaingó, 11 Dec 1974 (fl, fr), *Quarín et al. 2769* (CTES, RB); Ituzaingó, Isla Apipé, Pto. Vizcaino, 18 Nov 1976 (fl), *Schinini 13768* (CTES, F, MO). **Misiones:** Dep. L. N. Alem, 12 km S de Alem, ruta 4, 21 Nov 1986 (fl), *Cabral & Zardini 501* (CTES, SPF); Dep. San Ignacio, San Ignacio, 4 Feb 1947 (fr), *Medina 229* (LIL, MO, US); Candelaria, Santa Ana, 19 Dec 1945 (fr), *Montes 1592* (LIL, MO); Eldorado, 5 km S of Eldorado, Ruta Nacional 12, 22 Oct 1978 (fl), *Renvoize et al. 3213* (K, MO, NY).

EXCLUDED TAXA

Helietta barrancae M. E. Jones, *Contr. W. Bot.* 18: 47. 1933. = *Thouinia acuminata* S. Wats. (according to C. V. Morton, *Contr. U. S. Nat. Herb.* 29: 87–116).

Helietta trifoliata (Baill.) Mabb., *The Plant-book*: 268. 1989. *Picrella trifoliata* Baill., *Adansonia* 10: 151, t. 10. 1871. TYPE: "e Mexico, ut aiunt, tub. vl.," *Giesbrecht s.n.*, P.

Although the combination *Helietta trifoliata* appears also in *Index Kewensis* (Da-

vies, 1991: 150), it is not acceptable because *Picrella* Baill. was based on a specimen found in cultivation in Paris and supposed to be of Mexican origin, as already remarked by Small (1911), Standley (1923), and Engler (1931: 389), all of whom referred the genus to the Simaroubaceae. This monotypic genus is known so far only from the original scanty specimen (the holotype of *Picrella trifoliata*) which, as well as the diagnosis and illustration provided by Baillon (1871), shows at least five characters incongruent with those of *Helietta*: axillary inflorescences, apparently valvate petals, free carpels joined only by the style, a single ovule per locule, and leaflets not articulate at base.

Acknowledgments

The author thanks Jacquelyn A. Kallunki for useful advice and discussions, for her critical review of the manuscript, and for her companionship and assistance during my 1994 stay in New York; Patricia Holmgren and Enrique Forero for the good reception at NY during 1994; Emiko Naruto for preparing the figures of the shoots and rendering attractive my original drawings; Márcio Valentim Cruz for help with SEM work; Neuza Maria de Castro for help with sectioning leaflets to elucidate the nature of glandular trichomes; and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) for financial support for this research program.

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