Annals of the Missouri Botanical Garden

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Annals
of the
Missouri Botanical Garden

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ACIDOTON (EUPHORBIACEAE) IN CENTRAL AMERICA

**Acidoton nicaraguensis** (Hemsl.) Webster, comb, nov.

**Cleidion ? nicaraguense** Hemsl., Biol. Centr.-Amer. 3: 130, 1883.
**Gitara panamensis** Croizat, Jour. Arnold Arb. 26: 192, 1945.

As treated in the last monographic revision by Pax & Hoffmann (Pflanzenr. IV, 147, IX (Heft 68): 24-26, 1919), *Acidoton* is a small West Indian genus of two species. A few years after that treatment, Pax & Hoffmann described a new genus *Gitara* (Pflanzenr. IV, 147, XVII (Heft 85): 187, 1924) on the basis of a Venezuelan plant, and noted that it was very close to *Tragia*. Finally, Croizat (Jour. Arnold Arb. 26: 192, 1945) described *Gitara panamensis* on the basis of a specimen from Panama (Darien, betw Pinogana & Yavisa, Pittier 6543; holotype A; isotype US). He was correct in seeing an affinity between the Panamanian plant and *Gitara venezolana*, but neither he nor Pax & Hoffmann seems to have noticed a possible resemblance with *Acidoton*.

Recently, in attempting to fix the identity of *Cleidion ? nicaraguense* Hemsl., I found that the type specimen of *Gitara panamensis* Croizat agreed closely with Hemsley’s description, as well as a specimen from Nicaragua (Engelsing s.n., NY). Although I have not been able to examine Hemsley’s types (Nicaragua, Chontales, Tate 352, 455; presumably at K), there can be little doubt that we are dealing with a single species which ranges from Nicaragua to Panama.

The Central American species of *Acidoton* resembles the West Indian ones in having a large number of stamens (24-35), axillary inflorescences, and stinging hairs present on various organs. The apical tuft of small stinging hairs on the anthers is very similar in all of the species, and furnishes a good diagnostic character to distinguish *Acidoton* from *Tragia*. There can be no doubt that *Acidoton* is very close to *Tragia*, as suggested by Pax & Hoffmann when they proposed *Gitara*. However, the apically tufted anthers and large number of stamens clearly set *Acidoton* apart from most species of *Tragia*. One Mexican species, *T. bailloniana* Muell. Arg., which was made the basis for the genus *Zuckertia* by Baillon does agree with *Acidoton* in its large stamen number and apiculate anthers. For the present, it seems best to leave it in *Tragia* because of its climbing habit, but its status may well be subject to reevaluation.

The relationship between the Central American and Venezuelan taxa of *Acidoton* remains to be elucidated. They are doubtless closely related, and might possibly prove to be races of a single wide-ranging species. However, the differences in leaf shape and venation pointed out by Croizat appear to be sufficient to justify maintaining (*ad interim*) the Venezuelan taxon as a direct species: *Acidoton venezolanus* (Pax & Hoffm.) Webster, comb. nov.

*Gitara venezolana* Pax & Hoffm., Pflanzenr. IV, 147, XVII (Heft 85): 187, 1924.

As thus construed, *Acidoton* is now a Caribbean genus with six species: 3 in Hispaniola, 1 in Jamaica, 1 in Central America, and 1 in northern South America.

—Grady Webster, University of California, Davis.
A NEW SPECIES OF CAPERONIA (EUPHORBIACEAE)
FROM PANAMA

Caperonia neglecta Webster, sp. nov. (section Caperonia).

Annua, monoica, ca 2-5 dm alta; caulis inermis, ramosus, petiolis et foliis atque setulis glanduligeris atque trichomatibus hispidulis vestitis. Folia petiolata petiolisque 1.5-5 mm longis; stipulae lanceolatae, ciliatae, ca 1.5-4.5 mm longae; lamina plerumque elliptica, acuta, membranacea, ca 3-7 cm longa, 1-3 cm lata, basi obtusa vel rotundata, nervis secundariis rectis, margine serrulato. Racemi 1.5-3 cm longi, inferne 1-3 flores ♀ gerentes, ceterum flores ♂; bracteae hispidulo-ciliatae. Flos ♂: laciniae calycis 5, inaequales, sparsim hispidulae; petala 5, manifeste inaequalia, longiora 3 ca 1.5-1.8 mm longa; stamina 10, biverticillata, antheris 0.3-0.4 mm longis; ovarii rudimentum rotundatum, ca 0.25-0.3 mm longum. Flos ♀ : pedicellus hispidulus, 2.4-2.7 mm longus; laciniae calycis 5, subaequales, glanduligerae hispidulaeque, ca 1.5-2.2 mm longae; petala 5, subaequalia, exserta, anguste elliptica, 1.2-1.6 mm longa; ovarium hispidulum et glandulis fusiformibus vestitum; styli ca 1 mm longi, profunde 3-lobati. Capsulae 4.5-5.5 mm latae; semina fusca, 2.3-2.7 mm diam.

Panama. Panama: Camino del Boticario, nr Chepo, Pittier 4545 (holotype US); Tumba Muerto Rd. nr Panama City, Standley 29769 (US), 29815 (US).

This nondescript and apparently weedy species has remained undescribed for several years in the vain hope that a name could be found for it. The type collection was annotated by Kathe Hoffmann as Caperonia palustris (L.) St.-Hil.; and indeed all of the specimens have been misdetermined as that species. The plant does have a considerable superficial resemblance to C. palustris, due to its copious glandular pubescence and many-toothed leaf blades. However, it is sharply distinguished from that species by its pedicellate ribbed pistillate calyx, unequal male petals, entire pistillode, and hispidulous ovary. In some respects such as the hispidulous ovary and short inflorescence it resembles C. paludosa KL., but it differs in its elongated stipules, copious glandular pubescence, and pedicellate pistillate flower. In some ways C. neglecta shows more resemblance to various African species such as C. hirtella Beille, but seems to differ from all of these in the combination of a pedicellate pistillate flower with 3-lobed styles and lanceolate stipules. The apparent restriction of C. neglecta to weedy habitats, together with its sporadic occurrence, suggests the possibility of its being a comparatively recent introduction; but if so, the original population in Africa appears not to have been detected thus far.—Grady Webster, University of California, Davis.

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1 I wish to acknowledge the generous assistance of Dr. A. Robyns in the preparation of the Latin descriptions.
TWO NEOTROPICAL TAXA OF DALECHAMPIA (EUPHORBIACEAE)

1. Dalechampia hutchinsoniana Webster, sp. nov.

_Frutex_ 1.5 m altus, ramis stramineis laevibus. _Folia_ simplicia, glabra, elliptica vel oblonga, argute serrulata, apiculata, ca 1.5-3 cm longa, 0.5-1 cm lata, ad basin quintuplinervia, petiolis 1-3 mm longis; stipulae lanceolatae, acuminatae, 2.5-6 mm longae, striato-costatae. _Inflorescentiae_ solitariae, pseudo-axillares, pedunculis glabratis ca 3-6 cm longis; bracteae involucrales obovatae, atro-sanguineae, glabrae, quintuplinerviae, laccrato-dentatae, unguiculatae, ca 2-2.5 cm longae, 1 cm latae, stipellis lanceolatis 4-7 mm longis; bracteae _cymae_ 9 scariosae, minutae hirsutae, ca 2.5 mm longae; bracteae pleiochasiae primariae 4, subrotundatae vel oblongae, concaveae, evidenter glabrae (minutissime hirsutae), multinervosae, 3.5-4 mm longae, 3.5-6 mm latae, ± liberae; nectarium ca 5-6 mm latum, e bracteolis tenuibus fimbriatis pluribus compositum. _Flores_ ♂ ca 9 in quoque pleiochasio, pedicellis ad 3 mm longis; laciniae calycis saeppe 4, oblongo-lanceolatae, minutae hirsutae, 2.5-3 mm longae; columna staminalis cylindrica, dense hirsuta, 2-2.5 mm longa, antheris 24-28, ca 0.5-0.6 mm longis. _Flores_ ♀ 3, pedicellis ca 1.5 mm longis; laciniae calycis 7-9, linear-lanceolatae, 2-4 mm longae, pinnatifido-laciniate, laciniae glandulosae, glandulis intersepalis paucis ca 0.2 mm longis; ovarium fere 1 mm longum, dense hirsutum; columna stylaris ca 3.5-4 mm longa, 0.5-0.6 mm lata, minute hirsuta, stigmate dilatato-emarginato 1.2-1.3 mm diam. _Capsulae_ ut semina ignotae.

_Balsas_, 800 m, 30 May 1964 (holotype MO; isotypes DAV, UC).

This striking species, which appears to be endemic to a restricted region in northern Peru, is not closely related to any other. The shrubby stems, simple palmatinerved leaves, and pinnately lobed sepals suggest a relationship to sect. _Humiles_ Pax & Hoffm. (Pflanzenr. IV, 147, XII: 53, 1919). However, the dark reddish unguiculate involucral bracts and larger stamen number immediately distinguish it from any species in that section. The bracts and androecium of _D. stenosepala_ Pax & Hoffm., but all of those plants are twining vines. Probably this Peruvian species will have to be placed in a new supraspecific taxon.

2. Dalechampia cissifolia Poepp. & Endl. subsp. _panamensis_ (Pax & Hoffm.)

Webster, stat. nov.

_Dalechampia panamensis_ Pax & Hoffm., Pflanzenr. IV, 147, XII (Heft 68): 19, 1919.

The taxonomic identity of the only Panamanian _Dalechampia_ with compound leaves has remained rather uncertain up to the present. Mueller (Prodr. 15(2): 1241, 1866) based his _D. stenosepala_ on a Brazilian collection of Sello as well as one from Costa Rica (mistakenly ascribed to Panama by Mueller: 'inter Jose et
Puntarenas', Oersted; B, n.v.). Pax & Hoffmann (loc. cit.) restricted the name D. stenosepala to the Brazilian plant and separated the Central American plant as D. panamensis.

In their treatment of the species in sect. Triphyllae, Pax & Hoffmann placed D. panamensis adjacent to D. cissifolia, with which it is indubitably closely related. The leaf characters given in their key are most unconvincing as the Panama plants often have distinctly dentate rather than 'subentire' leaflets. The only characteristics in which Peruvian specimens of D. cissifolia appear to differ significantly include longer fruiting pedicels (up to 4 cm long) and calyx-lobes (up to 1.5 cm long as compared to 1 cm for Panamanian specimens).

It seems most reasonable to treat the Central American representatives of this complex as a subspecies of D. cissifolia; the South American plants would then fall into subsp. cissifolia. It is probable that D. stenosepala should also be included in D. cissifolia, but until critical comparisons are made no change in its status is suggested.—Grady Webster, University of California, Davis.

A REMARKABLE NEW PHYLLANTHUS (EUPHORBIACEAE) FROM CENTRAL AMERICA

During the preparation of a synopsis of the American taxa of Phyllanthus (Webster, ined.), it has proven necessary to describe a number of novelties. Among these is a Central American plant which occupies such an isolated position that it deserves special treatment. Although most of the New World species of Phyllanthus can be fitted into the classification proposed for the West Indian ones (Webster, Jour. Arnold Arb. 37-39, 1956-58), there are certain species which definitely do not belong to any of the previously established taxa; these, of course, are the most interesting ones.

The great majority of the woody species of American Phyllanthus belong to two subgenera with areolate pollen: Botryanthus and Xylophylla. However, others belong to the strictly American subg. Conami, and a few seem best classified in either the woody subgenera Kirganelia and Emblica1 or the mainly herbaceous subg. Phyllanthus. The South American species include a number of aberrant taxa which will be given detailed treatment later. In contrast, only a single North American species—the one described below—cannot easily fit into the subgeneric taxa already established. It, therefore, is necessary to create a new section for the species at the same time that it is formally described.

Phyllanthus section Calodictyon, sect. nov.

1Phyllanthus subg. Emblica (Gaertn.) Webster, stat. nov., based on Emblica Gaertn., Fruct. Sem. 2: 122, 1790.
Arbuscula monoica, glabra, ramificatione more sectionis Phyllanthi; cata-
phyllae induratae, deciuae; folia magna, chartacea, prominenter reticulata; cymulae
axillares, biseuales; flores calycis laciniis 5, disco ♂ segmentis 3 duplicibus, disco ♀ 5-angulato, staminibus 3, liberis, antheris muticis verticaliter dehiscentibus,
granis pollinis subglobosis tricolporatis tectatis perreticulatis, ovario loculis 3, stylis
bifidis alte connatis.

Type species: Phyllanthus tuerckheimii Webster. The name of the section
alludes to the attractive reticulate-veined leaves.

Phyllanthus tuerckheimii Webster, sp. nov.—Fig.1.

Arbuscula monoica, glabra, ramis subteretibus laevibus; cataphylla indurata,
brunnea, evidentia deciua, stipulis triangularibus ca 3.5-4 mm longis, crassis-
culis, lamina lanceolata; ramuli 12-20 cm longi, 2.2-3 mm diam, subcomplanati
angulative, plumbei, laeves, cum foliis 5-10; internodi um proximale 2-6 cm; in-
ternodia mediana plerumque 1-3 cm longa. Folia stipulis brunneis, induratis,
subpersistentibus, lanceolatis, ca 3-4 mm longis; petioli 3-4 mm longi; laminae chartaceae, ± ellipticae, plerumque 7-14 cm longae, 2.5-5 cm latae, abrupte acutae vel acuminatae, utrinque olivaceae et lucidae, venis vel umilisque prominentem reticulatis, marginibus planis. Inflorescentiae cymostae, cymulis bisexualibus in ramulis axillaribus; cymulae cum floribus pluribus, 2-4 ad eundum nodum. Flores ♂ pedicellis tenibus 5-9 mm longis; laciniae calycis 5, subaequalae, ellipticae vel obovatae, integrae, obtusae, ca 2.5-4 mm longae, 1.5-2.2 mm latae; discus ca 1.5-2.2 mm latus, segmentis 3 bilobis crassi et foveatis; stamina 3, filamentis libris 0.6-1.0 mm longis, antheris ovatis oblongisve obtusis 0.6-0.7 mm longis verticaliter dehiscentibus; pollinis grana subglobosa, tricolporata, colpibus ad polos convenientibus, exino crasso perreticulato. Flores ♀ pedicellis crassiusculis 6-9 mm longis; laciniae calycis 5, subaequalae, ± erectae, ellipticae vel obovatae, 4-5.5 mm longae, 2.5-4 mm latae, reticulatae nervatae; discus crateriformis, 5-an-gulatus, crassiusculus, prominenter foveatus, 2-3 mm latus, 0.6-0.8 mm altus; ovarium laeve; styli connati, columna 2.5-3 mm alta, apicibus bifidis vel bipartitis 0.9-1.2 mm longis gracilibus et patentibus. Fructu nisci seminaque ignoti.


This species, known only from the type collection, was determined on the printed labels as P. grandifolius L., but this is a double error. The plant was evidently mistaken for P. grandifolius sensu Muell.-Arg. non L. (DC., Prodr. 15(2): 329, 1866), which is the West Indian species correctly know as P. jug-landifolius Willd. This latter plant, belonging to sect. Asterandra in subg. Xylophylla, does somewhat resemble the Guatemalan species under discussion in its large reticulate-veined leaves. The massive pitted floral disk in P. juglandifolius also recalls that in P. tuerckheimii (Fig. 2). However, P. juglandifolius is very different in its dilated style-tips, connate horizontally dehiscent stamens, and especially in its areolate pollen grains which are typical for subg. Xylophylla and utterly different from the tricolporate coarsely reticulate grains of P. tuerck-heimii. True P. grandifolius L., which does occur in Guatemala, is even more different in its non-phyllanthoid branching and elaborately ramified inflorescences.

The overall configuration of the flowers in sect. Calodictyon would place the taxon in subg. Gomphidium (Baill.) Webster, a mainly Australasian group of species which approach the genus Glochidion in many respects. The ♂ flowers of P. tuerckheimii, with three free vertically dehiscent stamens and a disk of three massive duplex segments, definitely resemble those of various species of sect. Gomphidium from New Caledonia and New Guinea; the ♀ flowers, with a crateriform disk and bifid styles, suggest those found in New Guinean species of sect. Paragomphidium such as P. finschii K. Schum. (except that in the Guatemalan plant the styles are connate). The leaves are much like those of P. brassii White, from Queensland, but that species has dimerous ♂ flowers (4 calyx-lobes and 2 stamens) and free styles. Although the pollen grains of most taxa of subg. Gom-phidium are similar to those of sect. Calodictyon in being tricolporate with colpi meeting at the poles, the unbordered colpi and coarse reticulum of the Guatemalan plant are not matched in any of them.
On the basis of the totality of characters observed, the similarities of sect. *Calodictyon* with the taxa of subg. *Gamphidium* are so striking that the group apparently must be referred to that otherwise strictly gerontogeian subgenus. The only other American taxa of *Phyllanthus* which seem to show possible affinities to subg. *Gomphidium* are the South American species of sect. *Microglochidion*. These plants have an androecium even more *Gomphidium*-like in the apiculate anthers, and some species have entire styles. However, the 6- to 8-colporate pollen grains of sect. *Microglochidion* are very different from those found in sect. *Gomphidium*, and for this reason the South American species seem better placed in subg. *Emblica*, where similar pollen grains occur.

The placement of sect. *Calodictyon* within subg. *Gomphidium* admittedly creates a geographical anomaly, since the subgenus thus becomes one of the few euphorbiaceous taxa which shows an Australasian-Mesoamerican disjunction. However, somewhat similar patterns are exhibited, e.g. by *Sebastiania* (mostly New World but with 1 Fijian species) and *Stillingia* (American except for 2 In-
donesian species). The isolated position of sect. Calodictyon within subg. Gomphidium suggests that it is probably best regarded as a relict group which has persisted from a time when subg. Gomphidium and subg. Emblica were much better represented in the New World.—Grady Webster, University of California, Davis.

NOTES ON SOME AMERICAN SPECIES OF PHYLLANTHUS (EUPHORBIACEAE)

1. Phyllanthus abnormis Baill. var. riograndensis, var. nov. ab var. abnormi differt ramis et foliis semper dense viseido-scabridulis, glandulis reniformibus. Type: Texas, Starr Co, 3 mi W of Sullivan City, on sand in open scrub, 2 Apr 1941, Lundell & Lundell 9891 (MICH).

This striking variant of Phyllanthus abnormis replaces the typical form of the species in the lower Rio Grande Valley (Hidalgo, Starr, and Webb counties), and probably occurs on the Mexican side, although it has not yet been collected there. The laterally expanded disk-segments in the pistillate flower are so characteristic that at first encounter the Rio Grande plant might appear to be a distinct species. However, there is some evidence of intergradation with the glabrous plants which have narrow disk-segments, so it seems best to record this population as simply a local variety.

2. Phyllanthus longipes Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 153, 1940, non P. longipes (Wight) Muell.-Arg., Linnaea 32: 11, 1863. Type: British Honduras, El Cayo Dist, Vaca, 13 May 1938, Gentle 2619 (holotype F; isotypes MICH, MO). This plant is obviously not a Phyllanthus, and seems to represent a distinct species in the genus Gymnanthes. It may, therefore, take the name Gymnanthes belizensis Webster, nom. nov. Although similar to G. riparia (Schlecht.) Kl. and G. longipes Muell.-Arg. of Mexico, it seems to be distinct by virtue of its rigid leaves combined with long very slender fruiting pedicels.

3. Phyllanthus ventricosus Webster, sp. nov. (subg. Botryanthus). Frutex monoicus, ca 3 m altus, ramis teretibus persistentibus, ramulis juvenilibus minute ferrugineo-puberulis sed mox glabris. Folia alterna, chartacea, elliptica, obtusa acuminata, glabra, ca 5-9 cm longa 3-4 cm lata, nervis lateralis utroque latere ca 7-9 supra inconspicuis subitus prominulis reticulato-anastomosantibus, petiolis ca 1.5-2.5 mm longis, stipulis deltoido-lanceolatis 0.9-1.1 mm longis. Flores in cymulide pedicellis tenuibus ca 5-9 mm longis; laciniae calycis 6 biseriatae, oblongae vel ovatae, integrae, 1.2-1.5 mm longae, 0.7-0.9 mm latae; discus poculiformis, crassiusculus, ca 0.3-0.4 mm altus, 1 mm latus; stamina 3, ommino coalita in columnam venterosam umbonatum 0.8-0.9 mm altam; antherae ex apice columnae inclinatae, loculis saciformibus ca 0.5-0.6 mm longis; pollinis grana areolata, areolis polybrochatis, Flores pedicellis sparse puberulis sed glabrescentibus, ca 4-9 mm longis; laciniae calycis 6 biseriatae, oblongae vel
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obovatae, integrae, 1.3-1.8 mm longae, 0.6-0.9 mm latae; discus crateriformis ca 0.3-0.4 mm altus, 1.5-1.6 mm latus; ovarium triloculare, stylis liberris patentibus bifidis ca 0.5 mm longis ramis tenuibus. Capsulae (immaturae) laeves, castaneae, 7-8 mm longae; semina non vidi.

Type: Peru, Dept Loreto, Distr Iquitos, Rancho Indiana, overflowed creek, alt 110 m, Mexico 6414 (holotype MO 1188471; isotypes GH, UC, US).

The type collection of this species had been determined by Standley as Phyl-lanthus poeppigiannus Muell. Arg., which is indeed superficially similar in appearance. However, P. poeppigiannus is dioecious and has clearly different flowers: although the $\varphi$ flower is similar in having a cupulate disk, the stamens are only partially connate ($\frac{3}{4}$ to $\frac{1}{2}$ the filament lengths) into a slender column ca 1.5 mm high; and the $\varphi$ flowers are easily distinguished by their entire styles. Still, the 6-merous calyces and areolate pollen grains are similar in both species, and P. ventricosus may reasonably be assigned a position in subg. Botryanthus (Webster, Jour. Arnold Arb. 38: 49, 1958) not too far distant from P. poeppigiannus.—Grady Webster, University of California, Davis.

A SECOND SPECIES OF TETRORCHIDIDUM (EUPHORBIACEAE) REPORTED FROM PANAMA

Tetrorchidium gorgonae Croizat subsp. robledoanum (Cuatr.) Webster, stat. nov. Tetrorchidium robledoanum Cuatr., Brittonia 9: 81, 1957.

The first record of Tetrorchidium from Panama was established by Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. 4, 219, 1929) when he described T. euryphyllum from near Almirante (Prov Bocas del Toro). Since then, only two additional Panamanian collections of Tetrorchidium have been made; these represent a species different from T. euryphyllum in having smaller more prominently reticulate leaves. Perusal of the treatment of Colombian Tetrorchidium by Cua-trecasas shows that these recent Panamanian collections approach most closely T. robledoanum Cuatr. and T. gorgonae Croizat (Jour. Arnold Arb. 24: 170, 1943). In fact, the foliar glands in one Panamanian collection (Canal Zone, W of Gatun Locks, Johnston 1688, MO) resemble those of T. gorgonae in being distinctly stalked and well below the apex of the petiole, whereas in the other collection (Panama, Cerro Jefe, Duke 9415, MO) the foliar glands are at the top of the petiole as in T. robledoanum.

In assessing the affinity of the Panamanian collections, it appears that they agree more closely with T. robledoanum in having smaller nearly entire leaves. The inconstancy of the foliar gland character in the Panama specimens, and the rather close resemblance of all the plants involved, suggests that the best course of action is to place all these taxa under the earliest name, T. gorgonae, with the mainland plants being assigned to a separate subspecies.—Grady Webster, University of California, Davis.
BERNARDIA AND CLEIDION (EUPHORBIACEAE) IN PANAMA

Bernardia denticulata (Standley) Webster, comb. nov.


Beginning with Hemsley's description of Cleidion nicaraguense in 1873, a total of five species occurring in Panama have been referred to either Bernardia or Cleidion. Most of these are known only from one or few collections which are incomplete in several instances, so that the true generic affinities have remained obscure up to the present time. In the preceding note, Hemsley's species was disposed of by transferring it to Acidotom; it now remains to consider the others.

Croizat (Jour. Arnold Arb. 24: 166, 1942) noted a strong resemblance to Bernardia in the pubescence and columella of Cleidion denticulatum Standl.; however, he apparently felt that the seeds were more like Cleidion. Actually, the large seeds of the type collection (Cooper 606, Chiriqui Trail, Bocas del Toro) are in size and shape not unlike those of, e.g., Bernardia obovata I. M. Johnston (as observed in Johnston 3426, DAV), although seeds of the Panama plant differ in being distinctly mottled.

While the generic position of the plant from Bocas del Toro cannot be fixed with absolute certainty in the absence of male flowers, I believe that the leaves, fruits, and seeds are all compatible with Bernardia, and that the dilated columella in particular mitigates against retaining the species in Cleidion.

The other species of Bernardia from Panama, B. macrophylla Standley, differs from B. denticulata in its less elongated and more finely toothed leaves. When (as observed in Johnston 3426, DAV), although seeds of the Panama plant differ ences.

Finally, although two of the three Panamanian species described in Cleidion have to be removed, Cleidion woodsonianum Croizat (Jour. Arnold Arb. 24: 167, 1943) does appear to be a true Cleidion. Croizat himself later (Trop. Woods 88: 31, 1946) transferred the species to Adenophaedra, but this action seems to be unwarranted. Examination of one of the isotypes (Woodson et al. 1587, Salamanca, Canal Zone; NY) yielded a single small ♂ inflorescence with a few buds; these prove to have numerous stamens (well over 50) as in Cleidion, in contrast to the two or three characteristic of Adenophaedra.

In summary, these various taxonomic changes leave the roster of Panama taxa at two species of Bernardia and one species of Cleidion. Additional material of all three species is needed before their affinities to their congeners can be appraised.

—Grady Webster, University of California, Davis.
FLORA OF PANAMA

by Robert E. Woodson, Jr. and Robert W. Schery
and Collaborators

Part VI

FAMILY 97. EUPHORBIACEAE

by Grady L. Webster and Derek Burch

University of California, Davis, California and
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Trees, shrubs, herbs, or vines; stems sometimes succulent, sometimes with milky or colored sap. Leaves alternate or, less commonly, opposite (rarely whorled), petiolate; stipules free or connate, often caducous, obsolete or absent; blades pinnately or palmately veined, compound or simple and lobed or not. Inflorescences cymose, racemose, or spicate, sometimes aggregated in pseudanthia. Flowers unisexual, mostly actinomorphic; calyx in most taxa of 3-6 valvate or quincunxially imbricate lobes or segments, rarely absent; corolla of 3-6 petals, or often reduced or absent; glandular disc of receptacular or staminodal origin often present; stamens (1-3)-20(-400 or more), the filaments free or united, the anthers mostly 2-locular and dehiscing longitudinally; pollen grains most often 3-colporate but sometimes inaperturate or polytreme; gynoecium of (1-3) or 4(-20) united carpels, the ovary superior, with axile placentation, the ovules 1 or 2 per locule, anatropous or hemitropous, epitropous, inserted beneath an obturator, crassinucellate, often with a nucellar beak. Fruits typically capsular, of 3 elastically dehiscing cocci separating from a persistent columella but sometimes drupaceous (rarely baccate or samaroid); seeds 1 or 2 per locule, or (by abortion) solitary in the fruits, the seed coats crustaceous to bony, the endosperm usually copious (rarely absent), the embryo extending most of the length of the seed, the cotyledons usually broader than the radicle, plane or rarely folded.

A highly diversified family of at least 7,000 species in more than 300 genera. Despite the relative floristic poverty of Panama, it has an impressive array of 36 genera with native species and a few additional genera, such as Pausandra, may still be discovered during the course of further exploration. A considerable variety of exotic euphorbiaceous genera are presently cultivated in Panama, especially in the Canal Zone, and a few of these may eventually escape to a certain extent as

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2 Responsible for Genera 1-25.
3 Responsible for Genera 26-36.

components of the native vegetation. Exotic genera in the Phyllanthoideae include Antidesma and Breynia, while the Euphorbioideae are represented by Aleurites, Codiaeum, and Hevea.

Useful references:


Key to the Genera

a. Ovules paired in each cell of the ovary; sap never milky; leaves entire, unlobed, not glandular. [Subfam. Phyllanthoideae]
b. Petals present; stipules intra-petiolar; fruits massive, 2 cm long ..........1. Amanoa
bb. Petals absent; stipules not intra-petiolar; fruits smaller, rarely exceeding 1 cm long.
c. Indumentum of simple or branched hairs; fruits of 3 or more carpels, not indehiscent and 1-seeded; $ flower without pistillode.
d. Fruit of 4 or 5 (rarely 3) carpels, irregularly dehiscent; seeds with bluish fleshy outer coat and bony inner coat; $ flower with an- nular disc and 4 free stamens; dioecious shrub or tree 2. Margaritaria
dd. Fruit of 3 (rarely 2 or 4) carpels, dehiscent in most species; seeds neither fleshy nor bony; $ flower with stamens 3 or else disc ab- sent (in local taxa); monoecious or dioecious, habit various ...3. Phyllanthus
cc. Indumentum lepidote; fruit of 2 carpels, drupaceous, 1-seeded; $ flower with pistillode 4. Hyeronima
aa. Ovules solitary in each cell of the ovary; sap often colored or milky; leaves often lobed and/or with petiolar glands or marginal teeth. [Subfam. Euphor- bioideae].
e. Flowers not aggregated into pseudanthia.
f. Stamens fasciculate-ramified, anthers $; leaves peltate, palmately lobed; inflorescences terminal, paniculate; $ flowers distal 23. Ricinus
ff. Stamens not highly branched, anthers equal in number to stamens; leaves not peltate and palmately lobed; inflorescences terminal or lateral, not paniculate, if $, with $ flowers proximal (lower).
g. Inflorescences of small clusters of stalked globose involucres each enclosing 3-10 sessile flowers (involucres almost lacking in one species but form of inflorescences otherwise the same) 26. Pera
gg. Inflorescences not of pedunculate heads of sessile flowers.
h. Petals present at least in $ flowers, often conspicuous in both $ and $.
i. Anthers ± erect in bud, not distinctly inflexed; indumentum not lepidote or of branched hairs (except trichomes malpighiaceous in *Argythamnia*).

j. Stamens not over 10.

k. Inflorescence dichasial; seeds carunculate; pollen grains verrucose; leaves palmately veined or lobed ........................................................................5. *Jatropha*

kk. Inflorescence racemiform; seeds ecarunculate; pollen grains not verrucose, 3–6-colporate; leaves pinnately veined.

l. Leaves finely serrate, lateral veins distinctly parallel; trichomes simple or glandular (not malpighiaceous); pistillode present in Ç flower ..................................................................................10. *Caperonia*

II. Leaves entire, lateral veins not distinctly parallel; trichomes malpighiaceous (at least in part); pistillode absent in Ç flower ..................................................................................11. *Argythamnia*

jj. Stamens Þ (50 or more) .................................................................................6. *Garcia*

hh. Petals reduced or absent in both Ç and Ç flowers.

m. Calyx distinctly petaloid; inflorescences dichasial.

n. Stinging hairs absent; Ç flowers usually yellowish or greenish to purplish, stamens free, the disc intrastaminal ........................................1. *Manihot*

nn. Stinging hairs present (sometimes very sparse); Ç flowers whitish, stamens connate, disc extrastaminal .............................................8. *Cnidosecolus*

mm. Calyx not petaloid; inflorescences not obviously dichasial.

o. Styles connate, columnar, 2.5–5 cm long terminating in a fleshy disc; 2–3 cm wide; Ç flowers aggregated into a pedunculate fleshy cone; carpels more than 5 .........................................................................32. *Hura*

oo. Styles usually much shorter than 2.5 cm, if long-columnar then not ending in a broad disc; Ç flowers not aggregated into a fleshy cone; carpels usually less than 5, if more the fruit pome-like.

p. Floral bracts not with conspicuous paired basal glands; Ç calyx-lobes valvate (imbricate in *Omphalea*).

q. Not twining with stinging hairs; Ç flowers with 3 or more stamens (often 2 in *Omphalea*).

r. Carpels 2; styles elongated, free, ± entire and unlobed; stamens usually 8 ..................................................................................15. *Alchornea*

rr. Carpels 3 or 4, styles variously modified, stamens few or many, not consistently 8.

s. Shrubs or trees, not lianas; styles free or at least not united for most of their length into a column.

t. Anthers not vermiform; Ç bracts not strikingly larger or different from the Ç; inflorescences racemose or thyssid, not definitely spicate.

u. Stamens over 10.

v. Stamens over 50, Ç pedicel slender, 10–15 mm long styles bifid ........................................................................14. *Cleidion*

vv. Stamens not over 35.

w. Stamens 24–35, anthers with a minute apical tuft of stinging hairs; styles connate into a column, the ends undivided, papillose .............................................19. *Acidoton*

ww. Stamens less than 20, anthers without an apical tuft of stinging hairs, styles free or nearly so.

x. Styles deeply lacinate; Ç pedicels becoming 20–70 mm long; leaves without basal foliar glands ..................................................................................12. *Adelia*

xx. Styles 1 or 2 times bifid; Ç flowers sessile or sub-sessile; leaves with conspicuous foliar glands near the base ........................................................................13. *Bernardia*
uu. Stamens less than 10.
y. Disc absent in $\delta$ flower; stamens 3, anthers peltate, 4-locellate ........................................... 17. Tetrorchidium
yy. Disc of $\delta$ flower massive, central stamens 4-8, not peltate.
z. Pistillode present in $\delta$ flower; leaves triplinerved; fruits small, seeds compressed and with fleshy coat, less than 3 mm long ........................................... 16. Alchorneopsis
zz. Pistillode absent in $\delta$ flower; leaves pinnately veined; fruits massive, seeds spheroidal, 15 mm long or more, seed coat not fleshy ........................................... 18. Caryodendron
tt. Anthers vermiform; 9 bracts much larger than $\delta$ (or if not, ovary dense-verrucose); flowers spicate ........................................... 24. Acalypha
ss. Lianas; styles connate for most of their length into a column.
A. Stamens 19-24; $\delta$ calyx-lobes valvate; carpels 4, carinate; seeds lenticular, 15-17 mm broad; leaves acuminate .............. 21. Plukenetia
AA. Stamens 2(-3); $\delta$ calyx-lobes imbricate; carpels 3, sericeous; seeds compressed, 39-40 mm broad; leaves obtuse .......... 22. Omphalea
qq. Twining vine armed with stinging hairs; $\delta$ flowers with 2 stamens ... 20. Tragia
pp. Floral bracts with conspicuous basal glands; $\delta$ calyx-lobes imbricate or open.
B. Seed carunculate, dry; fruit capsular; petiole eglandular but sometimes with cupular glands at base of leaf blade.
C. Inflorescence spicate.
D. Columnella with a persistent hardened gynobase; $\delta$ calyx lobes and stamens 2 ........................................... 29. Stillingia
DD. Columnella without hardened gynobase after dehiscence of fruit; $\delta$ calyx-lobes and stamens usually 3 .............. 27. Sebastiania
CC. Inflorescence racemiform or paniculate ................. 28. Mabea
BB. Seed ecarunculate, either seed coat or capsule wall fleshy; petiole usually biglandular, the stipitate glands a little below the junction with the blade.
E. Fruit thin walled, capsular; seed coat fleshy; ovary 3 locular ........ 30. Sapium
EE. Fruit fleshy, indehiscent; seed coat dry; ovary 6-10 locular ... 31. Hippomane
e. Flowers aggregated into pseudanthia (see also 26. Pera).
F. Pseudanthium bilabiate, the flowers subtended by 2 large divergent palmately veined bracts; 9 flowers 3 at lower node, 6-12; styles connate to the stigmas; fruiting calyx covered with irritating hairs; vines ... 25. Dalechampia
FF. Pseudanthium radially symmetrical, or if bilaterally symmetrical then not subtended by divergent bracts; 9 flower solitary, terminal; $\delta$ in 5 groups around base of $\varphi$; styles free or connate; calyx obsolete; herbs, shrubs, or trees, never twining.
G. Cyathium spurred, strongly zygomorphic; glands hidden within spur ......................................................... 36. Pedilanthus
GG. Cyathium not spurred, overall appearance ± actinomorphic; glands on rim of cyathium.
H. Glands of cyathia solitary (rarely up to 5 on first few formed), exappendiculate ........................................... 34. Poinsettia
HH. Glands of cyathia usually 4 or 5, exappendiculate or with petaloid appendages.
I. Leaves all opposite, base inequilateral, veins chlorenchyma-sheathed, stipulate; main axis aborting within 2 nodes of cotyledons ........................................... 35. Chamaesyce
II. Leaves alternate, opposite or whorled, if opposite base ± equilateral, veins not chlorenchyma-sheathed, stipules often obsolete; main axis persisting or aborting only after an obvious stem has been produced ................................... 33. Euphorbia
1. AMANOA


Trees or shrubs, glabrous; monoecious. Leaves alternate, coriaceous, entire; short-petiolate; stipules persistent, oblique-decurrent, projecting between adaxial surface of petiole and stem ("intrapetiolar"). Inflorescences subsessile or shortly pedicellate, the densely bracteate clusters racemose or occasionally paniculate; sepals 5, firm, larger than the sometimes scale-like petals; disc not very conspicuous. Staminate flowers with stamens 5, the filaments free, shorter than the introrsely dehiscing anthers; pollen grains oblate, 3-5-colporate, echinate; pistillode conspicuous. Pistillate flowers with 3 carpels, the ovules 2 in each locule, anatropous, the styles connate, the stigmas thick, bifid, reflexed. Fruits capsular, massive, the endocarp often very thick, tardily dehiscent, the columella massive, tapering from the base; seeds usually 3 per capsule, ovoid or ellipsoid, smooth, not carunculate, thin-walled, the endosperm scanty or absent, the massive angled cotyledons filling most of the seed, the radicle short.

A small but somewhat heterogeneous genus of about 10 American and African species. The three African species are distinguished by larger floral bracts but on the whole appear to be correctly placed in the same genus as the neotropical taxa.

1. Amanoa guyanensis Aublet, Hist. Pl. Gui. Fr. 256, t. 101, 1775.—Fig. 1.

Tree, glabrous; twigs smooth, terete or somewhat angled. Leaves coriaceous; petiole 5-8 mm long, adaxially deeply furrowed; stipules inconspicuous, reddish, ca 1 mm high; blades elliptic to elliptic-oblong, rather abruptly cuspidate or acuminate, 8-13 cm long, 4.5-7 cm broad, rounded or obtuse to subcordate at the base, with 8-13 major and several minor veins on each side. Inflorescences on stiff lateral branchlets or branch-tips, subtended by reduced leaves or by scale-like bracts. Staminate flowers with pedicel shorter than the calyx; calyx-lobes 5, thick, ovate, ca 7-9 mm long; petals dark, unguiculate, ca 0.7-1 mm long, 1.1-1.4 mm broad; disc cupuliform, shallow, margin undulate, anthers ca 5 mm long; pistilloides massive, apically 3-lobed, ca 5 mm high, 2.5 mm in diam. Pistillate flowers with stout pedicel, becoming 1.5 cm long; calyx-lobes ovate-oblong, ca as long as in $\sigma'$; petals suborbicular, shortly unguiculate, finely denticulate, 1.5-1.7 mm long, 2-2.3 mm broad; ovary abruptly or gradually passing into the thick stylar column, the stigmas dilated, reflexed, ± crenulate at the ends. Capsule 2 cm long (in Panamanian specimen), thick; seeds ovoid, 1-1.5 cm long.

Rainforests, northern South America.

Canal Zone: nr mouth of Rio Chagres, flooded land, Johnston 1698 (GH, MO).

It seems rather remarkable that this species has been collected only once, since the collector noted that it was frequent in an area which has often been botanized. The identification of the Johnston collection as Amanoa guyanensis is made with some hesitation, since the specimen does not include flowers. The Panamanian plant appears to be quite similar to that from British Honduras determined by
Fig. 1. *Amanoa guianensis* Aublet: A, habit (ca ×1/2); B, male flower (ca ×7); C, female flower (ca ×5); D, ovary (ca ×7). After *La Cruz* 2514 (MO), British Guiana.
Standley (Trop. Woods 32: 15, 1932) as A. grandiflora Muell.-Arg. and made the type of a new species A. potamophila by Croizat (Amer. Midl. Nat. 29: 476, 1943). Until the neotropical populations of Amanoa can be carefully studied and the distinction between A. guyanensis and A. grandiflora worked out more satisfactorily, any identification of the Panamanian population must be provisional.

2. MARGARITARIA


Shrubs or trees; dioecious; foliage deciduous, new leaves appearing with flowers (or persistent in certain species), ramification distichous, branches all persistent with ± conspicuous lenticels. Leaves alternate, entire, chartaceous; short-petiolate; stipules entire, subpersistent. Inflorescences of clustered flowers on short floriferous branches or at proximal axils of leafy branches, rarely flowers solitary; gamosepalous, the calyx-lobes usually 4; apetalous; disc annular and entire in both sexes. Staminate flowers with long pedicels; stamens usually 4, free, the anthers extrorse in the bud, dehiscing longitudinally; pollen grains 3-colporate. Pistillate flowers with stout pedicels; ovary with 2-5 carpels, the styles free or united into a column, bifid to bipartite, ± dilated. Capsules irregularly dehiscent, the green reticulate exocarp usually breaking away from the pale membranous endocarp of each coccus, the cocci very fragile, fragmenting irregularly; seeds normally paired in each coccus, the outer seed-coat dark blue, thick and fleshy, the inner seed-coat thick and woody, achen-like, smooth or rugose, invaginated at the chalazal end, the endosperm copious, whitish, the embryo straight or nearly so, the cotyledons thin and flat, much longer than the radicle.

A very homogeneous genus of about 10 species, represented in most tropical regions except Australia and the Pacific Islands. Mueller (in DC., Prodr. 15(2): 414-418, 1866), on the basis of the tetramerous flowers, treated the group as three subsections of his sect. Cicca L., which also included the common Phyllanthus acidus (L.) Skeels. This unnatural arrangement has misled the majority of subsequent workers into treating Margaritaria as a section within Phyllanthus. Actually, however, it more closely resembles certain other genera of Phyllanthaceae such as Flueggea and Securinega than it does any species of Phyllanthus.

1. Margaritaria nobilis L. f., Suppl. Pl. Syst. Veg. 428, 1781.—Fig. 2.


Tree 5-10 m high; dioecious; branches subterete or angled, glabrous, usually with conspicuous lenticels. Leaves chartaceous; petioles ca 2-5 mm long; stipules elliptic to oblong, acuminate, 1.5-3 mm long; blades elliptic or oblong to ovate-lanceolate, ca 6-15 cm long, 2.5-5 cm broad, smooth above, glabrous or glaucous beneath and sometimes hairy along the veins, major veins mostly 7-12 on a side,
Fig. 2. *Margaritaria nobilis* L. f.: A, habit (×1½); B, female flower (×5); C, ovary (×8); D, male flower (×5); E, stamens (×8); F, anther (×20); J, fruit with 6 locules (×3); H, fruit with 5 locules (×5); I, seed (×5). A after Duke 5040 (MO); B-C after Woodson et al. 1364 (F, GH, MO); D-F after Broadway 4515 (MO), Tobago; H-I after White 164 (MO).
raised beneath, the veinlets scarcely raised beneath but often conspicuous, cuneate to rounded at the base, ± acuminate at the tip. Inflorescences of 2-several flowers per cluster or the ♀ sometimes solitary. Staminate flowers with pedicels ca 2.5-5 mm long; calyx-lobes 4, somewhat unequal (outer pair usually narrowly membranous), ca 0.9-1.7 mm long; anthers ca 0.4 mm long. Pistillate flowers with pedicels rather stout, becoming 5-14 mm long in fruit; calyx-lobes 4, similar to the staminate; disc 0.8-1.5 mm broad; ovary usually of 4 or 5 (rarely 3) carpels, the styles ca 1.5 mm long. Capsules mostly 8-11 mm in diam; seeds ca 3.5-4 mm long.

Mexico and Cuba south to Peru and Brazil, in both wet and dry forests.

BOCAS DEL TORO: Almirante, Cooper 381 (F), Changuinola, Dunlap 19 (F, US).
CANAL ZONE: Albrook, Dwyer 7124 (MO), Barro Colorado I, Shattuck 975 (MO, NY), Standley 41045 (US); Cerro Gordo, Standley 25988 (US); Chagres River, Pittier 3468 (US); Fort Hamilton, Mason & Harvey 6531 (US); Fort Sherman, Standley 30975 (US); Gamboa, Pittier 6650 (US); Gatun, Hayes 219 (NY); Miraflores, G. White 164 (MO, NY), P. White 131 (F, MO); Sosa Hill, Duke 4708 (MO). CHIRIQUI: Cerro Galera Chorcha, vic of Gualaca, Allen 5018 (F, MO). DARIEN: El Real, Duke 5040 (MO), Stern et al. 892 (MO); vic of El Real, Rio Tulea, Stern et al. 768 (DAV, MO); La Palma, Pittier 6603 (US); Rio Chucunauque, vic of Campamento Buena Vista, Stern et al. 919 (DAV, MO), betw Rio Membrillo and Rio Subcuti, Duke 6590 (MO), 8611 (MO); vic of Santa Fé, Rio Sabana, Duke 4154 (MO), Panama: Arraiján, Woodson et al. 19364 (F, GH, MO); Bella Vista, Mason & Valentine 6950 (US); Punta Paitilla, Standley 30913 (US); Rio Mamonica, 4 mi beyond Chepo, Duke 5577 (MO); Rio Tocumen, Standley 26725 (US); Sabana de Juan Corso, Pittier 4518 (F, US); San José I, Johnston 954 (GH, MO). SAN BLAS: headwaters of Rio Malatupu, Elias 1743 (MO, GH), 1750 (MO, GH, US).

This very widespread but not necessarily common plant exhibits a great deal of geographic variation. Mueller (in DC, Prodr. 15(2): 414-415, 1866; in Mart., Fl. Bras. 11(2): 70, 1874) recognized a considerable number of varieties which have not been listed in the synonymy of the species, as most of these are South American and have not yet been evaluated. The “variety” hypomalacus from Central America described by Standley is merely a sporadic pubescent form unworthy of taxonomic recognition. The plant described from Colombia as Phyllanthus heteromorphus (Rusby, Descr. S. Amer. Pl. 42, 1920) is perhaps the most distinctive geographic race due to its striking pubescence, but it has not been encountered in Panama.

Very closely related to M. nobilis is an African species, Margaritaria discoidea (Baillon) Webster. Like M. nobilis, the African species is widespread and very polymorphic. It is very difficult to find a single character which will separate all specimens of both species, but M. discoidea usually differs in having carpels mostly 3 (rarely 4, apparently never 5), shorter fruiting pedicels (3.5-6 mm) and smaller seeds (mostly 2.6-3.3 mm long). In the West Indies (Cuba, Bahamas, and Hispaniola) occur three endemic species of Margaritaria which are probably closely related to M. nobilis. All of these, however, differ in having scabridulous branchlets, and M. scandens (Wright ex Griseb.) Webster, the species most easily confused with M. nobilis, has obtuse leaves whitened with waxy points beneath. Evidently the morphological differentiation of populations has occurred with extreme slowness in Margaritaria, so that populations isolated for long geological periods have not diverged greatly.
3. PHYLANTHUS


Trees, shrubs or herbs of very diverse habit; monoecious or subdioecious, much less commonly dioecious; branching unspecialized (twigs then persistent, with spiral or distichous phyllotaxy) or (in many species) axes of two kinds: persistent, with spiral phyllotaxy and without flowers, and deciduous, with distichous phyllotaxy and often floriferous. Leaves usually alternate, entire, varying in size and texture; short-petiolate; stipules deciduous or persistent. Inflorescences usually axillary; flowers solitary or in reduced cymes, in some species cauliflorous or in pseudodeterminate thyrses; gamosepalous, 4-6 lobed; apetalous; disc usually present. Staminate flowers with mostly 3-6(2-15) stamens, the filaments free or connate; disc usually cut into segments; pollen grains sometimes spheroidal and 3-colporate but often with other patterns, small, intectate; pistillode absent. Pistillate flowers pedicellate or subsessile; calyx-lobes usually 5 or 6, usually entire; disc entire or cut into segments, rarely absent; carpels usually 3, the ovules 2 per locule, hemitropous, the styles free or united, bifid or variously divided or dilated. Fruits usually capsular, ± explosively dehiscent, less commonly baccate or drupaceous, the crustaceous cocci separating from a persistent columella; seeds usually 2 per locule (rarely only 1 developing), the seed-coat dry and crustaceous, smooth or sculptured, the endosperm cartilaginous, the embryo straight or slightly curved.

A diversified genus of perhaps 700 species, the majority of these belonging to the Old World. The genus has been subdivided by many authors, but the broad concept of Mueller-Argoviensis has been retained by most recent workers. The species may be grouped into about 10 subgenera, of which six are represented in Panama by either wild or cultivated species. The local species fall into two basically different types: those in subg. Isocladus Webster, with distichous leaves and undifferentiated branching, and the other species with deciduous and often floriferous branchlets; the latter have been designated as having 'Phyllanthoid' branching (Webster, Jour. Arnold Arb. 37: 102-114, 1956).

The so-called grosella or Otaheite gooseberry, P. acidus (L.) Skeels, is rather commonly cultivated in Panama and elsewhere in the American tropics. It is closely related to the native P. elsiae Urban but may be distinguished from that and other native species by its drupaceous fruits and the common occurrence of staminodes in the female flower. Both P. acidus and P. elsiae belong to subg. Cicca (L.) Webster, which has perhaps been the most widely recognized of all segregates from Phyllanthus. However, subg. Cicca is related to some African species of subg. Kirganelia (Juss.) Webster, and it seems more convenient therefore to retain it with Phyllanthus.

Various other species of Phyllanthus may be cultivated in Panama, but the only one recorded seems to be P. emblica L., which resembles P. acidus in having drupaceous fruits; but these eventually dehisce, and the plant is easily distinguished from P. acidus by its much smaller linear-oblong leaves.

Useful reference:
Webster, G. L., A monographic study of the West Indian species of Phyllan-
Flora of Panama (Family 97. Euphorbiaceae)


a. Monoecious herbs; axes all persistent; leaves distichous, none reduced to scales (subg. Isocladus).

b. Seeds minutely verruculose, ca 1 mm long or less; capsules ca 2 mm broad or less.

c. Filaments of stamens free; stems terete, at most narrowly winged

cc. Filaments of stamens united; stems compressed and distinctly winged

bb. Seeds smooth, 1.5 mm long or more; capsules ca 3 mm broad ... 3. P. hyssopifolioides

aa. Monoecious or dioecious herbs, shrubs, or trees; leaves on persistent axes reduced to scales, developed leaves and flowers present only on deciduous branchlets.

d. Dioecious shrubs or trees; cauliflorous; calyx-lobes and stamens usually 4, carpels usually 3, fruits with 1 or 2 developed cells, each with a single seed, pithy and indehiscent (subg. Cicca) 4. P. elsiae
dd. Monoecious, habit various, not cauliflorous (flowers axillary on deciduous branchlets); calyx lobes 5 or 6, stamens 3 (seldom 2); carpels usually 3, fruit capsular, dehiscent, each cell with 2 seeds.

e. Branchlets pinnatifid; plants woody or herbaceous; pollen grains reticular, colporate (subg. Phyllanthus).

f. Leaf-blades hispiduous beneath; ♀ flower subsessile; ovary distinctly roughened; seeds transversely ribbed 5. P. urinaria

ff. Leaf-blades smooth; ♀ flower definitely pedicellate; ovary smooth or nearly so; seeds striate or verruculose.

g. Leaf-blades usually oblique at the base; stipules narrow, 2 mm long or more; ♂ calyx-lobes 1.2 mm long or longer; pollen grains 4-colporate; seeds verruculose, 1.4-1.8 mm long 6. P. niruri
gg. Leaf-blades not oblique; stipules not over 1.3 mm long; ♂ calyx-lobes less than 1 mm long; pollen grains 3-colporate; seeds striate or ribbed, 0.8-1.3 mm long.

h. Cymules bisexual (1 ♂ and 1 ♀ flower); ♂ calyx-lobes narrowly obovate, 1 mm long or less, distinctly pointed at the tip; seeds with usually 5 or 6 distinct ribs 7. P. amarus

hh. Cymules unisexual; ♀ calyx-lobes broadly obovate, rounded at the tip, 1.4 mm long or more (in fruit); seeds with 10-12 delicate striae.

i. Filaments completely united, staminal column 0.25-0.4 mm high; pistillate disc angled or 5-lobed; seeds 1.1-1.3 mm long; stems sometimes thickened with aerenchyma below, leaves not narrowed towards tip 8. P. stipulatus

ii. Filaments only partially united, staminal column ca 0.1 mm high; pistillate disc divided into 3 narrow segments; seeds 0.9-1 (-1.1) mm long; stems never thickened with aerenchyma, leaves narrowed towards the tip 9. P. earibaeus

ee. Branchlets bipinnatifid; plants woody; pollen grains echinulose (subg. Conami).

j. Leaf-blades abruptly caudate-pointed, scabrous-roughened above; pedicel of ♀ flower scabridulous, 5-14 mm long; seeds 2.3-2.8 mm long 10. P. acuminatus

jj. Leaf-blades evenly narrowed to an acute or obtuse tip, smooth; pedicel of ♀ flower smooth, 10-15 mm long; seeds 2.2-2.4 mm long 11. P. anisolobus

*Herb,* annual or short-lived perennial, ca 1-3 dm high; monoecious, branches terete or narrowly winged; stems unbranched to pinnately branched. *Leaves* membranous to firm; petioles short, 0.5-1 mm long; stipules auriculate, 0.7-2 mm long; blades elliptic to obovate, obtuse to rounded or apiculate, 5-20 mm long and 2-10 mm broad, paler beneath, the reticulum of veinlets often distinct. *Cymes* with usually 1 or 2 staminate and 1 or 2 pistillate flowers. *Staminate flowers* with (5-) 6 calyx-lobes, 0.5-0.7 mm long; disc-segments 6; stamens 3, the filaments free, short, the anthers opening horizontally; pollen grains oblong, 4-colporate. *Pistillate flowers* with pedicels sharply reflexed, 1 mm long or less; calyx-lobes usually 6, 0.6-1.4 mm long, linear to oblong; disc entire or dissected; ovary usually smooth, the styles bifid, less than 0.5 mm long. *Capsules* 1.6-2 mm in diam; seeds 0.7-1 mm long, dull grayish-brown, verruculose.

Latitudinally the most widespread species of *Phyllanthus,* extending from Pennsylvania south to Argentina, and showing marked geographic variation. The Panamanian specimens appear to represent two subspecies:

1a. *Phyllanthus caroliniensis* subsp. *caroliniensis*.

Stems terete or flattened, not distinctly winged, usually with a number of lateral branches; plants of relatively weedy habitats.

**Canal Zone:** Ancon, Pittier 2761 (US); Balbo, Standley 28558 (US), 29289 (US). **Darien:** El Real, Burch et al. 1057 (MO). **Panama:** hills betw Capira & Potrero, Dodge & Hunter 8618 (MO); Taboga I, Standley 27832 (US, GH).


*P. stenopterus* Muell.-Arg. in DC, Prodr. 15(2): 399, 1866.

Stems terete, sharply and narrowly (ca 0.1 mm wide) winged, unbranched to copiously branched; plants of wet situations.

**Canal Zone:** Chagres, Fendler 273 pro parte (GH, NY, US); Fort Clayton to Corozal, Standley 29043 (US). **Chiriquí:** David airport, Lewis et al. 731 (GH, MO). **Panama:** vic of Chepo, Pittier 4610 (US), 4661 (US); Las Sabanas, Bro. Heriberto 147 pro parte (US); Race Track, Panama, Standley 27757 (US); Punta Paitilla, Standley 26236 (US); Ro Tocumen, Standley 26607 (US); San José I, Erlanson 443 (GH), Harlow 78 (GH), Johnston 185 (GH).


*Herb,* annual or short-lived perennial, up to ca 3 dm high, sparsely to freely branching; monoecious; branches distally flattened and with a sharp wing 0.2-0.25 mm across on each side, ca 1-1.2 mm wide (including wings only 0.7 mm or more wide on secondary branches). *Leaves* firm in texture; petioles usually less than 1 mm long; stipules auriculate, acuminate, ca 1-2 mm long; blades elliptic, obtusely but distinctly pointed, mostly 6-15 mm long and 2.5-5 mm broad, the primary veins sometimes distinct but not prominent, the secondary veins (and
sometimes all venation) obscure or invisible. **Cymules** with usually 1 or 2 ♂ and 1 or 2 ♀ flowers. **Staminate flowers** with pedicels usually less than 1 mm long; calyx-lobes usually 5, ca 0.5-0.7 mm long and broad; disc-segments 5, entire; stamens 3, the filaments united about halfway (sometimes less), less than 0.5 mm long, the anthers opening ± horizontally; pollen grains oblong, 4-colporate. **Pistillate flowers** with pedicels sharply reflexed, less than 1 mm long; calyx-lobes usually 5, ca 0.6-0.8 mm long, obovate; disc annular, entire; ovary smooth, the styles free, bifid, less than 0.4 mm long. **Capsules** ca 1.7-2 mm in diam; seeds ca 0.9-1 mm long, brownish, verruculose.

Mexico to Peru, usually in rather moist places.

**BOCAS DEL TORO:** Changuinola Valley, Dunlap 359 (F, US); id., 10-15 mi inland from mouth of Changuinola River, Lewis et al. 888 (DAV, GH, MO, US). **PANAMA:** sandy places on rocky shore, Boquerón waterfall, Río Boquerón, Steyermark & Allen 17234 (MO).

This species is related to *P. caroliniensis* and could easily be confused with *P. caroliniensis* subsp. *stenopterus*, which also has winged stems. However, the stems of subsp. *stenopterus* are terete, more delicate, and with wings narrower (ca 0.1 mm), and it also agrees with typical *P. caroliniensis* in its veiny leaves and free filaments of the male flowers. The leaves of *P. compressus* are thicker than those of *P. caroliniensis* and have a dull, leaden appearance which (when taken with the inconspicuous veins) is distinctive.


**Annual herb**, erect, completely smooth and glabrous; monoecious; main stem unbranched or nearly so, 1-2.5 dm high, 0.5-1 mm in diam, terete below, flattened above and with thin narrow wings 0.1-0.15 mm broad. **Leaves** with petioles 0.5-0.8 mm long; stipules ovate-lanceolate, acuminate, basally auriculate, ± denticulate, 1.2-1.5 mm long; blades ovate to oblong or elliptic, obtuse-acute at tip, 6-12 mm long, 2.5-5 mm broad, the lateral veins obscure to distinctly visible. **Inflorescences** unisexual, sexes at separate axils, the staminate in few-flowered clusters, the pistillate solitary. **Staminate flowers** with pedicels less than 1 mm long; calyx-lobes 5, obovate to broader than long, 0.6-0.7 mm long, 0.6-0.9 mm broad; disc-segments 5, cuneate to orbicular, thin, ca 0.2 mm in diam; stamens 3, the filaments free, ca 0.15 mm long, the anthers subglobose, 0.25-0.3 mm broad, dehiscing obliquely. **Pistillate flowers** with geniculate pedicels, 1 mm long or less; calyx-lobes 6, obovate to oblong, obtuse to subacute, (0.8-)1-1.2 mm long; disc-segments 6, cuneate, entire; ovary smooth, the styles horizontal, bifid, the style-branches dilated and thickened, appressed to the ovary, less than 0.2 mm long. **Capsules** subglobose, olivaceous, ca 3 mm broad; seeds 1.6-1.7 mm long, smooth, dull brownish with yellow coating.

Savannas, apparently in wet places, in several disjunct neotropical areas (Dominican Republic, Trinidad, Panama, northern South America).

CHIRIQUI: vic of Boquete, Llanos Francia, 3300 ft, Stern et al. 1161 (DAV, MO); COCLE: Penonomé, Ebinger 1020 (MO).
The recent (1959, 1960) collection of a widely disjunct population of this species in Panama is rather surprising, but as the plant is rather inconspicuous (and perhaps ephemeral), it may have been overlooked. It should be sought in savanna areas in other provinces.


Bush or tree, up to 15 m high, glabrous; dioecious; older twigs 5-15 mm thick sometimes with conspicuous lenticels; scale-leaves on permanent branches ± deciduous, blackish, indurate, ca 1.5 mm long. Deciduous branchlets 1-3 dm long, 1.3-1.8 mm thick, with ca 10-20 leaves, the median internodes ca 1-1.5 cm long. Leaves chartaceous; petioles 2.5-3.5 mm long; stipules lanceolate, blackish-brown, 0.8-1.2 mm long; blades mostly broadly elliptic to suborbicular, rather abruptly pointed, 3-5(-7) cm long, 2-4(-5) cm broad. Thrysiform inflorescences naked, clustered on spur-shoots; staminate axes mostly 1.5-7 cm long, the cymules with 10-20 flowers; pistillate axes mostly 3-6 cm long, the cymules with 1-4 flowers. Staminate flowers with calyx-lobes 4, 1-1.7 mm long; disc absent; stamens usually 4, the filaments free, ca 0.25 mm, the anthers dehiscing vertically; pollen grains 3-colporate. Pistillate flowers with pedicels 1-3 mm long; calyx-lobes 4, 0.8-1.3 mm long; disc absent; ovary of 3 (rarely 2) carpels, the styles connate at base, distally bifid, 1.8-2.3 mm long. Fruits oblate-spheroidal, usually 3-celled, 5-8.5 mm high, 5.5-10.5 mm broad, obtusely lobed, indehiscent, the outer layer soft and pithy, the inner hard and bony, fertile carpels usually 1 or 2 per fruit, each with 1 seed; seeds flattened, smooth, pale brown, ca 3.4 mm long.

Low forests along lagoons and rivers, usually near sea-level, southern Mexico to northern South America.

The ecology and distribution of this interesting species, which is closely related to the commonly cultivated P. acidus, has been discussed in an earlier publication (Jour. Arnold Arb. 38: 73-75, 1957). The tree is doubtless common along the estuaries of many rivers in Panama, as well as the other Central American countries. Phyllanthus chacoensis Morong of Argentina and Paraguay is even more similar than P. acidus, but differs in having invariably 2-celled fruits and shorter, broader styles. These few American species of subg. Cicca appear to be relicts of a very ancient distribution.


Herb, usually annual, erect or procumbent, up to 5 dm high; monoecious; main stems 1-3 mm thick, subterete with narrow sharp ridges decurrent from nodes; scale-leaves on main axes scarious, 2-3 mm long. Deciduous branchlets mostly 5-10 cm long, 0.5-0.75 mm thick, with 20-35 leaves. Leaves with very short petioles; stipules unequal, the longer 0.8-1.5 mm long, lanceolate; blades
mostly 8-25 mm long, 2-6(-9) mm broad, linear to oblong-obovate, obtuse or mucronulate at the tip, marginally hispidulous beneath. Cymules unisexual, the proximal nodes with solitary female flowers, the distal nodes with cymules of 5-7 male flowers. Staminate flowers with calyx-lobes 6, less than 0.5 mm long; disc-segments 6, crenulate; stamens 3, the filaments completely fused into a column, the anthers dehiscing vertically; pollen grains 4-colporate. Pistillate flowers with pedicels 0.5 mm long or less; calyx-lobes 6, linear to lanceolate, dorsally hispidulous, 0.6-0.9 mm long; disc entire or crenulate; ovary conspicuously papillate, the styles connate, bifid at the tips. Capsules 2.2-2.2 mm in diam, scurfy or nearly smooth, often reddish-blotched; seeds 1.1-1.2 mm long, light brown, with 12-15 sharp tranverse ridges on back and sides and often with 1-3 deep pits on the sides.

Of Old World origin, now widely distributed in tropical regions; a weed in moist habitats.


Annual herb 1-5 dm high, glabrous; monoecious; main stem smooth, terete, ca 1-2.5 mm thick, scale leaves scarious, becoming brownish, 1.5-3 mm long, narrow and acuminate. Deciduous branchlets mostly 5-10 cm long, 0.3-0.5 mm thick, subterete, smooth, with ca 15-30 leaves. Leaves thin; petioles 0.4-0.7 mm long; stipules linear-lanceolate, unequal, the longer of each pair 2-2.7 mm long; blades mostly ovate or elliptic, ca 7-17 mm long, 3-9 mm broad, acute or subacute at the tip, conspicuously oblique at the base, often conspicuously paler beneath. Cymules unisexual, the proximal 2-12 nodes of branchlets barren or with cymules of 3-7 staminate flowers, the distal nodes with solitary pistillate flowers. Staminate flowers with pedicels 1.2-1.8 mm long; calyx-lobes 5 (rarely 6), obovate or obcuneate, mostly 1.2-1.5 mm long; disc-segments 5, more or less papillate; stamens 3, the filaments ca 0.6-1 mm long, free or united to ⅓ their length in a column, the anthers dehiscing obliquely; pollen grains 4-colporate. Pistillate flowers with pedicels usually becoming 2.5-4.5 mm long; calyx-lobes 5, elliptic or obovate, obtuse or rounded at the tip, 1.5-2.7 mm long; disc patelliform, somewhat angled and thickened; ovary smooth, the styles free, ascending, bifid, 0.5-0.6 mm long, the branches capitate. Capsules smooth, stramineous, ca 3 mm in diam; seeds dark brown or fuscous, 1.4-1.8 mm long, verruculose.

One of the most widespread native American species, extending from central Texas south to northern Argentina.

Most of the material from Panama which has been called *P. niruri* proves to be misidentified; the species appears to be comparatively rare, especially since it has not been collected in the Canal Zone. It is easily separated from the more common *P. amarus* and *P. stipulatus* by its verruculose rather than striate seeds, longer stipules, and larger distinctly ribbed female calyx.


Annual herb, glabrous, erect, 1-5 dm high; monoecious; main stem smooth, terete, usually 1.5-2 mm thick; scale-leaves scarious, brownish, 1-2 mm long. Deciduous branchlets 4-12 cm long, ca 0.5 mm thick, subterete (never sharply winged), smooth or proximally roughened, with ca 15-30 leaves. Leaves thin; petioles 0.3-0.5 mm long; stipules lanceolate, 0.8-1.3 mm long; blades elliptic-oblong or somewhat obovate, mostly 5-11 mm long and 3-6 mm broad, rounded to apiculate at the tip, only slightly (if at all) inaequilateral at base, the margins smooth or obscurely roughened. Cymules mostly bisexual, the proximal 1 or 2 axils with stamineate flowers, the other axils each with one stamineate and one pistillate flower. Stamineate flowers with pedicels 0.6-1.3 mm long; calyx-lobes 5 (rarely 6), ovate or elliptic, 0.3-0.6 mm long; disc-segments 5, entire; stamens 3 (rarely 2), the filaments connate into a column 0.2-0.3 mm high, the anthers dehiscing obliquely or horizontally; pollen grains 3-colporate. Pistillate flowers with pedicels becoming 1-2 mm long in fruit; calyx-lobes usually 5, obovate-oblong, acute or apiculate, becoming 0.9-1 mm long; disc flat, deeply 5-lobed, sometimes irregular; ovary smooth, the styles free, ascending, shallowly bifid, less than 0.2 mm long. Capsules smooth, stramineous, 1.9-2.1 mm in diam; seeds sharply trigonous, light brown, 0.9-1 mm long, with 5 or 6 straight parallel ribs on the back.

Probably native to America, but now a circumtropical weed.

Canal Zone: Balboa, Standley 25280 (US), 25662 (US), 29255 (US); Barro Colorado I, Shattuck 308 (F); Colón, Piper 3878 (US); Culebra, Pittier 4773 (US); Fort Randolph, Standley 28595 (US); Fort San Lorenzo, Burch et al. 1032 (GH, MO, UC, US); Fort Sherman, Standley 30937 (US); Frijoles, Standley 31471 (US); Gatum, Standley 27315 pro parte (US); Mt Hope Cemetery, Standley 28853 (US); Margarita Swamp, Maxon & Valentine 7063 (US); Summit, Standley 30086 pro parte (US). Chiriquí: David airport, Lewis et al. 746 (GH, MO). Panama: sabanas N of Panama City, Bro. Paul 529 pro parte (US); San José I, Johnston 1315 (GH, MO, US).

This weedy plant, the most widespread and abundant species of *Phyllanthus*, has until recently been confused with *P. niruri*; its complicated nomenclatural history has been reviewed elsewhere (Jour. Arnold Arb. 37: 6-8, 1956; 38: 313-315, 1957). It is easily distinguished from *P. niruri*, however, by its equilateral leaf bases, bisexual cymules, and ribbed instead of verruculose seeds. It is more easily confused with *P. stipulatus*, but that plant has unisexual cymules and broader, more rounded pistillate calyx-lobes.

*Moeroris stipulata* Raf., Sylva Tellur. 91, 1838.


*Herb*, erect, usually annual, 2-5(-10) dm high; monoecious; main stem 1-2 mm thick or up to 4 mm and becoming spongy when plant grows in water; scale-leaves 0.5-1 mm long, scarious. *Deciduous branchlets* mostly 2-6 cm long, often reddish-tinged, smooth or scabridulous, with ca 15-30 leaves. *Leaves* smooth or minutely scabridulous on 1 or both sides; stipules lanceolate, 0.5-1 mm long; blades ovate or suborbicular, ca 3-10(-13) mm long, 2-4(-6) mm broad, obtuse to subtruncate at the tip, not unequal at the base. *Cymules* unisexual, the proximal axils barren or with cymules of 3-10 staminate flowers, the distal axils with solitary pistillate flowers. *Staminate flowers* with pedicels 0.4-0.7 mm long; calyx-lobes usually 5, obovate to orbicular, 0.5-0.9 mm long; disc-segments 5(-6), entire or crenulate; stamens 3 (rarely 2), the filaments connate into a column 0.25-0.35 mm high, the anthers dehiscing ± horizontally; pollen grains 3-colporate. *Pistillate flowers* with pedicels becoming 1.5-2.5 mm long; calyx-lobes 5, obovate, becoming 1.4-1.8(-2) mm long and 0.8-1.3(-1.5) mm broad, obtuse or rounded; disc 5-angled or lobed, sometimes asymmetric; ovary smooth, the styles free, 0.2-0.3 mm long, bifid, the tips subcapitate. *Capsules* ca 2.4-2.5 mm in diam, obscurely rugulose; seeds sharply trigonous, 1.1-1.3 mm long, light brown, with ca 10-12 delicate longitudinal striae.

Widespread in tropical America, often in wet places and sometimes growing in shallow water.

**BOCAS DEL TORO:** Carleton 271 (US). **CANAL ZONE:** Chagres, Fendler 273 pro parte (MO, US); Fort Kobbe, Johnston 1620 (GH). **CHIRIQUI:** El Boquete, Davidson 525 (US), Killip 3632 (US). **COCLE:** Penonomé, Ehinger 1023 (MO). **PANAMA:** San José I, Johnston 184 (GH), 1004 (GH); Chepo, Hunter & Steyermark s.n. (MO); Juan Díaz, Killip 3066 (US), Standley 26225 (US); Laguna de Portala, Pittier 4640 (US); Las Sabanas, Bro. Heriberto 147 pro parte (US); Matias Hernandez, Standley 28888 (US); Nuevo San Francisco, Standley 30761 (US); Pacora, Allen 997 (MO), Woodson et al. 733 (F, MO); Panama, Standley 27808 (US); sabanas N of Panama City, Bro. Paul 529 pro parte (US).


*Annual herb*; monoecious; main stem slender, erect, 1-3.5 dm high, 0.5-2 mm thick; scale-leaves 0.5-0.9 mm long, scarious. *Deciduous branchlets* mostly 3-7 cm long, smooth or minutely scabridulous, with ca 15-30 leaves. *Leaves* membranous, minutely scabridulous on both sides; petioles 0.3-0.4 mm long; stipules lanceolate, 0.5-0.8 (-1) mm long; blades elliptic to ovate-oblong (± narrowed towards the tip), apically obtuse, 4-8 mm long, 2-3.5 mm broad. *Cymules* unisexual, the staminate flowers several at proximal axils of branchlet, the pistillate flowers solitary and distal. *Staminate flowers* with pedicels 0.3-0.8 mm long; calyx-lobes 5, suborbicular, 0.4-0.6 mm long; disc-segments 5, glandular-crenate; stamens 3, the filaments ca 0.2-0.25 mm long, united below into a column, the
anthers 0.2-0.25 mm broad, dehiscing ± horizontally; pollen grains 3-colporate. **Pistillate flowers** with pedicels becoming 1.5-2 mm long; calyx-lobes 5, oblong to obovate, becoming 1.2-1.6 mm long in fruit, obtuse; disc dissected into 3 linear or lanceolate somewhat unequal segments 0.25-0.5 mm long; ovary smooth, the styles free, spreading, 0.25-0.3 mm long, bifid, the tips scarcely thickened. **Capsules** ca 2 mm in diam, obscurely rugulose; seeds 0.9-1.1 mm long, yellowish-brown, with ca 10 longitudinal striae and many fine cross-bars.

Lesser Antilles, northeastern South America, and Panama; a rather weedy species of moist or wet habitats.

**CANAL ZONE:** Balboa, Standley 29274 (US); Cerro Gordo, Standley 26034 (US); Fort San Lorenzo, Burch et al. 1031a (DAV, GH, MO, US); Gatun, Standley 27315 pro parte (US); betw Gamboa & Cruces, Pittier 3764 (US); summit, Standley 30086 pro parte (US). **PANAMA:** lower cloud forest, 2-3 mi S of Goofy Lake, rd to Cerro Jefe, 2000-2200 ft, Lewis et al. 248 (DAV, GH, MO, US); Las Sabanas, Bro. Heriberto 147 pro parte (US); San José I, Johnston 1004 (GH).

The recent discovery in Panama of this characteristically Lesser Antillean species is surprising, and represents a disjunction of at least 1000 miles. The Canal Zone collections suggest the possibility of a recent introduction, but the locality near Cerro Jefe on the other hand would seem to indicate indigenous status. The species may well have been overlooked simply because it so closely resembles *P. stipulatus*.


*P. conami* Sw., Prodr. 28, 1788 (pro parte, quoad descr.).

**Shrub** or small tree, 2-8 m high, sparsely branching; monoecious; branches of current year producing 3-6 deciduous branchlets; scale-leaves inconspicuous, pale, less than 2 mm long. **Deciduous branchlets** bipinnatifid (except for first of the season); primary axis 2-5 dm long, ca 2-3 mm broad, wing-angled, dorsally rough or hirsutulous, with ca 8-20 ultimate axes, each 5-20 cm long, with mostly 7-20 leaves. **Leaves** membranous to chartaceous; petioles adaxially roughened or hirsutulous, 1.5-3 mm long; stipules triangular, blunt, those on primary axis up to 1.3 mm long (somewhat smaller on ultimate axes), persistent, often reflexed; blades ovate or elliptic, lucid and scabridulous above, smooth beneath (except along veins), ca 2.45 cm long, 1.25 cm broad, abruptly and bluntly cuspidate-acuminate at the tip, usually obtuse at base. **Cymules** bisexual, on ultimate axes, with 5-20 staminate and a single pistillate flower. **Staminate flowers** with pedicels capillary, 3-4.5 mm long; calyx-lobes 6, biseriate, the outer narrowly oblong, ca 0.9-1 mm long, 0.4-0.6 mm broad, the inner round, ca 0.9-1.2 mm long and broad; disc segments 3, reniform, massive; stamens 3, the filaments connate into a short column 0.1-0.3 mm high, the anthers triangular-ovate, apiculate, dehiscing horizontally; pollen grains globose, with 3 short dorate colpi, pilate. **Pistillate flowers** with pedicels 5-12 mm long, slender, often angled, scabridulous at least below; calyx-lobes 6, biseriate, with narrow whitish margins, the outer
elliptic, 1.1-1.4 mm long, 0.5-0.9 mm wide, the inner broadly ovate, 1.5-1.7 mm long, 1.1-1.3 wide; disc cupuliform, massive, 3-lobed; ovary oblate, smooth, deeply sulcate, the styles free, flattened, spreading, 0.4-0.6 mm long, divided 1/4 to 1/2 their length. Capsules 4.5-5 mm in diam, conspicuously veiny, the columella massive, ca 2 mm long; seeds plano-convex, ca 2.5-2.8 mm long, reddish-brown, smooth with epidermis foveolate, sometimes with a rudimentary caruncle.

The most widespread woody American species of *Phyllanthus*, ranging from Mexico (Baja California, Tamaulipas) south through the West Indies and South America to northern Argentina (Jujuy, Salta).

**BOCAS DEL TORO:** Water Valley, von Wedel 870 (GH, MO), 996 (GH, MO), 1623 (GH, MO), 1789 (GH, MO), 2744 (GH, MO); Shepherd I, McDaniel 5170 (MO). **CANAL ZONE:** Balboa, Standley 25597 (US), 26488 (US); Barro Colorado I, Aviles 69 (F), 940 (F), Bailey & Bailey 343 (F, GH), 570 (F, GH), Bangham 382 (A, F), Ebinger 640 (MO), Salvoza 877 (A), Woodworth & Vestal 671 (A, F, MO); Cooch, Solo, Dwyer & Duke 7916 (MO); Culebra, Pittier 2216 (US); Curudu, Tyson 1039 (MO), 1313 (MO); Darien, Standley 31647 (US); France Field to Catival, Standley 30405 (US); Old Fort Lorenzo, Pippard 5921 (US); Fort Sherman Reservation, Mason & Valentine 6989 (US), 7002 (US); Gamboa, Standley 28359 (US); Gatun, Standley 27260 (US), Hayes 99 (NY); nr Miraflores Lake, Chiva-Chiva trail, Tyson 1339 (MO); Miraflores to Pedro Miguel, Pittier 3970 (F, US); Road C-21, Duke 5786 (MO); Summit, Woodson et al. 765 (A, F, MO), Standley 29587 (US). **CHIRIQUI:** Progreso, Cooper & Slater 223 (F, GH); Rio San Cristobal, 2 mi W of David, Tyson 916 (MO). **COCLE:** wet llanos betw Aguadulce and Antón, Woodson et al. 1212 (A, F, MO); betw Las Margaritas and El Valle, Woodson et al. 1734 (A, F, MO); El Valle, Dwyer 1840 (MO). **COLON:** Porto Bello, Ebinger 117 (MO). **PANAMA:** Chilibre, Dwyer 1036 (MO); camino de Las Sabanas, Bro. Heriberto 204 (GH, US); savanna-like areas nr top of Cerro Campana, Duke 5978 (MO).

11. **Phyllanthus anisolobus** Muell.-Arg. in DC., Prodr. 15(2): 382, 1866.—Fig. 3.


Shrub or tree, 3-8 m high, glabrous; monoecious; branches pale brown, smooth, scale-leaves inconspicuous. **Deciduous branchlets** mostly bipinnatifid, the primary axis 2-3.5 dm long, obtusely or sharply angled, green, smooth, usually with 5-10 lateral axes, each 8-30 cm long with 10-20 leaves. Leaves thin; petioles smooth, 2-3 mm long; stipules triangular, 0.6-0.8 mm long, subpersistent; blades broadly elliptic, evenly narrowed to a blunt or subacute tip, obtuse at the base, ca 2-5 cm long, 1.3-2.5 cm broad, smooth on both sides. **Cymules** bisexual, on the lateral branchlet axes, **♂** solitary, **♂** several. **Staminate flowers** with pedicels 3-7 mm long; calyx-lobes 6, 1.7-2.2 mm long, biseriate, the outer oblong, ca 0.7-0.8 mm broad, the inner elliptic, 1.2-1.8 mm broad (rarely lobes 5 and then subequal); disc of 6 massive rounded segments united by pairs into reniform glands ca 0.8 mm wide; stamens 3, the filaments connate into a column 0.8-1.2 mm high, the anthers deflexed atop the column, very deeply emarginate (anther-sacs stipitate), ca 0.4-0.5 mm in diam; pollen grains 3-collporate, reticulate. **Pistillate flowers** with smooth pedicels becoming 6-13 mm long; calyx-lobes 6, biseriate as in the **♂** flowers; disc of 6 segments united by pairs as in **♂**, these 3 reniform glands usually confluent to produce a 3-lobed cup; ovary smooth, the styles 0.7-1.1 mm long, erect or
Fig. 3. *Phylanthus anisolobus* Muell.-Arg.: A, habit (ca ×1/2); B, male flower (ca ×8); C, male flower with sepals removed (ca ×16); D, female flower (ca ×8); E, female flower with sepals removed (ca ×16). After Lewis et al. 1802 (MO).
ascending, bifid, the branches slender. *Capsules* ca 3 mm long; seeds mostly 2-2.4 mm long, pale brown, smooth with slightly raised reddish swellings, sometimes with a rudimentary caruncle.

Rainforest areas, often along streams, at lower altitudes (below 1000 m), Costa Rica to Colombia and Peru.

**cocciz**: along streams, vic of Finca Tomas Arias, El Valle de Antón, 600 m, Allen 3626 (F, MO, NY; hills N of El Valle de Antón, Lewis et al. 1802 (MO).

The recent collection of good flowering material of the plant at El Valle shows clearly that the species represented is *P. anisolobus*, which was described from a Peruvian specimen of Pavon. Furthermore, its agreement in vegetative characters with the Costa Rican *P. pittieri* indicates that that species is synonymous with *P. anisolobus*. Pax's description of *P. pittieri* as having 5 calyx-lobes appears to be misleading, as all Costa Rican specimens which otherwise agree with his description have 6-merous calyces; apparently he happened to dissect one of the rare staminate flowers with 5 calyx-lobes. In the Costa Rican, Panamanian and South American plants of this affinity there is a strong resemblance in the flowers which marks *P. anisolobus* as distinct: the deeply emarginate anthers, with each anther-sac distinctly stipitate, are especially characteristic and set the species apart from all other taxa in subg. *Conami*.

A collection from Darien (La Palma, Pittier 6600, US) may also represent this species, but the specimen lacks pistillate flowers and is not positively identifiable. It differs mainly in having simply pinnatiform branchlets with only 5-10 leaves; however, most species in subg. *Conami* may produce a few pinnatiform branchlets before the characteristic bipinnatiform ones. Additional collections from La Palma are needed to resolve the status of the population there.

4. *HYERONIMA*


*Trees* or shrubs; dioecious; lepidote indumentum on all parts (except in *H. ferruginea*). *Leaves* alternate, entire; petiolate; stipules small or large, deciduous. *Inflorescences* axillary, racemose (sometimes almost spicate), usually aggregated into panicles; bracts inconspicuous; flowers with calyx a shallowly lobed cup; apetalous; disc well developed. *Staminate flowers* on very short pedicels; disc a rather massive cup, subentire or variously lobed; stamens 3-6, inserted within the disc, the filaments free, projecting beyond the calyx at anthesis, the anthers with an enlarged connective, introrse in the bud, the two anther-sacs pendant and divergent at anthesis, dehiscing longitudinally; pollen grains prolate, 3-colporate, psilate. *Pistillate flowers* shortly pedicellate; disc cupuliform, subentire, more tenuous than in the Σ; ovary ovoid, lepidote, the styles very short or not developed,
the bifid punctiform stigmata sessile, the carpels 2 with 2 ovules per locule. *Fruits* drupaceous, thin-walled, 1-celled, usually 1-seeded; seeds not carunculate, endosperm present, the cotyledons broader than the radicle, plane.

A stenomorphic genus restricted to the tropical portions of the New World. About 30 species have been recognized, but all are closely related and the genus badly needs a careful taxonomic revision. *Hyeronima* is the neotropical counterpart of the gerontogean genus *Antidesma*, which has very similar floral structure. Although *Hyeronima* seems sufficiently distinct by virtue of its lepidote indumentum and unilocular fruit, the flowers of the two genera are so similar that Baillon's combining them is understandable.

The Central American species of *Hyeronima* are poorly understood. Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 610, 1937) recognizes 4 species, all present in Costa Rica. However, all the Panamanian collections available so far appear to belong to the single following species.

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Fig. 4 *Hyeronima laxiflora* (Tul.) Muell.-Arg.: A, habit (ca ×1/2); B, stalk showing large stipules (ca ×1/2). A after Carpenter 57 (F); B after Johnston 1798 (GH).
A tall tree up to 40 m high and over 1 m in diam with buttresses up to 1 m high or more; twigs subterete, angled, rather densely clothed, with orbicular peltate serrate-marginated scales 0.1-0.2 mm in diam. Leaves on flowering twigs smooth or slightly roughened above, sparsely lepidote on both sides (densely so when young); petioles (2-)3-9 cm long; stipules stalked, deciduous, lanceolate, 5-15 mm long, 1-4 mm broad (stipules inflated and leaves much larger on sucker shoots); blades generally broadly elliptic, ca 10-30 cm long, 5-19 cm broad, rather abruptly acuminate, obtuse to rounded at the base, the major veins ca 8-11 on a side, straight, at nearly a 45° angle, impressed above, salient beneath, the veinlets evident but often not conspicuous beneath. Panicles densely lepidote, 8 ca 9-17 cm long, 9 4-10 cm long; bracts on main axis resembling stipules; lateral axes mostly 4-6, unbranched, with minute bracts (less than 1 mm long). Staminate flowers with rigid pedicel ca ½ mm long; calyx cupuliform, shallowly and obscurely 3- or 4-dentate, densely lepidote; disc massive, ca as high as the calyx, subentire, fringed at the top with scaly hairs; stamens usually 4, the filaments elongating at anthesis to 0.6-0.8 mm or more, the anthers 0.4-0.5 mm long including the enlarged glandular connective; pistillode cylindric, ca 0.7-0.8 mm high, distally bifid, hirsutulous and with scaly trichomes. Pistillate flowers with stout pedicel, becoming 1.3-2 mm long in fruit; calyx similar to the 8, becoming ca 0.5-0.8 mm high; disc shallower and much thinner than in the 8, subentire, minutely pubescent along the rim; ovary ovoid, nearly 1 mm high, covered with peltate scales, the styles obsolete, the stigmas very small, punctiform, bifid. Drupe whitish, with an ellipsoidal bullate endocarp (2.5-)2.7-3.1 mm long and 2.4-2.6 mm in diam; seeds smooth, brownish, slightly over 2 mm long.

Rainforest at low altitudes, Panama to the Guianas.


The description is based on the Panamanian specimens only, and it is not certain that the plants really belong in the same species as Hyeronima laxiflora from the Guianas. Standley (Contr. U. S. Nat. Herb. 27: 233, 1928) reported the plants from the Canal Zone as H. alchorneoides Fr. Allemão; that species is very similar to the Panamanian plants in its small fruit and other floral characters, but differs in having larger flowers (calyx 1 mm high or more) with a more massive pistillode (ca 0.4-0.5 mm across the truncate end vs. ca 0.2 mm across the ± notched end of the more slender pistillode of H. laxiflora). The species of Hyeronima are all so closely related, however, that it is difficult to draw any clear lines. From the geographic distribution alone, one would expect the Panamanian
plants to belong to *H. oblonga* (Tul.) Muell.-Arg. var. *benthamii* (Tul.) Muell.-Arg., which is cited from Mexico and Costa Rica by Pax and Hoffmann [Pflanzenreich 81 (IV, 147, XV): 38, 1922]. However, that plant (as represented in Costa Rica) differs in its larger calyx, glabrous ovary and divided male disc.

Part of the taxonomic difficulty in *Hyeronima* may be due to a considerable amount of vegetative plasticity. Some specimens (e.g. Johnston 1798, Standley 303/5) have very large leaves up to 4 dm long or more and conspicuous cucullate stipules much broader (ca 1 cm or more) than usual. Such specimens appear to have been taken from saplings or sprout-shoots, and the leaves and stipules on reproductive twigs are never of such overgrown proportions. While it is not impossible that the Panamanian collections at hand may represent more than one species of *Hyeronima*, this is not proven, and it seems more probable that we are dealing with one variable taxon.

5. **JATROPHA**


*Curcas* Adans., Fam. Pl. 2: 356, 1763.

**Trees**, shrubs, or perennial herbs; monoecious or dioecious; stems with pale to distinctly colored latex. **Leaves** alternate, simple to lobed or divided, entire to conspicuously serrate; stipules often glandular or spinose. **Inflorescences** axillary or terminal, usually distinctly pedunculate, dichasial, ♀ flowers at proximal dichotomies and fewer than the ♂. **Staminate flowers** with 5 sepals, ± imbricate; petals 5, imbricate, free or coherent to connate, greenish or white to red; disc entire or dissected into segments; stamens mostly 8-12, the filaments connate, the anthers usually in 2(-6) whorls, dehiscing longitudinally; pollen grains globose, inaperturate, exine with massive hexagonal processes; pistillode reduced or absent. **Pistillate flowers** with 5 sepals, imbricate; petals as in ♀; disc annular or dissected; ovary of usually 3 carpels (rarely 2, 4, or 5), smooth, the ovules 1 per locule, the styles connate below or free, entire or bifid. **Fruits** capsular (but sometimes tardily dehiscent); seeds carunculate, with thin crustaceous testa, endosperm present, copious, the cotyledons broad, palmatinerved, the radicle short.

A pantropical genus of perhaps 150 species, with about 70-80 represented in America; only one species (*J. gossypiifolia*) is native in Panama. In addition to the three species enumerated below, various others are doubtlessly cultivated in gardens and may possibly be found escaped. *Jatropha podagrica* Hooker was described from Panama on the basis of a Seemann collection, but the original description makes it clear that this was a cultivated specimen; no indigenous Panamanian plants of the species have ever been discovered. From the Panamanian species described below, *J. podagrica* may easily be distinguished by its long-petioled peltate leaves, which are glaucous underneath.

Useful references:


a. Stipules glandular-dissected; leaf-blades deeply 3-5-lobed, with marginal glandular teeth; petals dark purplish-red, glabrous; stamens mostly 8 ....1. *J. gossypiifolia*

aa. Stipules entire or obscure, not glandular; leaf-blades entire to lobed half way to midrib, without marginal glandular teeth; petals paler, hirsutulous; stamens mostly 10.

b. Petals small (less than 1 cm long), greenish-yellow, hirsutulous over most of inner face; fruits semi-drupeaceous, tardily dehiscent; leaf-blades mostly deeply or broadly cordate at base, coarsely lobed, with 5-7 major veins at base ...............................2. *J. curcas*

bb. Petals larger (more than 1 cm long), bright red, hirsutulous only at base; fruits not fleshy, quickly dehiscent; leaf-blades rounded to narrowly cordate at base, entire or with small lateral or basal lobes, with 3-5 major veins at base ..........................................................3. *J. integerrima*

1. *Jatropha gossypiifolia* L., Sp. Pl. 1006, 1753.—Fig. 5.

*J. staphysagriifolia* Miller, Gard. Dict. ed. 8, 1768.

Subshrub or robust herb 1-2 m high, stems softly woody; branches glabrous. Leaves with petioles cylindric, 3-6 cm long, with branched glandular setae similar to those of the stipules; stipules parted to base into 2-4 slender branched glanduliferous setae ca 3-5 mm long; blades 3-5-lobed halfway to the base or more, 5-8 cm long, mostly 7-15 cm broad, palmatinerved, ± cordate at base, the lobes oblong or elliptic, acute or short-acuminate at the tip, closely glandular-denticulate along margins, pinnately veined. Dichasia terminal on branches, with lateral axes alternate; peduncle minutely puberulent, ca 2-4 cm long; bracts lanceolate, acuminate, glandular-ciliate, the lower ones 8-12 mm long. Staminate flowers with pedicels less than 2 mm long; calyx-lobes ovate-lanceolate, acuminate, with stalked capitata glands on margins, distinctly imbricate, 2-4(-5) mm long; petals obovate, dark reddish or purplish-red, ca 3-5 mm long; stamens 8, the filaments 2-3 mm long, connate or strongly coherent in the lower 1/3, the anthers ovate, 0.5-0.7 mm long; pistillode absent. Pistillate flowers with pedicels less than 5 mm long, puberulent; calyx-lobes similar to staminate but puberulent and becoming larger (5-7 mm long); ovary pubescent, the styles slender, ca 1.5 mm long, dilated into emarginate stigmata. Capsules subglobose, 3-sulcate, ca 1 cm in diam, glabrescent, slightly verruculose; seeds dark grayish, with small black specks, mottled grayish-brown, or dark chestnut brown, slightly compressed, 5.5-7.3 mm long, the caruncle massive, deeply laciniate, 1.2-1.9 mm deep, 2.1-3.3 mm broad.

Widespread in disturbed areas in tropical America; also introduced into the Old World.

**BOCAS DEL TORO:** vic of Chiriquí Lagoon, von Wedel 2919 (MO); Isla Colón, von Wedel 485 (MO). **CANAL ZONE:** Las Cruces trail, Hunter & Allen 666 (MO). **CHIRIQUI:** El Boquete, Pittier 3124 (US). **HERRERA:** Pesé Allen 800 (MO); road from Chítré to Divisa, Burch et al. 1366 (MO). **LOS SANTOS:** Playa de La Concepción, Burch et al. 1260 (MO). **PANAMA:** Isla Taboga, Woodson et al. 1529 (F, MO); nr beach at Nueva Gorgona, Duke 4485 (MO).
Fig. 5. *Jatropha gossypiifolia* L.: A, habit (×1/2); B, male flower (ca ×6); C, stamens (ca ×7); D, anther (ca ×10); E, female flower (ca ×10); F, seed (ca ×3). A after Allen 800 (MO); B-D after Burch et al. 1366 (MO); E after Klug 3374 (MO), Peru; F after Duke 4495 (MO).

Shrub or small tree ca (1-) 2-5 m high; branches and mature foliage glabrous. Leaves with petioles (3-) 9-15 cm long; stipules nearly obsolete, not evident on mature leaves; blades ovate, unlobed or coarsely (3-) 5-7-lobed (lobes extending less than halfway to midrib), palmatinerved with mostly 7 nerves and deeply or broadly cordate at base, mostly 10-25 cm long, 9-15 cm broad, sparsely puberulent when young but soon glabrescent. Dichasia terminal on branches, bisexual or often unisexual; axes tomentulose, glabrescent, becoming ca 10-25 cm long; peduncles mostly 4-10 cm long; lower bracts narrowly lanceolate, 2-15 mm long, entire (not glandular). Stamine flowers with puberulent pedicels, ca 1-5 mm long, articulated below the flowers; calyx-lobes 5, elliptic, blunt, entire (not glandular), scarcely imbricate, ca 2.8-3.5 mm long; petals ovate, greenish or yellowish-white, adaxially hirsute, ca 5-6 mm long; disc-segments 5, ellipsoid, erect, massive, ca 1 mm high; stamens (8-) 10, the filaments 2.2-3.7 mm long, connate below the middle, the anthers elliptic, 1-1.6 mm long; pistillode absent. Pistillate flowers with pedicels 5-9 mm long, up to 10-13 mm long in fruit, glabrous; calyx-lobes 5, oblong to lanceolate, foliaceous, obtuse or subacute at tip, entire, becoming ca 7-9 mm long; petals similar to the staminate; ovary glabrous, the styles slender, ca 1.5 mm long, connate in lower half, dilated into massive stigmata. Capsules ellipsoid, ca 3 cm long and 2 cm broad, more or less fleshy, at length drying and dehiscent; seeds blackish, encrustate-striate, 15-22 mm long, distinctly beaked beyond the hilum, the caruncle appressed to the beak, not massive, deeply lobed, ca 2 mm long and 3.5 mm broad.

Native probably to Mexico and Guatemala; widely distributed throughout the tropics as a medicinal or hedge plant, and often escaping.


J. hastata Jacquin, loc. cit. t. 173 fig. 54.

Shrub ca 2-4 m high; branches and foliage glabrous or sparsely hirsutulous. Leaves entire or often with a pair of small acute lobes below the middle; petioles mostly 3-7 cm long; stipules nearly obsolete, not evident on mature leaves; blades ovate to elliptic, abruptly short-acuminate, palmatinerved with 5(-7) main veins at the rounded or subcordate base, 5-15 cm long, 2.5-8(-13) cm broad. Dichasia terminal or pseudo-axillary, often bisexual; peduncles ca 5-10 cm long; lower bracts lanceolate, mostly 2-5 mm long, entire or obscurely glandular-dentate. Stamine flowers with pedicels mostly 5-8 mm long, articulate near the top; calyx ca 2.5-3.5 mm long, lobed about halfway, the lobes blunt, entire, not imbricate; petals elliptic-obovate, bright red, adaxially hirsute at base (glabrous
over most of inner face), 15-22 mm long; disc-segments 5, rounded, reddish, ca 0.5-0.7 mm wide; stamens 10, the filaments ca 5-7 mm long, connate over halfway into a column, the anthers linear to oblong-lanceolate, mostly 2.5-3 mm long; pistillode absent. *Pistillate flowers* with pedicels becoming 5-9 mm long, glabrescent; perianth similar to the ♀; ovary glabrous, the styles ca 2.5 mm long, slender, bifid, the stigmata linear. *Capsules* subglobose-cylindric (truncate), trisulcate, ca 12-13 mm long and broad; seeds fuscous, mottled with dark specks, slightly compressed, 9.6-10 mm long, 5.1-5.8 mm broad, the caruncle bipartite, flabellate-laciniate, ca 2 mm long, 3 mm broad.

A polymorphic species native to Cuba, now extensively cultivated in gardens in the Caribbean area. According to at least one herbarium record (*Duke 8519*), the plant has become established in the wild, and it may be expected as a common escape.


**Shrubs** or trees; monoecious; latex scanty. **Leaves** alternate, entire; petiolate; extipulate; pinnately veined. **Inflorescence** a terminal cluster (reduced cyme) with 1 or 2 pistillate and several stamine flowers; flowers with calyx perulate in bud, rupturing into 2 or 3 valvate segments; petals 6-13, narrow, sericeous, exceeding the calyx. **Stamine flowers** with persistent calyx; disc dissected into segments; stamens numerous (ca 30 to over 100), the filaments free; pollen grains globose, inaperturate, exine with massive hexagonal processes; pistillode absent. **Pistillate flowers** with stout pedicels; calyx deciduous; disc deeply lobed; ovary of 3 carpels, sericeous, the ovules 1 per locule, the styles short, thick, reflexed, bifid. **Fruits** capsular; seeds ecarunculate, the endosperm copious.

This small American genus includes only 2 species, the following and *G. parviflora* Lundell of eastern Mexico.

Useful reference:


1. **Garcia nutans** Vahl in Rohr, Skriv. Naturh. Selsk. Kjøbenhavn. 2: 217, t. 9, 1792.—Fig. 6.

**Shrub** or tree to 15 m high; twigs hispidulous to tomentulose. **Leaves** chartaceous to subcoriaceous; petioles 1-5 cm long; stipules absent; blades oblong to elliptic, abruptly acuminate to obtuse at the tip, obtuse to rounded at the base, mostly 8-19 cm long, 2.5-7 cm broad, sparsely to densely pilose beneath, the margins entire. **Stamine flowers** with hispidulous to densely pilose pedicels ca 1-3.5 cm long; calyx 6-13.5 cm long, tomentulose without; petals 6-13, linear to oblong-elliptic, pinkish to dark red, more or less hirsute, 10-17 mm long; disc-segments numerous, up to 1.5
Fig. 6. *Garcia nutans* Rohr: A, habit (ca × \( \frac{1}{4} \)); B, male flower (ca ×4); C, anther (ca ×12); D, seed (ca ×1). A after Matuda 3568 (MO), Mexico; B-D after Stern et al. 1872 (MO).
mm high, scattered over the pilose receptacle; stamens ca 60-150, the filaments mostly glabrous, ca 2.5-6 mm long, the anthers apiculate, 0.7-1 mm long. **Pistillate flowers** with tomentulose pedicels 1-3 cm long; perianth similar to the ♂; disc lobed, ca 2 mm high; ovary densely sericeous, the styles thick, 1.5-2 mm long, the stigmas fleshy, reddish to nearly black. **Capsules** 3-lobed, 3-seeded, 2-2.5 cm high, 3-4 cm in diam, sericeous; seeds globose, to 17 mm in diam.

According to Lundell, the species is native to eastern Mexico (San Luis Potosí to Chiapas), and other records represent escaped or cultivated plants. However, McVaugh (Brittonia 13: 187, 1961) has reported a wild population from Jalisco, and the Panamanian collection cited below would also appear to represent a native plant. The species may prove to be indigenous over a wide area from southern Mexico to Colombia.

**Manihot** Miller, Gard. Diet. ed. 4, 1754.

*Trees, shrubs, or herbs, with milky latex; monoecious; roots often tuberous. Leaves alternate, long-petiolate, stipulate; blades mostly palmately lobed or divided, without distinct foliar glands. Inflorescences terminal (sometimes pseudo-axillary) panicles, the pistillate several on basal branches, the staminate ± racemose along the central axis; flowers with a 5-merous uniseriate perianth (petaloid calyx), petals absent. **Staminate flowers** with distinctly gamosepalous calyx, lobes imbricate in bud; disc central, intrastaminal, entire or 5-lobed, lobes ± bifid; stamens 10, biseriate, the outer opposite the calyx-lobes, the filaments free, the anthers introrse, dehiscing longitudinally; pollen grains globose, periporate, exine clavate; pistilode rudimentary or absent. **Pistillate flowers** long-pedicellate; calyx more deeply lobed than in staminate flowers; disc pulviniform, staminodia sometimes present; ovary of 3 carpels, smooth to ribbed or winged, the ovules 1 per locule, the styles connate below, the stigmas dilated to lacerate. Fruits capsular; columella often persistent; seeds carunculate, with thin crustaceous testa, endosperm copious, the embryo with broad palmate veined cotyledons.

Over 150 species have been described in this strictly American genus, most of them from Brazil. The species of *Manihot* are notoriously difficult to discriminate, and the total number may be considerably reduced when the genus is monographically revised. In addition to the two species enumerated below, at least one other, *M. glaziovii* Muell.-Arg. (the Ceará rubber tree of Brazil), may be found in cultivation. It is readily distinguished by its arboreal habit, peltate leaves, and larger fruits (2 cm in diam or more).

Useful reference:

1. Leaves mostly with 7-9 lobes; ♂ calyces 12-14 mm long, glabrous within;
   ♂ disc ± entire; anthers glabrous; ovary not sharply ribbed or winged; seeds
   7-9 mm broad

   1. *M. guanensis*
aa. Leaves mostly with 3-5 lobes; ő calyces 3-4.5 mm long, pubescent within; ő disc 10-lobed; anthers apically puberulent; ovary (and fruit) sharply ribbed or winged; seeds 4-6.5 mm broad

1. Manihot gualanensis Blake, Contr. U. S. Nat. Herb. 24: 13, 1922.—Fig. 7.

Shrub 1-4 m high, glabrous. Leaves with petioles ca 8-25 cm long; stipules linear-lanceolate, attenuate-acuminate, ± split into segments, ca 9-10 mm or more, soon deciduous; blades cut nearly to base with (5-)7-9 lobes, the lobes oblongate, abruptly short-acuminate, glaucous beneath, the middle lobe ca 10-15 cm long and 3-4 cm broad, the lateral lobes smaller. Panicles ca 2 dm long, with a few basal pistillate flowers and numerous staminate flowers above; flowers mostly on reflexed pedicels. Staminate flowers with pedicels 7-10 mm long; calyx broadly campanulate, somewhat inflated, yellowish- or greenish-white, ca 12-14 mm long, glabrous, the calyx-lobes 5-8 mm long, deltoid-oblong, obtuse-apiculate; disc massive, convex, ca 4 mm wide; stamens 9 or 10, the filaments to ca 7.5 mm long, glabrous, the anthers oblong or linear, 2.5-3 mm long, glabrous; pistillode absent. Pistillate flowers with pedicels becoming 5-15 mm long in fruit; ovary glabrous, not winged. Capsules ca 1.5 cm long, valves rugose; seeds plumply lenticular (somewhat more convex abaxially), grayish to pale brownish flecked with dark brown, 9.9-9.7 mm long, 7.5-9 mm broad, the caruncle deltoid, not very massive, subentire, 1.5-2 mm long, 3.6 mm broad.

Guatemala south to Panama.

Canal Zone: Upper Chilibre R, ½-1 mi below Chilibre, Seibert 1506 (MO); Farfan Beach area, Tyson 1837 (MO), 4108 (MO). Darien: vic of Campamento Buena Vista, Rio Chucunaque above confluence with Rio Tuquesa, Stern et al. 864 (DAV, MO); vic of Yaviza, along Rio Chucunaque, edge of woods, Stern et al. 101 (DAV, MO).

The identification of these Panamanian specimens as M. gualanensis Blake is accepted on the advice of the expert in the group, Dr. David J. Rogers, who kindly determined one of the Tyson specimens.

The collections from Darien are vegetative, and their identification as M. gualanensis is uncertain; additional collections of wild cassava plants in Panama are much needed in order to establish whether more than one species is present. Hemsley (Biol. Centr.-Amer. Bot. 3: 121, 1883) cited M. carthagoides (Jacquin) Muell.-Arg. from Panama on the basis of a specimen from Paraíso, Canal Zone (Hayes 717). Without examining the specimen, it is impossible to determine whether the collection is really that species rather than M. gualanensis.


Herb or shrub, sometimes arborescent, ca 1-3 m high, glabrous. Leaves with petioles 5-17 cm long; stipules lanceolate, acuminate, 7-8 mm long, deciduous; blades mostly deeply 3-5-lobed (less commonly 7-lobed, or sometimes undivided);
Fig. 7. Manihot guianensis Blake: A, habit (×1); B, inflorescences (ca ×1½); C, flower (ca ×2); D, stamen (ca ×10); E, seed (ca ×2). A-D after Tyson 4108 (MO); E after Tyson 1837 (MO).
lobes mostly elliptic-lanceolate, acuminate, glaucous beneath, the middle lobe ca 9-17 cm long, (1-)2-5 cm broad, the lateral lobes mostly smaller. Panicles 0.5-1 dm long at anthesis, lengthening in fruit; flowers on spreading or somewhat reflexed pedicels. 

Staminate flowers with pedicels 4-6 mm long; calyx campanulate, yellowish-green, ca 3-4.5 mm long, glabrous outside; calyx-lobes ca 2-2.5 mm long, deltoid, densely puberulent within; disc 10-lobed (i.e. of 5 concrescent bilobed segments), ca 2 mm wide; stamens 10, the filaments unequal, the longer not over 2 mm long, the anthers linear-oblong, 1.8-2 mm long, those on shorter filaments with apical tufts of hairs; pistillode absent. 

Pistillate flowers with pedicels 7-12 mm long, becoming ca 1.5-2 cm in fruit; calyx-lobes 5, oblong-lanceolate, acute, ca 7.5-10 mm long; disc massive, ca 3-3.5 mm wide; ovary with 6 sharp ribs or wings, the styles ca 1.8-2 mm long, dilated and divided into several capitate tips. Capsules ca 1.5 cm long, 1.3 cm in diam, rugose and 6-winged; seeds compressed, bluntly beaked, grayish or pale brownish, dark-flecked, 7.1-9.3 mm long, 4.1-5.1 mm broad, the caruncle broadly deltoid, entire, 1.3-1.7 mm long, 2.8-3.2 mm broad.

Apparently native to South America; widely cultivated in the tropics, including Panama, where the plant at least occasionally escapes.

BOCAS DEL TORO: Chiriquicito, Seibert 1549 (MO). CANAL ZONE: Balboa, Standley 25509 (US), 25559 (US), 25563 (US); Balboa, Sosa Hill, Standley 25252 (US); Barro Colorado I, Shattuck 161 (GH, MO); Cerro Gordo, Pittier 2302 (US); Fort Randolph, swampy woods, Standley 28637 (US); Rio Pedro Miquel, Standley 29930 (US). PANAMA: Taboga I, Standley 27061 (US).

8. Cnidoscolus


Tree, shrubs, or herbs; monoecious; stems and leaves containing milky latex and armed with stinging hairs. Leaves alternate; petioles long, glandular at junction with blade; stipules usually present; palmately (rarely pinnately) veined, mostly palmately lobed, sometimes deeply parted and nearly compound. Inflorescences terminal (sometimes pseudo-axillary) dichasia, the pistillate flowers at the lower (proximal) nodes, the staminate at upper nodes; flowers with more or less petaloid calyx, usually white; apetalous. Staminate flowers with calyx gamosepalous, lobes imbricate in bud; disc annular; stamens 8-10(-25), the outer free and the inner connate (or all connate); pollen grains globose, periporate, clavate; filiform staminodes (pistillodes?) sometimes present atop staminal column. Pistillate flowers with calyx choisepalous, the sepals deciduous (or gamosepalous in some species); disc annular, sometimes with staminodes; ovary of 3 (rarely 5) carpels, the ovules 1 per locule, the styles ± free, several times bifid or laciniate (rarely once bifid), sometimes apically dilated. Fruits capsular (rarely drupaceous); seeds carunculate, with copious endosperm, the embryo straight, the cotyledons broad and longer than radicle.

An American genus of about 50 species, the majority in Mexico and Brazil. Although earlier confounded with Jatropha, Cnidoscolus is much closer to Manihot, which it resembles in its apetalous flowers and periporate pollen grains. Cnidos-
colus is unique, however, in its armament of painfully stinging hairs. The single native species, *C. urens*, belongs to an herbaceous complex in sect. *Jussieuia* (Houst.) Pax & Hoffmann.

**Useful reference:**


a. Herbaceous or only slightly woody, 0.5-2 m high; stems and leaves heavily armed with stinging hairs; leaves 3-5-lobed, lobes finely denticulate; petiolar gland of many small digitiform processes; pistillate flowers only 3-6 per inflorescence, sepals ca 3 mm long, styles incrassate

1. *Cnidoscolus urens* (L.) Arthur, Torreya 21: 11, 1921.—Fig. 8.

*Jatropha urens* L., Sp. Pl. 1007, 1753.

*I. adenophila* Pax & Hoffm., Pflanzenreich 63 (IV, 147, VII): 400, 1919.


Herb or softly woody subshrub 0.5-2 m high; stems densely armed with rigid stinging hairs 2-6 mm long. Leaves chartaceous; petioles mostly 3-12(-15) cm long, pubescent, sparsely to densely armed; junction of petiole and blade with a dense cluster (1.5-3 mm wide) of small digitiform glands; stipules split into a central subulate greenish part 2-5 mm long and several small lateral glands or gland-tipped setae; blades ovate or suborbicular in outline, 3-5-lobed, ± cordate at base, ca (5)-7-15 cm long, 8-18 cm broad, 5-7-palmatinerved, pubescent (often more densely so beneath), with stinging hairs along veins, the lobes oblong to oblanceolate, obscurely to sharply denticate, abruptly acute to acuminate. *Dichasia* terminal (or pseudoaxillary due to sympodial growth); peduncles sparsely to densely armed, 3.5-12 cm long; pistillate flowers ca 3-6 per inflorescence, at proximal axils; staminate flowers ca 10-25 per inflorescence, clustered at tips of second-order branches. *Staminatae flowers* sub sessile; disc pubescent and usually armate, sometimes
Fig. 8. *Cnidoscolus urens* (L.) Arthur: A, habit (×1/4); B, male flower, calyx split to show stamens (×21/4); C, seed (×2). A, C after *Burch et al.* 1337 (MO); B after *Burch et al.* 1157 (MO).

glabrous, the styles nearly free, ca 1.2-1.3 mm long, incrassate, twice bifid. Capsules usually armed with stinging hairs, ± rugose, ca 10-12 mm long; seeds oblong-ovate, somewhat compressed, 6.5-9.7 mm long, 3.5-5.1 mm broad, pale to dark brownish or grayish, ± flecked, minutely rugulose, distinctly beaked, the caruncle deltoid, 1.2-1.5 mm high, 2-3 mm broad.

Widely distributed from eastern Mexico south to Argentina, Paraguay, and Brazil.

**Canal Zone:** Balboa, *Standley* 25485 (US); Curundu, *McDaniel* 5180 (MO), *Tyson* 1045 (MO); Farfan Beach, *Dwyer* 3065 (MO), *Tyson* 1803 (MO); Gamboa, *Pittier* 3712 (US); Matachin, *Kuntze* 1921 (NY, US); vic of Miraflores Locks, *King* 5321 (TEX), *Stern*
et al. 81 (DAV, MO). COCLE: banks of Rio Grande, Burch et al. 1157 (MO); wet llanos betw Aguadulce and Antoní, Woodson et al. 1226a (A, MO, NY). DARIEN: vic of El Real, Rio Tuira, Stern et al. 454 (DAV, MO). HERRERA: Chitre to Divisa, Burch et al. 1357 (MO). LOS SANTOS: Monagré beach, ca 5 mi SE of Los Santos, Lewis et al. 1673 (DAV, GH, MO, US). PANAMA: Chepo, Dodge 10728 (F, MO), Duke 4061 (MO), Pittier 4740 (US, type coll. of C. adenophilus); Las Margaritas to Rio Mamoni, Duke 5867 (MO); nr Jenine, Rio Canita, Duke 3821 (MO); 13 mi SE of La Chorrera, King 5299 (TEX); betw Las Sabanas & Matias Hernández, Standley 31815 (US); Panama, Hayes 295 (NY); San José I, Erlanson 41 (GH), Harlow 82 (GH); Johnston 197 (GH); Taboga I, Macbride 2773 (F, US). VERAGUAS: hwy to Soná, 29 mi W of Santiago, King 5279 (TEX).

The Panamanian populations of C. urens are not only as proteanly variable as elsewhere in much of tropical America, but appear to fall into a bimodal variation pattern in which the extremes appear as though they were distinct species. West of the Canal Zone and on the islands in the Gulf of Panama appears a form with predominantly 5-lobed leaves densely pubescent beneath, large staminate flowers with long anthers (1.1 mm or more), and relatively large seeds up to 9.3 mm long, while in the Canal Zone and to the east are found plants with smaller mostly 3-lobed glabrescent leaves and smaller staminate flowers (anthers 0.6-0.8 mm) and seeds (mostly 6.5-7 mm long). It is this small-flowered form which was described by Pax and Hoffmann as a new species, C. adenophilus, partly on the basis of a bracteal character which seems to be nonexistent.

Although it might appear that two species are present in Panama if one compared a few sheets of the large-flowered form (e.g. Burch et al. 1157, Dwyer 3065, Johnston 197, Lewis et al. 1673) with sheets of the small-flowered form (e.g. Duke 5867, Pittier 3712, Stern et al. 81, Tyson 1045), closer inspection will show that the readily apparent morphological differences are not sufficiently closely correlated to permit the delimitation of two different species. In other parts of Mexico and Central America a similar kind of bimodal variation pattern occurs, but there too the characters do not show any geographically distinctive correlation. The varieties recognized by Mueller and by Pax and Hoffmann appear merely to represent individually striking biotypes rather than geographic races. The cytological study by Miller and Webster (Brittonia 18: 378, 1967) showed n = 18 in both small-flowered and large-flowered forms, although since only 3 populations were sampled, further counts would be desirable. The infraspecific variation of C. urens thus remains a baffling unsolved problem which evidently requires a considerably more sophisticated analysis than it has received so far.


Jatropha aconitifolia Miller, Gard. Dict. ed. 8, 1768.

Tree or arborescent shrub ca 3-8 m high; glabrous, stinging hairs sparse or absent except on petioles and leaf veins. Leaves thinly chartaceous; petioles ca 15-25 cm long, usually unarmèd or nearly so; junction of petiole and blade with a single median dark reniform gland ca 2-3 mm wide; stipules very inconspicuous;
blades as broad as or broader than long, usually 15-25 cm across and deeply cut, with 5 main lobes and 2 smaller basal lobes, the lobes oblong to obovate, often ± runcinate-pinnatifid, sharply toothed, acuminate. *Dichasia* terminal; peduncles ca 15-30 cm long, smooth or sometimes armed, the first branches opposite, the forks of dichasium compact, the inflorescence 3-6 cm across at anthesis, the axes of inflorescence densely and closely minutely pilose. *Staminate flowers* subsessile; perianth greenish-white, minutely pilose outside but usually unarmed, ca 10-14 mm long, the perianth tube distally dilated, 6-10 mm long, lobes roundish-oblong, 4-6 mm long; disc ca 1-1.5 mm across; stamens with filaments united for most of their lengths into a column, the outer ones 4-5 mm long, the inner 8-9(-12) mm long, the anthers ca 1.5 mm long; staminodes 3, 4-5 mm long. *Pistillate flowers* subsessile or on short pedicels 1-2 mm long; calyx-segments whitish, linear-oblong, deciduous, 5-7 mm long; disc similar to that of staminate flower; ovary pubescent, the styles 3-4 mm long, connate for 1 mm at base, 3-4-fid into narrow segments. *Capsules* unarmed, green, minutely rugose, 8-12 mm long; seeds elliptic, compressed, 6-8.5 mm long, 4-5.5 mm broad, pale to dark brown and mottled, the caruncle deltoid-cordate, 1.5-2 mm high, 2-2.8 mm broad.

Native probably to eastern Mexico according to McVaugh (The Mexican species of *Jatropha*, 13, Rubber Dev. Corp., 1943); widely cultivated in Central America as a hedgerow plant. The species is extensively grown in Panama, and at least one herbarium record (*Hunter & Allen 672*) suggests that it has become naturalized.

**Canal Zone:** Government forest, Las Cruces trail, *Hunter & Allen 672* (MO). **Veraguas:** 2 mi S of Canazas, *Tyson 3708* (MO).

**9. CROTON**


*Trees, shrubs, or herbs; monoeccious or dioecious; stems usually with colored sap, the indumentum (at least in part) stellate or lepidote. Leaves alternate; petiolate (petioles often with glands near the top); stipulate (stipules sometimes obscure or obsolete); blades pinnately or palmately veined, sometimes lobed, entire or serrate. Inflorescences spicate-racemose (or sometimes paniculate or subcapitate), terminal or axillary; bisexual racemes mostly with ♀ flowers solitary at proximal nodes, ♂ 1-several at distal nodes (sometimes at same nodes with ♀ ). *Staminate flowers* with 4-6 imbricate or (most often) valvate calyx-lobes; disc entire or dissected; petals usually 5 (rarely absent); stamens mostly 8-50, free, the filaments inflexed in bud; pollen grains globose, inaperturate, clavate; pistillode absent. *Pistillate flowers* with 4-10 (mostly 5-7) imbricate or valvate calyx-lobes; disc usually entire, rarely dissected, sometimes with staminodia; petals 5, often reduced or absent; ovary of 3 (rarely 2) carpels, the ovules 1 per locule; the styles ± free, once to repeatedly bifid or bipartite. Fruits capsular; seeds terete to compressed, dry, carunculate, endosperm present, the embryo with broad cotyledons. Nearly 1000 species have been described in this natural but polymorphic genus. The majority of the species are American, but most of these occur in South
America and the West Indies; about 80 distinct species have been recognized in continental North America.

Although Croton is relatively poorly represented in Panama, with only 13 species, these belong to 6 different sections which include most of the important neotropical groups within the genus. A very high percentage of the Panamanian specimens of Croton have been misidentified in the past, partly due to the obscure treatments in the literature and partly to some necessary nomenclatural changes. None of the species proposed from Panama since the original treatments by Klotzsch and Mueller can be maintained, and it does not appear that there are any endemic Panamanian species of Croton, except perhaps C. billbergianus.

Much of the difficulty in the genus appears to be the result of a misconception by previous workers that American species of Croton tend to be narrowly restricted in range. The experience gained during the preparation of this treatment shows that this does not acco rd with the facts; several common woody Panamanian species (e.g. C. schiedeanus, C. pungens and C. hircinus) range far beyond our boundaries into South America. A few species, C. panamensis especially, are quite variable and cannot be definitively treated in a local revision such as this. Finally, it must be admitted that the species in sect. Eluteria pose the greatest number of problems, since these taxa are similar to various extra-Panamanian ones, and both flowers and seeds are necessary to establish specific identities. These lepidote taxa of Croton need careful field study in Panama and adjacent regions before the treatment proposed here can be accepted as authoritative.

a. Stamine flowers petaliferous; leaves stipulate; indumentum various.

b. Indumentum lepidote; petals in ♀ flower reduced, similar to the ♂; leaves with deciduous stipules and eglandular petioles; inflorescences strictly axillary. (sect. Eluteria)

c. Stamens 9-12, filaments glabrous; anthers 0.6-0.8 mm long; petals of ♂ flower not lepidote or with only 1 or 2 scales; seeds mostly 7 mm long or less.

d. Leaves ± oblong-elliptic, pinnately veined; inflorescences mostly 2 cm long or more; pedicel of ♀ flower mostly 10 mm long or more

1. C. schiedeanus

dd. Leaves ovate, ± cordate and (3-)5-veined at base; inflorescences 1 cm long or less; pedicel of ♀ flower only 1-2 mm long

2. C. pseudoniveus

cc. Stamens 14-17 or if fewer then filaments hirsutulous; anthers 1-1.2 mm long; petals of ♂ flower lepidote; seeds 15 mm long or more.

e. Stamens (10-)11-13, filaments hirsutulous; leaves pinnately veined ♀ flowers mostly 3 or 4 per raceme; seeds 20-22 mm long

3. C. tenuicaudatus

ee. Stamens 15, filaments glabrous; leaves 3-5 veined at base; ♀ flowers mostly 1 or 2 per raceme; seeds 15-18 mm long

4. C. pyriticus

bb. Indumentum not lepidote, the trichomes mostly or entirely stellate or dendritic; petals in ♀ flower distinctly reduced or absent [sometimes fairly well developed in C. panamensis]; petioles with distinct glands at junction with blade [except in C. hircinus]; inflorescences terminal (at least in part).

f. Leaves unlobed (with obscure and rudimentary indications of lobing in C. hircinus); ♂ calyx-lobes usually distinctly valvate in the bud; receptacle of ♂ flower usually villose; seeds not tetragonal; habit various.
g. Lower cymules of inflorescence with both ♂ and ♀ flowers at the same nodes, styles bifid or bipartite. (sect. *Cyclostigma*)

h. Pistillate flowers distinctly pedicellate (pedicels mostly 3-6 mm long; inflorescences mostly 2-4 dm long; stamens 13-20; petals of ♂ flowers with villose margins; styles glabrous or nearly so; seeds less than 5 mm long) .................. 5. *C. panamensis*

hh. Pistillate flowers subsessile (pedicels becoming at most 2 mm long); inflorescences mostly 1-2 dm long; stamens 27-43; petals of ♂ flowers glabrous, margins minutely ciliate; styles distinctly stellate pubescent; seeds at least 5 mm long ...6. *C. pungens*

gg. Lower nodes of bisexual inflorescences with only ♀ flowers.

j. Styles twice to four times bifid; shrubs or trees (sect. *Croton*)

k. Pistillate calyx-lobes not prominently glandular-toothed; stamens 14-16; petioles with distinct apical glands.

l. Pistillate calyx-lobes elliptic to oblong, not accrescent, less than 5 mm broad; petals of ♂ flower not over 4 mm long; leaves 7-9-veined at base, entire, with petioles mostly 5-20 cm long .................. 7. *C. billbergianus*

ll. Pistillate calyx-lobes ovate, reduplicate-valvate, accrescent, becoming 7-8 mm long and broad; petals of ♂ flower 4.5-5 mm long; leaves mostly 5 veined at base, entire to denticulate, with petioles 1-3.5 cm long .............. 8. *C. fragrans*

kk. Pistillate calyx-lobes coarsely glandular-toothed below; stamens 10-12; petiolar glands obscure or obsolete .......... 9. *C. hircinus*

jj. Styles once bifid; annual herbs. (sect. *Geiseleria*)

m. Leaves coarsely and sharply serrate (major teeth usually not over 10 per side); stamens 8-10; styles less than 1.5 mm long, ± spreading .................. 10. *C. trinitatis*

mm. Leaves more finely and/or bluntly toothed; stamens 11; styles more than 1.5 mm long, ± erect.

n. Stems coarsely hispid; leaves mostly ovate, pointed at the tip, petiolar glands stalked; bracts with long gland-tipped processes; seeds 2.6-3.1 mm long .................. 11. *C. hirtus*

nn. Stems not coarsely hispid; leaves mostly elliptic or oblong, blunt at the tip, petiolar glands sessile; bracts eglandular; seeds 2.8-3.5 mm long ......................... [C. *glandulosus]*

ff. Leaf-blades deeply 3-5-lobed; ♂ calyx-lobes distinctly imbricate in bud; receptacle of ♂ flower glabrous; seeds tetragonal; annual herb. (sect. *Astraea*) .................................................. 12. *C. lobatus*

aa. Flowers apetalous; stipules and petiolar glands absent; leaves with stellate-lepidote indumentum above, lepidote beneath; stamens 10-12, filaments hirsutulous; styles 3 times bifid; seeds deciduously stellate, ca 5 mm long. (sect. *Drepanodium*) ........................................... 13. *C. punctatus*
1. **Croton schiedeanus** Schlecht., Linnaea 19: 243, 1847.—Fig. 9(E).

*C. perobtusus* Lundell, Phytologia 1: 405, 1940.

*Tree* ca 5-15 m high, trunk ca 1-2.5 dm thick; monoecious; indumentum lepidote. *Leaves* chartaceous; petioles lepidote, eglandular, ca 0.5-4 cm long; stipules densely lepidote, linear, capitulate, (1-)2.4 mm long, caducous and thus often appearing to be absent; blades elliptic to oblong, ca 7-22 cm long, 3-9 cm broad, glabrate above, lepidote beneath with scattered scales ca 0.1-0.2 mm across (the blade appearing greenish beneath, not silvery), the venation distinctly pinnate, the major lateral veins (ca 8-12 on a side) straightish, the base obtuse to rounded, the margins entire, the apex ± abruptly contracted to a ± obtuse acumen. *Inflorescences* axillary, racemiform, ca 2-10 cm long, bisexual or male, often fascicled in the axils; ♀ flowers 1 or 2 at the base; ♂ flowers many, distal; bracts subtending solitary flowers, inconspicuous, eglandular, less than 1 mm long. *Staminate* flowers with lepidote pedicels becoming ca 2.5-3.5 mm long; calyx-lobes 5, valvate, densely lepidote, shorter than the petals; receptacle villose; petals ca 1.3-2.1 mm long, glandular-punctate, densely villose-ciliate on the margins, glabrous on the back or with 1(-2) scales; stamens (9-)10 or 11, the filaments glabrous, ca 1.5-2.5 mm long, the anthers elliptic, 0.6-0.8 mm long. *Pistillate* flowers with stiff straight lepidote pedicels becoming 10-25 mm long; calyx-lobes 5, equal, triangular or ovate, shorter than the petals; disc annular, ± adnate to the calyx; petals ca 1.8-2.1 mm long, similar to the ♂; ovary densely lepidote, scales delicately denticulate, ca 0.3-0.4 mm in diam, the styles usually 3 times bifid, ca 3-3.5 mm long, the branches slender, glabrous, spreading. *Capsules* not seen entire; cocci lepidote, verrucose, ca 8.5-12 mm long, the columella slender, 6.5-8.2 mm long; seeds compressed, brownish, smooth, obtusely beaked, 6.2-7(-9.5) mm long, 4.4-5(-5.4) mm broad.

Widespread in lowland Mesoamerican rain forests (mostly below 500 m) from Mexico (Nayarit, Vera Cruz) south mainly along the Gulf coast to Costa Rica, Panama, Colombia, and Peru.


Although this species, the most common Panamanian *Croton* with lepidote indumentum, has usually been identified as *Croton glabellus* L., it apparently is correctly designated as *C. schiedeanus* Schlecht. True *C. glabellus* (*C. nitens* Sw.), which appears to be restricted to Jamaica and the Cayman Islands, is characterized by small stipules (scarcely over 0.5 mm long), hirsutulous filaments, small seeds (4.3-6.5 mm long), and short fruiting pedicels (1.5-9 mm). In contrast, the Panamanian plants discussed here have usually larger stipules, glabrous filaments, larger seeds, and longer fruiting pedicels; furthermore, they also differ in less
quantifiable characteristics such as thinner, larger leaves and more slender inflorescence axes. There can be little doubt that C. glabellus and C. schiedeanus are rather closely related, but there seems to be no reason not to treat them as distinct species.

2. **Croton pseudoniveus** Lundell, Phytologia 1: 449, 1940.

* croton or tree 5-6 m high; monoecious; twigs densely and smoothly lepidote. *leaves* thinly chartaceous; petioles lepidote glandular, mostly 10-30 mm long; stipules subulate-lanceolate, lepidote, 5-6.5 mm long; blades ovate, 6-12.5 cm long, 4-9 cm broad, green and sparsely lepidote on both sides (paler beneath), copiously and minutely glandular-punctate, 5-veined at base, with 4 or 5 additional lateral veins per side, the base narrowly cordate, the margins entire, the apex abruptly acuminate. *Inflorescences* axillary, spiciform, very compact and abbreviated (1 cm long or less), bisexual or ♀, with usually only 1 ♀ flower at base; bracts subtending solitary flowers. *Staminate flowers* with lepidote pedicels 0.9-1.5 mm long; calyx-lobes 5, valvate, triangular, lepidote, ca 1.5-1.6 mm long; receptacle villose; petals oblong to obovate, ca 2 mm long, densely villose on the margins, glandular-pustulate on the back, not lepidote; stamens 10 or 11, the filaments glabrous, 2-2.3 mm long, the anthers elliptic, pustulate on the connective, 0.6-0.7 mm long. *Pistillate flowers* with stout lepidote pedicels ca 1-2 mm long; calyx-lobes as in the ♂; disc ca 1.5 mm wide, irregularly segmented into 5 lobes, adnate to the calyx; ovary silvery-lepidote, the finely denticulate concave scales 0.7-0.8 mm wide, the styles free, spreading, ca 2.5-3 mm long, mostly 4 times bifid, the branches slender and glabrous. *Capsules* not seen; seeds (ex McVaugh, loc. cit.) 5.5 mm long.

Deciduous woodland, lowlands, western Mexico and Panama.

COCLE: Penonomé, roadside, Dwyer 1999 (MO). PANAMA: 5 mi E of Canita (23 mi E of Chepo), Tyson & Smith 4160 (MO).

The identification of these two Panamanian collections with a species heretofore recorded only from Mexico is made with some hesitation. However, the similarities in indumentum, inflorescence size, and stamen number are so impressive that the conspecificity of the Mexican and Panamanian specimens is at least a reasonable hypothesis. According to McVaugh (Brittonia 13: 160-165, 1961), the Mexican population of *C. pseudoniveus* is distinguished by its large stiff ovarian scales up to 1 mm wide. In the Panamanian plant the scales are only 0.7-0.8 mm wide, and thus are more comparable in size to *C. reflexifolius* H.B.K.; this latter species, known from lowlands of southern Mexico, resembles *C. pseudoniveus* in leaf shape and seed size but differs in its denser foliar indumentum and androecium of 15 or 16 stamens.

In terms of geographical position, one might have expected the plant from Coclé to resemble *C. niveus* Jacquin of northern coastal Colombia. However, that species, although similar in leaf shape, has a much denser foliar indumentum (at least dorsally), and—like *C. reflexifolius*—an androecium of ca 15 stamens. It seems possible that *C. niveus* and *C. reflexifolius* may prove to be conspecific when
better material is available for study; and if the stamen number is found to be inconstant, all of these lowland populations with ovate leaves and small seeds may prove to belong to a single variable species, *C. niveus*.

3. **Croton tenuicaudatus** Lundell, Phytologia 1: 451, 1940.

   *Tree* 6-18 (-30?) m high; monoecious; twigs with brownish scurfily hispidulous-lepidote indumentum. *Leaves* thinly chartaceous; petioles lepidote, glandular, (1-) 2-4.5 cm long; stipules narrowly lanceolate to subulate, densely lepidote, ca 2-4 mm long, soon deciduous; blades elliptic to elliptic-oblong, mostly 8-16 cm long, 5-8 cm broad, dark, minutely pubescent and sparsely lepidote above, paler beneath, minutely glandular-punctate, and sparsely lepidote (scales ca 0.1-0.2 mm wide); venation distinctly pinnate, the major lateral veins (ca 8-12 on a side) ± straight, the base rounded to truncate, the margins entire, ± abruptly contracted to an acuminate or caudate tip. *Inflorescences* axillary, racemiform, becoming 7-15 cm long, mostly bisexual, 1-2 per axil; ♀ flowers (1-)3 or 4 at the base; ♂ flowers many, distal; bracts subtending solitary flowers, inconspicuous, less than 1 mm long. *Staminate flowers* with lepidote pedicels 2.5-4.2 mm long; calyx-lobes 5, valvate, triangular, lepidote, ca 2.2-2.8 mm long; receptacle villose; petals elliptic to oblanceolate, 2.4-3.2 mm long, glandular-punctate, densely villose on the margins, lepidote on the back; stamens (10-)11-13, the filaments hirsutulous, 2.4-4.5 mm long, the anthers narrowly elliptic or oblong, 1-1.2 mm long. *Pistillate flowers* with stout lepidote pedicels 3.5-7 mm long at anthesis; calyx-lobes 5, equal, triangular or ovate, densely lepidote, 2.2-2.7 mm long; disc annular, adnate to the base of the calyx, ca 2.8 mm across; petals obovate, 2.2-2.9 mm long, similar to the ♀; ovary densely lepidote, scales minutely denticulate, ca 0.3-0.5 mm in diam, the styles usually 3 times bifid, ca 2.5-3.5 mm long, the branches slender, glabrous, spreading. *Capsules* not seen entire; cocci smooth, lepidote, ca 35 mm long, the columella winged, ca 25 mm long; seeds slightly compressed, concave-convex, reticulate-costate on sides and back, scarcely beaked, 20-22 mm long, 11-12 mm broad.

   Forests at intermediate altitudes (ca 800-1000 m), Costa Rica and western Panama.

   **Chiriquí**: betw Concepción & El Volcán, White 309 (MO), 316 (MO). **Coclé**: N of El Valle de Antón, Allen 3719 (MO).

   The identity of this Panamanian species appears certain, as the specimens collected in Chiriquí by White are a very close match for the type collection from Costa Rica (vic of El General, Skutch 2575 MICH). It is not certain that the fruiting collection from Coclé should be associated with the flowering specimens from further west, as the leaf shape is somewhat different and the petioles are shorter. If it does belong here, then *Croton tenuicaudatus* would appear to have the largest seeds of any species in its section.

Tree to 20 m high; monoecious; twigs densely lepidote. Leaves thinly chartaceous; petioles lepidote, eglandular, 1.5-6 cm long; stipules not observed (caducous?); blades ovate, mostly 8-12 cm long, 5-9 cm broad, greenish above, sparsely lepidote, densely lepidote beneath, brownish-silvery, densely and minutely glandular-punctate on both sides; blades 3-5-veined at the broadly cuneate to truncate base, the margins entire, rather abruptly contracted into a short acumen at the apex. Inflorescences axillary, racemiform, 1.5-5(-10) cm long, mostly bisexual, with 1 or 2 basal ♀ flowers; bracts subtending solitary flowers. Staminate flowers with lepidote pedicels ca 2 mm long; calyx-lobes 5, valvate, lepidote, ca 2.5 mm long; receptacle villose; petals obovate, ca 2-3 mm long, densely villose on the margins, lepidote on the back; stamens ca 15, the filaments glabrous, the anthers 1.1-1.2 mm long. Pistillate flowers with pedicels becoming 10 mm long; calyx-lobes nearly as in the ♂; petals obovate, ca 2 mm long, lepidote as the ♂; ovary silvery-lepidote, the styles free, spreading, several times bifid, up to 4 mm long, glabrous. Capsules not seen entire; cocci lepidote, obscurely verrucose, 21-23 mm long, the columella 15 mm long; seeds somewhat compressed, smooth, carinate dorsally, obscurely and obliquely grooved ventrally, dark brownish mottled with gray, apically mucronate, 15-18 mm long, 10-11 mm broad, the caruncle 2-2.2 mm wide.

Montane forests, Costa Rica and western Panama, at 1200-1500 m. chiri qui: El Boquete, 4000 ft, Davidson 865 (A, MO).

The description of this species has been adapted partly from Croizat's original diagnosis, as the single Panamanian collection lacks flowers. The status of *Croton pyriticus* must be judged as still very uncertain. It is extremely close to *C. eluterioides* Lotsy, from Guatemala, and may prove to be only a southerly geographic race of that taxon. Croizat distinguished *C. eluterioides* by its muricate fruit with smaller seeds (11 mm long); but a collection from El Salvador (Tucker 1229 DAV, UC) combines the muricate fruit of that species with the larger seeds of *C. pyriticus*.

There is also a striking resemblance between *C. pyriticus* and *C. niveus* Jacquin, described from the vicinity of Cartagena, Colombia. Both taxa have flowers with about 15 stamens, glabrous filaments, and similar leaves. Unfortunately fruiting specimens from the region of the type locality of *C. niveus* have not yet been collected. Since that plant furthermore appears to be a shrub growing in the lowlands rather than a tall tree in montane forests, it would appear premature to apply the name *C. niveus* to any collections available from Panama.

5. *Croton panamensis* (Kl.) Muell.-Arg. in DC., Prodr. 15(2): 546, 1866.—Fig. 9(F).

*C. denticulatum* KL, loc. cit.
*Croton steyermarkianus* Croizat, Jour. Arnold Arb. 21: 86, 1940.
*C. triumfetiioides* Croizat, loc. cit. 87.
Tree ca 5-30 m high, with trunk 0.7-6 dm thick; monoecious; young twigs ± scurfy with compact dendritic hairs. Leaves membranous or chartaceous; petioles scurfy 3-20 cm long, the glands at apex of petiole 2-6 (plus a cluster of smaller ones usually present on ventral side), stipules linear-lanceolate to subulate, 3-10 mm long; blades mostly ovate, (7-) 10-30 cm long, (2.5-) 7-23 cm broad, sparsely pubescent above with scattered dendritic and hirsute hairs (eventually glabrate), sparsely to densely tomentose beneath with stellate and dendritic hairs (these multiradiate, mostly 0.3-0.6 mm wide) and minutely glandular-dotted, 5-7-nerved at base, with ca 6-10 additional veins on either side, the veinlet reticulum prominent beneath, the base truncate to deeply cordate, the margins subentire to obscurely or rather prominently denticulate, the apex rather abruptly acuminate or caudate. Inflorescences terminal, usually bisexual, racemiform, (7-) 20-40 cm long, typically with the 5-20 proximal cymes distal (and sometimes the first proximal) cymes; bracts triangular or lanceolate, tomentose, inconspicuous, ca 1-1.5 mm long, subtending several flowers. Staminate flowers with stellate-tomentose pedicels ca 5-8 mm long; calyx-lobes 5, stellate-tomentose, triangular, 2-2.2 mm long; receptacle densely villose; petals obovate, 1.9-2.5 mm long, villose especially on the margins; stamens (13-) 14-18(-20), the filaments glabrous (except at base), 2-2.8 mm long, the anthers elliptic, 0.6-0.8 mm long. Pistillate flowers with stout stellate-tomentose pedicels (2-) 3-6 mm long; calyx-segments 5, whitish- or yellowish-tomentose outside, dark brownish inside, elliptic to oblong, ± valvate, 2.3-2.8 mm long, 1.3-1.8 mm broad; disc 2-3 mm wide, notched or lobed into 5 entire or toothed segments; petals filiform-subulate to rarely narrowly ligulate, 0.5-2.1 mm long, 0.1(-0.4) mm broad; ovary orange- or brownish-tomentose with stellate and dendritic hairs (hirsute radii ca 0.3-0.6 mm long), the styles free, bifid or bipartite, glabrous or rarely sparsely stellate at the base, (2.5-) 3-5 mm long, the slender branches mostly 2.5-3 mm long. Capsules subglobose, yellowish-brown, stellate-hispidulous, ca 6.5 mm diam, the columella slender, 3.3-3.5 mm long; seeds plump, brown, obscurely costate-roughened, 3.1-3.9 mm long, 2.6-2.8 mm broad, the caruncle ovate, ca 1 mm wide.

Lowland and montane forests, Central America (limits of distribution not clearly defined) to Colombia.

Bocas del Toro: Almirante, Cooper s.n. (F). Canal Zone: Albrook, Blum 767 (MO), Dwyer 6715 (MO); Barro Colorado I, Bailey & Bailey 439 (F), White 116 (MO); Corozal, Standley 27357 (US); Curundu, Harvey 5190 (F); El Paraíso, Pittier 2527 (US); Empire to Mandinga, Piper 3536 (US); Fort Sherman, Tyson & Ah Chu 1705 (MO); Gamboa, Ebinger 492 (MO); betw Gamboa & Cruces, Pittier 3773 (US); betw Gorgona & Mamei, Pittier 2695 pro parte (GH, NY); Las Cascadas Plantation, Standley 258111 (US), 29542 (US); Limón, Bro. Heriberto 25 (US); vic of Madden Dam & Alhajuela, Hunter & Allen 790 (MO); Matachin, Kuntze 1934 (NY), Pittier 2695 pro parte (US); Obispo, Hayes 135 (NY); Porlamar, Aguirre: Alto Lino, clearings, Bro. Maurice 737 (US); Bajo Mona, Davidson 480* (F, MO); id., mouth of Quebrada Chiquero, Río Caldera, Woodson et al. 1006* (MO); Cerro Horquetas, cloud forest, von Hagen & von Hagen 2110 (F); El Boquete, Pittier 2927 (US); id., 1 mi SW, Allen 4716 (MO); id., 1 mi S, King 5318* (UC); id., Finca Collins, cloud forest, Stern et al. 1134* (MO); id., Boquete to 3 mi N, Lewis et al. 597 (DAV, GH, MO, NY, UC, US); Quebrada Velo, vic of Finca Lerida, Allen 4678* (F, MO); Río Macho de Monte, 1 mi E of Cuesta de Piedra, Tyson 906 (MO); vic of San Félix, Allen 3649 (MO); Volcán Chiriqui, Potrero Muleto to summit, Woodson & Schery.
In the conservative circumscription adopted here, *C. panamensis* includes all the Panamanian representatives of sect. *Cyclostigma* which have pedicellate flowers. The species shows considerable variation in such characters as leaf size and density of pubescence, but none of the proposed segregate taxa appear specifically distinct in our area. The most striking variant occurs in the Boquete region of Chiriquí, where plants with hispid \( \sigma \) buds and upper leaf surfaces have been designated as *C. triumfettoides* Croizat (a species described from Costa Rica); these collections have been marked by asterisks in the list of specimens. It is possible that these plants may represent a montane ecotype, as they appear to occur mostly at 1200 m and above, whereas typical *C. panamensis* is found mostly below 1200 m. Nevertheless, the plants with hispid buds are so similar in most respects to those from lower altitudes that it does not appear warranted to treat them as a distinct species.

The type locality of *C. panamensis* happens to be in this same region of Chiriquí where the deviant populations occur, but Mr. H. K. Airy Shaw has kindly examined the type specimens (at Kew) of both taxa proposed by Klotzsch and reports that neither represents the hispid variant. The second 'species' of Klotzsch, *C. triumfettoides* Croizat (a species described from Costa Rica), is merely a trivial variation unworthy of any taxonomic recognition, as the leaf margins of *C. panamensis* vary from entire to distinctly denticulate throughout most parts of its range.

It may turn out that the present circumscription of *C. panamensis* is actually not conservative enough, for this species is in fact closely related to *C. draco* Schlecht. of Mexico and Guatemala. Typically, the more northerly species may be distinguished by its much broader foliaceous stipules; but the two taxa are much alike in other respects, and they may prove to intergrade in Honduras or Nicaragua. In that event, *C. panamensis* would have to be designated as a subspecies of *C. draco*.


Shrub or tree 1-5(-20?) m high; monoecious; young twigs with hispidulous stellate-tomentose indumentum. Leaves thinly chartaceous; petioles hispidulous-tomentose, (1-)2-6 cm long, the glands at apex of petiole 2-4, patelliform, distinctly stalked, 0.4-0.8 mm across (stalk ca 0.7-1.5 mm long); stipules linear to subulate, 1.5-4 mm long, sparsely stellate; blades ovate, ca 5-15 cm long, 2-10 cm broad, greenish above and rather sparsely pubescent with scattered oligoradiate stellate or short-stalked dendritic hairs, whitish-tomentose beneath with multiradiate dendritic hairs (ca 0.4-0.8 mm across), 5-7-nerved at base, with 3-6 additional...
veins on either side, the veinlet reticulum rather prominent beneath, the base usually cordate, the margins entire to finely denticulate, the apex abruptly acuminate. **Inflorescences** terminal (sometimes pseudoaxillary), bisexual or sometimes stamine, racemiform, (3-)10-22 cm long; bisexual inflorescences with 1-15 proximal ♀ cymes, distal cymes ♂; bracts lanceolate, acute to acuminate, tomentose, ca 1-3 mm long, each subtending several flowers. **Staminate flowers** with hispidulous-tomentose pedicels 3-8 mm long; calyx-lobes 5, triangular, stellate-tomentose, 2.2-2.5 mm long, 1.1-1.5 mm broad; receptacle densely villose; petals obovate, 2.3-2.9 mm long, 1-1.3 mm broad, glabrous except for the minutely ciliate margins; stamens 27-43, the filaments 2.5-3 mm long, glabrous and ± papillose, the anthers elliptic, 0.7-1 mm long. **Pistillate flowers** subsessile, the stout pedicels even in fruit only 1-2 mm long; calyx-segments 5, ± unequal, oblong to linear-lanceolate, valvate, 2.5-3.7 mm long, 0.7-1.6 mm broad, stellate-tomentose on both faces; disc obscure; petals (staminodia?) antheriform, callose, swollen, ca 0.3-0.4 mm long; ovary closely tomentose with tawny stellate hairs, the styles free, bifid, copiously stellate-pubescent, ca 4.4-4.5 mm long, divided more than 1/2 way to the base. **Capsules** obovoid, ca 6.5-7.5 mm long, yellowish, closely stellate-scurfy, the columella slender, apically 3-pronged, ca 5.5-6 mm long; seeds plump, dull to blackish brown, rugose-costate, 5.1-5.7 mm long, 3.6-4.1 mm broad, the caruncle ovate, ca 1.5 mm wide.

Montane forests, Costa Rica to Venezuela, Peru, and Brazil; in Panama occurring above 1000 m.

Chiriquí: Finca Lérida to Peña Blanca, Woodson & Schery 293 (MO); Paso Ancho to Monte Lirio, Allen 1474 (A, MO); Volcán de Chiriquí, llanos, Allen 978 (MO), 4855 (MO); id., Davidson 892 (A, MO; type coll. of Croton standleyi); id., Camiseta, Terry 1357 (MO, US).

Although at present known only from the Boquete region in extreme western Panama, this widespread species may be found on the higher summits in Darien. The type collection of Croton standleyi represents an unusually small-leaved form, but does not appear to show any important differences from C. pungens. A rather closely related species, Croton xalapensis H.B.K., does not occur in Panama so far as is known. It differs from C. pungens especially in lacking ♂ flowers at the lower ♀ nodes of the inflorescences.

7. **Croton billbergianus** Muell.-Arg., Linn. 34: 98, 1865; in DC., Prodr. 15(2): 582, 1866.—Fig. 9(A-D).

Shrub or tree ca 3-10 m high; monoecious; twigs and young foliage closely scurfy with stellate hairs ca 0.1-0.2 mm across. **Leaves** membranous or thinly chartaceous; petioles stellate-scurfy, ca (2-) 5-20 cm long, the glands at apex of petiole dorsal, sessile, petalliform, yellow, thickened, ca 1-1.5 mm across; stipules subulate-lanceolate, ca 5-7 mm long, densely scurfy, soon deciduous; blades mostly ovate, ca 7-25 cm long, 5-18 cm broad, glabrate and pustulate above, minutely glandular-punctate and sparsely to densely pubescent beneath with stellate hairs, 7-9-nerved at base, with 6-10 additional veins on either side distally, the base usually cordate, the margins entire, the apex abruptly short-acuminate.
Inflorescences terminal, bisexual, racemiform or paniculate (lateral axes mostly 1 or 2), ca 3-15 cm long, often with additional smaller sometimes unisexual racemes at proximal axils; ♀ flowers 3-8 at proximal axils of most inflorescence axes, ♂ flowers many, at distal axils; bracts linear, greenish, stellate, ca 1.5-3.2 mm long, subtending solitary flowers. Stamine flowers with stellate pedicels ca 3-5 mm long; calyx ca 3.5-4.5 mm long, divided ca 2/3 into 5 triangular lobes; receptacle densely villose; petals elliptic to narrowly oblong, 3.5-3.8 mm long, 1-1.5 mm broad, villose, not punctate; stamens 14-16, the filaments densely villose on the proximal half, 4-5 mm long, the anthers elliptic-oblong, 1-1.4 mm long. Pistillate flowers with spreading or reflexed stellate-tomentose pedicels ca 3-5 mm long, becoming 7-10 mm in fruit; calyx-lobes 5, subequal, elliptic or oblong, obtuse, entire, ca 4.5-5 mm long; disc parted into 5 obscure, massive segments ca 1-1.2 mm wide; petals absent; ovary densely tomentose with yellowish multiradiate stellate hairs ca 0.5-1 mm across, the styles basally connate into a stout column 0.5-1 mm high, densely stellate proximally, free ends 3-4.5 mm long, 2 or 3 times bifid, the tips slender. Capsules spheroidal, ca 8.5-9 mm diam, stellate-tomentose, the columella slender, 4.2-4.5 mm long; seeds plump, obovate, brownish, verrucose, slightly and obtusely beaked, 4.3-5 mm long, 3.1-4.1 mm broad, the caruncle with two broad lateral lobes, 0.8-1 mm long, 1.5-2.1 mm broad.

Lowland forests; endemic to Panama, so far as is known.

Although commonly collected in the Canal Zone, this species appears to be of rather restricted distribution. It is similar in many respects to C. hoffmannii Muell.-Arg. of Costa Rica, but that plant differs in its ferruginous indumentum, looser and larger stellate hairs on the lower leaf surface, and larger smoother seeds. Much more closely related is Croton pyramidalis J. D. Sm., of Guatemala and Honduras, which is the northern counterpart of C. billbergianus. Although C. pyramidalis may easily be recognized by its more densely stellate and often longer-acuminate leaves, reflexed ♀ calyx-lobes, and reddish (rather than yellowish) tomentum on the ovary, it is doubtless very close to the Panamanian plant. Further studies will probably show that it should be regarded as a subspecies of C. billbergianus.
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Shrub, sometimes arborescent, 2-10 m high; monoecious; twigs and foliage with indumentum of stellate and dendritic hairs. Leaves membranous or chartaceous; petioles densely stellate-tomentose, ca 1-3.5 cm long; glands at apex of petiole 2-6, patelliform, stalked, ca 0.5-0.8 mm diam (ca as broad as length of stalk); stipules elliptic or obovate, tomentose, the margins lacinate-toothed, ca 4-9 mm long; blades ovate to elliptic, ca 8-20 cm long, 4-12 cm broad, softly stellate or stellate-hispidulous (1 of the ascending radii often larger than the others) above, paler and more densely stellate (the ca 6-10-radiate hairs mostly 0.5-0.8 mm across) and minutely glandular-punctate beneath, mostly 5-(7-)nerved at base, with ca 5-8 additional veins on either side, the base obtuse or rounded to subcordate, the margins subentire or distinctly crenulate-denticulate, the apex rather abruptly short-acuminate. Inflorescences terminal (sometimes with additional axes in distalmost axils), bisexual or stamine, racemiform (or paniculate by aggregation), becoming ca 10-20 cm long; cymes unisexual, ♀ flowers 1-5 at proximal nodes; bracts elliptic-lanceolate, acuminate, ± lacinate-toothed, ca 2-4 mm long, subtending solitary flowers (or ♀ flowers sometimes several per bract). Stamine flowers with stellate-tomentose pedicels ca 6-9 mm long; calyx whitish stellate-tomentose, 4-5 mm long, divided ca ½ way or more into 5 triangular lobes; receptacle densely villose; petals obovate, ca 4.5-5 mm long, minutely glandular-punctate, densely whitish-ciliate along the margins and villose on the back; stamens 15 or 16, the filaments glandular-pustulate, glabrous, 3-3.7 mm long, the anthers elliptic-oblong, 1.2-1.3 mm long, glandular-pustulate on the connective. Pistillate flowers with stout tomentose pedicels 2-3 mm long; calyx-segments 5, whitish stellate-tomentose, broadly ovate, reduplicate-valvate, entire, ca 5-5.5 mm long and 4-4.5 mm broad (increasing to 7-8 mm long and broad in fruit); disc ca 2.5 mm across, cut into 5 reniform thickish segments; petals absent, replaced by tufts of stiff hairs; ovary minutely and closely pulverulent-scurfy (the trichomes ca 0.05 mm wide) and glandular-pustulate, the styles free, ca 4.5 mm long, basally thickened, distally 2-4 times bifid into slender tips. Capsules subglobose, closely glandular-scurfy, ca 7.5-8 mm across, the columella slender, ca 4.5 mm long; seeds plump, brownish, minutely beaked, obliquely costate on both faces, 4.3-4.5 mm long, 3.3-3.4 mm wide, the caruncle triangular, ca 1.2-1.5 mm broad.

Lowland forests, eastern Panama to northern Colombia and Venezuela.


The determination of this species as *Croton fragrans* seems relatively secure, since the reduplicate-valvate accrescent ♀ calyx, glandular-pustulate floral parts, and conspicuously toothed stipules provide very distinctive features. Although some of the Panamanian collections have been confused with *C. hoffmannii*
Muell.-Arg., that Costa Rican species differs in its distinctly imbricate calyx-lobes, more ferruginous pubescence on young parts, entire stipules, and villose rather than pustulate filaments. So far no collections of C. hoffmannii have been seen from western Panama, where it might be expected to occur.


*Shrub* or small tree 1-4 m high; monoecious; twigs rather coarsely hispid-stellate. *Leaves* thinly chartaceous, petioles rather sparsely stellate (± glabrescent), ca (0.5-)1-3(-5) cm long, the petiolar glands usually indistinct, sometimes capitulate and up to 1 mm long, usually ± confounded with glandular teeth at base of blade; stipules linear to subulate, capitulate-tipped and with 2 or more glandular-capitulate lobes toward the base, mostly 1.5-7 mm long; blades ovate to elliptic, ca (3-)5-11 cm long, (1.5-)2-7 cm broad, sparsely stellate or stellate-hispid above with 6-10-radiate hairs, sparsely stellate (hairs ca 0.5-1.2 mm wide) and densely glandular-punctate beneath, 7 (-9) nerved at base, with ca 3-6 additional veins on either side, the base rounded to narrowly cordate, the margins distinctly and sometimes coarsely dentate or duplicidentate (teeth 15-40 on each side), the apex acute to mostly cuspidate-acuminate. *Inflorescences* terminal, bisexual, racemiform, 5-17 cm long, with 3-7 solitary flowers at proximal axils, solitary flowers at distal axils; bracts lanceolate to linear, glandular-tipped and lobed as the stipules, 2-7 mm long under the flowers and shorter under the flowers. *Staminate flowers* with stellate pedicels 1.5-4.7 mm long; calyx-lobes 5, triangular, stellate-pubescent, glandular-punctate, 2-2.8 mm long, 1.3-2 mm broad; receptacle nearly glabrous, glandular-punctate (hairs mostly on filaments and petals); petals elliptic to obovate or spatulate, 2.5-3.5 mm long, 1-2 mm broad, glandular-punctate, densely barbate-hirsute on the lower margins; stamens 10-12, the filaments densely hirsutulous in the lower third, (1.5-)2-3.5 mm long, the anthers ovate to elliptic, 0.7-1 mm long (sometimes reduced). *Pistillate flowers* subsessile, the pedicel even in fruit only 1-2 mm long, the calyx-segments 5, subequal, narrowly lanceolate to linear, coarsely glandular-toothed below, stellate-pubescent, 3.5-5 mm long, 1-3 mm broad; disc cut into 5 dark round segments ca 0.6-0.8 mm wide; petals subulate, capitulate, 0.5-1.1 mm long; ovary densely stellate-tomentose, ± hispid at the apex, the styles free, ca 3-4 mm long, twice bifid (quadruplicate), ± stellate-hispidulous towards the base of the slender branches. *Capsules* subglobose, copiously stellate-pubescent, becoming ca 6 mm in diam, the columella slender, ca 3.5 mm long; seeds elliptic, slightly compressed, brownish, somewhat narrowed apically but not beaked, nearly smooth (minutely striolate), 3.8-4.2 mm long, 2.9-3.1 mm broad.

Lesser Antilles, northern coastal South America, and Panama, in lowland woods below 1000 m.
10. **Croton trinitatis** Millsp., Publ. Field Mus. Nat. Hist., Bot. Ser. 2: 57, 1900.—Fig. 9(G).


Annual herb, rather sparsely branching, ca 2-8 dm high; monoeocious; stems slender, sparsely to moderately appressed-pubescent with long-radiate stellate hairs (spreading hairs up to 1 mm long). Leaves membranous; petioles stellate-pubescent 0.5-3.5 cm long, the petiolar glands distinctly stalked, as long as to twice as long as broad, 0.3-0.6 × 0.2-0.5 mm; stipules greenish, ± subulate-tipped from a broader base, 0.4-1.1 mm long; blades oblong-deltoid to ovate, mostly 2-5 cm long, 1-4 cm broad, hispidulous-stellate above (hairs ca 0.2-0.8 mm across), radiate-stellate beneath (hairs ca 0.2-0.6 mm wide, 7-10-radiate), the veins at base 3(-5), with 3-5 additional veins on each side, the base obtuse, the margins coarsely serrate, major teeth ca 7-12 on a side, the apex acute. Inflorescences terminal or pseudoaxillary (in forks of branches), bisexual, ca 1 cm long or less, subsessile or with a short peduncle up to 0.5 cm long, with 2-4 proximal ¥ flowers and 5-8 distal ç flowers; bracts inconspicuous, greenish, pointed, less than 1 mm long, not or obscurely glandular at base. Staminate flowers with glabrous pedicels 0.3-0.6 mm long; calyx-lobes 5, with greenish sparsely hispidulous tips, ca 0.6-0.9 mm long; receptacle villose; petals ca as long as calyx-lobes, distinctly pointed; stamens 8-10, the filaments glabrous, 0.7-1 mm long, the anthers 0.25-0.3 mm long. Pistillate flowers with short densely pubescent pedicels which attain 1.5-2.6 mm long in fruit; calyx-lobes 5, subequal, ob lanceolate or spatulate, ca 2.5-3.3 mm long, stellate-hispidulous; disc obscure; petals subulate, ca 0.3-0.4 mm long; ovary densely hispidulous, the styles bipartite, 0.7-1.1 mm long, the tips ± spreading, not inrolled. Capsules ca 4.5 mm long, stellate-pubescent; seeds compressed, blackish-brown, smooth (minutely foveolate-reticulate), not beaked, 3-3.6 mm long, 2.2-2.5 mm broad, the caruncle bilobed, 0.4-0.5 mm high, 1.1-1.3 mm broad.

A widespread and rather common weed in the Caribbean area (Florida and the Bahamas south to Panama, Venezuela, and Trinidad); also occurring sporadically in much of South America.
This species was described by Mueller (DC., Prodr. 15(2): 686, 1866) under the name *Croton chamaedryfolius* Grisebach; however, Grisebach's name was based on *C. chamaedi*I. Grisebach's name was based on *C. chamaedryfolius* Lam., which is an *Acalypha*. Although often confused with *C. glandulosus* L., *C. trinitatis* is sharply different in its beakless seeds and fewer stamens; and it can usually be distinguished from that species by its more coarsely toothed leaves with smaller and more distinctly stalked petiolar glands.

11. *Croton hirtus* L’Her., Stirp. Nov. 17, t. 9, 1785.—Fig. 9(H).

*C. glandulosus* × *hirtus* (L’Her.) Muell.-Arg. in DC, Prodr. 15(2): 684, 1866.


Annual herb becoming mostly 1-4 dm high; monoecious; stems conspicuously retrorsely stellate-hispid (hairs ca 1.5-2.5 mm long). Leaves membranous; petioles of leaves on main stem stellate-hispidulous, ca 3-25 mm long; stipules greenish, subulate, subentire, sparsely stellate, ca (1.5-)2.5-4.5 mm long, the glands at apex of petiole 2, distinctly stalked, 0.5-1.2 mm long, 0.1-0.3 mm broad across the flattened head; blades elliptic to more commonly ovate, 2-6.5 cm long, 1.5-5 cm broad (or smaller in depauperate specimens), bright green and rather sparsely stellate-hispid above, minutely glandular-punctate beneath, stellate with 6-10-radiate hairs (radii spreading, hairs ca 0.3-0.8 mm across), the veins at base of larger leaves 5, with ca 3-6 additional veins on each side, the base cuneate, the margins of larger leaves coarsely crenate-duplicidentate, with ca 10-15 major teeth on each side, the apex acute or obtuse. Inflorescences terminal, (the branching pattern of well-developed plants ± dichasial), bisexual, (0.5-)1-2.5 cm long, usually nearly sessile and subtended by reduced leaves, with mainly 5-12 proximal solitary ♀ flowers and 4-7 solitary distal ♂ flowers; bracts greenish, linear-lanceolate to subulate, glandular-capitate, with 4 or more slender-stalked ellipsoid glands at base (representing bifid stipules), 2-5 mm long (or reduced distally). Staminate flowers with stellate-pubescent pedicels 0.5-1 mm long; calyx-lobes 5, elliptic, hispidulous-stellate, ca 1-1.5 mm long; receptacle glabrous or nearly so; stamens 11, the filaments 0.8-1.1 mm long, glabrous, the anthers elliptic, 0.4-0.5 mm long. Pistillate flowers subsessile, the stout stellate-pubescent pedicels becoming 0.5-1.5 mm long in fruit; calyx-lobes usually 4 (the 5th rudimentary or obsolete), linear...
to oblanceolate, distinctly unequal, the two larger 1.5-2.5 mm long and 0.4-1.1 mm broad, the two smaller 0.8-1.9 mm long and 0.2-0.3 mm broad (becoming somewhat larger in fruit); disc 5-angled, adnate to the base of the calyx-lobes; petals ellipsoidal, 0.2-0.3 mm long; ovary densely stellate-hispidulous, the styles connate at base or nearly free, ± erect, bifid or bipartite, 1.7-2.5 mm long, the style-branches slender, hispidulous, 1.5-1.8 mm long. Capsules subglobose, stellate-hispidulous, ca 3.5 mm diam, the columella slender, ca 2.8 mm long; seeds compressed, blackish-brown, smooth (minutely foveolate-reticulate), minutely beaked, 2.6-3.1 mm long, 1.8-2.3 mm broad, the caruncle broadly ovate, 0.4-0.6 mm long, 0.7-1.6 mm broad.

Widespread in disturbed habitats in tropical America.

**Canal Zone:** Balboa, Macbride & Featherstone 28 (F), 35 (F, GH), Standley 32152 (US); id., Sosa Hill, Standley 25276 (US); Barro Colorado I, Ebinger 245 (MO), 297 (MO); Gamboa, Greenman & Greenman 3158 (MO); Howard Air Force Base, SE of Kobbe Beach, Oliver & MacBryde 1878 (DAV, GH, MO); Miraflores Bridge, Dwyer 1004 (MO); Miraflores Locks, Stern et al. 76 (DAV, MO); Sosa Hill, Duke 4690 (DAV, MO); Darien: vic of Boquete, Ilanos Francia, Stern et al. 1209 (DAV, MO); Tole, Tyson et al. 4217 (MO). **Colón (?):** betw Las Margaritas and El Valle, Woodson et al. 1270 (A, MO, NY). **Panama:** vic of Chepo, Camino del Boticario, Pittier 4691 (US); Juan Franco, Bro. Heriberto 270 (US); sabanas N of Panama City, Bro. Paul 543 (US); San José I, East Harbor, Erlanson 246 (NY, US); id., Main Camp, Johnston 999 (GH).

Most of the reports of *Croton glandulosus* L. from Panama represent the present species (a smaller proportion prove to be *C. trinitatis*). No authentic Panamanian specimen of *C. glandulosus* has been seen, so that the species cannot be accepted as a member of the flora, although it may possibly be introduced in the future.

Despite the prevailing tendency of botanists to treat *C. hirtus* as a synonym of *C. glandulosus* (mainly due, one suspects, to the influence of Mueller's treatment), the two taxa are actually quite distinct. *Croton glandulosus* diverges sharply from *C. hirtus* in lacking the conspicuous hispid pubescence on the stems, and further differs in its sessile petiolar glands, less conspicuously toothed leaf-blades, and glandless floral bracts.

12. **Croton lobatus** L., Sp. Pl. 1005, 1753.—Fig. 9(I).


*Croton lobatus* & *seemannii* (KL) Muell.-Arg. in D.C., Prodr. 15(2): 669, 1866.

**Annual herb** becoming mostly 5-10 dm high; monoecious; stems sparsely stellate, soon glabrate. **Leaves** membranous, petioles stellate-pubescent, glabrescent, (2-)4-8 cm long, the glands at apex of petiole several on the ventral side, globular, minute (ca 0.1-0.15 mm wide); stipules lanceolate to setaceous, acute or acuminate, subentire, ca 0.7-2.5 mm long; blades deeply lobed into 3(-5) elliptic-lanceolate to obovate-lanceolate acuminate lobes, ca 3-7 cm long, 5-9 cm broad, hispidulous-strigose on both sides with a few scattered stellate hairs beneath, obscurely glandular-punctate; blades 3-5-nerved at base, lobes with ca 5-8 veins on each side, the base truncate to broadly cordate, the margins rather coarsely serrate or crenate,
central lobe with ca 5-20 teeth on each side. Inflorescences terminal but sometimes appearing axillary, bisexual, racemiform, mostly 7-15 cm long, with (1-)3-7 solitary ¥ flowers at proximal axils, cymules of 2-4 ç flowers at the 5-12 distal axils; bracts lanceolate, greenish, somewhat pubescent, often with basal lobes, ca 1-2.5 mm long under the ¥ flowers, somewhat smaller under the ç. Staminate flowers with glabrous pedicels ca 1.5-2.5 mm long; calyx-lobes 5, distinctly imbricate, elliptic, rounded at the tip, glabrous or very sparsely hispid, 1-1.2 mm long, 0.8-1 mm broad; receptacle glabrous; petals elliptic, glabrous, not punctate, 1.2-1.5 mm long, 0.5-1 mm broad; stamens (8-)12-15, the filaments glabrous, 0.9-1 mm long, the anthers broader than long, ca 0.3 × 0.4-0.5 mm. Pistillate flowers sub-sessile, the stellate pedicel becoming ca 2-3 mm long in fruit; calyx-segments 5, valvate, subequal or somewhat unequal, oblanceolate to linear, acute, greenish, sparsely hispidulous, ca 4.5-5.5 mm long, 1-1.5 mm broad, toothed with stalked glands in the lower half; disc dissected into 5 reniform segments ca 0.3-0.4 mm wide; ovary sparsely to densely pubescent with stellate and/or simple hairs, the styles essentially free, spreading, strigose-hispidulous, quadrifid in the distal half, glabrous or stellate-hispidulous, 2.5-3.5 mm long, the slender subulate branches 0.7-2.2 mm long. Capsules subglobose, 3-lobed, sparsely stellate, ca 6-6.5 mm in diam, the columella slender, ca 4 mm long; seeds oblong, tetragonal, brownish or fuscous, apically beaked, prominently rugulose-costate, 4.1-4.4 mm long, 2.2-3 mm broad, the caruncle reniform-peltate, 1.2-1.5 mm long and 1.9-2.2 mm broad when fully expanded (but often shrunk to smaller dimensions).

Common in weedy habitats, southern Florida and the Bahamas south to Peru and Brazil.

**Canal Zone:** vic of Rio Cocoi, Rd K-9, Stern et al. 346 (DAV, MO). **Panama:** Rio Abajo, Bro. Heriberto 284 (GH, NY, US).

The Panamanian population of this widespread weed was referred to var. secmannii by Mueller, but that variety appears to be synonymous with var. lobatus, since Linnaeus founded his species on a similar plant from Vera Cruz, Mexico. The Central American and West Indian populations of this species may prove to comprise a single geographic race characterized by glabrous to sparsely pubescent ovary and predominantly simple hairs on the upper leaf surface.


**C. maritimus** Walter, Fl. Carol. 239, 1788.

**Shrub** with spreading, flexible ± succulent branches, less than 1 m high; monoeious; twigs with dense indumentum of lepidote (but deeply lobed) scales. **Leaves** thickish; stoutish lepidote petioles 7-20 mm long, the petiolar glands and stipules absent; blades flexible-leathery, elliptic to more commonly ovate, ca 2-4 cm long, 1.2-3 cm broad, greenish and closely stellate-lepidote above (the scales ca 0.3-0.5 mm wide, with the 10-15 radii barely fused at base), pale and silvery-lepidote beneath (the densely overlapping scales ca 0.6-0.7 mm wide with ca 15-20
radii united \( \frac{1}{4} \) to \( \frac{1}{3} \) their length); blades 3-5-nerved at base, the other veins completely indistinct, the base rounded to subcordate, the margins entire, the apex acute. Inflorescences terminal, bisexual (reduced ones sometimes unisexual), distinctly pedunculate, ca 1-2 cm long, with 1 (rarely 2) basal \( \varphi \) flower and a pedunculate terminal capitulum of ca 4-6 \( \varphi \) flowers; bracts stellate-lepidote, caducous and inconspicuous, not over ca 1 mm long. Stamine flowers sub sessile or with short stout pedicels less than 1 mm long; calyx-lobes 5, imbricate, ovate to elliptic, obtuse, lepidote on the back, villose on the margins, ca 2.5 mm long and 1.2-1.6 mm broad; receptacle pilose; petals absent; stamens 10-12, the filaments hirsutulous, up to 1.5 mm long, the anthers elliptic, 0.8-0.9 mm long, the connectives pustulate. Pistillate flowers sub sessile, the stout pedicel only ca 1 mm long in fruit (fruits superficially appearing pedunculate when at the end of the inflorescence peduncle); calyx-lobes 5, subequal, imbricate, ovate to triangular, lepidote, entire, becoming 3-3.5 mm long, 1.8-2.3 mm broad; disc annular, adnate to the base of the calyx, 2.8-3.2 mm wide; petals absent; ovary densely lepidote (scales with ca 12-20 radii connate less than \( \frac{1}{3} \) their lengths, ca 0.5-0.9 mm wide), the styles free, spreading, 3 times bifid, stellate-lepidote below, ca 1.5-2 mm long. Capsules sub globose, 3-lobed, stellate-lepidote, ca 7-8 mm broad, the columella apically dilated-alate, ca 4-4.5 mm long; seeds plump, ovoidal, grayish or silvery with brownish spots or mottling, sparsely and deciduously stellate, 4.9-5.1 mm long, 3.9-4.2 mm broad, the caruncle massive, convex, subentire, ca 2.5 mm wide.

Deep sand on marine beaches, North Carolina south to Panama, with outliers in Bermuda and Cuba.

BOCAS DEL TORO: beach at Bar Mouth, Changuinola Valley, Dunlap 521 (F). CANAL ZONE: beach, vic of Fort Sherman, Standley 31196 (US). COLÓN: Colón, Riley 103 (US); beach nr Viento Frio, Pittier 4112 (US).

The distribution of this distinctive species is rather curious, since it forms a nearly continuous population (where substrates permit) along the entire Atlantic and Gulf coasts of the North American mainland, but offshore has invaded only Bermuda and western Cuba, being absent from areas such as the Bahamas where it might well be expected. The Panamanian plants, which represent the southernmost extension of the species and the section to which it belongs, appear very similar in all respects to those in North Carolina, at the opposite end of the range.

10. CAPERONIA

Caperonia St.-Hil., Hist. Pl. Remarq. Brésil 244, 1824.

Ditaxis sect. Caperonia (St.-Hil.) Baillon, Adansonia 4: 272, 1865.

Herbs, annual or perennial, sometimes rhizomatous or suffruticose; monocious (in Panamanian species). Leaves alternate, petiolate, stipulate; blade pinnately or palmately veined, margin serrate. Inflorescences axillary, usually bisexual, racemiform or spiciform, with 1-5 basal pistillate and several distal stamine flowers; bracts subtending solitary flowers. Stamine flowers with pedicels articulate; calyx usually 5-lobed, valvate in the bud; petals 5, often unequal, basally
adnate to the staminal column; disc absent; stamens 10, in 2 superposed whorls of 5, the anthers dehiscing longitudinally; pollen grains ± oblate-spheroidal, reticulate, 6-colporate (in Panamanian species), germ pores large; pistillode present. *Pistillate flowers* sessile or sometimes short-pedicellate; calyx-lobes typically 5, with 0-5 smaller supernumerary lobes; disc obsolete; ovary of 3 carpels, muricate and sometimes hispidulous as well, the ovules 1 per locule, the styles 3, ± deeply 3-7-lobed. *Fruits* capsular, verruculose; seeds spheroidal, ecarunculate, minutely foveolate, with narrow raphe, the endosperm copious, the cotyledons broader than radicle.

A predominantly American genus of 35-40 species, related to *Argythamnia* but separable by its glandular pubescence, leaf venation, pistillode-bearing staminate flowers, pollen grains, seed ornamentation, and chromosome number.

The taxa of *Caperonia* in Panama show the rather bewildering kind of variation they display elsewhere, and no less than 6 species have been proposed on the basis of Panamanian specimens. It is possible that some of the apparent variability is due to hybridization between *C. paludosa* and *C. palustris*, but there is really no convincing evidence for this. All of our taxa belong to sect. *Caperonia*; plants of sect. *Aculeolata* Pax & Hoffmann are strictly South American. *Caperonia castaneifolia* (L.) St.-Hil. has not been encountered in Panama; the records of it by Klotzsch (in Seemann, Bot. Voy. Herald 103, 1853) and Hemsley (Biol. Centr.-Amer. Bot. 3: 120, 1883) appear to have been founded on misdetermined specimens of *C. palustris*. Nevertheless, since it is very widespread in tropical America, it may eventually be detected in Panama. It may be distinguished by its complete lack of gland-tipped setae, ovate stipules, and subequal petals (the staminate exserted considerably beyond the calyx).

a. *Pistillate flowers* distinctly pedicellate (pedicel in fruit over 2 mm long); ovary hispidulous as well as muricate; styles 3-lobed; pistillode in 3 flowers entire; leaves closely and shallowly toothed ..............................1. *C. neglecta*

aa. *Pistillate flowers* sessile or nearly so (pedicel in fruit less than 1 mm long); styles mostly 5-7-lobed; pistillode in 3 flower apically lobed; leaves more sharply and remotely toothed.

b. Ovary muricate but not hispidulous; stipules lanceolate (mostly 2.5-5 times as long as broad); pistillate petals subequal, shorter than the calyx; stems and calyx-lanceolate. ..............................2. *C. palustris*

bb. Ovary hispidulous as well as muricate; stipules more or less ovate (mostly 1.5-2.5 cm long as broad); pistillate petals equaling or exceeding the calyx; stems with appressed non-glandular hairs only, the calyx with a few marginal gland-tipped setae; leaves narrowly lanceolate to linear. 3. *C. paludosa*


*Annual herb* with distinct taproot, ca 2-5 dm high; stems moderately to copiously branched, angled, striate, densely shaggy-hirsute with gland-tipped hairs and hispidulous-strigose with appressed sharp-pointed hairs. *Leaves* membranous; petioles pubescent ca 1.5-5.5 mm long; stipules lanceolate, ciliate with sharp-pointed hairs, ca 1.5-4.5 mm long, 0.4-0.9 mm broad; blades mostly elliptic, mostly 3-7 cm long and 1-3 cm broad, pubescent on both sides with both gland-
ular and pointed hairs, the veins and midrib raised on both sides, the secondary veins parallel and at right angles to primary ones (venation thus ± scalariform), the base obtuse or rounded, the margins shallowly serrate with mostly 15-30 teeth, the apex evenly narrowed or tapering to an acute point. Racemes 1.5-3 cm long, with 1-3 basal ♀ and several distal ♂ flowers; rachis pubescent as the stem; bracts with sharp hairs at the apex and on the margins. Staminate flowers with short hispidulous pedicels; calyx-lobes unequal (3 of them smaller and less deeply cut), sparingly hispidulous, 1-veined, acute or apiculate; petals obovate, distinctly unequal, the 3 larger ones ca 1.5-1.8 mm long and 0.6-0.8 mm broad, the two smaller ones ca 1.1-1.3 mm long and 0.5-0.6 mm broad; upper stamens with filaments about as long as or longer than the anthers, the lower stamens with filaments shorter than anthers, the anthers 0.3-0.4 mm long; pistillode entire, rounded, ca 0.25-0.3 mm long. Pistillate flowers with hispidulous pedicels becoming 2.4-2.7 mm long in fruit; calyx-lobes 5, subequal, convexly rounded on the back, tipped with a sharp seta, margins with gland-tipped and with sharp hairs, in fruit ca 1.5-2.2 mm long and distinctly longitudinally ribbed; petals subequal, narrowly elliptic, 1.2-1.6 mm long, 0.3-0.5 mm broad, exserted beyond the calyx-lobes; ovary densely hispidulous proximally, muricate distally, the styles ca 1 mm long, deeply 3-lobed, the lobes rather slender. Capsules 4.5-5.5 mm broad, greenish with reddish verrucae, the columella ca 1.5 mm long; seeds spheroidal, fuscous-brown, 2.3-2.7 mm in diam.

Known only from a few weedy localities in Panama.

**CANAL ZONE:** Corozal, brushy slope, Standley 27376 (US), 27386 (US). **PANAMA:** Camino del Boticario, near Chepo, Pittier 4545 (holotype US); Tumba Muerto Rd, nr Panama, grassy field, Standley 29769 (US); id., moist woods, Standley 29815 (US).

Pittier collected the type specimen of this species at the same locality with *C. palustris* and *C. paludosa*; but his specimen was annotated by Kathe Hoffman as *C. palustris*; Standley labeled his collections the same. Due to its copious glandular pubescence and many-toothed blades, *C. neglecta* does superficially resemble *C. palustris*, but is easily separated by its hispidulous ovary and unequal male petals. In many ways, *C. neglecta* is intermediate between the other two Panamanian species, having leaves and glandular hairs similar to those of *C. palustris* but the petals and hispidulous ovary of *C. paludosa*. This, and the sporadic occurrence of *C. neglecta* sometimes in association with the other 2 species, suggests the possibility of its being a hybrid between them. Against this, however, must be set the fact that *C. neglecta* has some unique characters not represented in either of its two Panamanian congensers, especially its pedicellate pistillate flowers and unlobed pistillode. Furthermore, it appears to produce viable pollen and seeds. There seems to be no sufficient reason, therefore, not to recognize it as a distinct species; but these questions certainly indicate the desirability of a thorough field study of the *Caperonia* populations in the savannas of western Panama province.

Croton palustris L., Sp. Pl. 1004, 1753.

Herb, usually annual, taprooted and also often rooting at the lower nodes; stems erect, suberete, striate, sometimes fistulose, usually not with prominent aerenchyma at base, ca 3-10 dm high, hirsute with gland-tipped hairs intermixed with appressed, relatively inconspicuous, sharp-pointed hairs. Leaves membranous; petioles 1.5-2.5 mm long, usually hispidulous and prominently pubescent with glandular hairs; stipules lanceolate, 2-4.5 mm long, 0.5-1.1 mm broad, often marginally ciliate with glandular and/or non-glandular hairs; blades variable in shape (ovate or elliptic to lanceolate or even linear lanceolate), mostly 4-10(-12) cm long, 0.5-5 cm broad, sparsely pubescent (with both glandular and non-glandular hairs) to glabrate on both sides, the midrib and veins (ca 6-15 on a side) prominent, the primary veins straight, the secondaries tenuous, perpendicular to primaries (venation thus ± scalariform), the base obtuse or rounded to subcordate, the margins rather sharply serrate and minutely scabrous, with ca (10-)15-35 teeth on a side, the apex broadly rounded to more often distinctly narrowed or pointed. Racemes spiciform, mostly 4-7 cm long, with (1-)2 or 3(-5) basal \( \varphi \) and several distal \( \varphi \) flowers; rachis hispidulous throughout, usually with glandular setae at least on the peduncle; bracts acute, persistent, glabrous. Staminate flowers with short glabrous pedicels; calyx glabrous, acutely lobed; petals 5, subequal, obovate, ca 1.5 mm long; stamens 10, the upper filaments as long as or longer than anthers, the lower filaments nearly contiguous to upper ones, shorter than the anthers, the anthers ca 0.5 mm long; pistilode apically 2-4-lobed, 0.6-0.8 mm high. Pistillate flowers subsessile, the very short glabrous pedicels less than 1 mm long even in fruit; calyx-lobes 5-9, usually unequal (with 4-6 larger inner lobes and 1-4 smaller outer ones), flattened, thin, not ribbed, acute, ordinarily copiously glandular-hirsute on margins and back, the longer ones ca 3.5-5 mm long in fruit; petals subequal, narrowly elliptic, pointed, (0.8-)1.3-1.9 mm long, 0.3-0.7 mm broad, not exserted beyond the calyx-lobes, ± deciduous; ovary glabrous proximally, densely glandular-muricate distally, the styles 1.1-1.7 mm long, usually deeply 5-7-lobed, the lobes slender. Capsules 5.1-5.7 mm in diam, stramineous-green with dark green verrucae; seeds spheroidal, fuscous, 2.4-2.7 mm in diam.

A widespread neotropical weed, usually of ditches, swamps, and other wet habitats, occurring from Florida and Louisiana south to Argentina and Uruguay.

**CANAL ZONE:** Balboa, Standley 26108 (US); Chiva-Chiva trail nr Mirafores Lake, Tyson 1383 (MO); Coco Solo, Elias & Kirkbride 1623 (GH, MO, US); Empire, Pittier 3728 (GH, US); Fort Kobbe, Duke 3959 (DAV, MO); France Field to Catival, Standley 30256 (US); Gamboa, Standley 28466 (US); Gatun, Duke 4303 (DAV, MO), Piper 5998 (US); Gorgas Lab, White 145 (F, MO); vic of Summit, Standley 26965 (US), Tyson & Blum 1993 (MO). **COLON:** vic of Sardinilla, 7-8 mi E of cement plant, Blum & Tyson 482 (MO). **DARIEN:** vic of El Real, Duke 4854 (MO) Stern et al. 617 (MO). **LOS SANTOS:** 3 mi S of Carreta, Burch et al. 1252 (MO). **PANAMA:** Camino de Las Sabanas, Bro. Heriberto 202 (GH, US); 5-6 mi E of Chepo, Duke 4034 (MO), 4035 (DAV, MO), Pittier 4546 (US); vic of El Llano, Duke 5500 (MO); Pacora, Woodson et al. 734 (F, MO); Panama, Juan Franco Racetrack, Standley 27683 (US); Rio Tater, Woodson & Scherly 595 (MO); San José I, Johnston 1042 (GH); Tocumen, Dwyer 1852 (MO). **PROVINCE UNKNOWN:** S. loc., Hayes 703 (K).
In Panama, this aggressive and highly variable weed has been found in gardens, fields, roadsidens, and swamps, often occurring together with C. paludosa. Some of the extremely narrowly-leaved variants of C. palustris suggest possible hybridization with C. paludosa, but other characters do not provide any convincing support for such a hypothesis.

Prain (in Fl. Trop. Afr. 6(1): 831, 1912) reported C. latifolia Pax from Panama on the basis of Hayes 703. However, examination of this specimen at Kew shows it is clearly a plant of C. palustris.

3. Caperonia paludosa Kl., London Jour. Bot. 2: 51, 1843.—Fig. 10.

C. stenomeris Blake, loc. cit.

Herb to 6 dm high, sometimes woody at the base; stems suberete, striate, often hollow-fistulose, sparingly hispidulous-strigose when young, soon glabrate, branches weak and often straggling. Leaves membranous or chartaceous; petioles usually hispidulous, 1-7 mm long; stipules ovate or triangular, 0.8-2.5 mm long, 0.5-1.1 mm broad (ca 1-2 times as long as broad), entire or marginally and apically hispidulous, not becoming reflexed; blades narrowly lanceolate to linear, ca 4-12 cm long, 2-7 mm broad, glabrous except for a few appressed hairs on midrib and veins, the primary veins ca 6-15 on a side, the secondaries ± perpendicular but often inconspicuously or invisible, the base narrow or rounded, the margins remotely and inconspicuously to sharply serrate, with ca 6-20 teeth on a side (sometimes subentire), the apex acute to acuminate. Racemes spiciform, 1.5-3 cm long, with 1 or (less commonly) 2 basal ℹ flowers; rachis appressed-hispidulous; bracts acute, entire or marginally hispidulous. Staminate flowers with short glabrous or hispidulous pedicels; calyx-lobes subequal, ca 1.4-1.5 mm long, acute, glabrous; petals obovate, subequal, or sometimes unequal, 1.2-2.2 mm long, 0.5-1 mm broad, the upper filaments longer than anthers, the lower shorter to slightly longer than the anthers, the anthers 0.4-0.5 mm long; pistillode cylindric, shallowly 3-lobed (sometimes barely emarginate), 0.4-0.9 mm long. Pistillate flowers subsessile, the glabrous pedicels less than 1 mm long in fruit; calyx-lobes 5 or 6 with 0-3 smaller outer lobes (or sometimes calyx of 3 large inner and 3 small outer lobes), flattish, thin, not ribbed, acute, sparsely glandular-setulose on the margins, to ca 2.5 mm long in fruit; petals subequal, equaling or exceeding the calyx-lobes at anthesis, 1.2-3 mm long, 0.6-1 mm broad; ovary strigose proximally, densely glandular-muricate distally, the styles ca 1.5 mm long or less, 4-5-lobed ½ to ⅔ their length, the lobes rather thick and fleshy. Capsules 4.8-5.1 mm in diam, strigose and muricate; seeds spheroidal, ca 2.4 mm long.

Marshes, swamps, and savannas, eastern Mexico to the Guianas.

Canal zone: betw Fort Clayton & Corozal, Standley 29093 (US). Ooclé: Aguadulce, Pittier 4922 (US); Las Margaritas to El Valle, Woodson et al. 1750 (F, GH, MO); Penonomé, Williams 212 (NY). Panama: Camino del Boticario, Chepo, Pittier 4547 (iso-
Fig. 10. Caperonia paludosa Kl.: A, habit (X1/4); B, male flower (X10); C, stamens (X20); D, female flower (X12); E, ovary (X15); F, fruit (X6); G, seed (X8). A-E after Woodson et al. 735 (MO); F-G after Dodge et al. 16912 (MO).
type of *C. panamensis* Pax & Hoffm., (US); La Joya, nr pond, Dodge *et al.* 16912 (MO); Juan Diaz, Standley 26224 (US); Las Sabanas, *Bro. Heriberto* 293 (NY, US), Killip 3121 pro parte (US); Matías Hernández, Pittier 6927 (holotype of *C. angusta*, US), Standley 28910 (US), 31987 (US); Nuevo San Francisco, Standley 30765 (US); wet savannas E of Pacora, Woodson *et al.* 735 (A, F, MO, NY); ditches & wet savannas nr Panama, Hayes 714 (K, NY); swamps nr Panamá, Seemann 119 (type coll. of *C. panamensis* Kl., K, BM); Rio Tapia, Juan Diaz, Killip 3121 pro parte (NY); Rio Tocumen, Standley 26571 (US).

The variable Panamanian populations of this species have been confusingly treated in the literature, and the synonymy has become excessively involved. However, despite the application of 4 names (2 of these fortuitously identical), only a single narrow-leaved species seems present in Panama, and it does not appear to be specifically different from the widespread *C. paludosa*. Mueller (in DC, *Prodr.* 15(2): 755, 1866) and Pax [Pfanzenreich 57 (IV, VI): 35, 1912] may have partially initiated the confusion by describing the pistillate flowers of *C. paludosa* as having rudimentary petals. In fact, however, examination of the type collection of *C. paludosa* (Schomburgk 109, K) shows that the pistillate flowers have petals ca 1.5-2 mm long, and are also well developed in the type collection of *C. panamensis* Kl. (Seemann 119, K). The petals are early deciduous in *C. paludosa*, which may account for these mistakes of description, and for the curious error made by Pax and Hoffmann in redescribing Klotzsch’s species under the same specific epithet.

Blake compounded all the confusion by uselessly renaming *C. panamensis* Pax & Hoffmann as *C. stenomeres*, and by proposing an additional species of *C. angusta* on the basis of a variant specimen (Pittier 6927, US) with 7-8-lobed pistillate calyx and a distinctly trilobed pistillode. Most of the Panamanian collections, however, resemble the type of *C. panamensis* Pax & Hoffmann in having the pistillate calyx 5- or 6-lobed. In any event, the plants with 7 or 8 pistillate calyx-lobes do not seem to be specifically distinct; whether the large number might be due to crossing with *C. palustris* must be tested by field observations.

11. ARGYTHAMNIA


Shrubs or herbs; monoecious (rarely dioecious); stems and foliage with indumentum of bifurcate (malpighiacous) hairs, often with purplish pigment. Leaves alternate; petioles short; stipules small; blades not glandular, entire or dentate. Inflorescences short, racemiform, bisexual, with one to several basal ♀ flowers; bracts small, subtending single flowers. Staminate flowers with calyx usually 5-lobed, valvate in the bud; petals 5, clawed at base, ± adnate to base of staminal column; disc dissected, segments opposite the calyx-lobes; stamens 5-15, monadelphous, the anthers 1-2(-3) seriate, 1-3 filiform staminodia sometimes present atop the column; pollen grains oblate, tectate, 3- or 4-colporate, bilaterally symmetrical; pistillode absent. Pistillate flowers with calyx 5-parted,
the lobes imbricate; petals 5, imbricate, entire, sometimes reduced; disc ± dissected into sometimes elongated segments; ovary of 3 carpels, the ovules 1 in each locule, the styles free or basally connate, the style-branches ± dilated at the tips. Fruits capsular; seeds subglobose, foveolate to reticulate, ecarunculate, endosperm present, the embryo straight, the cotyledons broader than the radicle.

An American genus of about 50 tropical or warm-temperate species, extending from southern U. S. to Argentina. The single Panamanian representative belongs to subg. Ditaxis (Vahl ex Juss.) Croiz.; a group often treated as a distinct genus because of its biseriate androecium of approximately 10 stamens.


**Shrub**; twigs with pale bark, densely pubescent when young, then glabrate. **Leaves** chartaceous; petioles 3-5 mm long; stipules ca 2-3.5 mm long, triangular, subulate-acuminate; blades lanceolate, 7-10 cm long, 2.5-4 cm broad, sericeous when young, glabrate above, pinnately veined, the base acute, the apex acuminate. **Racemes** 2-4.5 cm long, with 1 or 2 ♂ flowers and 3 or 4 ♀ flowers; rachis strigose; bracts ovate, acute, ca 3 mm long, pilose. **Staminate flowers** with pilose pedicels ca 2 mm long; calyx-lobes narrowly ob lanceolate, acuminate, pubescent, 5-5.7 mm long; petals oblanceolate, acute, ca 6-7 mm long, dorsally sericeous, ventrally with sparse indument, exserted beyond the calyx; disc-segments obscure; stamens 10, the anthers biseriate, ca 0.6-0.7 mm long, the staminal column ca 3.5 cm long, the filaments and the 4 or 5 staminodes pilose. **Pistillate flowers** with pedicels 1-2 cm long; calyx-lobes ovate, acuminate, becoming 7-9 mm long, pubescent; petals as in ♂, but shorter than the calyx (ca 4 mm long), pilose; disc-segments thick, glabrous; ovary densely sericeous, the styles ca 1.5 mm long, connate beyond the middle, pilose, bifid, the lobes dilated. **Capsules** (ex Pax & Hoffm., op. cit.) pilose, 6 mm long.

Endemic to Panama.

**Panama**: dry wooded hills, Alhajuela, Pittier 2360 (type coll. US); Chagres Valley, forests on limestone, Pittier 3450 (US).

As suggested by the descriptions of Pax and Hoffmann, this species appears to be closely related to the widespread *A. polygama* (Jacquin) O. Ktze., but differs in its longer racemes and narrower ♀ petals. Studies made on a more complete series of collections (including fruiting specimens) are needed to test whether the species is in fact distinct and endemic to Panama.

12. **ADELIA**


**Trees** or shrubs; dioecious; twigs often spinescent; indumentum of simple non-glandular trichomes. **Leaves** alternate, petiolate; stipules inconspicuous;
blades pinnately veined, eglandular, entire. Inflorescences axillary, glomerulate; flowers apetalous. Staminate flowers pedicellate; calyx-lobes 4 or 5, valvate; disc annular, thickened and fleshy; stamens 8-17, monadelphous at least at base (often appearing free in bud), the filaments slender, longer than the anthers; pollen grains 3-4-colpate, tectate, colpi operculate; pistillode minute or obsolete. Pistillate flowers long-pedicellate; calyx-lobes mostly 5 or 6, reflexed at anthesis; disc as in ♂; ovary usually of 3 carpels, pubescent, the ovules 1 per locule, the styles free or united at the base, deeply lacerate. Fruits capsular, dehiscing to leave a persistent columella; seeds smooth, ecarunculate, the endosperm fleshy, the embryo with broad thin cotyledons and short radicle.

A neotropical genus of about a dozen species, distributed from Mexico and the Bahamas south to Brazil. The Caribbean species are rather difficult to distinguish, and it is possible that some reductions will have to be made. Two species have been reported from Panama, but one of these is known only from a single incomplete collection, and its status is still not clear.

1. **Adelia triloba** (Muell.-Arg.) Hemsley, Biol. Centr.-Amer. Bot. 3: 130, 1883.—Fig. 11.


**Shrub** or tree up to 15 m high; dioecious; trunk slender to 2 dm thick; twigs pale, smooth, terete, with inconspicuous lenticels, not spinescent. *Leaves* chartaceous; petioles glabrate, ca 4-9 mm long; stipules lanceolate, inconspicuous, 1 mm long or less; blades elliptic to obovate, mostly 5-20 cm long, 2-7 cm broad, glabrous except for tufts of straight simple hairs in the axils of main veins beneath (rarely entirely glabrous), the major veins ca 5-8 on a side, straight, distinctly raised beneath, the veinlets forming a conspicuous reticulum beneath, the base tapering, narrowly-rounded to subcordate, the margins entire, the apex abruptly cuspidate-acuminate (acumen mostly 1-1.5 cm long). Inflorescences glomerulate, several to many flowers of each sex in dense axillary clusters. Staminate flowers with slender pubescent pedicels mostly 4-7 mm long; calyx-lobes 5, elliptic, pointed, ca 2-2.3 mm long, pubescent outside; disc fleshy, ca 1-1.3 mm in diam; stamens mostly 13-16, in 2 or more whorls (often 8 or 9 at base, 5 or 6 at the top), the filaments connate into a column ca 0.5-1 mm high, terminated by a pistillode, the filament tips slender, ca 1-1.5 mm long, the anthers blunt, ca 0.4 mm long. Pistillate flowers with glabrate pedicels becoming 2-7 cm long in fruit; calyx-lobes 6, lanceolate to linear-lanceolate, blunt or acute, 3-6.5 mm long, pubescent; disc as in ♂; ovary densely pubescent, the styles free, or shortly connate basally, spreading, deeply fimbriate-lacerate, ca (1.2-)1.5-3.5 mm long. Capsules trigonous, deeply emarginate-depressed at the top (coci connate only in lower ½ or ⅔), 7-11 mm in diam, 5.8-7.5 mm high, pubescent; columella slender, ± purplish-tinted, 3-pronged at tip, 3.5-4 mm long; seeds subspheroidal or sometimes distinctly oblate, 3.1-4.1 mm long, 3.4-4 mm in diam, smooth, grayish or waxy-whitened, with distinct raphe.
Fig. 11. *Adelia triloba* (Muell.-Arg.) Hemsley: A, habit (×1/2); B, female flower (×6); C, fruit, top view (×2); D, fruit, side view (×2); E, seed (×4). A-B after Blum & Dwyer 2106 (MO); C-E after Tyson 3493 (MO).
BOCAS DEL TORO: Almirante, Daytonia Farm, Cooper 394 (F); id., Cooper 428 (NY, US), 431 (A, F, GH, US); Changuinola Valley, Dunlap 218 (F, US), 434 (F); Water Valley, von Wedel 1541 (GH, MO). CANAL ZONE: Barro Colorado I, Shattuck 748 (F), 806 (F, MO), Wetmore & Abbe 35 (A, GH), 145 (GH), 153 (GH), Wilson 27 (F), Woodworth & Vestal 510 (A), 522 (A); Cerro Gordo, Pittier 2313 (US); Darien, Macbride 2696 (F), Standley 31549 (US), 31635 (US); Fort Sherman, Blum & Dwyer 2106 (MO), Johnston 1735 (GH, MO), Tyson 2106 (MO); 6 mi N of Gamboa, Tyson 3493 (MO); Gorgona to Mamei, Pittier 2249 (A, GH, US); Las Cascadas plantation, Standley 25815 (US); vic of Madden Dam, disturbed forest, Lewis et al. 4 (MO); Mamei, Hayes 498 (isotype K); Mojina Swamp, Allen 869 (MO); Quebrada Melgada, drowned forest and sabanas, Steyermark 17489 (MO, UC); Rio Agua Salud, nr Frioles, Piper 5861 (US). COCLE: Bismarck, above Penonomé, Williams 265 (NY, US). DARIEN: Garachiné, forests nr sea, Pittier 5510 (holotype of A. panamensis, US); Marraganti, Williams 638 (NY). PANAMA: Juan Díaz, Standley 30509 (US); Juan Díaz to Matías Hernández, Standley 31962 (US); Rio Tapia, Standley 30687 (US); Rio Tocumen, Standley 29447 (US).

This variable species, which is quite common in disturbed forests in the Canal Zone, is very similar to A. barbinervis Cham. & Schl. of Mexico and northern Central America. However, it clearly differs in the characteristically deeply lobed coccii of the fruit, less densely pubescent ovary, and more deeply divided styles.

The status of A. panamensis, described by Pax and Hoffmann on the basis of the single Pittier collection from Darien, is still difficult to evaluate. The spinescent branches and small leaves (ca 3-5 cm long) suggest the West Indian A. ricinella L., from which the Darien plant would appear to differ in its articulate fruiting pedicels and perhaps larger seeds. However, it should be noted that the spinescent branches and small leaves of Pittier's specimen occasionally occur in otherwise typical A. triloba (e.g. in Standley 30509 from Panama); and one specimen of A. triloba (Allen 869 from Mojina Swamp) has articulate fruiting pedicels. It is possible, therefore, that A. panamensis merely represents an aberrant variant from a drier habitat. The only distinctive character of the taxon not matched in A. triloba appears to be the large number of ♀ calyx-lobes (mostly 7-9 vs. 6 in A. triloba); but with only a single collection it is impossible to decide whether this feature characterizes a distinct population. Until further collections, including ♀ flowers, can be made in the area it seems best tentatively to regard A. panamensis as a local variation of A. triloba.

The resemblance of the type collection of A. panamensis to the West Indian A. ricinella brings up a further perplexing difficulty. Although it differs from A. triloba in various tendencies (e.g. more pronounced spininess, smaller leaves and seeds), A. ricinella is extremely close overall and not sharply separable by any one character (except possibly the fruit, if the capsules of the West Indian plants, not seen entire, prove not to be deeply trilobed). It might be more reasonable to treat these two taxa as allopatric subspecies of a single species.
13. BERNARDIA


Shrubs or subshrubs; monoecious or dioecious; indumentum of simple or stellate hairs. Leaves alternate, petiolate or subsessile, stipulate; blades pinnately veined (or trinerved at base), often with basal glands, (usually dentate). Inflorescences spike-like, unisexual when monoecious; ♀ flowers in elongate or contracted axillary spikes; ♂ flowers in usually few-flowered axillary or pseudo-terminal spikes; bracts subtending 1 ♀ or several ♂ flowers. Stamine flowers sessile or with short pedicels; calyx globose and entire in bud, splitting into 3 or 4 valvate lobes at anthesis; petals absent; disc absent or of minute interstaminal processes; stamens 3-20 or more, the filaments free, erect, the anthers dehiscing vertically; pollen grains 3-colporate, dehiscence, columnella persistent; seeds not carunculate, the endosperm fleshy, the cotyledons broad and flat.

A neotropical genus of 30 to 40 species, most highly developed in Brazil. Several species are known from Mexico, but only two from Panama, and only one other (B. brandegei Millsp.) has been reported from Central America.

a. Leaves oblanceolate to obovate, acuminate but not abruptly so, rather finely serrate (teeth ca 30-60 per side); basal foliar glands usually 2, inconspicuous above .................................................. 1. Bernardia macrophylla

aa. Leaves spatulate, abruptly cuspidate-acuminate, remotely serrulate (teeth ca 15-25 per side); basal foliar glands usually 4-6, conspicuous above ...... 2. B. denticulata


Shrub to 3 m high; dioecious; young stems suberete, pubescent with straight, unbranched, mostly antrorse hairs. Leaves thin; petioles densely pubescent, 5-10 mm long; stipules subulate-lanceolate, (1-)1.7-2.1 mm long, 0.5-1 mm broad, densely pubescent; blades obovate or oblanceolate, mostly 12-20 cm long, 3.5-7.5 cm broad, with sharp unicellular hairs on both faces, the basal glands usually 2, inconspicuous above, the midrib and veins prominently raised beneath, the primary veins mostly 9-12 on a side, straight, the veinlets at right angles to primaries, the base narrowed, acute, the margins shallowly crenate-dentate, with ca 30-60 teeth per side, the apex acuminate. Inflorescences unisexual; ♀ flowers in contracted racemes, ♀ flowers in contracted pseudoterminal spiciform racemes. Stamine flowers with calyx splitting into 4 or 5 unequal segments; calyx-lobes lanceolate, 3-veined, sparsely pubescent, 1.6-1.8 mm long, 0.7-1.1 mm broad; disc of minute dark clavate interstaminal processes; stamens 14, the filaments free, 0.9-1 mm long, the anthers ca 0.4 mm broad. Pistillate flowers sessile; calyx-lobes 5, subequal, ovate, acute, 5-veined, 1.6-1.8 mm long, 0.8-1.3 mm broad, densely pubescent outside; disc thin, cupuliform, 0.25-0.35 mm high, nearly glabrous;
ovary pubescent, the styles bifid, the lobes entire or again bifid, slightly over 0.5 mm long. Fruits not seen.

Endemic to Panama.

PANAMA: Río Tocumen, Standley 29389 (holotype US), 29380 (US), 29471 (US).

By virtue of its penninerved leaves with unbranched trichomes, this species appears to belong in sect. Polyboea (Kl.) Muell.-Arg. as defined by Pax [Pflanzenreich 63 (IV, 147, VII): 28, 1914]. Standley compared it with the West Indian B. corensis (Jacquin) Muell.-Arg., from which it differs in its larger more pubescent leaves, dioecious inflorescences, and larger stamen number. It is even closer to B. jacquiniana Muell.-Arg., which from descriptions scarcely differs except in having fewer stamens (9-12).


Tree ca 5 m high, trunk 2-2.5 dm thick; twigs antorsestrigose with simple pointed hairs ca 0.1-0.5 mm long. Leaves thinly chartaceous; petioles stout, densely hispidulous, ca 4-10 mm long; stipules not seen, apparently caducous; blades spatulate; 20-26 cm long, 4.8-8 cm broad, smooth and glabrate above with 4-6 shining roundish glands towards the base, sparsely hispidulous-strigose, the midrib and primary lateral veins (ca 7-9 on a side) raised beneath, the veinlet reticulum not very conspicuous, the base evenly tapered, narrowly acute, the margins shallowly and remotely crenulate-serrate, with mostly 15-25 teeth on a side, the tip abruptly short-acuminate. Pistillate inflorescences terminal, few-flowered, ca 1-5 cm long; ♂ inflorescences not seen. Pistillate flowers with stout sericeous pedicels ca 4 mm long in fruit; calyx-lobes 5, ovate or elliptic, sericeous, 2-2.2 mm long. Capsules not seen entire; valves of cocci ca 12-13 mm long, smooth, strigose, the columella dilated into 3 wings, ca 4.5-5 mm high, 7.5-8 mm broad; seeds plump, slightly compressed, not beaked, slightly carinate on the back, mottled dark brown against dark gray, ca 7.8-9.5 mm long.

Known only from the type collection in western Panama.

BOCAS DEL TORO: Chiriquí Trail, Buena Vista Camp, 1250 ft, Cooper 606 (holotype F; isotypes NY, Y).

The relationships of this species are still somewhat problematical, owing to the incompleteness of the single known collection. If correctly placed in Bernardia, the plant probably belongs in sect. Polyboea, but is not closely related to B. macrophylla nor to any other Bernardia in North America.
14. CLEIDION


_Trees_ or shrubs; monoecious or dioecious; with indumentum of simple hairs. _Leaves_ alternate, petiolate, stipulate; blades usually dentate, pinnately veined, often with glandular spots at the base. _Inflorescences_ axillary, thyroid or racemiform; bracts eglandular. _Staminate flowers_ ± pedicellate; calyx splitting at anthesis into 3 or 4 valvate lobes; petals and disc absent; stamens numerous (35-80), densely crowded on a convex receptacle, the anthers 4-loculate, connective ± apappendaged; pollen grains subglobose, 3-colporate, tectate, psilate; pistillode absent. _Pistillate flowers_ pedicellate; calyx-lobes 3-6, imbricate; disc and petals absent; _ovary_ of 3 (rarely 2) carpels, the ovules solitary in each locule, the styles elongated, free, bifid or bipartite. _Fruits_ capsular, of 3 (rarely 1 or 2) cocci, the columella slender; seeds roundish, ecarunculate, smooth, endosperm present, the cotyledons broad, thin.

About 20 species, mostly of southeastern Asia and Australasia, with a few species in South America and a single one in Africa. The Panamanian species is the northernmost American representative of the genus.


_Tree_ 4-5 m high; monoecious; twigs minutely scabrid-puberulous. _Leaves_ thinly chartaceous; petioles 5-23 mm long; stipules ovate-lanceolate, indurate, ca 1.5-2 mm long; blades elliptic to obovate, 7-13 cm long, 2-4.5 cm broad, minutely pustulate, glabrescent except along the veins (with tufts of hair in vein-axils along midrib), the veins ca 7 or 8 on a side, the veinlet reticulum prominulous beneath, the base cuneately narrowed, the margins crenate-serrate with 14-21 ± callose teeth on each side, the apex ± abruptly caudate-acuminate. _Inflorescences_ unisexual, axillary; ♂ racemes 5-15 cm long, rachis slender and minutely puberulous, with 2-5 flowers; ♀ thyrse (only 1 seen) ca 1 cm long, with several flowers crowded at each node. _Staminate flowers_ (seen only in bud) short-pedicellate; calyx-segments 3, elliptic, pointed, minutely sericeous-strigose externally; stamens numerous (over 50). _Pistillate flowers_ on slender pedicels becoming 10-15 mm long; calyx-lobes 6, biseriate, triangular, acuminate, sericeous, 0.9-1.2 mm long; _ovary_ of 3 carpels, sericeous, the styles ca 2.8 mm long, pubescent, bifid into 2 terete branches. _Capsules_ not seen entire, cocci ca 7.5 mm long, smooth, sparsely strigose, the columella slender, not apically dilated, 4.8-5.5 mm long; seeds roundish, plump, slightly beaked apically, 5 mm long, mottled brown-and-gray.

Endemic to Panama; known only from the type collection.

_Canal Zone:_ vic of Salamanca Hydrographic Sta, Río Pequení, ca 80 m, Woodson et al. 1587 (holotype A; isotypes MO, NY).
15. ALCHORNEA

Alchornea Sw., Prodr. 98, 1788; Fl. Ind. Occ. 2: 1153, t. 24, 1800.

Trees or shrubs; dioecious (in Panamanian species); indumentum of simple or stellate trichomes. Leaves alternate, petiolate, inconspicuously stipulate; blades pinnately or palmately veined (often triplinerved), commonly with glandular spots near the base, generally dentate. Inflorescences axillary, of spiciform racemes, the ♂ racemes often compound; bracts eglandular, each subtending 1-3 ♀ or 1-several ♂ flowers. Staminate flowers subsessile with calyx splitting at anthesis into 2-5 valvate lobes; petals absent; disc central, confluent with bases of stamens; stamens (in local species) usually 8, in 2 whorls of 4, the filaments short, the anthers dehiscing intorsely and longitudinally; pollen grains spheroidal, 3-colporate, colpi operculate; pistillode absent. Pistillate flowers sessile to short-pedicellate; calyx-lobes usually 4, imbricate; petals absent; disc obsolete; ovary of 2 carpels, ovules 1 per locule, the styles elongated, free, undivided. Fruits capsular, dicoccous, the columella persistent; seeds tuberculate, ecarunculate, with prominent ventral raphe, endosperm present, the cotyledons broad, thin, not curved.

In the narrow circumscription of Pax and Hoffmann [Pflanzenreich 63 (IV, 147, VII): 220, 1914], Alchornea comprises about 50 species, the majority of these American. As shown by Punt (Wentia 7: 82, 1962), Alchornea closely resembles such South American genera as Aparisthmium and Conceveiba in its operculate pollen grains. Critical studies may show, therefore, that Mueller (in DC, Prodr. 15(2): 899 et seq., 1866) was justified in defining the limits of Alchornea broadly.

The available Panamanian collections of Alchornea are inadequate to serve as the basis for a satisfactory treatment of the taxa. Four different species appear to be recorded at present, but additional Colombian species may be expected in Darien.

1. Alchornea costaricensis Pax & Hoffm., Pflanzenreich 63 (IV, 147, VII): 235, 1914.—Fig. 12.


Tree to 8 or 10 m high, with dense crown; twigs terete, glabrescent. Leaves chartaceous; petioles (1-)1.5-4(-9) cm long, pubescent, the hairs straight or sometimes stellate, minute; stipules very inconspicuous, less than 0.5 mm long, tri-
Fig. 12. *Alchornea costaricensis* Pax & Hoffm.: A, habit (ca \( \times \frac{1}{2} \)); B, female flower (\( \times 6 \)); C, fruit, top view (\( \times 2 \)); D, fruit, side view (\( \times 2 \)); E, seed (\( \times 4 \)). A-B after Blum 2106 (MO); C-E after Tyson 3493 (MO).
angular, pubescent; blades ovate- to elliptic-lanceolate, ca 8-15 cm long, 3-6 cm broad, stellate-pubescent when expanding, at length glabrate, usually with 2 foliar glands between midrib and basal nerves, the major veins mostly 5 or 6 on a side, basal pair nearly straight, prominently raised beneath, glabrate, the base obtuse to rounded, the margins rather sparsely crenulate-dentate (ca 6-10 glandular teeth on a side), the apex distinctly and rather abruptly acuminate (acumen ca 1-2 cm long). Spikes stellate-pubescent; ♂ axes unbranched mostly 3-8 cm long, with ca 20-30 nodes, flowers mostly 4-6 per bract; ♀ 2-8(-10) cm long, with mostly 6-15 flowers. Staminate flowers subsessile; buds oblate-subglobose, 1.2-1.5 mm in diam; calyx-lobes 3 or 4; stamens with filaments shorter than anthers, confluent with the disc, the anthers oblong or elliptic, ca 0.7-0.8 mm long. Pistillate flowers subsessile; calyx ca 1.5 mm high, 4-lobed about 1/2 way to base, densely pubescent; disc not evident; ovary ellipsoid, densely pubescent, ca 1.5 mm high, the styles distinct, unlobed, tapering to long-attenuate tips, 7.5-10 mm long, 0.7-0.9 mm wide at base, stellate-pubescent on the non-stigmatic portion. Capsules obscurely stellate or glabrate, ca 5-6 mm high, 6.5-8.5 mm broad; seeds elliptic, brownish, irregularly tuberculate, 4.8-5.3 mm long, 4.4-4.8 mm broad.

Rain forests, Costa Rica and Panama.

BOCAS DEL TORO: Carleton 163 (US); Almirante, Cooper 348 (F, NY, US), 443 (F, NY, US); Changuinola Valley, Cooper & Slater 103 (F, NY, US), 155 (US), Dunlap 23a (MO). CANAL ZONE: Christophersen 198 (type coll. of f. longispicata, US); Barro Colorado I, Aviles 950 (F), Kenoyer 660 (US), Standley 31234 (US), 41006 (US); Fort Randolph, Standley 28719 (US); Fort San Lorenzo, Tyson & Blum 3666 (MO); Fort Sherman, Standley 31039 (US); Madden Dam, Alston 8904 (BM), Dwyer & Robyns 18 (MO); Rio Paraiso, Standley 29861 (US); Summit, Standley 25805 (US); rd to Tortuguilla Cove, Johnston 1815 (MO).

This species appears to be the most common Alchornea in western Panama and the only one in the Canal Zone. Its eastern limit is still undetermined, although the meager available records suggest that it is replaced in Darien by A. triplinervia Muell.-Arg. In extreme western Panama (i.e. Bocas del Toro) A. costaricensis is sympatric with A. latifolia, a species with which it has been much confused in herbaria. The two species may ordinarily be rather easily distinguished vegetatively by texture (stiffer in A. latifolia) and leaf pubescence (vein axils barbate beneath in A. latifolia); furthermore, the ♂ spikes of A. costaricensis are unbranched, in contrast to the compound ones of A. latifolia. Probably A. costaricensis is actually more closely related to such South American species as A. glandulosa Endl. & Poeppig; that species is very similar, although seemingly differing in its thinner leaves with a larger number of foliar glands. Possibly A. costaricensis is only a geographical race of the wide-ranging and variable A. glandulosa, but until a monographic study can be made, it seems more convenient to maintain it as distinct.


Tree ca 5-15 m high; twigs glabrous. Leaves coriaceous; petioles nearly or quite glabrous, mostly 2-5 cm long; stipules very inconspicuous; blades ovate or
elliptic, typically 8-20 cm long, 3-8 cm broad (to 30 × 20 cm on sprout-shoots), completely glabrate except for scattered stellate hairs beneath and barbate tufts of long hair in axils of major veins, foliar glands usually 2-4, near base on upper side and often paired on lower side, the major veins ca 5-8 on a side, the basal ones strongly raised beneath, extending nearly or quite half the blade length, the veinlets forming an irregular and usually very distinct reticulum, the base rounded to subcordate, the margins crenate-dentate (typically with 11-14 glandular teeth on a side), the apex obtuse to short-acuminate. Spikes axillary; ♂ spikes mostly compound, main axis typically 5-15(-30) cm long, with ca 15-25 nodes, the 4-10 lateral axes ca 0.5-3 cm long; ♀ spikes simple or with 1 or 2 basal branches, 3-20 cm long, with 8-20 flowers. Stamineate flowers sub sessile, ca 1.5 mm broad in bud; calyx-lobes 2-4, ca 1.5 mm long or less, glabrous except for a few apical hairs; stamens 8, the anthers ca 0.7-0.8 mm long. Pistillate flowers with pedicels very stout, in fruit ca 1-1.5 mm long and almost as thick, glabrous; calyx-lobes 4, lanceolate, acute or acuminate, ca 2-2.8 mm long, sparsely pubescent; ovary stellate-pubescent, the styles mostly 10-20 mm long. Capsules usually dicoccous, 5-7 mm long, 8-10 mm in diam; seeds stramineous, tuberculatc, ca 5.8-6.3 mm long, 4.8-5.6 mm broad.

Widespread in the Greater Antilles and much of Central America, mostly in rainforest.

BOCAS DEL TORO: Changuinola Valley, Cooper & Slater 134 (F, NY, US); Laguna Chiriquí, Hart 122 (US).

The specimen of Hart is the only 'typical' collection of A. latifolia seen from Panama. The collection made by Cooper & Slater is atypical in having leaves with fewer teeth and very narrow bases; however, the prominent vein reticulum and barbate leaf-axils are characteristic of A. latifolia. Certain other specimens of Alchornea from the Changuinola River valley (especially Dunlap 23a) resemble A. latifolia in leaf shape but appear to belong in A. costaricensis on the basis of most other characters. It seems possible that the 2 species may be hybridizing in western Panama, and intensive field studies there would be of much interest.


Tree to 15 m high; twigs stellate-puberulent. Leaves membranous to thinly chartaceous; petioles stellate-puberulent, 1-8 cm long; stipules 0.4-0.6 mm long, basally puberulent; blades elliptic to ovate, ca 5-15 cm long, 3-11 cm broad, early glabrate above, minutely stellate-pubescent beneath especially along the veins, with several (mostly 6-10) elliptical glandular spots near the base above, 3-veined at the base with 1-3 additional pairs of lateral veins, the veinlet reticulum prominulous beneath, the 3 major veins barbate in axils with minor laterals, the base rounded to subcordate, the margins shallowly and remotely serrulate with 6-10 glandular thickened ± incurved teeth on each side, the apex rather abruptly acuminate. Spikes stellate-puberulent; ♂ spikes mostly compound, ca 5-14 cm long, mostly with 3-5 lateral axes; ♀ spikes unbranched, 3-10 cm long.
Staminate flowers subsessile, ca 1 mm broad in bud; calyx-lobes 2 or 3, acute, glabrous, less than 1 mm long; stamens 7 or 8, the anthers 0.5-0.6 mm long, blunt. Pistillate flowers subsessile; calyx-lobes 4, lanceolate, acute, ca 1-1.5 mm long, pubescent; ovary stellate-tomentulose, the styles stellate-pubescent, mostly 9-11 mm long. Capsules and seeds not seen.

Forests, Costa Rica to Venezuela and Peru.

darien: rain forest at crest, Caná-Cuasi trail, Terry & Terry 1575 (MO).

The identity of the single Panamanian collection is not absolutely certain, as only ♂ flowers are present. The small leaf size suggests the widespread A. triplinervia (Spreng.) Muell.-Arg., which is known to reach Colombia, and this collection was in fact cited by Standley and Steyermark (Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 150, 1940) as that species. However, the thinner leaf texture, foliar glands, and small ♂ buds all indicate a probable closer affinity of the Darien plant to A. glandulosa.


Tree ca 8 m high, trunk ca 1.5 dm in diam; twigs pubescent. Leaves chartaceous; petioles stout, 9-11 cm long, minutely stellate-pubescent; stipules not evident; blades ovate or elliptic, 24-27 cm long, 15-18 cm broad, 3-nerved at base with 3 or 4 additional strong veins on each side of midrib, the veins and veinlets corrugate-impressed above, conspicuously raised beneath; lamina copiously stellate-pubescent beneath, glabrate above, basal foliar glands mostly 2 on each side, plane beneath, raised above, the base rounded to subcordate, the margins shallowly toothed (glandular teeth ca 15-17 on a side) to the base, the tip rounded with an abrupt short acumen. Spikes (♀, the ♂ unknown) fascicled 2-4 on nodes below the leaves, 6-12 cm long, with ca 10-15 flowers, rachis densely stellate-pubescent. Staminate flowers unknown. Pistillate flowers subsessile (pedicels less than 1 mm long); calyx-lobes pubescent, ca 1 mm long or less; ovary stellate-pubescent, the styles 10-15 mm long, very slender, glabrous. Capsules (immature) glabrate, ca 7-9 mm in diam.

Forests, Panama and Colombia.


Despite the lack of staminate flowers, the characters of the Darien collection agree so well with the descriptions of A. grandis that there can be little doubt as to its assignment. This represents a considerable extension of range, since A. grandis has heretofore been reported only from the type collection in Colombia (Tumaco, Hinds s.n.; K, n.v.), about 400 miles to the south.
16. Alchorneopsis


Trees; dioecious; twigs and foliage glabrous or minutely pubescent with simple hairs. Leaves alternate, petiolate, exstipulate; blade triplinerved, biglandular at base beneath, the margins entire to remotely crenulate. Inflorescences axillary (± fascicled), spiciform; ♀ flowers in glomerules, ♂ flowers solitary at each node; bracts inconspicuous, eglandular. Staminate flowers subsessile or pedicellate; calyx splitting at anthesis into 3 or 4 valvate lobes; petals absent; disc massive, hirsutulous; stamens 5-8 (mostly 6), the filaments free, the anthers dehiscing introrsely and longitudinally, the outer locule-halves larger than the inner, with enlarged glandular connective; pollen grains subglobose (slightly oblate), 3-collporate, tectate (psilate); pistillode ± 3-lobed. Pistillate flowers pedicellate; calyx-lobes 4 or 5, slightly imbricate; petals absent; disc annular, pulviniform, hirsutulous (± confounded with the base of the ovary); ovary of 3 carpels, 1 ovule per locule, the styles free, short, recurving, undivided, papillate. Fruits capsular, the columella persistent, massive; seeds flattened, ecarunculate, the outer coat fleshy, the inner coat reticulate- striate, the cotyledons broad and thin.

A neotropical genus of three known species, all very similar and questionably distinct. The superficial vegetative resemblance of plants in this genus with Alchornea is remarkable, but the indumentum of simple rather than stellate hairs permits their separation even in the vegetative condition. The ♂ inflorescences are similar in both genera, but those of Alchorneopsis are never branched, and the ♂ flowers always have a pistillode. The short styles of the ♀ flower of Alchorneopsis are very divergent from the elongated ones of Alchornea, and the seeds of the two genera are very different. The resemblances between Alchornea and Alchorneopsis must therefore be ascribed to parallelism, the two genera both having their origin within subtribe Mercurialinae but apparently not from an immediately common ancestry. The similarities in anther and seed structure in fact suggest that Alchorneopsis may be more closely related to Tetrochidium than to any other neotropical genus of Euphorbiaceae.


A. nemoralis Martius & floribunda (Bentham) Baillon, Adansonia 5: 239, 1865.

Tree to 20 m high; twigs terete, glabrous or minutely scabridulous. Leaves chartaceous; petioles minutely scabridulous, ca 1-5 cm long; blades elliptic, 5-15 cm long, 3-8 cm broad, glabrous except for minute hairs along veins beneath, 3-veined at base, with mostly 2 or 3 additional major veins on either side, the veinlet reticulum prominulous beneath, the basal foliar glands foveate-excavated, the base acute to obtuse, the margins subentire to remotely crenulate, the apex
abruptly pointed or acuminate. *Inflorescences* densely appressed-puberulous; ♂ racemes 5-12 cm long, ♀ racemes 2-4 cm long. *Staminate flowers* with puberulent pedicels 0.5-1.5 mm long; calyx-lobes 3, sparsely strigose, elliptic, acute, 1.2-1.5 mm long; disc copiously hirsutulous; stamens 5-7 (mostly 6), the filaments glabrous, 1.3-2 mm long, the anthers elliptical, 0.5-0.6 mm long, the prominent connective nearly or quite as long as the anther-sacs; pistillode glabrous, trinit, 0.4-0.7 mm high. *Pistillate flowers* with puberulent pedicels 1-1.5 mm long in fruit; calyx-lobes 3 or 4 [in Panamanian material], ovate, strigose, 0.7-0.9 mm long; disc massive, 1.1-1.2 mm diam; ovary 1.1-1.3 mm high, pubescent, the styles spreading, coarsely papillate, undivided or obscurely bifid at the tip, ca 0.5 mm long. *Capsules* not seen entire; cocci wrinkled, glabrate, 3-4 mm long, the columella persistent, broadly 3-winged (ovate in outline), 0.7-1 mm high; seeds lenticular (thicker basally), blackish beneath the pale outer coat, striate with discrete or somewhat anastomosing ± discontinuous ribs (ca 10-12 on the back), 2.2-2.5 mm long and broad.

Rain forests, Panama to the Guianas and northern Brazil (Amazonas, Pará).


The single Panamanian collection represents an extension in range limits of *A. floribunda* of more than 800 miles from the type locality on the Rio Vaupés in NW Brazil. The assignment of Williams' specimen to this species must be provisional since it bears only fruits (the above description has been augmented by examination of 3 Brazilian specimens: *Ducke 10292, 13501, 18513; all RB*). All 3 species of *Alchorneopsis* are imperfectly known, so that comparisons are difficult. The seed size of the Panama collection is closer to *A. trimera* Lanj. of Surinam than to *A. portoricensis* Urban (which has seeds 3 mm long, fide Pax & Hoffmann). The ♀ calyx of the Panamanian plant, with both 3 and 4 lobes, is intermediate between the 3-merous calyx of *A. trimera* and the 4- or 5-merous calyx of the Brazilian *A. floribunda*. It seems probable that the three 'species' of *Alchorneopsis* are merely geographic races of a single wide-ranging species, but in any event the Panamanian plant can appropriately take the earliest species name in the genus, *A. floribunda*.

17. TETRORCHIDIO


*Trees* or shrubs; dioecious (sometimes monoecious ?); branches with simple or malpighiaceous hairs. *Leaves* alternate; petioles usually with stalked glands; stipules glandular; blades pinnately veined, entire to dentate. *Inflorescences* axillary, ♂ flowers in spiciform thyrses, ♀ flowers in racemes (sometimes branched and paniculate). *Staminate flowers* sessile or subsessile; calyx-lobes 3, imbricate, ventrally ribbed; petals absent; disc absent; stamens 3, opposite the calyx-lobes, free, the filaments very short, the anthers extrorse, peltate, 4-loculate; pollen grains 3-colporate, intectate, psilate; pistillode small or obsolete. *Pistillate flowers*
subsessile or pedicellate; calyx-lobes 3, imbricate; petals absent; disc cupuliform or dissected into 3 lobes; ovary of 2 or 3 carpels, ovules 1 per locale, the styles free, short, bifid, the style branches sometimes dilated. Fruits capsular, thin-walled; seeds rounded, ecarunculate, the outer seed-coat fleshy, the inner foveolate, endosperm present, the cotyledons broad, flat.

About 15 species, the majority (sect. Tetrochidium) American, but with 5 species [sect. Hasskarlia (Baillon) Pax & Hoffmann] in Africa characterized by dense catkin-like staminate spikes. Two allopatric, rather poorly known, species occur in Panama.

Useful reference:


Tree, to 25 m high with trunk ca 1 dm thick; dioecious. Leaves membranaceous or thinly chartaceous, clustered near ends of branches; petioles 1-4 cm long; stipules glandular, ca 1 mm long; blades elliptic to obovate, 14-21 cm long, 6-13 cm broad, minutely strigose-pubescent with malpighiaceous hairs on both faces, the midrib and primary veins (5-6 per side) prominently raised beneath, the veinlets distinctly raised to form a prominent reticulum, the base cuneate, the margins entire but with 1 to 2 cyathiform glands at or above the middle, the apex abruptly short-acuminate. Inflorescences axillary; ♂ thyrses 4-8 cm long; rachis densely strigose, 2 racemes 3-6 cm long, rachis more coarsely yellowish-strigose. Staminate flowers subsessile; calyx-lobes fleshy, suborbicular, ca 0.9-1.1 mm long, densely strigose without; stamens apparently adnate to base of calyx-lobes, the filaments indistinct, the anthers cordate-reniform, with broad round connective opposite midrib of calyx-lobes, 0.8-1.1 mm wide. Pistillate flowers subsessile (pedicels ill-defined, ca 0.5 mm long, becoming ca 1 mm long in fruit); calyx-lobes ovate-deltoid, ca 1 mm long; disc cupulate, ca 0.8-1 mm high, lobed, enclosing most of the ovary before anthesis; ovary glabrous, 2-locular, the styles dilated, reflexed over the ovary to form a cap ca 0.5-0.7 mm high and 0.8-1.3 mm broad. Capsules (immature) ca 5 mm in diam.

Rainforests, Costa Rica and Panama.

BOCAS DEL TORO: vic of Almirante, Buena Vista camp, Chiriquí Trail, 450 m, Cooper 621 (holotype F; isotypes GH, Y).


*Tree* or shrub 4-7 m high; dioecious, branches minutely strigose. *Leaves* chartaceous; petioles 0.5-1.5 mm long; stipules triangular, pubescent, ca 1 mm long; blades elliptic to obovate, 7-12 cm long, 3-5.5 cm broad, sparsely strigose with malpighiaceous hairs on both faces, the midrib and primary veins (4-6 on a side) prominently raised on both faces, the veinlets forming a distinct reticulum, the base cuneate, the margins subentire (with 2-4 inconspicuous glandular teeth on each side), narrowed to an abruptly short-acuminate tip. *Inflorescences* axillary; *♂* thyrses 2-6 cm long, rachis densely strigose; *♀* racemes 2-6 cm long, densely strigose. *Staminate flowers* subsessile; calyx-lobes triangular, densely strigose, ca 0.8-0.9 mm long; anthers subsessile, 0.8-0.9 mm wide. *Pistillate flowers* with pedicels 1.3-2 mm long; calyx-lobes ovate, obtuse, strigose, 0.9-1.1 mm long; disc cupulate, 0.8-0.9 mm high, enclosing 1/2 the ovary or more at anthesis; ovary glabrous, 2-locular, the styril cap nearly disciform, 0.4-0.5 mm high, 1.2-1.8 mm broad. *Fruits* not seen.

Eastern Panama, Colombia, and (fide Cuatrecasas) Ecuador.

The two collections from Panama unfortunately have only flowers, and fruiting collections are much desired. The plant from the Canal Zone appears to be very similar to the type collection of subsp. *robledoanum* except in its more proximally inserted petiolar glands. The collection from Cerro Jefe has a placement of glands more like that of subsp. *robledoanum*, but it also shows a certain similarity to *T. euryphyllum*. The exact status of all these taxa cannot be resolved until more complete Panamanian collections, with flowers of both sexes as well as fruits, are obtained.

18. CARYODENDRON

*Caryodendron* Karsten, Fl. Columb. 1: 91, t. 45, 1858.

*Centrodicus* Muell.-Arg. in Martius, Fl. Brasil. 11(2): 325, t. 102, 1874.

*Trees*; dioecious; twigs with simple hairs. *Leaves* alternate, petiolate, stipulate; blades pinnately veined, usually with basal glandular spots, entire. *Inflorescences* unisexual; *♂* flowers in simple or compound terminal spiciform thyrses, *♀* flowers in terminal few-flowered racemes; bracts eglandular. *Staminate flowers* subsessile, several per bract; calyx segments 3, valvate; petals absent; disc massive, pulviniform, central, ± pubescent; stamens 4-7, usually with 1 central in the disc and 1 or 2 whorls of 3 exterior to the disc; the filaments free, abruptly inflexed near the top, the anthers introrse, dehiscing obliquely, connective protrusive; pollen grains subglobose (somewhat oblate), 3-colporate, tectate (tectum perforatum), triangular in polar view; pistillode absent. *Pistillate flowers* with
stout pedicels; calyx-lobes 5 or 6, imbricate; petals absent; disc annular; ovary of 3 carpels (rarely 2 or 4). Fruits capsular, the cocci thick-walled, smooth; seeds ovoid to globose, large (over 1 cm long), endosperm present, the cotyledons broad and flat.

Only three known species, the following Panamanian one and two from South America.


*Tree* 4-6 m high; twigs and foliage glabrous. *Leaves* chartaceous; petioles 1.2-3 cm long; stipules not seen [early deciduous, leaving an oblique scar]; blades elliptic- or oblanceolate-oblong, 19-26 cm long, 5-7 cm broad, with 2-4 glandular spots above near the base, the midrib and main primary veins (ca 6-8 on a side) raised beneath, the veinlet reticulum rather prominent on both sides, the base cuneate, the margins entire, recurved, with a truncate or emarginate acumen at the apex. *Inflorescences* terminal, unisexual; *♂* spike compound, with main axis ca 7 cm long and 4.5 mm broad, bearing 2 lateral axes 8-14 cm long and 2-2.5 mm thick; rachis of *♂* spike minutely antrorse-strigulose, the bracts minutely glandular punctate, subtending bracteolate clusters of several *♂* flowers. *Stamine flowers* [not seen fully expanded] nearly sessile; calyx-segments 3, glabrous, ca 1.5-1.8 mm long; stamens 6 or 7, usually with 1 central, the filaments ca 0.8-0.9 mm high, the anthers ca 0.4-0.5 mm long; disc densely hirsute. *Pistillate flowers* not seen; fruiting pedicel massive (nearly 4 mm thick). *Capsules* not seen entire; cocci ca 2 cm long, 2-2.5 mm thick, densely and closely tomentulose outside, the columella ca 1.7 cm long; seeds spheroidal, smooth, pale brownish, prominently carinate dorsally, obscurely and obliquely costate ventrally, with prominent raphe, 15.8-16.5 mm long, 14.4-15 mm broad.

Endemic to western Panama, on the basis of available records.


This species is extremely close to *C. grandifolium* (Muell.-Arg.) Pax of Brazil. Standley noted the resemblance, but felt that the Panamanian plant differed specifically in its narrower leaves, smaller flower clusters, and thicker *♂* spikes. Actually, only the latter character seems very impressive. The only floral characters noted which might be diagnostic are the smaller anthers of *C. angustifolium* (0.4-0.5 mm vs. 0.8-0.9 mm; but this might reflect merely the immaturity of Panamanian material examined), and its hirsute floral disc, which is much more densely pubescent than that in the *♂* flower of *C. grandifolium*. Despite the undoubted resemblance of the two taxa, therefore, it seems best to maintain them as distinct species for the time being. *Caryodendron orinocense* Karsten, the original species of the genus, appears to differ in its more highly branched ♀ inflorescence and (if *Ducke* 1072, RB belongs here) larger fruits and seeds.
19. ACIDOTON

**Acidoton** Sw., Prodr. 84, 1788; Fl. Ind. Occ. 954, 1800, nom. gen. cons.


Shrubs or small trees; monoeocious or dioecious. Leaves alternate, petiolate, stipulate; blades pinnately veined, entire or dentate. Inflorescences axillary clusters or racemes; bracts eglandular, subtending solitary flowers. Staminate flowers pedicellate or subsessile; calyx-lobes 3-5, valvate; petals absent; disc absent (or confounded with the fleshy receptacle); stamens ca 24-60, the filaments free, glabrous, the anthers extrorse, dehiscing longitudinally, the anther-connective with an apical tuft of stinging hairs; pollen grains ellipsoid, tectate, inaperturate. Pistillate flowers pedicellate; calyx-lobes 5-6, narrow, ± imbricate; petals and disc absent; ovary of 3 carpels, pubescent (at least in part) with stinging hairs, the ovules 1 per locule, the styles connate below, spreading above, undivided, strongly papillose. Fruits capsular, valves ± armed with stinging hairs; seeds round, ecarunculate.

A small Caribbean genus of six species (Jamaica, Hispaniola, Central America, Venezuela). The genus is very closely related to *Tragia*, but differs in its habit and more numerous stamens with the anther-connective terminating in a tuft of stinging hairs.

1. **Acidoton nicaraguensis** (Hemsley) Webster, Ann. Missouri Bot. Gard. 54: 191, 1967.—Fig. 13.


Shrub or small tree; dioecious; young branches appressed-hirsute, glabrescent, not spinose. Leaves thinly chartaceous; petioles 3-7 mm long; stipules lanceolate, acuminate, ± longitudinally ribbed or striate, 3.5-5.5 mm long; blades elliptic to obovate, ca 10-20 cm long, 3.5-7.5 cm broad, glabrescent except along veins beneath, the midrib and veins (ca 5-8 on a side) distinctly raised beneath, the veinlets prominulous, particularly on underside forming a rather conspicuous reticulum, the base rounded, the margins coarsely crenate-toothed above the middle (ca 4-8 teeth on a side), the apex ± abruptly caudate-acuminate (acumen ca 1.5-2.5 cm long). Inflorescences unisexual; ♀ racemes 1-2 cm long, with 7-10 flowers; ♀ racemes becoming 4-6 cm long, with 3-5 flowers; bracts ca 2-3 mm long, acute; inflorescence rachis and bracts strigeois-hirsute. Staminate flowers with pedicels ca 2 mm long; calyx-lobes 3, lanceolate, pubescent, 3-3.5 mm long; disc not evident; stamens 24-35, free, the filaments glabrous, 1-2 mm long, the anthers ellipsoid, 0.35-0.5 mm long, the apical tuft of stinging hairs ca 0.1 mm long. Pistillate flowers with ± recurving pedicels becoming 3-9 mm long; calyx-lobes lanceolate, acuminate, pubescent, ca 1 mm long at anthesis; disc absent; ovary densely pubescent with both stinging and simple hairs, the styles connate into a stout column 1-1.3 mm high, the free style-ends about as long as the column, recurving, densely papillose.
Fig. 13. *Acidoton nicaraguensis* (Hemsley) Webster: A, habit (ca ×1/2); B, female flower (ca ×6); C, male flower (ca ×8); D, anther (ca ×20); E, dehisced coccus (ca ×3); F, seed (ca ×3). A after Englesing 141 (MO), Nicaragua; B-D after Pittier 6543 (US); E-F after Duke 8320 (MO).
Capsules not seen entire, valves ca 7 mm long, glabrescent, the columella trifurcate distally, 1.5-1.8 mm high; seeds globose, ca 4 mm in diam.

Forests, Nicaragua and Panama.


Vines (suffruticose herbs or shrubs in extra-Panamanian species); monoecious; with stinging hairs. *Leaves* alternate, petiolate or sessile, stipulate, entire to toothed or lobed. *Inflorescences* bisexual, racemiform, opposite the leaves or terminal on lateral branches; flowers 1-several at proximal nodes; bracts small, subtending solitary flowers. *Flowers* apetalous; calyx 3-6-lobed; disc absent. *Staminate flowers* with articulate pedicels; calyx-lobes valvate; stamens 2-5 (-8), the filaments connate below, the anthers dehiscing longitudinally; pollen grains spheroidal, reticulate, 3-collate with colpi operculate (rarely inaperturate); pistillode small or absent. *Pistillate flowers* pedicellate; calyx-lobes imbricate; ovary of usually 3 carpels, hispid with stinging hairs, sometimes with dorsal horns, the ovules 1 per locale, the styles united at least at base, unlobed, often papillate. *Fruits* capsular, the columella persistent, with 3 apical points; seeds subglobose, smooth or nearly so, ecarunculate, endosperm present, cotyledons foliaceous.

A variable genus of more than 100 species, about 60 in the New World, but only a single species in Panama. It is easily distinguished from all other local *Euphorbiaceae* by the combination of twining habit and stinging indumentum.

Useful reference:


1. **Tragia volubilis** L., Sp. Pl. 980, 1753.—Fig. 14.


*Twining vine*; stems and foliage ± densely covered with stinging hairs. *Leaves* thin; petioles 0.5-2.5 cm long; stipules ovate-lanceolate, acuminate, greenish, ca 2-4 mm long; blades elliptic-oblong, 2.5-7 cm long, 0.7-2.5 cm broad, above sparsely and beneath more densely beset with stinging hairs, mostly 5-veined at base, the base subcordate to distinctly cordate, the margins sharply serrate (teeth 8-20 on a side), the apex acute to acuminate. *Inflorescences* opposite the leaves (sometimes apparently axillary), becoming ca 1-2.5 cm long, usually with a single basal ♀ flower, remaining nodes (ca 15-25) with ♂ flowers; ♀ bracts mostly trifid, ♂ bracts entire. *Staminate flowers* with minutely hispidulous pedicels ca 1.1-1.6 mm long, articulate somewhat below the middle (stumps remaining after dehiscence of flower shorter than to as long as the subtending bract); calyx-lobes 3, elliptic, acute, 0.8-0.9 mm long, 0.5-0.6 mm broad; stamens 2 [in Panamanian specimens], the filaments thick and fleshy, free, shorter than the anthers, the
Fig. 14. *Tragia volubilis* L.: A, habit (ca ×1/4); B, female flower (ca ×10); C, ovary (ca ×10); D, male flower (ca ×20); E, stamen (ca ×30); F, normal 3-coccus fruit (ca ×4); G, fruit with prominent horns (ca ×4); H, seed (ca ×4). After Lewis et al. 1653 (MO).
anthers elliptic, 0.3-0.4 mm long. **Pistillate flowers** with hispidulous pedicels which elongate greatly in fruit to (1-)1.5-2.5 cm long; calyx-lobes 6, ± biseriate, lanceolate, acute, greenish, reflexed in fruit, increasing from ca 1.2 to ca 1.8 mm in length; ovary densely hispidulous with stinging hairs, the styles basally connate into a column 0.4-1.2 mm high, the tips spreading or usually tightly inrolled. **Capsules** hispid with stinging hairs, dimorphic, some of the normal 3-coccous type and ca 6 mm in diam, others zygomorphic, with 2 prominent dorsal horns up to 4 mm long, the columella slender, apically dilated into 3 flattened blades, 1.6-1.8 mm long; seeds round, ellipsoid, grayish with reddish-brown ridges (alveolate-reticulate, the color contrast lost in age), ca 2.5 mm long.

Common and widespread in tropical America from Mexico and Cuba south to Peru, Argentina, and Uruguay; also reported from Africa (where it is presumably introduced).

**CANAL ZONE:** Balboa, moist thickets, Standley 25472 (US), 26051 (US), 27173 (US); betw Corozal & Ancon, Pittier 6741 (US). **HERRERA:** secondary woods, 12.5 mi S of Ocú, Lewis et al. 1653 (DAV, GH, MO, US).

Although Pax and Hoffmann [Pflanzenreich 68 (IV, 147, IX): 50, 1919] reported var. *lanceolata* from Panama (on the basis of Williams 549, n.v.), the specimens examined by me have distinctly serrate leaves and accord well with the typical variety. The plant is doubtless much more widely distributed in Panama than the herbarium records indicate, but has evidently been avoided by most collectors.

**21. PLUKENETIA**


*Lianas*; young stem apices puberulent with simple hairs. **Leaves** alternate, petiolate, stipulate (stipules small and deciduous); blades entire or dentate, palmately or pinnately veined, usually stipellate and with a pair of sessile glands at base. **Inflorescences** axillary, narrowly paniculate or thyrsoid, ±; flowers 1 or 2 at the base of ± inflorescences, ± flowers in ± abbreviated distal monochasia; bracts small, eglandular. **Staminate flowers** pedicellate; calyx splitting into usually 4 lanceolate segments; petals absent; receptacle slightly to distinctly conical; disc of interstaminal segments or absent; stamens 10-40, the filaments free or ± basally adnate to the receptacle, the anthers ± 4-lobed, apiculate; pollen grains oblate, 3-colpate, tectate; pistillode rudimentary or absent. **Pistillate flowers** with stout pedicels; calyx-segments 4 or 5, barely imbricate; petals and disc absent; ovary of 3 or 4 carpels, ovules solitary in each locule, the styles connate at least half way, the style-tips entire or obscurely bilobed. **Fruits** large, capsular, cocci smooth to carinate or winged, rather thick-walled; seeds globose to lenticular, smooth, ecarunculate, endosperm present, the cotyledons ovate, palmately veined.

In the broad circumscription of Bentham (Gen. Pl. 3: 327, 1880), this is a rather variable genus of about 15 species from tropical regions except Australia. Proposed segregate genera such as *Anabaenella, Angostylidium, Apodandra,
Elaeophora, Fragariopsis, and Pterococcus are each distinguished by only one or two characters, whereas they all have much in common with the typical element (*Plukenetia volubilis* L.) in habit, flowers, pollen, and fruits. Since these segregate taxa each have only one to three species, the utility of fragmenting the *Plukenetia* complex to such an extent seems questionable.

1. *Plukenetia volubilis* L., Sp. Pl. 1192, 1753; Pax & Hoffm., Pflanzenreich 68 (IV, 147, IX): 14, 1919.—Fig. 15.


*Liana*; twigs minutely appressed-pubescent, glabrescent. *Leaves* membranous; petioles mostly 3-8 cm long; stipules brownish, glabrous, ovate-lanceolate, 1-1.5 mm long; blades ovate, ca 7-13 cm long, 5-12 cm broad, glabrate and shining above, glabrate or sparsely hirsutulous and paler beneath, ventrally with 2 prominent ellipsoidal shining marginal glands (ca 1.5-2 mm long) near the base, major veins at base of blade 3, the remainder of blade pinnately veined (3 or 4 major laterals on either side), the veinlet reticulum conspicuous, the base truncate to subcordate, the margins finely to rather coarsely denticulate, the apex abruptly caudate-acuminate. *Inflorescences* axillary, ♀️, ca 3-8 cm long at anthesis, becoming up to 15-20 cm long in fruit; ♂️ flowers solitary at lowermost nodes, ♀️ flowers in clusters at distal nodes. *Staminate* flowers with pedicels ca 1-1.5 mm long; calyx-segments generally 4, lanceolate, acute, 1.8-2.5 mm long; receptacle conical, 0.7-1.5 mm high; disc obsolete; stamens 19-24, inserted spirally on the receptacle, the filaments 0.3-0.6 mm long, the anther-sacs bipartite, the locules discrete (hence anthers 4-partite), 0.3-0.4 mm long, the connective apex blunt and glandular. *Pistillate* flowers with pedicels becoming 10-15 mm long; calyx-lobes oblong-lanceolate, 1.8-2.2 mm long, 0.9-1 mm broad; ovary of 4 glabrous carinate carpels, the stylar column 11-25 mm long, slender, the stigmas thick, bilobed. *Capsules* deeply 4-lobed, oblate, up to ca 2 cm high, 3.5 cm broad, the cocci thick and rigid; seeds lenticular with thinner margins, reticulate-venose, brownish-mottled, 15-17 mm broad.

Lowland rain forests below 1000 m, Lesser Antilles and Panama south to Peru, Bolivia, and Brazil.

**LOS SANTOS:** betw Los Santos & Guarare, in thickets, Woodson et al. 1201 (A, MO, NY).

The single Panamanian collection bears only small (immature?) fruits, and the above description has been augmented by reproductive details from some extra-Panamanian specimens (Ecuador, *Mexia* 7309; Bolivia, *Krukoff* 10082, *Steinbach* 7352; all UC). Although the collection from Los Santos accords reasonably well with South American material of *P. volubilis* L., more complete Panamanian collections are needed in order to make the identity of our representative a certainty.
22. OMPHALEA


Shrubs, lianas, or small trees, with clear latex; monoecious. Leaves alternate (sometimes approximate at ends of branches), distinctly petiolate, stipulate; blades large, pinnately veined but often 3-nerved at base, entire to deeply lobed, usually with 2 large glands at junction with petiole. Inflorescence paniculate (a compound thyrse); floral bracts often conspicuous and foliose; cymules ♂ or ♀. Staminate flowers short-pedicellate; calyx-lobes 4, decussate (rarely 5 and imbricate); petals absent; disc patelliform, fleshy, entire; stamens 2 or 3, the filaments connate, the connectives of anthers connate into a large fleshy disciform mass with anthers at
the periphery, the anthers dehiscing obliquely; pollen grain oblate, 3-colpate, tectate (psilate); pistillode absent. *Pistillate flowers* short-pedicellate; calyx-lobes 4 (rarely 5); petals absent; disc annular, sometimes indistinct; ovary of 3 carpels, with 1 ovule in each locule, the styles connate into a stout column which is entire or barely 3-lobed at the apex. *Fruits* fleshy but ultimately dehiscing into 3 1-seeded woody cocci; seeds subglobose, ecarunculate, endosperm present, the cotyledons broad, cordate at base.

A primarily American genus of 15 species, most of these in the West Indies, only three species known from the Old World. Most of the American species are known from very few collections, and careful field work is still needed to determine whether there are significant differences in fruit characters, etc. In addition to the one species known from Panama, two others have been described from Central America by Hemsley. The relationships between these taxa remain to be carefully investigated.

1. *Omphalea diandra* L., Sp. Pl. ed. 2, 1377, 1763; Muell.-Arg. in DC., Prodr. 15(2): 1135, 1866; Pax & Hoffm., Pflanzenreich 52 (IV, 147, V): 20, 1912.—Fig. 16.


*Liana* up to 30 m high; main stems 5 cm thick or more; bark exuding reddish or purplish sap when cut. *Leaves* firmly chartaceous; petioles (1-)2-11 cm long; stipules ca 2-2.5 mm long, pubescent; blades elliptic to oblong, ca 8-21 cm long, 5-15 cm broad, pubescent beneath or sometimes glabrate, the veins at base 3 or 5, with 2 or 3 additional pairs of main veins, the veinlet reticulum conspicuous beneath, the glands at base of blade massive, rounded, sessile, ca 1.2-2 mm wide, the base rounded to truncate or subcordate, the margins entire, the apex mostly bluntly obtuse. *Inflorescences* paniculate, ca (1-)2-5 dm long, with a few lateral axes toward the base, these ca 1-15 cm long, sometimes again branched, bearing many ♀ and a few ♂ flowers which are central in ♂ cymes or solitary at ends of ultimate axes; bracts on lower parts of axes lanceolate, densely pubescent, 2-3 mm long, biglandular near the base; bracts on distal parts of axes foliaceous, ca 2-3.5 cm long, 1.5-5 mm broad, glabrate, biglandular well above the base (ca 4-8 mm). *Staminate flowers* with pedicels becoming 1.5-2.5 mm long; calyx-lobes 4 (rarely 5), biseriate, unequal, the inner pair ± cochleately enveloping the androecium, fleshy, at anthesis 1.5-2.7 mm long, 1.7-2.6 mm broad, glabrous except for the ± ciliate margins; disc fleshy, ± adnate to base of calyx-lobes, ca 1.5-2.2 mm across; stamens 2 (rarely 3), the androecium (dilated connectives) disciform, fleshy, 1-1.5 mm wide, the anthers 0.6-0.8 mm long. *Pistillate flowers* on pedicels ca 1-2 mm long; calyx-lobes 4 and decussate (rarely 5), ovate, fleshy, 1.5-2 mm long and about as broad, pubescent or nearly glabrous; disc thin, circular, ca 1.2 mm wide, hidden under the ovary; ovary ca 3-4 mm high, ovoid, sericeous, the stilar column stout, sericeous, 2-2.5 mm long, the stigmas erect, ca 0.2 mm long.
Fig. 16. Omphalea diandra L.: A, habit (ca ×1/2); B, inflorescences (ca ×1/2); C, inflorescence bract (ca ×1); D, female flower (ca ×6); E, male flower (ca ×4); F, stamens, top view (ca ×10); G, stamens, side view (ca ×10); H, seed (ca ×1/2). A after Duke 4906 (MO); B-G after Wright 1990 (MO), Cuba.
Fruits fleshy, pomiform, ca 8-12 cm in diam, at length dehiscent (?); seeds compressed, rounded, 3.9-4.5 cm broad, brown, rugulose.

West Indies to South America (Peru and Brazil), usually in lowland rain forests or swamp forests; present in Central America along the Caribbean lowlands from Honduras to Panama.

Bocas del Toro: Old Bank I, vic of Chiriqui Lagoon, von Wedel 1921 (GH, MO).

Canal Zone: Barro Colorado I, Aviles 22h (F), Bangham 504 (A, F), Shattuck 619 (F), Wetmore & Woodworth 58 (A), Woodworth & Vestal 613 (A); Fort Randolph, Standley 28645 (US); beach thicket, vic of Fort Sherman, Standley 30921 (US), 31191 (US); Lion Hill Sta, Hayes 660 (BM, K).

Darien: Cativo Swamp, 5 mi downstream from El Real, Duke 4306 (MO); along Rio Tuira below El Real and Piriaque I, Stern et al. 889 (MO).

Panama: San Jose I, West Loop Rd, Erlanson 110 (GH); id., Long Beach, Johnston 599 (GH), 1183 (GH, MO); id., Playa Grande, Johnston 720 (GH). Veraguas: Isla Coliba, Dwyer 1622 (DAV, MO), Seemann 635 (possibly an isotype of var. panamensis, BM).

Johnston (Sargentia 8: 177, 178, 1949) has presented a valuable description of the plant as it occurs on San Jose Island. However, his decision to separate the Panamanian plants as a species separate from O. diandra is not convincing. As Klotzsch noted in the original description of his variety panamensis, the leaf shape of O. diandra is quite variable. Seemann's specimen has floral bracts which are about as long as those found in plants elsewhere, and its inflorescence is similar also. Perhaps the Panamanian population does represent a reasonably distinctive geographic race characterized by glabrate leaves with blunt tips and usually only 3 prominent veins at base. Until the genus is monographically revised, it can be conveniently referred to as O. diandra var. panamensis Kl.

23. RICINUS


Shrubs or trees (in tropical regions); twigs and foliage glabrous, sap watery. Leaves alternate, petiolate (petioles long, ± glanduliferous at apex), stipulate (stipules fused into a caducous sheath); blade peltate, palmately 7-11-lobed, serrate. Inflorescences terminal (sometimes appearing opposite the leaves or axillary due to sympodial growth), paniculate, the proximal nodes with cymes of several ♂ flowers, the distal cymes ♀ or ♀; bracts papery, glandular at base; the flowers with valvate calyx, apetalous, disc absent. Staminate flowers pedicellate; calyx calytrate in bud, splitting into 3-5 segments at anthesis; stamens ∞ (up to 1000), the filaments partially connate into fascicles at base, irregularly branched; pollen grains spheroidal, tectate, 3-colporate, colpi narrow; pistilode absent. Pistillate flowers pedicellate, with calyx similar to the ♂; ovary of 3 carpels, mucrate, the ovules 1 per locule, the styles connate below, bifid, the branches usually conspicuously papillate. Fruits capsular, echinate (or smooth in some cultivars), the columella wing-dilated above; seeds elliptic, somewhat compressed, smooth, mottled, carunculate, the endosperm copious, the cotyledons foliaceous and palmately veined.

A monotypic genus native to the Old World; probably African in origin, but now widely distributed in tropical and warm-temperate regions.
Ricinus communis L., Sp. Pl. 1007, 1753.

Shrub or tree, usually 2-5 m high; twigs (in most varieties) glaucous. Leaves thin, glabrous; petioles 1-2 dm long or more, the gland at apex of petiole on dorsal side of blade, single or sometimes paired, patelliform, dark, subsessile, ca 2-3 mm across; stipules ca 1-1.5 cm long, caducous, leaving a prominent annular scar; blades mostly 7-9-lobed, ca 1 dm across or more (up to 1 m), peltate, the lobes lanceolate, acuminated, pinnately veined, the margins serrate with ± glandular teeth. Panicles terminal, bisexual, the 3-10 lowermost nodes with clusters of several ♀ flowers, the distal nodes ♂ (a few intermediate nodes often ♀); bracts papery, associated with dark patelliform glands. Staminate flowers with articulate pedicels ca 5-15 mm long; calyx-lobes lanceolate, acute, ca 4-9 mm long; androecium ca 5-7 mm wide, the anthers 0.3-0.4 mm long. Pistillate flowers with pedicels becoming mostly 1.5-3 cm long in fruit; calyx-lobes mostly 5, lanceolate, acute, ca 3-4 mm long, persistent or deciduous; ovary coarsely muricate, the styles bifid or bipartite, reddish, densely papillose, ca 3-4 mm long. Capsules ordinarily echinate, 12-21 mm in diam, the columella wing-dilated distally, ca 1 cm long or more; seeds ellipsoidal, somewhat flattened, diversely mottled, 9-22 mm long, 4.5-9 mm broad.

Native probably of Africa; cultivated in Panama (as elsewhere in the tropics) and tending to escape in highly disturbed areas.

colón: Gatun Lake, Goodyear Estate, Seibert 1521 (MO). los santos: Pocri, bridge at Río Purio, Dwyer 2486A (MO).

24. ACALYPHA


Herbs, shrubs, or rarely trees; monoecious or dioecious; indumentum of simple hairs or glands. Leaves alternate, petiolate, stipulate; blades pinnately or palmately veined, undivided, entire or dentate. Inflorescences spicate, terminal or axillary; spikes unisexual or bisexual; ♀ flowers several at each node, subtended by a minute bract; ♂ flowers 1-3 at each node, subtended by a usually large foliaceous, lobed bract; the flowers apetalous, disc absent. Staminate flowers sub sessile; calyx parted into 4 valvate segments; stamens 4-8, the filaments free or basally connate, the anther-sacs pendent, unilocular, elongated and veriform; pollen grains oblate-spheroidal, 3-5 pseudoporate, tectate, psilate; pistillode absent. Pistillate flowers sub sessile (pedicellate in a few species); calyx-lobes 3-5, imbricate; ovary of 3 (rarely 1 or 2) carpels, the ovules solitary in each cell, the styles free or basally connate, several times divided into filamentous segments (rarely bifid or entire). Fruits capsular, sometimes surrounded by the accrescent ♀ bract; seeds ovoid, usually carunculate, smooth to pitted or tuberculate, endosperm present, the embryo straight.

A homogeneous genus of some 400 species, the majority American. The greatest concentration of species is in the Caribbean region, but Panama is rather poorly represented. In addition to the nine native species enumerated below, at least one
other is represented by a single ♀ collection from Darien (Río Balsa, Duke 8795, MO). Although its identity is uncertain in the absence of ♂ flowers, it may prove to be A. cancana Muell.-Arg. (in DC, Prodr. 15(2): 869, 1866), described from northwestern Colombia. The plant resembles A. macrostachya but is easily distinguished by its more velutinous pubescence and more slender ♂ spikes.

Cultivated plants of A. wilkesiana Muell.-Arg. and A. hispida Burm. f. may be found in the Canal Zone and elsewhere, but neither species appears to have become naturalized.

a. Pistillate flowers pedicellate, the minute subtending bracts not becoming foliaceous (subg. Linostachys)
   b. Pistillate inflorescences terminal, paniculate; leaves without resinous dots beneath
      bb. Pistillate inflorescences axillary, racemose; leaves with minute resinous dots beneath
      aaa. Pistillate flowers sessile, the subtending bracts becoming conspicuous and foliaceous (subg. Acalypha)
   c. Herbs or shrubs; ♂ bracts with rounded to acute or short-acuminate tips.
      d. Shrubs; spikes all axillary.
         e. Leaves palmately veined at base; ♂ bracts with 10-25 acute lobes, subtending solitary flowers; spikes mostly unisexual.
            f. Pistillate spikes with 15-65 bracts; ♂ bracts in fruit 5-8 mm long, shallowly toothed (lobes cut ca ¼ to ½ way to base); ♂ spikes 3-5 mm thick; capsules smooth .......... 3. A. costaricensis
               ff. Pistillate spikes with 1 or 2 bracts; ♂ bracts in fruit 4 mm long, more deeply toothed (lobes cut ca ½ way to base); ♂ spikes less than 2 mm thick; capsules verruculose .......... 4. A. leptopoda

cc. Herbs; ♂ spikes terminal, ♂ axillary; ♂ bracts obtusely 5-7 lobed

dd. Herbs; ♂ spikes terminal, ♂ axillary; ♂ bracts subentire, subtending 2 or 3 flowers; spikes mostly bisexual, with 1 or 2 ♂ bracts at base; capsules verruculose .......... 5. A. diversifolia

ee. Leaves pinnately veined; ♂ bracts subentire, subtending 2 or 3 flowers; spikes mostly bisexual, with 1 or 2 ♂ bracts at base; capsules verruculose .......... 6. A. septemloba

1. Acalypha costaricensis (O. Ktze.) Knobl. ex Pax & Hoffm., Pflanzenreich 85 (IV, 147, XVI): 16, 1924.—Fig. 17.


Shrub 0.5-4 m high; monoecious or dioecious; stems greenish, glabrate to sparsely appressed-hirsutulous. Leaves membranous; petioles (1.5-)3-8 cm long, sparsely strigose to glabrate; stipules lanceolate, pubescent, flat, dark, 2.5-3.5 mm long; blades elliptic to slightly obovate, mostly 8-23 cm long 3.5-12 cm broad, glabrous (except along veins) and minutely pubescent, 3-nerved at base but other-
Fig. 17. Acalypha costaricensis (O. Ktze.) Knobl.: A, habit (ca ×1/2); B, female flower (ca ×7); C, fruit (ca ×8); D, seed (ca ×8). A after Yuncker et al. 8463 (MO), Honduras; B-D after Godfrey 66583 (MO), Costa Rica.
wise pinnately veined (veins 8-10 on a side), the narrowed base rounded to truncate, the margins coarsely dentate (12-25 teeth on a side), the apex acuminate. Inflorescences unisexual; ♀ flowers in terminal compound racemes (panicles) 10-25 cm long, with ca 15-35 lateral branches, the longer of these 3-7 cm long; ♂ flowers in axillary spikes mostly 5-20 cm long, ca 1.5-2.5 mm thick, peduncles ca 1 cm long or less. Pistillate flowers solitary; bracts linear-lanceolate, acuminate, pubescent, ca 0.5-1 mm long, pedicels 0.5-1 mm long at anthesis; calyx-lobes 5, lanceolate, 0.9-1.2 mm long; ovary densely and prominently verrucose-hispidulous, the styles free, basally thickened, 1.3-2 mm long, distally laciniate into 5-10 narrow segments. Capsules ca 3 mm broad, densely verrucose with cylindrical dark purplish processes; seeds plumply ovoid (nearly globose), slightly beaked apically, light brown, smooth (minutely foveolate), 1.6-1.8 mm long, the caruncle small (ca 0.1 mm long) or obsolete.

Lowland rain forests, below 1000 ft, Honduras to Panama.


Shrub or small tree 2-8 m high; monoecious or dioecious; stems villose with ± appressed hairs. Leaves with slender villose petioles 3-12 cm long; stipules linear-lanceolate to subulate, pubescent, 2.5-4 mm long; blades membranous, ovate to ovate-lanceolate, acuminate, mostly rounded to subcordate at the base, generally 8-15 cm long, 5-9 cm broad, above strigose or glabrate, beneath sparsely to densely villose and dotted with small (0.05-0.1 mm) shining resinous droplets, 5-nerved at base but pinnately veined above (veins ca 6-8 on a side), the margins coarsely crenate-dentate (25-35 teeth on a side). Inflorescences unisexual, axillary; ♀ flowers in slender racemes ca 5-15 cm long, with ca 10-40(-60) flowers, short pedicellate; ♂ flowers in spikes ca 3-8 cm long, 1-2 mm thick, rather loosely flowered and becoming ± interrupted proximally, sessile or with peduncles ca 1-2.5 cm long. Pistillate flowers solitary; bracts very small, scarcely more than 0.5 mm long, pubescent; pedicels 1.1-3 mm at anthesis, attaining 1-3 mm in fruit; calyx-lobes 5, lanceolate, 0.6-0.8 mm long, pubescent; ovary densely verrucose and dotted with resinous droplets, the styles free, basally verruculose, 2-2.5 mm long, distally laciniate into ca 5-10 narrow segments. Capsules ca 2 mm broad, densely verrucose with greenish processes and hispidulous; seeds plumply ovoid (nearly globose), slightly beaked apically, light brown, smooth (minutely foveolate), ca 0.9-1.1 mm long, the caruncle nearly obsolete.

A widespread and polymorphic species, from British Honduras south to Brazil and Paraguay.

Pax and Hoffmann [Pflanzenreich 85 (IV, 147, XVI): 17, 1924] referred the Pittier collection from Taboga Island to var. paniculata Muell.-Arg. (DC., Prodr. 15(2): 802, 1866), on the basis of the sparse indument and truncate leaf-bases. However, it remains to be demonstrated that the six varieties recognized by Pax and Hoffmann are geographically defined races, and there seems to be no need to apply any subspecific names to the Panamanian populations of A. villosa.


A. macrostachya c macrophylla (H.B.K) Muell-Arg. in Mart., Fl. Bras. 11(2): 345, 1874.

Tree, or sometimes shrub, ca 3-8 m high; monoecious or dioecious; trunk ca 3-5 cm diam; stems nearly glabrous to densely tomentose. Leaves membranous; petioles glabrous to densely tomentose (2-)4-20 cm long; stipules broadly lanceolate to linear-lanceolate, acuminate, flat, sparsely to densely pubescent, 5-13 mm long; blades ovate to ovate-lanceolate, ca 10-20 cm long, 5-15 cm broad, glabrate to tomentose on both surfaces, 5-7-nerved at base, mostly with 6-10 veins on each side, the base barely to distinctly cordate, the margins crenate-serrate with 25-60 teeth on a side, the apex abruptly acuminate. Inflorescences axillary, spicate, normally unisexual; ♀ spikes becoming 15-30 cm long, loosely flowered, with ca 15-65 bracts, sometimes distinctly pedunculate; ♂ spikes ca 6-20(-40) cm long, densely flowered, 3-5 mm thick, sessile or short-pedunculate. Pistillate flowers solitary; bracts broader than long, ± reniform, 2.5-3.1 mm long, 4.4-5 mm broad, increasing and foliaceous in fruit to 5-8 mm long, with ca 11-20 shallow acute or acuminate lobes mostly 1.5-2.2 mm long, ± strigose-hirsute especially along the veins; calyx-lobes obscure; ovary densely hispid-tomentose, the styles free, strigose-hispid on the back, pinnatifid along their entire length into stoutish segments (the longer subequal to the style), mostly 3-4 mm long. Capsules 3.3-3.7 mm in diam, hispid, not glandular; seeds ellipsoid, narrowed at one end, brownish-gray, smooth (minutely foveolate), ca 1.9-2 mm long, the caruncle an ill-defined whitish streak up to ca 1.5 mm long.

Common and widespread from southern Mexico to Peru, Bolivia, and Brazil.

BOCAS DEL TORO: Changuinola River, 10-15 mi S of mouth, Lewis et al. 878 (MO); Changuinola Valley, Lincoln Creek, Dunlap 432 (GH, NY); Chiriqui Lagoon, Water Valley, von Wedel 1640 (GH, MO), 2158 (MO); Western Valley, von Wedel 2701 (GH, MO). CANAL ZONE: Barro Colorado I, Aviles 934 (F), Shattuck 843 (F), 843b (MO, US), Standley 31353 (US), Woodworth & Vestal 439 (A), 561 (A); Cerro Galero, Stern & Chambers 31 (MO); Empire to Mandinga, Piper 5470 (US), 5482 (US); Frijoles, Allen 917 (MO), Piper 5821 (US); Gamboa, Bro. Heriberto 24 (US); 6 mi N of Gamboa, Tyson 3487 (MO); Gatuncillo, Piper 5625 (US); Las Cascadas Plantation, nr Summit, Standley 29514 (US);

*A. lotii* J. D. Sm., *Bot. Gaz.* 20: 544, 1885.

*Shrub* to 3 m high; monoecious; branches with spreading pubescence. *Leaves* membranous; petioles tomentulose, mostly 2-8 cm long; stipules linear-lanceolate, tip subulate, 7-17 mm long, glabrous; blades ovate to ovate-lanceolate, mostly 5-18 cm long, 2.5-9 cm broad, glabrate except for tufts of hairs in axils of veins beneath and with minute reddish glands (disappearing in age), 5-7 veined at base but pinately veined above (with ca 5-7 additional lateral veins on each side above the basal ones), the base obtuse to rounded or subcordate, the margins rather coarsely serrate (teeth ca 25-40 on a side), the apex acuminate. *Inflorescences* axillary, spicate; 2 spikes mostly 1-bracted (and then simulating solitary flowers), occasionally 2-bracted (rarely more), conspicuously stalked, the peduncle 10-20 mm long, lengthening to 40 mm in fruit; 3 spikes at more proximal axils, ca 2-7 cm long, loosely flowered, ca 1.5 cm across, the peduncles 1-2 cm long. *Pistillate flowers* solitary, enveloped in subtending bract, sessile; bracts ca 3 × 6 mm at anthesis increasing to 4 × 9-10 mm in fruit, cut ca 1/2 way in 13-17 lanceolate acuminate lobes ca 1.5-2 mm long (lobes becoming ± deltoid in fruit), strigose-hispidulous; ovary densely hispidulous-tomentose, the styles free, erect, nearly glabrous, ca 4-5 mm long, divided in the distal 2/5 into 10-12 subulate-tipped segments. *Capsules* verruculose-hispidulous; seeds ellipsoidal, slightly beaked, grayish-brown, smooth, ca 1.5-1.7 mm long, the caruncle obscure.

*Woods* and thickets (often second-growth), 500-1800 m, southern Mexico to western Panama.


The Panamanian specimens of *A. leptopoda* are probably all referable to var. *glabrescens* Muell.-Arg., but it is doubtful if that name has much significance. Although *A. leptopoda* is a rather variable species, its races have never been carefully analyzed.
5. Acalypha diversifolia Jacquin, Hort. Schoenbr. 2: 63, t. 244, 1797.


A. leptostachya × carpinifolia Muell.-Arg., Linnaea 34: 35, 1865.


A. diversifolia × carpinifolia (Muell.-Arg) Muell.-Arg., loc. cit.

Shrub 2-4 m high; monoecious; stems glabrous or sparsely pubescent. Leaves chartaceous; petioles 0.5-2 cm long; stipules lanceolate, subulate-acuminate, sub-indurate, distinctly convex at base, glabrate, (2.5-)4-8 mm long; blades elliptic to ovate- or obovate-lanceolate, (5-)8-15 cm long, (2-)2.5-6(-8) cm broad, ± glabrate except along the veins and minutely pubescent, pinnately veined (veins ca 5-7 on a side), the base narrowed, obtuse or subcordate, the margins crenate-serrate (teeth ca 20-40 on a side), the teeth sometimes callose, the apex abruptly acuminate. Inflorescences axillary, spicate; spikes sessile, bisexual, with 1 or 2 up to 6 ♀ bracts at the base, or entirely ♂; ♀ spikes (or parts of spikes) ca 3-8 cm long, loosely to densely flowered, 1.5-4 mm thick. Pistillate flowers sessile, 2-3 per bract; bracts ± ovate, ca 3-4.5 mm long and broad, shallowly 6-8-toothed (typically with 1 large central acute lobe and 2 or 3 much smaller lateral teeth), nearly or quite glabrous, foliaceous in fruit; ovary densely hispidulous-muriculate, the styles free, slightly hispidulous at base, ca 1.5-2 mm long, divided in the distal half into a number of slender lobes. Capsules verruculose-hispidulous, 2.2-2.3 mm diam; seeds ellipsoidal, indistinctly beaked, grayish, nearly smooth (minutely foveolate), ca 1.2-1.5 mm long, the caruncle not well-defined.

Common in thickets or montane rain-forest, southern Mexico to Peru, Bolivia, and Brazil.

BOCAS DEL TORO: Changuinola Valley, Cooper & Slater 114 (A, GH, NY, US), 1977 (GH), Dunlap 236 (F, US); vic of Chiriqui Lagoon, von Wedel 1041 (MO); id., Old Bank I, von Wedel 1993 (GH, MO); id., Water Valley, von Wedel 935 (GH, MO), 958 (GH, MO), 1587 (GH, MO). CANAL ZONE: Barro Colorado I, Elmore X7 (GH, US), Miller 2972 (MO), Shattuck 22 (MO), 311 (F), 733 (F, MO, US), 842 (F, MO, US), 1141 (F), Standley 40835 (US), Woodworth & Vestal 325 (A, MO); Chagres, Fendler 281 (GH, MO, US); Chiva-Chiva Trail, Mazon & Harvey 6528 (US); Empire to Mandinga, Piper 5488 (GH, US), 5516 (NY, US); Fort Randolph, Standley 28713 (US); 29851 (US); Fort San Lorenzo, Tyson & Blum 3684 (MO); Fort Sherman, Standley 30054 (US), 31000 (US), 31105 (US); vic of Frijoles, Allen 920 (MO), Mazon 4702 (NY, US), Piper 5781 (GH, US), Standley 27561 (US); George, Allen 470 (US), Mcgannon 1084 (US), Miller 1824 (US), Galena Point, Blum & Dwyer 2148 (MO), 2149 (MO); Gamboa, Standley 28394 (US); betw Gatun and Fort Sherman, Johnston 1729 (GH, MO); Gatun, Hayes s.n. (GH), Bro. Heriberto 111 (GH, NY, US), Standley 27289 (US), 2149 (MO); Gorgona, Mazon 4743 (US); Juan Mina, Piper 5693 (US); Las Cascadas Plantation, Standley 25742 (US), 25935 (US), 29642 (US); Obispo, Standley 31676 (US); Old Fort San Lorenzo, Piper 5972 (US); Rio Grande, nr Culebra, Pittier 2528 (GH, NY, US); Rio Indio de Gatun, Pittier 2811 (GH, NY, US); Rio Paraíso, Standley 29888 (US); Rio Providencia, 12 mi S of Colon, Tyson & Blum 2943 (MO), Chiriqui: Peninsula de Burica, vic of San Bartolomé, Woodson & Schery 920 (MO, NY), EXCL.: El Valle de Anton, Allen 1668 (MO), Bro. Maurice 775 (US), Miller 1834 (MO, US). DARIEN: vic of Canál, Williams 954 (US); Cerro Piriaque, Tyson et al. 3819 (US); vic of Pinogana, Pittier 6550 (US); betw Pinogana and Yaviza, Allen 263 (MO). HERRERA: vic of Ocu, Río Posoancho, Stern et al. 1732 (MO). LOS SANTOS: Quebrada Bejuco, 16 m S of Macaracas, Tyson et al. 2911 (MO); Quebrada Ocho Paso,


"Herb, evidently perennial from rhizome-like base; monoeious; to ca 0.5 m high; stems slender, spreading, with strigose or recurved hairs. Leaves membranous; petioles mostly 0.5-1.7 cm long; stipules lanceolate, acuminate, dark, pubescent, ca 1.5-2.2 mm long; blades ovate, ca 2-4 cm long, 1.5-2.8 cm broad, conspicuously strigose on both sides and with minute reddish glands beneath, 5-veined at base, the base truncate to rounded, the margins crenate-serrate (ca 10-25 teeth on a side), the apex acute. Inflorescences spicate; spikes unisexual, at distant nodes; ♀ spikes terminal, sessile or sub sessile, cylindrical, densely flowered, ca 1-2 cm long, 3-4 mm broad; ♂ spikes axillary, ± sessile, densely flowered, 0.7-1.2 cm long, 2-2.5 mm thick. Pistillate flowers 2 per bract; bracts ± ovate, mostly with 7 gland-tipped obtuse lobes cut ca ½ way, becoming ca 3-3.5 mm broad; calyx-segments 3, elliptic, pointed, pubescent, ca 0.7-0.8 mm long; ovary densely hisrate-hispid and muricate, the styles glabrous or nearly so, rather thick, ca 2.2-3.3 mm long, with 2-5 distal subulate branches. Capsules not seen; seeds [ex Muell.-Arg.] ovoid, minutely foveolate, ca 1 mm long.

Mountains, Costa Rica and western Panama.

Kuntze's *R. irazuensis*, although described as having 3-5-lobed ♀ bracts, agrees so closely with *A. septemloba* in other respects that it is probably synon-ymous.


"Herb to ca 1 m high; stems glabrate, with minute glandular droplets on young tips. Leaves membranous; petioles minutely puberulent, glabrate, 5-14 cm long; stipules linear-lanceolate, acuminate, glabrate, 11-13 mm long; blades ovate, ca 7-20 cm long, 4-12 cm broad, completely glabrate (hairs rare and scattered on veins), strongly 3-veined (and with 2 much weaker veins) at base, otherwise pinately veined (ca 8 additional major veins on a side), the base rounded or truncate, the margin serrate (teeth 22-35 on a side), the apex acuminate. Inflorescences spicate, unisexual, ♀ spikes terminal and often in the upper axils as well, 6-11 cm long, loosely flowered, with ca 30-50 bracts, 1-1.5 cm across; ♀ spikes axillary, ca 1-2.5 cm long, with peduncles 5-20 mm long. Pistillate flowers paired, sessile; enveloping bracts glabrous 7-10.5 mm long (or smaller in depauperate plants), cut ca ½ way into 9-12 lanceolate, attenuate-acuminate lobes, the middle ones ca 5-6 mm long; calyx-lobes obscure; ovary minutely hispidulous, the styles free,
sparsely and obscurely hispidulous at base, distally laciniate into ca 6-10 subulate lobes 1.5-2.5 mm long. **Capsules** glabrous; seeds ovoid, beaked, prominently rugose, 2.5-2.8 mm long.

Weedy habitats. Mexico to Peru.

**BOCAS DEL TORO:** Chiriquicito, to 5 mi S along Rio Guarumo, Lewis et al. 2077 (BM, DAV, GH, MO, US). Chiriqui: 2 mi SW Guabala, Tyson et al. 4248 (MO).


**Herb,** apparently annual; monoecious; stem and branches with appressed-incurved hairs intermixed with spreading ± gland-tipped hairs. **Leaves** membranaceous; petioles 1-3.5 cm long; stipules lanceolate, pubescent, 0.7-1.3 mm long; blades ovate, mostly 2-8 cm long, 1.5-5 cm broad, glabrate except for straight hairs on veins beneath, 5-veined at base, the base rounded to subcordate, the margins rather coarsely serrate (12-20 teeth per side), the apex abruptly short-acuminate. **Spikes** terminal and axillary; ♀ spikes terminal, short-pedunculate (peduncle ca 2-7 mm long), ellipsoidal to cylindrical, ca 1-4 cm long, 1.5-3.5 cm broad, sometimes with a terminal pedunculate ebracteate ♀ flower; ♂ spikes axillary, ± interrupted, ca 2-5 mm long, with peduncles 1-5 mm long. **Pistillate flowers** solitary, sessile; bracts densely hispid with sharp hairs ca 1-2 mm long and shorter mostly gland-tipped hairs, 4.5-7 mm long, with 3-5 lobes, the longer central lobes ca 3-5 mm long, deltoid with a green subulate tip mostly 2-4 mm long; ovary hispidulous and with glandular-capitate hairs, the styles unbranched, 2-7 mm long. **Capsules** glabrate; seeds ellipsoid or ovoid, smooth (minutely foveolate), grayish, 1.1-1.1 mm long, the caruncle inconspicuous, ca 0.3-0.4 mm long.

A widespread weed in the Caribbean area, from southern Louisiana and the Bahamas south to Panama, Colombia, and Venezuela.

**CANAL ZONE:** vic of Miraflores Lake, Tyson 1391 (MO); Miraflores Locks, Tyson 1259 (MO). **CÓLÓN:** vic of Sardinilla, 7-8 mi E of cement plant, Blum & Tyson 490 (MO). **DARIÉN:** El Real to Pinogana, Stern et al. 285 (DAV, MO). **PANAMA:** sabanas N of Panama City, Bro. Paul 519 (US); Panama Viejo, Duke 5708 (MO); Taboga I, Pittier 3555 (US), Standley 27033 (US), Woodson et al. 1515 (MO, NY).


**Herb** ca 2-5 dm high; stems moderately to densely pubescent with ± incurved, appressed hairs, gland-tipped hairs absent. **Leaves** membranaceous; petioles densely pubescent, mostly 1-2.5 cm long; stipules lanceolate, acuminate, pubescent, ca 1.5-2.5 mm long; blades ovate, mostly 3-6 cm long, 1.5-3 cm broad, strigose-hirsute above, glabrate beneath except on the veins, 5-veined at base, the base cuneate, the margins crenate-serrate (12-18 teeth on a side), the apex acute. **Spikes** all axillary; ♀ spikes with peduncles 6-12 mm long, ellipsoidal to short-cylindrical,
ca (1-)1.5-2 cm long, 1-1.5 cm broad, usually with a terminal projection 4-7 mm long bearing 5-10 nodes of ♀ flowers (and occasionally a terminating ebracteate ♀ flower); ♂ spikes densely pubescent, uninterrupted, ca 5-20 mm long, with peduncles 3-25 mm long. Pistillate flowers solitary, sessile; bracts hispid with sharp hairs ca 0.5-1.5 mm long and slender gland-tipped hairs (ca 0.5-1 mm long), 4-8 mm long, with 5 lobes (plus occasionally 1 or 2 smaller extra lobes), the longer central lobes mostly (1.5-)2.5-5 mm long, deltoid with a green subulate tip 0.8-3 mm long; ovary apically 3-carinate, hispidulous, not glandular, the styles 1.7-4 mm long, with 3-5 distal branches. Capsules sharply carinate, hispid to hispidulous; seeds ellipsoidal, smooth (minutely foveolate), grayish, 1.2-1.3 mm long, the caruncle 0.4-0.6 mm long.

A widespread neotropical weed, from Mexico south to Peru, Bolivia, and Brazil.

**BOCAS DEL TORO:** Changuinola River, Stork et al. 6 (US), 127 (US); Chiriquicito to 5 mi S along Rio Guarumo, Lewis et al. 2135 (DAV, MO); Isla Cokán, vic of Chiriquí Lagoon, von Wedel 2821 (GH, MO, NY). **Canaal zone:** Ancon, Piper 5818 (US); Balboa, Standley 32115 (US); Fort San Lorenzo, Burch et al. 1044 (DUKE, F, MO); Fort Sherman, Tyson & Blum 3774 (MO); Frijoles, Ebiner 630 (MO); Gamboa, Bro. Heriberto 65 (US), Pittier 4791 (US), Standley 28358 (US); Gatun, Hayes 237 (NY), Piper 5997 (US), Standley 27313 (US); Mirafores Lake, White & White 195 (MO); betw Peluca Hydrographic Sta & Quebrada Peluca, Steyermark & Allen 17237 (MO); Quarry Heights, Dwyer 2602 (MO); Sosa Hill, Standley 25241 (US). **CHIRIQUI:** vio of Boquete, Davidson 634 (A, MO, US), Lewis et al. 419 (DUKE, F, GH, K, MO, NY, UC, US), Bro. Maurice 734 (US), Pittier 2912 (NY, US), Woodson & Schery 715 (MO); W slopes of Cerro Horqueta, Allen 4380 (MO); vic of Puerto Armuelles, Woodson & Schery 821 (GH, MO). **DARIEN:** El Real, Duke 5039 (MO); El Real to Pinogana, Duke S129 (MO); vic of Yape, Allen 865 (GH, MO). **PANAMA:** 5-6 mi E of Chepo, Duke 4016 (DAV, MO); Corozal Rd, nr Panama, Standley 26814 (US); Juan Diaz, nr Rio Tapia, Maxon & Harvey 6743 (US); San José I, Johnston 900 (GH). **VERAGUAS:** 5 mi E of La Mesa, Blum & Tyson 673 (MO).

**Acalypha aristata** H.B.K. was reported from Panama by Pax and Hoffmann [Pflanzenreich 85 (IV, 147, XVI): 23, 1924] on the basis of a specimen collected at Gamboa (Pittier 4791). However, that collection actually represents *A. arvensis*, and no specimens of *A. aristata* have been seen from Panama. Nevertheless, since the latter occurs in northern Colombia, it may eventually be detected here. Although vegetatively similar and probably closely related, it may be readily distinguished from *A. arvensis* by its terminal ♀ spikes and 2-flowered ♀ bracts.

**25. DALECHAMPIA**


Undershubs or perennial herbs; mcnoecious; stems often scandent or twining, with irritating hairs. Leaves alternate, petiolate, stipulate, and usually with a pair of stipels at apex of petiole; blades simple to palately lobed or divided. Inflorescences terminal on axillary short-shoots (or apparently axillary when side-shoots are contracted), bisexual, distinctly pedunculate, flowers subterminated by conspicuous bilabiate involucr of 2 stipulate bracts; bracts simple to palately lobed, often white or colored; flowers in contracted cymes; ♀ cymbule proximal, 3-flowered, subterminated by 2 or 3 bractlets; ♂ flowers in a pleiochasium of several 1-3-flowered
cymules, associated with a pulviniform nectary compounded from modified bractlets of suppressed ♂ cymules. Staminate flowers with articulated pedicels; calyx globose and entire in bud, splitting into 3-6 valvate segments at anthesis; disc and petals absent; stamens (5-)10-35(-90), the filaments connate into a stout column, the anthers dehiscing longitudinally; pollen grains oblong, coarsely ornamented with a massive reticulum; pistillode absent. Pistillate flowers pedicellate or subsessile; calyx-lobes 5-12, imbricate, usually ± lobed or pinnatifid, accrescent in fruit; disc and petals absent; ovary of 3 (rarely 4) carpels, the ovules 1 per locule, the styles connate into an elongated column, often dilated into a peltate compound stigma. Fruits capsular, of 3(-4) elastically dehiscent cocci, the endocarp crustaceous or woody, the columella persistent; seeds globose or ellipsoid, not carunculate, endosperm present, the cotyledons broad.

This taxonomically isolated genus of some 125 species cannot be confused with any other in Panama. The characteristic bilabiate involucre is often conspicuously colored, creamy white as in *D. scandens* and *D. tiliifolia* or pinkish as in *D. dioscoreifolia*, and seems to remain green at anthesis only in *D. cissifolia*. Observations of pollinators, which are nearly lacking for the entire genus, would be well worth the effort by investigators in Panama.


*Perennial vine* (but often flowering the first year); stems woody and thickened at base, above twining and climbing, 1.5-5 mm thick or more; aerial stems subterete, somewhat channeled, green, ± hispid, the young tips densely hispid-puberulent. *Leaves* alternate; stipules becoming reflexed and brownish, ovate-lanceolate, acute, pubescent and ciliate abaxially, nearly glabrous adaxially (except near base), obscurely striate, (2-)3-5.5 mm long, 1.5-3 mm broad; petiole ± hispid as the stems, subterete, 2-12 cm long; stipels greenish, lanceolate, 1-3 mm long, glandular at base, ciliate and pubescent (especially abaxially); blades thinly to rather stiffly chartaceous, cordate at base, above greenish, rather sparsely pubescent, and somewhat rugose, beneath paler and more densely pubescent; usually deeply 3-lobed, sometimes 5-lobed, the lobes cut more than 1⁄2 way to the base,
rarely unlobed, usually with 5 main veins at base, mostly 3-10 cm long and 2.5-11 cm broad, the lateral lobes asymmetrically elliptic or ovate, abruptly acute or acuminate, the middle lobe elliptic-oblong or -obovate, abruptly narrowed to a short acuminate tip, 2-7 cm long, 1-5 cm broad, the veins conspicuously raised beneath, the tertiary veinlets tending to be scalariformly parallel. Inflorescences 1 or 2 on short axillary shoots (axis usually 5-10 mm long), subtended by reduced leaves; peduncles 2.5-5 cm long at anthesis, becoming 4-6 cm long in fruit. Involutural bracts 3-lobed ca halfway to the base, minutely glandular-toothed along the margin, generally 5-veined from the base, at anthesis distinctly whitish (lobe-tips sometimes remaining green), (1.5-)2.5-3 cm long and broad later turning green and becoming (2-)3-3.5 cm long and broad, pubescent with both crisped and stinging hairs (less densely to very sparsely so on the adaxial side); stipules reflexed, asymmetrically ovate- or oblong-ovate or lanate, greenish, ciliate-pubescent on both sides, ca 4-7.5 mm long. Pistillate cyme sub sessile, 3-flowered; adaxial bractlets 2 or coalesced into 1, ca 3-6 mm high, whitish, broader than high, sericeous on both sides, margins ciliate but not glandular, crassifolius hairs sparse, the abaxial bractlet ca 4-6 mm high, oblong, somewhat greenish, similarly pubescent, crassifolius hairs absent. Stamineate cyme terminal, peduncle densely hispatalus, 2.5-3.5 mm long; involuyl 2-lipped, subglabrous, ca 2.4 mm high and 6-7.5 mm broad, with mostly 9 or 10 \( \varphi \) flowers in 3 cymes; ciliate bractlets forming 2 laminate masses, the secretion copious and resinous. Stamineate flowers with pedicels short and stout (1 mm long or less); buds ca 2 mm in diam, appearing glabrous (minutely hispidulous with crassifolius hairs), splitting at anthesis into (3-)4 acute green lobes; stamens ca 25-35, the staminal column ca 1-1.3 mm long, the filament tips free, 0.1-0.2 mm long, the anthers deeply 4-sulcate, ca 0.4-0.6 mm long. Pistillate flowers subsessile at anthesis; calyx-lobes 8-12, unequal, deeply fimbriate lobed, the lobes ca 3-5 on a side, subulate, gland-tipped; ovary minutely hispidulous, oblate, the style cylindrical, 4-8 mm long, abruptly dilated distally into peltate stigma ca 0.8-1.3 mm across. Central fruiting pedicel up to ca 1.2 cm long, lateral pedicels shorter; fruiting calyx-lobes mostly 5-9 mm long, 0.4-0.8 mm broad, with conspicuously gland-tipped cilia, sharp-pointed hairs ca 1.5 mm long and minute crassifolius hairs (less than 0.5 mm long). Capsules oblate, ± smooth (minutely hispidulous), ca 8.5-10 mm in diam, the cocci distinctly carinate, ca 5.5-7.5 mm long; seeds subglobose, smooth, with ricinoid brown-and-gray mottling, (3-)3.5-4(-4.6) mm across.

Widespread in tropical America, often in secondary shrubbery; reported from Africa but such reports still lack confirmation.

**Canal Zone:** Balboa, Standley 32142 (US). Cocle: Aguadulce, Pittier 4933 (NY, US).

**Panama:** Corozal Rd, Standley 26766 (US); Exposición, Bro. Heriberto 278 (US); Las Sabanas, Bro. Heriberto 196 (US), Standley 25883 (US); Panama, Bro. Paul 514 (US); San José I, Johnston 396 (GH, MO), 839 (GH); Taboga I, Woodson et al. 1549 (MO), 1590 (A, MO).

Although *D. scandens* is probably the most widespread species in the genus, it is surprisingly uncommon in Panama compared to *D. tiliifolia*. Pax & Hoffmann [Pflanzenreich 68 (IV, 147, XII): 34, 1919] refer the Cocle collection of Pittier...
to var. mollis rather than to var. scandens. However, some of the other collections from Panama have involucral bracts smaller than 3 cm and it seems doubtful that this is a valid diagnostic character. Whatever subspecific taxa may be recognized in a monographic study of D. scandens, our Panamanian plants rather closely resemble the West Indian ones and thus will probably remain with the nominate variety.

2. Dalechampia tiliifolia Lam., Encycl. Méth. Bot. 2: 257, 1786.—Fig. 18.

Clambering vine; stems twining, 2-4 mm thick, striate-ribbed, retrorsely incurved-pubescent. Leaves alternate; stipules 3-5 mm long, caducous; petiole pubescent as the stem, (1.5-)2.5-14 cm long; stipels lanceolate, 1-3.5 mm long, pubescent, more or less glandular at the base; blades polymorphic, of 3 kinds—(a) undivided blades: ovate, cordate and 5-veined at the base, (6-)10-16 cm long, (5-)7-11 cm broad; (b) blades with one lateral lobe (as in Sassafras); and (c) 3-lobed blades, lobed more deeply than ⅓ way to the base, 7-16 cm long, 8-17 cm broad, the middle lobe oblong to obovate, ± abruptly acute or acuminate, (4-)6-11 cm long, (2-)2.5-4(-6) cm broad; margins finely serrulate or subentire, the lamina densely pubescent to tomentose beneath, with a reticulum of conspicuously raised veins. Inflorescences 1 or sometimes 2 per short axillary shoot, the axis (3-)7-25 cm long; peduncles (1-)1.5-4 cm long at anthesis, becoming (1-)2.5-7 cm long in fruit, the involucral bracts broadly ovate, 3-toothed at the tip (middle tooth 3-7 mm long), generally 7-9-veined from the base, tomentose on both sides, distinctly whitish at anthesis, (2-)3.5-5(-6) cm long, becoming green in fruit, (3.5)4-6 cm long; stipules 2-4.5 mm long. Pistillate cyme with auriculate adaxial bractlet, subglabrous, the margins ciliate, 5.5-6.5 mm high, 10-11 mm broad; abaxial bractlet broadly ovate or obovate, 5-7 mm high, 8-11 mm broad. Staminate cyme with stout peduncle 3.5-5 mm long, sparingly to densely hirsutulous; involucel 2-lipped, subglabrous; lip facing bract entire, reniform, 2.5-3 mm high, 7-10 mm broad, the lip facing female cyme 3-parted, the lateral lobes broadly obovate, the center lobe oblong to obovate; ♂ flowers 9 or 10; ceriferous bractlets conspicuously fimbriate at the tips, secretion resinous and sticky. Staminate flowers with slender pedicels 4-8 mm long, articulated at about ⅔ height; mature buds ca 3-4 mm in diam; calyx-lobes (3-)4-6, 3.3-3.8 mm long; stamens (25-)30-45, the staminal column rather slender, 2.5-4 mm long, the free filaments densely hispidulous. Pistillate flowers with calyx-lobes 9-12, fimbriately lobed (ca 6-10 gland-tipped lobes on each side); ovary densely hispidulous, the style cylindrical, slender, 7-12 mm long, the stigma peltate-concave, 1.3-2.7 mm in diam. Central fruiting pedicel ca 1-1.8 cm long, laterals shorter; fruiting calyx-lobes mostly 8-13 mm long, 0.9-2 mm broad, with densely hispid subulate lobes. Capsules 9.5-10.3 mm in diam, densely hispid, the cocci 6.5-8.5 mm long; seeds somewhat compressed, elliptic in outline, (3.3-)3.7-4.8 mm long, ricinoid-mottled.

Widespread in tropical America from Honduras to Brazil, not attaining such high latitudes as D. scandens.
Fig. 18. *Dalechampia tiliifolia* Lam.: A, habit (ca \( \times \frac{1}{2} \)); B, inflorescence (ca \( \times 1 \)); C, ovary (ca \( \times 2 \)); D, female flower, calyx lobe (ca \( \times 5 \)); E, male flower (ca \( \times 5 \)); F, anther (ca \( \times 10 \)); G, seed (ca \( \times 4 \)). After von Wedel 2154 (MO).
BOCAS DEL TORO: Changuinola Valley, *Dunlap* 395 (F, GH); Water Valley, von Wedel 1730 (GH, MO), 2154 (MO). CANAL ZONE: Ancon, *Bro. Celestine 61* (US), Williams 42 (NY, US); Balboa, *Standley* 25529 (US), 26093 (US); Balboa Heights, *Greenman & Greenman* 5064 (MO); Barro Colorado I, Brown 153 (F), Wetmore & Abebe 156 (F, GH); Cerro Gordo, *Standley* 26011 (US); Chagres, *Fendler* 279 (GH, MO); Chiva-Chiva trail, *Piper* 5716 (US); Colón to Empire, *Crawford* 415 (NY); Culebra, *Pittier* 2153 (US); Curund, *Harvey* 5223 (F); Darien, *Macbride* 2700 (F), *Standley* 31648 (US); Empire to Mandinga, *Piper* 5440 (US); Farfan Beach to Palo Seco, *Burch et al.* 1411 (MO), *Hunter & Allen* 443 (NY, MO); Fort Randolph, *Standley* 28721 (US); Gamboa, *Standley* 28491 (US); Gatun, *Standley* 27305 (US); Miraflores, *White & White* 46 (MO), *Blum* 2060 (MO); Obispo, *Hayes* 165 (GH), 791 (NY); Punta Paitilla, *Piper* 5420 (US); Summit, *Tyson* 2783 (MO). CHIRIQUI: San Félix, *Pittier* 5128 (US).


*Climbing vine; stems 1-2.5 mm thick, subterete, ± retrorsely pubescent. Leaves alternate; stipules reflexed, obliquely lanceolate, pubescent, 2.5-6 mm long; petiole pubescent, mostly 2.5-7.5 cm long; stipels lanceolate, 1.3-4.2 mm long; blades chartaceous, cordate at base, appearing glabrate on both sides except on veins, beneath paler and minutely hispidulous, 3-foliolate (rarely 5-foliolate), mostly 8-15 cm long, the margins undulate-dentate, the lateral lobes asymmetrically elliptic, the middle lobe narrowly elliptic-oblong to obovate, acute to acuminate, ca 6-14 cm long, 1-4 cm broad, petiolule 2-6 mm, the veins raised beneath but veinlets not conspicuously so. Inflorescences axillary and solitary to leaves on main stem (i.e. terminating reduced axillary branches less than 5 mm long); peduncle 1-2 cm long at anthesis, attaining up to 2.5 cm long in fruit. Involutral bracts 3-lobed ca halfway to base or sometimes nearly or quite unlobed, apparently greenish even at anthesis, with 5 main veins from the base, the margins ciliate and minutely dentate or subentire, 1.4-2.3 cm long, 1.3-2.5 cm broad, ca 1.5-2.5 × 1.6-2.9 cm in fruit, glabrous on both sides (but with minute stingy hairs on veins and some veinlets), the middle lobe of bract oblong, acute, 6-16 mm long, 3.3-7 mm broad, the stipules reflexed, 2.2-6 mm long. Pistillate cyme with 2 adaxial bractlets, discrete, obovate, subglabrous, the margins stiffly ciliate, ca 1.5-2 mm long, 1-1.5 mm broad; abaxial bract broadly oblong, ciliate-margined, ca 2.5-3.5 mm long. Stamine cyme with stout peduncle, very short (ca 1 mm long or less); involucre 2-lipped, subglabrous, 1.5-2 mm high, 5-8 mm broad, the lips reniform, entire; ♀ flowers 8 or 9; ceriferous bractlets truncate (not fimbriate), not
very resinous. **Staminate flowers** with pedicels ca 2-3 mm long, articulated at ca \(\frac{3}{4}\) its length above the base, sparsely hispidulous; buds ca 1.5-2 mm in diam; calyx-lobes 4 or 5, reflexed; stamens 23-26, the staminal column stout, not over 1 mm long. **Pistillate flowers** with calyx-lobes 7-11, unequal, deeply pectinate-lobed (4-6 lobes on either side); ovary densely hispidulous, the style slender, clavate-thickened on one side above the middle, 5-6 mm long, the stigma concave, oblique, slightly expanded, ca 0.6-1 mm across. Central fruiting pedicel up to 1 cm long; fruiting calyx-lobes 5-9 mm long, 0.3-0.6 mm broad, lacinuli ca 0.5-1 mm long, bristly. **Capsules** minutely hispidulous, 6.6-8.5 mm in diam, the columella ca 2.5-3 mm long, the cocci 5-7 mm long; seeds subglobose, (2.8-)3-3.7 mm long, ricinoid-mottled.

Tropical rain forest, Guatemala to Peru (and perhaps further south and east).

**Canal Zone:** Cerro Gordo, nr Culebra, Pittier 2331 (lectotype US 67561; isotype NY); trail betw Gamboa and Cruces, Pittier 3775 pro parte (F, US); woods nr Gatun, Hayes s.n. (GH), 7 (NY), 482 (NY, US); Las Cruces, Pittier 3775 (GH, US); Miraflor, White 123 (F, MO); Old Fort Loreno, mouth of Rio Chagres, Piper 5978 (US). **Colón:** Franc Field to Catival, Standley 30275 (US). **Panama:** Camino de las Sabanas, Lewis et al. 2123, (MO), which unfortunately lacks flowers, resembles *D. cissifolia* in its trifoliolate leaves but differs in having hirsute stems and larger stipules (nearly 1 cm long). Discovery of flowering material will doubtless show it to be a species new to Panama and perhaps new to science.


*Climbing vine*; stems 2-3 mm in diam, pubescent, subterete. **Leaves** alternate; stipules reflexed, lanceolate, long-acuminate, appressed-pubescent, ca 3-7 mm long; petiole pubescent with incurved hairs and sometimes with stinging hairs, mostly 2-5 cm long; stipels lanceolate, gland-tipped and usually glandular at base, 1.3-3.2 mm long; blades chartaceous, undivided, ovate with cordate base, usually 5-veined from the base, abruptly short-acuminate at the tip, mostly 7-15 cm long, 5-11 cm broad, pubescent on both sides but more or less glabrate in age, the margins crenately toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath. **Inflorescences** axillary (i.e. terminating reduced axillary branches ca 3-7 mm long); peduncle 1-1.8 cm long at anthesis, becoming 1.8-2.3 cm long in fruit. **Involucral bracts** ovate-cordate, caudate-acuminate at the tip, 5-veined from the base, pink or white with darker red or purple veins, the margins lacerate-toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath. **Inflorescences** axillary (i.e. terminating reduced axillary branches ca 3-7 mm long); peduncle 1-1.8 cm long at anthesis, becoming 1.8-2.3 cm long in fruit. **Involucral bracts** ovate-cordate, caudate-acuminate at the tip, 5-veined from the base, pink or white with darker red or purple veins, the margins lacerate-toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath. **Inflorescences** axillary (i.e. terminating reduced axillary branches ca 3-7 mm long); peduncle 1-1.8 cm long at anthesis, becoming 1.8-2.3 cm long in fruit. **Involucral bracts** ovate-cordate, caudate-acuminate at the tip, 5-veined from the base, pink or white with darker red or purple veins, the margins lacerate-toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath. **Inflorescences** axillary (i.e. terminating reduced axillary branches ca 3-7 mm long); peduncle 1-1.8 cm long at anthesis, becoming 1.8-2.3 cm long in fruit. **Involucral bracts** ovate-cordate, caudate-acuminate at the tip, 5-veined from the base, pink or white with darker red or purple veins, the margins lacerate-toothed to subentire, the veins distinctly raised on both sides but more conspicuously so beneath.
involucel glabrous, of 4 distinct, broadly imbricate, chartaceous to subcoriaceous concave bracts; \( \sigma \) flowers 8 or 9; ceriferous bractlets fimbriate. **Staminate flowers** with pedicels ca 3.5-6 mm long, articulate near the top, glabrous below the articulation, hispidulous above; calyx-lobes 4, appressed-hispidulous without; stamens ca 20-30, the staminal column slender, 2.5-3.5 mm long, glabrous. **Pistillate flowers** with sepals 6-11, deeply plicate-lobed, pubescent; ovary densely hispidulous, the style columnar, appressed-hispidulous, 3-5.5 mm long, the stigma peltate-disciform, ca 2-3.5 mm across. **Central fruiting pedicel** 1.9-2.5 cm long; fruiting sepals mostly 8-10 mm long, deeply dissected into rigid acuminate lanceolate lobes 2-5 mm long, lobes densely armed with stinging hairs. **Capsules** deeply 3-lobed, ca 12 mm in diam, the columella ca 5 mm long; seeds turgid, more or less cubical, asymmetrically crested, with low transverse ribbing, dark-mottled, 4.7-5.5 mm long.

Lowland rain forest, Costa Rica to Peru.

**BOCAS DEL TORO:** Almirante, Blum 1325 (MO); Bocas del Toro, von Wedel 239 (MO), 263 (MO), 365 (MO); Chiriquí Lagoon, von Wedel 1114 (MO), 1263 (MO), 1381 (MO); Water Valley, von Wedel 599 (MO), 1489 (MO), 1764 (MO), 1780A (MO), 1818 (MO). **CANAL ZONE:** Barro Colorado I, Shattuck 618 (F, US), Wetmore & Abbe 11 (A, F, GH), 11A (A); Las Cascadas Plantation, nr Summit, Standley 26724 (US). **COLÓN:** France Field to Catival, Standley 30232 (US), 30318 (US), 30356 (US). **PANAMA:** Cerro Azul, Duke 9334 (MO); Chepo, Duke 4075 (DAV, MO); El Llano to Rio Mamoni, Duke 5933 (MO); Rio Tocumen, Standley 26758 (US).

5. **Dalechampia friedrichsthali** Muell.-Arg., Flora **55**: 45, 1872; Pax & Hoffm., Pflanzenreich **68** (IV, 147, XII): 52, 1919.

**Climbing vine**; stems ca 2-2.5 mm thick, terete, minutely pubescent and also sparsely hirsute. **Leaves** alternate; stipules reflexed, lanceolate, acuminate, striate, minutely pubescent and ciliate, 8-12 mm long; petiole pubescent as the stem, 5.5-9.5 cm long; stipels lanceolate, pubescent, glandular at base, 1.8-3 mm long; blades chartaceous, ovate, abruptly short-acuminate, deeply cordate at base (basal lobes overlapping), sometimes with a prominent tooth 3-5 mm long on one side, sparsely hirsute above, closely and minutely puberulous beneath, 7-14 cm long, 5-10 cm broad, the margins subentire (finely and inconspicuously dentate), the veins and veinlets very prominently raised beneath. **Inflorescences** axillary and solitary to leaves on the main stem, the involucre terminating a peduncle-like branch 7.5-10 cm long; leaf at base of peduncle with caducous blade, represented only by stipules; true peduncle only 1-2 cm long, hirsute above. **Involucral bracts** evidently pale at anthesis, ovate, shallowly 3-lobed at the tip, the middle lobe cuspidate-acuminate, ca 8-9 mm long, the blade becoming ca 3 cm long, margins lacerate, minutely pubescent and also hispid (especially on veins and lobes), 5-veined at the base and contracted into a thick petiole ca 1.5-2 mm long; stipules subequal, pubescent and hispid-ciliate, 12-13 mm long, 3.5-5 mm broad. **Pistillate cymule** with 2 adaxial bractlets, discrete, asymmetrically obovate, obscurely toothed, 5-5.5 mm long, the margins hispid-ciliate but not glandular; abaxial bractlet broadly ovate-reniform, ca 4.5 mm long, over 6 mm broad, crenate-toothed, pubescent as the adaxial bractlets. **Staminate cymule** with peduncle stout, min-
olutely pubescent, ca 1.5-2 mm long; involucel of 4 distinct, broadly imbricate, firmly chartaceous concave bracts, each ca 4-5 mm high and 7-8 mm broad; ♀ flowers ca 10; ceriferous bractlets conspicuously fimbriate distally. Staminate flowers with pedicels 2-3 mm long, hispidulous, articulate near the top; buds ca 1.5-2.5 mm in diam; sepals 4 or 5; stamens (18-)25-33, the staminal column 1.3-2 mm long, hispidulous. Pistillate flowers with sepals 5-8, ovate-oblong, lacerate-fimbriate (but rachis broader than lobes), densely pubescent, 1.7-2.2 mm long at anthesis; ovary deeply 3-lobed, minutely short-hispidulous, the style slender, antrorsely minutely hispidulous below, 9.5-10 mm long, slightly dilated distally into a concave stigma 1-1.2 mm across. Capsules with cocci (ex Pax & Hoffmann) 8 mm long; seeds ca 4 mm across, slightly rugulose, mottled.

Known only from two collections, one in Costa Rica, incorrectly cited as Guatemala by Mueller, the other the Panamanian collection cited below.


This evidently rare species also belongs in sect. Dioscoreifolieae and is obviously related to D. dioscoreifolia, but not closely so. The much longer hypododium, more short-petiolate involucral bracts, and longer styles with smaller stigmas clearly set D. friedrichsthulii apart.

26. PERA


Trees; dioecious or rarely monoecious. Leaves alternate, simple, petiolate; stipules small or obsolete. Inflorescences axillary consisting of small clusters of stalked globose involucres each enclosing 3-10 sessile flowers; involucres 1-2 bracteolate at base, opening laterally at anthesis or valvate or, in one species, almost lacking. Staminate flowers 3-10, not all fully formed; calyx gamosepalous with 3 acuminate lobes; stamens 2-5, the filaments short and free or longer and basally connate, the anthers dorsifixed near base and longitudinally dehiscent; pollen grains prolate, tectate, 3-colporate. Pistillate flowers 2-5; naked; ovary 3-carpellate each with a single ovule, the 3 short styles connate basally. Fruit capsular, somewhat woody, dehiscent valvate; seeds ovoid or obvoid, compressed, smooth, shiny, carunculate.

A tropical American genus of about 25 species, two of which are reported from Panama.

a. Involute well developed, enclosing flower buds before anthesis ............. 1. P. arborea

aa. Involute absent or represented by a minute scale ................................ 2. P. aperta

1. Pera arborea Mutis, Vet.-Akad., Stockholm, Nya Handl. 5: 299, t. 8, 1784.—Fig. 19.

Tree to 20 m, glabrous or strongly lepidote and glabrate; dioecious. Leaves somewhat coriaceous; petioles to 2 cm long, deeply channeled to obscurely winged; stipules obsolete; blade elliptic to obovate, 6-12 cm long, 3-5.5 cm wide, the base
Fig. 19. *Pera arborea* Mutis: A, habit, fruiting branch (×1½); B, branch with flower buds (×2); C, fruit (×2½); D, seed (×3); E, involucre cut away to show male flower (×8); F, unopened involucre containing male flowers (×8). A, C, D after Tyson & Blum 4058 (MO); B, E, F after Johnston 478 (MO).
rounded to acute, the margin entire, the apex bluntly to sharply acuminate. *Staminate flowers* 5-10 in each involucre, the bracteoles unequal with the larger ca 1 mm long, the involucre 3 mm diam, dehiscence lateral; calyx to 1.5 mm long, strongly toothed; stamens 4-6. *Pistillate flowers* usually 3 per involucre, the peduncle rarely more than 6 mm long before anthesis, the bracteoles and involucre resembling *S*. Capsule ellipsoid to obovate, ca 12 mm long, on stalk to 4 mm long, the surface coarsely ruminate with rather sharp edged wrinkles; seed obovoid, somewhat compressed, ca 5 mm long, black, shiny, the caruncle obvious.

British Honduras, Panama and Colombia. The tree is not particularly conspicuous and may be more frequent in moist forests than the rather small number of collections would suggest.

**Canal Zone:** Fort Sherman Reservation, *Maxon & Valentine* 6975 (NY, US). **Cocle:** vic of El Valle de Anón, Allen 775 (F, MO). **Colón:** nr Fato, Pittier 4096 (F, NY, US), 4250 (US). **Darien:** forests nr Pinogana, Pittier 6574 (US). **Panama:** Cerro Azul, *Dwyer* s.n. (MO), *Tyson & Blum* 4058 (MO); Rio Tapia, *Standley* 30674 (K, US); San José I, *Johnston* 15 (GH, MO), 233 (GH, MO), 411 (GH, MO), 447 (GH), 478 (GH, MO).


Tree to 6 m, young shoots crustate-lepidote. Leaves somewhat coriaceous; petioles to 2 cm long; stipules obsolete; blade oblong, ca 5 cm long, 2-4 cm wide, the base rounded to cuneate, the margin subentire, somewhat revolute, the apex shortly acuminate. *Staminate flowers* not seen. *Pistillate flowers* 2-5, the peduncle slender, ca 1 cm long, the bracteoles ca 2 mm long, no involucre or the merest trace present. *Fruit* not seen.

**Canal Zone:** hills S of El Valle de Anón, Allen 2506 (holotype US; isotype MO).

The overall appearance of the type specimen of this species is very close to that of *P. arborea*, but the absence or extreme reduction of the involucre is a clear distinguishing feature. The peduncle is also longer than that of the buds of most collections of *P. arborea* examined. Few other collections of this genus from areas similar to the type locality of *P. aperta* have been seen, and in their absence Croizat’s judgement that this is more than an aberrant individual must be accepted.

Known only from the type collection.

27. SEBASTIANIA

*Sebastiania* Spreng., Neue Entd. Pflanzenk. 2: 118, pl. 3, 1821.

Shrubs trees or herbs; monoecious or dioecious. Leaves alternate (rarely opposite), simple, petiolate; stipules small; blade serrulate or entire. Inflorescences spicate, terminal or opposite the leaves (or rarely axillary), usually bisexual. *Staminate flowers* in clusters of 2-3 or solitary at distal nodes, subtending bracts biglandular; calyx 3-lobed; petals and disc absent; stamens 3 or 2, the filaments free or basally connate and anthers extrorse; pollen grains subglobose, tectate, 3-colporate. *Pistillate flowers* solitary or rarely in small groups at base of spike,
About 90 species, three in the Old World tropics, most of the remainder in Brazil. The single representative in Panama is a small annual which has little superficial resemblance to the majority of species in the genus.
1. **Sebastiania corniculata** (Vahl) Muell.-Arg. in DC., Prodr. 15(2):1168, 1866.—Fig. 20.

*Tragia corniculata* Vahl, Eclog. Amer. 2: 55, pl. 19, 1798.

Herb, annual; monoecious; stem sparsely branched, slender, ascending to 50 cm, hirsute or glabrate. Leaves alternate, membranous; petioles to 2 mm long; stipules minute; blade linear-lanceolate 16-32 mm long, 3-5 mm wide, hirsute or glabrous, the base obtuse to rounded, somewhat inequilateral, the margin serrate, sometimes obscurely so, the apex acute, often acuminate. Inflorescences bisexual with a female flower at the base of a male spike or unisexual with the solitary female flowers interaxillary. Staminate flowers in 10-12 flowered spikes 3-7 mm long borne opposite the leaves, the subtending bracts toothed, ca 1/4 mm long, the pedicels ca 1/2 mm long; calyx-lobes broadly obovate ca 1/2 mm long; stamens 3, free. Pistillate flowers solitary, the pedicel ca 1/2 mm long; calyx-lobes elliptic, dentate, less than 1 mm long; ovary glabrous or sparsely hirtellous with 6 horn-like processes distally, the styles shortly connate. Capsule truncate-globose, ca 3.5 mm diam, the distal processes ca 1 mm long with additional flaps of tissue of a similar size developing on the sides of some fruits, the persistent columella ca 3 mm long, broadening from a slender base; seeds subcylindric, to 2.5 mm long, minutely pitted, the caruncle stipitate.

An inconspicuous member of the flora of the savannas and grassland of cut-over areas.

CoCle: Nata, Allen 824 (F, MO). Panama: nr Las Sabanas, Standley 40782 (US); along drowned Rio Azote Caballo, Dodge et al. 16840 (MO).

28. **MABEA**


Shrubs or trees with milky latex; monoecious. Leaves alternate, simple, petiolate; stipules usually obsolete; blade expanded, entire or toothed. Inflorescence racemose or paniculate, terminal, usually bisexual. Staminate flowers numerous, usually ternate in groups of 2-5 at upper nodes with each group subtended by a conspicuously biglandular bract; calyx small of 3-5 broad lobes; petals and disc absent; stamens numerous or rarely 2-3, the anthers almost sessile on a convex receptacle, extrorse; pollen grains somewhat prolate, tectate, 3-colporate. Pistillate flowers few, solitary (rarely 2-4 on branched peduncle) at basal nodes, subtending bract glandular to varying degrees; sepals 3-6, unequal, acute; petals and disc absent; carpels 3, each with 1 ovule, the styles connate in a long colum, free and simple above. Fruit capsular, endocarp hard, the columella persistent after dehiscence; seed carunculate, smooth or somewhat warty.

About 40 species, all in tropical America and with no more than three or four as far north as Central America. As treated here, the Panamanian specimens fall into two taxa, one of which shows a wide range of variation.

a. Leaves elliptic to lanceolate, usually 3-5 times as long as wide, the apex sub-acuminate; stamens 15-25 per flower .......................... 1. *M. montana*
aa. Leaves broadly elliptic to ovate-elliptic, usually less than 3 times as long as wide, apex strongly long-acuminate; more than 30 stamens per flower .......................... 2. *M. occidentalis*
1. *Mabea montana* Muell.-Arg. in DC., Prodr. 15(2): 1151, 1866.—Fig. 21 (A-C).

Shrub or small tree. Leaves membranous; blade 7-12 × 1.5-3 cm, elliptic to lanceolate, the upper surface sometimes shiny, the base rounded, the margin serrate (sometimes obscurely so), the apex somewhat acuminate and often mucronate. Inflorescence a raceme of groups of ♂ flowers, ♀ usually solitary. Staminate flowers in groups of 3-5, the subtending biglandular bract at or near the base of the peduncle; calyx gamosepalous, the broad lobes fused for most of their length; stamens 15-25. Pistillate flowers 2-5, solitary at basal nodes, a single ♂ flower sometimes sharing the node, subtending bract eglandular; sepals 6, 3 much larger than the others. Capsule ovoid, to 16 mm long; seed ovoid, to 10 cm long, somewhat laterally compressed, dark brown, smooth.

Reported from Venezuela and Colombia, and in Panama most common in the lowland forests around the Canal Zone.

**Canal Zone:** vic of Ancon, Piper 6022 (US), 6034 (US); Ancon Hill, Killip 39554 (US), Piper 5550 (US), 5570 (US), 5583 (US), Standley 28156 (US), 26364 (K); low hill N of Balboa, Gillespie P-30 (F); Balboa heights, Greenman & Greenman 5074 (MO); Corozal Standley 27634 (US); beach area Fort Kobbe, Duke 4227 (MO); Howard Air Force Base, SE of Kobbe beach, Oliver & MacBryde 1881 (GH, MO); woods nr Panama, Hayes 715 (K). **Coclé:** Perignoné Williams 53 (NY). **Darién:** Rio Cucunati at Puente Quemado, Duke 8816 (MO). **Panama:** Taboga I, Macbride 2831 (F, US), Miller 1841 (US), Pittier 3586 (US).

2. *Mabea occidentalis* Bentham, Hooker's London Jour. Bot. 6: 364, 1854.—Fig. 21 (D).

Shrub or small tree. Leaves membranous to subchartaceous; blade 8-15 × 3-5 cm, broadly elliptic to ovate-elliptic, the upper surface usually shiny, the base obtuse to rounded, the margin subentire to bluntly serrate and often undulate, the apex strongly long-acuminate. Inflorescence a raceme of groups of ♂ and solitary ♀ flowers. Staminate flowers in groups of 3, the subtending biglandular bract at or near the base of the peduncle; calyx gamosepalous, the broad lobes fused for ca ½ length; stamens 30-45. Pistillate flowers 3-7, solitary at basal nodes, subtending bract eglandular or obscurely glandular; sepals 6, acute, subequal. Capsule ovoid, 11-17 cm long; seed ovoid, ca 8 mm long, slightly laterally compressed, smooth or obscurely warty.

Central America and northern South America to Brazil. Most of the collections seen from Panama have come from the Province of Panama or the Canal Zone, and the plant is most common in rather wet forests.

**Canal Zone:** Balboa Standley 29302 (US); Barro Colorado I, Brown 2 (F), 7 (F), 8 (F), 9 (F), 14 (F), 169 (F), Frost 56 (F), Killip 40025 (US), Shattuck 253 (A, F), Standley 31448 (US), 41033 (US), Wetmore & Abbe 29 (A, F, GH) Woodworth & Vestal 369 (A, F), Wilson 54 (F); nr Fort Randolph, Standley 28662 (US); 29882 (US); Galena Point, Blum & Dwyer 2147 (MO); nr Gatun, Hayes s.n. (F, GH, K, MO, NY, US); Gatun Station, Hayes 52 (NY), 118 (GH, US), 461 (NY); betw Gatun & Lion Hill, Pitter 2565 (US); Matachin, Cowell 196 (NY), 200 (NY); vic of Miraflores Lake, White 188 (MO); Obispo, Standley 31698 (US); Quebrada Ancha, Steyermark & Allen 17106 (MO); Quebrada La Palma, Dodge & Allen 17348 (F, K, NY, US); Rio Chagres, 1 mi above Madden Lake, Duke 4456 (MO); Rio Paraiso, above East Paraiso, Standley 29899 (US);
Fig. 21. **Mabea montana** Muell.-Arg.: A, habit (×1/2); B, young fruit (×4); C, male flower cluster (×4). A, C after Standley 25156 (US); B after Piper 6022 (US). **M. occidentalis** Bentham: D, leaf (×1/2). After Johnston 1137 (MO).
s. loc., Lee 1 (F, MO). colón: summit of Cerro Santa Rita, Allen 5102 (F, MO); Juan Mina plantation, Río Chagres above Gamboa, Allen 4142 (F, MO). Darien: vic of La Palma, Pittier 5502 (US); Rio Sambu, 0-5 mi above Río Venado, Duke 9260 (MO); San José River, Duke & Bristan 405 (MO); ca 2 mi N of Santa Fé, Duke 10249 (J. A. Duke pers. herb.). Panama: Cerro Jefe, Dwyer & Gauger 7364 (MO), Tyson 3399 (MO), Tyson et al. 3209 (MO), 3351 (MO), 4355 (MO), 4366 (MO); upper Mamoni River, Pittier 4486 (US); vic of El Llano, Duke 5846 (MO); Río La Maestra, Allen 21 (F, MO); Río Tapia, Standley 28135 (US); Río Tocumen, Standley 26728 (US); San José I, Erlanson 162 (GH, US), Johnston 408 (GH, MO), 1137 (GH, MO), 1053 (GH); Taboga I, Standley 28003 (US). san blas: inland from airport at Mandinga, Duke 8906 (MO). Veraguas: rd betw San Francisco & Santa Fé, Stern et al. 33725 (MO, US).

The specimens from Panama show a great deal of variation but could not be assigned with any degree of satisfaction to the varieties cited by Pax [Pflanzenreich 52 (IV, 147, V):33, 1912] in his treatment of the whole genus. One collection from the E slope of Cerro Jefe (Tyson et al. 3351) and Allen 5102 from 1200-1500 ft in Colón were particularly sturdy specimens, but apart from this overall larger size no differences were found from other collections. Several collections appeared to differ in the size of the female calyx, but no other distinguishing features were found. It seems possible that additional field work and study of complete specimens would allow some division of this taxon.

29. STILLINGIA

Stillingia Garden ex L., Mant. PI. 19, 1767.

Perennial herbs, shrubs or small trees, glabrous throughout; monoecious. Leaves alternate, opposite or verticillate, simple, petiolate; usually with glandular filiform stipules and often with 2-3 cyathiform or scutelliform glands at the base of the blade. Inflorescence terminal, spicate, bisexual. Staminate flowers at distal nodes, solitary or in compressed cymes, subtending bracts biglandular; calyx 2-lobed; apetalous; disc absent; stamens 2, the filaments connate at base, the anthers extrorse; pollen grains ellipsoid to spheroid, usually 3-colpate. Pistillate flowers solitary at proximal nodes; sepals 5, usually distinct; petals absent; carpels 3 or 2, each with 1 ovule, the styles connate at base, simple. Fruit capsular, a hardened gynobase persisting after dehiscence; seed carunculate or not, rugulose or smooth, the endosperm mealy.

A genus of 25-30 species of the tropics and subtropics. All are from the New World except three in Madagascar and one in Fiji, but only one has been reported from Panama and this is known from only two collections.

Useful Reference:


Shrubs or subherbaceous from a woody rootstock, spreading or erect to 1.5 m. Leaves membranous, alternate or subverticillate; petiole to 5 mm long; stipules
obliterated; blade elliptic, 3-5.5 cm long, 1-2.2 cm wide, the base acute with 2 cyathiform glands, the margin serrulate, the apex acute. Inflorescence to 7 cm long. Staminate flowers sessile in 3-5-flowered cymules, subtending bracts elliptic; calyx ca 1 mm long. Pistillate flowers sessile; sepals narrowly elliptic, ca 3 mm long; styles ca 3 mm long. Capsules obvoid, shallowly 3-lobed, to 1.8 cm diam, the lobes of gynobase 3-9 mm long; seed subspherical, ca 6 mm diam, smooth, shiny, the caruncle small.

CHIRIQUI: Boquete, savannas alt 4000 ft, Davidson 750 (A, F, P, MO, US); Boquete, Seemann s.n. (K).

30. SAPIUM


Excoecaria Muell.-Arg. in DC., Prodr. 15(2): 1201, 1866 (pro parte).

Trees or shrubs, glabrous; monoecious or rarely dioecious; milky latex in stems. Leaves alternate, simple, petiolate, usually with two glands near apex; stipules small. Inflorescences spicate, terminal, bisexual. Staminate flowers in several-flowered clusters at distal nodes, subtending bract biglandular; calyx gamosepalous, 2-3-lobed; corolla and disc absent; stamens 2 or 3, the filaments free or connate at base, the anthers extrorse; pollen grains subglobose, tectate, 3-colporate. Pistillate flowers solitary at proximal nodes, subtending bracts usually biglandular; calyx gamosepalous (2-)3-5-lobed, sometimes obscurely so; corolla and disc absent; carpels 3 (rarely 2), each with a single ovule, the 3 styles simple, usually connate at least at base, the stylar column often early-deciduous. Fruit capsular, sometimes fleshy or somewhat woody, the columella usually persistent; seeds rounded, outer seed-coat fleshy, ecarunculate.

A genus of about 100 species, pantropical but with the majority from the New World.

The genus has the reputation of being difficult taxonomically, and this seems well justified with the incomplete specimens available in most herbaria. Dr. E. Jablonski of the New York Botanical Garden is working actively in the group, and it is unfortunate that this treatment must appear before he has published further. Separation of taxa and assignment of names is made here with some trepidation, particularly since the ranges that he gives for South American species (Phytologia 14: 441-449, 1967) already cast some doubt on the correctness of some of my decisions.

a. Spikes in clusters of 3-5 (rarely fewer); $\delta$ flowers 2-5 at each node .... 1. S. aucuparium
   aa. Spikes solitary; $\delta$ flowers usually more than 5 at each node.
   b. Petiole without glands or with only vestiges near junction with blade; leaf-apes $\pm$ plane .................................................. 2. S. eglandulosum
   bb. Petiole with 2 prominent glands near junction with blade; leaf-apes $\pm$ cuculate.
   c. Leaves somewhat coriaceous, elliptic to obovate; styles fused only at base, strongly reflexed ........................................... 3. S. caudatum
   cc. Leaves membranous, elliptic-lanceolate; styles fused for much of length, not reflexed ........................................... 4. S. biglandulosum
1. *Sapium aucuparium* Jacquin, Enum. Pl. Carib. 31, 1760.—Fig. 22.

*S. anadenum* Schum. & Pittier, loc. cit., pl. 11.

Tree to 20 m; monoecious. Leaves membranous; petiole 2-3 cm long with the two glands at or near the apex, subopposite or alternate, stipitate to obsolete; stipules obsolete; blade elliptic to obovate, 9-12 × 3-5 cm, often rather glossy on both surfaces, the secondary veins many, parallel for most of their length, leaving midrib ± at right angles, the base obtuse, sometimes unequal, the margin subentire to regularly strongly tufted, the apex acuminate, sometimes cucullate. Spikes in clusters of 3-5 (rarely fewer), to 10 cm long, bisexual. *Staminate flowers* in groups of 2-3 (-5), the subtending bract prominent in young spikes, deltoid, to 3 mm long, caducous, the basal glands persistent, prominent; calyx minute to ca 1 mm long, 2-lipped; often caducous; stamens 2. *Pistillate flowers* 8-15, singly at the basal nodes of the spike, the bract equaling ♂, caducous but basal glands persistent, smaller than in ♂; calyx cupular of two unequal segments, free almost to base;
ovary orbicular, the styles simple, to 2 mm long, connate for ca ½ length, erect, upper half uncinate, the whole stylar column caducous leaving a short rounded peg. Capsule ovoid, to 8 mm long; seed flattened-ovoid.

Cuba, Jamaica, Central and northern South America. Quite widely distributed in Panama with no clear altitude or environmental preference.


The application of this name and of S. biglandulosum (L.) Muell.-Arg. follows that of Croizat (Jour. Arnold Arb. 24: 174 et seq., 1943).


Shrub or small tree (in Panama); monoecious. Leaves membranous; petiole 2-3 cm long, eglandular or with vestiges at base of blade; stipules obtuse, to 3 mm long, somewhat sheathing in young stems; blade obovate-elliptic, 13-18 × 5-7 cm, glabrous, the base acute, the margins entire or obscurely serrate, the apex long-acuminate, plane. Spikes solitary, to 7 cm long, bisexual. Staminate flowers in groups of 5-7, the bracts short, broad, to ½ mm long, the basal glands prominent, cupular, persistent; calyx cupular, ca 1 mm long, 2-lipped; stamens 2. Pistillate flowers 3-5, singly at the basal nodes, the bract short, as in S. eglandulosum, prominently biglandular, the glands cupular; calyx cupular, 3-lobed; ovary orbicular, the styles simple, to 3 mm long, fused for half length, the upper half reflexed. Capsule not seen.

Brazil, Peru and Colombia. The two Panamanian collections represent an entirely credible extension of the range from that shown by Jablonski (op. cit.).

DARIEN: ascent of Cerro Pirre from Rio Pirre S of El Real, Duke 5334 (MO); Cerro Pirre, Duke & Elias 13665 (MO, NY).


Tree to 10 m; monoecious. Leaves somewhat coriaceous; petiole 1.5-4.5 cm long, the 2 stipitate glands at or near apex; stipules ovate, to 1 mm long or obsolete; blade elliptic to obovate (8-)13-17 × 2.5-5 cm, upper surface usually dull, the base obtuse, the margin irregularly toothed to subentire, the apex somewhat attenuate, usually strongly cucullate. Spikes solitary, bisexual. Staminate flowers in groups of 7-10, bract short and broad, ca ½ mm long, biglandular, the glands small; calyx ca ½ mm long, cupular, scarcely lobed; the stamens 2. Pistillate flowers 5-10, solitary at basal nodes, the bract as in S. eglandulosum, caducous leaving two prominent glands larger than in S. eglandulosum; ovary orbicular, styles simple, ca 2 mm long fused only at base and remainder of length reflexed to lie on surface of ovary, deciduous leaving a rounded peg. Capsule ovoid, somewhat stipitate, to 8 mm long; seed ovoid, flattened laterally, surface warted.

Range doubtful; the species was described from Panama.
FLORA OF PANAMA (Family 97. Euphorbiaceae)


The syntypes cited for this name (Pittier 2603, 3713, 4058) were collected from a single tree at different seasons and show a remarkable diversity of leaf characters. The rest of the specimens from Panama are a good match for one or other sheet. It seems unlikely that a plant that ranges so widely in Panama should be restricted to that country, and it is probable that Dr. Jablonski will have other thoughts on the validity of this name. The Panamanian specimens have resemblances to Schumann & Pittier’s S. oligoneurum and S. thelocarpum of Costa Rica and with the widely ranging S. hippomane G. F. W. Meyer, and may well prove not to be distinct.

Pittier described another species from Panama, S. giganteum (Contr. U.S. Nat. Herb. 20: 128, 1918). No authentic material of this has been seen, but from the description it falls within the range of variation of S. caudatum as used here.


Tree to 10 m; monoecious. Leaves membranous; petiole ca 1 mm long, the 2 apical glands prominent; stipules to 1 mm long, ovate; blade elliptic-lanceolate, 8-11 × 1.5-2 cm, glabrous, the base acute, the margin coarsely and evenly serrate, inrolled on drying, the apex somewhat attenuate and cucullate. Spikes solitary at apex of short laterals, to 8 cm long, bisexual or all ♂. Staminate flowers in groups of 7-10, the subtending bract lingulate, to ½ mm long, biglandular, the glands sometimes obsolete; calyx ca 1 mm long, 2-3 lipped; stamens 2. Pistillate flowers 1-8, singly at basal nodes, rather distant, the bract deltoid, fimbriate, biglandular; calyx cupular, 2-lobed; ovary orbicular, styles simple, fused for most of length and slightly expanded at apex, soon deciduous leaving a rounded peg. Capsule broadly ovoid, to 1 cm long, smooth; seeds broadly ovoid flattened laterally, the surface warty.

Panama and northern South America, perhaps to Brazil. A number of the Panamanian collections are from areas near the sea, but the species does not appear restricted to one altitude or habitat.

CANAL ZONE: upper Chilibre River, 1 mi below Chilibre, Seibert 1514 (MO, NY, US); Culebra I, Hayes s.n. (GH); Fort Amador, Tyson 2026 (MO); Las Sabanas, Bro. Celestine 109 (US), Pittier 6681 (US). COCAL: Agudaluce, Pittier 4951 (NY, US); N rim El Valle de Antón, Allen 1915 (type coll. of Stillingia haematantha GH, MO); vic of Las Uvas, Allen 2575 (A, F). LOS SANTOS: Pediasia, Dwyer 2495 (MO). PANAMA: Bella Vista,
One more group of specimens remains without a name. All have elliptic leaves 20-35 × 5-9 cm with an obtuse to rounded base, coarsely and evenly serrate margin and attenuate apex which may be somewhat cucullate. The veins are arcuate, prominent below, and the petiole has a pair of stipitate glands a little below the junction with the blade. The stipules are deltoid, to 2 mm long. All the shoots have a succulent appearance which suggests that they may be sucker growth or water shoots, and those of the sheets which include collection notes describe the plant as a shrub. None include any flowering or fruiting material. They do not unequivocably match any American material in the herbarium of the Missouri Botanical Garden, and will not be included in this treatment in the hope that later, more complete collections will enable someone to make good the omission.

31. HIPPOMANE


Trees or shrubs with milky latex, glabrous; monoecious. Leaves alternate, simple, petiolate, with a single gland at junction with blade; stipules caducous; blade ovate-cordate, the base rounded, the margins bluntly serrate, the apex acute to short acuminate. Inflorescences terminal, spicate, bisexual. Staminate flowers clustered in several-flowered glomerules at the distal nodes, subtending bracts biglandular at base; calyx 2-3-lobed; apetalous; disc absent; stamens 2, the filaments connate, the anthers extrorse; pollen grains sub-globose, tectate, 3-colporate. Pistillate flowers solitary at proximal nodes; calyx 3-parted; apetalous; disc absent; carpels 6-9, the styles simple, connate at base, spreading above, the ovary smooth with one ovule per locule. Fruit drupaceous, apple-like, red or yellow; seeds ovoid, compressed, ecarunculate.

A genus of two or three species, one widespread in the Caribbean area, the others endemic to Hispaniola.

1. Hippomane mancinella L., Sp. Pl. 1191, 1753.—Fig. 23.

Tree to 10 m, much branched forming a rounded crown, the bark gray or red, often lichen covered. Leaves on slender petioles 3-5 cm long; blades ovate to elliptic, 5-10 cm long, 4-6 cm wide just below middle, somewhat shiny above with veins slightly raised particularly on drying, the base rounded to subcordate, the margin crenulate with 8-12 shallow teeth, the apex short-acuminate. Inflorescences to 10 cm long, stout, 1-2 9 flowers at base. Staminate calyx ca 1 mm long, the lobes broadly ovate. Pistillate calyx ca 3 mm long, ovate and somewhat acuminate. Fruit globose, to 3.5 cm diam, smooth; seed dark, ca 6 mm long.

Widespread and locally common near the upper edge of beaches from Florida and the Bahamas through Central America and the Antilles to Colombia and Venezuela.
Fig. 23. *Hippomane mancinella* L.: A, habit (×⅔); B, male flower (×10); C, female flower (×10). A-B after Christopherson 173 (US); C after Standley 30777 (US).
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32. HURA


Trees, trunk with hard conical spines; monoecious. Leaves alternate, simple, long-petiolate, with 2 round glands at junction with blade; stipules caducous. Inflorescences unisexual. Stamineate flowers in terminal long-pedunculate fleshy conical spikes, each flower sheathed by a membranous bract which ruptures at anthesis, sessile; calyx cupulate, denticulate; disc absent; stamens numerous, the filaments connate, the anthers in 2-several verticels, longitudinally dehiscent; pollen grains oblate, ternate, 3-colporate. Pistillate flowers solitary in uppermost leaf axils or rarely at base of male spike, long-pedicellate; calyx broad-cupulate, 5-toothed to subentire; disc absent; ovary of 5-20 carpels, each with a single ovule, the styles connate into a long column, dilated into radiating lobes at the apex. Fruit an explosively dehiscing woody capsule; seeds laterally compressed, ecarunculate.

Two neotropical species, widely planted as living fence posts. Only one has been collected in Panama.

1. Hura crepitans L., Sp. Pl. 1008, 1753.—Fig. 24.

Trees to 25 m, but often kept much lower when used as living fence posts. Leaves on petioles to 20 cm long; blade ovate to orbicular, 12-25 cm long and 7-15 cm wide, prominently pinnerved, sparsely long-pubescent on the lower surface, the base cordate, the margin crenate with teeth often glandular tipped, the apex acuminate to subcuspidate. Stamineate flowers 60-80 on conical fleshy axis 2-4.5 cm long, peduncle to 10 cm long; calyx to 1 mm long; staminal column to 2 mm long with 2-3 verticels of anthers, the third rarely complete. Pistillate flowers with pedicels to 5 cm long; calyx 3-5 mm long, truncate, or rarely shallowly 5-toothed; stylar column 2.5-5 cm long, the fleshy apical disc to 1 cm diam with radiating tips an additional 1 cm long. Capsule woody, oblate, to ca 8 cm diam, 3-5 cm long, dehiscing explosively into ca 15 crescentic cocci; seeds smooth, flattened, suborbicular, to 2 cm diam.

Costa Rica, the West Indies, Panama to tropical South America.

The other species, H. polyandra Baillon, is easily distinguished by the several verticels of anthers in its male flowers. There are no obvious vegetative differences but the range of this species seems to lie north of that of H. crepitans with overlap chiefly in Costa Rica.

BOCAS DEL TORO: Changuinola to 5 mi S at junction, Rios Changuinola & Terebe, Lewis et al. 832 (GH, MO, UC, US); vic of Chiriquí Lagoon, von Wedel 1165 (MO), 1519 (MO), 2466 (MO), 2638 (MO), 2750 (MO), Seibert 1561 (US). CANAL ZONE: Ancon,
Fig. 24. *Hura crepitans* L.: A, habit (×1/2); B, male flower (×10). A after Allen 280 (MO); B after Allen 4501 (MO).

Herbs shrubs or trees, sometimes succulent, milky latex in all parts; monoecious or rarely dioecious. Leaves opposite, whorled or alternate, often serially on the same plant, simple; sometimes caducous particularly in succulent forms; usually petiolate except in succulents; stipules present or absent, sometimes glandular. Inflorescence a cyathium, the 5 cup-like lobes alternating at their tips with 4-5 glands, these with or without appendages. Staminate flowers in 4-5 cymes, the subtending bracteoles partly fused to the involucre or reduced or absent; naked; monandrous; pollen grains subglobose, reticulate to tectate, 3-colporate, sometimes operculate. Pistillate flowers terminal, solitary; perianth of 3-6 united sepals or absent; ovary 3-celled each with a single ovule, the styles 3, free or joined basally, usually partly bifid. Fruit capsular (rarely drupaceous); seed ± ovoid, angled or terete, the surface smooth or variously sculptured, with or without caruncle.

A genus of about 1200 species as used here. The diversity of plant form and detail of the reproductive structures have led a number of workers to suggest that the strong unifying feature of the cyathial inflorescence would better be considered a tribal than a generic character; a number of more "natural" genera would then be formed as segregates of the Linnaean Euphorbia. The most recent discussion of this, a fine account by Webster with a full bibliography (Jour. Arnold Arb. 48: 303-430, 1967), takes the reasonable position that until such segregates can be defined in an unequivocal way they should not be separated as genera even though these would represent evolutionary units. Webster allows that a diagnosis can be made of Chamaesyce and accepts it "diffidently" as a genus, but treats all other segregates which have been proposed as part of Euphorbia L. Much the same disposition is made here. I have less hesitation in accepting Chamaesyce as a distinct genus, and have also accepted Poinseltia at that rank even though in Central America as a whole the boundary between this taxon and Euphorbia subg. Agaloma (Raf.) House is not always distinct. In Panama these two genera are easily distinguishable in the field, and I feel that it is more informative to treat them in this way than to maintain them in Euphorbia L.

a. Leaves all whorled; trees or large shrubs; stems articulate ..................I. E. cotinifolia
aa. Leaves alternate, opposite or both, sometimes also with a whorl at one node; herbs, often vining; stems not obviously articulate.
b. Capsule glabrous.
c. Seed terete, surface smooth; cyathia ca 2 mm diam, the glands 4, dark, the appendages equaling glands, ciliate-pubescent above .................. 2. E. dwyeri
c. Seed strongly angled, surface deeply punctate with pits in regular longitudinal rows; cyathia ca 1 mm diam, the glands 4 or 2, green, the appendages obsolete (Panamanian specimens) to prominent and white several times size of gland, glabrous .................................. 3. E. graminea

bb. Capsule pubescent, especially when young.
d. Leaves ovate to subcordate, rarely larger than 1 X 1 cm; glands usually 4, appendages deeply 3-4 parted; capsule ca 1.5 mm diam; seed ca 1 mm long, surface deeply pitted ............................................. 4. E. oeymoidea
dd. Leaves ovate-lanceolate 3.5-6 X 1-2 cm; glands 2, appendages entire or obsolete; capsule ca 3 mm diam; seed ca 2.5 mm long, surface papil-late ............................................... 5. E. oerstediana


Tree, head strongly branched, to 10 m, branches terete, articulate, glabrous. Leaves ternate (rarely alternate at some nodes); stipules obsolete; petiole 2-6 cm long, slender; blade ovate, 4-6 X 3-5 cm, green, glabrous or with scattered short hairs, the base rounded, sometimes obscurely peltate, the margin entire, the apex truncate to emarginate. Cyathia in terminal cymes, often forming showy panicles with up to 30 on each of 6-12 laterals at the tip of a branch, campanulate, ca 3 mm diam, the lobes broad, fimbriate and often white at their apices; glands 5(4), brown, the appendages larger than glands, white. Fruit not seen from Panamanian material; a Mexican collection (Pringle 6069 MO) has capsules broadly ovoid, to 6 mm diam, sparsely pubescent; seed ovoid, ca 2.5 mm long, somewhat angled, the surface deeply pitted with pits ± in rows and occasionally also warted, ecarunculate.

Mexico through Central America to northern South America. Occasionally planted as living fence posts and probably introduced to the West Indies for this reason.


A very striking small tree similar to this taxon but with bright red leaves is often seen in Central America as a hedge plant. An example from Panama is Duke 8454 (MO) from a cemetery in Mulatuppu, Comarca de San Blas. Its taxonomic position is not clear but it is probably the entity which Klotzsch & Garecke described as Alectorocotonum caracasemum (Abh. Akad. Berlin, Phys.-Math. 1860: 40, 1860). In making the transfer to Euphorbia Boissier (in DC., Prodr. 15(2): 60, 1862) describes it as having cymes of 3-7 cyathia. This and the color and possibly thinner texture of the leaves may be enough to warrant its separation at specific rank, but further collections from all parts of the range are needed to be sure whether this is the case or if it would better be treated as a subspecific segregate of E. cotinifolia.

_Herb_, stems terete, glabrous, not articulate, sparingly branched, sprawling, to 1.5 m long. _Leaves_ alternate through most of plant, opposite above a 3-leaved whorl; stipules obsolete; petiole 2.5-6 cm long, slender; blade ovate-lanceolate, 3.5-6 × 2-3.5 cm, thin, green (drying darker above than below), glabrous except for scattered short hairs on the under surface, the base cuneate to rounded, sometimes obscurely peltate, the margin entire, the apex obtuse to rounded or emarginate and mucronulate. _Cyathia_ in groups of 2-5 on short dichotomizing laterals, funnelform-campanulate, 2 mm long, 2 mm in diam; peduncle to 4 mm long; glands 4, dark, the appendages equaling glands and with short spreading hairs on upper surface simulating a ciliate edge to the gland, occasionally glabrous. _Capsule_ broadly ovoid, 4 × 4 mm, glabrous; seed ovoid, 3 mm long, smooth, terete, ecarunculate.

Known only from the type collection from a trail to the lower edge of a cloud forest at an altitude of 5000-5800 ft.

chiriqui: Cerro Horqueta, NW of Boquete, Dwyer et al. 434 (holotype MO; isotypes GH, K, US).


_E. picta_ Jacquin, Coll. 3: 178, 1790.

_Herb_, stems terete, not articulate, branching from base, sprawling to 1.5 m long. _Leaves_ alternate, becoming opposite above; stipules obsolete; petiole to 2 cm long; blade oblong-elliptic to sublinear or rarely ovate, 2.5-4(-8) × 0.5-1.5(-5) cm, green, short pubescent or glabrous, the base acute to obtuse, the margin entire, the apex acute. _Cyathia_ terminal on dichotomizing upper branches, funnelform, ca 1 mm diam; glands 2-4, minute, exappendiculate (extra-Panamanian specimens often with large white appendages). _Capsule_ broadly ovoid, ca 3.5 mm diam, glabrous; seed ovoid, 1.5 mm long, angular, deeply punctate with pits in regular longitudinal rows, ecarunculate.

Southern Mexico to northern South America. A very variable species in all parts of its range. It may, in fact, be a complex of separable taxa but many of the segregates made to date are unconvincing.

canal zone: Farfan beach area, Tyson et al. 3171 (MO). darien: trail from Río Pucro to Quebrada Maskia, Duke 13054 (MO); vic of Yape, Allen 860 (F, MO). province unknown: s. loc., Seemann 1241 (BM), 1649 (BM).


_Herb_, stem not articulate, much branched, scandent to 1 m. _Leaves_ alternate at base, opposite above; stipules obsolete; petiole to 1.5 cm long, slender; blade broadly truncate-ovate to subcordate, ca 1 × 1 cm on main stems, much smaller on laterals, thin, sparsely long pubescent on each surface, the base truncate or short-acuminate, the margin entire, the apex obtuse. _Cyathia_ terminal on branched laterals, campanulate, ca .75 mm diam; glands usually 4, the appendages
larger than gland, deeply 3-4-parted. Capsule ovoid, to 1.5 mm diam, long pubescent; seed ovoid, 1 mm long, angular, surface deeply pitted, ecarunculate.

Central America and probably northern South America.

canal zone: Farfan Beach area, Tyson et al. 3170 (MO). Herrera: rd from La Avena to Pesé, Burch et al. 1289 (GH, MO, UC, US).

5. Euphorbia oerstediana (Kl. & Gke.) Boiss. in DC, Prodr. 15(2): 59, 1862.

Herb, stems terete, glabrous except at tips, not fully articulate, sparingly branched, erect to 9 inches. Leaves alternate, sometimes opposite near apex of stems; stipules obsolete; petiole ca 1 cm long; blade thin, ovate-lanceolate, 3.5-6 × 1-2 cm, scattered short hairs on each surface, the base obtuse to rounded, the margin entire, the apex obtuse to mucronate. Cyathia in small terminal groups, campanulate, ca 1 mm diam; glands 2, the appendages green, the margins entire, upright or obsolete. Capsule broadly ovoid, ca 3 mm diam, densely pubescent particularly when young; seed ovoid, 2.5 mm long, surface papillate, minutely carunculate.

Central America, West Indies and northern South America. Known from only one collection in Panama, but probably more common than this would indicate and simply overlooked since it is a very inconspicuous member of the flora of wooded areas.

Herrera: rd from La Avena to Pesé, Burch et al. 1316 (MO).

Another species, *E. apocynoides*, was described by Klotzsch on the basis of material collected by Seemann (in Seemann, Bot. Voy. Herald 99, 1853). The only material seen, a probable type sheet from BM, is not full enough to allow a decision on its identity. The leaves suggest the Mexican *E. fulgens* Karwinsky, but the single cyathium present is closer to that of the group containing *E. oerstediana* and *E. lancifolia* Schlecht. (Boissier's sect. Dichilium); Klotzsch's description, on the other hand, stresses the articulation of the stems which suggests sect. Alectororoctonum. No sensible disposition can be made of this taxon until more material is available and it is to be hoped that the increased collecting activity in the Republic will continue to add to our knowledge of this genus.

34. POINSETTIA


Euphorbia sect. Poinsettia (Graham) Baillon, Étude générale du groupe des Euphorbiacées 284, 1858.

Herbs, annual or perennating, or shrubs, milky latex in all parts; monoecious. Leaves opposite or alternate; petiolate; stipules absent or minute; blades expanded, green, those subtending the inflorescences ("floral bracts") red, purple, or white in some species. Inflorescence a cyathium, these in terminal condensed dichasial or pleiochasia; lobes 5, the involucral glands cup-like, exappendiculate, usually
one but rarely up to 5 in central cyathia. Staminate flowers few to many; naked; monandrous; pollen grains subglobose, usually tectate, 3-colporate. Pistillate flower terminal, solitary; naked; ovary 3-celled, each with a single ovule, the styles 3, joined at base, bifid for most of length. Fruit a capsule dehiscent at sutures; seed ovoid, somewhat angled, surface variously sculptured, the caruncle small or absent.

A New World genus of about 12 species, probably centered in Mexico. Two of the weedy species are found wild in Panama and a third, P. pulcherrima (Graham) Willd., is widely cultivated for its showy bracts. This species, “Poinsettia” of the florist trade and “flor de Pascua” in most of Latin America, is a large shrub with brilliant red, pink or white leaves subtending the inflorescence, and with cyathia 5 mm or more in diameter. It may well be naturalized in the Republic.

Useful reference:


a. Cyathial gland with a circular opening; floral bracts green or purple spotted but never red at the base; seed angular 1. P. heterophylla

aa. Cyathial gland bilabiate; floral bracts green or red at base; seed not strongly angled 2. P. cyathophora

1. Poinsettia heterophylla (L.) Kl. & Gke., Monatsb. Akad. Berlin 1859: 253, 1859.—Fig. 25 (A, B).

E. geniculata Ortega, Hort. Mat. Dec. 18, 1797.

Herb, annual or perennating. Stem ascending, to 7 dm long, dark green. Leaves alternate at base, opposite above; blades membranous, 5-11 × 2-5 cm, pandurate, obovate or elliptic, rarely lanceolate, entire or dentate, glabrous or hairy, green sometimes purple-splashed or pale at the base but never red. Cyathia glabrous without, the gland stipitate, terete with a slightly flared round opening. Capsule glabrous, broadly truncate-ovoid, to 4 mm long, 5 mm wide; seed truncate-ellipsoid, to 2.5 mm long, somewhat angular, the surface coarsely tuberculate.

Widely distributed as a weed in tropical America, and extending into Florida, Louisiana and Texas.
Fig. 25. Poinsettia heterophylla (L.) Kl. & Gke.: A, habit ($\times \frac{1}{4}$); B, cyathium ($\times 6$). A-B after Siebert 1536 (MO). P. cyathophora (Murray) Kl. & Gke.: C, cyathium ($\times 6$). C after Lewis et al. 682 (MO).
2. **Poinsettia cyathophora** (Murray) Kl. & Gke., *Monatsb. Akad. Berlin* 1859: 253, 1859.—Fig. 25(C).


*Herb*, annual or perennating. *Stems* ascending, to 5 dm long (one collection to 16 dm), green, somewhat glaucous. *Leaves* alternate at base of plant, opposite above; blades membranous, 5-10 × 1-3 cm, pandurate, ovate, ovate, lanceolate or sub-linear, entire or dentate, glabrous or sparsely long-hairy, green, those subtending the inflorescence often bright red at the base or throughout. *Cyathia* glabrous or sparingly short-pubescent, the gland flattened, strongly bilabiate. *Capsule* glabrous, broadly ovoid, to 4 mm long, 5 mm wide; seed truncate-ellipsoid, to 3 mm long, scarcely angled, the surface tuberculate.

Common in waste places in the eastern United States and the West Indies, present as a weed of disturbed areas in much of the remainder of the United States, Central America and northern South America, as well as parts of the Old World.

**BOCAS DEL TORO:** *vic of Chiriqui Lagoon*, *von Wedel 1313* (MO), 2607 (MO), 2926 (MO); *Isa Colón*, *von Wedel 139* (MO); *Careening Cay*, *von Wedel 575* (MO). **CHIRIQUI:** *ca 14 mi N of David*, *Lewis et al. 682* (MO).

This species is much less common than *P. heterophylla* in Panama, which upholds Dressler’s observation (loc. cit.) of the relative frequency of the two in the tropics.

Each of the two species shows great variation in vegetative characters, particularly leaf shape, but observations in the field do not support the authors who have separated and named taxa on this basis.

35. **CHAMAEYCE**


*Herbs* or subshrubs, annual or short perennating, prostrate to ascending or erect, milky latex in all parts; monocious; the main axis aborting, the secondary axes few to many, rarely rooting at nodes. *Leaves* opposite, simple; petiolate with stipules interpetiolar, distinct or joined; blades expanded, with chlorophyll-bearing cells mainly in a sheath around veins and colorless areas in between, the base inequilateral, the margin entire or serrate. *Cyathia* terminal but appearing axillary, solitary at nodes or clustered in cymules; lobes 5 approximating glands; glands 4 or with fifth vestigial, alternating with lobes, with petaloid appendages (these rarely obsolete). *Staminate flowers* few to many; naked; monandrous; pollen grains subglobose, tectate, 3-colporate. *Pistillate flowers* terminal, solitary; naked; ovary 3-celled each with a single ovule, the styles 3, free or joined basally, partly bifid. *Fruit* capsular, almost always fully exerted and not splitting cyathium...
at maturity; seed ovoid, angled or terete, the coat smooth or variously sculptured, ecarunculate.

Plants of disturbed habitats, most abundant in rather dry situations and succumbing quickly to competition in more favorable sites.

A genus of about 250 species, of world-wide distribution but with by far the largest number of species in the New World. The genus is poorly represented in Panama by comparison with neighbouring countries, and of the 10 species found six are known from five or fewer collections of each.

Recent works include:


a. Capsule pubescent, at least when young.
   b. Plant erect or ascending; cyathia in short-stalked leafy dichasia ..........1. *C. lasiocarpa*
   bb. Plant prostrate or decumbent; cyathia in glomerules or on condensed leafy laterals.
   c. Cyathia borne in dense lateral and terminal leafless glomerules ..........2. *C. hirta*
   cc. Cyathia borne on condensed leafy laterals.
   d. Capsule not fully exserted, splitting cyathium at maturity; glands subcircular, appendages usually all equal in size ..........3. *C. thymifolia*
   dd. Capsule fully exserted and not splitting cyathium at maturity; glands rimming cyathium, appendages unequal in size with one pair very long and often concealing capsule.
   e. Glandular appendages pubescent on underside ..........4. *C. densiflora*
   ee. Glandular appendages glabrous on underside ..........5. *C. dioica*

aa. Capsule glabrous.
   f. Leaf margins entire.
   g. Plants prostrate to decumbent; stipules distinct, deeply lanciniate ..........6. *C. ammannioides*
   gg. Plants erect to sprawling; stipules united, short-cleft or fringed ..........7. *C. buxifolia*
   ff. Leaf margins serrate, at least in upper ½.
   h. Capsule more than 2 mm long; seed to 1.8 mm long ..........8. *C. bahiensis*
   hh. Capsule less than 2 mm long; seed rarely longer than 1 mm.
   i. Cyathia in almost leafless lateral and terminal glomerules; capsule subspherical, less than 1.4 mm long ..........9. *C. hypericifolia*
   ii. Cyathia in leafy lateral and terminal dichasia; capsule oblong-ovoid, more than 1.6 mm long .............10. *C. hyssopifolia*

Three other common weeds of the American tropics are to be expected in Panama: *C. ophthalmica* (Pers.) Burch is like a delicate plant of *C. hirta*, but may be distinguished by the position of its glomerules of cyathia which are always terminal; *C. prostrata* (Ait.) Small and *C. serpens* (H.B.K.) Small are each small prostrate plants. The first is easily distinguished by its capsule, stiff-hairy only on the angles, and the second by its joined, scale-like white stipules and the fact that it frequently roots at the nodes.


_Herb_, annual, ascending to 5 dm. _Stems_ to 4 mm diam at woody base, densely tomentose. _Leaves_ membranous; stipules joined, deltoid, tufted or deeply bifid; blades ovate-lanceolate somewhat falcate, 8-20 × 3-4 mm, densely gray-pubescent, the base rounded, the margin sharp-serrate, the apex acute to obtuse. _Cyathia_ solitary in lateral and terminal short-stalked, leafy dichasia, densely pubescent; glands small, the appendages to three times as long and broad as gland, white, or obsolete. _Capsule_ tomentose, sometimes glabrate, broadly ovoid, 1.5-2 × 2 mm; seeds oblong-ovoid, to 1 mm long, strongly 4-angled, the faces flat with 2-4 deep transverse ridges.

Greater Antilles, Central America and northern South America. Only three Panama collections can be placed with assurance under this name. Even these are rather closer in appearance to _C. hyssopifolia_ (from which it differs chiefly in pubescence) than is usual over most of the range of the two species.

**Canal zone:** Corozal to Pedro Miguel, Cowell 407 (F, NY), Los Santos: 3 mi S of Carreta, Burch et al. 1234 (F, GH, K, MO, UC, US). **Panama:** Panama Viejo, Duke 5732a (MO).


_Euphorbia hirta_ L., Sp. Pl. 454, 1753.


_Herb_, annual; decumbent to 3 dm. _Stems_ few, to 2 mm diam, tomentose and with abundant multicellular hairs which are often brown or purple, rarely merely tomentose. _Leaves_ membranous; stipules distinct or joined at base, somewhat lacerate, to 1 mm long; blades ovate to lanceolate, often rhombiform, 10-35(-55) × 5-15(-25) mm, glabrate on upper surface, green or red often with purple spot, the base rounded to cuneate, the margin serrate, the apex obtuse to acute. _Cyathia_ in dense terminal and axillary glomerules formed of condensed leafless dichasia, strigose; glands minute, purple, the appendages obsolete to three times as wide as gland. _Capsule_ strigose, ovoid, to 1 mm long, 1 mm wide; seed cuneiform, 0-8 mm long, 0.4 mm wide above base, the angles subequal, the faces concave, obscurely transversely ridged or wrinkled, tan, red-brown or gray.

A pantropical weed. Widespread and extremely common in all disturbed areas in Panama.

**Bocas del Toro:** Bocas del Toro I Airport, Lewis et al. 787 (MO, UC, US); vic of Chiriqui Lagoon, von Wedel 539 (MO); Old Bank I von Wedel 1868 (MO); Water Valley, von Wedel 1748 (MO). **Canal zone:** Ancon, Greenman & Greenman 5009 (MO); western slope of Ancon Hill, Seibert 111 (MO); Barro Colorado I, Hayden 1 (MO), McDaniel 3027 (FSU, MO), Woodworth & Vestal 408 (F); id, Miller Trail, Shattuck 41 (F); vic of Corrosion Lab, Duke 4441 (DAV, MO); Stern et al. 63 (MO); Chagres, Isthmus of Panama, Fendler 274 (BM, K, MO, W); Culebra I, Duke 4632 (DAV, MO); Fort Clayton, Cardenas Creek area, Tyson 1290 (FSU), Dwyer 2787 (MO); Fort Kobbe, Duke 3907 (MO), 3932 (MO), Woodson et al. 1429 (F); Fort San Lorenzo, Burch et al.
1967] 

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1029 (GH, K, MO, UC, US); E of Gatun locks, Duke 4298 (DAV); Gamboa, Petersen s.n. (F); vic of Salamance Hydrographic Sta, Rio Pequeni, Woodson et al. 1616 (F, MO); Soza Hill, Duke 4659 (DAV, MO), chimiqui: David airport, Lewis et al. 744 (GH, K, MO, UC, US). coele: Rio Hato airstrip, Burch et al. 1140 (F, GH, K, MO, NY). colón: Colon, vacant lot, MacBrade & Featherton s (F), Rodway s.n. (K); 2.4 mi S of Piña, Lewis et al. 1850 (GH, MO, US). Durien: vic of Boca de Cude, Allen 893 (F, MO); El Real, Burch et al. 1053 (GH, MO, US); Rio Sabana, Leopold III 106 (MO); 2 mi E Santa Fe, Tyson et al. 4826 (MO); vic of Santa Fe, Duke 9486 (MO). Herrera: Rd from La Avena to Pesé, Burch et al. 1286 (MO, UC); banks of Rio Santa Maria, Burch et al. 1200 (GH, MO); rd betw Las Minas & Pesé, Burch et al. 1346 (K, MO), 1348 (GH, MO, UC, US); 12.5 mi S of Ocu, Lewis et al. 1660 (GH, MO, US). Los Santos: Playa de la Concepción, Burch et al. 1263 (F, GH, MO, NY). Panama: Isla Taboga, Woodson et al. 1502 (F, MO); Panama City, Petersen s.n. (F); rd to Oluj de Agua, ca 5 mi N of Panama City, Stimson 5052 (DUKE, MO).


Euphorbia thymifolia L., Sp. Pl. 454, 1753.

Herb, annual, perennating by thick rootstock, prostrate, forming mats to 4 dm diam. Stems 1-2 mm thick, villous-pubescent or tomentose on upper surface, often glabrate, naked on under surface, green or light brown. Leaves membranous; stipules distinct, linear, toothed; blades obleng-elliptic, 4-10 × 2-5 mm, the upper surface usually glabrous, the lower sparsely tomentose, glabrate, green or yellowish, the base oblique or subequilateral on side shoots, the margin coarsely serrate, the apex rounded to acute. Cyathia solitary or in pairs or even few-flowered glochimel at nodes of condensed leafy laterals; glands broadly elliptic or subcircular, pink or red, the appendages small. Capsule strigose, long-ovoid, 0.8-1 mm long, 1 mm wide below equator, not fully exerted but splitting cysthium at maturity; seed conical-ovoid, to 0.9 mm long, 0.5 mm wide below equator, strongly 4-angled, the faces concave, obscurely transversely ridged, tan-colored.

New World tropics and subtropics. Widespread and common in the Republic. Its small size allows it to survive in places in which the larger weedy species would be damaged.


Euphorbia densiflora (Kl. & Gke.) Kl. in Peters, Reise Mossamb, 94, 1862.

_Herb_, annual or perennating, prostrate or decumbent. Stems 1-2 mm thick, densely long-pubescent particularly at sides, hairs multicellular, often purple. _Leaves_ membranous; stipules distinct, sublinear; blades obliquely oblong, 10-20 × 5-9 mm, sparsely pubescent, the base strongly oblique, the margin serrate, the apex obtuse. _Cyathia_ densely clustered on short leafy laterals, white-pubescent; glands rimming cyathium, one pair often obsolete, deep red, the appendages in two unequal pairs, one a mere rim to their glands (or absent when glands are obsolete), the other auriculate and extended laterally, deep red, pubescent on lower surface, often concealing capsule. _Capsule_ densely pubescent, broadly ovoid to 1.8 mm long; seeds angular-ovoid, ca 1 mm long, the faces deeply transversely ridged.

Central America and northern South America. Not uncommon in the Republic but probably confined to the medium altitude regions in which it has already been collected.


_Herb_, perennial or at least perennating, prostrate in dense mats. Stems to 1 mm thick, wooly-pubescent. _Leaves_ membranous; stipules distinct, linear; blades elliptic, ca 4 mm long, 1-1.3 mm wide, sparsely pubescent on each side, the base acute, the margin serrate, the apex acute. _Cyathia_ solitary at nodes of short condensed laterals, densely pubescent; glands elliptical, rimming cyathium, the two pairs sometimes unequal, dark red, the appendages in two unequal pairs, the larger pair auriculate, glabrous, often concealing capsule. _Capsule_ and seed not seen from Panama—capsule pubescent, ovoid, ca 1.4 mm long; seed angular-ovoid with lateral ridges in South American specimens.

Probably restricted to South and Central America but part of a closely related group that extends into the West Indies and southern United States. This species is included reluctantly on the basis of a single collection which is too sparse to be absolutely certain that it is not an extreme form of _C. thymifolia_.

_COCLE:_ Rio Hato reservation, InterAmer Hwy, _Tyson & Blum_ 2555 (MO).


_Herb_, annual or perennating, prostrate or decumbent forming loose mats to 6 dm diam. Stems 1-2 mm thick, not rooting at nodes, glaucous, often suffused
Leaves often slightly fleshy; stipules distinct, deeply laciniate into 3-6 linear segments; blades oblong-elliptic, 6-12 × 2.5-6 mm, glaucous often suffused red, the base obtuse, the margin entire, the apex obtuse to mucronate. Cyathia solitary, terminal on branches of lateral shoots near tips of main stems, glabrous; glands subcircular, somewhat stipitate, the appendages usually obsolete. Capsule glabrous, broadly ovoid, 1.8-2.1 × 2-2.4 mm; seed ovoid, to 1.8 mm long, 1.3 mm diam at equator, obscurely 3-angled from apex for ca ½ length, terete at base, smooth, white.

Coastal sands of Florida, Mexico, Cuba, Guatemala and northern South America. Represented from Panama by only two collections.

**Canal zone:** Chagres, Fendler 276 (F, K, MO), 277 pro parte (W—probably numbered in error). **Veraguas:** mouth of Rio Concepción, Lewis et al. 2786 (MO).
7. Chamaesyce buxifolia (Lam.) Small, Fl. SE. U.S. 712, 1903.

E. flexuosa H.B.K., loc. cit. 55.

Subshrub, perennial, erect to ascending, nearly decumbent in shifting sand. Stems to 6 dm long, to 8 mm diam at naked woody base, glabrous, green becoming darker. Leaves somewhat fleshy; stipules united, to 1 mm long, ligulate or deltoid, short cleft or fringed, white; blades ovate to elliptic, 5-12 × 3-6 mm, glabrous, yellowish to dark green and glaucous, the base truncate to cordate, obscuring stem, the margin entire, the apex obtuse. Cyathia solitary at upper nodes; glabrous without, densely ciliate in throat; glands transversely elliptic, brown, fleshy, the appendages as wide as gland, white, the margin entire or undulate. Capsule glabrous, subspherical 1.5-2 mm long, 2.2-5 mm wide; seed broadly ovoid, 1.3 mm long, 1.2 mm wide, the angles mere ridges except near apex, the faces plump, convex, the surface obscurely pitted, ashen.

Coastal sands of Florida, the Antilles, the Bahamas, Central America and northern South America.

Lamarck’s name is retained for this species in spite of the case made for the adoption of E. mesembrianthemifolia Jacquin in recent floras of the West Indies and by Dugand when publishing the combination in Chamaesyce (Phytol. 13: 385, 1966). While Jaquin’s description (Enum. Pl. Carib. 22, 1760 and Sel. Stirp. Amer. 150, 1763) suggests that his epithet could be applied to this plant, no authentic material has been found, and I hesitate to upset a well-understood usage without some incontrovertible evidence.

BOCAS DEL TORO: Old Bank I, vic of Chiriqui Lagoon, von Wedel 2130 (MO), SAN BLASS Sunset I, Duke 8863 (MO); Irandi airport, Duke 6509 (MO); Perme, Cooper 226 (F).
PROVINCE UNKNOWN: S. loc., Pittier 4108 (F).


Euphorbia bahiensis (Kl. & Gke.) Boiss. in DC., Prodr. 15(2): 24, 1862.

Herb, annual or perennating, trailing or erect to 5 dm. Stems, 2-4 mm diam, usually dark particularly at nodes. Leaves membranous; stipules joined, shortly-deltoid, fringed; blades oblong-elliptic to obovate 15-30 × 6-12 mm, those on laterals much smaller, glabrous, the base truncate or cordate, the margin serrate, sometimes obscurely so, the apex obtuse to rounded. Cyathia solitary in lateral dichasia, glabrous; glands elliptic, the appendages obsolete to prominent, white. Capsule glabrous, broadly ovoid, to 2.5 mm long, 3 mm diam; seed ovoid to 1.8 mm long, strongly 4-angled, the faces flat, wrinkled.

Coastal sands from Rio de Janeiro to Costa Rica with a single collection known from Jamaica. The Atlantic Coast of Panama has few of the sand beaches on the upper parts of which this plant grows but the recent intensive collecting produced two colonies and it would be surprising if more are not found as the remoter beaches are visited.

_Euphorbia hypericifolia_ L., Sp. Pl. 454, 1753.

**Herb**, annual or perennating, erect to ascending to 4 dm. Stem to 3 mm diam at somewhat woody base, tan to dark brown. Leaves membranous; stipules joined and sheathing with margin serrate, or, at upper nodes, separate, entire or deeply 2-4 cleft; blades ovate-elliptic to elliptic-ovoblate, somewhat falcate, 15-35 × 8-14 mm, glabrous, green, the base rounded or cuneate, the margin serrate, the apex acute. Cyathia in short-stalked, lateral and terminal congested dichasia forming glomerules with a few basal leaves, glabrous; glands subcircular, the appendages obsolete or prominent, entire, white or pink. Capsule glabrous, subterhical, to 1.2 mm diameter; seed ovoid, to 0.8 mm long, 0.5 mm wide, strongly 4-sided, the faces flat or convex, wrinkled, light brown.

New World tropics and subtropics. There are remarkably few collections from Panama of this plant which is extremely common in other parts of its range. The numbers of collections of this and the following species seem to be an accurate representation of their relative frequency and the plant is by no means common in the Republic.

**BOCAS DEL TORO**: Isla Colón, vic of Chiriqui Lagoon, von Wedel 2829 (MO); Bocas del Toro I airport, Lewis et al. 786 (GH, MO). **CANAL ZONE**: Ancon, Greenman & Greenman 5010 (MO), 5071 (MO); Barro Colorado I, McDaniel 5023 (MO); Chagres, Fendler 275 (BM, F, K, MO); Upper Chilibre River, Seibert 1504 (MO); Chiva Chiva trail nr Miraflores Lake, Tyson 1388 (FSU); Fort San Lorenzo, Burch et al. 1030 (K, MO, NY, UC, US), Tyson 1577 (FSU), Tyson & Blum 3702 (MO); Galena Point, Blum & Dwyer 2144 (MO); Pedro Miguel, Bro. Heriberto 13 (F), Colón: Colón, Rose 22076 (NY).

**BARIEN**: vic of Campamento Buena Vista, Rio Chucunaque above confluence with Rio Tuquesa, Stern et al. 872 (MO); El Real, Burch et al. 1052 (F, GH, MO), 2 mi E of Sante Fé, Tyson et al. 4815 (MO). **PANAMA**: Cerro Azul at 2000 ft, Tyson 2058-A (MO); Canita 18 mi E of Chepo, Tyson & Smith 4137 (MO); Panama City, Burch et al. 1417 (MO). **SAN BLAS**: Soskatupu, Duke 10181 (MO).


**Herb**, annual or perennating; erect, ascending or decumbent, to 6 dm. Stem to 4 mm thick at somewhat woody base, glabrous or sparingly long pilose near base, straw-colored or darker brown. Leaves membranous; stipules joined or nearly free at upper nodes, almost obsolete to deltoid, 0.8 mm long, margin short-fringed; blades variable, glabrous or sparsely long pilose, linear-lanceolate, 15-35 × 3-6 mm, the base subcordate, the margin serrate only near the acute apex, to ovate-elliptic, somewhat falcate, 10-30 × 6-10 mm, the base rounded to subcordate, the
margin serrate, the apex obtuse. Cyathia terminal and axillary in short-stalked diffuse or compact leafy dichasia, glabrous; glands transversely elliptic or sub-circular, the appendages obsolete to prominent, white or pink. Capsule glabrous, truncate-cuneiform to broadly ovoid, 1.5-2 mm long, 1.6-1.8 mm wide; seed oblong-ovoid, to 1 mm long, 0.5 mm wide, 4-angled, the faces flat with transverse ridges, brown or black, angles sometimes light.

New World tropics and subtropics and an adventive weed in the Old World. A common weed throughout the Republic, particularly where man’s activities have left disturbed ground. This taxon is very variable in other parts of its range but none of the extreme forms which may prove worthy of recognition seem to occur in Panama.

**BOCAS DEL TORO:** Bocas del Toro I airport, Lewis et al. 785 (F, GH, MO, NY); vic of Almirante, Cooper 87 (F), 107 (F); Changuinola, Lewis et al. 818 (GH, K, MO, UC, US), Carleton 75 (NY); Changuinola valley, Dunlap 54 (F); Isla Colón, vic of Chiriquí Lagoon, von Wedel 2800 (MO, NY), 2954 (F, MO, NY); s. loc., von Wedel 141 (MO), 183 (MO). CANAL ZONE: New York. von Wedel 141 (MO), 183 (MO), 257 (NY), 277 (F, K, MO), 290 (F, K, MO), Corozal to Pedro Miguel, Cowell 401 (NY); Culebra I. Duke 463 (DAV, MO); ca 1 mi N of Fort Clayton, Stimson 5193 (DUKE, MO), Shattuck 783 (MO), CANAL ZONE: Albrook Air Foree Base, Tyson 1104 (MO); vie of Balboa, Seibert 381 (K, MO, NY); Balboa, Macbride & Featherstone 36 (F); Barro Colorado I, Aviles 21 (F), Bailey & Bailey 155 (F), 155a (F), Ebiner 34 (F), Hood 1020 (F), Shattuck 493 (F), Woodworth & Vestal 409 (F); Culebra I. Duke 463 (DAV, MO); ca 1 mi N of Fort Clayton, Stimson 5193 (DUKE, MO), Shattuck 783 (MO), COLOMBO, Duke 3952 (MO); Fort Sherman, Burch et al. 1012 (K, MO, NY, UC); ca 6 mi N Gamboa, Tyson 1509 (FSU); E of Gatun Locks, Duke 4301 (DAV); Gatun Sta, Hayes 675 (NY); Miraflores, Dwyer & Hayden 1005 (MO), White 174 (MO); Santa Rita trail, Cowell 158 (NY). CHIRIGUI: vic of Boquete, Davidson 601 (F, MO), Dwyer & Hayden 7615 (MO); David airport, Lewis et al. 738 (GH, K, MO, NY, UC, US); Rio San Pedro, Dwyer & Hayden 7768 (MO). Coclé: betw Porto Posada & Penonomé, Williams 165 (NY); Río Hato airstrip, Blum & Dwyer 2481 (MO), Burch et al. 1155 (F, GH, MO, US). COLÓN: María Chiquita, E of Rio Piedras, Dwyer & Kirckbide 7795 (MO); vic of Rio Piedras, Blum et al. 2545 (MO). DARIEN: El Real, Burch et al. 1051 (GH, MO, UC, US); 0-4 mi up Río Sabana from Santa Fé, Duke 4168 (MO). HERRERA: rd from La Avena to Pesé, Burch et al. 1288 (K, MO, NY); ca 10 mi S of Ocú, Tyson et al. 2864 (MO). LOS SANTOS: ca 3 mi S of Carreta, Burch et al. 1222 (K, MO, NY); 5-6 mi from Chiréte on rd to Las Tablas, Burch et al. 1221 (MO, UC, US). PANAMA: nr Arraijan, Woodson et al. 1380 (F, MO, NY); NE of Hacienda La Joya, Dodge et al. 16905 (MO); Panama Viejo, Duke 5732 (MO); Panama City, Duke 4010 (MO); PanAmer Hwy 5-6 mi E of Chepo, Duke 4021 (DAV, MO); Río Pacora nr confluence with Río Corso, Duke 12002 (MO). PROVINCE UNKNOWN: s. loc., Seemann 196 (BM).

36. PEDILANTHUS


Shrubs, succulent, becoming woody, usually erect to ascending and only sparsely branched, often somewhat zig-zag, milky latex in all parts. Leaves alternate, distichous; short petiolate; stipules small; blades expanded, fleshy, entire, early deciduous. Cyathia in axillary or terminal cymes, subtending bracts opposite; involuclral bracts 5, partly connate, forming a slipper-shaped structure made up of a widely lobed ventral pair sometimes with glands on the dorsal edges, a basally asymmetric lateral pair with glands on the dorsal edges, and a dorsal bract with glands on each edge. Staminate flowers numerous, naked; monandrous; pollen grains ellipsoid, 3-lobed in equatorial view, usually intectate, 3-colporate. Pistillate
flower terminal, solitary; naked; ovary 3-celled each with a single ovule, the styles 3, bifid, connate for most of length. Fruit a capsule or indehiscent; seed ovoid, smooth or tuberculate, ecarunculate.

A tropical American genus of 14 species centered in Mexico. Only a single species is represented in Panama, and all collections (at least from naturally occurring plants), fall in the typical subspecies. The genus has been monographed by Dressler (Contr. Gray Harb., Harv. Univ. 182: 1-188, 1957), who treats exhaustively the variants that may be found as cultivated plants or escapes.


 *Shrub* to 1.5 m, branches terete, puberulent but soon glabrate, often leafless. *Leaves* somewhat succulent; stipules blunt, dark brown; petiole 3-8 mm long; blade elliptic-ovate, 6-10 × 2.4 cm, the base cuneate, the apex acute or somewhat attenuate; sparsely puberulent above, more densely so below. *Cymes* condensed, the subtending bracts flushed red, puberulent; involucrle to 14 mm long, the bracts green at base, deep red above, puberulent within, glabrous without. *Capsule* ovoid, to 6 mm long, 7 mm diam, glabrous; seed ovoid, obscurely angled, to 5 mm long, the surface smooth, gray.

This is the most widely ranging species of the genus and this subspecies alone spans the mainland area from Mexico to northern South America. In Panama it is most common at medium elevations, but it (and possibly some distinct cultivars) may frequently be seen as low hedges in most provinces.

**Canal Zone:** Tabernilla, Cowell 276 (NY). **Cocle:** Aguadulce, Pittier 5000 (US); La Pintada, Hunter & Allen 514 (MO); Penonomé, Williams 229 (NY, US). **Herrera:** vic of Ocú, Stern et al. 1737 (MO). **Panama:** Alahuela, nr Madden Dam, Dodge et al. 16824 (GH, MO, S); Taboga I, Macbride 2804 (F, US), **Veraguas:** Canazas, Tyson 3622 (MO); headwaters of Rio Canazas, Allen 196 (F, MO).

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