A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS *

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With five plates

Sect. 18. Orbicularia (Baill.) Griseb. Fl. Br. W. Ind. 34. 1859.

Dimorphocladium Britton, ibid. 74.

Shrubs with phyllanthoid branching, axes smooth and glabrous; leaves with mesophyllar sclereids, mostly coriaceous, stipules (at least proximal ones) mostly persistent. Monoecious; cymes male and bisexual, female flowers usually only one per cyme. Male flower: calyx-lobes 6 (rarely 5); disk-segments free or coalescent; stamens 3–7, filaments united entirely or below into a column; pollen grains areolate. Female flower: calyx-lobes 6 (rarely 5); disk tenuous to rather massive; ovary sessile or slightly stipitate; styles free or connate below into a column, the free ends bifid, style-branches often revolute at the tips. Capsule oblate, veins conspicuous or obscure; seeds trigonous, verruculose.

TYPE SPECIES: Orbicularia phyllanthoides Baill. [= Phyllanthus orbicularis HBK.]

Although a well-marked and apparently monophyletic group, which here is given essentially the same circumscription as that of Carabia (Ecol. Mon. 15: 335. 1945), sect. Orbicularia is rather difficult to characterize as distinct from neighboring sections in subg. Xylophylla. The most closely related section, from which sect. Orbicularia has probably been derived, is sect. Williamia. The species of the latter with sclerified "leaves (subsect. Incrustati) can be distinguished from the present group only by their incrustate axes and lacerate style-tips.

After a prolonged study which has been pursued intermittently over a period of several years, the following treatment of sect. Orbicularia is presented with some diffidence. Despite personal field observations in Cuba in 1951 and 1953 and the analysis of a considerable number of herbarium specimens, a definitive resolution of the taxonomic problems in the group has not been achieved. Field studies have been of value in demonstrating (to the author's satisfaction, at least) that some of the confusion in the literature is traceable to the striking differences in leaf form brought about by different ontogenetic changes and/or responses to different ecological situations. Thus it appears that the very glossy and

* Continued from volume XXXIX, p. 100.
foveolate leaf on which *P. foveolatus* was described is only the older, more coriaceous one of *P. myrtilloides* ssp. *erythrinus*; and the convex, very glossy leaf which supposedly characterizes *P. coelophyllus* is merely the kind of leaf developed by *P. baracoensis* in drier situations. However, a much more serious difficulty to a satisfactory classification in the section is the extreme range of variability of some species, particularly *P. myrtilloides* and *P. orbicularis*. It is also possible that in certain instances hybridization has further complicated the picture by giving rise to anomalous specimens which appear to transgress the rather indistinct specific lines. It would be extremely difficult to account for the several peculiar forms from the Sierra de Nipe (described by Urban as species) except on the supposition that they represent the results of crosses between *P. chamaecristoides* and *P. phlebocarpus*. Finally, it must be remarked that Urban's usually sound taxonomic judgment failed him when treating sect. *Orbicularia*, for he described numbers of "paper species" (such as *P. breviramis, P. cardiophyllus*, and *P. melanodiscus*) which cannot be retained at any taxonomic rank.

In attempting to formulate a usable and objective classification of sect. *Orbicularia*, it has been necessary to abandon, in part, a purely morphological standard for delimitation of taxa and to rely heavily on the principle of geographical replacement as formulated by Huxley (New Systematics 36. 1940) and elucidated by Van Steenis (Fl. Mál. ser. I. 5(3): cxcv–cxcvi. 1957). The result is that, whereas Alain in the "Flora de Cuba" (1953) recognized 19 Cuban species referable to sect. *Orbicularia*, only 7 are accepted in the present treatment. It is realized that this may

appear excessively radical especially since it leads to some apparent inconsistencies, but nevertheless it seems the closest approximation to the facts of nature that can be devised at this time. It is doubtful that the accumulation of additional material will bring any improvement as long as it can be analyzed only by orthodox herbarium methods; a completely satisfactory classification of the section must surely await an extensive population analysis with emphasis on cytological methods.

### KEY TO THE SPECIES

1. Leaves spatulate, acute at the base, rigidly coriaceous, the margin neither reflexed nor revolute.
   2. Stipules dimorphic; leaf-blades of main stem 2–4 cm. long; branchlets 8–10 cm. long. .................. 58. *P. formosus*
   2. Stipules subequal; leaf-blades of main stem, if unreduced, not over 1.5 cm. long; branchlets at most 5 cm. long.
      3. Pedicel of female flower mostly over 10 mm. long; anthers sessile or nearly so atop the column; calyx bright pink or purplish. .......................................................... 59. *P. comosus*
      3. Pedicel of female flower less than 5 mm. long; filaments united about half-way, the anthers long-stipitate; calyx whitish or faintly pinkish-tinged. .......................................................... 60. *P. orbicularis*

1. Leaves, if spatulate, not rigidly coriaceous nor with plane margins.
2. Stamens mostly 5–7 (rarely 4, very rarely 3); leaves not all expanding with the flowers, not prominently reticulate on both sides with raised veins.
3. Styles usually more than 1 mm. long, united into a column mostly 0.5 mm. high or more.
   4. Pedicel of female flower mostly more than 3 mm. long (if exactly 3 then anthers stipitate and cataphylls deciduous). .................. 61. *P. myrtilloides*
   4. Pedicel of female flower mostly less than 3 mm. long (rarely to 3.5 mm.).
      5. Filaments of stamens mostly 1.5–2.5 mm. high, united in the lower half; branchlets mostly with less than 10 elliptic to orbicular leaves; cataphylls persistent. 60. *P. orbicularis*
      5. Filaments of stamens not over 1 mm. high, completely united or nearly so; branchlets mostly with 15–45 oblong to obovate, often falcate, leaves; cataphylls deciduous. .......................................................... 62. *P. chamaecristoides*

3. Styles free or barely united at base, mostly less than 1 mm. long.
4. Cataphylls subpersistent; branchlets 3–6 cm. long; leaves with petiole less than 1 mm. long, blade obovate or obcuneate, 3–7 mm. long, prominently apiculate; outer calyx-lobes (of both sexes) narrowly oblong, mostly less than 1 mm. broad. 63. *P. scopulorum*
4. Cataphylls deciduous; branchlets mostly 6–12 cm. long; leaves with petiole 1–2.5 mm. long, blade broadly elliptic to orbicular, mostly 10–20 mm. long, at most obscurely apiculate; calyx-lobes subequal, the outer 1 mm. broad or more. .......................................................... 64. *P. nummularioides*

2. Stamens mostly 3 (rarely 2 or 4); leaves and flowers expanding together,
leaf-blades with a prominent raised reticulum on both sides; styles free or nearly so, spreading, less than 1 mm. long. P. phlebocarpus


Low shrub (4–6 cm. high ex Shafer), sparsely branching; main stems terete, stout (c. 5 mm. thick), more or less incrusted by the persistent stipules, foliage clustered at top. Leaves of main stems (i.e., those subtending branchlets) apparently not reduced to cataphylls: stipules blackish, indurate, acicular-lanceolate, 8–11 mm. long, attenuate-acuminate, the thin scarious lacerate margins more or less deciduous. Leaf-blades narrowed to an ill-defined petiolar base c. 4–7 mm. long, rigidly coriaceous, spathulate, 20–40 mm. long, 6–9 mm. broad, rounded and marginate at the tip (apiculum of young leaf early deciduous), acute at the base; above olivaceous, sublucid, smooth; minutely foveolate. The impressed midrib distinct, the lateral veins (c. 10–12 on a side) less prominent; beneath paler, midrib strongly raised proximally, lateral veins obscure; margins differentiated beneath, thin and acute, plane. Deciduous branchlets spreading to erect, 8–10 cm. long, 0.8–1 mm. thick, olivaceous, densely papillate-scabridulous, terete below, somewhat compressed above, with up to 23 leaves; first internode 8–13 mm. long, median internodes 3–5 mm. long. Leaves: stipules persistent, mostly 3.5–7 mm. long, midrib portions becoming blackish and indurate, strikingly dimorphic: one of each pair oblong-lanceolate, abruptly acuminate, with broad scarious conspicuously lacerate margins, the other narrowly linear-lanceolate, attenuate-acuminate, with very narrow entire scarious margins. Petiole 1 mm. long or less. Leaf-blades as on main stems but much smaller: asymmetrically obovate or broadly oblong, 6–11 mm. long, 3.5–5 mm. broad.

Male flower [not seen, description ex Urban]: Calyx-lobes 5, ovate, reddish. Stamens 4; filaments (in bud) apparently connate; anthers free, connective broad, anther-sacs discrete, dehiscing longitudinally.

Female flowers and fruits unknown.

Type: Cuba, Oriente, trail from Camp La Barga to Camp San Benito, damp thickets, alt. 450–900 m., 22–26 Feb. 1910, Shafer 4102 (NY, LECTOTYPE). The original holotype in Herb. Krug & Urban (B) presumably has been destroyed.

Distribution: known only from the type collection (MAP XXVIII).

Although still imperfectly known, P. formosus is obviously a distinctive and isolated species on the basis of its vegetative characteristics, particularly the large unreduced leaves of the primary axes and the dimorphic stipules. Technically, the branching of the species could scarcely be called phyllanthoid in view of the apparent failure of the leaves on the main axes to become reduced to cataphylls. However, it is possible that such
Habit of *Phyllanthus formosus* Urb. (Shafer 4102 [NY]).
reduction may be found to occur when additional specimens are collected. Furthermore, since the branchlets are deciduous and similar to those of *P. comosus* and since the reduction of leaves to cataphylls is often very tardy in that species, it appears that in *P. formosus* true phyllanthoid branching occurs but is masked by the reversion of cataphylls to expanded leaves.

The rigid spathulate leaves of *P. formosus* are so similar to those of *P. comosus* that the two species must be rather closely related, although when better material of *P. formosus* is available there may prove to be important distinctions in the reproductive parts. The proposal by Britton to erect a separate genus *Dimorphocladium* for *P. formosus* is quite without merit. The description of this genus was occasioned mainly by the fact that Britton failed to realize that the distinction between permanent axes and deciduous branchlets, which he noticed in *P. formosus*, also occurred in many other species of *Phyllanthus*.

   (PLATE XXIX, figs. A–B).


Glabrous diffusely branching shrub c. 0.5–2 m. high, with short leafy branchlets often clustered at branch-tips; branches at first smooth, angular, reddish-brown, waxy, becoming terete, greyish, and with fissured bark in age, c. 1.5–3 mm. thick. Leaves of branches often unreduced on lower portions (similar to branchlet leaves), but distally becoming abruptly reduced to cataphylls. Cataphylls blackish, indurate, more or less persistent: stipules triangular to lanceolate, 0.6–1 mm. long, 0.5–0.6 mm. broad, acuminate; blade acicular, c. 0.5–0.8 mm. long. Deciduous branchlets mostly 0.5–2 (–3) cm. long, 0.3–0.5 mm. thick, stramineous, with flaky deciduous waxy coating, furrowed, terete, with (3–) 4–8 (–15) leaves; first internode 1.5–3 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules persistent, triangular-lanceolate, 0.5–0.8 mm. long, 0.25–0.4 mm. broad, brownish, the scarious tips reflexed. Petiole 0.7–1.5 mm. long. Leaf-blades rigidly coriaceous, obovate to narrowly spathulate, (7–) 9–16 mm. long, 2.5–5 (–6) mm. broad, obtuse to rounded or slightly emarginate at the apex (rare individual blades with a short inconspicuous apiculum), narrowly acute at the base; young leaves more or less pinkish-or purplish-tinged; mature leaf-blade above bright green, subfoveolate (with a minute subhexagonal reticulum of raised cell walls), midrib slightly raised; beneath somewhat paler, midrib plane, lateral veins obscure; margins subdifferentiated, not especially thickened, plane.

Monoecious; flowers mostly solitary, usually only one female flower per branchlet (at the third or fourth node), other flowers male (occasionally a male and female flower at the same axil).

Male flower: pedicel capillary, 10–15 mm. long. Calyx pinkish (in life); calyx-lobes 5 or 6, membranous, crystalliferous, rather unequal, oblong to spathulate, (3.2–) 3.5–4 mm. long, 1.5–2.5 mm. broad, obtuse or
rounded at the tip, entire, midrib branching, veins more or less anastomosing. Disk a fleshy more or less 3-angled ring (the 5 or 6 disk-segments completely coalesced), plane, entire, crimson-colored when fresh. Stamens 5 or 6; filaments connate into a slender sometimes apiculate column 1–1.8 mm. high, less than 0.3 mm. thick; anthers subsessile (free parts of filaments about as long as or shorter than the anthers), crowded into a single whorl atop the column (i.e., attached at more or less the same level, although 2 or 3 may be inner to the others), broadly ovate and definitely emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs divaricate, well-separated on the connective, dehiscing obliquely or horizontally; pollen grains c. 22–29 μ in diameter.

Female flower: pedicel slender, curving, (10–) 12–17 (–21) mm. long, terete below, angled above, purplish. Calyx pink, becoming darker in fruit; calyx-lobes 6, chartaceous, subequal (outer ones narrower), elliptic-oblong to spatulate, 3.5–5 mm. long, 1.8–3 mm. broad, obtuse or rounded at the tip, entire, midrib pinnately branched, veins more or less anastomosing (obscure in fruiting calyx). Disk obtusely 5- or 6-angled, plane, crimson when fresh, with a thickened narrow entire rim. Ovary nearly sessile, prominently ribbed along the septa; styles erect, connate below into a column c. 0.5–0.7 mm. high (or sometimes nearly free), divergent above, c. 0.8–1.2 mm. high (not counting rolled-up portion), parted c. 1/3 to 1/2 their lengths; style-branches divergent, entire, cirrinitely revolute, narrowed to the tips.

Capsule oblate, c. 4–4.5 mm. in diameter, smooth, stramineous, not veiny; valves more or less retained within the marcescent calyx. Seeds trigonous, symmetric or sometimes slightly asymmetric, 2–2.6 mm. long, 1.3–1.6 mm. radially, 1.1–1.7 mm. tangentially, when mature dark brown with rows of slightly raised reddish-brown dots; hilum subterminal, elliptic, c. 0.3 mm. long.

**Type:** Cuba, Shafer 4242.

**Distribution:** serpentine lowlands and hills, northeastern Cuba (Map XXVIII).

**Cuba. Oriente:** Cerro de Miraflóres, Cananova, León, Clemente, & Howard 20302 (MICH); León 21161 (GH); Webster 3883 (GH, MICH, NY, US); savanna southeast of Playa de Vaca, Jervis 1650 (GH, MICH); Moa, Mrs. Bucher 96 ex p. (SV); serpentine hills near mouth of Río Yamaniguéy, Shafer 4242 (NY, Lectotype; F, US, Isotypes).

This species, because of the delicate purplish-pink tingeing of leaf-margins and flowers, is one of the most attractive of the West Indian species of Phyllanthus. Unfortunately, it does not appear to lend itself to cultivation, for attempts to germinate seeds were entirely unsuccessful. In the Cerro Miraflóres, the species was observed to grow in the low scrub (charrascal) on rocky serpentine soil, associated with such characteristic Moa plants as Dracaena cubensis, Euphorbia heleneae, and Scaevola wrightii.

Although *P. comosus* is probably most closely related to *P. formosus*, as has been discussed under the latter, it in some respects resembles local
populations of *P. orbicularis*. Both species were observed growing in the same localities at Playa de Vaca and Cerro de Miraflores, but never exactly at the same site (i.e., plants of the two species were never observed to grow side by side). In these two areas *P. orbicularis* appears to occupy somewhat lower altitudes, but their detailed ecological relationships remain to be elucidated. The presence of *comosus*-like features such as spatulate leaf-blades on the local specimens of *P. orbicularis* suggests transfer of characters between the two species. However, it is also possible that part, or all, of this similarity may be due to the fact that the eastern race of *P. orbicularis* is closely related to *P. comosus*; this is suggested by the fact that spatulate leaf-blades occur in *P. orbicularis* in areas considerably outside of the known range of *P. comosus* (e.g., the Sierra de Nipe and Maraví River near Baracoa). The verification of any hypothesis of the modification of *P. orbicularis* by “introgression” of *P. comosus* characters must therefore be tested with the alternative possibility in mind.


Glabrous shrub c. 0.5–2 m. high, usually diffusely branching, lateral branches sometimes reduced to short-shoots; branches c. 1.5–3 mm. thick, reddish brown becoming greyish, bark sometimes breaking into thin plates. Cataphylls blackish, indurate, not reflexed, more or less persistent: stipules lanceolate, (1.5–) 2–3 mm. long, acuminate, entire or denticate; blade linear-lanceolate, c. 1.5–2 mm. long. Deciduous branchlets sometimes clustered on spur-shoots, (0.5–) 1–3 (–5) cm. long, 0.3–0.8 mm. thick, reddish brown, subterete, smooth, with (2–) 3–8 (–11) leaves; first internode (2–) 4–8 (–10) mm. long, median internodes mostly 2–6 mm. long. Leaves: stipules reflexed, persistent, lanceolate, (1–) 1.5–2 (–2.5) mm. long, acuminate, scarious to indurate, margins entire. Petioles 0.3–1 mm. long. Leaf-blades coriaceous, sometimes very thick and rigid, plane or convex, broadly elliptic or obovate to suborbicular or obcuneate (sometimes broader than long), c. 5–10 (–12) mm. long, 5–13 mm. broad, rounded or emarginate at the tip (apiculum obsolete or minute), acute to rounded or often emarginate at the base; above olivaceous, in age plumbeous or dark brown and mottled, veins obscure to conspicuously raised and reticulate, foveolate; beneath yellowish or brownish, midrib and laterals (c. 4–6 on a side) slightly raised, branching crookedly, the reticulum often prominent; margins differentiated (with narrow epidermal
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cells) but no thicker than blade, plane or occasionally reflexed but never revolute.

Monoecious; cymules with mostly 2–5 flowers, male or bisexual, female flowers one per cymule.

Male flower: pedicel 2–5 (–7) mm. long. Calyx whitish or pink-tinged; calyx-lobes 6 (rarely 5), membranous or chartaceous, subequal, elliptic or oblong to obovate or spatulate, (2–) 2.5–4 (–5) mm. long, 1.3–2 mm. broad, obtuse and entire at the tip, midrib sparingly to conspicuously branched. Disk-segments usually 6, flat or concave, rather fleshy, cuneate or quadrate, c. 0.3–0.5 mm. broad, closely contiguous or sometimes united in pairs, dark red (drying brownish). Stamens mostly 6 (less commonly 5 or 7, rarely 3 or 4); filaments (1–) 1.5–2.5 mm. long, unequal (3 anthers usually distinctly higher) erect, united usually about halfway into a column c. 0.8–1.3 mm. long; anthers stipitate in two whorls (free portion of filament usually much longer than anthers), ovate, dehiscing more or less vertically or obliquely (occasionally lower anthers horizontal or nearly so), c. 0.2–0.3 mm. long, 0.3–0.5 mm. broad; pollen grains (21–) 23–27 (–29) μ in diameter.

Female flower: pedicel 0.5–2.5 (–3.5) mm. long. Calyx whitish or pinkish-tinged; calyx-lobes 6, subequal, scarious or chartaceous, elliptic or oblong to spatulate, 3–4 (–6) mm. long, 1.5–2.5 (–3.5) mm. broad, obtuse at the tip, entire, midrib usually conspicuously branched but veins often obscure. Disk hexagonal, flat, rim slightly thickened, entire, red (drying brownish). Ovary sessile or slightly stipitate; styles erect and connate into a column (0.3–) 0.5–0.8 (–1.2) mm. high, free ends erect to recurved, parted usually c. ¼ their length (rarely parted to the column), tips of style-branches often revolute.

Capsule 3–3.8 mm. in diameter, reddish brown, smooth or slightly rugulose, veins obscure. Columella 1.2–1.8 mm. long. Seeds trigonous, sometimes asymmetric, (1.6–) 1.8–2.2 (–2.4) mm. long, 1.1–1.4 (–1.6) mm. radially and tangentially, reddish brown with rows of dark slightly raised points; hilum elliptic, 0.3 mm. long, micropylar end rarely obscurely carunculate.

Collected flowering and fruiting throughout the year.

Type: "Insula Cubae prope Regla et Havana," Humboldt (P, type collection).

Distribution: thickets, serpentine barrens, Cuba (Maps XXV and XXVI).

Cuba. Without specific locality, Sessé et al. 4565 (F, probably type collection of P. rotundifolius). Pinar del Río: San José de Sagua to San Marcos, Shafer 11969 (F, NY, US); La Cajalbana area, Acuña & Alain 15669 (SV), Ekman 10474 (S), León & Charles 4959 (NY), Webster 4650, 4655 (GH); Bahía Honda, León (MT), Wilson 9412 (F, NY, US), Wright 1942 ex p. (GOET, S); Cuabal de Lechua near San Claudio, Ekman 12988 (S). Havana: Regla and Havana, Humboldt (P, type collection); Madruga, Britton et al. 613 (NY), León 3328 (NY), Van Herman 15328 (SV); Guanabacoa, Loma de la
Jata, Ekman 16535 (S), Shafer & León 12055 (NY). Matanzas: cuabales NW of Pan de Matanzas, Ekman 16476 (MICH, S); Cuabal del Espinal, east of Canasi, León & Roig 12949 (NY); Tetes de Camarioca, Britton et al. 14078 (F, GH, NY, US). Las Villas: Motembo, sabana, León 9368 (NY); Santa Clara, Britton et al. 6187 (NY), Britton & Cowell 13304 (NY, US). Camagüey: La Ciega, Caobilla, Acuña 13518 (US); hills near Camagüey, Britton et al. 13232 (F, GH, NY, US); Camagüey to Santayana, Britton 2416 (F, NY, US); Sabana de la Matanzas, Roig, Luaces, & Arango (SV). Oriente: Holguin, at base of Cerro de Fraile, Ekman 3223 (S); Holguin, Aguasclaras, Ekman 7660

MAP XXVI. Distribution of P. orbicularis HBK.

(MICH, S); base of Loma Pilón, near Holguin, Shafer 1213 (F, NY, US); Holguin, Holguin to Mayari, Wright 1942 ex p. (GH, GOET); Sierra de Nipe, along creek 5 km. south of Woodfred, Howard 6132 (GH, MICH, NY, US); Mayari, Rio Miguel, Alain et al. 5845 (GH); Cananova, Cerro de Miraflores, Marie-Victorin et al. 21493 (A, MT), Webster 3884 (GH, MICH, NY, US); Playa de la Vaca, Acuña 12505, 13159 (SV), Clement 3655 (GH, MT, US), Marie-Victorin et al. 21475, 21747 (A, MT), Webster 3867 (GH, MICH, NY, US); Moa, Mrs. Bucher 95, 96 ex p. (NY, SV); plain between Moa and Yaguanque, León et al. 20289 (NY); hills near mouth of Rio Yamaniguey, Shafer 4246 (F, NY, US); pinelands near sea-shore, Río Maravi, near Baracoa, Ekman 4032 (S).

PLATE XXIX. FLOWERS OF SECT. Orbicularia.

Phyllanthus orbicularis is the commonest and most widespread woody species of the genus in Cuba; it occurs always in relatively dry serpentine areas in scrub thickets, savannas, or palm barrens. In its original publication the species was also said to occur in “opacatis Orinoci prope Carichana,” but this record remains unconfirmed and is surely an error; Humboldt must have confused the Cuban plant with a South American species of sect. Microglochidion. It is apparent, even on superficial inspection, that the species contains a number of strikingly divergent local populations. The most outstanding of these is represented by Ekman 7660 from the vicinity of Holguín, which has much larger flowers than plants from all other localities. However, there is also a notable difference between plants of the eastern and western parts of the islands, so that it is possible to recognize two major subspecific races: a western race characterized by smaller male flowers, branchlets with more leaves, and thinner leaves with the nerves conspicuous above; and an eastern race with larger male flowers, shorter few-leaved branchlets, and thick rigid leaves with the nerves obscure above. The boundary between the two races would be drawn west of the Sierra de Xipe, and if the differences were really sharp two subspecies could be defined. It does not seem worth-while to recognize any formal subspecific categories, however, in view of the impossibility of defining two natural subspecies which could be separated by a key. In the case of the number of leaves per branchlet, there appears to be a cline running from Pinar del Río, where the mode is commonly 6 to 8, to the Moa region of Oriente, where it is usually 4 to 5. Unfortunately the number of samples with male flowers is too small to demonstrate whether there is a cline in this character too, but it seems not unlikely.

There appears to be a considerable amount of fluctuating or random variability within P. orbicularis, particularly with regard to stamen number and stylar configuration. In the original description of the species the stamen number was given as 4–10, and Mueller noted it as 6–9, rarely to 12. These reports have not been confirmed, for although a few flowers with only 4 (or very rarely 3) stamens have been observed, none have been seen with more than 7. In view of the large range of variation in the species, it is not impossible that flowers with 10, or even 12, stamens occur but it seems more likely that the observations in the literature are erroneous. There is yet another factor which must be considered in attempting to account for the variation patterns shown by P. orbicularis. It is possible that the distinctive characters of the eastern race of the species may be partially the result of hybridization with P. comosus. The obovate leaves with acute bases and the spatulate calyx-lobes of the Moa plants of P. orbicularis strongly suggest the influence of P. comosus. In the Cerro de Mirafloros both species were seen growing together in the scrubland, where there certainly does not appear to be any ecological barrier to their crossing. However, no plants with intermediate characters were observed and it could not be determined whether or not hybridization is occurring at the present time.
Glabrous bushy shrub or small tree c. 0.5-4 m. high; branches of current year straight, slender (c. 1–3 mm. thick), smooth, terete, sometimes furrowed or cracking open, dark brown or greyish. Cataphylls blackish, indurate, often reflexed, more or less deciduous: stipules triangular to lanceolate, mostly 1–3 mm. long, acute to acuminate, entire or denticate; blade linear-lanceolate, c. 0.5–1.5 mm. long. Deciduous branchlets spreading or ascending, (2–) 3–8 (–11) cm. long, 0.3–0.8 mm. thick, stramineous or olivaceous, subterete, more or less smooth, with mostly 8–18 (–25) leaves; first internode mostly 2–12 mm. long, median internodes mostly 2–10 mm. long. Leaves: stipules reflexed, subpersistent or often mostly deciduous, subentire, lanceolate, acute or acuminate, the proximal ones partly or entirely blackish and indurate, c. 1–3 mm. long and 0.4–0.8 mm. broad, the distal ones brownish and scarious, c. 0.5–1 mm. long. Petioles mostly 1–2.5 mm. long. Leaf-blades chartaceous to rigidly coriaceous, spathulate to obovate or suborbicular, mostly 8–25 mm. long and 4–15 mm. broad, obtuse to rounded or sometimes emarginate at the tip, the scarious apiculum obsolete or up to c. 1 mm. long, acute to rounded or rarely subcordate at the base; above olivaceous or plumbeous, dull to sublucid (or sometimes polished in age), veins plane or slightly raised, obscure to subprominent (veinlets obscure); beneath yellowish or whitish, midrib, main lateral veins (c. 3–5 on a side) and sometimes the veinlets slightly raised, reticulum subprominent to obscure; margins plane to conspicuously revolute.

Monoecious; proximal cymes usually with 2 or 3 male flowers, some distal cymes unisexual with 1 female and 1–3 male flowers, or flowers subsolitary (rarely 2 female flowers per axil).

Male flower: pedicel mostly 7–15 (–25) mm. long. Calyx whitish or pinkish-tinged; calyx-lobes 6 (rarely 5), membranous or somewhat fleshy, subequal or sometimes quite unequal, the outer lobes oblong to obovate, the inner ovate to spathulate, c. 1.7–3 mm. long, obtuse or rounded and entire to denticate at the tip, midrib branched or unbranched. Disk-segments usually 6, flat, thin or somewhat fleshy, roundish or squarish, free or occasionally connate, mostly 0.4–0.5 mm. across. Stamens 6 (rarely 5, very rarely 4); filaments connate into a column 0.7–2 mm. long; anthers sessile to stipitate (the free distal portions of filaments up to 0.8 mm. long), broadly ovate, mostly 0.25–0.4 mm. long and 0.3–0.5 mm. broad; anther-sacs divergent, the upper (inner) dehiscing more or less vertically, the lower (outer) dehiscing more or less horizontally, slits apically contiguous but not confluent; pollen grains c. 18–26 μ in diameter.

Female flower: pedicel slender, c. 3–15 (–20) mm. long. Calyx whitish, greenish, or sometimes pinkish-tinged; calyx-lobes 6 (rarely 5), scarious to subcoriaceous, subequal, elliptic or oblong to obovate (inner lobes often broader); larger lobes c. 3–4 (–4.5) mm. long, mostly 1.5–2.5 mm. broad, obtuse or rounded at the tip, entire or denticate, midrib usually more or
less branched but veins often obscure. Disk plane, tenuous to rather mas-

ve, more or less angled, sometimes inconspicuously pitted. Ovary sessile,

smooth, 3-sulcate, ribless or inconspicuously carinate; styles united c. ½

their length into a column c. 0.5–1.5 mm. high, free ends bifid or parted
to the column, style-branches tapering to slender more or less revolute
tips.

Capsule oblate, c. 2–2.7 mm. high, 3–4 mm. in diameter, dark reddish brown, veins subprominent or completely obscure. Columella c. 1.5–2 mm.

long. Seeds trigonous, sometimes slightly asymmetric (one face carinate),

1.5–2.2 mm. long, 1–1.5 mm. radially and tangentially, reddish brown becoming fuscos, with regular or irregular rows of dark slightly raised points; hilum subterminal, elliptic to triangular, c. 0.3–0.4 mm. long, micropylar end sometimes (in ssp. *spathulijolius*) carunculate.

In the greatly enlarged circumscription here adopted, *P. myrtilloides*

is a variable polytypic species common and widespread in the serpentine lands of northern Oriente province, Cuba. It may appear excessively con-
servative to combine such different plants as *P. spathulijolius*, with chartaceous narrowly obovate revolute leaves and whitish or greenish flowers, and *P. erythrinus* with plane nearly orbicular coriaceous leaves and at least the floral disk dark reddish or purplish. It must be admitted that — due to insufficient sampling — clear zones of intergradation be-
tween the five taxa have not been demonstrated, and indeed in most cases intermediate specimens have not been observed. However, the five taxa in the *P. myrtilloides* complex have *in toto* neatly allopatric and adjoining ranges, and display varying combinations of essentially a single overall pattern of characteristics. Although these taxa could still be maintained as five closely related species, their degree of relationship is so close that it seems more realistic to regard them as five unusually distinctive subspecies.

KEY TO THE SUBSPECIES

1. Anthers all stipitate, dehiscing vertically or obliquely; fruiting pedicel c. 3–7 (rarely to 9) mm. long; leaves prominently apiculate (at least when young), not or scarcely revolute. ssp. *myrtilloides* (61b)

1. Anthers not all stipitate, at least the lower whorl sessile or subsessile and dehiscing more or less horizontally; fruiting pedicel mostly 8–20 (rarely as low as 5) mm. long; leaves various.

2. Style-branches adaxially auriculate, recurving from the top of the stylar column; leaves plane, not revolute. ssp. *alainii* (61c)

2. Style-branches not auriculate; leaves various.

3. Young leaves and floral disk dark reddish or purplish; leaves neither strongly apiculate nor revolute; staminal column mostly 1.5–2 mm. long. ssp. *erythrinus* (61a)

3. Young leaves and floral disk greenish or at least not purplish; leaves strongly revolute.

4. Cataphylls reflexed; staminal column 0.5–1 mm. long; larger calyx-

lobes of male flower c. 2 mm. long, midrib unbranched; seeds 1.9–2.2 mm. long. ssp. *shaferi* (61d)
4. Cataphylls not reflexed; staminal column 1–1.7 mm. long; large calyx-lobes of male flower c. 2.5 mm. long or more, midrib branched; seeds 1.6–1.8 mm. long. \ldots\ ssp. *spathulifolius* (61e)


*Phyllanthus melanodiscus* Urb. ibid.


Shrub 0.5–3 m. high; cataphylls not reflexed, stipules 1–2 mm. long, the tip deciduous, the blade c. 1–1.5 mm. long. Branchlets (2.5–) 4–8 (–11) cm. long, often bright yellow proximally, with (6–) 8–17 (–25) leaves; first internode (4–) 6–12 (–15) mm. long, median internodes 4–12 mm. long. Leaves: proximal stipules c. 1–1.5 mm. long, distal stipules c. 0.5–0.8 mm. long; petioles c. 1.5–2.5 (–3.5) mm. long; leaf-blades chartaceous to coriaceous, conspicuously purplish when young, mostly broadly elliptic to suborbicular, mostly 13–25 mm. long and 10–18 mm. broad, the apiculum very short (0.3 mm. long or less) or obsolete; margins plane or reflexed but never definitely revolute.

Male flower: pedicel 10–20 mm. long; calyx more or less purplish-tinted; calyx-lobes mostly 2.5–3 (–3.5) mm. long, 1.8–2 mm. broad, midrib usually conspicuously branched; stamens 6, staminal column (1–) 1.5–2 mm. long; anthers substipitate (free portions of filaments about as long as to shorter than the anthers), dehiscing vertically or obliquely. Female flower: pedicel (5–) 10–20 mm. long; calyx-lobes (3–) 3.5–4 mm. long, 1.5–2.5 mm. broad, midrib more or less branched; disk flat, colored dark reddish or purplish; styles erect, coherent or usually connate into a column c. 0.5–0.8 mm. high, free ends parted c. \(\frac{3}{4}\) their length. Seeds 1.6–1.8 mm. long, 1.1–1.3 mm, radially and tangentially.


**TYPE:** Cuba, Oriente, *Wright 1943.*

**DISTRIBUTION:** scrub or pineland, mountainous serpentine areas, eastern Cuba (Map XXVII).

**CUBA. ORIENTE:** Sierra de Moa, alt. 800 m., *Alain 3414* (GH); Baracoa, El Yunque, north side, *Ekman 3546* (S, TYPE COLLECTION of *P. cardiophyllus*); between Taco and Nibujon, charrascales, pinelas, *Ekman 3724* (S, TYPE COLLECTION of *P. melanodiscus*); pinelands, road between Baracoa and Florida, *Ekman 3080* (S); Lomas de Cuaba [Duaba], *Ekman 4265* (S); upper valley of Río Navas, thickets by river, *Shafer 4412* (GH, NY); Loma Santa Teresa, near El Yunque,
Shafer 7734 (NY), 7736 (F, GH, NY); Camp La Gloria, south of Sierra Moa, Shafer 8271 (NY, holotype of Orbicularia foveolata); pine woods. Baracoa, Underwood & Earle 1349 (NY); Sierra de Moa, c. 20 km. south of Moa lumber mill, Webster 3899 (GH, MICH, NY, US); pine near Baracoa, Wright 1943 (GOET, holotype; G, GH, isotypes). A sterile specimen from Charrascos de Peña Prieta, Toa, Alain 3597 (GH), is probably referable to this subspecies.

Of the five subspecies of _P. myrtilloides_, the present one appears to be the most widespread and also the most xerophilous. Although it has been collected in river thickets (Shafer 4412), it seems to be mainly a plant of open pinelands, so that ecologically it corresponds more to _P. baracoensis_ than to any of the other subspecies of _P. myrtilloides_. The purplish color of the unfolding leaves and floral disk is most conspicuous in the living plant and at once distinguishes it so well that in the field it might be taken for a distinct species. However, in almost all respects except pigmentation ssp. _erythrinus_ is very similar to ssp. _myrtilloides_, although it can be distinguished by its shorter stipules, non-apiculate leaves, and usually longer fruiting pedicel.

Despite its rather formidable synonymy, ssp. _erythrinus_ does not appear to be an unusually polymorphic taxon. The two species proposed by Urban, _P. cardiophyllus_ and _P. melanodiscus_, are trivial variants. Alain (Flora de Cuba 3: 51, 1953) has already reduced the latter, and the supposed difference in leaf-shape of _P. cardiophyllus_ is quite inconsequential. In contrast, Britton's _Orbicularia foveolata_ (which Alain has transferred to _Phyllanthus_) cannot be disposed of so easily. The holotype (Shafer 8271) is a nearly sterile specimen with strikingly shiny coriaceous suborbicular leaves which are conspicuously foveolate due to the prominent anticlinal walls of the hexagonal epidermal cells. Shafer noted on the label that the flowers were white, which would be unusual for the usually pinkish-flowered plants of ssp. _erythrinus_; unfortunately, the floral material is too inadequate to provide the necessary additional information as to floral characters. However, the glossy leaves which are supposedly the main distinguishing feature of _P. foveolatus_ can be matched closely by those on older branches of a plant encountered in the Sierra Moa (Webster 3899) probably not far from Shafer's original locality. It thus appears that the proposed species _P. foveolatus_ was founded on a specimen which differs from typical ssp. _erythrinus_ only in its ontogenetic stage (and possibly also in its development in a drier environment). Foveolate-leaved specimens may be expected throughout the range of the subspecies.


Bush or small tree c. 2–4 m. high; cataphylls more or less reflexed, stipules mostly 1–1.5 mm. long, blade c. 1 mm. long. Branchlets (3–)
5–11 cm. long, with 10–15 (–20) leaves; first internode 2–7 mm. long, median internodes 3–7 mm. long. Leaves: proximal stipules 1.5–3 mm. long, distal stipules c. 1 mm. long or less; petioles c. 1–2.5 mm. long; leaf-blades chartaceous or subcoriaceous, elliptic to suborbicular, mostly 10–20 (–27) mm. long and 7–14 (–17) mm. broad, obtuse to rounded or sometimes emarginate and, when young, conspicuously apiculate at the tip (apiculum c. 0.5–1 mm. long, more or less deciduous in age), acute to obtuse at the base, margins plane or reflexed (or at most slightly and casually revolute).

Male flower: pedicel 5–12 mm. long; calyx whitish (drying reddish), calyx-lobes c. 2–3.2 mm. long, the outer elliptic-oblong and c. 0.8–1.5 mm. broad, the inner obovate and c. 1.2–1.8 mm. broad, midrib unbranched or nearly so; disk-segments free; stamens 6 (rarely 5), staminal column mostly 1–1.5 (–1.8) mm. long, anthers usually stipitate (free portion of filaments definitely longer than at least the inner anthers), dehiscing vertically or obliquely.

Female flower: pedicel 3–7 (–9) mm. long; calyx greenish white (drying reddish), calyx-lobes mostly 3–4 (–4.5) mm. long and 1.5–2.5 mm. broad, midrib unbranched or nearly so; styles erect and connate into a column c. 0.5–1 mm. high, the free ends bifid c. 1/2 their length. Seeds c. 1.5–2 mm. long, 1–1.3 mm. radially and tangentially.

**Type**: Cuba, Oriente, *Wright 1438* ex p.

**Distribution**: rain-forest, mountains of Oriente province, Cuba (Map XXVII).


In its usual phase, as in the Monteverde region, ssp. *myrtilloides* is distinguishable from the remainder of the species by the definitely stipitate anthers, the free portions of the filaments approaching the elongated condition as in *P. orbicularis*. The collection from the lake at the top of Monte Galano (*Alain 3837*) is quite atypical in having small male flowers with the anthers nearly sessile on the staminal column. However, since it agrees with ssp. *myrtilloides* in its reflexed cataphylls and short fruiting pedicel, it is classified here provisionally.

The present subspecies is certainly closely related to ssp. *erythrinus*, but clearly differs in its apiculate leaves, usually reflexed cataphylls, and lack of purplish coloration in leaves or flowers; furthermore, ssp. *myrtilloides* appears to be a more mesophytic plant. However, it is not certain that these variable morphological characters will still provide valid distinctions when additional collections become available. Another closely related plant is ssp. *alainii*, which is vegetatively similar but differs in its auriculate styles and shorter filaments.
Maps XXVII-XXIX. Distribution of some species of sect. *Orbicularia*.
61c. **Phyllanthus myrtilloides** ssp. alainii, ssp. nov.\(^{22}\)  

(PLATE XXIX, fgs. G–H).

Shrub; cataphylls more or less spreading (not reflexed), stipules c. 1.5 mm. long, with deciduous tips, the blade c. 1.5 mm. long. Branchlets 4–8 cm. long, with c. 9–15 leaves; first internode 1.5–4 mm. long, median internodes 3–8 mm. long. Leaves: proximal stipules 2–3.5 mm. long, distal stipules c. 1 mm. long; petioles c. 1.5–2.5 mm. long; leaf-blades chartaceous, broadly elliptic or obovate, c. 10–25 mm. long and 8–15 mm. broad, the apiculum obsolete or nearly so, acute or obtuse at the base, margins plane or recurved.

Male flower: pedicel c. 10–15 mm. long; inner (larger) calyx-lobes c. 2.5–3 mm. long and 1.8–2.7 mm. broad, anthers sessile or subsessile atop the column, the upper dehiscing vertically, the lower more or less horizontally. Female flower: pedicel 7–15 mm. long; calyx-lobes mostly 3.5–4 mm. long and 2–3 mm. broad, venation obscure; disk flat, tenuous; styles erect and connate up to the bifurcation point into a column c. 1 mm. long, style-branches reflexed from top of column, adaxially auriculate, less than 1 mm. long, revolute at the tips. Seeds c. 2.1 mm. long, 1.4 mm. radially and tangentially.

**TYPE:** Cuba, Oriente, *Alain et al. 5475*.

**DISTRIBUTION:** Sierra Cristal, Oriente province, Cuba (Map XXVII).


This apparently not uncommon plant of the Sierra Cristal vegetatively resembles ssp. *shaheri* and ssp. *spathulifolius* and is, in fact, quite closely allied to the former subspecies. However, its auriculate style-branches, non-revolute leaves and large male flowers are in sum so distinctive that it merits recognition as a distinct entity. There is also a definite vegetative resemblance between ssp. *alainii* and ssp. *myrtilloides* but the leaves of ssp. *alainii* are not apiculate, the female pedicel is usually longer, and the androecium of completely connate filaments is quite different from that of ssp. *myrtilloides*.

It seems appropriate to name this plant for Brother Alain, the assiduous botanist of the Colegio de la Salle, Vedado, Habana. His recent collections

\(^{22}\) **Phyllanthus myrtilloides** ssp. alainii, ssp. nov.

*Frutex stipulis cataphyllorum patentibus 1.5 mm. longis; ramulis 9–15-foliatis; foliis chartaceis ellipticis obovatis 10–25 mm. longis, nec apiculatis nec revolutis; flore masculo lacinis calycis 2.5–3 mm. longis, columna staminum 0.7–1.1 mm., antheris sessilibus; flore femino pedicello 7–15 mm. longo, lacinis calycis plurumque 3.5–4 mm. longis, columna styllum c. 1 mm., stigmatibus auriculatis, reflexibus, revolutis; semina c. 2.1 mm. longa.*
Phyllanthus myrtilloides ssp. shaferi (Urb.), stat. nov.


Shrub 1–3 m. high; cataphylls usually reflexed, stipules c. 1–1.5 mm. long, blade up to 1.5 mm. long but often greatly reduced. Branchlets 2–6 cm. long, with c. 10–16 (–18) leaves; first internode 1.5–4 mm. long, median internodes 2–6 mm. long. Leaves: proximal stipules c. 1–2.2 mm. long, distal stipules c. 0.5–1.3 mm. long; petioles c. 0.8–1.5 (–2.5) mm. long; leaf-blades chartaceous often becoming convex and coriaceous, broadly elliptic to obovate or sometimes suborbicular, c. 6–10 (–15) mm. long, (3–) 4–8 (–10) mm. broad, rounded at the tip, the conspicuous apiculum (of juvenile leaves) deciduous, margins usually conspicuously revolute.

Male flower: pedicel 6–15 mm. long; calyx-lobes mostly 1.7–2.1 mm. long and about as broad, midrib branched or unbranched; disk-segments rather massive, free; stamens 6 (rarely 5), staminal column 0.5–1 mm. high, anthers sessile on the column, upper dehiscing vertically, lower horizontally. Female flower: pedicel 7–15 mm. long; calyx-lobes c. 3–4 mm. long and 1.7–2.5 mm. broad, midrib branched but veins obscure; disk rather massive; styles united very nearly to the bifurcation point into a column (0.5–) 1–1.5 mm. high, style-branches sharply reflexed from the top of the column, the tips revolute. Seeds 1.9–2.2 mm. long, 1.2–1.5 mm. radially and tangentially.

Type: Cuba, Oriente, Shafer 1715.

Distribution: serpentine regions, Sierra de Nipe, Cuba (Map XXVII).

Cuba. Oriente. Sierra de Nipe: Cayo del Rey, Arroyo Canapú, Apr., May 1940, Carabia 3603, 4086 (GH, MICH, NY); pinar de Mayari, Carabia 3626 (GH, MICH, NY); Salto del Sojo, Carabia 3723 (GH, NY); along Río Piedra in pinelands, alt. c. 500 m., 3 July 1914, Ekman 1786 (MICH, S); charrascales, at stream, 25 July 1914, Ekman 2196 (S); Bayate prope Río Piedra, 18 F 1915, Ekman 4671 (S, sterile); ad marginem Río Piñoto, 20 Apr. 1919, Ekman 9501 (S); La Planch, July 1941, Howard 6181 (GH, MT, NY, US); pinelands, La Casimba, 27 July 1940, León & Alain 19235 (MICH); pinelands, crest of Sierra Nipe, alt. 600–700 m., 16–18 Oct. 1941, Morton & Acúa 3110 (US); near streamlet, pinales southeast of Paso Estanía; 1–2 May 1909, Shafer 1715 (NY, lectotype; F, isotype); Arroyo del Medio, above the falls, alt. 450–550 m., 22 Dec. 1909, Shafer 3266 (F, GH, NY, US). Sierra Cristal: border of Río Miguel, Mayari, 2–7 Apr. 1956, Alain, Acúa & López Figueiras 5940 (GH).

In the Sierra de Nipe ssp. shaferi is a very common plant along watercourses. As illustrated by Marie-Victorin (Contr. Inst. Bot. Univ. Montr. 68: 62. 1956), it has a distinctive aspect with small convex revolute leaves and pendent long-pedicellate flowers. However, it is very closely related to ssp. alainii, and the auriculate style-branches and non-revolute leaves
of the latter are the only really distinctive characters. Also similar to ssp. *shaferi* is ssp. *spathulijolius* of the Moa region, but that plant has narrower leaves, longer staminal column, and different styles.


Shrub 0.5–3 m. high; cataphylls deciduous, not reflexed, stipules (0.6–1–1.5 mm. long, blade c. 0.5–0.8 mm. long. Branchlets (2–3–6–8) cm. long, with mostly 7–12 (–15) leaves; first internode c. 2–5. mm. long, median internodes 4–8 mm. long. Leaves: proximal stipules c. 0.7–1.5 mm. long, distal stipules c. 0.4–0.7 mm. long; petioles c. 1–1.5 mm. long; leaf-blades chartaceous, obovate or spatulate, 7–13 mm. long and 5–9 mm. broad, obtuse or rounded at the tip (apiculum nearly obsolete even in young leaves), acute at the base, margins usually distinctly revolute.

Male flower: pedicel 8–16 mm. long; calyx whitish; calyx-lobes mostly 2–3 mm. long and 0.7–1.8 mm. broad, midrib distinctly branched; disk-segments free; stamens 6 (rarely 5), staminal column (1–) 1.2–1.5 (–1.7) mm. high, anthers substipitate to sessile (free portion of filament at most about as long as or slightly longer than anther). Female flower: pedicel (6–) 8–13 mm. long; calyx greenish white; calyx-lobes mostly 3–3.5 mm. long, 1.2–2 mm. broad, midrib branched but veins inconspicuous; styles erect, coherent or connate into a column c. 0.5 mm. high, free ends parted c. \( \frac{1}{2} \) their length, the style-branches divergent, tips revolute. Seeds 1.6–1.8 mm. long, 1.1–1.3 mm. radially and tangentially, often carunculate.

**Type:** Cuba, Oriente, *Wright 1438b*.

**Distribution:** riparian woods, northern Oriente province, Cuba. (MAP XXVII).

**Cuba. Oriente:** Monte Grande de Centeno, south of Moa, 4 Aug. 1945, León, Alain, & Clemente 22673 (MIC); bank of Río Moa, c. 20 km. south of Moa, 21 July 1951, *Webster 3896* (GH, MIC, NY, US), 3897 (GH, MICH); margin of Río Castro near Sagua de Tanamo, 3 Apr. 1861, *Wright 1438b* (GOET, H OLOTYPE; G, S, W, ISOTYPES).

In many respects, including its general aspect, ssp. *spathulifolius* is a very distinctive group and might be thought to merit specific distinction, although Gomez de la Maza long ago reduced it to a variety of *P. myrtilloides*. Vegetatively ssp. *spathulifolius* is not unlike ssp. *alainii* of the Sierra Cristal but its styles are much more similar to those of ssp. *myrtilloides*. In the Sierra Moa, ssp. *spathulifolius* was observed growing with *Exostema* in the bed of the Río Moa within a few miles of a small population of plants of ssp. *erythrophyllum*. Here the two plants appear so different
from one another, both morphologically and ecologically, that they gave
the impression of being distinct species. However, when the other related
populations in Oriente are taken into consideration, they are seen to be
merely at the opposite ends of a nearly continuous spectrum.

The locality cited for Wright's collection has been taken from a label
on an isotype sheet of ssp. myrtilloides (GH). There is no material of
the type collection of ssp. spathulifolius in the Gray Herbarium (due,
preumably, to the vagaries of distribution), but circumstantial evidence
suggests that the label cited above belongs with specimens of ssp. spathuli-
folius.


Low shrub c. 1-2 m. high; branches straight, c. 1-4 mm. thick, terete,
dark brown, smooth or furrowed. Cataphylls blackish, indurate, some-
times reflexed, glabrous or puberulent, deciduous: stipules lanceolate,
c. 1.5-3 mm. long, acuminate, entire or denticulate; blade narrowly lanceo-
late, c. 1-1.5 mm. long, acuminate, entire. Deciduous branchlets ascend-
ing or spreading, c. 3-7 (-13) cm. long, 0.25-0.5 mm. thick, stramineous
to reddish brown, subterete, with mostly 15-45 leaves; first internode
1-5 mm. long, median internodes 1-4 mm. long. Leaves: stipules reflexed,
persistent or deciduous, triangular-lanceolate, acuminate, the proximal
ones partly or entirely blackish and indurate, 1-2.5 mm. long, the distal
ones brownish and scarious, 0.5-1 mm. long. Petioles 0.3-1.2 mm. long.
Leaf-blades brittle-chartaceous to subcoriaceous, sometimes convex, ellip-
tic or oblong (and sometimes falcate) to obovate or spathulate, 3-10 mm.
long, 2-5 (-7) mm. broad, subacute to obtuse or rounded and obscurely
to prominently apiculate at the tip, acute to obtuse (sometimes inequi-
lateral) at the base; above olivaceous or plumbeous, dull or sublucid
(sometimes glossy in age), midrib and lateral veins slightly raised, sub-
prominent to obscure; beneath pale, sometimes whitish or yellowish, mid-
rib and steeply ascending lateral veins (c. 5-7 on a side) slightly raised,
prominent to obscure, lateral veins nearly or quite unbranched; margins
plane, reflexed, or revolute.

Monoecious; flowers mostly solitary, the proximal male, occasional
distal ones female; male flowers sometimes paired.

Male flower: pedicel 2.5-7 mm. long. Calyx greenish white (more or
less reddish when dried); calyx-lobes normally 6, more or less membranous,
biseriate, c. 1.5-2 mm. long, the outer lobes elliptic or oblong, 0.8-1.3 mm.
broad, the inner lobes broadly elliptic to obovate, 1.1-1.7 mm. broad; lobes
obtuse or rounded and entire or minutely denticulate at the tip, midrib
simple or with steeply ascending lateral veins. Disk-segments normally
6, roundish or squarish, somewhat fleshy, entire, c. 0.3-0.5 mm. across.
Stamens usually 6 (rarely 5 or 7), filaments united into a rather stout
sometimes apiculate column 0.5-0.9 mm. high; anthers subsessile (the
free portion of the filament usually shorter than the anther) in 2 approxi-
mate whorls atop the column, broadly ovate, rounded across the top, c.
0.2-0.3 mm. long, 0.3-0.4 mm. broad; anther-sacs divergent or divaricate,
dehiscing vertically (upper whorl) or horizontally (lower whorl), the slits not confluent; pollen grains 18–23 (–26) μ in diameter.

Female flower: pedicel 0.3–2 (–2.5) mm. long, smooth, slender, angled. Calyx greenish white (drying reddish); calyx-lobes normally 6, chartaceous-scarious, subequal, elliptic-oblong, to subulate, c. 2.5–3 mm. long, 1–1.7 mm. broad, rounded or obtuse at the tip, entire or obscurely denticate, midrib obscure and unbranched or nearly so. Disk thin and flat, 6-lobed or angled, crenulate or entire. Ovary sessile, inconspicuously sulcate or ribbed; styles erect, mostly 1.3–2.5 mm. high, united below into a column c. 0.8–1.5 mm. high, parted \( \frac{2}{3} \) to \( \frac{3}{5} \) their length; style-branches usually sharply reflexed from the point of bifurcation, c. 0.7–1.2 mm. long, divergent, narrowed to slender sometimes revolute tips.

Capsule oblate, c. 3.5 mm. in diameter (or slightly less), dark reddish brown, essentially smooth, veins obscure. Columella 1.2–1.5 mm. long. Seeds trigonous, symmetric or slightly asymmetric, 1.6–1.7 mm. long, 1–1.2 mm. radially, 1–1.3 mm. tangentially, dark greyish- or reddish-brown, with evenly spaced rows of slightly raised dots; hilum subterminal, elliptic or ovate, c. 0.2–0.3 mm. long.

The two subspecies of this rather widespread plant appear different in so many respects that some workers might be reluctant to combine them. In almost all instances, they can be distinguished vegetatively because of the hirtellous cataphylls of ssp. chamaecristoides. However, the male and female flowers are nearly identical (within the usual range of variation) in both groups and the allopatric range adds support to the probability that we are here dealing with subspecies which replace one another geographically rather than with distinct "Linnaean" species. The practical task of characterizing \( \textit{P. chamaecristoides} \) taxonomically is made more difficult by the fact that ssp. chamaecristoides and ssp. baracoensis appear to hybridize with two different species, \( \textit{P. phlebocarpus} \) and \( \textit{P. scopulorum} \), respectively.

The species most closely related to \( \textit{P. chamaecristoides} \) are probably \( \textit{P. myrtilloides} \) and \( \textit{P. scopulorum} \). Subspecies \( \textit{shaferi} \) of \( \textit{P. myrtilloides} \) is vegetatively somewhat similar and also has connate filaments and a rather similar stylar column, although it differs in its much longer pedicels. A much greater vegetative similarity is shown by \( \textit{P. scopulorum} \), but that species has much shorter, free styles and also usually longer pedicels.

**KEY TO THE SUBSPECIES**

Cataphylls and branchlet stipules hirtellous; leaf scarcely or not apiculate, margins plane or reflexed. ............................................ ssp. \textit{chamaecristoides}

Cataphylls and branchlet stipules glabrous; leaf with a usually conspicuous reflexed apiculum, margins usually revolute. ................................. ssp. \textit{baracoensis}

62a. \textit{Phyllanthus chamaecristoides} ssp. \textit{chamaecristoides}

\textit{Phyllanthus apiculatus} Urb. op. cit. 184–185 (non \textit{P. apiculatus} Merr., 1920).
Terminal cones of cataphylls conspicuously scurfy-hirtellous; cataphylls caducous. Branchlets (2.5–) 4–7 (–13) cm. long, with mostly 25–45 (–55) leaves. Leaves: stipules at first copiously hirtellous on both faces and margins, later becoming more or less glabrate; leaf-blades mostly asymmetrically elliptic or oblong, often more or less falcate, with an obscure or obsolete apiculum at the tip, more or less inequilateral at the base (one side acute, the other obtuse), c. 6–10 mm. long, 2–4 mm. broad; margins plane or reflexed, not revolute.

Female flower: pedicel 0.9–1.4 mm. long; stylar column c. 0.9–1.5 mm. high.

Collected in flower Feb., June, July, Nov.; in fruit Nov.

**TYPE:** Cuba, *Ekman 2127.*

**DISTRIBUTION:** thickets and savannas, sepentine soil, Sierra de Nipe (Map XXVIII).


This population, which can be distinguished from all others in sect. _Orbicularia_ by its hirtellous cataphylls, is known (in the typical form, at least) only from the southern part of the Sierra de Nipe. The specimen of ssp. _baracoensis_ collected in the Sierra de Nipe by Carabia probably comes from the northern part of the range, but it is not yet clear how close the distributional limits of the two subspecies approach one another.

The collection from the Arroyo Piedra (*Ekman 4655*), on the basis of which Urban proposed the species _P. apiculatus_ (locs not differ from other collections in any important respect. The leaves are somewhat less falcate and the stipules even more densely hirtellous, but the floral structure is essentially the same.

62b. _Phyllanthus chamaecristoides_ ssp. _baracoensis_ (Urb.), stat. nov.

_(PLATE XXIX, figs. K–L)._ 


_Phyllanthus coelophyllus_ Urb. loc. cit.

Terminal cones of cataphylls completely glabrous; cataphylls deciduous. Branchlets 2–5 (–8) cm. long, with (12–) 15–25 (–35) leaves. Leaves: stipules glabrous; leaf-blades symmetric, becoming convex, broadly rhombic-ovate to spatulate, with a usually conspicuous reflexed more or less deciduous apiculum, 3–7 (–9) mm. long, 2–5 (–7) mm. broad; margins recurved or usually strongly revolute.

Female flower: pedicel 0.3–2 (–2.5) mm. long; stylar column (0.6–) 0.8–1.1 (–1.4) mm. high.

Collected in flower and fruit Jan.–Aug.

**TYPE:** Cuba, *Ekman 4326.*
DISTRIBUTION: pinelands, thickets, and stream-banks, serpentine areas, eastern Cuba (MAP XXVIII).

CUBA. ORIENTE. Sierra de Nipe: Loma del Winch, Carabia 3821 (MICH, NY). Moa region: pinares de Moa, Acuña (SV 13154); Moa, Mrs. Bucher 31, 96 (SV); Rio de la Sabana, Yagueque, near Cananova, León, Marie-Victorin, & Clement 20706 (MICH); Cerro de Miraflores, León 21147 (MICH); La Breña woods, León, Clement, & Alain 22496 (MICH); Playa de Vaca, Marie-Victorin, Clement, & Alain 21462 (MT); Centeno, bordos del rio, Marie-Victorin, Clement, & Alain 21471 (MT); charrascal del Cerro de Miraflores, Marie-Victorin, Clement, & Alain 21491 (MT); Moa, pinède, Marie-Victorin & Clement 21748 (MT); ravines, Cerro de Miraflores, Webster 3888 (GH, MICH); pine-land between Cerro de Miraflores and Moa, Webster 3893 (GH, MICH); Baracoa region: Minas de Iberia ad Taco Bay, Ekman 3839 (S, isotype of P. coelophyllus); charrascales near Río Macaguaniagua, Ekman 4326 (S, holotype; NY, S, isotypes); Mesa de Prada, Jauco, León 11771 (NY, SV).

In contrast to ssp. chamaecristoides, ssp. baracoensis is a much more widely distributed plant, extending from the Sierra de Nipe on the west to near the eastern tip of the island at Jauco. The Carabia collection from the Sierra de Nipe is rather surprising, since it is far disjunct from the rest of the known population, and one would rather have suspected that ssp. chamaecristoides would occur at the Loma del Winch. However, the collection is quite typical for ssp. baracoensis, although the leaves are unusually small, and there is no doubt as to its determination.

The group most closely related to ssp. baracoensis (besides ssp. chamaecristoides) is P. scopulorum, which has a very similar habit and which occurs together with ssp. baracoensis in the Moa region. In this area ssp. baracoensis shows an increase in female pedicel length; in Webster 3893, for example, the pedicels are up to 3.5 mm. long, or at the border of the size-range of P. scopulorum, but the long united styles of the specimen place it definitely in ssp. baracoensis. More nearly intermediate is Marie-Victorin et al. 21746 (MICH, MT; not cited above), which has female pedicels 6–8 mm. long as in P. scopulorum but united styles as in ssp. baracoensis. The origin of these aberrant specimens is still not clear, but if P. scopulorum is really a distinct species there is certainly a strong presumption that it hybridizes with ssp. baracoensis.


Glabrous bushy shrub up to 1–2 m. high; branches straight, brittle, c. 1–2.5 mm. thick, terete, bark dark brown or greyish, smooth or furrowed, sometimes wax-incrusted. Cataphylls blackish, indurate, reflexed, largely persistent: stipules triangular-lanceolate, (1.5–) 2–3 mm. long, 0.5–1 mm. broad, long-attenuate at the tip, entire or obscurely denticulate; blade lanceolate, c. 1–2 mm. long, 0.5 mm. broad. Deciduous branchlets ascending or spreading, mostly 3–5 (–6) cm. long, 0.2–0.4 mm. thick,
stramineous becoming greyish, subterete, with c. 15–25 (–30) leaves; first internode 1–2.5 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules reflexed, lanceolate, acuminate-attenuate, entire or denticulate at the base, the proximal ones blackish, indurate, persistent, mostly 1.5–3.5 mm. long, the distal ones scarios, brownish, subpersistent, 0.5–1.5 mm. long. Petioles olivaceous or stramineous, 0.4–0.8 mm. long. Leaf-blades flexibly coriaceous, mostly obovate or obcuneate, sometimes falcate, mostly 3–6 (–7) mm. long, 1.5–4 (–5) mm. broad, broadly obtuse to rounded or subtruncate at the tip, the conspicuous attenuate apiculum of the juvenile blade reflexed and deciduous in age, acute at the base; above olivaceous, sublucid (or glossy in age), very minutely foveolate, veins somewhat raised and subprominent to quite obscure; beneath paler, greenish or whitish, often with waxy atoms or minutely scabridulous, midrib and lateral veins (c. 3–5 on a side) much more prominent than above, usually raised, veinlets obscure; margins usually conspicuously revolute (at least in older leaves).

Monoecious; cymes mostly with 1 or 2 flowers; proximal cymes male, occasional distal cymes bisexual or with a single female flower.

Male flower: pedicel 3–6 mm. long. Calyx usually pinkish-tinged; calyx-lobes 6, biseriate, membranous, 1.5–2.5 mm. long, the outer linear- to oblong-obovate, c. 0.5–0.8 mm. broad, the inner obovate or spatulate, c. 0.8–1.2 mm. broad; lobes obtuse or rounded at the tip, entire or obscurely denticulate, midrib usually unbranched or nearly so. Disk-segments 6, squarish, concave, rather fleshy, minutely pitted, c. 0.2–0.3 mm. across. Stamens 6 (rarely 7), filaments united into a slender column 0.5–0.9 mm. high; anthers sessile or subsessile in 2 approximate whorls atop the column, broadly ovate, rounded or truncate across the tip, c. 0.2–0.25 mm. long, 0.4–0.5 mm. broad; anther-sacs divergent or subparallel, dehiscing vertically (upper anthers) or horizontally (lower anthers), the slits not confluent; pollen grains c. 18–23 μ in diameter.

Female flower: pedicel becoming (3–) 4–8 (–12) mm. long. Calyx usually pinkish-tinged; calyx-lobes 6, thin, biseriate as in the male, c. 1.7–2.3 mm. long, the outer c. 0.5–0.8 mm. broad, the inner c. 0.8–1.3 mm. broad, obtuse or rounded at the tip, entire or obscurely denticulate, midrib sparsely branching but veins usually obscure. Disk undulate-lobed or divided into segments, somewhat thickened, dark. Ovary sessile, with inconspicuous sutural ribs or bands; styles free or sometimes connivent or coherent, erect, ascending, or spreading, c. 0.3–0.7 mm. high (i.e., to point of bifurcation), bifid; style-branches usually reflexed, about as long as base of style, the tips slender, inturned or revolute.

Capsule oblate, c. 3–3.5 mm. broad, dark reddish brown, smooth, with yellowish sutural stripes and rather conspicuous veins. Columella 1.2–1.5 mm. long. Seeds trigonous, slightly asymmetric, carinate on one of the lateral faces, 1.4–1.7 mm. long, 1.1–1.3 mm. radially and tangentially, reddish-brown with even rows of raised dots; hilum subterminal, roundish, c. 0.25–0.3 mm. across.

Collected in flower and fruit April through July.
WEBSTER, WEST INDIAN PHYLLANTHUS

Type: Cuba, Shafer 4006.

Distribution: pinelands, northeastern Oriente province, Cuba (Map XXIX).

Cuba. Oriente: Moa region: Camino Delta no. 1, Acuña 12497 (SV, US), 12498 (US); Yagrumaje del medio, Clément 3620 (MT); chemin du Cayo Chiquito, Clément 3650 (GH, MT, US); Sierra de Moa, edge of creek in pine woods 15 km. southwest of Compañía de Moa mill, Howard 5854 (GH, MT, NY, US); charrascal del Coco, south of Moa, León, Clemente, & Alain 22637 (MICH); Jicotea rivulet, pinelands, east of Moa, León, Clemente, & Howard 20165 (MICH); pineland between Río Moa and Río Yagrumaje, Webster 3756 (MICH); banks of Río Cayoguan c. 3–4 mi. upstream from delta, Webster 3800 (GH, MICH, NY), 3803 (MICH); ecotone between hardwoods and pine-land, Cayo Chiquita, 8 km. south of Moa, Webster 3849 (GH, MICH); thickets near Camp Toa, alt. 400 m., Shafer 4006 (NY, Holotype).

This species endemic to the Moa region grows both in pinelands and streambeds, although in the latter habitat it is sometimes replaced by P. myrtilloides ssp. spathulifolius. From both that plant and from P. chamaecristoides ssp. baracoensis, it is distinguished by its much shorter free styles, while in pedicel length it is intermediate between them. As previously mentioned, there is a distinct possibility that it hybridizes with ssp. baracoensis and it is conceivable that it may cross with ssp. spathulifolius as well.

In many respects P. scopulorum is intermediate between P. phlebocarpus and P. chamaecristoides ssp. baracoensis; it has the free styles and long female pedicel of the former combined with the stamen number and vegetative features of the latter. The possibility that it is in fact a hybrid population must therefore be considered. However, weighing against such an assumption is the fertility of P. scopulorum and the fact that in the Moa region it is much commoner and more widespread than P. phlebocarpus. Consequently, P. scopulorum is here provisionally accepted as a distinct species.

The typification of P. scopulorum presents additional difficulties, because the type specimen is entirely sterile and originated somewhat outside of the known range of the species as determined by the remainder of the collections. Until Shafer’s type locality can be revisited, therefore, it is not certain that the name P. scopulorum is really applicable to the plant of the Moa region described above. However, until more evidence is forthcoming the Shafer specimen is best considered conspecific with the others.


Low shrub (becoming 1 m. high, Ekman); branches erect, straight, slender (c. 1.5–3 mm. thick), smooth, suberete, reddish brown. Cataphylls blackish, indurate, reflexed, more or less deciduous: stipules lanceolate, 2–3 mm. long, 0.5–1 mm. broad, attenuate-acuminate, entire, glab-
rous; blade very similar, c. 2–3 mm. long. Deciduous branchlets (4–) 6–12 (–15) cm. long, 0.4–0.7 mm. thick, stramineous to reddish brown, subterete, smooth, with mostly 10–20 (–25) leaves; first internode (2–) 4–8 mm. long, median internodes (2–) 4–11 mm. long. Leaves: stipules reflexed, lanceolate, entire, the proximal ones blackish, indurate, mostly persistent, 1.5–2.5 mm. long, the distal ones scarious, brownish, sub-persistent, c. 0.7–1.1 mm. long. Petiole 1.5–5 mm. long. Leaf-blades firmly chartaceous, broadly elliptic or obovate to suborbicular, mostly 10–20 (–23) mm. long and 7–17 mm. broad, rounded or subtruncate and minutely apiculate at the tip (apiculum of distal leaves not over c. 0.2 mm. long), obtuse to rounded at the base; above olivaceous, dull or sub-lucid, very minutely foveolate, midrib and lateral veins plane or somewhat sunken, often prominent; beneath yellowish- or greyish-green, midrib and main lateral veins (c. 4 or 5 on a side) more or less equally raised, veinlets also raised and reticulum subprominent; margins thin, scarious, plane or reflexed but not revolute.

Monoecious [but female flowers sparse and specimens thus occasionally appearing to be entirely male]; cymules mostly with 2–4 male flowers, occasional distal cymules with 1 female and 1–3 male flowers.

Male flower: pedicel capillary, 5–12 mm. long. Calyx whitish; calyx-lobes 6, membranous, subequal, elliptic to obovate, mostly 1.5–2.5 mm. long, 1–1.5 mm. broad, obtuse at the tip, subentire, midrib simple or pinnately branched. Disk-segments 6, roundish, entire, not evidently pitted, c. 0.2–0.3 mm. broad, free or united by pairs. Stamens 6 (rarely 5); filaments united into a column c. 0.5–0.9 mm. high; anthers briefly stipitate (free portion of filament c. 0.2–0.5 mm. long) or the outer sub-sessile, ovate, emarginate, c. 0.25–0.3 mm. long and 0.3–0.4 mm. broad; anther-sacs divergent, the slits confluent at the apex, the inner (upper) dehiscing more or less vertically, the outer dehiscing more or less horizontally; pollen grains 18–26 μ in diameter.

Female flower: pedicel slender, 8–17 mm. long, terete below, angled and slightly thickened above. Calyx whitish; calyx-lobes 6, thin, sub-chartaceous, subequal, oblong to broadly elliptic or obovate, c. 2–3.2 mm. long, 1.2–2 mm. broad, obtuse or subacute at the tip, entire or obscurely denticulate, midrib pinnately branched. Disk entire and 6-angled or cut into distinct segments 0.4–0.5 mm. across, flat or undulate, not massive. Ovary sessile; styles free or slightly coherent at the very base, erect or ascending, bifid c. ½ their length, the undivided portion c. 0.3–0.5 mm. long, the branches slightly spreading to sharply curving.

Capsule not seen entire (probably c. 4 mm. in diameter); valves reddish brown, smooth, not veiny, c. 2.5 mm. long. Seeds [not seen fully mature] c. 1.5 mm. long, reddish-brown, with rows of slightly raised dots.

Collected in flower and fruit Oct.—Feb.

TYPE: St. Domingo, Bertero (G, holotype; MO, W, isotypes).

DISTRIBUTION: pinelands, Central Hispaniola (Map XXV).

DOMINICAN REPUBLIC. La Vega: pine forests on rocky slopes north of
As the sole representative of sect. *Orbicularia* outside of Cuba, *P. nummularioides* is of particular phytogeographic interest. All of the Allard and Ekman collections are from the same mountain area north of Piedra Blanca and Ekman (in a note on a label) has suggested that Bertero may have collected the plant at the same place, since the Loma Peguera is near the road between Sto. Domingo [Ciudad Trujillo] and Santiago. The complete isolation of this small population strongly suggests its origin by long-distance dispersal from Cuba.

The relationships of *P. nummularioides* are rather difficult to determine. In a number of respects, including reflexed cataphylls and essentially free styles, it closely resembles *P. scopulorum*. However, since that plant has such a different aspect and also differs by the several characters shown in the key, it may not be the most closely related species. Much more similar vegetatively is *P. myrtilloides*, especially ssp. *erythrinus*, which differs, however, in its larger flowers, purplish coloration, and connate styles. It is possible that *P. nummularioides* should be considered only a subspecies of *P. myrtilloides* but it is retained at specific rank for the time being because its free styles, at any rate, distinguish it from all forms of that polytypic species.


*Phyllanthus breviramis* Urb. op. cit. 192.
*Phyllanthus estrellensis* Urb. op. cit. 188.

Glabrous shrub; branches straight, slender (c. 1.5–3 mm. thick), smooth, terete, becoming dark greyish or brown. Cataphylls blackish, indurate, soon deciduous: stipules broadly triangular, c. 1–1.5 mm. long, acute, entire; blade linear-oblong, 1–1.2 mm. long. Deciduous branchlets erect or ascending, 2–6 cm. long, 0.4–0.5 mm. thick, stramineous, terete or obtusely angled, smooth, with mostly 7–12 (–20) leaves; first internode 2–8 (–10) mm. long, median internodes 2–8 mm. long. Leaves: stipules reflexed, deciduous, triangular-lanceolate, entire, the proximal ones blackish and indurate, the distal ones brown and scarious, 0.6–1 mm. long, up to 0.5–0.6 mm. broad. Petioles c. 1–2 mm. long, stramineous. Leaf-blades thinly chartaceous, broadly elliptic or obovate to suborbicular, (8–) 10–18 (–20) mm. long, (6–) 8–13 (–19) mm. broad, mostly retuse or emarginate at the tip (apiculum completely obsolete), obtuse to truncate or subcordate at the base; above olivaceous, dull to lucid, midrib, veins, and veinlets, yellowish, plane or raised, anastomosing in a fine but prominent reticulum; beneath yellowish, dull to lucid, midrib, lateral veins (c. 4–6 on a side), and veinlets prominently raised in a conspicuous reticulum; margins unthickened, plane.

Monoecious; proximal cymules with 1 or 2 male flowers, occasional
distal cymules with a solitary female flower (often only one female flower on a branchlet).

Male flower: pedicel 2.5–4 (–6) mm. long. Calyx whitish; calyx-lobes normally 6 (rarely 4 or 5), membranous, biseriate, subequal, oblong or obovate (inner lobes somewhat broader than outer), 1–1.5 (–1.8) mm. long, 0.6–0.9 (–1.2) mm. broad, midrib unbranched. Disk-segments isomeric with calyx-lobes, roundish or squarish, obscurely stipitate, entire, minutely foveolate, 0.25–0.4 mm. across. Stamens 3 (rarely 2 or 4), filaments completely connate into a slender column c. 0.4–0.6 mm. high; anthers sessile atop the column, united by the connectives, ovate, c. 0.25–0.4 mm. broad; anther-sacs divergent, dehiscing obliquely or horizontally, the slits not confluent; pollen grains (14–) 16–20 (–22) μ in diameter.

Female flower: pedicel very slender, 6–9 mm. long, slightly thickened above. Calyx whitish; calyx-lobes 6, thin, biseriate, subequal, oblong to narrowly obovate, 1.5–2 mm. long, 0.8–1.2 mm. broad, rounded and entire or obscurely and minutely denticulate at the tip, midrib unbranched or nearly so. Disk 6-lobed or divided into 6 discrete, squarish, somewhat thickened, dark segments. Ovary sessile, minutely verruculose, 3-sulcate; styles very shortly basally connate into a column c. 0.2 mm. high, thence spreading, the free ends parted c. ¾ their length, the branches c. 0.2–0.4 mm. long, divergent, the narrowed tips recurved. Capsule not seen entire; valves c. 2.5 mm. long, greenish or reddish-tined, with a rather conspicuous reticulum of sunken veins. Columella 1.2–1.3 mm. long. Seeds asymmetrically trigonous (carinate on one face), 1.3–1.6 mm. long, 1–1.2 mm. radially and tangentially, reddish brown, with fine more or less evenly spaced reddish-brown slightly raised dots; hilum subterminal, rounded-triangular, c. 0.3–0.4 mm. across.

Collected in flower Apr.–May; in fruit May, July, Oct.

**Type:** Cuba, *Ekman 2271a.*

**Distribution:** scrubland and savannas, on serpentine, northern Oriente province, Cuba (Map XXIX).


The following more or less aberrant collections are probably also referable here:

**Cuba. Oriente:** Bayate, *Ekman 2018* (S; det. by Urban as *P. aff. norlinii* ?); Loma de Estrella, savanna, *Ekman 2271b* (S, HOLotype of *P. estrellensis*), 2272 (S, NY; TYPE COLLECTION of *P. norlinii*).

As here interpreted, *P. phlebocarpus* is a rather widespread and variable
plant of open vegetation on serpentine lands, extending from Sierra de Nipe to Moa. Usually the species is easily recognizable by its broad, thin leaves which are conspicuously reticulate on both sides, unlike those of any other species of sect. Orbicularia. The androecium of 3 stamens and the short spreading nearly free styles also sharply distinguish it. Furthermore, *P. phlebocarpus* appears to differ from other species of the section in being at least partially deciduous, the flowers and new leaves developing together on the expanding branchlets during the renewed growing season in April or May. In other species the flowers appear in sequence as each branchlet successively matures. Urban's proposed species *P. breviramis* was based on a specimen of *P. phlebocarpus* in the spring "flush" of growth. The "pistillode" described by him is merely the apiculate tip of the staminal column, and in all essential respects the specimen does not deviate from typical *P. phlebocarpus*.

Heretofore, the status of *P. phlebocarpus* has been obscured (in the literature and in herbaria) by the existence in the Sierra de Nipe of anomalous plants with narrower leaves, shorter petioles, and a variable stamen number of 3–5; on the basis of such specimens Urban described two new species, *P. estrellensis* and *P. norlindii*. However, the circumstances of the collection of these specimens casts strong suspicion on the validity of these proposed concepts as representing true species in nature. It is notable that Ekman collected the type specimens of all three "species" at the same locality (i.e., savanna at Loma Estrella) and, in fact, confounded *P. estrellensis* and *P. phlebocarpus* under the same number; this appears significant, since Ekman rarely made mixed collections of different species. The only other collection which has been referred to *P. norlindii* (Ekman 2018) was also taken at the same locality with *P. phlebocarpus* (Ekman 2019) and — judging from the consecutive collection numbers — again from adjacent plants.

The known occurrence of *P. estrellensis* and *P. norlindii* only in conjunction with *P. phlebocarpus* suggests that they may represent only some sort of modification of that species. It is possible that they represent hybrid forms between *P. phlebocarpus* and *P. chamaecristoides* ssp. *chamaecristoides*, for the latter was also collected by Ekman at both localities; and the leaf-shape, petiole and pedicel-length, and stamen-number of *P. estrellensis* and *P. norlindii* are more or less intermediate between the two putative parental species, *P. estrellensis* suggesting a backcross with *P. phlebocarpus*, and *P. norlindii* being more truly intermediate. The type specimen of *P. norlindii* is copiously flowering and fruiting, and the pollen fertility is about 80%, but the seeds do not appear to be viable. However, it should be stated clearly that evidence of hybridity is thus far purely circumstantial and is advanced only as a working hypothesis. The situation is complicated by the intrinsic variability of *P. phlebocarpus*. For example, such specimens as Carabia 4068, although typical for *P. phlebocarpus* in floral characters, have leaf-shapes which match those on sheets of *P. estrellensis* and *P. norlindii*. Whatever their genetic constitution the plants to which those two names have been applied would appear
to be classifiable under \( P. \) phlebocarpus. It does not seem necessary at the present time to designate them by formula, even if their hybrid origin could be demonstrated.

The relationships of \( P. \) phlebocarpus are not easy to determine, owing to its isolated position within sect. Orbicularia. Vegetatively it resembles some forms of \( P. \) myrtilloides, particularly ssp. erythrinus, and this is perhaps its closest definable affinity.


Shrubs with phyllanthoid branching; branchlets often borne on spur-shoots; leaves chartaceous, stipules subpersistent. Monoecious, cymules bisexual. Male flower: calyx-lobes 5; stamens 3 or less commonly 4, filaments united; pollen grains with large areoles. Female flower: calyx-lobes 5, often deciduous; disk shallowly cupuliform; styles free, bifid, branches rather thick. Capsule massive, the exocarp somewhat fleshy, cocci indehiscent; seeds asymmetric, smooth.

**Type species:** Phyllanthus subcarnosus Wright ex Muell. Arg.

The single variable species of this section occupies an isolated position in subg. Xylophylla and it is possible that it should be referred to subg. Cicca instead. The female flower resembles that of the commonly cultivated \( P. \) acidus (sect. Cicca), the subindehiscent fruit that of \( P. \) elsiae (sect. Aporosella), and the leaf venation and branch-spur formation that of \( P. \) pseudocicca (sect. Ciccopsis). Probably sect. Ciccopsis should be regarded as the most closely related group in subg. Cicca. Among the sections of subg. Xylophylla, perhaps the most similar is Asterandra, which has leaves with somewhat similar petiolar ridges, male flowers with three (or more) monadelphous stamens, areolate pollen grains, and a globose fruit which is fleshy until rather late in ontogeny.

The areolate pollen grains of \( P. \) subcarnosus (Pl. IX, fig. 41) are of particular interest since they can be regarded as derived from a microspore with three confluent bordered colpi such as that of \( P. \) acidus (Jour. Arnold Arb. 37: 240. 1956). If the areolate grains of the other taxa in subg. Xylophylla can be shown to have evolved from the microspore of \( P. \) subcarnosus, then sect. Omphacodes would have to be regarded as a phylogenetically important group and possibly the most primitive group within subg. Xylophylla. However, the specialized fruit, reduced androecium, and peculiar styles of sect. Omphacodes offer rather formidable obstacles to such an evolutionary hypothesis. Furthermore, it is by no means impossible that the areolate pollen grains of sect. Omphacodes have been derived independently of those in the other sections of the subgenus. It is true that the areolate grains of sect. Macreaa can be distinguished from those of subg. Xylophylla by the different placement of the germ-pores, while in sect. Omphacodes there is no such difference. Thus there is a slight presumption in favor of the idea that the pollen of sect. Omphacodes may be primitive within subg. Xylophylla but the case is by no means
proved. Until some of the South American species which appear also to lie in the "neutral zone" between subgenera *Cicca* and *Xylophylla* can be critically studied, the phylogenetic position of sect. *Omphacodes* must remain somewhat uncertain.


Glabrous shrub or tree c. 2–4 m. high; branches straight, distally c. 3–6 mm. thick, terete or sometimes distinctly angled, smooth, dark brown or grey, lenticels inconspicuous. Cataphylls indurate, brownish, not reflexed, persistent: stipules triangular, blunt or acute at the tip, 1.5–2 (–2.5) mm. long, 1–2 mm. broad; blade linear-lanceolate, c. 1.5–2.5 mm. long. Deciduous branchlets borne scattered on main branches or clustered on lateral spur-shoots, mostly 7–15 (–25) cm. long and 1.5–2.5 mm. thick, compressed, sharply wing-angled, stramineous, smooth, with 5–12 (–15) leaves; first internode mostly 10–30 mm. long, median internodes c. 10–30 mm. long. Leaves: stipules appressed, persistent or (distally) sometimes completely deciduous, triangular-lanceolate, acuminate, 1.2–2.5 mm. long, 0.8–1.5 mm. broad, brownish, entire, the base becoming more or less indurate, the scarious tip often breaking off. Petioles 1.5–4 (–5) mm. long, brownish, with two straight or slightly undulate adaxial ridges decurrent from the blade. Leaf-blades chartaceous, elliptic or slightly ovate (less commonly obovate or suborbicular), 3–11 cm. long and 2–7 cm. broad (reduced blades at proximal nodes smaller), emarginate or obtuse to subacute and with a brownish more or less deciduous apiculum up to 0.5 mm. long at the tip, obtuse to rounded or occasionally subcordate at the base; above olivaceous to silvery, obscurely to conspicuously foveolate, the depressed or plane midrib rather conspicuous, the lateral veins obscure; beneath paler or silvery, more or less obscurely foveolate, the midrib salient (and excurrent at the apex), the lateral veins (c. 5–7 on a side) slightly raised, anastomosing short of the margin, enclosing subprominent reticula of veinlets; margin unthickened or scarcely so, plane or recurved.

Monoecious; cymes bisexual (proximal ones sometimes entirely male), of one female and several male flowers.

Male flower: pedicel capillary (slightly thickened above), c. (3–) 4–6 mm. long. Calyx whitish (in life); calyx-lobes 5, subequal, more or less spreading, suborbicular to broadly elliptic or obovate, 1.3–2.7 mm. long and 1–1.8 mm. broad (at full anthesis, somewhat smaller in mature bud stage), subentire, thickened at the junction with the fleshy receptacle but distally thin, the midrib unbranched. Disk-segments 5, free or casually united, somewhat fleshy, squarish to triangular or round, obscurely pitted, c. 0.25–0.5 mm. across. Stamens 3 or less commonly 4, filaments connate into a column (0.3–) 0.5–0.8 mm. high; anthers subsessile atop the column, more or less ascending, c. 0.25–0.3 mm. long and 0.35–0.5 mm. broad;
anther-sacs divergent, the slits apically contiguous but not confluent, dehiscing obliquely; pollen grains spheroidal, c. 20–22 µ in diameter, with large polybrochate mostly pentagonal areoles c. 1/3 the diameter of the grain.

Female flower: pedicel becoming (8–) 10–20 mm. long, terete and slender below, dilated and sharply angled above. Calyx-lobes 5, chartaceous, caducous (falling at anthesis and represented only by prominent scars) or sometimes persistent and becoming reflexed in fruit, elliptic-oblong to obovate, c. 1.8–2.5 mm. long, 1.2–1.8 mm. broad, subentire, centrally thickened with very thin scarious margins, the midrib unbranched. Disk shallowly cupuliform, tenuous, the undulate margin not pitted, c. 0.25–0.4 mm. high but always much shorter than the ovary. Ovary subglobose; styles free, spreading, bifid nearly to the base, the divergent thickened and rather fleshy branches c. 0.5–0.7 mm. long, blunt at the tips.

Capsule subglobose, when dried 6–13 mm. in diameter, the exocarp fleshy but apparently thin, drying reddish brown; cocci more or less indehiscent, the outer and inner walls firmly united. Columella not seen. Seeds asymmetrically trigonous, those of each pair often unequal, (3–) 3.5–5 mm. long, (2–) 2.7–3.3 mm. broad, shiny reddish brown, smooth (sometimes very obscurely striate); hilum subterminal, c. 0.7 mm. long; micropylar end often with a small yellowish caruncle.


TYPE: Cuba, Wright 1946.

DISTRIBUTION: infra-mangrove coastal scrub and inland mountainous areas, Cuba and Hispaniola (Map XXX).

CUBA. PINAR DEL Río: Mendoza, in forests at Boquerón, Ekman 18746 (S, SV); behind manglares, halfway between Malas Aguas and San Cayetano, Webster 4683 (GH, MICH); Sierra de los Organos, grupo del Rosario, San Diego de Tapia, at the edge of the Río Maní-Maní (= Río San Miguel), Ekman 12665 (S); Zambumbia Hill, Rangel, León 12715 (MICH, NY); Río San Miguel from Volador to Mal Paso, Wilson 9374 (F, GH, NY, US); Toscano, in woods bordering manglares, Wright 1946 (G, Holotype; F, GH, GOET, MO, P, S, Isootypes); Toscano, at Las Calaveras, woods bordering on manglares, Ekman 17427 (S); Morillo, forest bordering on manglares, Ekman 17401 (S).

ORIENTE: Puerto Padre, Curbelo X91 (NY, SV); Sierra Maestra, Río Yara, Nagua, in thickets, Ekman 14180 (S), León 10980 (NY); Sierra de Nipe, at base of Loma Mensura, Ekman 3157 (S); Sierra de Nipe, El Taller, prope Río Piloto in dumetis, Ekman 9676; Cerro de Cananova, Sagua de Tánano, Clemente & Crisógono 6234 (GH, Isootype of P. leonis); Río de la Sabana, Yaguanque, Cananova, León et al. 20724 (MICH); El Yunque, Baracoa, Bucher (SV 14556); Farallon La Perla, Shaffer 8747 (NY); woods at the foot of Sierra de Imías, Imías, León 12137 (NY); rocky banks of Jauco River, Jauco, León 11843 (NY, SV).


As here circumscribed, P. subcarnosus is a highly variable species occurring in scattered localities in Cuba and Hispaniola. Although widespread, it has been collected only rarely in the fertile condition, and its
variation pattern presents many puzzling aspects. Originally it appeared that the population from Oriente province, described by Alain as *P. leonis*, could be recognized as a subspecies distinct from the Pinar del Río plants on the basis of the following features: longer branchlets (up to 30 cm.) and leaves (mostly 5–10 instead of 3–5 cm. long), larger male calyx-lobes (2 mm. long or more) and female pedicels, usually persistent rather than deciduous female calyx-lobes, and larger capsules (9–13 mm. as compared to 6–7 mm. in the very few capsules measured from Pinar del Río) and seeds (4.5–5 mm. long as opposed to 3–3.8 mm.). This would appear to be an impressive number of distinctions, but it must be remembered that the size measurements are mostly based on inadequate sampling and that, in most instances, there is either some overlap in the range of variation or else a relatively narrow gap. When the Hispaniolan plant is taken into account, the single collection of Poiteau is sufficient to erase some of the supposed distinctions, for it has the large capsules of *P. leonis* combined with the small male flowers of typical *P. subcarnosus* and is intermediate in leaf-size.

![Map of Cuba](image)

**Map XXX.** Distribution of *P. subcarnosus* Wr. ex Muell. Arg.

It is still possible that when better samples are available from most areas of the range of *P. subcarnosus* it may prove feasible to distinguish two or more subspecific taxa; the leaf-shape of the Hispaniolan plants is distinctive, and the specimens from the Sierra de Nipe have unusually large leaves. However, it is outside the province of this study to base the systematic disposition on any such hypothetical prediction. Consequently, for the time being no subspecific entities are recognized within *P. subcarnosus*, with the proviso that a much more intensive study of the variation is indicated.

One of the major difficulties in the analysis of the present species is the lack of adequate floral material. It is not possible, for instance, to decide conclusively whether the variation in size of the male flowers is purely random or follows a geographical pattern. When sect. *Omphacodes* was first described, the stamen number was given as 3. This proves to be the prevalent but not the exclusive number, for a count of 50 flowers from *Webster 4683* yielded a score of 38 flowers with 3 stamens and 12 flowers
with 4. This tendency toward a higher stamen number is of interest in view of the tetramerous condition of the androecium in some of the probably related sections of subg. Cicca. In contrast to the stamen number, no deviations were observed in the number of calyx-lobes and carpels, which were constantly 5 and 3, respectively.

The ecological behavior of *P. subcarnosus* is very interesting and merits field study. On the northern coast of Pinar del Rio it occurs in the shrubby woods directly behind the mangrove zone, associated with such plants as *Eugenia axillaris* and *Comocladia dentata*; Curbelo's collection from Puerto Padre probably came from a similar habitat. However, it occurs inland both in the serpentine areas of the Sierra de Nipe and the calcareous regions of the Sierra Maestra. If it has really been derived from subg. *Cicca*, then it is probable that the original habitat of the species was in the sub-mangrove zone as in *P. elsiar* and *P. acidus*. The distribution of the present-day populations of *P. subcarnosus* may illustrate therefore, an important West Indian evolutionary phenomenon, viz., the colonization of inland areas by plants which have migrated along halophytic shoreline areas.


Slender shrubs or trees with palm-like habit, the trunk with branchlets clustered at the apex; cataphylls inconspicuous; branchlets pinnatifid; leaves chartaceous, stipules reflexed. Monoeious; cymes mostly bisexual. Male flower: calyx-lobes 5, disk-segments coalescent into a massive ring; stamens 3–7, filaments united; anthers dehiscing horizontally or downwards; pollen grains areolate. Female flower: calyx-lobes 5 (6); disk as in male; styles erect, connate about halfway, the tips dilated, horizontally spreading. Capsule dry at maturity, cocci rather massive; seeds rounded, mottled, smooth, thick-walled.

**Type species:** *Asterandra cornifolia* (HBK.) Kl. [= *Phyllanthus juglandifolius* Willd. ssp. *cornifolius* (HBK.) Webster.]

Section *Asterandra*, although comprising only a single polytypic species, has a rather broad distribution which includes most of the West Indies and tropical South America. It is certainly very closely related to sect. *Oxalistylis*, which has very similar leaves and flowers but differs in its usually hirsutulous leaves and axes, free male disk-segments, longer styles with differently shaped stigmas, and thin-walled ridged or striate seeds. Possibly further study will show that the two sections should be combined, in which case *Oxalistylis* would have priority as a sectional epithet.


*Phyllanthus grandifolius* sensu Muell. Arg. in DC. Prodr. 15(2): 329. 1866; et auct. seq., non L.
Shrub or tree 1.5–10 m. high, the slender simple or sparsely branching trunk often with branchlets clustered at the apex in the manner of a palm; axes nearly smooth (minutely scabridulous on the youngest parts) or minutely hirtellous. Cataphylls inconspicuous, reflexed: stipules chartaceous, lanceolate, c. 1.7–2.5 mm. long. Deciduous branchlets 25–120 cm. long, 2–5 mm. thick, olivaceous, smooth or minutely hirtellous, more or less angled, with c. 15–45 leaves; first internode 15–70 mm. long, median internodes 10–50 mm. long. Leaves: stipules triangular-lanceolate, soon reflexed, c. 1–2.5 mm. long, 0.8–1.5 mm. broad, chartaceous, olivaceous. Petiole glabrous or scabridulous, 2–5 mm. long, the leaf-blade margins decurrent on the adaxial side as two strongly undulate and conspicuous flanges. Leaf-blades chartaceous, elliptic- or oblong-lanceolate (proximal ones broadly elliptic to suborbicular), c. 5–20 cm. long, 2.5–6 cm. broad, abruptly short-acuminate, obtuse to cordate at the base; above olivaceous, smooth, the midrib, veins, and veinlets all evident but scarcely raised; beneath paler (sometimes glaucous), smooth or minutely scabridulous, sometimes minutely scurfy or hirtellous on the midrib and major veins, midrib salient, lateral veins (c. 6–10 on a side) and veinlets rather prominently raised, forming a conspicuous reticulum; margins unthickened, plane or recurved.

Monoecious; branchlets most often floriferous at every node; cymules simple to thrice compound, the peduncle up to 2 mm. long, more or less adnate (and flowers thus slightly supra-axillary); female flowers up to 3 or 4 in proximal axils, usually 1 or 2 in middle region of branchlet, often lacking distally (distal cymules thus entirely male); male flowers 2–10 per cymule, rarely solitary or absent.

Male flower: pedicel capillary, c. 10–20 mm. long. Calyx yellowish-green or greenish-white; calyx-lobes 5, chartaceous (rather fleshy at the base), somewhat unequal, the outer lobes elliptic or oblong and narrower, the inner lobes broadly elliptic to obvate or suborbicular, c. 1.8–3 mm. long and 1.5–2.5 mm. broad, blunt and often sparsely denticate at the tip, otherwise entire, the scarious margin narrow and indefinite, the (1–) 3–5 nerves usually obscure. Disk annular, 5-angled, very massive, usually deeply pitted, 1.5–3 mm. across. Stamens 3–7, filaments connate into a rather massive column 1–1.5 mm. high and 0.5–0.75 mm. thick; anthers sessile atop the column, horizontal or deflexed below the umbonate top of the column, mostly c. 0.6–0.7 mm. long and 0.7–0.8 mm. broad (reduced ones smaller); anther-sacs subparallel, not confluent, dehiscing horizontally or obliquely downward; pollen grains 23–30 μ in diameter.

Female flower: pedicel slender, 5–30 mm. long, smooth or rarely scabridulous, obscurely angled. Calyx yellowish green; calyx-lobes 5, herbaceous, rather thick, subequal or distinctly unequal, elliptic or oblong to obvate, in fruit becoming 2–4 mm. long and 1.2–2.5 mm. broad, obtuse or rounded and entire or obscurely denticate at the tip, the midrib slightly raised on both sides, the laterals obscure. Disk massive, 5-angled, closely resembling the male. Ovary smooth, carinate; styles erect, connate about
halfway into a thick column, the flattened dilated tips bifid or emarginate, c. 0.5–0.7 mm. long, more or less horizontally spreading.

Capsule oblate, trigonous, deeply sulcate between the cocci, c. 7–12 mm. high and 9–17 mm. in diameter, smooth and glabrous, not veiny. Columella 4–6 mm. long, massive. Seeds plano-convex, plump, when mature 4.2–6 mm. long, 3.2–4 mm. broad, irregularly brown-and-gray mottled, smooth; hilum central, raphe linear-triangular.

It was shown previously (Jour. Arnold Arb. 37: 10. 1956) that Mueller’s application of the name \( P. \) grandifolius to this West Indian and South American species was an erroneous adoption of horticultural practice, the true \( P. \) grandifolius L. being a Mexican species of subg. Botryanthus. As here interpreted, \( P. \) juglandifolius is a very widespread and polymorphic species which ranges over the West Indies and much of tropical South America.

**KEY TO THE SUBSPECIES**

Leaves mostly elliptic-lanceolate, obtuse to rounded at the base, c. 5–11 (rarely to 15) cm. long, glabrous beneath; stamens 3–5; fruiting pedicel 6–11 (–14) mm. long; mature capsule mostly 10–12 mm. in diameter. 

67a. **Phyllanthus juglandifolius** ssp. juglandifolius

(PLATE I, fig. 4; PLATE XXX, figs. C–D).

*Phyllanthus grandifolius* \( \gamma \) genuinus Muell. Arg. in DC. Prodr. 15(2): 329. 1866 (ex p.); non *P. grandifolius* L. 
*Phyllanthus quinquefidus* Sesse & Moc. Flora Mex. ed. 2. 212. 1894.

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**PLATE XXX. FLOWERS OF SECTS. Omphacodes, Asterandra, Epistylium, and Glyptocharum.**

WEBSTER, WEST INDIAN PHYLLANTHUS
Shrub or treelet 1.5–3 m. high; branchlets 25–60 (–75) cm. long, smooth or minutely scabridulous, with (12–) 15–35 leaves; leaf-blades elliptic-lanceolate (less commonly oblong-lanceolate), c. 5–11 (–15) cm. long, 2.5–5 cm. broad. Male flower: calyx-lobes 1.8–2.5 mm. long, 1.2–2.5 mm. broad; disk 1.5–2 mm. across; stamens mostly 3 or 4, less commonly 5. Female flower: pedicel becoming 6–11 (–15) mm. long; fruiting calyx-lobes 2–2.8 mm. long. Capsule c. (5–) 7–8 mm. high and (9–) 10–12.5 mm. in diameter; mature seeds 4.5–5.5 mm. long, 3.2–4 mm. broad.

Collected flowering February through October; fruiting April through December.

Type: *Herb. Willdenow* (B, holotype). The type sheet has no exact data, but from Willdenow’s description it appears to have been taken from a plant cultivated in the Berlin Botanical Garden.

Distribution: mainly Greater Antilles, a disjunct population occurring in Brazil (Map XXXI).


WEBSTER, WEST INDIAN PHYLLANTHUS


Phyllanthus grandifolius β salzmanni Muell. Arg. ibid.
Phyllanthus grandifolius γ genuinus Muell. Arg. ibid. (ex p.).

Shrub or palm-like tree 2–10 m. high; branchlets (40–) 50–100 (–120) cm. long, smooth or hirtellous, with (25–) 30–45 leaves; leaf-blades oblong-lanceolate, (10–) 13–17 (–20) cm. long, 3–5 (–7) cm. broad, glabrous beneath or sometimes hirtellous along the midrib and main veins. Male flower: calyx-lobes 2.1–3 mm. long, 1.5–2.8 mm. broad; disk 1.8–3 mm. across; stamens mostly 6, less commonly 5 or 7 (mostly 5 in Trinidad plants). Female flower: pedicel becoming (10–) 15–25 (–30) mm. long; fruiting calyx-lobes c. 3–4 mm. long. Capsule c. 8–12 mm. high, (10–) 12–15 (–17) mm. in diameter; mature seeds 4.5–5.5 mm. long [6 mm. ex Urban], 3.5–4 mm. broad.

Collected flowering (in Trinidad) in June; fruiting in June and August.


DISTRIBUTION: widespread in tropical South America, reaching its northern limit in Trinidad (MAP XXXI).

TRINIDAD: without specific locality, Finlay (TRIN 2462), Von Rohr 91 (C); Moruga, Britton & Broadway 2463 (GH); Cedros, L’Enviense, Broadway (TRIN 8538); San Fernando Hill, Lewis (TRIN 9164); 12 mile post, Peñal Rock Road, Williams (TRIN 12172); Southern Watershed Reserve, Williams (TRIN 12179).

The following specimens are representative of the South America material studied of this subspecies:


ECUADOR. GUAYAS: Balao, Eggers 14123 (A); south of Milagro, Hitchcock 20567 (GH). MANABI: near Guale, Haught 3067 (GH).

PERU. LORETO: Lower Río Huallaga, Santa Rosa, Williams 4880 (F).

VENEZUELA. ZULIA: Maracaybo, Moritz 260 (GH); Perija, Maracaibo, Karsten (W).

Urban (Repert. Sp. Nov. 15: 404. 1919) accepted P. cornifolius as a species distinct from P. juglandifolius on the basis of its leaf-shape, longer female pedicels, supposedly differently shaped style-tips, and larger fruit. He cited from Trinidad Broadway 2727 (unfortunately not examined dur-
ing the present study) and described the capsule as 14 mm. high, 18 mm. in diameter, and with seeds 6 mm. long. These dimensions, while presumably correctly stated, are larger than those observed in any other specimen; and the distinctive features of *P. cornifolius* as presented by Urban thus appear impressive. However, it is significant that his discussion is cautiously restricted to a comparison of the Trinidad collection with the West Indian specimens only of *P. juglandifolius*. When the variation throughout the entire range of both taxa is analyzed, the fluctuation and overlap of characters together with the complete geographical replacement of the two is strongly indicative that the populations in question are best ranked as subspecies of a single variable species.

![Map XXXI. Caribbean distribution of *P. juglandifolius* Willd.: small dots, ssp. *juglandifolius*; large dots, ssp. *cornifolius*.](image)

Our knowledge of the variation patterns within ssp. *cornifolius* is very fragmentary in comparison with that of ssp. *juglandifolius*, which is at once homogeneous and better represented by herbarium specimens. However, although the scarcity of comparable herbarium material makes it impossible at this time to prove whether or not there is a significant overlap in measurements, it is clear that the mean values of many dimensions (e.g., height, length of branchlets and fruiting pedicels, size of leaves, and diameter of fruits) in ssp. *cornifolius* are definitely larger than those in ssp. *juglandifolius*.

The Trinidad population of *P. juglandifolius* is no better known than
the South American ones with respect to the number of fertile collections available; but in any event it appears to be somewhat transitional between the two subspecies. For example, the leaves are always glabrous as in ssp. *juglandifolius*, but in size and shape they are wholly characteristic of ssp. *cornifolius*. Again, the stamen number in the Trinidad plants appears to be mainly 5, which is the number of overlap between the subspecies; and a single flower of *Von Rohr 91* had only 3 stamens. This is the only instance within ssp. *cornifolius* of a number lower than 5, so that it may simply be a completely exceptional occurrence; but the examination of a good series of male flowers from Trinidad is needed to clarify the matter.

The detailed distribution of ssp. *cornifolius* on Trinidad is interesting in that all collections have been made in the southwestern corner of the island, San Fernando Hill being the point farthest north. Judging from the vegetation map of Beard (Nat. Veg. Trinidad, *frontisp.* 1946), the plant is generally found in the semi-evergreen seasonal forest, where it presumably plays the part of a pioneer plant as ssp. *juglandifolius* was observed to do in Cuba.


*Epistylium* Sw. Fl. Ind. Occ. 1100. 1800.


*Phyllanthus* sect. *Catastylium* Griseb. ibid.

Shrubs or trees with phyllanthoid branching; branchlets pinnatifid, clustered at the apex of the more or less unbranched stem; leaves chartaceous or coriaceous, stipules persistent. Monoecious; cymules bisexual, borne on racemiform axillary or cauline thyrses. Male flower: calyx-lobes 4 or 5; disk-segments 4 or 5; stamens 2 or 3, filaments united; anthers more or less deflexed; pollen grains areolate. Female flower: receptacle and base of calyx massive; calyx-lobes 5, erect; disk tenuous, lobed or parted into 5 segments; stigmas massive, sessile atop ovary or terminating an elongated gynoecium. Capsule dry at maturity, angled; seeds 2 or possibly sometimes 1 per locule.

**Type species:** *Omphalea axillare* Sw. (= *Phyllanthus axillaris* (Sw.) Griseb.)

As here construed, sect. *Epistylium* comprises three species endemic to Jamaica which have the palm-like habit of sect. *Asterandra* and show a similar calciphilous habitat preference. Although the latter section differs from sect. *Epistylium* in its woodier seeds, much more massive floral disk, and very different inflorescence, its resemblance (at least to *P. cladanthus*) in habit, stipules, anthers, and styles suggests a rather close relationship. However, some of the representatives of subg. *Cicca*, especially *P. acidus* (sect. *Cicca*), also are suggestively similar to sect. *Epistylium* in the production of cauliflorous thyrses; and the tetramerous flowers, reduced fe-
male disk, and tendency to reduction in seed number in sect. Cicca represent a much closer approach to the condition in sect. Epistylium than do the corresponding features in sect. Asterandra. On the other hand, the tricolporate pollen grains, free stamens, and very different styles of sect. Cicca would appear to preclude an intimate relationship with sect. Epistylium. Another possibly related group is sect. Omphacodes, which does have areolate pollen grains and which shows some vegetative resemblance to the Jamaican plants. However, in that section cauliflory does not occur, and the stipules and styles are very different. It is most difficult to decide whether the resemblance between Epistylium and Cicca is genetically significant, or whether the various floral similarities may not rather be simply correlated with the cauliflorous condition. The multiple and seemingly contradictory affinities of sect. Epistylium pose a most interesting problem for further and more intensive investigation.

If the nature of the ties between Epistylium and its possible ancestors is obscure, the affinity in a different direction is much more clear. Undoubtedly related to sect. Epistylium and probably descended from it is sect. Hemiphyllanthus, which scarcely differs in anything more than pubescent axes and bipinnatifid branchlets. The leaf venation of the Haitian P. maleolens and P. myriophyllus is similar to that of P. cladanthus, and the massive receptacle and styal column of P. cauliflorus is not unlike that of P. ovatus or P. megapodus. The more highly modified species of sect. Xylophylla are also related to sect. Epistylium, either directly or via sect. Hemiphyllanthus.

The three species of sect. Epistylium, although clearly differing both in floral and vegetative characters, are so obviously related that no purpose would be served in separating P. cladanthus into a separate sect. Castrastylium; Mueller recognized the weakness of the distinctions but out of inertia recognized two sections. The least specialized of the three species is clearly P. cladanthus, which has 3 or 4 stamens and a subglobose ovary. Its reflexed stipules are much more like those of sect. Asterandra than are the stipules of either P. cauliflorus or P. axillaris.

KEY TO THE SPECIES

1. Stipules lanceolate, reflexed, not fused with branchlet; branchlets subterete; leaves oblong-lanceolate, chartaceous; male flower with 5 calyx-lobes and 3 stamens. 68. P. cladanthus

1. Stipules triangular, massive, not reflexed, more or less fused to branchlet; male flower with 4 calyx-lobes and 2 stamens.
2. Branchlets angled, not flattened; leaves chartaceous, oblong-lanceolate; inflorescences at least partially cauleine; pedicel of female flower 2–3 mm. long or more; ovary extended into a long styal column. 69. P. cauliflorus
2. Branchlets flattened; leaves coriaceous, mostly elliptic; inflorescences strictly axillary to leaves on branchlets; female flower subsessile; ovary ellipsoid (styal column confounded with upper part of ovary). 70. P. axillaris

Phyllanthus cauliflorus sensu Griseb. Fl. Br. W. Ind. 33. 1859; non Omphalea cauliflora Sw.


Slender tree c. 5–10 m. high; trunk c. 1 dm. thick or less, usually unbranched, smooth and reddish brown when young, becoming greyish. Cataphylls coriaceous, reflexed: stipules triangular or broadly lanceolate, c. 2.5–4 mm. long, 1.7–4 mm. broad, blunt, greyish; blade narrower. Deciduous branchlets steeply ascending, (15–) 20–60 cm. long, c. 2–4 mm. thick, reddish brown, smooth, terete or somewhat angled, with c. 10–20 leaves; first internode (3–) 5–8 (–12) cm. long, median internodes c. 1.5–3 cm. long. Leaves: stipules persistent, reflexed, indurate, lanceolate, 2.5–5 mm. long, 1.5–2.5 mm. broad (becoming broader with age), acuminate or blunt-tipped, dark reddish brown and polished. Petioles 4–7 mm. long, the laminar flanges adaxially decurrent. Leaf-blades chartaceous, ovate- to more commonly oblong-lanceolate, abruptly acuminate, 9–15 cm. long, 3–5.5 (–7) cm. broad, obtuse to rounded or rarely subcordate at the base; above olivaceous, the incised midrib prominent, the delicate lateral veins plane or very slightly raised; beneath paler, sublucid, the salient midrib proximally keeled, the main lateral veins (c. 8–12 on a side) and veinlets tenuous but raised, forming a conspicuous reticulum; margins plane or narrowly reflexed.

Monoecious; cymules usually bisexual, borne on naked thyrses, the latter usually fascicled at old nodes on main axis; additional thyrses sometimes produced on branchlets. Thyrses (2–) 5–20 cm. long, with c. 7–15 nodes; larger thyrses often compound, with up to 15 lateral axes and with conspicuous indurate cataphylls proximally. Cymules each with 1 female and up to c. 10 male flowers.

Male flower: pedicel slender, 3–8 mm. long. Calyx pinkish (ex Proctor); calyx-lobes 5 (rarely 6), thin and scarious, unequal: outer lobes oblong to elliptic, c. 1–1.5 mm. long and 0.8–1.2 mm. broad; inner lobes broadly obovate to suborbicular, c. 1.3–1.8 mm. long and 1.2–1.7 mm. broad; lobes rounded at the tip, entire, the midrib simple or sparingly branched above the middle. Disk-segments 5 (rarely 6), dark, roundish, thickened, pitted, crenulate, concave, c. 0.3–0.6 mm. across. Stamens 3 (rarely 4); filaments completely connate into a column c. 1 mm. high; anthers sessile atop the column, steeply deflexed (almost upside-down), (0.6–) 0.7–1 mm. long, 0.5–0.8 mm. broad; anther-sacs subparallel, dehiscing pseudo-vertically (actually obliquely downwards), the slits not confluent; pollen grains mostly 25–30 µ in diameter, with c. 15 oligobrochate areoles per amb, areoles c. 4–6 µ across.

Female flower: pedicel slender and terete (dilated only just beneath the calyx), c. 7–15 mm. long. Calyx pinkish; calyx-lobes 5, erect, strongly imbricate, somewhat unequal, fleshy with thin scarious margins, mostly
broadly elliptic to suborbicular, c. 1.3–1.7 mm. long, 1–1.5 mm. broad, entire and rounded at the tip, the midrib sparsely branching. Disk a very inconspicuous membranous crenate ring (with small teeth alternating with the calyx-lobes), hidden under the ovary. Ovary subglobose, c. 1.5–2 mm. high and 2.5–3 mm. broad at (or shortly after) anthesis, shallowly sulcate; styles undeveloped, the dilated petaloid stigmas (style-tips) sessile, massive, more or less triangular, bluntly auriculate apically, crenulate along the distal margin, c. 0.5–1.5 mm. high and 1.3–2 mm. broad.

Capsule (not seen fully mature) oblate, bluntly trigonous, c. 8 mm. in diameter, smooth, not veiny. Seeds (immature) 2 per locule, c. 2.5 mm. long, brownish.


**TYPE:** Jamaica, Wilson (GOET, fragment of **TYPE**).

**DISTRIBUTION:** limestone hills, west central to eastern Jamaica (MAP XXXII).


**PORTLAND:** John Crow Mountains, mist forest on dogtooth limestone 1.5 miles southwest of Ecclesdown, alt. c. 1000 ft., 6 Aug. 1954, Webster & Wilson 5161 (A).

**ST. THOMAS:** woodlands, eastern slopes of south end of John Crow Mountains, 10 Mar. 1909, Harris & Britton (F, JAM, NY, US); Big Level, wooded limestone hill, alt. 1500–2000 ft., 16 Mar. 1956, Proctor 11800 (GH).

Although it was the basis for the separate section *Catastylium* established by Grisebach, *P. cladanthus* is too closely related to *P. cauliflorus* to be maintained in a distinct group. Vegetatively it so closely resembles that species that Grisebach confounded them, but Mueller was able to straighten out the confusion. However, even in the sterile condition *P. cladanthus* is ordinarily readily distinguishable from *P. cauliflorus* by its very different reflexed stipules.

Harris, in his detailed notes made on this species as he encountered it near Troy, remarked of the flowers that they were “produced along the main stem and branches, below the clusters of leaves, and extending downwards for a considerable distance. Occasionally the side branches are covered with flower fascicles.” This description would appear to indicate that *P. cladanthus*, like *P. cauliflorus*, produces axillary inflorescences on the branchlets in addition to the usual cauliflorous ones.

The distribution of *P. cladanthus* parallels that of numerous other Jamaican species in the great disjunction between the western localities in the “cockpit” country at Troy and the eastern stations in the John Crow Mountains. There are no apparent differences between the specimens of the two areas, although the variation has certainly been inadequately sampled heretofore. There are no obvious habitat differences in the intervening region where the species does not occur, and such areas as Mt. Diablo, at least, are so well known that it is unlikely the species has escaped detection there.

(PLATE XXX, figs. J–K).

*Omphalea cauliflora* Sw. Prodr. 95. 1788.

*Epistylium cauliflorum* (Sw.) Sw. Fl. Ind. Occ. 1099, pl. 22, figs. e, f, h. 1800.


Slender tree with usually unbranched trunk, becoming c. 5–6 m. high. Cataphylls not observed. Deciduous branchlets 25–55 cm. long, mostly 2.5–3 mm. thick, olivaceous or reddish-brown, distinctly angled, smooth, with 8–20 leaves; first internode 6–12 cm. long, median internodes c. 1.5–3.5 cm. long. Leaves: stipules persistent, not reflexed (tip appressed or spreading), indurate and rather massive, becoming more or less fused with the branchlet, triangular, c. 3–4 mm. long and 2.5–3 mm. broad on lower part of branchlet but decreasing to only 1.5 mm. long distally, blunt-tipped, greyish. Petioles 3–7 mm. long, the laminar flanges adaxially decurrent. Leaf-blades chartaceous or subcoriaceous, flexuous, ovate- to more commonly oblong-lanceolate, 7–14 cm. long, 3–6 cm. broad, abruptly short-acuminate, obtuse to rounded or subcordate at the base; above more or less lucid when dried, the midrib incised, the lateral veins and veinlets plane or slightly raised, subprominent; beneath sublucid, the midrib carinate and very prominent, the lateral veins (c. 8–10 on a side) and veinlets raised, forming a prominent reticulum; margins plane (or slightly and narrowly reflexed).

Monoecious; cymules bisexual, borne on naked thyrses, the latter usually fascicled at nodes on spur-shoots from main trunk but sometimes also produced one or two together in axils of leaves on branchlets (axis of thyrse sometimes reduced so that flowers may appear to be in axillary clusters). Thyrses c. 3–18 cm. long, with 4–20 nodes; cymules each with 1 female and several male flowers.

Male flower: pedicel slender, 3–5 mm. long. Calyx yellowish green; calyx-lobes 4, rounded at the tip, biseriate, unequal: outer lobes elliptic-oblong, c. 0.9–1.2 mm. long, inner lobes suborbicular or broader than long, 1.4–1.8 mm. long and 1.3–2.1 mm. broad; midrib of outer lobes simple, or inner lobes often sparingly branched distally. Disk-segments 4, dark, rather massive, entire, c. 0.25–0.6 mm. across. Stamens 2; filaments completely connate into a column c. 0.6–1 mm. high; anthers sessile atop the column, triangular-ovate, blunt-tipped, c. 0.5–0.7 mm. long, 0.4–0.6 mm. broad; anther-sacs subparallel, dehiscing obliquely downward or almost horizontally, the slits not apically confluent; pollen grains 15–18 μ in diameter, areoles mostly polybrochate, c. 7 or 8 per amb, c. 5–6 μ across.

Female flower: pedicel becoming 2–3.5 mm. long, slender and subterete below, rather abruptly incrassate and angled above. Calyx blood-red (ex Swartz); calyx-lobes 5, erect, strongly imbricate, massive and fleshy at the base, elliptic to suborbicular, at anthesis c. 1–1.2 mm. long and 0.9–1.2 mm. broad, later increasing up to 1.8 mm. long, rounded at the tip, entire,
midrib distally sparsely branched. Disk divided into 5 thin, erect, oblong segments 0.2 mm. long or less. Gynoeicum cylindrical-ellipsoidal (i.e., the massive stylar column about as long as and nearly as broad as the ovary proper); stylar column increasing to 1.5–2.5 mm. long soon after anthesis; stigmas massive, more or less triangular, bluntly auriculate and obcordate (apically channelled), subentire along the distal margin (often with a downwardly projected lateral lobe), c. 0.4–0.7 mm. high and as broad or broader.

Capsule (not seen mature) ovoid, pointed, obscurely ribbed, dark, not veiny. Seeds (not seen) 2 per locule (ex Swartz).

**Type:** montane forests, western Jamaica, Swartz (C, G, S; syntypes).

**Distribution:** wooded limestone hills, western Jamaica (Map XXXII).


On the basis of available collections, it appears that Mueller and Fawcett and Rendle were correct in accepting Swartz's distinction between *P. cauliflorus* and *P. axillaris*. The two species are much more closely related to one another than to *P. cladanthus*, having in common the peculiar incrassate stipules, nearly indentical male flowers, and elongated gynoeicium.

Swartz distinguished *P. cauliflorus* from *P. axillaris* by its greater height, longer oblong leaves, cauliflorous inflorescence, more elongate gynoeicum, and beaked fruit with two seeds in each locule (instead of solitary as in *P. axillaris*). In general these distinctions are still largely valid, although a few qualifications are necessary. Recent collections of *P. axillaris* show that it is not necessarily only 2–4 ft. high as stated by Swartz but may attain over 3.5 m. in height. Furthermore, *P. cauliflorus* does not produce exclusively cauline inflorescences, for they are partially axillary in Britton & Hollick 2027. However, this does not efface the inflorescence distinction since, as far as is known, *P. axillaris* is never cauliflorous, and *P. cauliflorus* always produces some cauline flowers.
The validity of the fruit characters suggested by Swartz must still rest on his personal observations, since herbarium material is inadequate. His descriptions are so accurate in other respects that there is no reason to doubt his ascription of paired seeds in the locules of *P. cauliflorus* and solitary ones in the locules of *P. axillaris*. However, it remains to be proved whether this distinction will hold when a large number of capsules of both species can be examined.

70. **Phyllanthus axillaris** (Sw.) Muell. Arg. in DC. Prodr. 15(2): 412. 1866; Fawc. & Rend. Fl. Jam. 4: 258–259. 1920.

(PLATE XXX, figs. L–O).

**Omphalea axillaris** Sw. Prodr. 95. 1788.

*Epistylium axillare* (Sw.) Sw. Fl. Ind. Occ. 1097. pl. 22, figs. a–d, g, i–k. 1800.

*Omphalea epistylium* Poir. Encycl. Meth. Suppl. 4: 140. 1816.


**Diasperus axillaris** (Sw.) O. Ktze. Rev. Gen. 2: 598. 1891.

Glabrous shrub c. 0.5–3.5 m. high, with usually unbranched trunk topped by crown of branchlets. Cataphylls not seen. Deciduous branchlets 20–40 cm. long, c. 2–4 mm. thick, greyish and subterete proximally, reddish-brown and flattened (and more or less marginally angled) distally, with c. 15–25 leaves; first internode 6–8 cm. long, median internodes quite variable in length (successive pairs of nodes sometimes approximate). Leaves: stipules persistent, triangular, mostly 2–4 mm. long and 2.5–3.5 mm. broad (smaller at tip of branchlet), not reflexed (tip more or less spreading), massive and indurate, becoming more or less fused with the branchlet, blunt-tipped, greyish. Petioles 2.5–4 mm. long, with decurrent adaxial laminar flanges, sometimes corrugate-fissured. Leaf-blades coriaceous, sometimes quite rigid, ovate- to elliptic-lanceolate, (6–) 8–11 cm. long, (2.5–) 3–5.5 cm. broad, abruptly short-acuminate, mostly obtuse to rounded at the base; above drying dull plumbeous or brownish grey, the midrib incised but veins and veinlets distinctly raised and prominent; beneath sublucid, often coppery when dried, the midrib carinate, the lateral veins (c. 5–8 on a side) and veinlets raised, forming a very prominent reticulum; margins slightly and narrowly reflexed.

Monoecious; cymules bisexual, each usually with one female and several male flowers, borne on short naked thyrses c. 1–3 cm. long which are apparently always axillary to leaves on branchlets (i.e., flowers never cauline).

Male flower: pedicel slender, mostly 3–5 mm. long. Calyx yellowish green; calyx-lobes 4, rounded at the tip, entire, biseriate, unequal: outer lobes elliptic, c. 1–1.3 mm. long and 0.7–1.2 mm. broad; inner lobes sub-orbicular or broader than long, c. 1.3–1.5 mm. long and 1.7–2 mm. broad; midrib simple or sparingly branched distally. Disk-segments 4, dark, massive, rugose-crenulate, concave, c. 0.3–0.5 mm. across. Stamens 2; filaments completely connate into a column c. 0.9–1.2 mm. high; anthers sessile atop the column, nearly horizontal, triangular-ovate, blunt-tipped,
c. 0.7–0.8 mm. long and 0.5–0.6 mm. broad; anther-sacs subparallel, dehiscing horizontally or slightly obliquely downwards, the slits not apically confluent; pollen grains c. 21–25 μ in diameter.

Female flower: pedicel sub-obsolete, less than 1 mm. long. Calyx cream-colored or greenish; calyx-lobes 5, erect, strongly imbricate, massive and fleshy at base, elliptic to suborbiculur, c. 1–1.3 mm. long and 0.8 (outer) to 1.3 (inner) mm. broad, rounded at the tip, entire, midrib simple or sparsely branched distally. Disk divided into 5 thin, erect, oblong segments c. 0.1–0.2 mm. long. Ovary ellipsoid, at or shortly after anthesis c. 1.5–1.8 mm. high and 1–1.3 mm. broad; styles undeveloped (confounded with ovary), the dilated stigmas sessile atop the ovary, massive, more or less triangular, bluntly auriculate and obcordate (apically channelled), subentire along the distal margin, c. 0.5–0.7 mm. high and 0.7–1 mm. broad.

Capsule trigonous, green (ex Howard); valves dark reddish brown, c. 5 mm. long. Columella c. 2.5 mm. long. Seeds solitary in each locule (ex Swartz), c. 3.5 mm. long, slightly over 2 mm. across the back, pale brown with dark brown slightly raised more or less elongated flecks; hilum submedian, triangular, c. 0.3 mm. long.

Collected in flower Apr. (Swartz), July, Sept.; in fruit July.

Type: mountains of western Jamaica, Swartz (G, syntype).

Distribution: limestone areas, western Jamaica (Map XXXII).


From the other two species of sect. Epistylium, P. axillaris is readily distinguishable on account of its shorter, thicker leaves, flattened branchlets, and axillary inflorescences. Apparently it also differs in its solitary rather than paired seeds, as pointed out by Swartz, although this requires confirmation. The gynoecium of P. axillaris appears to be intermediate between that of P. cladanthus and that of P. cauliflorus but this appearance may be deceptive. The complete loss of any distinction between style and ovary in P. axillaris might represent a further modification of the long-styled gynoecium of P. cauliflorus. This would appear the more probable, since in other respects—such as its more rigid leaves and flattened branchlets—P. axillaris appears to be the most specialized representative of sect. Epistylium.


Dendriform small shrub with pinnatifoliate branchlets; cataphylls indurate; leaves coriaceous, margins revolute, stipules indurate and persistent. Monoecious; cymes mostly unisexual. Male flower: calyx-lobes 4, disk-segments coalescent into a massive ring; stamens 2, filaments united; anthers dehiscing horizontally; pollen grains areolate. Female flower:
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calyx-lobes 5; disk massive; styles dilated, lacerate. Capsule globose, not sulcate; seeds dark, fissured.

**Type species:** *Phyllanthus chryseus* Howard.

The single species of this monotypic section is so distinctive in many features, such as its small indurate cataphylls and stipules, revolute leaves golden beneath, very massive disk, and fissured seeds, that it cannot be regarded as closely related to any other group. As noted by Howard, the leaves and cataphylls show some resemblance to those of *P. subcarnosus* (sect. *Omphacodes*), but of course the flowers are completely different. The closest floral similarity is perhaps to be found in sect. *Asterandra*, where there is a very apparent resemblance in the floral disk and styles; however, the vegetative parts in sect. *Asterandra* are quite dissimilar. The Jamaican species of sect. *Epistylium* are vaguely similar but differ in many important respects, such as inflorescence, floral disk, and styles. Possibly *P. chryseus* could be regarded as a xerophytic derivative (adapted to serpentine) of the mesophytic and calciphilous *P. juglandijolius*, but if so the affinity must be indirect. *Phyllanthus chryseus* is an excellent example of a highly specialized relict species of ancient origin.


(PLATE XXX, figs. P–Q).

Glabrous shrub resembling a miniature tree, with bluish-green foliage, the erect woody unbranched stem 2–8 dm. high, 5–7 mm. thick, reddish brown and pruinose above, greyish below. Lower leaves of stem with petioles 5–10 mm. long, leaf-blades elliptic or oblong-ovate, rounded or obtuse at the tip, c. 6–8 cm. long and 2.3–4 cm. broad; upper leaves reduced to cataphylls: stipules triangular-lanceolate, acuminate, 3.5–5.5 mm. long, 2–3 mm. broad, oblique at the base, indurate, smooth, reddish brown and polished, with a single excentric keel; blade linear-lanceolate, 2.5–5 mm. long. Deciduous branchlets mostly 10–20 cm. long, 1.5–2.5 mm. thick, olivaceous, smooth, distinctly flattened but not sharply angled, with mostly 8–20 (–25) leaves; first internode (of well-developed branchlets) 25–55 mm. long, median internodes 10–35 mm. long. Leaves: stipules persistent, triangular, 1–2 mm. long, 0.9–1.8 mm. broad, bluntly pointed, shining and indurate, reddish brown. Leaf-blades rigidly coriaceous, broadly elliptic to orbicular (or sometimes broader than long), c. 2–4.5 cm. long, 1.5–3.5 cm. broad, rounded or emarginate at the tip (the minute scarious apiculum reflexed), obtuse to rounded (or sometimes truncate or subcordate) at the base; blades distinctly reddish when young, when mature bluish green above (turning olivaceous or plumbeous on drying), minutely foveolate, the midrib usually incised, other veins obscure; beneath golden-yellow (or greenish yellow) when living, turning coppery when dried, the midrib salient, laterals (c. 5 on a side) slightly raised but inconspicuous; margins thickened, conspicuously revolute.

Monoecious, cymules usually unisexual; two proximal nodes of branch-
let most often with racemiform cymules of 3 (less commonly up to 7) male flowers; subsequent nodes with solitary female flowers alternating with male cymules at somewhat irregular intervals.

Male flower: pedicel slender, 4.5–7.5 mm. long. Calyx greenish or reddish-tinged, the receptacle massive; calyx-lobes 4, coriaceous, biseriate (strongly imbricate in the bud), subequal, suborbicular (mostly broader than long), 2.8–4.5 mm. long, 4.5–6 mm. broad, rounded at the tip, entire, midrib with well-developed but rather inconspicuous branches. Disk very massive, squarish in outline, surrounding the androecium (inclosing it in a hollow), deeply pitted, greenish in life but turning reddish when dried. Stamens 2; filaments completely connate into a slender column less than 1 mm. high; anthers sessile atop the column, discrete (separated by a notch on each side, the connective between the anther-sacs emarginate so that there may appear to be 4 anthers), semicircular-notched in outline, c. 0.4–0.5 mm. long, 0.7–0.8 mm. broad; anther-sacs divergent, curved, dehiscing horizontally, the slits not confluent; pollen grains 18–21 μ in diameter; areoles polybrochate, 5 or 6 per amb, 5- or 6-sided, c. 6–9 μ across.

Female flower: pedicel slender, 11–17 mm. long, terete or obscurely angled, slightly and gradually broadened upwards. Calyx greenish, the receptacle massive; calyx-lobes 5, coriaceous, spreading at anthesis, broadly ovate, c. 4–7 mm. long and broad, rounded at the tip, entire, midrib conspicuously branched. Disk massive, 5-angled, smooth, entire, yellowish at anthesis (drying reddish brown). Ovary sunken in the disk, capped by the petaloid style-tips (stigmas), these free, spreading and horizontally appressed, sessile, obtuse, 1.5–2 mm. long, 2.3–2.7 mm. broad, yellowish, conspicuously lacerate.

Capsule spheroidal, c. 7.5 mm. in diameter, reddish brown, rugulose, not veiny. Columella slender, 4.5–6 mm. long. Seeds trigonous, symmetric, c. 4.7–5 mm. long, 2.6–3 mm. radially and tangentially, very dark reddish brown (sometimes nearly black), deeply and irregularly transversely or somewhat obliquely fissured on back and sides; hilum submedian, narrowly elliptic, c. 0.4–0.5 mm. long.

Collected in flower and fruit May, July.

**Type:** Cuba. *Howard 5829.*

**Distribution:** endemic to a small area of serpentine hillsides in the Moa region, eastern Cuba.


One of the most distinctive endemic species of the serpentine flora of Moa, *P. chrysceus* appears to be confined to a very narrow range south of
Moa between the Río Cabañas and the Río Yagrumaje. In the field it presents a striking appearance due to its miniature-tree habit and stiff round leaves bluish above and yellowish beneath (cf. photograph taken by Marie-Victorin, Contr. Inst. Bot. Univ. Montreal 68: 164. 1956). Although so restricted in range, the plant was locally quite common, associated with such characteristic Moa species as Scaevola wrightii and Anastaphia recurva.


Shrubs or small trees with phyllanthoid branching; axes incrustate or tomentulose; branchlets bipinnatifid, leaves well-developed at least on ultimate axes, leaf-blades membranous to coriaceous. Monoeious; cymules unisexual or bisexual, produced only on ultimate axes of branchlet. Male flower: calyx-lobes 5; disk-segments 5; stamens 2–6, filaments free or united; anthers dehiscing obliquely or horizontally; pollen grains areolate. Female flower: calyx-lobes 5; disk cupuliform, dissected, or obscure; styles free or connate, branches erect to reflexed. Capsule trigonous, cocci fragile; seeds trigonous, verruculose or (in *Phyllanthus maleolens*) smooth.

**Type species:** Phyllanthus ovatus Poir.

Geographically, ecologically, and morphologically, sect. Hemiphyllanthus is one of the most distinctive groups of West Indian Phyllanthus. The bicentric distribution of the section, the representatives of which occur in two widely disjunct areas (southwestern Haiti and the Lesser Antilles), raises most interesting problems regarding the past migrations of the group. All of the six species of the section agree in being rain-forest calciphiles, and they probably all have the palm-like ("schopfbäumchen") habit characteristic of pioneer plants of rain-forest areas. The bipinnatifid branchlets have a distinctive tomentum of reddish multicellular scales except in *Phyllanthus maleolens*, the branchlets of which are merely incrustate.

The most specialized fern-like Lesser Antillean species, such as *P. mimosoides*, are so distinctive in appearance that they do not appear to belong with any other taxa. However, they can be related (via *Phyllanthus ovatus*) to the two representatives in Hispaniola, and the latter show a definite resemblance to the Jamaican section *Epistylium*. *Phyllanthus maleolens* of the present section has leaves and stipules similar to those of *P. cauliflorus* in sect. *Epistylium*, and the flowers of *P. maleolens* are rather similar to those of *P. cladanthus*. The most important morphological gap between sects. *Epistylium* and *Hemiphyllanthus* is of course the difference between their pinnatifid and bipinnatifid branchlets. Assuming that there is a close relationship between *P. cauliflorus* and *P. maleolens*, it is easy to suggest a hypothesis of the origin of the bipinnatifid branchlets of sect.
Hemiphyllanthus. If the axillary thyrses which sometimes appear on the branchlets of *P. cauliflorus* were to become thickened, rigid, and leafy, the result would be a bipinnatifid branchlet like that of *P. maleolens*, with leaves on both orders of axes but with flowers confined to the ultimate axes. Whatever the exact course of evolution, it is apparent that the phylogenetic origin of sect. *Hemiphyllanthus* is to be sought within sect. *Epi-stylium*.

The disjunct distribution of the representatives of sect. *Hemiphyllanthus* is reflected in the distinct morphological differences between the Hispaniolan and Lesser Antillean species-groups, which could be defined as subsections if any formal subdivision were worthwhile. The origin of the section must have been to the west of the Lesser Antilles, possibly in Hispaniola, and the radiation in which *P. mimosoides* has taken the leading part must represent a later burst of evolution. It is notable that in sect. *Hemiphyllanthus*, in contrast to such groups as sect. *Orbicularia*, the species are much more sharply defined, only the most elementary taxonomic judgment being required to distinguish them.

Another aspect of the phylogeny of sect. *Hemiphyllanthus*, certainly of no small interest, is its relationship to sect. *Xylophylla*. It is clear that the compound phylloclade of most representatives of that group is homologous with the bipinnatifid branchlet of the present section; and it is furthermore evident that the two sections are related and that *Hemiphyllanthus* is the less specialized of the two (in vegetative characters, at least). However, this is not the same thing as saying that sect. *Xylophylla* was derived from sect. *Hemiphyllanthus*. As discussed under the former, the relationship of the two sections can perhaps best be stated as one of more or less coordinate origin.

### KEY TO THE SPECIES

1. Stipules of branchlets thickened, indurate, and blackish; leaf-blades well-developed on both primary and ultimate branchlet axes; pedicel of female flower slender and terete, 3 mm. long or longer.

2. Branchlets merely incrustate; leaves coriaceous, shiny above, 10–35 mm. long; stamens 3, filaments free, dehisce obliquely upwards. .................................................. 72. *P. maleolens*

3. Stipules of branchlets scarious, neither indurate nor blackened; leaves of primary branchlet axes reduced to cataphylls; pedicel of female flower thickened and fleshy or else less than 3 mm. long.

2. Leaves ovate or elliptic, symmetric at base, mostly 30–50 mm. long; styles undivided, united into a column 2.5–3.5 mm. high which is exserted beyond the calyx. .................................................. 74. *P. ovatus*

3. Pedicel of female flower at anthesis dilated into an incrassate recepta-
cle usually broader than the calyx; styles fused into a massive column higher than the ovary; cataphylls of primary branchlet axis densely tomentulose when young; ultimate axes of branchlet with mostly 15–25 leaves, blades mostly 18–30 mm. long. .... 75. *P. megapodus*

3. Pedicel of female flower more slender; styles free or shortly connate, spreading or reflexed; cataphylls of primary branchlet axis glabrous; ultimate axes of branchlet with mostly 30–60 leaves (or more), blades 5–13 mm. long.

4. Pedicel of female flower more slender; calyx-lobes 1.5–3 mm. long, spreading; styles spreading; stamens 3; leaves smooth beneath. .... 76. *P. mimosoides*

4. Pedicel of female flower incrassate above, calyx-lobes not over 1 mm. long, erect; styles reflexed and appressed to outside of calyx; stamens usually 5; leaves minutely scabridulous beneath. .... 77. *P. acacioides*


Slender tree 2–8 m. high, with unbranched trunk, evil-smelling (fide Ekman); main axis reddish-incrustate. Deciduous branchlets bipinnatifid; primary axis 25–50 cm. long, (2–) 3–4 mm. thick, leafy (but leaves often very soon deciduous), ferruginous-incrustate on younger parts (smoother and greyish in age), terete, with c. 12–30 nodes; first internode c. 3–5 cm. long, median internodes c. 1–3 (–4) cm. long. Leaf-blades of primary axis similar to those on ultimate axes but rather smaller; stipules persistent, more or less spreading or reflexed at the tip, indurate, broadly ovate-triangular (often broader than long), c. 1.5–2.5 mm. long, 1.5–3.5 mm. broad, blunt-tipped, greyish. Ultimate axes ascending, mostly 6–13 cm. long (occasional axes only 3–5 cm. long), c. 1.3–2 mm. broad, reddish brown and incrustate, more or less flattened, sharply wing-angled between the stipules, with 10–25 (–30) leaves; first internode 2.5–5 mm. long, median internodes 3.5–6 mm. long (internodes up to 10–12 mm. long on sterile axes). Leaves: stipules persistent, more or less reflexed, becoming blackish and somewhat indurate, c. 1.2–2.2 mm. long, bluntly pointed, more or less decurrent. Petioles reddish brown, plano-convex, 1–2 (–2.5) mm. long. Leaf-blades subcoriaceous, elliptic or slightly obovate, (10–) 15–35 mm. long, (5–) 10–20 (–25) mm. broad, retuse at the tip (the minute apiculum of young leaves deciduous), symmetrically acute or obtuse at the base; above olivaceous, lucid, the nerves (except the midrib) inconspicuous; beneath paler, yellowish green, the midrib conspicuous and raised, the lateral veins (c. 4 or 5 on a side) raised, somewhat crooked, giving off a few subanastomosing veinlets; margin usually narrowly revolute.

Monoecious; cymules axillary, on ultimate axes of branchlet, bisexual, of 1 female and up to 8 or 10 male flowers; bracteoles thickened and indurate.
Male flower: pedicel slender, 4–7 mm. long. Calyx yellowish, sometimes reddish-tinged; calyx-lobes 5, chartaceous, broadly elliptic or obovate, convex and sometimes cuculata, somewhat unequal, 1.2–1.5 mm. long outer lobes c. 0.75–1 mm. broad, inner lobes c. 1–1.4 mm. broad, rounded at the tip, entire, midrib sparsely branched or unbranched in smallest lobes. Disk-segments 5, suborbicular, entire, slightly thickened, c. 0.25–0.4 mm. broad. Stamens 3; filaments free, up to 0.4–0.5 mm. long or anthers appearing subsessile; anthers ovate, rounded and emarginate at the tip, c. 0.5–0.7 mm. long, 0.6–0.9 mm. broad; anther-sacs subparallel or divergent, dehisce longitudinally (more or less obliquely), slits apically contiguous but not confluent; pollen grains c. 22.5 µ in diameter, with c. 9–11 polybrochate areoles per amb, germ-pores conspicuous.

Female flower: pedicel 6–10 mm. long, slender, terete below, angled above, straight or curved. Calyx-lobes 5, chartaceous, spreading at anthesis (more or less reflexed in fruit), unequal, oblong to obovate, 1–1.2 mm. long, 0.6–1 mm. broad, obtuse at the tip, entire, midrib incontinuously branched. Disk somewhat fleshy, 5-angled, crenulate. Ovary oblate, siliuate; styles free or slightly connate at the base, erect, 0.7 mm. high, bifid, sharply bent at the crotch, style-branches somewhat dilated and flattened, one or both toothed or again bifid.

Capsule oblate, trigonous, c. 5 mm. in diameter, dark reddish brown, obscurely rugulose. Columella stout, c. 1.3–1.5 mm. high and nearly as broad. Seeds asymmetrically trigonous (plano-umbonate), c. 2.5–2.7 mm. long, 1.7–2 mm. radially and tangentially, light brown, smooth; hilum submedian, ovoid, partly extending onto the lateral face, c. 0.6–0.7 mm. long and 0.4–0.5 mm. broad.

Collected in flower June-Sept.; in fruit July, Sept.

**Type**: Haiti, Ekman H6849.

**Distribution**: mountains, southwestern Hispaniola (Map XXXI'').

**Haiti. Ouest**: Morne des Commissaires: Grand-Gosier, Morne Sinclilio, alt c. 1300 m., 3 Sept. 1926, Ekman H6849 (S, Holoype); Grand-Gosier, Ravine-Fanchon, alt. c. 1675 m., 4 Sept. 1926, Ekman H6880 (A, S); Boucan Chat, alt. 1600 m., 10 June 1942, Holdridge 1266 (GH, MO); Mare Sal, alt. 1600 m., 28 July 1942, Holdridge 1381 (GH, MICH, MO, US).

**Dominican Republic. Barahona**: Cordillera de Bahoruco, Sierra de los Comisarios, above Gros-Figuier, alt. 1500 m., 29 Sept. 1926, Ekman H6782 (S).

The offensive odor from which this species takes its name was noted by Ekman only for the plant encountered in Barahona, and was not mentioned by Holdridge. Since the production of a distinct odor by the vegetative part of the plant (Ekman's specimen bears no flowers) is a distinctly unusual, if not unique, character in Phyllanthus, Ekman's observation needs to be confirmed. The formation of an unpleasant odor at night has been reported for P. epiphyllanthus, but this appears to be associated with flowering.

The citation of specimens from both Hispaniolan republics is somewhat
misleading, for the total range of *P. maleolens* is apparently confined to
the Morne des Commissaires, and it barely crosses the international line
into the Dominican Republic. According to the collectors' notes, the
species grows in "Laubwald" (broadleaf forest) on calcareous soil at higher
altitudes than those known for any other West Indian species of subg.
*Xylophylla*.

The closest relative of *P. maleolens* is certainly its counterpart in the
Massif de la Hotte, *P. myriophyllus*. That plant, however, not only differs
in its smaller flowers with shorter pedicels, dimerous androecium, and re-
flexed styles, but vegetatively — by virtue of its smaller leaves and tomen-
tulose axes — resembles the Lesser Antillean species. Distinctly similar

to *P. maleolens* in several respects is *P. ovatus* of Martinique, which has
however, completely different female flowers with highly modified styles.

Since in many respects — notably its lack of tomentum, large leaves,
free stamens, and unmodified female flower — *P. maleolens* is the least
specialized of the members of section *Hemiphyllanthus*, its extra-sectional
affinities are of particular interest. There is no doubt that these affinities
are all with the Jamaican sect. *Epistylium*, despite the fact that all three
species of that group have simply pinnatifid branchlets. Each one of the
three species shows some similarity to *P. maleolens*, *P. cauliflorus* in its
stipules, *P. cladanthus* in its comparatively long pedicels, and *P. axillaris*
in the flattened branchlets. It would appear, therefore, that *P. maleolens*
evolved from the common ancestor of the three living species of sect.
*Epistylium*.  

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MAP XXXIII. Distribution of the species of sect. *Hemiphyllanthus*.

(PLATE XXXI, figs. C–D).

Slender shrub or tree c. 2–3 m. high, with unbranched trunk. Deciduous branchlets bipinnatiform; primary axis 30–80 cm. long, 3–4 mm. thick, leafy (leaves subpersistent), densely scurfy with ferruginous tomentum (becoming glabrate on older parts), terete, with 40–110 nodes; first internode 10–25 mm. long, median internodes 5–10 mm. long. Leaf-blades of primary axis precisely as on ultimate axes; stipules at first broadly triangular and reddish brown, c. 1.5–2.5 mm. long, the tip deciduous, the blackish, massive, indurate base persistent, c. 1.5–2.5 mm. broad. Ultimate axes ascending or spreading, (5–) 7–14 cm. long, 0.7–1 mm. broad, chestnut-brown, conspicuously fluted with obtuse ribs recurrent from the stipule-bases, tomentulose between the ribs with simple pale to dark ferruginous hairs, with 25–70 leaves; first internode c. 1 mm. long, median internodes 1.5–2.5 mm. long. Leaves: stipules persistent, recurrent at the base, at first ovate-lanceolate and c. 1 mm. long (with denticulate margin), later the tip inflexed and base incrustate, blackish, indurate, c. 0.7–1 mm. broad. Petioles reddish-brown, 0.3–0.4 mm. long. Leaf-blades firmly chartaceous, smooth on both sides, broadly elliptic-oblong or ovate-oblong, (4–) 5–7 mm. long, (2.5–) 3–4.5 mm. broad, obtuse or bluntly apiculate at the tip, symmetrical and obtuse to truncate or subcordate at the base; above dark olivaceous, dull, the nerves completely obscure or the plane midrib visible; beneath pale green, lucid, the midrib raised, the lateral veins (c. 4 or 5 on a side) ascending, inconspicuous, veinlets not visible; margins slightly thickened and subrevolute.

Apparently monoecious (possibly sometimes dioecious); cymules axillary, on ultimate axes of branchlet, the proximal with 3–5 male flowers. the distal with some male and some bisexual cymules (each of the latter with a single female flower).

Male flower: pedicel capillary, 2–4 mm. long. Calyx yellowish white; calyx-lobes 5, thin and scarious, obovate or suborbicular, unequal, c. 1–1.2 mm. long, 0.7–1.1 mm. broad (the outer narrower), obtuse or acute, entire or obscurely crenulate, midrib simple or sparsely branched. Disk-segments 5, oval, thin and flattened, entire, c. 0.25 mm. across. Stamens 2; filaments connate into a column c. 0.3 mm. high; anthers subsecissile, broadly ovate, rounded and minutely emarginate at the tip, c. 0.3 mm. long and 0.5 mm. broad; anther-sacs divergent, dehiscing more or less horizontally, the slits not apically confluent; pollen grains c. 16–18 μ in diameter, with c. 5–7 polybrochate areoles per amb.

Female flower: pedicel 3–3.5 mm. long at anthesis, slender, only very slightly and gradually broadened upwards, terete, smooth, reddish brown. Calyx yellowish white; calyx-lobes 5, membranous, more or less spreading, unequal: outer lobes obovate-oblong c. 1 mm. long and 0.6–0.7 mm. broad; inner lobes suborbicular, c. 1.2 mm. long and broad; lobes entire, midrib unbranched. Disk conspicuous, fleshy, 5-angled, crenulate. Ovary oblate, shallowly sulcate; styles slightly connate at the base, flattened,
dilated, c. 0.7 mm. long, parted c. \( \frac{3}{4} \) to \( \frac{1}{5} \) their length, the branches reflexed over the ovary (but remaining inside the outspread calyx), tapering to acute tips. Fruit unknown.

Collected in flower May, Nov.

**Type:** Haiti, *Ekman H 140.*

**Distribution:** mountains, western end of southern peninsula of Haiti (Map XXXIII).


Not only is *P. myriophyllus* interesting as yet another example of the remarkable endemism of the Massif de la Hotte, but it is phylogenetically significant in being transitional between the large-leaved species *P. maleolens* and the “mimosoid” species of the Lesser Antilles. It seems unlikely, however, that *P. myriophyllus* can be regarded as directly ancestral to *P. mimosoides* or its relatives; it rather illustrates a parallel reduction in leaf-size to that which can be traced from *P. ovatus* to the small-leaved Antillean species.


(PLATE XXXI, figs. E–F).


Shrub 1–4 m. high, with usually unbranched trunk; stem ferruginous-tomentulose at the apex, becoming more or less glabrate below. Cataphylls inconspicuous, indurate, very similar to those of main axis of branchlet. Deciduous branchlets bipinnatiform; primary axis (8–) 10–25 cm. long, c. 2.5–3 mm. thick, distally ferruginous-tomentulose, proximally sparsely hairy or glabrate, subterete, with 10–20 (–35) leaves; first internode 20–60 mm. long, median internodes mostly 10–20 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, spreading or somewhat reflexed, indurate, ovate-triangular, 1–2 mm. long, 1.3–2.3 mm. broad, obtusely pointed, brownish or greyish; blade narrower, 1–1.2 mm. long. Ultimate axes ascending, when well developed c. 5–15 cm. long, 1–1.5 mm. broad, olivaceous, angled or somewhat flattened, smooth and glabrous, with mostly 5–20 (–30) leaves; first internode mostly 5–15 mm. long, median internodes mostly 5–20 mm. long. Leaves: stipules persistent, sometimes reflexed, indurate, triangular-lanceolate, mostly 1–1.5 mm. long, acuminate, entire. Petioles not sharply set off from blade, c. 0.5–1.5 mm. long. Leaf-blades chartaceous, smooth on both sides, symmetrically
or asymmetrically elliptic or ovate, mostly 30–50 mm. long and 20–35 mm. broad, sometimes (especially on distal part of branchlet) only 15–30 mm. long and 10–20 mm. broad, acute or subacute at the tip, acute or obtuse at the base; above olivaceous or plumbeous, minutely foveolate, midrib incised and prominent but other veins obscure; beneath paler, more or less smooth, the midrib conspicuous and raised, the lateral veins (c. 5–7 on a side) somewhat raised, ascending, straight, veinlets obscure; margins unthickened, plane or narrowly recurved.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules male and distal ones bisexual (of 1 female and c. 6–8 male flowers), or all bisexual.

Male flower: pedicel thickened upwards, 1.5–3.5 mm. long. Calyx drying reddish brown; calyx-lobes 5 (rarely 6), chartaceous, oblong-oblanceolate to suborbicular, subequal, c. 1.5–1.8 mm. long, 1.1–1.6 mm. broad, obtuse or rounded at the tip, entire with narrow pale scarious margins, midrib unbranched. Disk-segments 5, more or less reniform, entire, somewhat thickened, inconspicuously pitted, c. 0.4–0.6 mm. across. Stamens 3 (rarely 4); filaments completely connate into a column c. 0.4–0.6 mm. high; anthers sessile atop the column, fused by their connectives (androecium plane on top, 3-lobed), triangular-ovate, obtuse, c. 0.4–0.6 mm. broad; anther-sacs discrete, divergent, dehiscing horizontally; pollen grains c. 22–25 μ in diameter, with c. 15 oligobrochale areoles per amb.

Female flower: subsecisile at anthesis, the thick fleshy obpyramidal pedicel lengthening in fruit up to 1.5–2.2 mm. long. Calyx-lobes 5, coriaceous, erect at anthesis (spreading or reflexed in fruit) strongly imbricate, more or less unequal, ovate or elliptic, 2–2.7 mm. long, 1.5–2.5 mm. broad, obtuse at the tip, midrib apparently unbranched. Disk somewhat fleshy, crenulate or notched, dark reddish brown. Ovary oblate; styles completely united into a thick fleshy urn-shaped column c. 2.5–3.3 mm. high (far exceeding the ovary); stigmas (undivided style-tips) triangular, obtuse, more or less spreading, subentire, c. 0.4–0.7 mm. long.

Capsule not seen entire; valves c. 4 mm. long, dark reddish brown, not veiny. Columella 2.7 mm. long. Seeds (not seen fully mature) somewhat asymmetrically trigonous, c. 4 mm. long and 2.5 mm. radially and tangentially, light brown with irregular rows of slightly raised dark reddish-brown dots; hilum ovate-triangular.


TYPE: Martinique, Herb. Poiret.

DISTRIBUTION: forested regions, Martinique (MAP XXXIII).

MARTINIQUE: without specific locality, Herb. Lamarck (G, P); Herb. Poiret (P, TYPE COLLECTION); Sieber Fl. Martin. 224 (F, GOET, MO, P, W); Hauteurs de la Grand-Rivière, de Case-Pilote, Morne-Rouge, 1880, 1899, Duss 53 (F, GH, MO, NY, US), 4057 (NY, US); Hauteur de la Case-Pilote, July 1870, Hahn 323 (K, P); Case-Naoire, collines peu buisées, Feb. 1868, Hahn 406 (A, G, P); same locality, Feb. 1869, Hahn 643 (P); taillis a lisiers forestiers et alturales, Morne Vert, Bernadette, alt. 560 m., 17 July 1942, Stehle 5065 (F).
In its occurrence in moist forested regions of northern Martinique, *P. ovatus* conforms with the ecological preference of other species of the section. According to Stehle it is found at the margin of the forest, and is thus heliophilous as well as mesophytic. The species is certainly very distinct but is perhaps most closely related to *P. maleolens*, from which it differs in its tomentulose axes, thinner more pointed leaves, thickened female pedicel, and connate nearly entire styles. Also related to *P. ovatus* is *P. megapodus*, which has somewhat similar female flowers but which vegetatively is much closer to *P. mimosoides* and *P. acacioides.*

As was pointed out previously (Contr. Gray Herb. 176: 62. 1955), the referral of *P. ovatus* to *Glochidion* by Pax and Hoffman on the basis of its undivided styles is unjustified, since it contradicts all other indications of affinity. Mueller was correct in reversing himself as to the generic disposition of this species, even though he did not place it in the proper circle of relationship. There is indeed a certain similarity between the stylar column of *P. ovatus* and the much shorter one of *P. botryanthus* (the species associated with it by Mueller), but the two species are only distantly related, and the gynoecial resemblance must be ascribed to parallel evolution.


Shrub or small tree up to 3–5 m. high, presumably with the habit of *P. mimosoides*. Cataphylls indurate, densely tomentulose: stipules and blade triangular-lanceolate, recurving, c. 2.5–3 mm. long. Deciduous branchlets bipinnatif form: primary axis 20–40 cm. long, 2–3 mm. thick, sparsely tomentulose and soon glabrate, smooth, terete, with (6–) 10–18 nodes; first internode 50–130 mm. long, median internodes mostly 15–40 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, appressed or reflexed, subindurate, triangular-lanceolate, c. 2.5–4 mm. long, 1.5–2.5 mm. broad, acuminate (but tip often broken off), auriculate at the base, densely reddish-tomentulose (when young; more or less glabrate in age); blade lanceolate, usually spreading or reflexed, reddish-tomentulose, c. 2–3 mm. long. Ultimate axes ascending, (5–) 7–15 (–18) cm. long, 0.8–1.3 mm. broad, olivaceous or stramineous, flattened ventrally (above) and angular-convex dorsally (beneath), with ribs deciduous from stipules on both sides, smooth and glabrous, with (13–) 15–25 (–27) leaves; first internode (1–) 3–7 mm. long, median internodes 4–9 mm. long. Leaves: stipules more or less deciduous, not reflexed, scarious, lanceolate, c. 1–1.8 mm. long, reddish, more or less ciliate at apex and on margins (tomentulose when young), decurrent at the base. Leaf-blades subsessile (petioles ill-defined, c. 0.5 mm. long or less), chartaceous, smooth on both sides, asymmetrically broadly oblong or obovate, sub-
falcate, (12–) 18–30 mm. long, (5–) 8–15 mm. broad, obtuse or rounded and apiculate at the tip, at base oblique on adaxial side; above olivaceous, minutely foveolate, veins inconspicuous; beneath midrib conspicuously raised, lateral veins (c. 7 or 8 on a side) straight and slightly raised, veinlets completely obscure; margins not especially thickened, plane or recurved.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules with 1–5 male flowers; distal cymules either male or of a solitary female flower, or sometimes bisexual (with 1 female and 1 or 2 male flowers).

Male flower: pedicel slender, 3–5 mm. long. Calyx whitish; calyx-lobes 5, membranous, somewhat spreading, broadly elliptic to obovate, subequal, c. 1.8–2.5 mm. long, 1.3–2.1 mm. broad, obtuse or rounded at the tip, entire, midrib unbranched. Disk-segments 5, roundish, rather thin, entire, c. 0.3–0.5 mm. across. Stamens 3; filaments connate into a column c. 0.5–0.8 mm. high; anthers subsessile atop the column, discrete, emarginate, c. 0.3 mm. long and 0.6–0.7 mm. broad; anther-sacs spheroidal, divaricate, dehiscing horizontally, slits not apically confluent; pollen grains c. 21–24 µ in diameter, with c. 15 areoles per amb.

Female flower: pedicel at anthesis c. 1.5–2 mm. long, terete and slender at the very base but above greatly dilated, obpyriform, fleshy, as broad as or broader than the calyx; fruiting pedicel c. 3–4 mm. long and 1.3–2.2 mm. broad (when dried). Calyx-lobes 5, thick and fleshy, at anthesis stiffly erect and imbricate-connivent around the ovary, elliptic to obovate (becoming obovate-oblong in fruit), c. 1.8–2.5 mm. long and 1.2–2 mm. broad, obtuse at the tip, entire, midrib unbranched. Disk nearly obsolete (scarcely 0.1 mm. high, or less, with 5 small points alternating with the calyx-lobes). Ovary oblate-spheroidal, smooth; styles erect, united into a massive column c. 2 mm. high and nearly as broad; style-branches reduced to blunt apical projections or becoming up to 1 mm. long.

Capsule not seen entire; valves c. 5.5 mm. long. Columella massive,
2–2.8 mm. long. Seeds (not seen mature) slightly over 3 mm. long, with evenly spaced slightly raised reddish-brown dots.

**Type:** Martinique, *Sieber Fl. martin. 396.*

**Distribution:** Dominica and Martinique, probably in upper montane rain-forest (Map XXXIII).

**Dominica:** forest clearings or along river, Fon Puy, a lesser peak of the western ridge of Morne Diablotin, alt. c. 1000 m., 14 Apr. 1940, W. & B. Hodge 2841 (GH); forest, Hampstead, 1903, Lloyd 640 (F, NY).

**Martinique:** *Sieber Fl. martin. 396* (W, holotype; BR, G, L, MO, P, isotypes).

In Dominica *P. megapodus* is apparently a rare plant of the upland rain forests, where it appears to replace the much more common lowland species, *P. mimosoides*. It is not yet clear, however, whether the replacement is so complete that the two species are allopatric. The record from Martinique requires confirmation, since it is not certain that all the plants distributed by Sieber under the “Flora Martinicensis” or “Flora Trinitatis” labels were actually collected on those two islands. Of course, if *P. megapodus* is as uncommon on Martinique as on Dominica it may have escaped detection since the visit of Sieber’s collector, Kohaut.

Although in aspect it resembles *P. mimosoides* so markedly that Mueller interpreted it as merely a large-leaved form, *P. megapodus* has very different female flowers which are much more like those of *P. ovatus*. Vegetatively *P. megapodus* is well distinguished from *P. mimosoides* having fewer than 20 ultimate axes per branchlet instead of 30–60 or more, tomentulose branchlet cataphylls, and larger leaves. From *P. ovatus*, *P. megapodus* differs in its non-exserted stylar column, smaller asymmetrical leaves, and especially in its hypertrophied female pedicel. In the last feature *P. megapodus* appears to represent the generic extreme, although it is somewhat approached by the thickened pedicel of *P. acacioides*.

76. **Phyllanthus mimosoides** Sw. Prodr. 27. 1788; Fl. Ind. Occ. 1101–1102. 1800; Muell. Arg. in DC. Prodr. 15(2): 380–381. 1866.

(Diagram XXXI, figs. I–J).

**Diasperus mimosoides** (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

Shrub c. 1–5 m. high, with a slender usually unbranched trunk and a terminal crown of leafy branchlets; stem apex ferruginous-tomentulose, older parts glabrate. Cataphylls indurate; stipules triangular, recurving, c. 2–2.5 mm. long, becoming acropetally displaced to flank the base of the branchlet; blade c. 1.5 mm. long. Deciduous branchlets bipinnatifid; primary axis (20–) 30–70 (–100) cm. long, 2–4 mm. thick, more or less ferruginous-tomentulose (proximally becoming glabrate), terete, with (20–) 30–60 (–100) nodes; first internode (25–) 40–100 (–130) mm. long, median internodes (5–) 7–15 (–20) mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, not reflexed, more or less indurate, lanceolate, (2–) 2.5–4 mm. long, 0.7–1.3 mm. broad, acuminate,
stramineous or reddish, with a dark sharply demarcated subtriangular fleshy basal area; blade thinner, scarious, linear-lanceolate, attenuate-acuminate, sometimes obscurely marginally ciliate below, mostly 2–3.5 mm. long and 0.2–0.5 mm. broad. Ultimate axes ascending, (3–) 5–10 (–12) cm. long, 0.5–0.9 mm. broad, olivaceous, flattened and angled with sharp ridges decurrent from stipules, smooth and glabrous (except for one or few tufts of hairs often present on internodal part of dorsal ridge), with (20–) 30–60 (–80) leaves; first internode c. 1–1.5 (–2) mm. long, median internodes c. 1–3 mm. long. Leaves: stipules persistent, not reflexed, scarious, lanceolate, mostly 1–1.5 (–1.8) mm. long, acuminate, decurrent at the base (adaxial margin running down center of the axis as a ridge). Leaf-blades subsessile (petioles only 0.2–0.4 mm. long), thinly chartaceous, smooth on both sides, asymmetrically oblong or oblong-ovobovate and often falcate, c. 5–11 (–13) mm. long, 2–4 (–6) mm. broad, mostly rounded or subtruncate and apiculate at the tip, at base abruptly oblique on adaxial side and straight on abaxial side; above olivaceous, minutely foveolate, veins obscure; beneath pallid, midrib slightly raised and running out into apiculum, lateral veins (4–6 on a side) ascending, straight, inconspicuous or quite obscure; margins unthickened, plane or slightly revolute.

Monoecious; cymules axillary, on ultimate axes of branchlet; proximal cymules with usually 1 or 2 male flowers; distal cymules male or a few with a single female flower, this solitary or accompanied by 1 or 2 males; bracteoles fimbriate.

Male flower: pedicel capillary, 1–3.5 mm. long. Calyx whitish; calyx-lobes 5, thin and scarious-membranous, spreading, oblong-elliptic to broadly elliptic (outer lobes narrower), (0.8–) 1–1.5 mm. long, c. 0.5–1.3 mm. broad, obtuse at the tip, entire, midrib unbranched (or branches very obscure), usually somewhat raised on ventral surface. Disk-segments 5, roundish, flattened, smooth, entire, c. 0.2–0.3 mm. across. Stamens 3; filaments connate into a stout or slender column 0.2–0.8 mm. high; anthers subsessile atop the column, discrete, very broadly ovate, obtuse, emarginate, 0.2–0.3 mm. long, 0.3–0.6 mm. broad; anther-sacs divaricate, dehiscing horizontally, the slits apically contiguous, discrete or confluent; pollen grains 16–18 μ in diameter, with c. 7–10 polybrochate areoles per amb.

Female flower: pedicel scarcely evident at anthesis, in fruit becoming 0.5–1.5 (–2) mm. long, smooth, terete, not markedly dilated above. Calyx whitish; calyx-lobes 5, thin and membranous or scarious, spreading from anthesis onwards, subequal, elliptic-oblong to obovate or spatulate, c. 1.5–2.5 mm. long (or up to 3 mm. long in fruit), 0.4–1.5 mm. broad, obtuse and entire at the tip, midrib unbranched. Disk divided into 5 reddish-brown linear to filiform segments 0.2–0.5 mm. long (or the smaller one or two reduced to short points). Ovary spheroidal, deeply sulcate; styles united below into a column 0.3–0.8 mm. high (or sometimes nearly free), ascending or spreading, the free ends c. 1.5–2 mm. long, divided ½
to \( \frac{3}{2} \) their length into two slender divergent, often twisted terete branches with bluntly pointed tips.

Capsule oblate-spheroidal, c. 4–5 mm. in diameter, olivaceous or dark reddish-brown, not veiny. Columella slender, 1.2–2.5 mm. long. Seeds trigonous, sometimes rather asymmetric, 1.5–2.5 mm. long, 1.2–2 mm. radially and tangentially, light brown with evenly spaced slightly raised reddish-brown dots; hilum rounded-triangular, 0.7–1 mm. across.

Collected in flower Feb.–Oct.; in fruit Feb.–Aug.

TYPE: Antigua, de Ponthieu (ex Swartz, 1788). The type collection is probably represented by the Ponthieu collection in the herbarium of the Conservatoire Botanique (G), and by a fragment in Swartz's herbarium (S); but neither of these has any definite indication of locality. A sheet collected by Ponthieu on Dominica and cited by Swartz in the “Flora Indiae Occidentalis” was examined at the British Museum; but this can hardly be considered the type. Since the sheet at Geneva has been annotated as “peut-etre l'échantillon dulequel Swartz a fait la description” and since it is a more ample specimen than that at Stockholm, it is here chosen as the lectotype.

DISTRIBUTION: rain-forest areas, Lesser Antilles (Map XXXIII).

ANTIGUA: de Ponthieu (G, lectotype; S, isotype; both presumably from Antigua).

MONTSERRAT: Ryan (BM, C); Fergus Mountain, Shafer 340 (F, NY); West (W).

GAUDELOUPE: without specific locality, Duchassaing (C, GOET, P), L'Herminier (P), Perrottet (G), Quentin 389 (P), Richard (P); Bassin Bleu, Duss 208 (P); Bois des Bains-Jaunes, du Matouba, de Bouillante, etc., alt. 450–990 m., Duss 2445 (F, GH, NY, US); Matouba, Forstrom (S); Sofaya, above Ste. Rose, alt. 700 m., Holdridge 449 (NY); Ste. Rose, alt. 20 m., Ouestel 852 (US); Plateau du Palmiste, Rodriguez 4669 (A, P); mornes basaltiques, Honelmont, Stehlé 205 (US); hauteurs de Vernon, Petit-Bourg, alt. 450 m., Stehlé 266 (A, S, US); Comperon près Font arabe, alt. 200 m., Stehlé 2630 (US).

DOMINICA: without specific locality, Bryant (NY), Fishlock 35 (NY), Imray 315 (GOET), de Ponthieu (BM), Ramage (BM); St. Hilaire Trace, alt. 300 m., J. S. Beard 645 (A, US), P. Beard 1460 (S); Sugarloaf prope Prince Rupert, Eggers 770 (G, GOET, P, W), 1064 (US); bank of St. Mary's River, at mouth of Pegoua River, Hatton Garden Estate, near sea level, W & B. Hodge 3075 (GH); along stream 1 mile north of Calibishie, W. & B. Hodge 3172 (GH); Carib trail from Salybia to Hatton Garden, W. Hodge 3219 (GH); Pegoua River, Deux Branches, Concorde Valley, W. & B. Hodge 3439 (GH); Hampstead River, c. 2 miles from mouth, La Chaudière, alt. 100 m., W. & B. Hodge 3558, 3662 (GH).

MARTINIQUE: dans le haut de la rivière de la Grande-Rivière, Duss 2045 (NY).


By far the commonest and most widespread species of the section, P. mimosoides is apparently the only one which has been taken into cultivation, where it has attracted the interest of morphologists; illustrations
showing its distinctive habit have been published by Goebel (Organogr. Pflanz. 84. 1898) and Troll. The species is abundant on Guadeloupe, where it is called “batard de fougere”, and Dominica, where it is referred to as “tamarin grand bois”. According to Beard (Nat. Veg. Windward & Leeward Isl. 106. 1949) it forms an extensive ground stratum in the secondary rain-forest on Montserrat. On Martinique, in contrast, Duss (Fl. Phanerogam. Ant. Fr. 23. 1897) found it very rare; and the species has presumably become extinct on Antigua. The record of Wickström (Kgl. Vet. Acad. Handl. [Stockholm] 1825: 423. 1826) from St. Barthélemy, based on a Forsstrom collection, is surely erroneous and perhaps was based on misdetermined specimens of P. amarus which are preserved in the Riksmuseet, Stockholm. One would in any event not expect a mesophytic species such as P. mimosoides to occur on a low barren island such as St. Barthélemy. The collection from Trinidad, Sieber 153, offers greater difficulties. It is possible that this record is correct, but unless the collection was made from a cultivated plant it represents a remarkable range extension. The failure of subsequent collectors to encounter the plant on Trinidad suggests that Sieber’s locality may be erroneous, and in any event the record needs confirmation.

In view of its wide distribution, it is not surprising that P. mimosoides is a rather variable species; the populations on each island tend to be somewhat different from those on neighboring islands. The plants of Dominica are perhaps the most divergent, differing from those of Guadeloupe and Montserrat in their somewhat larger leaves, flowers, and seeds. Some characters, such as the size of male flowers and degree of stylar union, appear to be intrinsically variable in all populations. However, even those which show some geographical correlation are not sufficiently well-marked to justify the recognition of subspecific taxa.

Although P. acacioides is vegetatively quite similar to P. mimosoides, its female flowers (as noted in the key) are so different that there can be no doubt the two species are perfectly distinct. There is also an obvious resemblance between P. mimosoides and P. megapodus, but the latter is not only vegetatively different but also has female flowers which are even more dissimilar than are those of P. acacioides. It is possible that the larger size of vegetative and floral parts in the Dominican population of P. mimosoides may be partly attributable to hybridization with P. megapodus, although there is no direct evidence for this, but in any event this would not prove that P. megapodus is the most closely related species. The sum of the evidence would appear to suggest that P. mimosoides is closest to P. acacioides in morphological characters, but is distinctly isolated even from that species.


Slender shrub with habit of P. mimosoides, up to 4 m. high; stem densely reddish-tomentulose near apex, glabrate below. Cataphylls indurate: stip-
ules triangular, appressed, acuminate, c. 2 mm. long; blade lanceolate, convex, nearly 2 mm. long. Deciduous branchlets bipinnatifid; primary axis c. 30–50 cm. long, 1.5–2 mm. thick, reddish- or purplish-tomentulose, becoming more or less glabrate, scabridulous, terete, with c. 40–70 nodes; first internode 15–25 mm. long, median internodes 5–9 mm. long. Leaves of primary axis reduced to cataphylls: stipules persistent, not reflexed, more or less indurate, triangular or triangular-lanceolate, c. 1.2–1.8 mm. long, 1–1.7 mm. broad, acuminate, stramineous or reddish, entire and glabrous, with dark fleshy basal area as in P. mimosoides; blade about as long as stipules, lanceolate, long-acuminate, strongly convex on back. Ultimate axes ascending, 5–11 cm. long, 0.5–0.6 mm. broad, purplish-brown to olivaceous, more or less flattened and bluntly angled with ridges current from the stipules, glabrous (occasionally with a few deciduous tufts of hair proximally), usually scabridulous, with 35–60 leaves; first internode 1.5–2.5 mm. long, median internodes 1.5–3 mm. long. Leaves: stipules persistent, not reflexed, scarious, lanceolate, 1–1.3 mm. long, 0.2–0.3 mm. broad, acuminate, marginally ciliate when young (otherwise glabrous), adaxially decurrent at the base. Petioles 0.3–0.5 mm. long. Leaf-blades subchartaceous, asymmetrically oblong- or obovate-falcate, c. 6–11 mm. long, 2–4 mm. broad, obtuse or abruptly subacute at the tip (apiculum more or less deciduous), at base oblique on adaxial side and straight on abaxial side; above olivaceous, smooth, veins obscure; beneath pallid (albescent), finely and densely scabridulous, midrib raised and running to tip, lateral veins obscure; margins somewhat thickened, plane or reflexed.

Monoeious; cymules axillary, on ultimate axes of branchlet; cymules mostly bisexual, of 1 female and 1 or 2 male flowers, but perhaps sometimes unisexual; leaves subtending flowers at branchlet tip sometimes reduced to scales.

Male flower: pedicel capillary, c. 2.5–5 mm. long. Calyx-lobes 5, chartaceous, elliptic or obovate, c. 1–1.3 mm. long, 0.7–1 mm. broad, obtuse or rounded at the tip, entire, midrib unbranched. Disk-segments 5, roundish to cuneate, somewhat fleshy, smooth, entire, c. 0.25–0.4 mm. across. Stamens usually 5 (rarely 4 or 6); filaments completely connate into a stout column 0.3–0.5 mm. high; anthers subsessile, one or two slightly displaced in rare androecia of 6 stamens, anthers in two superposed whorls, discrete, ovate, obtuse, c. 0.2 mm. long, 0.2–0.3 mm. broad; anther-sacs divaricate, flattened, dehiscing horizontally, slits apically contiguous but discrete; pollen grains c. 13–14 μ in diameter, with c. 5 or 6 polybrochate areoles per amb.

Female flower: pedicel c. 0.7–1.3 mm. long at anthesis, broadly dilated above. Calyx-lobes 5, thick and fleshy, at anthesis stiffly erect and imbricate-connivent around the ovary, broadly elliptic or ovate to suborbicular, c. 0.5–0.8 mm. long and broad, rounded at the tip, entire, midrib unbranched. Disk nearly obsolete (reduced to a tenuous ring with minute projections at angles). Ovary smooth, subspheroidal; styles united at the base into a very short and stout column, bifid c. 3/5 their length, in
bud erect and slightly protruding above the calyx, at maturity greatly elongating; styal branches flattened, becoming 2–2.5 mm. long. tapering from base to the acute tips, sharply reflexed on outside of calyx.

Capsule not seen entire; valves c. 3 mm. long, reddish-brown. Seeds trigonous, c. 1.5 mm. long, light brown.

**TYPE:** Tobago, *Eggers 5840.*

**DISTRIBUTION:** endemic to Tobago (Map XXXIII).

**TOBAGO:** near Lot 42, shaded cool places, 21 Apr. 1913, *Broadway 4189* (F, G, GH, MO, W); in sylvis Montis Morne d’or, alt. 500 m., *Eggers 5840* (K, lectotype); St. George–Castara Road, 27 May 1930, *Marshall* (TRIN 12384).

Broadway described this plant as a gregarious single-stemmed shrub with the appearance of *Jacaranda caerulea* and growing in shaded cool places. The female flowers are remarkable for the great change in styal configuration associated with anthesis; in the bud the styles are erect and protrude slightly above the calyx, but at anthesis they elongate greatly and recurve abruptly so that they are appressed to the outside of the rather fleshy calyx.

Although not all the diagnostic characters cited by Urban are dependable, *P. acacioides* clearly differs from *P. mimosoides* not only in its distinctive styles but also in its reduced female disk, pentamerous androecium, and whitened scabridulous undersurface of leaf-blade. Because of its distribution, *P. acacioides* might be taken for an outlying species derived from a disjunct population of *P. mimosoides*. However, the fact that the female flower of *P. acacioides* shows a greater resemblance to that of *P. ovatus* than it does to that of its “sister” species shows that great caution must be observed in proposing phylogenetic speculations. Thus although *P. mimosoides* is overall the species most similar to *P. acacioides*, it should not be regarded as necessarily its direct ancestor.


*Xylophylla* L. Mant. 2: 147–148. 1771.
*Hexadema* Raf. Sylva Tellur. 92. 1838.
*Lomanthes* Raf. ibid.

Shrubs or small trees with phyllanthoid branching; axes smooth and glabrous; cataphylls of main stem indurate, clustered at the apex in a scaly cone; branchlets bipinnatifid with ultimate axes transformed into usually leafless phylloclades, or (in *P. epiphyllanthus*) entire branchlet converted into phylloclade; nodes represented by marginal notches, leaves usually all reduced to scales, occasionally well-developed. Monoecious;
cymules unisexual or bisexual, produced at notches of phylloclades. Male flower: calyx-lobes 6 (rarely 5); disk-segments usually 6 and discrete; stamens normally 3 or rarely 4 (very rarely 5), filaments united at least at the base; anthers dehiscing more or less horizontally; pollen grains globose, areolate. Female flower: calyx-lobes 6 (rarely 5); disk of discrete segments or cupuliform to urceolate; styles free or connate below, style branches often again lobed or bifid. Capsule oblate, smooth to tuberculate; seeds trigonous or sometimes (when only 1 per locule) ovate and flattened, verruculose.

**Type species:** *Phyllanthus epiphyllanthus* L. (*Xylophylla latifolia* L., ex p.).

This West Indian section of about 10 specific and subspecific taxa includes some of the most familiar representatives of the genus; the type species, *P. epiphyllanthus*, was the first American member of the genus to become well-known in Europe. Because of their unusual morphological features, plants of sect. *Xylophylla* have received considerable attention from both horticulturists and morphologists, but except in the little-quoted work of Dingler (Flachsprosse der Phanerogamen. 1885) few attempts have been made to understand the evolution and relationships of the phylloclade-bearing species of *Phyllanthus*.

As here construed, sect. *Xylophylla* has a circumscription narrower than that of Mueller (DC. Prodr. 15[2]: 427-432. 1866) or Pax and Hoffman (Naturl. Pflanzenfam. 19c: 64-65. 1931). These authors included, in addition to the West Indian species, four or five phyllocladiferous Brazilian species such as *P. klotzschianus* and *P. flagelliformis*. Convergent evolution has progressed so far that on superficial inspection certain forms of *P. klotzschianus* and *P. montanus* might almost appear to be conspecific. However, an attentive examination of the flowers belies this impression, for the flowers of the Brazilian species differ in many details, including their deeply emarginate anthers, and their tricolporate coarsely reticulate pollen grains are completely different from the areolate grains of the West Indian species. It therefore appears certain, as suggested earlier in this study (Jour. Arnold Arb. 37: 111. 1956), that the Brazilian species have evolved phylloclades quite independently of the West Indian ones; they are to be transferred to sect. *Choretropsis*.

As emended, sect. *Xylophylla* comprises only West Indian species, all except two of which are confined to Jamaica. At the present time sect. *Xylophylla* gives the appearance of a successful group in which evolution is probably actively in progress. Several of the species, particularly *P. epiphyllanthus* and *P. angustifolius*, occur in large and conspicuous populations, which show signs of incipient speciation. The representatives of the section afford a most interesting epitome of the evolutionary process as it occurs in many groups of higher plants on the Caribbean islands, and merit more intensive study than has been accomplished here.

The relationships of sect. *Xylophylla* are plainly closest to sects. *Epistylium* and *Hemiphyllanthus*, the former appearing to be the group from
which both sect. *Xylophylla* and sect. *Hemiphyllanthus* were derived. An hypothesis of the probable origin of bipinnatifid branchlets has already been mentioned under the latter group. The peculiar branchlet structure of sect. *Xylophylla* is thus a specialization involving the replacement of the original leaves of a bipinnatifid branchlet by the expanded axes themselves. However, the relationship of *P. montanus*, the most primitive species of sect. *Xylophylla*, to *P. cauliflorus* and *P. axillaris* of sect. *Epistylium* is so striking that it seems possible that sect. *Xylophylla* may have arisen from sect. *Epistylium* coordinate with, rather than derived from, the less specialized sect. *Hemiphyllanthus*.

In order to make clear the homology between the branchlets in the present section and those in sect. *Hemiphyllanthus*, the terminology used for vegetative structures in the species descriptions has been slightly modified from that presented in the introductory section of this study. The compound phylloclade, as illustrated in text-fig. 5, is here described as a branchlet with the ultimate axes transformed to phylloclades, the branchlets of all species of sect. *Xylophylla* being regarded as modifications of bipinnatifid branchlets as in sect. *Hemiphyllanthus*. In *P. montanus*, which is the most primitive species of sect. *Xylophylla*, the primary branchlet axis is unmodified and the term phylloclade is applicable only to the lateral ultimate axes. In *P. angustifolius* the primary axis is flattened and as green as the ultimate axes, so that the branchlet of this species can be regarded as a truly compound phylloclade. Finally, in the most specialized species, *P. epiphyllanthus*, the lateral axes are suppressed and the dilated primary axis of the branchlet serves directly as a simple phylloclade.
Although it cannot be used as a key character, due to its relative infrequency of occurrence, the production of leaves on the usually leafless phylloclades of sect. *Xylophylla* is a phenomenon of some taxonomic interest; the tendency toward suppression of leaves parallels, as might be anticipated, the trend toward an increasingly leaf-like character of the branchlet axes. In *P. montanus* leaves commonly occur on seedling phylloclades and sprout-shoots and, in a diminutive form, may sometimes be produced on normal branchlets. In *P. latifolius* and *P. angustifolius* leaves normally occur on seedlings and also appear on wound-shoots, and this is probably true of *P. proctoris* as well. In *P. arbuscula* and *P. epiphyllanthus*, on the other hand, leaves have never been observed at any stage in ontogeny.

The identification and taxonomic analysis of the Jamaican species of sect. *Xylophylla* is beset with a number of practical difficulties due to the high percentage of sterile specimens; flowering in some species appears to be erratic and infrequent. The key has been constructed with this in mind and should be workable even for sterile specimens as long as they are not sprout-shoots or unusual modifications.

**KEY TO THE SPECIES**

1. Phylloclades borne distichously on main axis of deciduous branchlet.

2. Branchlet slow-growing, rather long-persistent, main axis greyish or brownish, not colored as the phylloclades; pedicel of female flower 0.5–1.5 mm. long. 78. *P. montanus*

2. Branchlets expanding rapidly, not long-persistent, main axis greenish and of consistency of lateral axes (phylloclades).

3. Pedicel of female flower only 0.5–1.5 mm. long; disk of female flower dissected into lobes or segments; phylloclades more or less rhombic-lanceolate, with mostly 20–50 nodes; apical cone 10–15 mm. broad, cataphylls scarcely or not ciliate 79. *P. latifolius*

3. Pedicel of female flower mostly 2 mm. long or more; disk of female flower entire; phylloclades elliptic- to obovate-lanceolate.

4. Cataphylls of main axis remaining brown or grey, ciliate (if at all) only toward the base; phylloclades mostly 1–2 cm. broad with 20–40 nodes; ovary smooth. 80. *P. arbuscula*

4. Cataphylls of main axis becoming dark or blackish-brown, copiously ciliate on margins at least when young; phylloclades mostly 0.5–1 cm. broad with 10–25 nodes, often subopposite at end of branchlet axis.

5. Phylloclades (floriferous axes) lanceolate, mostly well over 3 mm. broad, with (8–) 10–20 (24) nodes; styles not dilated, the ends 3–5-fid into slender tips. 81. *P. angustifolius*

5. Phylloclades (floriferous axes) narrowly linear, only 1–3 mm. broad, with 7–10 (13) nodes; styles dilated and flattened, ends merely crenulate, forming a sort of calyptra over the ovary. 82. *P. proctoris*

1. Phylloclades each representing an entire branchlet, borne scattered directly on main stem. 83. *P. epiphyllanthus*

*Xylophylla montana* Sw. Prodr. 28. 1788.

*Diasperus montanus* (Sw.) O. Ktze. Rev. Gen. 2: 600. 1891.

Shrub or small tree, usually c. 2–5 m. high; branches 2–8 mm. thick, terete, smooth, greyish-brown. Apical cone inconspicuous, c. 2 mm. long and 2–2.5 mm. broad; cataphylls deciduous, pale, thickened, deltoid, not over c. 1.5 mm. long, blunt, entire; blade about as long, massive. Branchlets ascending, bipinnatiform, ultimate axes transformed into phylloclades; primary (penultimate) axis 5–30 (–40) cm. long, 1.5–3 mm. broad, proximally terete, distally often flattened, greyish or brownish, with 7–20 (–30) lateral axes; first internode (0.5–) 1.5–4 cm. long, median internodes mostly 0.5–2 cm. long. Cataphylls of primary axis subpersistent or deciduous; stipules ovate, thickened, mostly 1–1.5 mm. long, blunt, entire or sparsely ciliate; blade shorter or about as long. Phylloclades flexible or rather stiff, elliptic to lanceolate (rarely linear-lanceolate), obtuse to long-attenuate at the tip, 3–20 cm. long, 0.5–3 cm. broad, with 10–30 (–50) slightly notched nodes; midrib conspicuous, more or less plane or salient beneath, veins tenuous and not very prominent; margins slightly (if at all) differentiated. Euphylls rarely produced except on sprout-shoots, blade elliptic, up to 11 mm. long and 6 mm. broad, obtuse or subacute at the tip, acute at the base, distinctly paler beneath, midrib prominent but veins and veinlets rather obscure. Cataphylls of ultimate axes reddish brown, scarious with often narrow, paler margins; stipules suborbicular-ovate, auriculate, 0.5–1.3 mm. long, 0.4–0.8 mm. broad, subentire or denticulate; blade subulate, less than 1 mm. long.

Monoecious; cymules usually bisexual, pulviniform, each with a single (rarely 2) female flower and c. 3–12 male flowers.

Male flower: pedicel slightly thickened, stiff, 1–3 mm. long. Calyx usually reddish-tinged; calyx lobes 5, chartaceous or hard-scarious, erect to somewhat spreading, unequal, one or two outer lobes usually elliptic to ovate, less than 1 mm. long, inner lobes suborbicular, c. 1.5 mm. long and broad, blunt-tipped, midrib simple or very sparsely branched above. Disk-segments 5, rather massive, roundish concave, c. 0.4–0.5 mm. across. Stamens 3; filaments completely connate into a column c. 0.5 mm. high; anthers sessile atop the column, broadly deltoid, blunt or emarginate, c. 0.2–0.25 mm. long and 0.3–0.4 mm. broad; anther-sacs dehiscing horizontally; pollen grains 17–21 μ in diameter.

Female flower: pedicel stout, c. 0.5–1.5 mm. long. Calyx greenish or (ex Swartz) dark purplish; calyx-lobes 5 or 6, at anthesis somewhat fleshy and erect, becoming scarious and spreading in fruit, subequal (outer lobes narrower), c. 1–1.5 mm. long, 0.8–1.5 mm. broad, more or less denticulate, midrib unbranched. Disk divided into distinct thin, petaloid segments c. 0.2–0.3 mm. long. Ovary ellipsoid or oblate, smooth, shallowly sulcate; styles free, spreading or ascending, sometimes slightly recessed into the
top of the ovary, c. 0.3–0.5 mm. long, bifid, the tips blunt, sometimes dilated.

Capsule oblate, rounded-trigonus, c. 4 mm. in diameter, reddish brown, sometimes somewhat glaucous, rugulose, not veiny. Columella c. 1.8 mm. long. Seeds asymmetrically trigonous (plano-umbonate), 1.7–1.9 mm.

Maps XXXV–XXXVII. Distribution of some Jamaican species of sect. Xylophylla.

long, 1.2–1.4 mm. broad, reddish, verruculose with rather densely spaced slightly raised dots; micropylar end sometimes carunculate.


Type: western Jamaica, Swartz (s, holotype).
**Phyllanthus montanus** is a species with most interesting features, since it clearly is the most primitive living representative of sect. *Xylophylla* and furthermore is obviously related to the species of sect. *Epistylium*. The primary axis of the branchlet of *P. montanus* is so similar to the branchlet of *P. axillaris*, even to the stipules, that a reasonably close affinity between the two species seems undeniable. One difficulty in assessing the relationships of *P. montanus* is that it is an extraordinarily variable species in its vegetative features. Specimens from Peckham Woods, which have short, often twisted branchlets with short lateral axes, scarcely suggest any relationship to a species of sect. *Epistylium*, but two unusual collections made near Somerset by Proctor have long primary axes with an unmistakable resemblance to those of *P. axillaris*. Despite these differences, intraspecific variability of *P. montanus* does not appear to show any definite geographic correlation, and there is no necessity to describe subspecific taxa.

Although it is the most isolated species in the section, *P. montanus* shows certain points of resemblance to *P. latifolius* — specifically, the short pedicels and dissected female disk — which suggest that the latter is its closest relation within the section. However, *P. latifolius* is vegetatively much more like the other species of the section in having a definitely modified primary branchlet axis, and its relation is certainly not very close.

79. **Phyllanthus latifolius** Sw. Fl. Ind. Occ. 1109. 1800.  
(PLATE XXXI, figs. O–P; PLATE XXXII).

*Xylophylla latifolia* L. Mant. 2: 221. 1771 (ex p.; excl. typ.).  

Shrub or small tree c. 1–4 m. high; branches of current year's growth 3–5 mm. thick, terete, brownish or greyish. Apical cone conspicuous, c.
10–15 mm. long and broad, irregular in outline. Cataphylls of main axis deciduous, scarios-indurate; stipules lanceolate, (4–) 6–10 mm. long, acuminate, squarrose; blade 3.5–11 mm. long. Branchlets ascending, bipinnatifrom, ultimate axes transformed into phylloclades; primary axis (5–) 8–20 cm. long, (1–) 1.5–2 mm. broad, flattened, edges obtuse, olivaceous, smooth, with (4–) 7–12 (–15) lateral axes (phylloclades); first internode (1–) 2–4 (–8) cm. long, median internodes mostly 1–2 cm. long. Cataphylls of primary axis deciduous; stipules and blades linear-lanceolate, attenuate-acuminate, c. 1–2 mm. long, reddish brown, not ciliate. Phylloclades usually rigid, most often rhombic- or obovate-lanceolate but sometimes (especially on sprout-shoots) narrowly lanceolate, (3.5–) 5–8 (–10) cm. long, (0.7–) 1.5–3 cm. broad, narrowed (often abruptly so) to a blunt or sometimes caudate tip, with (15–) 20–50 (–60) nodes; midrib more or less prominent, veins steeply ascending, tenuose or subprominent; margins not differentiated. Euphylls occasional on sprout-shoots: blade obovate, c. 3–5 mm. long, acute at the tip and base, midrib rather prominent beneath but veins otherwise obscure. Cataphylls of ultimate axes suborbicular, convex, trifid, not over c. 0.5 mm. long, reddish brown, ciliate.

Monoecious; cymules male or (more often) bisexual, with 1 female and several (up to c. 10) male flowers.

Male flower: pedicel c. 1–3.5 mm. long. Calyx reddish; calyx-lobes 6, scarios-membranous, spreading (at least at the tips), subequal, obovate, c. 0.7–1.3 mm. long and 0.4–0.9 mm. broad (occasional outermost lobes greatly reduced), entire, midrib unbranched. Disk-segments 6, not pitted, c. 0.2–0.3 mm. broad. Stamens 3; filaments (0.5–) 0.7–0.9 mm. long, united below into a stout column c. 0.3–0.7 mm. high; anthers broadly ovate, emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther sacs dehiscing more or less horizontally, pollen grains 15–19 μ in diameter.

Female flower: pedicel 0.5–1.5 mm. long. Calyx reddish; calyx-lobes 6, scarios or chartaceous, spreading, obovate or suborbicular, 0.5–0.8 mm. long, 0.4–0.7 mm. broad, entire, midrib unbranched. Disk separated into 6 lobes or segments c. 0.2–0.4 mm. across. Ovary oblate or turbinate, siliate, smooth; styles basally connate into a short column 0.2–0.4 mm. high; style-tips spreading, c. 0.6–0.8 mm long, with mostly 3–5 lobes (occasional style-tips merely bifid).

Capsule oblate, c. 4 mm. in diameter, reddish brown, rugulose, not veiny. Columella c. 1 mm. long. Seeds asymmetrically trigonous, c. 2 mm. long, 1–1.2 mm. broad, reddish brown, verruculose with slightly raised dots.

Collected in flower June, July, Sept.; in fruit July.

Type: Jamaica, Browne (Herb. Linn. 1105–1 LINN; holotype).

Distribution: dry rocky areas, southern Jamaica (Map XXXVI).

Jamaica: without specific locality, Browne (LINN), Jacquin (BM), March (GH), Masson, Shakespeare (BM), St. Catherine: near Salt Island, Healthshire Hills, Britton 3058 (NY), Harris & Britton 10532 (JAM, US); 2 mi. NNW of Guanaboa Vale P.O., 900 ft., Proctor 7151 (MICH); Horse Cave, Hillshire Hills, Proctor 7602 (GH); near Bartons, c. 5 mi. north of Old Harbor, alt.
Habit of *Phyllanthus latifolius* Sw., growing on limestone hilltop near Barton's, St. Catherine Parish, Jamaica (Webster & Wilson 4862). Left-hand figure, $\times \frac{1}{10}$; right-hand figure, $\times \frac{1}{4}$. 


Phyllanthus latijolius has a relatively restricted distribution, being known thus far only from dry hills in St. Catherine and St. Andrew parishes, although it may eventually be found to overlap into Clarendon and St. Thomas. It is perhaps the most xerophytic species in the section, although some forms of P. angustijolius and P. epiphyllanthus also occur in similarly dry habitats. The detailed distribution of P. latijolius offers some interesting problems with regard to the interaction between species. On Long Mountain, it was found to occupy the dry, lower southwestern slopes, while P. angustijolius occupied the northeastern slopes of the relatively mesophytic woods on top. This suggests an ecological separation between the species, but in some areas (e.g., Portland Ridge) P. angustijolius grows in habitats which are the sort occupied by P. latijolius. It is striking that the two species have never been observed growing side by side, even where (as at Long Mountain) their populations are in close proximity; this mutual exclusiveness, which suggests the effects of competition, deserves to be investigated critically from the ecological point of view.

As has been mentioned above, P. latijolius approaches closer to P. montanus than any other species of the section. The characters which suggest such a relationship — the dissected female disk and short pedicel — are also the ones which serve to separate P. latijolius from its close relative, P. arbuscula. These two species have the same kind of cataphylls and rather similar phylloclades, but those of P. latijolius are often thicker, more rhombic, and with denser clusters of flowers. The plants of P. angustijolius which occur within the range of P. latijolius may usually be easily distinguished from "narrow-leaved" forms of the latter by their blackish, ciliate cataphylls and phylloclades with fewer nodes which are often paired at the branchlet-tip.

80. Phyllanthus arbuscula (Sw.) Gmel. Syst. 2: 204. 1791.

(PLATE XXXI, figs. Q–S).

_Xylophylla arbuscula_ Sw. Prodr. 28. 1788.
_Xylophylla angustijolia_ b. _linearis_ Sw. ibid.
_Phyllanthus linearis_ (Sw.) Sw. _Fl._ Ind. Occ. 1113. 1800.
_Xylophylla speciosa_ (Jacq.) Sweet, _Hort. Brit._ ed. 1. 360. 1827.
_Genesiphyla speciosa_ (Jacq.) Raf. _Sylva Tellur._ 92. 1838.
_Phyllanthus linearis a genuinus_ Muell. Arg. in DC. Prodr. 15(2): 430. 1866
(excl. descr.).
Phyllanthus coxianus Fawc. & Rend. ibid.
Phyllanthus swartzii Fawc. & Rend. ibid. 67.

Shrub or small tree up to 7 m. high, usually with a single main trunk and a few erect branches, these c. 3–5 mm. thick, smooth, light brown or greyish. Apical cone as broad as long, c. 5–10 mm. across, outline irregular due to exsertion of phyllocladal cataphylls; cataphylls deciduous, pale, thickened: stipules deltoid to lanceolate, 2.5–7 (–9) mm. long, 1–3 mm. broad, obtuse to acuminate, entire (rarely ciliate toward the base); blade deltoid to lanceolate, acuminate, about as long as the stipules. Branchlets ascending, bipinnatiform, ultimate axes transformed into phylloclades; primary axis (2.5–) 5–25 (–30) cm. long, 1–2.5 mm. broad, compressed and obtusely angled, adaxially sulcate, greyish green, with 4–16 lateral axes (phylloclades); first internode 1.5–5 (–6) cm. long, median internodes 0.5–2.5 mm. long. Cataphylls of primary axis mostly deciduous (occasional ones more or less persistent): stipules linear-lanceolate, (1.5–) 3–6 (–8) mm. long, acuminate, entire (or rarely sparsely ciliate toward the base), pale brown, basally auriculate; blade linear-lanceolate, about as long as the stipules. Phylloclades thin and flexible to somewhat rigid, elliptic to lanceolate, (2.5–) 4–11 cm. long, (0.5–) 1–2 (–2.7) cm. broad, tapering (sometimes abruptly) to an acute or acuminate tip, often paler (yellowish) beneath, with (10–) 20–40 (–50) conspicuously notched nodes; midrib and veins very often conspicuous and raised on both sides; margins usually with a distinctly differentiated rim running between notches. Euphyls never observed, even on seedlings. Cataphylls of phylloclades reddish brown, fragile and readily breaking off at the base, trifid (stipules united to the blade), tips acuminate, c. 0.5–1 mm. long; base auriculate, auricles ciliate-dentate.

Monoecious; cymules bisexual, of 1 female and c. 3 or 4 males, or proximal cymules male.

Male flower: pedicel capillary, (1.5–) 2–5 (–8) mm. long. Calyx cream-colored or greenish to scarlet; calyx-lobes 6 (rarely 5), membranous to coriaceous, more or less unequal, outer lobes obovate to elliptic and inner lobes ovate, or all lobes ovate, 1–2 mm. long, 0.8–1.8 mm. broad. Disk-segments 6, roundish, entire, thin, flat, c. 0.3–0.6 mm. across. Stamens 3; filaments 0.3–0.6 (–0.8) mm. high, united into a massive column 0.2–0.5 mm. high; anthers emarginate, 0.25–0.4 mm. long, 0.4–0.6 mm. broad; anther-sacs dehiscing horizontally; pollen grains c. 18–21 μ in diameter.

Female flower: pedicel thicker than in male, stiff, (2.5–) 3.5–10 (–14) mm. long at anthesis, increasing to 6–15 mm. long in fruit. Calyx-lobes cream-colored or greenish,* membranous to coriaceous, erect to spreading, c. 1–1.5 (–3) mm. long and broad (reduced outer lobes often smaller), obtuse (outer lobes sometimes with a brownish scarious tip), entire, midrib unbranched. Disk annular or shallowly cupuliform to urceolate and

* or scarlet in western populations.
enclosing the ovary, up to c. 1 mm. high. Ovary oblate, smooth; style free and spreading or basally united and then more or less erect, stylar column up to 1 mm. long; style-ends often twice bifid, tips with 3 or 4 lobes.

Capsule oblate, trigonous, c. 4–5 mm. in diameter, dark reddish brown, rugulose, not veiny. Columella 2–2.2 mm. long. Seeds asymmetrically trigonous (plano-umbonate), 2.7–3.3 mm. long, 2–2.5 mm. radially and tangentially, with irregular longitudinal lines of slightly raised reddish-brown dots.


**Type:** Jamaica, Catherine Hill, *Swartz* (BM, holotype; S, isotypes).

**Distribution:** upland areas, Jamaica (Map XXXVIII).

This species consists of some distinctive populations but no clear-cut subspecies. The specimens are cited according to these races, which are lettered but not named; the proposed species to which each race roughly corresponds is given in parentheses.

Race A. Calyx scarlet, fleshy or coriaceous, lobes erect; disk of female flower urceolate, enclosing the ovary; styles united into a column as high as or higher than the ovary; (*P. dingleri*).


Race B. Calyx scarlet, more or less coriaceous; disk of female flower partially enclosing the ovary; styles united into a definite column; seeds often 1 per locule; phylloclades often small and thick; (*P. coxianus*).


Race C. Calyx whitish, or partly pinkish-tinged, thin-textured; disk of female flower covering c. ½ ovary or less; styles slightly united or nearly free; phylloclades broad and thin; (*P. inaequaliflorus*).

Race D. Calyx whitish or greenish, membranous; disk of female flower covering less than $\frac{1}{2}$ the ovary; styles free or very nearly so, spreading; phylloclades usually broad and thin; (P. speciosus).

JAMAICA: without locality (probably St. Andrew), March (GOET), Swartz (S, probably ISOTYPE), Wright (W). ST. ANDREW: John Crow Peak, Bancroft (J.P. 1263) (JAM); Silver Hill, Hylton (JAM); Catherine Hill, Swartz (BM, HOLOTYPE). PORTLAND: Haycock Mt., above Balcarres, alt. 2750–3500 ft., Proctor 8074 (JAM); Spring Bank, 2.5 mi. WSW of Port Antonio, Proctor 6722 (MICH). ST. THOMAS: House Hill to Cuna Cuna Gap, alt. 550–725 m., Maxon 8966 (NY, US); Corn Puss Gap, Webster & Wilson 4893 (A, JAM, MICH); Mansfield, near Bath, alt. 300–500 m., Maxon 2404 (NY, US); Big Level, alt. 2200–2500 ft., Webster & Proctor 5517 (A, JAM, MICH).

The long synonymy of *P. arbuscula* is a good indication of the extraordinary variability of this common Jamaican species. For a long time an attempt was made by the writer to distinguish the species proposed by Fawcett and Rendle, first on the specific level and then on the subspecific. After prolonged consideration, however, any attempt to distinguish sub-

MAP XXXVIII. Distribution of *P. arbuscula* (Sw.) Gmel., showing variation in floral characters according to races described in text. Small circles indicate sterile specimens.

specific taxa within *P. arbuscula* has been abandoned, for although "subspecies" could be recognized and grouped in a key, this would give a misleading impression of permanence and solidity to what are more probably clines, rather than geographically delimited subspecies. If one compares a flowering specimen of the Dolphin Head race (A), with one from the Blue Mountains race (D), it appears at first glance that two different species are at hand; but if the specimens are taken instead from the area in the center of the island, between Troy and Mt. Diablo, serious difficulties immediately arise. All combinations of the characters mainly concerned (flower color and texture, female disk size, and stylar configura-
tion) can be found within a relatively small area. Thus, in Manchester parish, Proctor 11605 from Somerset represents "good" P. dingleri, with red flowers, urceolate female disk, and united styles; but the Brown and Wullschlægel collections from Mandeville and Fairfield are, despite their peculiar phylloclade shape, scarcely different from the typical form of the species in the Blue Mountains; and Stearn 387, with whitish flowers but united styles, is transitional to the Dolphin Head type. Similar examples could be added if it seemed necessary to elaborate the point, that the characters which appear so distinct at the two extremities of the island undergo "dissolution" in the center. The situation might possibly be interpreted as representing that of two extensively hybridizing subspecies, but the area of intermediates would probably be so large that such a classification would serve no useful purpose. The variation is so evidently clinal in character that it would be extremely interesting to map it in detail but, unfortunately, the large number of sterile specimens makes a thorough analysis impracticable at this time.

A character of especial interest is the common occurrence in plants of the Cockpit Country race (B) of capsules in which all or some of the locules produce only a single seed. As is usual in the Phyllantheae, the single seeds are so differently shaped that they look quite unlike the paired ones. Unfortunately, it is not yet possible to estimate the taxonomic importance of this feature because seeds are not known from the other three races. Thus far it appears that the production of solitary seeds is confined (in sect. Xylophylla) to P. arbuscula.

The name Xylophylla arbuscula, the basis for that here accepted for this species, was reduced by Swartz himself to the synonymy of P. speciosus Jacq., a course subsequent writers have followed. It has been assumed that Swartz withdrew his own name because of Jacquin's priority in publication, but Mr. William Stearn (personal communication) has discovered evidence that Swartz's name was actually the earlier. Swartz may have withdrawn his proposed name out of modesty or perhaps because Jacquin's was published under the correct genus; but in any event, the plant collected by Swartz in the Blue Mountains must take the name of P. arbuscula. Phyllanthus arbuscula is rather closely related to P. latifolius but, as has been discussed under that species, it clearly differs both in floral and vegetative characters. More closely related is the species from the John Crow Mountains which must unfortunately remain undescribed because of lack of floral material. In contrast, P. angustifolius is much less similar morphologically since it has dark, ciliate cataphylls, usually narrower indistinctly veined phylloclades with fewer nodes, and a rugulose ovary. However, at least one specimen (Webster & Proctor 5517) has characteristics intermediate between P. arbuscula and P. angustifolius, suggesting that it may represent a hybrid. The peculiar plant named P. linearis by Swartz may possibly represent a cross between P. proctoris and P. arbuscula; but narrow-leaved forms of the latter sometimes occur normally (e.g. March, GOET), so that in this case the situation is not entirely clear.

(PLATE XXXI, figs. T–U).


*Phyllanthus cognatus* Spr. Syst. 3: 23. 1826.

*Hexadena angustifolia* (Sw.) Raf. Sylva Tellur. 92. 1838.


*Phyllanthus linearis β cognatus* (Spr.) Muell. Arg. op. cit. 430.


Shrub up to c. 3 m. high; branches 2.5–5 mm. thick, reddish brown or greyish. Apical cone usually rounded in outline (cataphylls with tips parallel or inflexed) and c. 3–4 mm. in diameter, but sometimes up to 5 or 6 mm. in diameter and irregular, the cataphyll tips somewhat divergent (but not squarrose); cataphylls deciduous, light brown to blackish brown, scarious-indurate: stipules usually broadly ovate, c. 1.5–2 mm. long and about as broad, less commonly lanceolate and up to 5 mm. long, margins always copiously ciliate when young (becoming more or less glabrate in age); blade ovate to lanceolate, about as long. Branchlets bipinnatifid, ultimate axes transformed into phylloclades; primary axis 3–12 (–14) cm. long, 1.2–2.5 mm. broad, flattened with acute edges, pale green as phyllolocades, with 4–8 (–12) lateral axes; first internode (1–) 2–5 (–6) cm. long, median internodes mostly 0.5–2 cm. long. Cataphylls of primary axis usually with deciduous tips: stipules and blade lanceolate, not fused, c. 0.7–1.5 mm. long, copiously ciliate when young, becoming dark reddish brown and glabrate with a narrow whitish margin. Phylloclades usually flexible, elliptic- or oblanceolate, c. 3–10 (–13) cm. long, (0.2–) 0.5–1 (–1.2) cm. broad, obtuse to bluntly acuminate at the tip, with (8–) 10–25 nodes; veins occasionally distinct but more often obscure and phylloclades merely longitudinally furrowed or channelled; margins not differentiated.

Monoeious; cymules male or bisexual, of mostly 1 or 2 (rarely 3) female and c. 2–5 male flowers.

Male flower: pedicel (1–) 2–6 mm. long. Calyx reddish or cream-colored: calyx-lobes 6 (rarely 5), membranous, more or less spreading, subequal or sometimes unequal (outer lobes then narrower), elliptic to broadly obovate, (0.8–) 1–1.5 (–2.3) mm. long, entire, midrib unbranched. Disk-segments usually 6, thin, flat, entire, roundish, c. 0.2–0.5 mm. across, sometimes united in pairs or obsolete. Stamens 3 or less commonly 4 (rarely 5); filaments 0.4–0.8 (–1) mm. long, united for usually ½ their length or more into a column 0.3–0.7 mm. high, free ends spreading; anthers emarginate, c. 0.2–0.3 mm. long, 0.4–0.5 mm. broad; anther-sacs rounded, dehiscing more or less horizontally; pollen grains c. 18–25 μ in diameter.

Female flower: pedicel (1–) 2–4 (–7) mm. long. Calyx yellowish-green to pinkish; calyx-lobes 6, scarious, subequal or distinctly unequal, elliptic
to ovate, 1–1.5 (–2.2) mm. long, 0.7–1.5 (–2) mm. broad, entire, mid-rib unbranched. Disk plane or shallowly cupuliform, c. 0.25 (–0.5) mm. high, rim undulate or crenulate. Ovary sulcate, rugulose; styles c. 0.6–1 mm. long, free or basally united into a very short column not over c. 0.3 mm. high, somewhat flattened, shallowly to deeply 3–4-lobed, lobes slender.

Capsule oblate, 3–4 mm. in diameter, reddish brown, rugulose, not veiny. Columella 1–1.8 mm. long. Seeds trigonous, 1.4–2.6 mm. long, 1–2 mm. radially and tangentially, reddish brown to fuscous, with finely raised dots.

Collected in flower and fruit throughout the year, but many collections sterile.

**Type:** Jamaica, Browne (LINN, HOLOTYPE).

**Distribution:** seacoasts and lower altitudes inland, usually on limestone, Swan Islands, Cayman Islands, and Jamaica (MAPS XXXIV and XXXVII).

**Swan Islands:** Eastern Swan Island, Moyne 6, 12 (K); Larger Island, Nelson 103, 104, 105 (GH); “Crane Island”, 1897, Sharples (GH).

**Cayman Islands.** Grand Cayman: Georgetown, 1888, Fawcett (K); 1891, Hitchcock (MO); 1 mi. SE of Georgetown, Kings G.C.–202 (BM, NY); east end, Kings G.C.–116 (BM, NY); Grape Tree Point, Proctor 11974, 11976 (GH). Cayman Brac: 1888, Fawcett (K); 1924, Matley (BM); east end, Kings C.B.–70 (BM, NY).

**Jamaica:** without specific locality, Bertero (MO; TYPE COLLECTION of P. coenatus), MacFadyen (K), Shakespeare (BM), Szwarcz (BM, S), Wolle (GH). Hanover: Orange Bay Point, Harris 10262 (JAM); Lucea, 1891, Hitchcock (MO). Westmoreland: Negril, near lighthouse, Britton & Hollick 2075, 2075a (NY), M. Farr (GH), Harris 10233 (JAM, P, US), Webster & Wilson 5062 (A, JAM, MICH); Negril Hills, 0.5 mile east of Little Bay, Proctor 11150 (GH). St. Elizabeth: Yardley Chase, Britton 1157 (NY), Harris 9666 (JAM, US); Merriman’s Point, Proctor 15335 (GH). Trelawny: Jackson Town, Hunnewell 19767; 1 mi. NW of Stewart Town, Pierce 24 (MICH); Florida Beach, Falmouth, West & Arnold 808 (GH). St. Ann: east of Rio Bueno, Patrick 306 (JAM); Discovery Bay (Dry Harbour), Diognium 86 (JAM), T. Farr (GH), Hunnewell 15304, 18845 (GH); Runaway Bay, Orcutt 6119 (MO, US); St. Ann’s Bay, Gully Road, Britton 2515 (NY, HOLOTYPE of Xylophylla contorta); Ocho Rios, Hunnewell 18843 (GH), Proctor 9566, 15533 (A). Clarendon: Round Hill, Proctor 9481 (GH); Portland Ridge, Howard 12007 (A), von der Porten (JAM), Webster 5111 (A, JAM, MICH). St. Catherine: Bog Walk, Crawford 817 (NY); Great Goat Island, Britton & Hollick 1891 (NY, US), Harris 9334 (JAM, NY), 9339 (A, NY, US); Lazaretto, Proctor 9969 (GH); Port Henderson Hill, Webster & Wilson 4925 (A, JAM, MICH). St. Mary: Cabarita Island, off Port Maria, Proctor 7549 (GH), 7550 (JAM). St. Andrew: Cinchona, Harris 8592 (MO, NY); between Pleasant Hill and Green Valley, Macion & Killip 1058 (A, GH, NY, US); Long Mountain, Davis (MICH), Proctor 7338 (JAM), 7387 (GH), Webster 4857 (A, JAM, MICH). Portland: Uncommon Hill, Proctor 8558 (JAM); Port Antonio, Britton 879 (NY), 930 (NY, US), Fredholm 3187 (US), Hitchcock (MO). St. Thomas: road to Hagley Gap, Harris 5830 (NY, US); Sheldon Road, Harris 12889 (GH).
JAM, NY, US); Yallahs River, Purdie (K); Plantain Garden River, near Whitehall, Proctor 7421, 11778 (GH); Morant Point, Bengry (GH), Britton 4105 (NY), Webster 5558 (A, JAM, MICH).

The following collections include plants which presumably were cultivated or naturalized:


Few species of Phyllanthus have a more interesting distribution than does P. angustifolius; the occurrence of the plant outside of Jamaica only on the Swan and Cayman Islands is an indication that the migrational history of this species may provide the key to some of the Pleistocene biogeographical problems of the Caribbean. Typically, P. angustifolius is a xerophytic species of dry littoral areas, often on cliffs or platforms of dogtooth limestone near the sea; however, it occurs inland at a number of localities (notably in the Blue Mountains) and thus shows some adaptability to colonizing different habitats. In the southeastern end of the John Crow Mountains it may at the present time be interbreeding with P. arbuscula.

Morphologically, P. angustifolius and its sister species P. proctoris are distinguished by their dark ciliate cataphylls, often in a distinctly small apical cone, and by the narrow phylloclades which are often paired at the end of the primary branchlet axes. Although closely related, P. proctoris appears to be sufficiently distinct by virtue of the floral characters mentioned below.

Phyllanthus angustifolius is a rather variable species and individual specimens often look distinctive. A form with narrow, elongated and often twisted phylloclades sometimes occurs and was the basis for the proposed Xylophylla contorta of Britton. In the vicinity of Port Antonio occurs a form with unusually large flowers, but it does not diverge sufficiently to warrant taxonomic recognition. The specimens from the Cayman Islands and Swan Islands are quite typical for the species and show no unusual features; this may indicate that the migration of the species there took place relatively recently.

82. Phyllanthus proctoris, nom. nov. (PLATE XXXI, figs. V–W).

Phyllanthus linearis sensu Griseb. Fl. Br. W. Ind. 35. 1859; Muell. Arg. in DC. Prodr. 15(2): 430. 1866 (excl. P. cognatus); et Fawc. & Rend. Fl. Jam. 4: 266. 1920; non P. linearis (Sw.) Sw.

Shrub up to 3 m. high; branches of current year's growth c. 1.5–2.5 mm. thick, terete, greyish-brown. Apical cone roundish, c. 2.5–3 mm. long and 2–2.5 mm. broad, smooth in outline; cataphylls of main axes deciduous, blackish and scarious: stipules triangular-lanceolate, c. 0.8–1.7 mm. long,
blade lanceolate, about as long. Branchlets pinnatiform, ultimate axes transformed to phylloclades; primary axis (3–) 5–13 cm. long, 1–2 mm. broad, flattened, edges obtuse, pale green as ultimate axes, with c. (4–) 6 or 7 lateral axes; first internode (1–) 2–6 cm. long, median internodes mostly 0.7–1.5 cm. long. Cataphylls of primary axis deciduous; stipules lanceolate, c. 1 mm. long, basally auriculate, densely ciliate marginally (when young; soon glabrate), reddish brown; blade about as long as the stipules. Phylloclades thin and flexuous, linear-lanceolate, c. (3–) 4–11 cm. long, 0.1–0.35 cm. broad, attenuate to the tip, finely striate or sulcate longitudinally (veins obscure) with 7–10 (–13) nodes; margins not differentiated. Euphylls not observed. Cataphylls of ultimate axes basally auriculate, c. 0.5–0.8 mm. long, prominently ciliate on margins (when young).

Monoecious: cymes male or bisexual, of 1–3 male flowers and/or 1 female flower.

Male flower: pedicel 2–3.5 mm. long. Calyx presumably greenish; calyx-lobes 6, membranous, more or less spreading, subequal, elliptic to obovate, 0.8–1 mm. long, 0.6–1 mm. broad, entire, midrib unbranched. Disk segments 6, roundish, c. 0.2 mm. across. Stamens 3; filaments united into a column 0.2–0.25 mm. high; anthers subsessile atop the column, c. 0.15 mm. long and 0.25 mm. broad; anther-sacs dehiscing horizontally; pollen grains 14–17 μ.

Female flower: pedicel mostly 2–3 mm. long. Calyx presumably greenish; calyx-lobes 6, unequal, the outer one or two usually brownish and scarious, only 0.7–0.9 mm. long; inner lobes chartaceous, broadly obovate, c. 1–1.2 mm. long, 0.8–1.2 mm. broad, entire, midrib unbranched. Disk shallowly cupuliform, irregularly notched, c. 1.2 mm. across. Ovary sub-globose, smooth; styles divergent, dilated, obtuse with crenulate distal margin, c. 0.5–0.9 mm. long, 0.5–0.8 mm. broad, horizontally spreading or reflexed over the ovary and forming a calyptra. Fruit and seeds unknown.

Collected in flower Jan.

**Type:** Jamaica, *Purdie*.

**Distribution:** seacoast and inland hills, western Jamaica (*Map XXXVII*).


This species has long been misunderstood, owing to the fact that Swartz’s type represents a peculiar plant which has not been recollected. It is clear from details of his description (such as pedicels 4 lines long and styles bifid) that Swartz’s *P. linearis* (Fl. Ind. Occ. 113–114. 1800) cannot be the same as the plant described above and accepted as *P. linearis* by Grisebach, Mueller, and Fawcett and Rendle. The long pedicels suggest an
affinity of Swartz’s plant with *P. arbuscula* which has been confirmed by examination of the type specimen of *P. linearis*. The latter is not typical for *P. arbuscula* and may possibly be a hybrid, but in any event Swartz’s name cannot be applied to the present plant.

Since a new name is required, it seems appropriate to name the plant for Mr. George Proctor of the Institute of Jamaica. Although he has not collected this species, his extensive gatherings of representatives of sect. *Xylophylla* and of other Jamaican groups of *Phyllanthus* have supplied valuable data during this study.

The closest relative of *P. proctoris* is certainly *P. angustifolius*, with which it agrees in having darkened ciliate cataphylls and often paired phylloclades at the end of the main branchlet axis. However, the phylloclades of *P. proctoris* are consistently narrower than all except a few aberrant forms of *P. angustifolius*, and no specimen of the latter has such highly modified styles. Thus although the two species are certainly very closely related, they nevertheless appear to be quite distinct.


Shrub or small tree generally 1–3 m. high, trunk slender, erect, sparsely to considerably branched; branches of current year’s growth 2.5–10 mm. thick, reddish brown becoming greyish, smooth, lenticels very inconspicuous. Apical cone usually small, c. 2–4 mm. in diameter. Cataphylls persistent, reddish brown becoming greyish, indurate, massive, the stipules fused with the blade in the lower half or entirely coalescent into a deltoid scale, c. 2.5–5 mm. long, more or less marginally ciliate when young but later often appearing entire. Phylloclades flexible to rigid, borne c. 0.5–1 cm. apart on terminal branches, or densely clustered on lateral spur-shoots, simple, often extremely variable in size and shape: linear to oblongate, straight to markedly falcate, (3–) 5–25 (–32) cm. long, (0.3–) 0.5–2.3 cm. broad, long-attenuate to truncate at the tip, with 7–40 nodes, these mostly in the distal half; midrib raised and rather conspicuous on both sides, lateral veins departing at an acute angle, tenuous, neither raised nor conspicuous; nodes mostly conspicuous along the margin, forming distinct notches, each with a dense cushion of persistent bracteoles. Euphylls never observed; cataphyll blade partially to completely united with its stipules, c. 0.8–1 mm. long, copiously ciliate along the margin, reddish brown, delicate and evanescent (scarcey evident except on young expanding phylloclades).

Monoecious; cymules usually bisexual, each with 1–3 female and several to many male flowers.

Male flower: pedicel capillary to thickish, 1–2.5 mm. long. Calyx usually reddish- or pinkish-tinged; calyxlobes usually 6, subequal to very unequal, erect or spreading, sometimes connate below, oblong to ovate or obovate (sometimes broader than long), c. 0.8–1.3 mm. long, outer lobes often with dark brownish scarious fimbriate tips. Disk-segments usually 6, discrete or sometimes united in pairs, tenuous to massive, sessile to
pedicellate, more or less foveolate-pitted, 0.25–0.5 mm. broad. Stamens 3 (rarely 4 or with the rudiment of a fourth); filaments partially to wholly united into a slender to massive column; anthers stipitate to sessile atop the column, broadly deltoid, more or less emarginate, 0.15–0.25 mm. long and 0.25–0.5 mm. broad; anther-sacs rounded, dehiscing horizontally or slightly deflexed; pollen grains c. 16–20 μ in diameter.

Female flower: pedicel rather stout, curved, often greatly thickened above, 0.5–2.5 mm. long. Calyx usually reddish- or pinkish-tinged; calyx-lobes 6, chartaceous, erect or spreading, equal or unequal, oblong to obovate (or broader than long), 0.7–1.5 mm. long, 0.5–1.5 mm. broad, entire or outermost lobes with dark brownish scarious ciliate tips, midrib unbranched. Disk variable, patelliform to urceolate and enclosing the ovary. Ovary smooth to conspicuously tuberculate, sulcate; styles free or shortly united into a column; style-ends spreading or deflexed, mostly dilated and irregularly 5–8-lobed.

Capsule oblate, trigonous, c. 3.5–4 mm. in diameter, dark reddish brown, not evidently veiny, smooth to incrustate-tuberculate; valves 2.5–3.2 mm. long. Columella c. 1.5 mm. long. Seeds asymmetrically trigonous, 1.4–2.1 mm. long, 1–1.6 mm. broad, smooth, dark reddish brown.

Collected in flower and fruit throughout the year.

*Phyllanthus epiphyllanthus*, vegetatively the most specialized species of sect. *Xylophylla*, is also the most widespread. It clearly appears to be closely related to and presumably has been derived from *P. angustifolius*, its simple phylloclades corresponding to the main axis of the branchlet of that species. In floral characters the two plants are very similar but *P. epiphyllanthus* usually has shorter pedicels and a greater number of stylar branches. The extensive populations of *P. epiphyllanthus* may be grouped into three distinctive and rather sharply defined subspecies which can be separated by the following key.

### KEY TO THE SUBSPECIES

1. Stipules of cataphylls completely fuse with the blade into an entire scale (rarely the extreme tips free); female disk c. 1/4 the height of the ovary or less (rarely to 1/3); calyx-lobes free to base, spreading at anthesis.  
   ssp. *epiphyllanthus*

2. Disk covering 1/3 to 1/2 of the ovary; calyx-lobes only barely united at base.  
   ssp. *dilatatus*

3. Disk urceolate, entirely enclosing the ovary; calyx-lobes only barely, if at all, united at base.  
   ssp. *domingensis*

83a. *Phyllanthus epiphyllanthus* ssp. *epiphyllanthus*  
(PLATE XXXI, figs. X–Y).

Phyllanthus foliis lanceolatis serratis: *crenis floriferis* L. Hort. Cliff. 439. 1738 [excl. ref. Sloan.].

*Phyllanthus epiphyllanthus* L. Sp. Pl. 981. 1753.

*Xylophylla jalcata* Sw. Prodr. 28. 1788.

*Phyllanthus epiphyllanthus* β *genuinus* Muell. Arg. in DC. Prodr. 15(2): 428. 1866; in part [excl. ref. Linden et Schomb.].


*Xylophylla epiphyllanthus* (L.) Britton in Small, Fl. Florida Keys 76. 1913.


Shrub 0.5–2.5 m. high; cataphylls of branches with stipules and blade completely fused into a deltoid scale (rarely the extreme tips becoming free) (1.5–) 2.5–4 (–5) mm. long. Phylloclades flexible to rigid, linear to oblanceolate, often falcate, 2.5–20 cm. long, 0.3–2 cm. broad, truncate to attenuate at the tip, with (7–) 9–30 (–35) nodes.

Male flower: pedicel slender, 1–3 mm. long. Calyx-lobes spreading, usually in two dissimilar whorls, the outer oblong to obovate, c. 0.5–1 (–1.5) mm. long and 0.5–0.9 (–1.3) mm. broad, the inner ovate to orbicular or broader than long, 0.7–1.5 mm. long and broad. Filaments mostly united $\frac{1}{2}$ to $\frac{3}{4}$ their length into a column 0.2–0.6 (–0.9) mm. long.

Female flower: pedicel becoming 0.5–2 mm. long. Calyx-lobes spreading, similar to the male, the outer c. 0.5–1 mm. long and broad, inner c. 0.8–1.3 mm. long and broad. Disk patelliform or shallowly cupuliform, at most not over 0.2 mm. high, usually enclosing the basal $\frac{1}{4}$ of the ovary (rarely to $\frac{1}{2}$). Ovary rugulose to conspicuously tuberculate, at least above; styles nearly free or less commonly united into a column up to 0.5 (rarely to 1.3) mm. high, style-tips spreading, distally lacerate, 0.5–1 mm. long. Capsule apically rugulose to conspicuously tuberculate, 3–4.2 mm. in diameter, valves 2.2–3 mm. long. Seeds 1.4–2.1 mm. long, 1–1.6 mm. broad.

**Type:** Herb. Hort. Cliffort. (BM). The specimen was probably collected in the Bahamas by Catesby and given to Linnaeus by Miller.

**Distribution:** widespread in the West Indies, mostly on limestone rock, often near the sea (Map XXXIV).

Rendle), "mutton parish" (in Barbuda, ex Beard), "duddy bush" (in Cayman Islands), "farine à zombi," "farine chaude," "langue à chat" (in Guadeloupe), and "panetela" (in Cuba). Roig (Dict. Bot. Nombres Vulg. Cub. ed. 2. 2: 743. 1953) considers that the Cuban name alludes to the pleasant nocturnal aroma of the flowers, which resembles a certain kind of pastry; the epithet "farine chaude" from Guadeloupe would appear to be derived in the same way. This distinctive nocturnal fragrance is interesting, since it has not been observed in any other species of the genus.

The report of Stehle and Quentin (Fl. Guad. 2(1): 51. 1937) from St. Barthélémy is doubtless correct and refers to this subspecies, but most other reports of *P. epiphyllanthus* from localities other than cited herein are to be regarded with suspicion. The record of *P. epiphyllanthus* from Jamaica on the basis of a Purdie specimen at Kew (Fawc. & Rend. Fl. Jam. 4: 261. 1920) can presumably be discounted, since numerous subsequent collectors have encountered only *P. angustijolius* along the shores of that island. Since Purdie is known to have collected on Puerto Rico and Guadeloupe (Urban, Symb. Ant. 3: 107. 1902), his specimen may have been taken on either of those islands. The report of *Xylophylla epiphyllanthus* from the Florida Keys by Small (Flora Florida Keys 76. 1913) is based on a misidentification of a doubtfully indigenous specimen of *P. angustijolius*. Lemée (Fl. Guyane Fr. 2: 263. 1952) has recorded *P. epiphyllanthus* from French Guiana on the basis of an ambiguous citation by Aublet (Hist. Pl. Guy. Fr. 2: 853. 1775), but if Aublet encountered the plant there it must have been cultivated. The only disjunct record which cannot be positively rejected is that from Trinidad by Sieber, but the failure of recent collectors to confirm it strongly suggests that Sieber's plant too may have been taken from cultivation.

Subspecies *epiphyllanthus* consists of many isolated populations which may be grouped into three races. The plants of the Bahamas and eastern Cuba have relatively short phylloclades with fewer nodes and a distinctly tuberculate fruit. The plants from Matanzas and Las Villas are vegetatively similar to the Bahaman ones but have peculiarly dilated more or less calyptriiform styles. The populations of Puerto Rico and the Lesser Antilles tend to have longer phylloclades (up to 20 cm. long) with more nodes, and nearly smooth capsules. However, the Barbados population is vegetatively so like the Bahaman that it breaks down the distinction between that race and the Lesser Antillean one; and, since it is not certain that the distinctive styles of the central Cuban race are a consistent character, it does not seem necessary to define formal varieties within the subspecies. The peculiar distributional relationships of ssp. *epiphyllanthus* demand further investigation. Typically the subspecies is (like *P. angustijolius*) a littoral plant of coral benches, but in central Cuba and Puerto Rico it occurs in upland rain-forest. In both eastern Cuba and Hispaniola, on the other hand, it does not appear to go inland, but is instead replaced by ssp. *dilatatus* and ssp. *domingensis* respectively. In areas where mountainous regions approach near the coastline, it might be expected that ssp.
83b. *Phyllanthus epiphyllanthus* ssp. *domingensis*, ssp. nov. 23

*Phyllanthus epiphyllanthus* β *genuinus* Muell. Arg. in DC. Prodr. 15(2): 428. 1866 (ex p., excl. typ.).

Shrub or small tree, 1–2 m. high or more (up to 10 m., ex Jiménez); cataphylls of branches massive, 3–6 mm. long, blade and stipules fused at base (c. lower 1 mm.) but distally free. Phylloclades more or less rigid, narrowly linear to broadly oblanceolate, straight to distinctly falcate, 10–31 cm. long, (0.4–) 0.7–1.3 (–2.5) cm. broad, usually long-attenuate at the tip, with (15–) 20–40 nodes.

Male flower: pedicel distally thickened, 1–2.5 mm. long. Calyx-lobes subequal, basally connate above the receptacle into a cup c. 0.2–0.3 mm. high; free ends of lobes erect, obovate, 0.8–1.3 mm. long and broad. Disk-segments mostly 0.2–0.3 mm. across. Filaments almost completely united into a column 0.5–0.8 mm. high. Female flower: pedicel becoming 1.3–2 mm. long. Calyx-lobes erect, basally connate into a cup c. 0.4–0.5 mm. high; free ends of lobes broadly obovate, 0.8–1.2 mm. long and broad, becoming up to 1.5 mm. long in fruit. Disk cupuliform, c. 0.3–0.5 mm. high, usually enclosing the ovary for about ⅓ to ½ its height, crenulate-rimmed. Ovary smooth; styles free or united below the middle, dilated and channelled distally, c. (0.3–) 0.5–0.7 mm. high, the deflexed limb lobed but lobes often inturned and thus margin appearing entire. Entire capsules not seen; valves 2.8–3.2 mm. long; seeds 1.7–1.9 mm. long, 1.2–1.4 mm. broad.

**TYPE:** Dominican Republic, *Ekman H12642*.

**DISTRIBUTION:** wooded hillsides, sandy or calcareous soil, northern Hispaniola (Map XXXIV).

**HISPANIOLA:** “St. Domingue,” Poiteau (G), Richard (P).

**HAITI. Nord:** Cap Haitien, slopes of Morne Haut du Cap, alt. 500 m., *Ekman H2727* (S, US).


Vegetatively, ssp. *domingensis* closely agrees with ssp. *dilatatus* in its unfused cataphylls and usually elongated or broadened phylloclades. It

= *Phyllanthus epiphyllanthus* ssp. *domingensis*, ssp. nov.

Cataphyllis trifidis; lacinis calycis ad basin connatis; filamenti omnino coalescit; disco feminino cupuliforme 0.3–0.5 mm. alte; ovario laeve; stylis liberis vel infere connatis.
is transitional between ssp. *dilatatus* and ssp. *epiphyllanthus* in its floral characters, having the smooth ovary of the former but a shallow female disk tending toward that of the latter; however, its basally cupulate calyx is different from either of the other two subspecies. On the whole, ssp. *domingensis* is much more closely related to ssp. *dilatatus* than to ssp. *epiphyllanthus*.


*(PLATE XXXI, fig. Z).*


Shrub or small tree up to c. 3 m. high; cataphylls of branches massive, 2–4 mm. long, the linear-lanceolate stipules and blade fused in the lower 1 mm. but distally free. Phylloclades more or less rigid, linear to oblongolate, straight or somewhat curved (5–) 10–20 cm. long, (0.3–) 0.7–2.5 (–2.8) cm. broad, with c. 20–30 nodes.

Male flower: pedicel 1–3 mm. long. Calyx-lobes subequal, erect (tips sometimes flaring), barely if at all connate below, obovate, 0.8–1.2 mm. long, 0.6–1.5 mm. broad. Filaments completely united into a rather slender column 0.5–0.8 mm. high. Female flower: pedicel 1–2 mm. long; calyx-lobes subequal or somewhat unequal, oblong to broadly obovate, 0.9–1.3 mm. long, 0.5–1.3 mm. broad; disk urceolate, longitudinally ribbed, entirely enclosing the ovary, 0.8–1.3 mm. high; ovary smooth; styles 0.5–0.8 mm. high, free or more commonly united into a column 0.3–0.6 mm. high, style-tips spreading or reflexed, adaxially channelled, with 3 or 4 lobes. Capsule 3.5–4 mm. broad, smooth; valves 2.8–3.3 mm. long; seeds 1.8–2.1 mm. long, 1.4–1.5 mm. broad.

**Type:** Cuba, Wright 1951.

**Distribution:** calcareous uplands, eastern Cuba (Map XXXIV).

**Cuba. Oriente:** valley of Rio Cauto, Linden 2140 (G, P); Sierra de Nipe, Rio Piloto, Ekman 3391 (S); Monte Picote, Ekman 7408, 9130 (S); Caridad de los Indios, Jervis 1369 (GH, MICH); Monte Libano, San Fernandez, Ekman 10271 (S); El Palenquito, alt. 600 m., Eggers 4844 (GOET, P); cliffs (paredones), Monteverde, Wright 1951 (G, holotype; GOET, MO, NY, P, US, isotypes; data ex NY); Baracoa, pinelands on road to Florida, Ekman 3989a (S); top of El Yunque, 1955 Harvard Trop. Bot. Course 469 (GH).

The epithet *dilatatus* assigned to this taxon by Mueller is not wholly appropriate, for some forms such as that represented by Linden 2140 have long narrow phylloclades as in ssp. *epiphyllanthus*. On the basis of the much more extensive material which has become available since Mueller's treatment, it is now apparent that ssp. *dilatatus* cannot be distinguished vegetatively from ssp. *epiphyllanthus* except by its cataphylls. Even the "typical" broad-bladed form of ssp. *dilatatus* (as Wright 1951) can be matched by phylloclades from Bahaman populations of ssp. *epiphyllanthus*
(e.g., Coker 524 and Britton & Millspaugh 6294 from Long Island). The diagnostic characters of ssp. *dilatatus* reside not in the vegetative parts but rather in the distinctive female flowers. No form of ssp. *epiphyllanthus* has such a highly developed female disk and, if it were not for the transitional character of the plants placed in ssp. *domingensis*, the population in the inland parts of Oriente province would have all the attributes of a distinct species.

ACKNOWLEDGMENTS

The basic framework of this study was constructed during the writing of a doctoral dissertation which was submitted at the University of Michigan in 1953. The inspiration for the investigation was given by Dr. Rogers McVaugh, who suggested the need for detailed study of *Phyllanthus* and who directed the research program with sympathy and understanding. Professor H. H. Bartlett generously supported field work in the southern United States, Cuba, and Jamaica, criticized the manuscript with thoroughness, and revised (and in many instances entirely recast) the author’s attempts at scientific Latin. Dr. W. H. Wagner, Jr. gave valuable advice and encouragement on morphological techniques and suggested some important improvements in terminology. Financial assistance from the Research Club of the University of Michigan and from a Rackham Fellowship greatly expedited completion of the dissertation.

Investigations on the West Indian species of *Phyllanthus* were continued at Harvard University under a National Science Foundation fellowship kindly sponsored by Dr. Reed C. Rollins and Dr. I. W. Bailey, who made available various needed facilities. Dr. Richard A. Howard assisted in many ways, including supporting field work in Jamaica, furnishing many interesting specimens, and imparting freely of his extensive knowledge of Caribbean plant life.

Dr. Roy N. Jervis, of East Texas State College (Commerce), made possible field work in Cuba in 1951, collected extensive series of specimens, and generously supplied a valuable series of outline maps drafted by himself. Mr. Bernard Lewis and other staff members of the Institute of Jamaica materially assisted in the success of field work on that island in 1954. Mr. George Proctor, of the Institute, aided in many ways in these explorations, and has since forwarded both living and dried collections of unusual interest. Dr. Kenneth A. Wilson collaborated helpfully on the Jamaican field work throughout the summer of 1954. Special collections or materials of West Indian species of *Phyllanthus* were also furnished by Hermano Alain (Colegio de la Salle, Havana), Ing. Julian Acuña (Santiago de las Vegas), Dr. E. P. Killip, and Dr. Fred A. Barkley.

Several persons have lent assistance in the preparation of illustrations. Dr. Ding Hou kindly furnished the drawings for Plates XIII and XIV; Mrs. Martha Szerlip Wittels applied her talented pen to the execution of Text-fig. 4 and Plates V, VIII, and IX; and Dr. Richard A. Scott took most of the photographs used for Plates VI, VII, XI, and XII. Photo-
graphs of type specimens were taken at the University of Michigan through the courtesy of Dr. McVaugh. The other drawings were skillfully reconstructed from the author's sketches by his wife, Dr. Barbara D. Webster. In addition to the outline maps of Cuba and Jamaica furnished by Dr. Jervis, outline maps of Caribbean America and the Western Hemisphere from Goode's series of base maps (University of Chicago) were utilized in preparing distribution maps. For the publication of all of these illustrations in their present form and for the execution of those not specifically mentioned, the author is alone responsible.

Particular gratitude is expressed to Dr. C. E. Kobuski and to Dr. Carroll E. Wood for their forbearance and patience in editing what must have appeared to be a never-ending manuscript.

Finally, the author wishes to record his particular indebtedness to his wife, Barbara, for her untiring and indispensable assistance. Not only has she contributed by typing manuscript, inking in most of the line drawings, and preparing mounts for microscopic study, but she has with great understanding provided encouragement throughout the extended period in which this manuscript has taken its final form.

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Corrections

37: 92. Changes in concept during the course of this work have resulted in a total of 83 West Indian species (instead of "90-odd") of Phyllanthus, of which about 75 are indigenous.
37: 99. Read 1,000 pages for 1,000 species.
37: 120. Read 1450 μ instead of 4150 μ for P. pachystylus.
37: 219. Phyllanthus elegans has not been introduced into the West Indies; it has been confused here with P. pulcher.
37: 256. Read Phyllanthus hyssopifolioides HBK. for Phyllanthus hyssopifolius HBK.
37: 345. Sect. Apolepis (Subg. Conami) will not run down properly in the key to subgenera unless the expression "entirely woody" under lead 2 is ignored.
38: 177. Read Cyclanthera for Cyllanthera.
38: 298. Plate XXII, A is more applicable here than XXII, B.
38: 323. Read fig. B for fig. A under P. fadyenii.
APPENDIX I*

ARTIFICIAL KEY TO THE WEST INDIAN TAXA OF PHYLLANTHUS

1. Branching not phyllanthoid (i.e., ultimate axes persistent, their subtending leaves not reduced to scales).
   2. Herbs; stamens free; pedicel of female flower and seeds less than 2 mm. long. ........................................... Sect. Loxopodium (37: 346)
   2. Shrubs or trees; stamens connate; pedicel of female flower and seeds more than 2 mm. long. ......................... Sect. Elutanthos (39: 51)

1. Branching phyllanthoid (i.e., ultimate axes deciduous, their subtending leaves usually reduced to scales).
   2. Branchlets with normal leaves, not greatly dilated.
   4. Specimens with flowers.
      5. Stamens (including anthers) wholly confluent into a circumcissile synandrium.
         6. Dioecious; stipules blackened and indurate; column of synandrium 1 mm. or more high. .......... P. dimorphus (Sect. Phyllanthus) (38: 341)
         6. Monoecious; stipules paler and thinner; column of synandrium less than 1 mm. high. .......... Sect. Cyclanthera (38: 177)
      5. Stamens not wholly confluent.
         6. Dioecious.
            7. Trees; flowers in cauliflorous thyrses. ..................... Sect. Aporoella (38: 72)
      6. Monoecious (male flowers sometimes soon deciduous and specimens then appearing female).
         7. Annual herb; stamens 5, entirely free. .................. Sect. Floribundi (38: 51)
         7. Habit various; stamens, if 5, at least partially connate.
            8. Flowers, at least in part, in naked thyrses.
               9. Stamens free; styles bifid, slender .................. Subg. Cissa (38: 60)
               9. Stamens united; styles thickened or 3–4 lobed.
                  10. Anthers dehiscing vertically; disk of female flower urceolate, enclosing the ovary. .... Sect. Emblica (38: 75)
                  10. Anthers dehiscing horizontally; disk of female flower much shorter, not enclosing the ovary. .... Sect. Epistylium (39: 153)
            8. Flowers in cymules axillary to normal leaves.
               9. Ovary with c. 9 or 10 carpels, styles minute and aggregated into an irregular mass; androecium of

*Numbers in parentheses refer to volume and page number of the taxon under which the unknown plant may be traced to species.
5 stamens united in two sets. 

Sect. Anisonema (38: 56)

9. Ovary with only 3 carpels, styles otherwise.

10. Annual or perennial herbs; stamens 2 or 3; styles bifid, free except at the base, never greatly dilated or united into an erect column.

11. Leaves as broad as or broader than long (c. 5–10 mm.); stamens 3, free; female disk dissected into 6 segments. 

Sect. Apolepis (38: 371)

11. Not with this combination of characters. 

Subg. Phyllanthus (38: 170)

10. Shrubs or trees; stamens 2–15; styles various, often united into a column.

11. Calyx-lobes dark red with lacerate margins; stamens 2, filaments united; axes reddish-hirsutulous. 

Sect. Eriococcus (38: 360)

11. Calyx-lobes at most minutely denticulate, never lacerate. 

Subg. Xylophylla (39: 68)

4. Specimens with fruits only.

5. Fruits woody or fleshy, indehiscent or tardily dehiscent.


Sect. Anisonema (38: 56)

6. Fruits drupeaceous or woody.

7. Cocci firmly united, not separating. Subg. Cicca (38: 60)

7. Cocci at length separating.

8. Leaves linear-oblong, 2–5 mm. broad. 

Sect. Emblica (38: 75)

8. Leaves much broader. 

Sect. Omphacodes (39: 142)

5. Fruits dry, dehiscent.

6. Herbs; seeds less than 2 mm. long.

7. Leaves orbicular or broader than long. 

Sect. Apolepis (38: 371)

7. Leaves otherwise. 

Subg. Phyllanthus (38: 170)

6. Shrubs or trees; seeds often 2 mm. long or more. 

Subg. Xylophylla (39: 68)

3. Branchlets bipinnatifid (primary axis bearing several to many lateral axes).

4. Calyx-lobes 6; pubescence not reddish; leaves (at least the petioles) and female pedicels scabridulous or hirsutulous. 

Sect. Nothoclema (38: 363)

4. Calyx-lobes 5; pubescence more or less reddish; leaves and female pedicels smooth and glabrous. 

Sect. Hemiphyllanthus (39: 163)

2. Branchlets with at least the lateral axes modified to phylloclades, leaf-blades usually greatly reduced or absent. 

Sect. Xylophylla (39: 179)
APPENDIX II

WEST INDIAN SPECIES EXCLUDED FROM PHYLLANTHUS

(Cicca antillana A. Juss. Tent. Euphorb. pl. 4, fig. 13B. 1824.) = **Margaritaria nobilis** L. f. Suppl. Pl. 428. 1781.


(Croton glabellum L. Syst. ed. 10, 1275. 1759.) = **Croton lucidus** L. (as to type, not as to Fawcett and Rendle's application). Fawcett and Rendle cited as basionym *Croton glabellum* L. Amoen. 5: 409. 1760 (non Syst., 1759), which supposedly is the plant accepted below as an *Astrocasia*; but this procedure is, of course, inadmissible under present rules of nomenclature.

= **Margaritaria hotteana** (Urb. & Ekm.) Webster, Jour. Arnold Arb. 38: 66. 1957.

= **Savia sessiliflora** (Sw.) Willd. Sp. Pl. 4: 771. 1806.


**Phyllanthus nobilis** (L. f.) Muell. Arg. in DC. Prodr. 15(2): 414. 1866.  
= **Margaritaria nobilis** L. f. Suppl. Pl. 428. 1781.


= **Savia sessiliflora** (Sw.) Willd. Sp. Pl. 4: 771. 1806.

**Phyllanthus scandens** (Griseb.) Muell. Arg. in DC. Prodr. 15(2): 415. 1866.  


**Phyllanthus virens** (Griseb.) Muell. Arg. in DC. Prodr. 15(2): 415. 1866.  
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