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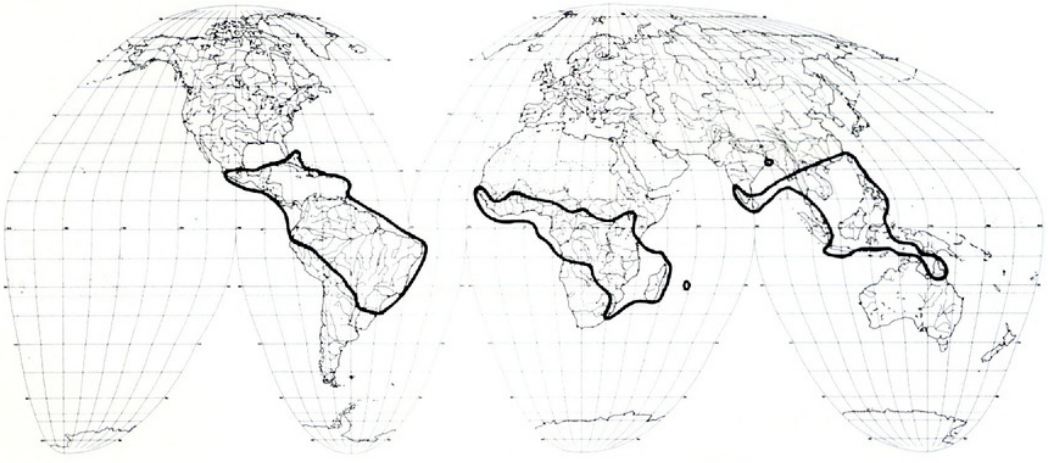
A REVISION OF MARGARITARIA (EUPHORBIACEAE)

GRADY L. WEBSTER

AMONG THE SMALLER GENERA of Euphorbiaceae subfamily Phyllanthoideae Pax, *Margaritaria* has a particularly broad distribution (MAP 1) in both the New and Old World tropics (except for the Pacific islands). The name (in the form *Margaritifera*), alluding to the characteristic pearly white endocarp of the fruit, was first used by Hermann (1689), and the plant was illustrated by Plukenet (1692). Although the genus was established by Linnaeus filius in 1781, nearly two centuries passed before it achieved general acceptance in the taxonomic literature. Because the younger Linnaeus included two different genera of plants in the original description, a taxonomic understanding of the genus was slow in developing. Antoine de Jussieu (1789) and Adrien de Jussieu (1824) both regarded *Margaritaria* as a genus of uncertain position, although the latter described a West Indian form of *M. nobilis* as *Cicca antillana* A. Juss. and, on the basis of an observation by Choisy, reported a possible relationship of *Margaritaria* with *Cicca* L. Baillon (1858) treated *Margaritaria* in a rather confused manner, placing various species in four different sections of *Cicca* as well as in the separate genus *Zygospermum* Baillon.



MAP 1. World distribution of *Margaritaria* (generalized). Base maps from Goode series, © University of Chicago.

Mueller Argoviensis (1866) continued this association between *Cicca* and *Margaritaria* but clarified the relationships to some extent by removing *Cicca disticha* (= *Phyllanthus acidus* (L.) Skeels) to a separate subsection of *Phyllanthus* sect. *Cicca* (L.) Mueller-Arg.

Baillon and Mueller saw that the Old World taxa described under *Prosorus* Dalz. by Dalzell (1852) and Thwaites (1856) were related to the New World *Margaritaria*. However, they failed to realize that the taxa *Margaritaria/Prosorus* do not belong in close juxtaposition with *Cicca* (*sensu stricto*). Bentham (1880), who rejected *Margaritaria* as being founded on a mixture of taxa, did point out that *Prosorus* was discordant with *Cicca* because of its tricarpellate fruit. Hooker (1887) judiciously maintained *Cicca* and *Prosorus* as separate sections of Indian *Phyllanthus*. However, this felicitous disposition of Hooker was ignored by Pax (1890) and Pax and Hoffmann (1931), who lumped *Cicca* and *Margaritaria* together in *Phyllanthus* sect. *Cicca*. Although occasional writers of floras (e.g., Britton & Millspaugh, 1920; Gamble, 1924) maintained *Margaritaria* or *Prosorus* as distinct genera, most conservative botanists have followed the usage of Mueller and of Pax, at least until the rehabilitation of *Margaritaria* by Webster (1957) and Airy Shaw (1966).

As I have pointed out earlier (Webster, 1957, 1968), *Margaritaria* is really quite distinct from *Phyllanthus* (including *Cicca*) and indeed is closer to *Flueggea* Willd. in Phyllantheae subtribe Flueggeinae Mueller-Arg. (Webster, 1975). The unique seeds, with fleshy exotesta and thick, bony endotesta, separate *Margaritaria* from all other Phyllantheae. The fruits of most species of *Margaritaria*, with a brittle, irregularly shattering, papery endocarp (FIGURES 5, 6), are equally distinctive. Staminate material of *Margaritaria* may be distinguished from that of *Flueggea* by the lack of a pistillode, and from that of *Phyllanthus* by the annular disc subtending a tetramerous androecium. The resemblance with *Phyllanthus* sect. *Cicca* that impressed 19th century botanists is very superficial indeed, since *Cicca* differs markedly in its drupaceous fruits with thin-walled, dry seeds and in its very different vegetative structure (with typical phyllanthoid branching, the ultimate axes being short lived and deciduous, in contrast to the persistent, unspecialized branches of *Margaritaria*).

Morphologically, the species of *Margaritaria* are all rather similar, and the dioecious character of the plants makes it rather difficult to construct workable keys to individual specimens. Most taxa are deciduous shrubs or small trees that grow in seasonal forest or bush vegetation. The habit of *Margaritaria* agrees with that of many other unspecialized Euphorbiaceae; Hallé *et al.* (1978) cite *M. discoidea* as an example of the architectural model of Roux, in which the sapling axis has spiral phyllotaxy but the leaves on the branchlets are distichous. To judge from my own observations of *M. nobilis* as well as from indications in the literature, all of the species in the genus would seem to belong to the model of Roux. The entire leaves, with short petioles and distinct stipules, vary relatively slightly in morphology. Flowers, often produced at the proximal nodes

of expanding new axes, are usually in anthesis before the current crop of leaves is mature. Opler, Frankie, and Baker (1976) have reported that in the seasonal forest in Guanacaste, Costa Rica, *M. nobilis* flowers about two weeks after the first spring rain in April or May, and only remains in flower about three days. Other *Margaritaria* populations in African and Asian monsoon forests may show similar flowering behavior. The tetramerous calyx is rather similar in all species, and the annular floral disc is so constant that it provides a good generic character. In all normal staminate flowers (FIGURE 12), the stamens are consistently 4, and the filaments are nearly always free. The tricolporate, semitectate pollen grains of *Margaritaria* are typical of many unspecialized Phyllantheae and are very similar to those of such genera as *Flueggea* (Punt, 1962; Köhler, 1965).

The pistillate flowers of *Margaritaria* (FIGURES 11, 13) have calyx and disc similar to that of the staminate. The main differential characters are found in the ovary, which has from 2 to 6 carpels. Mueller (1866) used carpel number as a diagnostic character in defining subsections of his sect. *Cicca*, but its value in indicating phylogenetic relationships is not very great. Carpel number has been independently reduced to 2 in the West Indies (*M. hotteana*), the Indian Ocean islands (*M. anomala*), and Australia (*M. dubium-traceyi*); within the American *M. nobilis* it fluctuates from 3 to 6 in such an unstable manner that it cannot be used to define subspecific taxa. However, despite some overlap, the pattern of carpel number distribution is distinctively different in *M. nobilis* and the closely related *M. discoidea* (TABLES 1, 2).

The fruits of most species of *Margaritaria* are different from those of all other Phyllantheae. The endocarp is thin, papery, and hyaline, and easily shatters to expose the fleshy seeds (FIGURES 5, 6). The seeds are even more distinctive, with their metallic blue-green, fleshy sarcotesta (exotesta), bony sclerotesta (endotesta), and large hilum. These seeds would appear to be morphologically adapted for bird dispersal; van der Pijl (1969), in fact, discusses *M. nobilis* as an example of "deceitful" ornithochorous seeds (although the sarcotesta is sufficiently thick that the notion of deceit is perhaps here misplaced). The sclerotesta of the seed furnishes a useful systematic character, since it varies considerably in size and sculpturing. It is distinctively rugose in *M. indica* and *M. rhomboidalis*, but smooth in most other taxa.

Cytologically, *Margaritaria* appears to be diploid with a base number of 13 ($2n = 26$), like many unspecialized taxa of subfamily Phyllanthoideae (Webster & Ellis, 1962; Mangenot in Bancilhon, 1971). Although there are only two published counts (for *M. discoidea* and *M. nobilis*), the uniformity of the genus makes it appear unlikely that additional counts would reveal any significant cytological diversity.

Ecologically, species of *Margaritaria* might fairly be characterized as plants of secondary successions in tropical, seasonal climates, although they may also be found in climax or evergreen forests. Adjanohoun (1964) reported that *M. discoidea* is common in secondary stages of moist forest

TABLES 1, 2. **Carpel number variation in American and African taxa of Margaritaria.**

1. Carpel numbers of individual fruits (all specimens pooled).

Species	Number of collections	Number of fruits	Percentage of fruits with carpel number 2	3	4	5	6
M. nobilis							
West Indies	34	290	0	2.8	28.6	67.2	1.4
Mesoamerica	53	462	0	12.6	78.4	8	1.1
South America	113	1025	0	4.2	68.5	25.3	2.0
Overall	200	1777	0	6.1	64.6	27.6	1.7
M. discoidea							
subsp. *discoidea*	71	1405	1.4	88.3	10.3	0	0
subsp. *nitida*	34	294	1.4	97.0	1.4	0	0
Overall	105	1699	1.4	89.8	8.7	0	0
M. obovata	16	240	21.7	77.5	0.8	0	0

2. Distribution of carpel number by collections.

M. nobilis	3	3/4	4	4/5	5	5/6	6	3/4/5	4/5/6	3/4/5/6	Total
West Indies	1	1	2	18	8	1	0	1	2	0	34
Mesoamerica	1	16	24	7	2	3	0	0	0	0	53
South America	0	15	31	39	12	6	0	4	5	1	113
Overall (%)	1	16	28.5	32	11	5	0	2.5	3.5	0.5	200

M. discoidea	2	2/3	3	3/4	4	2/3/4	Total
subsp. *discoidea*	0	2	44	24	0	1	71
subsp. *nitida*	0	2	29	2	0	1	34
Overall (%)	0	3.8	69.5	24.8	0	1.9	105
M. obovata (%)	0	50	43.8	6.2	0	0	16

in West Africa but also invades savannas. To judge from the data on herbarium specimens, *M. nobilis* displays a similar ecological amplitude in America.

Analysis of specimens from the great areas inhabited by *M. nobilis*, *M. discoidea*, and *M. indica*, in America, Africa, and Asia, respectively, shows a considerable amount of ill-defined fluctuating morphological variability, as one might expect to find in extensive panmictic populations. Only in Africa is there more than one distinct mainland continental species. Speciation has occurred mainly in the Caribbean and Indian Ocean islands and thus appears to reflect a "peripheral" effect; i.e., the definitive geo-

graphic segregation of islands seems to have been prerequisite to speciation, at least outside Africa.

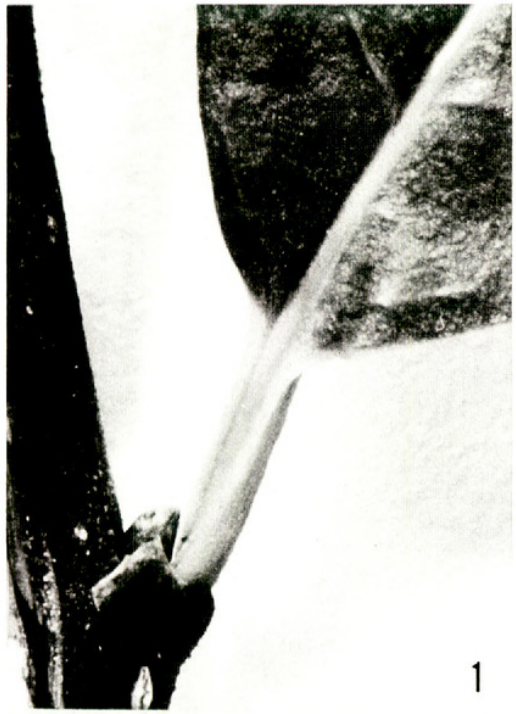
Reconstruction of phylogenetic relationships in *Margaritaria* must be based mainly on comparison of living species, in view of the paucity and questionableness of the fossil evidence. Mädel (1962) has noted the resemblance between the wood of the Upper Cretaceous *Paraphyllanthoxylon* and the living *Margaritaria discoidea*. Bailey (1924) established the genus *Paraphyllanthoxylon* on the basis of similar Cretaceous wood from Arizona; more recently Cahoon (1972) has described *P. alabamense* from Cenomanian/Turonian rocks in central Alabama. The large diameter (1 m. or more) of some of the Alabama logs is so uncharacteristic of living species of *Margaritaria* that the generic assignment appears dubious; in fact, even if these various Cretaceous "species" of *Paraphyllanthoxylon* are euphorbiaceous, it is doubtful if one could defend a closer systematic assignment than simply the tribe Phyllantheae. Since the pollen of *Margaritaria* is no more distinctive than the wood, it seems unlikely that forthcoming paleobotanical evidence will offer any clues very useful in reconstructing the phylogeny of the genus.

The morphological diversity found in Africa and Madagascar indicates that this region may be designated as the most likely homeland for *Margaritaria*, as was suggested earlier for another genus of Phyllantheae, *Meineckia* Baillon (Webster, 1965). The ornithochorous dispersal of *Margaritaria* would seem to allow a fairly high probability for successful transoceanic long-distance migration; however, the failure of the genus to invade the Pacific islands suggests that its dispersibility may be somewhat limited. As far as the intercontinental distribution of *Margaritaria* is concerned, there does not appear to be enough evidence for a decision to be made between the alternative models of transoceanic dispersal or migration over rafting tectonic plates. However, when the distribution patterns of other Phyllantheae such as *Meineckia* and *Flueggea* are taken into account, one may perhaps best explain the distribution of *Margaritaria* by postulating both expansions and contractions from a once more nearly continuous range (probably achieved without extensive long-distance dispersal).

SYSTEMATIC TREATMENT

Margaritaria Linnaeus f. Suppl. Pl. 66. 1781. *Cicca* sect. *Pseudo-Cicca* Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus* sect. *Cicca* subsect. *Paracicca* Mueller-Arg. Linnaea **32**: 50. 1863. *Phyllanthus* sect. *Cicca* subsect. *Margaritaria* (L. f.) Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: *Margaritaria nobilis* L. f.

Prosorus Dalz. Jour. Bot. Kew. Misc. **4**: 345. 1852. *Cicca* sect. *Prosorus* (Dalz.) Baillon, Étude Gén. Euphorb. 619. 1858. *Phyllanthus* sect. *Cicca* subsect. *Prosorus* (Dalz.) Mueller-Arg. in DC. Prodr. **15**(2): 416. 1866. *Phyllanthus* sect. *Prosorus* (Dalz.) Hooker f. Fl. Brit. India **5**: 305. 1887. TYPE: *Prosorus indicus* Dalz. (= *Margaritaria indica* (Dalz.) Airy Shaw).



FIGURES 1–4. Leaf bases of *Margaritaria*: 1, *M. scandens* (*Correll 43522*), showing adaxially channeled petiole, × 5; 2, *M. hispidula* (*Appert 107*), showing nonchanneled petiole, × 8; 3, *M. rhomboidalis* (*Leandri et al. 2195*), showing adaxially channeled petiole, × 8; 4, *M. luzoniensis* (*Otanes 17955*), showing nonchanneled petiole, × 8.

Zygospermum Thwaites ex Baillon, Étude Gén. Euphorb. 620. 1858. TYPE: *Zygospermum zeylanicum* Thwaites ex Baillon (= *Margaritaria cyanosperma* (Gaertner) Airy Shaw).

Wurtzia Baillon, Adansonia I. **1**: 186. *t. 7, figs. 5, 6.* 1861. TYPE: *Wurtzia tetracocca* Baillon (= *Margaritaria tetracocca* (Baillon) Webster).

Cicca sect. *Ciccoides* Thouars ex Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus* sect. *Cicca* subsect. *Ciccoides* Mueller-Arg. in DC. Prodr. **15**(2): 418. 1866. TYPE: *Cicca anomala* Baillon (= *Margaritaria anomala* (Baillon) Fosberg).

Calococcus Kurz ex Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. **27**: 48. 1864. TYPE: *Calococcus sundaicus* Kurz ex Teijsm. & Binn. (= *Margaritaria indica* (Dalz.) Airy Shaw).

Dioecious shrubs or trees (rarely scandent); foliage usually deciduous, new leaves appearing with flowers (or sometimes evergreen); phyllotaxy on branches distichous; branches persistent, bark usually lenticellate in age. Leaves mostly chartaceous, pinnately veined; veins brochidodromous; margins entire; petioles short; stipules entire or denticulate, deciduous or subpersistent. Flowers in clusters at proximal axils of expanding leafy branches (or on short shoots); pistillate (occasionally) and staminate (rarely) flowers solitary. Staminate flower: pedicel elongated, often capillary, not articulated; sepals 4, biseriate, often unequal (outer pair usually narrower), membranous or chartaceous, entire or denticulate, midvein usually sparsely branched; disc annular, entire or shallowly lobed, adnate to base of calyx (reduced or absent in a few taxa); stamens 4, the filaments free (rarely basally connate), the anthers extrorse in bud, dehiscing longitudinally, muticous; pollen grains subglobose, 3-colporate, semitectate; pistillode absent. Pistillate flower: pedicel terete or flattened, not articulated; calyx and disc similar to staminate; ovary with 2 to 6 carpels, the styles free or basally connate, bifid to bipartite, often somewhat dilated, ovules 2 per locule, hemitropous. Fruit capsular, more or less irregularly dehiscent, the green exocarp separating from the thin, papery endocarp (in most taxa); seeds normally paired in each locule, the outer coat (sarcotesta) fleshy, bluish, the inner coat (sclerotesta) thick, woody or bony, smooth or rugose, invaginated at the chalazal end, the endosperm copious, whitish, the embryo straight or slightly curved, with cotyledons thin and flat, much longer than the radicle.

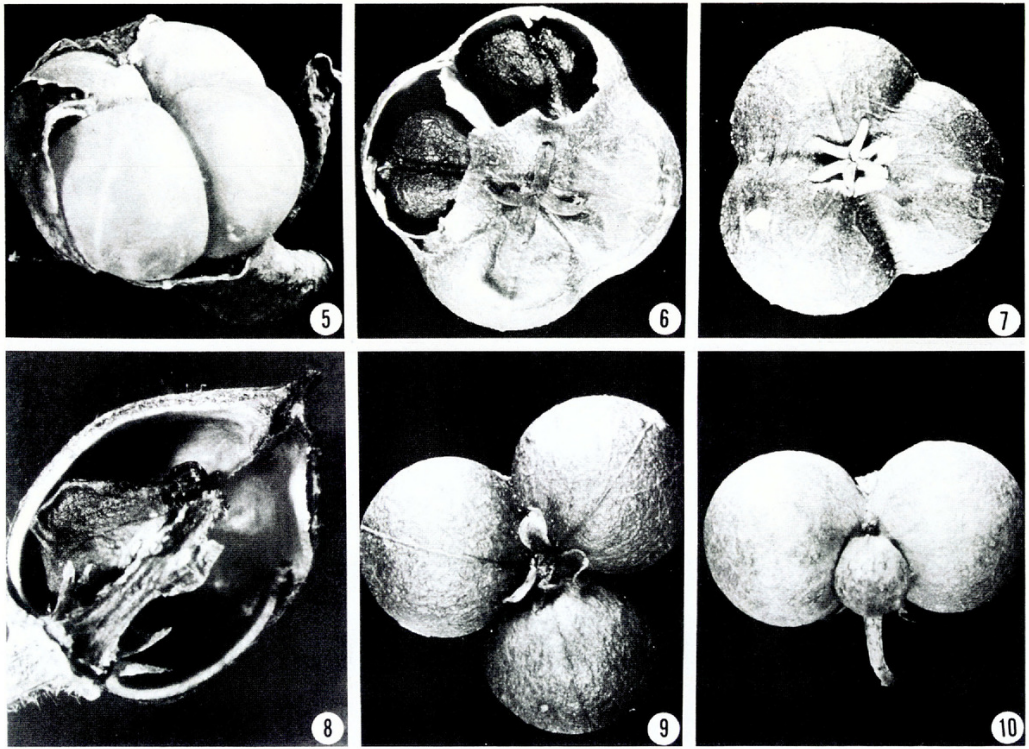
As here interpreted, *Margaritaria* is a relatively homogeneous genus of 14 species that are all rather closely related. The most distinctive group is Baillon's section *Ciccoides*, with 2-carpellate fruits that do not have a thin, papery endocarp (FIGURE 8). Although *M. dubium-traceyi* of Australia has similar fruits, it does not appear to be immediately related to *M. anomala* of Madagascar and the Mascarenes, the type of sect. *Ciccoides*. It does not seem expedient, therefore, to recognize any subgeneric taxa within *Margaritaria*.

KEY TO THE SPECIES OF MARGARITARIA

1. Ovary glabrous, or if hirtellous then not deeply lobed.
   2. Filaments free.
      3. Fruits irregularly dehiscent, the endocarp thin, hyaline, papery.

4. Endotesta of seed smooth or nearly so.
   5. Branch tips not spinose.
      6. Branches glabrous or hirsutulous but not finely scabridulous; stipules lanceolate, not basally cordate.
         7. Petioles adaxially channeled; leaf blades rounded to acuminate; young twigs glabrous or hirsutulous.
            8. Carpels mostly 4 or 5 (rarely 3 or 6); styles free or nearly so; stipules 2–5 mm. long; seeds 2–4 mm. long; leaves usually acuminate. ..... 1. *M. nobilis.*
            8. Carpels mostly 3 (rarely 2 or 4); stipules 5–10 mm. long or if shorter then styles distinctly connate; leaves rounded to acuminate. .... 2. *M. discoidea.*
         7. Petioles not adaxially channeled; leaf blades obtuse or rounded at tip; young twigs reddish hirsutulous; carpels 3. ..... 6. *M. luzoniensis.*
      6. Branches usually finely scabridulous; stipules lanceolate or ovate, basally cordate, cuspidate-acuminate; carpels 3 or 4.
         9. Anthers 0.5–0.7 mm. long; staminate disc over 1 mm. across; carpels mostly 3; leaves more or less glaucous beneath, stipules pale. ..... 3. *M. scandens.*
         9. Anthers 1.2–1.4 mm. long; staminate disc obsolete; carpels mostly 4; leaves not glaucous beneath, stipules dark and indurate. ..... 4. *M. tetracocca.*
   5. Branch tips slender, spinescent, scabridulous when young; stipules lanceolate, pale; carpels 2. ..... 5. *M. hotteana.*
4. Endotesta of seed distinctly rugose or ribbed; carpels 3; plants glabrous.
   10. Staminate disc well developed; veinlet reticulum not distinctly prominulous; carpels 3.
      11. Staminate calyx lobes 1–1.6 mm. long; anthers 0.5–1 mm. long; pistillate flowers often 2 or 3 per axil. ..... 7. *M. indica.*
      11. Staminate calyx lobes 3.3–3.7 mm. long; anthers 1.8–2 mm. long; pistillate flowers solitary. ..... 8. *M. cyanosperma.*
   10. Staminate disc obsolete or absent; veinlet reticulum distinctly prominulous; carpels 2 or 3. ..... 9. *M. rhomboidalis.*
3. Fruits tardily dehiscent, the endococci not extremely thin and hyaline; leaves mostly rounded to emarginate; carpels 2.
   12. Leaves and fruits glabrous.
      13. Endotesta of seed smooth; leaf venation not prominulous; anthers 0.8–1.4 mm. long. ..... 10. *M. anomala.*
      13. Endotesta of seed rugose; leaf venation prominulous; anthers 0.3–0.5 mm. long. ..... 11. *M. dubium-traceyi.*
   12. Leaves and fruits hispidulous or hirsutulous; leaf venation prominulous. ..... 12. *M. hispidula.*
2. Filaments distinctly connate; leaves not over 2 cm. long, rounded to emarginate; carpels 2 or 3, glabrous. ..... 13. *M. decaryana.*

1. Ovary hirtellous (rarely glabrous), deeply lobed, 1 or 2 of the 3 carpels often abortive; petioles not adaxially channeled; endococci hyaline-papery. ..... 14. *M. obovata.*



FIGURES 5–10. Fruits of *Margaritaria*. 5, 6, *M. nobilis* (*Gentle 508*): 5, 4-carpellate fruit, exocarp peeling back to expose papery endocarps; 6, endocarps of 2 carpels broken away to show paired seeds inside; both × 5. 7, *M. discoidea* subsp. *discoidea* (*Linder 125*), intact 3-carpellate fruit, × 5. 8, *M. hispidula* (*Appert 107*), longitudinal section of fruit showing firmly adherent endocarp, × 7. 9, 10, *M. obovata* (*Mwasumbi LMB 10477*): 9, 3-carpellate fruit; 10, fruit with third carpel abortive; both × 4.5.

1. Margaritaria nobilis Linnaeus f. Suppl. Pl. 428. 1781. *Phyllanthus nobilis* (L. f.) Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: Surinam, *Dahlberg s.n.* (LINN). FIGURES 5, 6.

Margaritifera arbor Sirinamensis Hermann, Paradisi Batavi Prodr. 352. 1689.

Euonymus Margaritifera pentacoccus Americana Plukenet, Phytographia, *t. 176, fig. 4.* 1692.

Margaritaria alternifolia L. in Alm, Pl. Surinam. 16. 1755, *nomen illegit.*

Cicca antillana A. Juss. Euphorb. Gen. Tent. 108. *t. 4, fig. 13B.* 1824. *Phyllanthus antillanus* (A. Juss.) Mueller-Arg. Linnaea **32**: 51. 1863. *Phyllanthus antillanus β pedicellaris* Mueller-Arg. *ibid. Phyllanthus nobilis antillanus* (A. Juss.) Mueller-Arg. in DC. Prodr. **15**(2): 415. 1866. *Margaritaria nobilis* var. *antillana* (A. Juss.) Stehlé & Quentin, Catal. Fl. Guad. **2**: 47. 1937. TYPE: St. Thomas, *Riedlé s.n.* (P-JU).

Cicca surinamensis Miq. Linnaea **21**: 479. 1848. *Phyllanthus antillanus α concolor* Mueller-Arg. Linnaea **32**: 51. 1863. TYPE: Surinam, *Hostmann 622* (U, lectotype).

Cicca pavoniana Baillon, Étude Gén. Euphorb. 618. 1858. *Phyllanthus nobilis ζ pavonianus* (Baillon) Mueller-Arg. in DC. Prodr. **15**(2): 415. 1866. TYPE: Peru, *Pavon s.n.* (P, holotype, *n.v.*; G, isotype).

Cicca antillana var. *γ pedicellaris* Griseb. Mem. Am. Acad. II. **8**: 158. 1860. TYPE: Cuba, Farallones, *Wright 584a* (GOET, holotype; G, GH, S, isotypes).

Phyllanthus nobilis β guyanensis Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866. TYPE: French Guyana, *Sagot 1153* (G, holotype; U, isotype).

Phyllanthus nobilis γ peruvianus Mueller-Arg. in *ibid.* TYPE: Peru, *Spruce 4472* (G, holotype).

Phyllanthus nobilis δ brasiliensis Mueller-Arg. in *ibid.* TYPE: Brazil, Minas Gerais, *Claussen s.n.* (G, holotype; A, isotype).

Phyllanthus nobilis ε riedelianus Mueller-Arg. in *ibid.* TYPE: Brazil, *Riedel s.n.* (*n.v.*).

Phyllanthus nobilis var. *θ martii* Mueller-Arg. Fl. Brasil. **11**(2): 70. 1873. TYPE: Brazil, *Martius 2813* (M).

Phyllanthus nobilis var. *panamensis* Mueller-Arg. *ibid.* TYPE: Panama, *Sutton Hayes 749* (M, lectotype).

Phyllanthus heteromorpha Rusby, Descr. S. Am. Pl. 42. 1920. TYPE: Colombia, *H. H. Smith 1716* (NY, holotype; MO, U, isotypes).

Phyllanthus nobilis var. *hypomalacus* Standley, Carnegie Inst. Publ. **461**: 68. 1935. *P. antillanus* var. *hypomalacus* (Standley) Lundell, Phytologia **1**: 337. 1939. TYPE: Mexico, Campeche, *Lundell 897* (F).

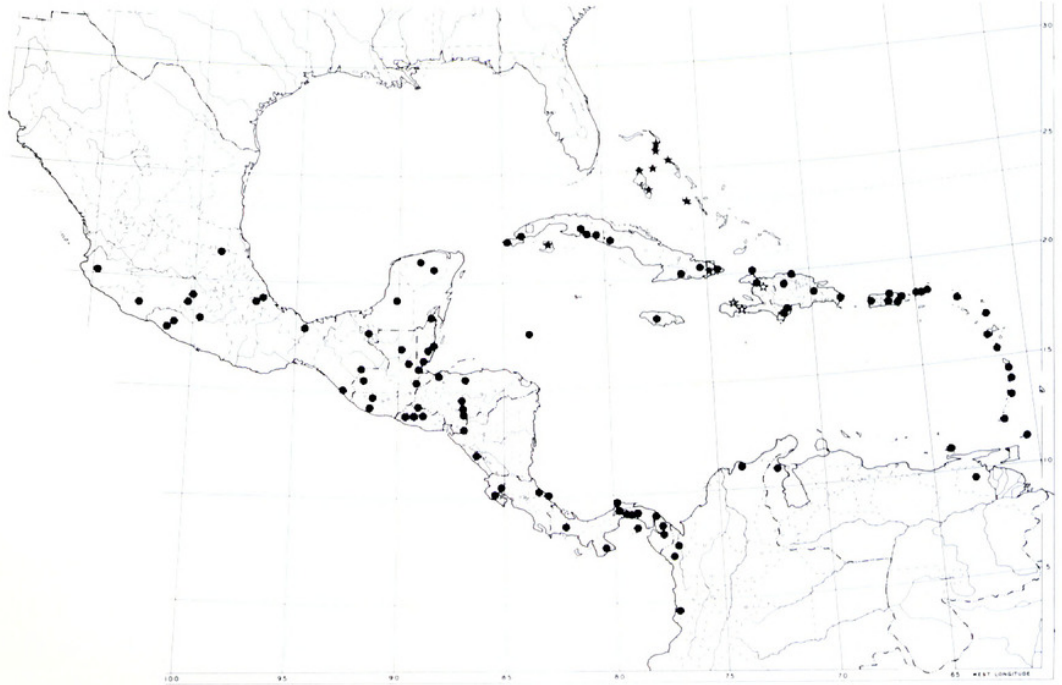
Celastrus tetramerus Standley, Contr. U. S. Natl. Herb. **23**: 679. 1923. TYPE: Mexico, Iguala Canyon, *Pringle 10319* (US).

Deciduous shrub or tree to 20 meters high; branches glabrous or rarely hirtellous, subterete or angled, becoming prominently lenticellate; foliage deciduous (perhaps sometimes evergreen). Leaf blades chartaceous, elliptic or oblong to oblanceolate, mostly 6–15 cm. long, 2.5–5 cm. broad, acuminate, obtuse to cuneate at base, decurrent on petiole, glabrous or sometimes hirsutulous beneath along the veins, sometimes glaucous beneath; major veins mostly 7 to 12 on a side, veinlet reticulum prominent beneath but scarcely prominulous; margins plane; petiole ca. 2–5 mm. long, distinctly channeled adaxially; stipules caducous to more or less

persistent, pale and scarious, elliptic- to oblong-lanceolate, acuminate, 1.5–3(–4.5) mm. long. Staminate flowers several per axillary cluster; pedicels ca. 2.5–8 mm. long, glabrous; sepals biseriate, glabrous, 0.9–1.7 mm. long, 0.7–1.5 mm. broad (outer pair usually narrower); disc 1–2 mm. across; stamens 4, free, filaments becoming 1–2 mm. long, the anthers elliptic or oblong, 0.5–1.1 mm. long. Pistillate flowers 1 to several per axil; pedicels subterete, glabrous, becoming 5–12(–16) mm. long; sepals 4, biseriate, the inner ones 1.5–2.5 mm. long, 1.5–2.5 mm. broad (outer ones usually narrower); disc 0.8–2.5 mm. across; ovary usually of 4 (65%) or 5 (28%) (rarely 3 or 6) carpels, not deeply lobed, the styles free or basally connate, 1.5–3 mm. long, bifid. Fruits subglobose to oblate, moderately lobed, 7.5–11 mm. in diameter, dehiscing irregularly, endocarps papery; seeds with thick, bluish green sarcotesta, the endotesta smooth, planoconvex, (2–)2.7–4 mm. long, 1.9–3.7 mm. broad.

DISTRIBUTION. Seasonal, rain, or riparian forests, mostly at lower elevations (up to 1000 meters); Mexico and Cuba south to Peru and Brazil (MAPS 2, 3).

REPRESENTATIVE SPECIMENS (cited to indicate range limits). **Mexico.** JALISCO: 2.5–4 mi. N. of La Cuesta, *McVaugh et al. 21190* (DAV, MICH). SAN LUIS POTOSÍ: Tamazunchale, *Lundell & Lundell 7259* (A). **Central America: Belize.** Corozal, *Gentle 508* (MO, US). **Guatemala.** *Petén, Lundell 3432* (GH). **El Salvador.** Chalaltenango, *Allen 7040* (F, US). **Honduras.** YORO: Morazán, *Webster et al. 12000* (DAV). SWAN IS.: Great Swan, *Proctor 32543* (DAV). **Nicaragua.** Volcán Santiago, *Maxon 7680* (GH, US). **Costa Rica.** Limón, *Shank & Molina 4199* (F, US). **Panama.** Barro Colorado Is., *Foster 1192* (DAV, MO). **West Indies: Cuba.** LAS



MAP 2. Distribution of *Margaritaria* in the Caribbean. Solid dots, *M. nobilis*; squares, *M. tetracocca*; solid stars, *M. scandens*; open stars, *M. hotteana*.

VILLAS: Buenos Aires, *Jack 7401* (A). ORIENTE: Río Yao, *Webster 4150* (DAV, GH); Farallones, *Wright 584a* (GH); Charco de Toro, *Wright 1933* (GOET). PINAR DEL RÍO: Mendoza, *Ekman 18086* (NY). **Haiti.** Morne Birgonne, *Ekman H2627* (A). **Dominican Republic.** Monción, *Ekman H12997* (DAV, S). **Puerto Rico.** Fajardo to Luquillo, *Sintenis 1553* (GH). **Jamaica.** Troy, *Harris 8698* (GH). **Virgin Islands.** ST. THOMAS, *Eggers 173* (GH). ST. JOHN, *Raunkiaer s.n.* (C). **Lesser Antilles.** ANTIGUA: Blubber Valley, *Box 1493* (A). GUADELOUPE: Vieux-Fort, *Webster, Ellis, & Miller 9157* (DAV, MICH, U). DOMINICA: Carholm Estate, *Ernst 1949* (DAV, US). MARTINIQUE: Ste.-Luce, *Hahn 964* (GH). SABA: *Boldingh 2198* (U). ST. LUCIA: Morne la Sorcière, *Proctor 18169* (DAV). ST. VINCENT: Letchwood Valley, *Beard 613* (A, NY, U). GRENADA: Union, *Proctor 17174* (A, DAV, U). GRENADINES: Mustique, *G. W. Smith 128* (GH). **Tobago.** Scarborough, *Broadway 4043* (GH, S, U). **Trinidad.** Cedros, *Broadway TRIN 7411* (TRIN). **South America: Colombia.** Puerto Berrio, *Haught 2180* (A, US). **Venezuela.** Isla Margarita, *Johnston 332* (GH); Delta Amacuro, *Wurdack & Monachino 39689* (US). **Guyana.** Kanuku Mts., *A. C. Smith 3509* (A, U, US). **Surinam.** Paramaribo, *Kappler 1625* (MO). **French Guiana.** Cayenne, *Broadway 345* (GH, US). **Ecuador.** El Recreo, *Eggers 15744* (S, US). **Peru.** Iquitos, *Asplund 14631* (US). **Bolivia.** Buenavista, *Steinbach 7374* (A). **Paraguay.** Estrella, *Hassler 10906* (M). **Argentina.** Posadas, *Ekman 1460* (S). **Brazil.** SANTA CATARINA: Itajai, *Klein 959* (US).

This widespread species is rarely abundant in any one locality, since it appears to belong to successional stages of vegetation. It displays a considerable amount of morphological variation, and Mueller in his final treatment (1873) recognized no less than nine varieties, of which seven were confined to various regions of South America. After considerable study of the available specimens, I have concluded that it is not profitable to attempt to demarcate any subspecific taxa, since the variation in morphological characters appears to be clinal, without any prominent discontinuities. Pubescent forms, designated by Standley as *Phyllanthus nobilis* var. *hypomalacus*, occur promiscuously mixed with glabrous ones. There is a tendency for 3-carpellate fruits to occur more commonly in Mexico and Central America, but they also occur in Paraguay and sporadically elsewhere; 5- and even 6-carpellate fruits are found in the Amazon basin and Colombia, but many West Indian specimens are also largely 5-carpellate (TABLES 1, 2).

The nomenclature and typification of this widespread American species of *Margaritaria* presents several problems. Linnaeus (in Alm, 1775) described two species, *M. oppositifolia* and *M. alternifolia*, that are illegitimate because the generic name *Margaritaria* was not validly published at that time. In 1781 Linnaeus filius assigned a different name, *M. nobilis*, probably because he combined the two taxa of 1775 (even though he expressed doubt about their conspecificity). It is not evident which specimen of those in the Linnaean Herbarium was collected by Dahlberg (as cited in the protologue), but I believe that the sheet labeled *M. alternifolia* can reasonably be taken to be the holotype. Wheeler (1939, a, b) suggested that both the generic name and the specific epithet of *Margaritaria nobilis* should be rejected because of the original inclusion of discordant elements; but under current rules of nomenclature, it appears

MAP 3. South American distribution of *Margaritaria nobilis*.

that Mueller (1866) salvaged the names by excluding the combretaceous element and thus achieving a satisfactory typification.

2. **Margaritaria discoidea** (Baillon) Webster, Jour. Arnold Arb. **48**: 311. 1967. *Cicca discoidea* Baillon, Adansonia I. 1: 85. 1860. *Phyllanthus discoideus* (Baillon) Mueller-Arg. Linnaea 32: 51. 1863; in DC. Prodr. **15**(2): 416. 1866. TYPE: Gambia, Albreda, *Heudelot 102* (P, lectotype).

Shrubs or trees to 20 (rarely 30) meters high; branches subterete or angled, glabrous or hirsutulous when young, becoming prominently lenticellate; foliage usually deciduous. Leaf blades chartaceous, elliptic or oblong, mostly acute to acuminate at apex, acute to obtuse at base, mostly 3–15 cm. long, 2–4(–5.5) cm. broad, glabrous beneath or sometimes hir-

sutulous (especially along veins); major veins usually 5 to 12 on a side, raised beneath, veinlet reticulum usually prominent beneath and sometimes prominulous; margins plane; petiole ca. 3–7 mm. long, usually distinctly channeled adaxially; stipules caducous (sometimes subpersistent), blunt to acuminate or acute-apiculate, mostly 4–8(–10) mm. long (occasionally only 2.5 mm. at first nodes of annual growth). Staminate flowers several per cluster; pedicels glabrous or hirsutulous, 2–5(–7) mm. long; sepals 4, subequal, the larger (inner) ones 0.8–1.5(–2) mm. long; disc thin, entire or minutely crenulate, (0.5–)1.0–1.8 mm. across; stamens 4, the filaments free or slightly united at base, 0.8–2 mm. long, the anthers ellipsoid, 0.4–1.4 mm. long. Pistillate flowers mostly 1 to 3 per axil; pedicels rather stout, subterete or angled, becoming (2–)3–8(–14) mm. long; sepals 4, subequal, oblong to ovate, the outer ones ca. 0.8–1.2 mm. long and broad, the inner ones 1.0–3.3 mm. long; disc rather thick, 1.5–2.7 mm. across; ovary usually of 3 carpels (90%), rarely of 2 (1.5%) or 4 (8.5%), the styles connate basally into a column 0.2–2 mm. high, with tips spreading, 0.8–1.5 mm. long, bifid. Capsules subglobose to oblate, scarcely to distinctly (but not deeply) 3-lobed, (5.5–)6–9(–11) mm. in diameter, endococci thin and papery; seeds with thin to thick sarcotesta, the endotesta smooth, plano-convex, (2–)2.3–3.2(–3.9) mm. long.

DISTRIBUTION. Deciduous forests or woodlands, sometimes in rainforests, most often in successional communities, from sea level to ca. 1000 meters elevation; western to eastern and southeastern Africa (MAP 4).

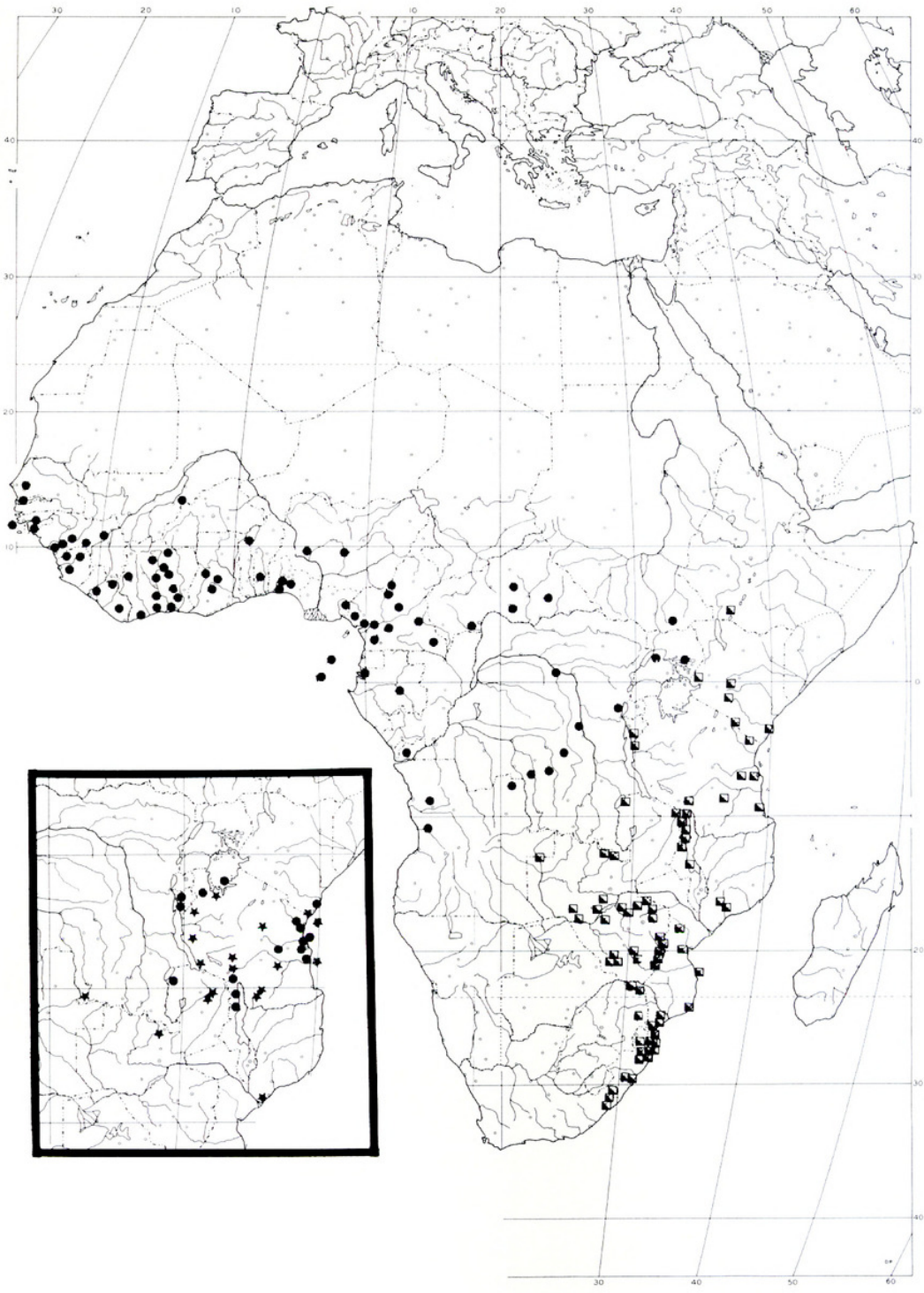
As noted by Radcliffe-Smith (1976), this widespread African species shows a great deal of variability. However, in contrast to *Margaritaria nobilis*, it exhibits a fairly clear differentiation into western and eastern populations that may be conveniently distinguished as subspecies. Although there is some overlap of characters, most specimens can be rather confidently assigned according to the characters detailed in the following key:

Stipules mostly 5–10 mm. long (at distal nodes); larger staminate sepals 1.1–1.5 mm. long; anthers mostly 0.4–0.7 mm. long; fruiting pedicels mostly 1.5–6 mm. long; stylar column 0.2–0.8(–1.1) mm. high; endotesta of seed mostly 2.5–3.5 mm. long; leaf blades mostly acute to acuminate at tip. . . . . subsp. 2a. *discoidea*.

Stipules mostly 2–5 mm. long (at distal nodes); larger staminate sepals 1.5–3 mm. long; anthers 0.8–1.4 mm. long; fruiting pedicels mostly 5–13 mm. long; stylar column 0.7–2 mm. high; endotesta of seed mostly 3.5–4.8 mm. long; leaf blades mostly obtuse to rounded at tip. . . . . subsp. 2b. *nitida*.

2a. Margaritaria discoidea subsp. discoidea. FIGURE 7.

Leaf blades mostly acute to acuminate at tip (occasionally obtuse); stipules usually caducous, generally acute to acuminate, (3–)5–8(–10) mm. long. Staminate flowers with sepals unequal, inner (larger) ones 1.1–1.5



MAP 4. Distribution of *Margaritaria* in Africa. Solid dots, *M. discoidea* subsp. *discoidea*; half-filled squares, *M. discoidea* subsp. *nitida*. Inset: *M. obovata* (solid dots; stars indicate localities cited by Radcliffe-Smith).

mm. long; disc (0.8–)1–1.3(–1.8) mm. across; anthers 0.4–0.7 mm. long. Pistillate flowers with pedicels becoming (1.5–)2.5–8(–13) mm. long; ovary of 3 carpels (88%), rarely of 2 (1.5%) or 4 (10.5%); stylar

column (0.2–)0.4–0.8(–1.1) mm. high; capsules (5.5–)6–8.5(–9.5) mm. across; endotesta of seed (2–)2.3–3.3(–3.5) mm. long.

DISTRIBUTION. Seasonal to evergreen rainforests, mostly below 1000 meters; Senegal to Angola, Zaire, and along the Rift Valley in eastern Africa (MAP 4); mainly in secondary vegetation (see Aubréville, 1959). Only a small portion of the specimens seen from West Africa are cited here.

REPRESENTATIVE SPECIMENS. **Angola:** Cuanza N., Cazengo, *Gossweiler 4692* (COI, NY, P). **Cameroon:** Bipindi, *Zenker 2890* (P, US). **Central African Empire:** Boukoko, *Tisserant 501* (P). **Ivory Coast:** Rasso, *Aubréville 560* (A, P). **Benin:** Cabolé, *Chevalier 23780* (P). **Gabon:** Libreville, *Klaine 1031* (A, P). **Gambia:** Albreda, *Heudelot 102* (P). **Ghana:** Asokroa, Kumasi, *Darko 595* (MO). **Guinea:** entre Konkouré et Timbo, *Chevalier 12499* (P). **Guinea-Bissau:** Fulacunda, *Espirito Santo 2162* (COI). **Liberia:** Barclayville, *Baldwin 11125* (NY). **Mali:** cercle de Kita, *Vuillet 247* (P). **Nigeria:** Ijebu, Oluasogo, *Ross 62* (MO, NY). **Senegal:** Thies-Diourbel, Kaolak, *Berhaut 1091* (P). **Sierra Leone:** Njala, *Deighton 1109* (MO). **Sao Tome & Principe:** Príncipe, *Espirito Santo 221* (COI); São Tomé, *Espirito Santo 3850* (COI). **Sudan:** Equatoria, Torit Rirt, *Andrews 1740* (K). **Togo:** Tamberma, *Kersting 343* (A). **Uganda:** Kipayo, *Dümmer 367* (MO, US); Teso, Serere, *Chandler 1063* (PRE). **Zaire.** EQUATEUR: Lukolela, *Chapin 598* (US). KIVU: Kalehe, *Pierlot 729* (BR), *Troupin 12520, 12595* (BR); Lueki, *Donie 2093* (MO). ORIENTALE: Isangi, *Léonard 1391* (MO).

Margaritaria discoidea subsp. *discoidea* is very similar morphologically both to the American *M. nobilis* and to the oriental *M. indica*. It appears closer to the American taxon because of the smooth endotesta of the seed and the tendency to have 4-carpellate fruits. However, no collections of *M. discoidea* subsp. *discoidea* having only 4 carpels have been seen; 65% of the collections have only 3 (or 2 and 3) carpels, and although 34% of the collections have both 3 and 4 carpels, the 4-carpellate fruits are always a small minority (TABLES 1, 2). Plants of *M. nobilis* from Mexico and Central America come closest to this condition, but 4-carpellate fruits there are nearly always in the majority. This difference in distribution of carpel number suggests to me that the American and African plants are best assigned to two different species. Staminate specimens of the three taxa are difficult or sometimes impossible to distinguish, and one could argue that the three taxa should be treated as a single circumtropical polymorphic species. However, the eastern African populations here accepted as a subspecies of *M. discoidea* would be difficult to accommodate in such a classification, and our knowledge of the populations still appears inadequate to justify such extreme lumping.

2b. **Margaritaria discoidea** subsp. **nitida** (Pax) Webster, comb. et stat. nov. *Flueggea nitida* Pax, Bot. Jahrb. 19: 76. 1894. TYPE: Mozambique, Quilimane, *Stuhlmann 559* (*n.v.*; the original specimen at B presumably having been destroyed, I hereby designate as neotype the following collection: Mozambique, entre Nampevo e Mugeba, *Grandvaux Barbosa & Carvalho 2950* (K)).

Flueggea fagifolia Pax, Pflanzenw. Ost.-Afr. C, 236. 1895. TYPE: Tanzania, Kilimanjaro, *Volkens 1737* (K, lectotype).

Phyllanthus ? amapondensis Sim, Forests Forest Fl. Colony Cape Good Hope, 325. *t. 141, fig. 2.* 1907. TYPE: South Africa, Pondoland, Egossa Forest, *Sim 2608* (PRE, holotype).

Leaf blades mostly obtuse or subacute at tip, occasionally rounded or emarginate, rarely acuminate; stipules caducous or persistent, 2.5–5(–6) mm. long; inner (larger) staminate sepals (1.5–)1.8–2.5(–3) mm. long; staminate disc 0.5–1.1(–1.5) mm. across; anthers 0.8–1.4 mm. long; pistillate flowers with pedicels becoming (5–)6–10(–13) mm. long; ovary nearly always of 3 carpels (97%), very rarely of 2 or 4 (1.5% each), styles usually connate ½ to ¾ their lengths, the column 0.8–2 mm. high; capsules (9–)10–13 mm. in diameter; endotesta of seeds (3.5–)3.8–4.8 mm. long.

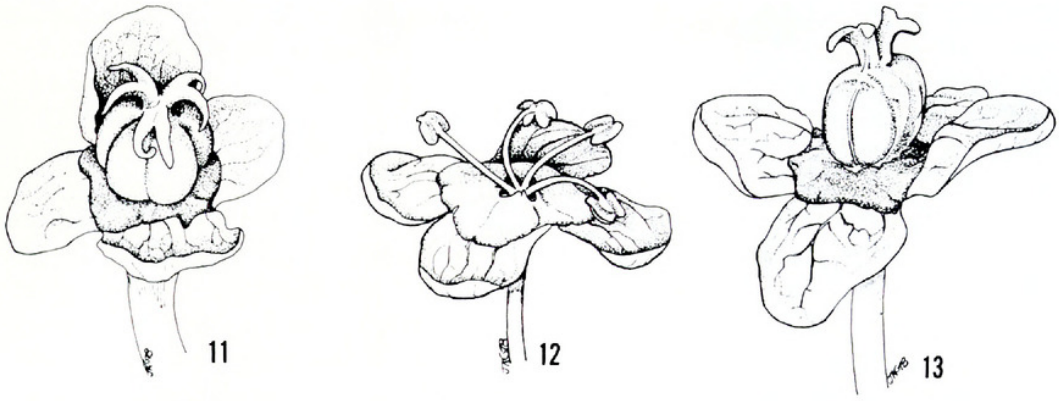
DISTRIBUTION. Burundi and southwestern Ethiopia south to Rhodesia and South Africa (MAP 4); a large number of additional specimens are cited by Radcliffe-Smith (1976).

SPECIMENS EXAMINED. **Burundi:** Bururi, Kigwena, *Reekmans 3192* (PRE). **Ethiopia:** S. Sidamo, *Chaffey 132* (K). **Kenya.** CENTRAL: Nyeri, *Porter 933* (PRE). COAST: Kilifi, Sokoke, *Gisau SOK6* (PRE). NAIROBI: Nairobi, National Museum grounds, *Mwangangi 1768* (MO); Coryndon Museum grounds, *Williams 427* (K, PRE); Chiromo, *Agnew 7784* (MO), *Gillett 16593* (MO). WESTERN: Kakamega Forest, *Drummond & Hemsley 4797* (PRE, K). **Malawi.** CENTRAL: Salima, *Robson & Steele 1613* (PRE). NORTHERN: Chendo River, between Fort Hill and Chisenga, *Robson & Fanshawe 556* (PRE); Chitipa Distr., Kaseye, *Pawek 13359* (DAV); Karonga Distr., 5 mi. W. of Karonga, *Pawek 12112* (DAV); Mzimba Distr., 1¼ mi. SE. of Mzambazi Mission, *Pawek 11960* (DAV); Nkhata Bay Distr., road to Nkhata Bay from Mzuzu, *Pawek 12046* (DAV). **Mozambique.** GAZA: Macia, S. Martinho do Bilene, *Grandvaux Barbosa 8338* (COI); entre Chissano e Licilo, *Grandvaux Barbosa & Lemos 7970* (COI, K). INHAMBANE: Sul do Save, Nhacoongo, *Macedo & Balsinhas 1101* (PRE); Bazaruto Is., Pont Estone, *Mogg 28639* (PRE). MAPUTO: Muntanhane, *Balsinhas 237* (PRE); Lourenço Marques, *Borle 174* (PRE), *Hornby 2880* (PRE); Bela Vista, Floresta do Licauti, *Lemos & Balsinhas 259* (PRE); Vila Luiza, *Grandvaux Barbosa & Lemos 7907* (COI). MANICA E SOFALA: Buzi, Reserva Florestal do Mucheve, *Fidalgo de Carvalho 703* (PRE); Mt. Gorongosa, *Muller & Gordon 1396* (PRE). ZAMBEZIA: entre Nampevo e Mugeba, *Grandvaux Barbosa & Carvalho 2590* (K); Quelimane, Lugela-Moruba, Namagoa Plantation, *Faulkner 314* (K). **Rhodesia.** MANICALAND. Chipinga Distr.: Makosa hills, *Phelps 197* (PRE); Mwangazi Gap, *Farrell 163* (PRE); Dotts Drift, *Goodier 664* (PRE). Melsetter Distr.: Umvumuvumu River, *Armitage 158* (PRE); Lusitu Valley, Ngorima Reserve, *Wgoni 65* (MO). Stapleford Distr.: Mt. Wuza, *Goldsmith 26749* (PRE). Umtali Distr.: 25 mi. S. of Umtali, *Drummond 5049* (PRE); Christmas Pass, *Gilliland 1260* (PRE); Umtali Golf Course, *Chase 5150* (MO). MASHONALAND NORTH. Darwin Distr.: Chiswiti Reserve, *Phipps 2358* (PRE). Urungwe Distr.: Deve, *Goodier 459* (PRE); Msukwe River, *Wild 4160* (MO, PRE); Urungwe, *Lovemore 311* (MO, PRE). Lomagundi Distr.: Mangula, *Jacobsen 2498, 2971* (PRE). MASHONALAND SOUTH. Mrewa Distr.: Shawnoye River bridge, *Moll 592* (NY). MATABELELAND. Sebungwe Distr.: Kariangwe Hill, *Lovemore 175* (NY, PRE); Suainga, *Lovemore*

487 (PRE); Victoria Falls, *Wilson s.n.* (A). Matopos Distr.: Moth Shrine Koppie, *Plowe 1320* (NY); Besna Kobila, *Miller 1991* (MO, PRE); Quaringa, *Miller 2522, 3295* (PRE). VICTORIA. Chibi Distr.: Madzivire Dip, *Moll 385* (NY). **South Africa.** CAPE OF GOOD HOPE: Pondoland, Egossa Forest, *Sim 2608, 19618* (PRE). NATAL: Hlabisa, *Ward 2677, 2819* (PRE); Hluhluwe Game Reserve, *Codd 9627* (PRE); *Fakude 20* (PRE), *Pegel 102* (PRE); Mbizatsheni, *Ward 6058* (PRE); Wall's farm, *Gerstner 5006* (PRE). Ingwavuma Distr.: Maputa, *de Winter & Vahrmeijer 8601* (PRE), 16 mi. from Ndumu toward Ingwavuma, *Moll 4353* (PRE); confluence Pongola/Usutu, *Dutton s.n.* (PRE); Ndumu Game Reserve, *Strey & Moll 3751* (NY), *Tinley 406* (PRE), *Ward 2474* (PRE). New Hanover Distr.: Benvie, Karkloff, *Moll 3374* (PRE). Port Shepstone Distr.: Amanzimtoti, *Ward 6038* (PRE); Isipingo Flats, *Ward 6715* (PRE). Westville Distr.: Mologodhlo Valley, *Haycroft s.n.* (PRE). TRANSVAAL: near Lothian, *Chief Forestry Res. Officer 81* (PRE); Kruger National Park, Dzundweni Hill, 12 mi. SE. of Punda Maria, *Codd & Dyer 4591* (PRE), Zoutpansberg, *Codd & Dyer 4545* (PRE). SWAZILAND: Hlatikuhu Forest, *Forestry Herb. 5324* (PRE). **Tanzania.** KIGOMA: Kigoma, *Humbert 7185* (P). KILIMANJARO: Am Himo, *Volkens 1737* (K). MBEYA: Kyimbila, *Stolz 1744 (ex. p.), 1770* (A, MO). MOROGORO: Vigude, Kilosa Distr., *Semsei 5987* (MO); Ulugurus, *Bruce s.n.* (P); Mahenge, *Schlieben 1467* (P). MTAWARA: Lindi, *Schlieben 5460* (M, P, S). TANGA: Lushoto Distr., Ndola Reserve, *Semsei 2966* (PRE), Lushoto-Gare track, *Semsei 3190* (PRE). **Uganda.** BUNYORO: Foweira, *Bagshawe 1572* (US). **Zambia.** LUAPULA: Kafulwe Mission, Lake Mweru, *White 3600* (MO). NORTHWESTERN: Balovale Distr., Chavuma, *White 3490* (MO, PRE). SOUTHERN: Mazabuka Distr., Kanchale, *White 6326* (NY); Victoria Falls, *Burtt Davy 601* (PRE); Siburu Forest, Sekute Chieftancy, *Bainbridge 705* (NY); Mapanza, Chomo, *Robinson 2506* (PRE). WESTERN: Zimbabwe, Chipopo Falls, *Mullin 89/51* (NY); Ndola, *Fanshawe F731* (BR).

The status of the eastern African populations of *Margaritaria discoidea* remains controversial. Radcliffe-Smith (1976), while recognizing *M. obovata* at varietal rank, grouped all other forms of eastern African *Margaritaria* in *M. discoidea*. However, although there are overlaps of measurement in most characters in the eastern and western African populations, I believe that they are modally distinctive enough to merit separation at the subspecific level. Specimens somewhat intermediate between subsps. *discoidea* and *nitida* are known from Sudan, Uganda, and Zaire. However, the sampling of collections from these areas is still not very good, so the position of the boundary line or zone between the two subspecies is not yet well defined.

3. **Margaritaria scandens** (Wright ex Griseb.) Webster, Jour. Arnold Arb. 38: 66. 1957. *Cicca antillana* var. *α glaucescens* Griseb. Mem. Am. Acad. II. 8: 157. 1860. *Phyllanthus antillanus ε glaucescens* (Griseb.) Mueller-Arg. Linnaea 32: 51. 1863. *Cicca scandens* Wright ex Griseb. Nachr. Ges. Wiss. Göttingen 1865: 165. 1865. *Phyllanthus scandens* (Griseb.) Mueller-Arg. in DC. Prodr. 15(2): 415. 1866. *Diasperus scandens* (Griseb.) O. Kuntze, Rev. Gen. Pl. 2: 601. 1891. TYPE: Cuba, Oriente, Monteverde, *Wright 1437* (GOET, holotype). FIGURES 1, 11.



FIGURES 11–13. Flowers of *Margaritaria*: 11, *M. scandens* (*Brace 168*), pistillate; 12, *M. hotteana* (*Ekman H8909*), staminate; 13, *M. hotteana* (*Ekman H8919*), pistillate; all × 7.5.

Phyllanthus bahamensis Urban, Symb. Antill. 3: 289. 1902. *Margaritaria bahamensis* (Urban) Britton & Millsp. Bahama Fl. 220. 1920. LECTOTYPE: Andros, Red Bays, *Northrop s.n.* (GH, lectotype).

Straggling or somewhat scandent shrub or small tree up to 5 meters high; branches scabridulous when young, reddish and becoming more or less smooth in age; foliage evergreen, or partly deciduous. Leaf blades firmly chartaceous, elliptic to obovate or lanceolate, mostly 3–7 cm. long, 1.5–2.5 cm. broad, obtuse or bluntly pointed at tip, cuneate at base, decurrent on petiole, often glaucous beneath; major veins ca. 7 to 12 on a side, not conspicuous above, beneath raised, the veinlet reticulum often prominent but not prominulous; margins plane or recurved; petioles 3–7 mm. long, distinctly adaxially channeled; stipules ovate-lanceolate, scarious, becoming more or less indurate and subpersistent, cordate, acuminate, (1–)1.5–2.5(–3.5) mm. long. Staminate flowers few to several per axil (rarely solitary); pedicels stout, 2–5 mm. long; sepals biseriate, ovate to elliptic, the outer pair 1–1.7 mm. long, 1–1.4 mm. broad, the inner pair 1.4–2.1 mm. long, 1.2–1.9 mm. broad; disc thickish, 1.2–2.1 mm. across; stamens 4, free, the filaments becoming 0.5–1.3(–2) mm. long, the anthers elliptic, 0.5–0.7(–1) mm. long. Pistillate flowers 1 to 3 per axil; pedicels subterete, (1.5–)3–7(–9) mm. long; sepals 4, biseriate, subequal, 1.5–2.3 mm. long and broad; disc thick, 2.3–3 mm. across; ovary of 3 (less commonly 4) carpels, the styles free, spreading, 1–1.5 mm. long, bifid. Fruits oblate, shallowly 3-lobed, 7–10 mm. in diameter, irregularly dehiscent, endococci papery; seeds with thick blue-green sarcotesta, the endotesta smooth, plano-convex, 2.7–4.2 mm. long, 2.4–3.5 mm. broad.

DISTRIBUTION. Hammocks, pine forests, and evergreen forests; Bahamas and Cuba (MAP 2).

SPECIMENS EXAMINED. **Bahamas.** ANDROS. N. Andros: Mangrove Cay, *Brace 4867* (NY); Nicholls town, *Correll & Evans 43929* (NY); Conch Sound, Strachan Hill, *Brace 6924* (NY); road to Conch Sound, *Brace 6784* (NY); road to Louisa Coppice, *Brace 6270* (A); 2 mi. NW. of Love Hill, *Hill 3027, 3035* (NY); Mastic

Point, *Brace 6983* (NY); Crow Hill, *Small & Carter 8720* (NY); Smith Hill, *Small & Carter 8678* (NY); 1 mi. N. of Smith's Hill, *Correll 43522* (NY). ELEUTHERA: Spanish Wells, *Coker 328* (NY); The Bluff, *Russell 1* (DAV). GREAT ABACO: road to Hole-in-the-wall, 6 mi. below intersection with Sandy Point Rd., *Correll & Meyer 44559* (NY); California Road, *Brace 2037* (NY). GREAT EXUMA: Stuart Manor, *Correll 44107* (NY). NEW PROVIDENCE: Nassau, *Brace 3906*, (NY), *Curtiss 183* (A, NY); Farringdon Road, *E. G. Britton 3043* (NY); Fort Charlotte Rd., *Brace 7147* (NY); Maiden-hair Coppice, *Wilson 8394* (NY), *E. G. Britton 3435* (NY); between Love and Gambier, *Degener 19140* (A, NY); Waterloo, *Britton & Brace 741* (NY), *Degener 19139* (A, NY); Blue Hills, between Lake Cunningham and Lake Killarney, *Webster, Samuel, & Williams 10514* (DAV). **Cuba.** LA HABANA: Isle of Pines, *Jennings 678* (NY). ORIENTE: Mt. Libano, 1860, *Wright s.n.* (GOET); La Perla, Monteverde, *Wright 1437* (GOET, holotype; BR, F, G, GH, NY, S, W, isotypes).

Several barren specimens from Oriente Province, Cuba, are distinctive in their thick, revolute leaves with a thick, waxy, glaucous bloom beneath: Lomas de Duaba, near Baracoa, *Ekman 4236* (S); Moa, La Brena, *León & Clemente 23339* (MICH); Toa, charrascos de Pena Prieta, *Alain 3481* (DAV); Pico Galano, Toa, *Alain 3761* (DAV). These may represent a form of *Margaritaria scandens* or perhaps an undescribed species.

There is still some uncertainty as to the application of the name *Margaritaria scandens* because the species has not been re-collected in Cuba since Wright's original gatherings. From these incomplete specimens, it is difficult to be absolutely certain that the Bahama plants are conspecific. However, until the Cuban population can be restudied, it seems best to treat *M. bahamensis* as a synonym of *M. scandens*. Unfortunately, I had earlier (Jour. Arnold Arb. 39: 208. 1958) mistakenly treated *M. bahamensis* as a synonym of *M. tetracocca* rather than of *M. scandens*.

4. **Margaritaria tetracocca** (Baillon) Webster, Jour. Arnold Arb. 38: 66. 1957. *Wurtzia tetracocca* Baillon, Adansonia I. 1: 187. 1861. TYPE: Cuba, Oriente, *Wright 583* (G, holotype; GOET, isotype).

Cicca antillana var. *β virens* Griseb. Mem. Am. Acad. II. 8: 158. 1860. *Phyllanthus antillanus β virens* (Griseb.) Mueller-Arg. Linnaea 32: 51. 1863. *Cicca virens* (Griseb.) Wright ex Griseb. Nachr. Ges. Wiss. Göttingen 1865: 166. 1865. *Phyllanthus virens* (Griseb.) Mueller-Arg. in DC. Prodr. 15(2): 415. 1866. *Diasperus virens* (Griseb.) O. Kuntze, Rev. Gen. Pl. 2: 601. 1891. TYPE: Cuba, Oriente, *Wright 584* (GOET, lectotype; G, GH, S, isotypes).

Shrub to 3 meters high; branches subterete, scabridulous at least when young; foliage evergreen. Leaf blades firmly chartaceous, elliptic or oblong, 3–9 cm. long, 1.5–3.5 cm. broad, obtuse or bluntly pointed at tip, cuneate at base, decurrent on petiole, shining above, paler but not glaucous beneath; major veins ca. 7 to 12 on a side, inconspicuous above, raised beneath, veinlet reticulum rather conspicuous beneath but not very prominulous; margins more or less revolute; petioles 4–7 mm. long, adaxially channeled; stipules ovate, basally auriculate, acuminate, hardly scarious, becoming dark and indurate, 1.5–2.7 mm. long. Staminate flow-

ers several per cluster; pedicels stout, 2–3 mm. long; sepals biseriate, 1.8–2.5 mm. long, the inner ones ca. 1.7–2.5 mm. broad (outer ones narrower); disc obsolete; stamens 4, free, the filaments 0.5–0.8 mm. long, the anthers oblong, 1–1.3 mm. long. Pistillate flowers solitary; pedicels subterete, scabridulous, 2.5–5.5 mm. long; sepals 4, biseriate, subequal, ovate, 1.5–2.3 mm. long, 1.2–2.1 mm. broad; disc rather thin, 1.5–1.8 mm. across; ovary of 4 (rarely 3) carpels, apically indented, the styles 1.5–2 mm. long, connate basally into a column 0.4–0.7 mm. high, bifid. Fruits oblate, shallowly to rather deeply 4-lobed, apically depressed, 9–10 mm. in diameter; seeds apparently with a thin sarcotesta, the endotesta smooth, plano-convex, 2.7–3.2 mm. long, 2.7–2.9 mm. broad.

DISTRIBUTION. Endemic to montane forests; Cuba and Hispaniola (MAP 2).

SPECIMENS EXAMINED. **Cuba.** ORIENTE: "Cuba Orientali," 1856–57, *Wright 583* (G, GOET); Monteverde, 1859–60, *Wright 584* (G, GH, GOET); Pinal de Santa Ana, *Eggers 5026* (A). PINAR DEL RÍO: Pan de Guajaibón, *Acuña & Alain 18549, 18550* (HAC), *Alain & Acuña 2999* (US). **Haiti.** SUD: Massif de la Hotte, central group, St. Louis du Sud, Bonnet-Carré, ca. 1150 m. alt., *Ekman H9234* (S).

Margaritaria tetracocca is still a poorly known species, but it appears to be quite distinct from the much more common and more widely distributed *M. scandens*. The absence of a glaucous bloom on the underside of the leaves in *M. tetracocca* is characteristic, although some forms of *M. scandens* also lack this character. However, the stipules of *M. tetracocca* are consistently different in their auriculate base and indurate texture, so even barren specimens can be distinguished from *M. scandens*.

The specimens from Pinar del Río and from Haiti are somewhat divergent from the type collection, and the Haitian plant in particular may — when better known — prove to be subspecifically or even specifically distinct.

5. **Margaritaria hotteana** (Urban & Ekman) Webster, Jour. Arnold Arb. 38: 66. 1957. *Phyllanthus hotteanus* Urban & Ekman, Arkiv Bot. 22A(8): 61. 1929. TYPE: Haiti, *Ekman H8909* (S, holotype; G, isotype). FIGURES 12, 13.

Low, straggling shrub; twigs slender, scabridulous when young, lenticellate in age, some twig tips becoming spinescent. Leaf blades thinly chartaceous, elliptic or oblong to obovate, 1–2.5 cm. long, 0.4–0.8 cm. broad, obtuse or rounded (and sometimes minutely apiculate) at tip, cuneate at base, decurrent on petiole, slightly shiny above, green and paler beneath; veins obscure above, midrib prominently raised beneath, major veins 5 to 10 on a side, veinlet reticulum fine and not prominulous; margins plane or slightly recurved; petioles 1–3 mm. long, adaxially channeled; stipules lanceolate, scarious, pale, mostly deciduous, 0.7–2 mm. long. Staminate flowers 1 to 3 per axil; pedicels slender, 3–6 mm. long;

sepals biseriate, oblong to obovate, 1.3–2 mm. long, 1.0–1.7 mm. broad (outer ones narrower); disc 4-angled, minutely scabridulous, 1.5–2.2 mm. across; stamens 4, free, the filaments 1–1.5 mm. long, the anthers elliptic, 0.5–0.6 mm. long. Pistillate flowers solitary; pedicels subterete, 2–3 mm. long; sepals 4, biseriate, the outer ones ovate, the inner ones oblong-elliptic, 1.7–1.8 mm. long, 1.3–1.7 mm. broad; disc 4-lobed, ca. 1.5 mm. across; ovary of 2 carpels, the styles nearly free, spreading, somewhat dilated, bifid, 0.7–1 mm. long. Fruits not seen.

DISTRIBUTION. Endemic to forests on limestone; southern Haiti (MAP 2).

SPECIMENS EXAMINED. **Haiti.** SUD: Massif de la Hotte, Morne Rochelois, Miragoane, towards Charlier, 14 Aug. 1927, *Ekman H8909* (G, S); Grande-Caïmite, Source-Fantasque, 20 Aug. 1927, *Ekman H8919* (S); St.-Michel de l'Atalaye, Morne la Cidre, limestone crags, ca. 750 m., *Ekman H8364* (S).

As noted by Ekman (ms.), the habit of this species is very similar to that of *Flueggea acidoton*; however, despite the lack of fruits, the floral disc clearly indicates that the plant belongs to *Margaritaria*. The scabridulous twigs suggest an affinity to *M. scandens* and *M. tetracocca*, but it differs from those species in its slender, spinescent branch tips, smaller leaves, and bicarpellate ovary.

6. **Margaritaria luzoniensis** (Merr.) Airy Shaw, Kew Bull. 20: 387. 1966. *Phyllanthus luzoniensis* Merr. Philip. Jour. Sci. Bot. 7: 404. 1912. *Prosorus luzoniensis* (Merr.) Airy Shaw, Kew Bull. 16: 343. 1963. TYPE: Luzon, Pampanga Prov., *Curran FB 17698* (A, lectotype). FIGURE 4.

Tree to ca. 10 meters high; foliage deciduous; twigs subterete, reddish-hirsutulous when young, glabrate in age, lenticellate. Leaf blades thinly chartaceous, elliptic to obovate, (2–)2.5–5 cm. long, 1–2.5 cm. broad, obtuse to rounded at apex, cuneate at base, slightly decurrent on the petiole above, beneath paler and hirsutulous when young (glabrate in age); veins (5 to 8 on a side) and veinlets anastomosing in a prominent reticulum, prominulous especially beneath; margins plane; petiole mostly 2–4 mm. long, slightly laterally flanged but not adaxially channeled; stipules caducous, brownish-scarious, lanceolate, hirtellous, ca. 1–1.5 mm. long. Staminate flowers several per axillary cluster; pedicels 4–6(–8) mm. long, hirsutulous; sepals biseriate, hirsutulous, the outer ones ovate, 1.3–1.6 mm. long, 0.8–1 mm. broad, the inner ones obovate, 1.6–2 mm. long, 1.1–1.5 mm. broad; disc thin, 0.5–0.9 mm. across; stamens 4, the filaments free, becoming 0.8–1.5 mm. long, the anthers elliptic, 0.6–0.7 mm. long. Pistillate flowers solitary; pedicels subterete, hirsutulous, 8–17 mm. long; calyx and ovary not seen in flower. Fruits subglobose, 6–10 mm. in diameter, 3-carpellate, columella more or less persistent; seeds with distinct dark sarcotesta, the endotesta smooth, plano-convex, 4.1–5.1 mm. long, 2.6–3.1 mm. broad.

DISTRIBUTION. Dry forests, lower elevations; endemic to Luzon.

SPECIMENS EXAMINED. **Philippines. Luzon.** BATAAN: Corregidor Is., *Curran FB 13225* (A, US). NUEVA ECIJA: Mt. Umingan, *Ramos & Edaño BS 26282* (US). PAMPANGA: Mt. Arayat, *Curran FB 17698* (A, lectotype). PANGASINAN: Umingan, *Otanes BS 17834* (A, US).

Airy Shaw (1971) has questioned the distinctness of *Margaritaria luzoniensis* from *M. indica* on the basis of certain specimens of the latter that have small fruits. Actually, in the one collection (*Ramos & Edaño BS 26282*) of *M. luzoniensis* with mature fruit, the seeds are larger than those of *M. indica*. A better seed character is provided by the surface of the endotesta, which is smooth in *M. luzoniensis* and at least somewhat (often pronouncedly) rugose in *M. indica*. The small, blunt leaves with non-channeled petiole (FIGURE 4) and reddish pubescence of *M. luzoniensis* make it easily recognizable even in the barren condition, and there appears to be no reason not to give it specific rank.

7. **Margaritaria indica** (Dalz.) Airy Shaw, Kew Bull. 20: 387. 1966. *Prosorus indicus* Dalz. Jour. Bot. Kew Misc. 4: 345. 1852. *Phyllanthus indicus* (Dalz.) Mueller-Arg. Linnaea 32: 52. 1863; in DC. Prodr. 15(2): 417. 1866. TYPE: India, Deccan, *Dalzell s.n.* (K).

Phyllanthus stocksii Mueller-Arg. Linnaea 32: 151. 1863. TYPE: India, *Stocks & Law s.n.* (G).

Calococcus sundaicus Kurz ex Teijsm. & Binn. Nat. Tijdschr. Nederl. Ind. 27: 48. 1864. *Phyllanthus sundaicus* (Kurz) Mueller-Arg. in DC. Prodr. 15(2): 1272. 1866. *Diasperus sundaicus* (Kurz) O. Kuntze, Rev. Gen. Pl. 2: 599. 1891. TYPE: "in freto sundaico," *Teijsmann s.n.* (holotype, presumably BO, *n.v.*; G, isotype).

Phyllanthus indicus f. *vestita* J. J. Sm. Bijdr. Booms. Java 12: 87. 1910. TYPE: Java, G. Watoedodol, *Koorders s.n.* (BO, *n.v.*).

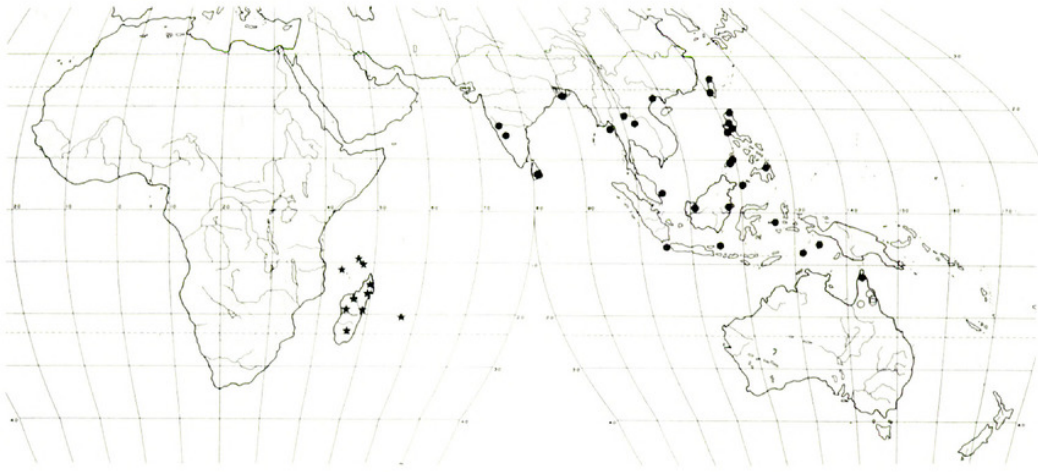
Glabrous trees up to 25 meters high; foliage deciduous; twigs brownish, more or less prominently lenticellate, subcompressed. Leaf blades thinly chartaceous, elliptic to oblong-lanceolate, ca. 5–13 cm. long, 3–6 cm. broad, distinctly and sometimes abruptly acuminate at tip, cuneate to rounded at base and more or less adaxially decurrent on the petiole, usually paler beneath; veins (mostly 8 to 12 on a side) and veinlets prominulous beneath; margins plane or incurved; petiole mostly 5–8 mm. long, adaxially channeled; stipules caducous, brownish-scarious, lanceolate, more or less acuminate, 2.5–4.5 mm. long. Staminate flowers several per axillary cluster; pedicels ca. 4–6 mm. long; sepals 4, biseriate, the outer ones ovate, 1–1.5 mm. long, 0.6–1 mm. broad, the inner ones obovate, 1.3–1.8 mm. long, 1–1.5 mm. broad; disc adnate, smooth or somewhat rugulose, 0.6–1.5 mm. across; stamens 4, the filaments free, becoming 0.7–1.5 mm. long, the anthers elliptic or oblong, 0.6–0.9 mm. long. Pistillate flowers 1 to 3 per axil; pedicels subterete, 8–21 mm. long; sepals 4, biseriate, ovate to oblong, entire, ca. 1.5–2 mm. long; disc entire, adnate, 1.8–2.8 mm. across; ovary almost always of 3 (very rarely 4) car-

pels, the styles free or basally connate, spreading, ca. 1.5–2 mm. long, bifid. Fruits subglobose, scarcely lobed, irregularly dehiscent, (7–)9–12 mm. in diameter, endococci papery; seeds with rather thickish, bluish sarcotesta, the endotesta usually distinctly rugose or furrowed on back, plano-convex, (3.5–)3.9–4.8 mm. long, (2.7–)3–3.7(–4.2) mm. broad.

DISTRIBUTION. Mostly in lowland (below 1000 meters) deciduous or semi-evergreen monsoon forests; India and Ceylon to Thailand, Formosa, Indochina, the Philippines, Indonesia, and Australia (MAP 5). Additional localities in Java are cited by J. J. Smith (1910), and other oriental localities are given by Airy Shaw (1963, 1976).

SPECIMENS EXAMINED. **India.** Kanara, *Talbot 1173* (K). MYSORE: 20 mi. S. of Belgaum, *Ritchie 1343* (GH); Hassan Distr., Yettinahalla, *Saldanha 13263* (K), *Nicolson et al. HFP 80* (MO); Shiradi ghat, *Saldanha 13140* (MO). **Sri Lanka:** Nannapurawa, Moneragala Distr., *Waas 663* (MO). **Burma:** Bassein Distr., Chaungtha Is., *Lace 3034* (K). **Thailand:** Chaiyaphum Distr., *van Beusekom et al. 4207* (K, MO); Lampang, Wang Fen, *Winit 1957* (K); Saraburi, Phu Kae, *Chamroerngsri 2* (K). **Vietnam.** TONKIN: Dam-ha, *Tsang 30219* (A, S); Ha-coi, *Tsang 29583* (A, S). **Malaysia.** PAHANG: Pulau Chibeh, P. Tioman, *Corner SFN 29829* (A). **Indonesia.** SUMATRA: without locality, *Forbes 2733* (GH). JAVA: Semarang Prov., *Koorders 26478* (A); Semarang, Kedoeng djati, *Koorders 25521* (WAG). MOLUCCAS: Soela, P. Mangoli, *Koorders 29901* (A); Tanimbar, Otimmer, *Koorders 24236, 24268* (A). **Philippines.** LUZON: Cagayan Prov., Abulug, *Alejandro FB 27438* (A, US); Prov. Camarines, *Alvarez FB 22655* (A, US). MINDANAO: Agusan subprov., *Miranda FB 22943* (A, US); Butuan subprov., *Weber 1195* (US). PALAWAN: Palawan Is., *Cenabre et al. FB 28004* (A), *Elmer 13132* (GH), *Fénix BS 15589* (A, US), *Natividad 23361* (US); Puerto Princesa, *Cenabre FB 29209, FB 29210* (A); Inahit, *Vidal 1729* (A). SULU: Tawitawi, *Ramos & Edaño BS 44303* (A).

This widespread species has a curiously spotty distribution which perhaps reflects vagaries of collecting. I have not seen any collections from



MAP 5. Distribution of *Margaritaria indica* (solid dots), *M. dubium-traceyi* (open circles), and *M. anomala* (stars; more detailed distribution within Madagascar given in MAP 6).

China, although Tsang's collections from Viet Nam were made only a few miles from the border. Since it has been found in Taiwan (Keng, 1951), it may be expected in Hainan. Keng (1955) suggested that the plant is probably introduced in Taiwan, but this seems rather improbable in view of the fact that it is scarcely, if ever, deliberately cultivated anywhere. Airy Shaw (1963) reported the species from China (Kwantung), Borneo (Sarawak), and the Kangean Islands; and more recently (1971) he has extended the range to New Guinea.

Margaritaria indica is very closely related to the African *M. discoidea*, from which it cannot be surely distinguished except by virtue of the rugose endotesta of the seed. Airy Shaw (1971) notes that some Philippine specimens suggest possible intergradation with *M. luzoniensis*; however, the available sampling of specimens is still far too scanty, and field investigations will be necessary to come to any conclusions about changes in taxonomic status.

8. **Margaritaria cyanosperma** (Gaertner) Airy Shaw, Kew Bull. 20: 387. 1966. *Croton ? cyanospermus* Gaertner, Fruct. Semin. Pl. 2: 120. *pl. 107*. 1791. *Prosorus gaertneri* Thwaites, London Jour. Bot. 8: 272. 1856. *Prosorus cyanospermus* (Gaertner) Thwaites, Enum. Pl. Zeyl. 281. 1861. *Phyllanthus cyanospermus* (Gaertner) Mueller-Arg. Linnaea 32: 51. 1863; in DC. Prodr. 15(2): 416. 1866. TYPE, *n.v.*; neotype: Ceylon, *Thwaites CP 2601* (PDA, holotype, *n.v.*).

Zygospermum zeylanicum Thwaites ex Baillon, Étude Gén. Euphorb. 620. *pl. 27, fig. 11*. 1858. TYPE: Ceylon, *Thwaites* (P, *n.v.*).

Glabrous tree; foliage deciduous; twigs brownish. Leaf blades thinly chartaceous, elliptic, ca. 5–9 cm. long, 2–4 cm. broad, cuspidate-acuminate at tip, cuneate at base; veins (ca. 5 to 10 on a side) and veinlets prominulous; margins plane; petioles 4–8 mm. long, adaxially channeled; stipules deciduous, lanceolate, scarious, acuminate, ca. 3–4 mm. long. Staminate flowers several per cluster; pedicels mostly 8–10 mm. long; sepals 4, biseriate, reticulate veined, the outer ones oblong, ca. 3.5–4 mm. long, 1.4–1.8 mm. broad, the inner ones obovate, 3.5–4 mm. long, 2.2–2.7 mm. broad; disc rather tenuous, 0.8–1 mm. across; stamens 4, the filaments free, 0.5–0.7 mm. long, the anthers linear-oblong, 1.8–2 mm. long. Pistillate flowers solitary; pedicels slender, 15–17 mm. long, 2.2–3 mm. broad; disc adnate and very tenuous (nearly obsolete), ca. 2 mm. across; ovary of 3 carpels, the styles free or nearly so, ca. 0.9–1.3 mm. long, bipartite, tips rather slender. Fruits subglobose, ca. 9–10 mm. in diameter, the columella persistent, slender, 6–6.5 mm. long, the endococci papery; seeds with thickish, dark sarcotesta, the endotesta deeply rugose-furrowed, plano-convex, (3.2–)3.5–4.5 mm. long, 3.5–4.0 mm. broad.

DISTRIBUTION. Endemic to Sri Lanka.

SPECIMENS EXAMINED. **Sri Lanka:** without specific locality, *Thwaites CP 2155*

(A), *CP 2601* (GH, L). Thwaites (1856) cited Ambagamowa and Ratnapoor districts, but the species seems not to have been re-collected in recent times.

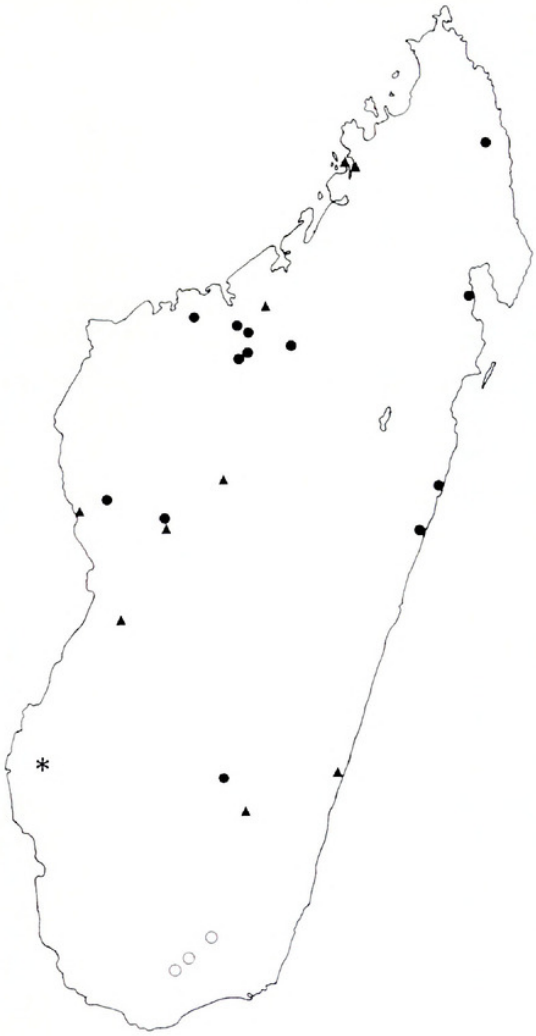
Although the rugose endotesta of the seed suggests an affinity with *Margaritaria indica,* the large staminate flowers set *M. cyanosperma* apart from all of the other species in the genus. Unfortunately, the species remains poorly known, and the typification of its name remains somewhat doubtful. It is impossible to tell from Gaertner's description, based on the fruit alone, which of the two species of *Margaritaria* on Sri Lanka should take the epithet *cyanosperma.* According to Dr. W. Frey, of Universität Tübingen (pers. comm.), the "type material" of Gaertner's is missing and presumed lost. However, since Thwaites (1856) clearly distinguished the two species, I am (in the absence of any contrary evidence) following his usage in assignment of names and am designating the specimen cited by him as neotype.

9. **Margaritaria rhomboidalis** (Baillon) Webster, comb. nov. *Cicca ? rhomboidalis* Baillon, Adansonia I. 2: 51. 1861. *Phyllanthus ? rhomboidalis* (Baillon) Mueller-Arg. Linnaea 32: 52. 1863, in DC. Prodr. 15(2): 417. 1866; Leandri, Not. Syst. Paris 6: 199. *fig. V.* 1938. Fl. Madagascar 111(1): 97. *fig. XV, 6–11.* 1958. TYPE: Madagascar, Ambongo, *Perville 664* (P, lectotype). FIGURE 3.

Shrub or small tree ca. 3–8 meters high; twigs pale, subterete; foliage deciduous. Leaf blades chartaceous to subcoriaceous, elliptic to obovate, ca. 2–5(–7) cm. long, 1.5–3 cm. broad, mostly obtuse to acute at tip, cuneate and often inequilateral at base, usually greenish on both sides (sometimes more or less glaucous beneath); veins (ca. 7 to 12 on a side) and veinlets conspicuous, prominulous especially beneath; margins plane or slightly reflexed; petioles 3–7(–13) mm. long, plane to adaxially channeled; stipules caducous, brownish, scarious, oblong-lanceolate, 1.2–4 mm. long. Staminate flowers several per axillary cluster; pedicels 3–5 mm. long; sepals 4, biseriate, ovate, entire, 1.8–2.5 mm. long, 1.3–1.7 mm. broad; disc obscure or absent; stamens 4, the filaments free, 0.5–1.2 mm. long, the anthers oblong, (0.8–)1–1.4 mm. long. Pistillate flowers solitary; pedicels compressed-angled, becoming 4–12(–20) mm. long; sepals 4, biseriate, ovate, entire, 2–3.2 mm. long; disc obscure or absent; ovary of 2 or 3 carpels, the styles usually basally connate, column 0.8–1.2 mm. high, the tips bifid and recurving, 0.5–1 mm. long. Capsules subglobose, irregularly dehiscent, mostly 8.5–10(–12) mm. in diameter, the endococci thin and papery, the columella more or less persistent, ca. 4–5 mm. long; seeds with thickish sarcotesta (whitish on drying), the endotesta more or less ribbed or rugose, 2.8–4.5 mm. long, the hilum varying in position from adaxial to abaxial, ca. 0.5–0.8 mm. across.

DISTRIBUTION. Endemic to Madagascar, mostly in deciduous forest or scrub at 300 meters or below (MAP 6).

SPECIMENS EXAMINED. **Madagascar.** FIANARANTSOA: bassin de la Menarahaka,



MAP 6. Distribution of *Margaritaria* in Madagascar. Solid dots, *M. anomala*; open circles, *M. decaryana*; triangles, *M. rhomboidalis*; asterisk, *M. hispidula*.

à l'est d'Ihosy aux environs d'Ambinda, *Capuron 11621, 11623* (P); Ankirihitra, près du mont Tsitondroina, *Perrier de la Bâthie 1346* (P); forêt de Belambo, nord de Marohala, *SF 16238* (P). MAJUNGA: forêt de Tsiampihy [Tsiempihy], *Leandri, Capuron, & Razafindrakoto 2195* (P); l'Antsingy, vers Ambodiriana, *Leandri, Capuron, & Razafindrakoto 2338* (P), *Leandri & Saboureau 2720, 3069* (P). TULEAR: Tsingy du Bemaraha, *Leandri 948, 954* (P).

This species, which appears to be rather common and widespread in Madagascar, resembles *Margaritaria indica* in the rugose endotesta of the seed, but differs in the distinctly prominulous leaf venation, obscure staminate disc, larger anthers, and connate styles.

10. **Margaritaria anomala** (Baillon) Fosberg, Kew Bull. 33: 185. 1978.

Cicca anomala Baillon, Étude Gén. Euphorb. 619. 1858. *Phyllanthus anomalus* (Baillon) Mueller-Arg. Linnaea **32**: 52. 1863; in DC. Prodr. **15**(2): 418. 1866. TYPE: "Madagascar," *du Petit-Thouars s.n.* (P, holotype).

Flueggea major Baillon, Étude Gén. Euphorb. 593. 1858; Adansonia I. **2**: 42. 1861. *Phyllanthus hysteranthus* Mueller-Arg. Linnaea **32**: 52. 1863 (*nomen superfl.*). TYPE: Mauritius, *Bouton s.n.* (P, holotype).

Flueggea ? eglandulosa Baillon, Étude Gén. Euphorb. 593. 1858. *Phyllanthus erythroxyloides* Mueller-Arg. in DC. Prodr. **15**(2): 418. 1866; Leandri, Fl. Madagascar **111**(1): 94. *fig. XV, 1–5.* 1958. *Phyllanthus eglandulosus* (Baillon) Leandri, Catal. Pl. Madagascar, Euphorb. 23. 1935. *Phyllanthus anomalus* subsp. *erythroxyloides* (Mueller-Arg.) Leandri, Not. Syst. Paris **6**: 191. 1938. TYPE: Madagascar, Ambongo, *Perville 662* (P, holotype).

Phyllanthus cheloniphorbe Hutchinson, Kew Bull. **1918**: 204. 1918. *Margaritaria anomala* var. *cheloniphorbe* (Hutch.) Fosberg, Kew Bull. **33**: 185. 1978. TYPE: Aldabra, *Abbott s.n.* (K, lectotype; US, isotype).

Glabrous shrub or small tree 1–6 meters high; bark scaly or in strips; foliage partly or wholly deciduous; twigs brownish, smooth, subterete or compressed. Leaf blades thinly chartaceous, elliptic to obovate or spathulate, (2–)3–6(–10) cm. long, 1.5–4(–6) cm. broad, rounded or emarginate to obtuse or bluntly cuspidate at tip, cuneate at base (more or less decurrent on petiole), usually paler (sometimes glaucous) beneath; veins and veinlets obscure to prominent but veinlet reticulum usually not prominulous beneath; leaf margins more or less incurved to revolute; petiole 2–6 (–10) mm. long, plane or adaxially somewhat channeled; stipules caducous, brownish-scarious, oblong-lanceolate, acuminate or blunt and apiculate, 2.5–5 mm. long. Staminate flowers several per axillary cluster; pedicels mostly 3–5 mm. long; sepals 4, biseriate, usually the outer ones 1.2–2 mm. long, 1–1.3 mm. broad, ovate, entire, the inner ones larger, 1.5–2.3 mm. long, 1.3–2 mm. broad; disc adnate, smooth or rugulose, mostly 0.5–1 mm. across; stamens 4, the filaments free, becoming 1–1.5 mm. long, the anthers 0.8–1.4 mm. long. Pistillate flowers solitary or less often paired at proximal axils of annual increment of growth; pedicels more or less compressed and angled, 5–15(–20) mm. long; sepals 4, biseriate, ovate to oblong, entire, 1.5–2.5 mm. long; disc entire, adnate, 1–2.2 mm. across; ovary of 2 (very rarely 3) carpels, the styles free or basally coherent, ca. 0.8–1.5 mm. long, bifid, with the branches more or less sharply reflexed. Fruits subglobose or laterally compressed, indehiscent or irregularly dehiscent, 6–8 mm. in diameter, endococci not developed (wall layers not separating), columella not persistent; seed with thin, bluish sarcotesta, the endotesta smooth (rarely somewhat rugose), more or less planoconvex or trigonous-lenticular, (2.7–)3.5–5.5 mm. long, the hilum adaxial, circular, sub-basal, 0.9–1.2 mm. across.

DISTRIBUTION. Scrub or seasonal forests below 1000 meters; Madagascar, Aldabra, Astove, and Mauritius (MAPS 5, 6). Reported from Cosmoledo by Fosberg (1978).

SPECIMENS EXAMINED. **Aldabra Islands.** Without further locality, 1892, *Abbott s.n.* (US). ÎLE MICHEL: scrub on sandy champignon, *Fosberg 49357* (DAV). MIDDLE ISLAND: scrub, moderately rough limestone, *Fosberg 49582, 49666, 49671* (DAV). SOUTH ISLAND: scrub on flat limestone, *Fosberg 48848, 48961, 49029, 49309, 49401* (DAV). **Astove Island:** Grand Anse, scrub on moderately

rough limestone, *Fosberg 49715, 49736* (DAV). **Comoro Islands.** Without further locality, *Boivin s.n.* (K, P). GRANDE COMORE: Moroni, *d'Alleizette s.n.* (L). **Madagascar.** DIEGO SUAREZ: forêt entre Ambondsofe et Ambodimagoro, plateaux calcaires, 250 m., *Humbert 18993* (P). FIANARANTSOA: vallée d'Ihosy, 800–1000 m., rochers siliceux, *Humbert 2998, 2998ter* (P). MAJUNGA: Berizoka, *Perrier de la Bâthie 339* (P); collines seches, Maevatanana, *Perrier de la Bâthie 339bis* (P); vallée de Menavava, *Perrier de la Bâthie 339ter* (P); bois secs, Bemarivo, *Perrier de la Bâthie 9527* (P); vallée de la Betsiboka à Marovoay, 50 m., bois du terrains arenacés, *Humbert & Perrier de la Bâthie 2353* (P); Ambongo, *Perrier de la Bâthie 662* (P); Ankarafantsika, Tsaramandroso, *Ramamoujisoa 2029* (P); Ankaraobato, Distr. Mitsinjo, *SF 5386* (P); station forestière de Marohogo, Majunga, *SF 7967* (P); forêt de Morarano, Marohogo, *SF 8069* (P); forêt Tsimembo,, Antsalova, *SF 8248* (P). TAMATAVE: côte littoral est, Baie d'Antongil, *d'Alleizette s.n.* (L); Andevoranto, Ambila-Lemaitso, *Ramasokoto 1524* (P); Tampina, forêt littorale, *Perrier de la Bâthie 13318* (P). TULEAR: Mandena-Ft. Dauphin, *SF 6609* (P). **Mauritius:** without further locality, *Ayers s.n.* (K), *Blackburn s.n.* (K), *Boivin s.n.* (P), *Bouton s.n.* (A, K), *Commerson s.n.* (P), *Duljeet MAU 11640, MAU 16638* (MAU), *Grey s.n.* (K); lisière des bois au Pouce et dans l'Anse Courtois, *Boivin s.n.* (P); Mt. Corps de Grade, *Friedmann 2620* (P); *Coode et al. 5021, 5022* (K); Montagne Ory, *Friedmann & Lorence 2626bis* (P); Petite Rivière, dry forest, *Herb. Royal Gardens Pamplemousse 139* (K); Plaine des Roches, *Julien MAU 14164* (MAU); Ferme Cascade, *Vaughan MAU 1611* (MAU).

Hooker (1887) treated *Margaritaria anomala* as a synonym of *M. indica*, apparently on the basis of some Wallich specimens misidentified by Mueller (1866). However, although staminate specimens are difficult to distinguish, the indehiscent, 2-carpellate fruits of *M. anomala* are very different from the dehiscent, 3-carpellate ones of *M. indica*.

Leandri (1958) has attempted to separate *Phyllanthus anomalus* from *P. erythroxyloides* on the basis of fruit and leaf shape. However, as noted by Coode (1978), the type specimen of Petit-Thouars was probably collected on Mauritius rather than on Madagascar. There is unfortunately some uncertainty in applying the name *Phyllanthus erythroxyloides*, since Baillon's allusion to the obsolete floral disc in his brief description (of *Flueggea eglandulosa*) would suggest that he might have had material of *Margaritaria rhomboidalis*. However, the leaves of the type collection (*Pervillé 662*) lack the prominulous venation characteristic of *M. rhomboidalis*, and the pistillate flower does have a disc. At any rate, the Mauritius and Madagascar populations clearly seem to be conspecific, and the name *M. anomala* applicable to both.

Fosberg (1978) has separated the populations from Aldabra and adjacent islands as var. *cheloniphorbe*. However, he does not cite any diagnostic characters, and although the Aldabra specimens do tend to have thicker and more rounded leaves, I can find no significant and consistent differences in leaves, flowers, or fruits between the plants of Aldabra and those of Mauritius and Madagascar.

11. **Margaritaria dubium-traceyi** Airy Shaw & Hyland, Kew Bull. 31: 357. *fig. 1.* 1976. TYPE: Queensland, *Hyland 7937* (K, holotype, *n.v.*).

Glabrous shrub or tree to 5 meters high; twigs terete, grayish, with scattered lenticels. Leaf blades chartaceous to subcoriaceous, ovate to elliptic-oblong, 4–6(–9) cm. long, 2–3.5(–5.5) cm. broad, emarginate, rounded or obtuse (rarely minutely apiculate) at tip, cuneate at base (distinctly decurrent on petiole), olivaceous; veins (ca. 6 to 9 on a side) and veinlets prominulous on both sides in a prominent reticulum; margins plane; petiole distinctly laterally carinate or adaxially channeled; stipules caducous. Staminate flowers several per axillary cluster; pedicels capillary, 10–13 mm. long; sepals 4, biseriate, elliptic to obovate, subequal, the outer ones ca. 1.2–1.3 mm. long, 0.8 mm. broad, the inner ones 1.5–1.8 mm. long, 0.8–1 mm. broad; disc angular, ca. 1 mm. across; stamens 4, the filaments united in pairs at base, 1.5–2.5 mm. long, the anthers elliptic, 0.3–0.5 mm. long. Pistillate flowers (not seen, descr. ex Airy Shaw) 1 or 2 per axil; pedicels slender, subterete or angled, 4–8 mm. long; sepals 4, biseriate, ca. 1 mm. long; ovary of 2 carpels, the styles basally connate, ca. 1 mm. long, bifid, branches spreading. Fruits subglobose or elliptic, more or less indehiscent (tardily splitting from apex), 5–7 mm. in diameter, endococci corneous (not tenuous and hyaline); seeds with bluish sarcotesta very tenuous except at base, the endotesta more or less ridged or grooved on back, wedge shaped, ca. 3.1–3.7 mm. long and 2.1–2.9 mm. across the back, the hilum basal, 0.2–0.3 mm. across.

DISTRIBUTION. Seasonal deciduous or eucalypt forests, below 600 meters; northern Queensland.

SPECIMENS EXAMINED. **Australia. Queensland.** BURKE DISTR.: Haydon Creek, Croydon–Normanton Road, alt. 60 m., *Hyland 5121* (DAV). COOK DISTR.: Springmount Road, 17°10′S, 145°15′E, alt. 550 m., *Hyland 5594* (K); betw. Chillagoe and Mungana, alt. 390 m., *Hyland 5838* (DAV); S. Palmer River cachement, 16°15′S, 144°40′E, alt. 480 m., *Hyland 5895* (DAV). Additional Queensland localities, cited by Airy Shaw (1976), have been indicated on MAP 5.

The relationships of *Margaritaria dubium-traceyi* are uncertain. The rugose endotesta of the seed suggests a possible affinity to *M. indica*, although the fruit is quite different and more similar to that of *M. anomala*. Possibly *M. dubium-traceyi* is a specialized derivative of *M. indica*, comparable to the vegetatively somewhat similar *M. luzoniensis*, and the resemblances in fruits with *M. anomala* are due to convergence.

12. **Margaritaria hispidula** Webster, sp. nov. FIGURES 2, 8.

Ab aliis speciebus Madagascariensibus differt foliis venis prominulis, infra hispidulis, capsulis mox dehiscentibus.

Tree 8 meters high; twigs subterete, whitish-hispidulous at tips, glabrate below, not prominently lenticellate. Leaf blades subcoriaceous,

shiny and subglabrous above, copiously hispidulous-hirsutulous beneath, ovate or elliptic to obovate, obtuse or subacute at tip, cuneate to rounded at base, ca. 2.5–4.5 cm. long, 1–2.5 cm. broad; major veins (6 to 8 on a side) and veinlet reticulum distinctly prominulous on both sides; margins plane or recurved; petioles 3–6 mm. long, copiously hispidulous-hirsutulous, not adaxially channeled; stipules oblong-lanceolate, scarious, pale brownish, 2.5–3.5 mm. long. Flowers not seen. Fruiting pedicels subterete, 9–11 mm. long, hispidulous; carpels 3, the styles (on immature fruit) ca. 2 mm. long, united about halfway into a column; fruits subglobose, 6–7 mm. in diameter, hispidulous, tardily dehiscent, the endocarp tough, 0.2 mm. thick, not fragile and papery; mature seeds not seen.

DISTRIBUTION. Known only from the type collection (MAP 6).

SPECIMEN EXAMINED. **Madagascar.** TULEAR: Befandrianda-Sud, neben Regenteich, 150 m. alt., *P. Otto Appert 107* (K, holotype).

It is regrettable that this species has to be proposed as new on the basis of such imperfect material. Vegetatively, it is similar to *Margaritaria rhomboidalis*, but its very different fruits suggest a closer relationship to *M. anomala* or *M. dubium-traceyi*. Although we cannot be certain of its affinities until better material is collected, I feel sure that the Appert collection represents a species distinct from the known Madagascan taxa.

13. **Margaritaria decaryana** (Leandri) Webster, comb. nov. *Phyllanthus decaryanus* Leandri, Not. Syst. Paris 6: 198. 1938; Fl. Madagascar 111(1): 98. *fig. 18, 1–5*. 1958. TYPE: Madagascar, Imangory, *Decary 8937* (P).

Phyllanthus decaryanus var. *manambia* Leandri, Mém. Inst. Sci. Madagascar 8B: 228. *fig. 6, 1–5*. 1957. TYPE: Madagascar, between Tsivory and Imanombo, *Capuron 8543* (P, lectotype).

Glabrous shrub or small tree; twigs subterete, smooth, grayish or brownish; foliage deciduous. Leaf blades membranous, broadly elliptic or suborbicular to spathulate or obcordate, 1.0–1.8 cm. long, rounded to emarginate at tip, cuneate at base, green on both sides (somewhat paler beneath); major veins mostly 3 or 4 on each side, veinlet reticulum somewhat prominulous beneath; margins plane; petioles ca. 3–5 mm. long, adaxially channeled; stipules persistent or caducous, oblong, scarious, acute and more or less denticulate-fimbriate distally, 1.0–2.5 mm. long. Staminate flowers several per cluster; pedicels slender, 4–6 mm. long; sepals subequal, becoming reflexed, elliptic or ovate, obtuse, entire or obscurely denticulate at apex, 1.6–2.1 mm. long, 1.1–1.8 mm. broad, disc entire, thin, ca. 0.7–1 mm. across; stamens 4, the filaments connate below, mostly 1.5–2.2 mm. long (staminal column 0.8–1.5 mm. long), the anthers oblong, 0.8–1.1 mm. long. Pistillate flowers solitary or paired; pedicels angled-compressed, ca. 3–4 mm. long; sepals 4, subequal, 2–2.5 mm. long, 1.5–2.5 mm. broad; disc thin, entire, ca. 1.5 mm. across; ovary

of 2 or 3 carpels, the styles more or less erect, 1.5–2 mm. long, basally connate, distally bifid. Fruits not seen.

DISTRIBUTION. Xeric scrub; southern Madagascar (MAP 6).

SPECIMENS EXAMINED. **Madagascar.** TULEAR: restes de bush, entre Tsivory et Imanombo, *Capuron 8543, 8543bis* (P); environs d'Ampandrandava, entre Bekily et Tsivory, *Seyrig 242B* (P).

If I am correct in associating Leandri's var. *manambia* with his *Phyllanthus decaryanus*, then the species is well characterized by its monadelphous androecium and small suborbicular leaves. Leandri refers to the species and variety as each having 2-locular ovaries, but actually they appear to be 2-locular in *Capuron 8543bis* and 3-locular in *Seyrig 242B*.

14. **Margaritaria obovata** (Baillon) Webster, comb. nov. *Flueggea obovata* Baillon, Adansonia I. 2: 41. 1861 (non *Securinega obovata* Mueller-Arg. 1866). *Securinega bailloniana* Mueller-Arg. in DC. Prodr. 15(2): 451. 1866. *Flueggea bailloniana* (Mueller-Arg.) Pax, Bot. Jahrb. 19: 76. 1894. TYPE: Zanzibar, *Boivin s.n.* (P, holotype). FIGURES 9, 10.

Margaritaria discoidea var. *triplosphaera* Radcliffe-Smith, Kew Bull. **30:** 680. 1976. TYPE: Tanzania, Songea, *Milne-Redhead & Taylor 8373* (K, holotype, *n.v.*).

Shrub or tree 2–10 meters high; branches subterete, reddish- or brownish-hirtellous at growing tips, glabrate and grayish in age; foliage usually deciduous. Leaves chartaceous; blades mostly obovate or spathulate, (1–)2–4(–5) cm. long, 1–3 cm. broad, usually rounded or very obtuse at tip, cuneate at base, above smooth, beneath more or less glaucous and hirtellous especially along midrib; major veins mostly 7 to 12 on a side, raised beneath, veinlet reticulum more or less prominulous; margins recurved or narrowly revolute; petioles usually hirsutulous, not adaxially channeled, 2–4(–5.5) mm. long; stipules caducous, lanceolate, acuminate, ca. 2–3.5 mm. long. Staminate flowers several per axil; pedicels glabrous, 3–5 mm. long; sepals biseriate, the outer ones oblong, 1.5–2 mm. long, 0.7–1 mm. broad, the inner ones broadly obovate, (1.5–)2–2.5 mm. long, 1.2–1.6 mm. broad; disc 0.5–1 mm. across; stamens 4, the filaments becoming 1.3–1.8 mm. long, the anthers linear-oblong, (0.6–)0.8–1 mm. long. Pistillate flowers solitary or paired; pedicels often hirsutulous, mostly 2.5–6 mm. long in fruit; sepals 4, subequal, oblong, hirsutulous on back, 1.6–2.5 mm. long, 1.3–2 mm. broad; disc thin, 1.7–2.0 mm. across; ovary deeply trilobed, hirsutulous; carpels 2 (22 percent) or 3 (78 percent), very rarely 4, the styles free or nearly so, spreading, bifid to bipartite, 1.2–1.5 mm. long. Capsules deeply 2- or 3-lobed (most often only 2 carpels well developed), mostly 10–12 mm. in diameter, the cocci subspheroidal, usually hirsutulous, the endocarp hyaline-papery; endotesta of seed plano-convex, smooth or grooved on back, 3.8–4.5 mm. long.

DISTRIBUTION. Scrubland, deciduous forest, or savanna woodland, sea level to ca. 1000 meters; Burundi and Kenya south to Mozambique. Radcliffe-Smith (1976) cites a large number of additional localities, including records from Zaire and Zambia (MAP 4).

SPECIMENS EXAMINED. **Burundi.** BUBANZA: colline Muzinda, 900 m., *Lewalle 1240* (MO); Randa, savane boisée, 900 m., *Lewalle 2635* (NY). BURURI: Mutambara, forêt claire, 1000 m., *Reekmans 1077* (MO); Rumone, forêt claire sur rochers, 900 m., *Lewalle 1604* (MO). **Kenya.** COAST: Kilifi, Sokoke, *Gisau SOK6* (PRE), *SOK11* (K, PRE). **Malawi.** NORTHERN: Karong Distr., 2 mi. N. of Chilumba in Vinthukhutu Forest Reserve, *Brachystegia* woodland, 1800 ft., *Pawek 12064* (DAV). **Tanzania.** COAST: Pande Hill, 80 km. WNW. of Dar-es-Salaam, 250 ft., wooded grassland, *Harris, Tadros, & Mwasumbi BJH 3616* (MO); Umbungo, scrubland, 50 m., *Mwasumbi LBM 10477* (MO); Kisarawe Distr., *Semsei 3682* (PRE); 21 mi. S. of Dar-es-Salaam on Kilwa Rd., 150 m., *Harris & Rodgers BJH 3970* (MO). MOROGORO: Kilosa, *Semsei 3332* (PRE). NORTHERN: probably from Ukerewe Is., *Father Conrads 6035* (PRE). SOUTHERN HIGHLANDS: Kyimbila Distr., *Stolz 1744 (ex p.)* (A, MO, P), *1771* (A, GH, MO, NY, P, PRE). TANGA: Korogwe Distr., Kwamarukanga, *Shabani 57* (PRE); Mkono, 30 km. E. of Handeni, 518 m., *Archbold 1728* (MO). ZANZIBAR: *Sacleux* (P); Kidichi, 300 ft., *Faulkner 2751* (NY).

This distinctive species, which is widespread in east Africa, is sympatric with *Margaritaria discoidea* over essentially all of its range and has often been confounded with it, although Pax clearly distinguished the two in 1895 (under the names *Flueggea bailloniana* and *F. nitida*). Radcliffe-Smith (1976) provides thorough documentation of its distribution and discusses its relationship with *M. discoidea*, but conservatively treats it as a variety. However, *M. obovata* is clearly distinguished by the deeply lobed fruit (FIGURE 9), the usually distinctive pubescence (on fruits as well as leaves), and leaves with blades that are not decurrent on the petiole as adaxial flanges (a very useful character pointed out by Radcliffe-Smith). In this genus where distinguishing characters are difficult to find, *M. obovata* is much more clearly marked than most taxa, and I believe that it deserves full specific status.

DOUBTFUL AND EXCLUDED TAXA

Margaritaria oppositifolia L. in Alm, Pl. Surinam. 16. 1775, *nomen illegit.* = Combretaceae (Mueller-Arg. in DC. Prodr. **15**(2): 414. 1866).

Phyllanthus ankarana Leandri, Bull. Soc. Bot. France **81**: 452. 1934. TYPE: Madagascar, Ankara, *Perrier de la Bâthie 1174* (P, *n.v.*). Although Leandri referred this species to *Phyllanthus* section *Prosorus*, the staminate disc of separate segments is not correct for *Margaritaria*. In the later treatment by Leandri (Fl. Madagascar **111**(1): 102. *fig. XVI, 4, 5.* 1958), it is clear that the plant is a true *Phyllanthus*, neither of sect. *Cicca* nor of *Margaritaria*.

Phyllanthus flacourtioides Hutch. Kew Bull. **1915**: 48. 1915. SYNTYPES: Mozambique, Lourenço Marques, *Schlechter 11598, 11634* (K, *n.v.*). Hutchinson related his species to *Margaritaria discoidea*, and his description suggests that it may be a form of *M. discoidea* subsp. *nitida*. However, if

Hutchinson's description of the staminate specimen is correct, it cannot be a *Margaritaria*.

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