A MONOGRAPHIC STUDY OF THE WEST INDIAN SPECIES OF PHYLLANTHUS

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With two plates

SYSTEMATIC TREATMENT

In the following pages are treated all of the species of Phyllanthus, whether spontaneous or cultivated, which have been observed in the West Indies. For the purposes of this study the West Indian region is defined as the area bounded by (and including) Bermuda and the Bahamas on the north, Swan Island and the Providencias on the west, and Curaçao, Trinidad, and Tobago on the south; the Florida Keys, as well as Margarita and the smaller islands off the Venezuelan coast, are therefore excluded. The inclusion (for reasons of convenience) of Trinidad, which has a predominantly South American flora, results in the mustering in of two species which are otherwise South American; but by and large the species here included represent a strikingly self-contained assemblage for such a large and diverse area, encompassing as it does a broad range of latitude and great diversity of climates, geological formations, and vegetational zones.

One of the most troublesome problems which faces anyone who wishes to investigate a West Indian Phyllanthus is that of deciding if the plant at hand actually belongs to the genus. The following purely artificial key to the West Indian representatives of Phyllantheae is therefore presented with the aim of facilitating determination. It should be noted that the tribe Phyllantheae is here circumscribed in a narrow sense, comprising the subtribe Phyllanthinae and part of the Andrachninae of Pax (Natürl. Pflanzenfam. ed. 1, 3(5): 14, 1890), or the subtribes Glochidiinae, Phyllanthinae, Andrachninae, and Wielandiinae of Pax and Hoffmann (Natürl. Pflanzenfam. ed. 2, 19c: 32–33, 1931). It is evident that further research will result in interpretations of the tribes and subtribes radically different from the arrangement of Pax and Hoffmann.

ARTIFICIAL KEY TO WEST INDIAN GENERA OF PHYLLANTHAE

A. Plants in flower

1. Branching phyllanthoid
   Phyllanthus

2. Petals present, at least in male flower; stamens 5.
   3. Monoecious subshrub, microphyllous, the leaves only 1–2 mm. long
      Andrachne

3. Dioecious shrubs or trees with much larger leaves.
   4. Petals about as large as the calyx-lobes; pistillode peltate; petiole
      c. 2 cm. long or more
      Astrocasia

* Continued from volume XXXVII, page 268.
4. Petals much smaller than calyx-lobes; pistillode slender, usually lobed; petioles much shorter ........................................ Savia

2. Petals absent.
   3. Pistillode present, stamens 5; dioecious shrubs or trees.
      4. Male flowers subsessile, glomerate; leaves chartaceous, triplinerved, narrowly peltate ................................. Chascotheca
      4. Male flowers pedicellate; leaves coriaceous, pinnately nerved, never peltate .................................................. Securinega

3. Pistillode absent.
   4. Stamens 4; floral disk annular; dioecious tree ............ Margaritaria
   4. Stamens 3; floral disk not annular; monoecious or dioecious herbs or shrubs ................................. Phyllanthus

B. Plants in fruit

1. Branching phyllanthoid ........................................ Phyllanthus
1. Branching not phyllanthoid.
   2. Petioles 2 cm. long or more; fruiting pedicels 4 cm. long or more, the calyx-lobes deciduous from the massive receptacle .............. Astrocasia
   2. Petioles, and usually fruiting pedicels, much shorter.
   3. Leaves only 1–2 mm. long .................................. Andrachne
   3. Leaves larger.
   4. Branches glabrous.
      5. Fruit not separating regularly into cocci; seed-coat fleshy without, bony within, the hilum deeply excavated Margaritaria
      5. Fruit regularly dehiscent into 3 cocci; seed coat neither fleshy nor bony, the hilum not excavated.
       6. Seed bullate-rugose, the hilum abaxial ................. Chascotheca
       6. Seed otherwise.
          7. Leaves coriaceous and narrowly spathulate, or else branches ending in spines ............................... Securinega
          7. Leaves otherwise; branches never spiny.
          8. Herbs or subshrubs, or if shrubby (P. botryanthus) then fruits borne on "naked" thyrses . Phyllanthus
          8. Trees; fruit axillary to foliage leaves .............. Savia

4. Branches pubescent.
   5. Branches hirtellous with spreading hairs ............... Phyllanthus
   5. Branches sericeous-pilose with appressed hairs .......... Savia

Once a doubtful specimen has been assigned to Phyllanthus, the task of determining it to species may still appear rather formidable. The first step should always be to decide whether or not the branching is phyllanthoid (cf. Jour. Arnold Arb. 37: 104 et seq. 1956). Since the sex and number of flowers produced per node is often an important character, it should be kept in mind that this can often be determined even from a branch that has lost most of its flowers; the number of pairs of persistent bracteoles usually give a good indication of the number of flowers, and the stumps or scars of the female flower pedicels are usually distinctly larger in diameter than those of males.

Flower-parts should be measured in water at a magnification of 15 to 50 diameters if exact correspondence with the descriptions is desired. How-
ever, in practice measurements taken from dried organs on the herbarium specimen are often accurate enough. It should be kept in mind, however, that the measurements apply in most cases to fully mature organs. Since some structures, particularly staminal and stylar columns, may undergo great elongation at anthesis, due allowance must be made for measurements taken from the bud.

The height of the staminal column, when there is more than a single whorl of anthers, is measured from the base to the attachment of the upper whorl of anthers. The length and breadth of the anthers are given in relation to their morphologically longitudinal axes. As discussed in the section on floral morphology, the direction of dehiscence of the anther is expressed topographically, i.e., in relation to the long axis of the entire flower rather than of the individual stamen.

Because of the diverse stylar configurations in the genus, it is difficult to express the dimensions in consistent terms. If the styles are erect and united, the height of the stylar column is given. If they are free and spreading, the length given in the descriptions refers to the purely topographical extent to which they can be straightened out when moistened. The degree of division of the style, on the other hand, refers to its total length and takes into account any twists which cannot be uncoiled.

The size, shape, and ornamentation of the seeds furnish excellent characters for purposes of identification. The stated dimensions are understood to apply in relation to the longitudinal (vertical) axis of the seed as it sits in the capsule. Thus the radial dimension is measured along either of the lateral faces or on the flat face if one of them is carinate, while the tangential is the width of the seed when lying on its back. Since the capsules of many species tend to dehisce — even if immature — when the specimen is dried, immature seeds may often be found mixed with the mature ones. This makes it difficult to determine the actual range in seed size, particularly since in some species the two seeds of a locule are normally unequal in size. Usually, however, one can distinguish well-developed seeds by their plumpness, more well-defined ornamentation, and less shiny surface.

The specimens cited in this work have been made available through the courtesy of the curators of the following institutions: Arnold Arboretum (A); Botanisches Museum, Berlin-Dahlem (B); British Museum (Natural History), London (BM); Jardin botanique de l’Etat, Brussels (BR); Botanical Museum and Herbarium, Copenhagen (C); Chicago Natural History Museum (F); Conservatoire et Jardin botaniques, Geneva (G); Gray Herbarium (GH); Systematisch-Geobotanisches Institut, Universität Göttingen (GOET); Science Museum, Institute of Jamaica, Kingston (JAM); Herbarium, Royal Botanic Gardens, Kew (K); Rijksherbarium, Leyden (L); Herbario de la Salle, Vedado, Habana (LS); University Herbarium, University of Michigan, Ann Arbor (MICH); Missouri Botanical Garden, St. Louis (MO); Herbier Marie-Victorin, Institut

1 Herbarium abbreviations are the standard ones of Lanjouw and Stafileu, Index Herbariorum ed. 2 (1954), except for the Science Museum, Institute of Jamaica, which is unlisted.

Niruri Adans. Fam. Pl. 2: 356. 1763.
Urinaria Medic. Malvenfam. 80. 1787.

Trees, shrubs, or herbs of very diverse habit. Branching either unspecialized — the phyllotaxy spiral or distichous —, or phyllanthoid, i.e., the spiralled leaves on main axes reduced to cataphylls which subtend deciduous branchlets with distichous leaves. Leaves varying greatly in size and texture but always entire, and glabrous in most species; petiole always much shorter than the blade; stipules deciduous or persistent, often indurate. Plants monoecious or subdioecious, rarely dioecious; inflorescences axillary (sometimes pseudoterminal), or more or less greatly reduced cymes, these aggregated into thyrses in some species; the individual flowers bibracteolate. Flowers apetalous; calyx gamophyllous, 4–6-lobed, the lobes imbricate in the bud (decussate in calyces with 4 lobes); disk nearly always present in the flowers of both sexes. Male flower pedicellate; stamens 2–15, mostly 3–6; filaments free or connate; anthers free or connate, almost invariably extrorse; disk usually divided into segments alternating with the calyx-lobes, less commonly undivided; pistillode absent; pollen grains oblong to globose, with various ornamentation patterns, small (c. 15–35 μ in diameter). Female flower pedicellate or subsessile; calyx-lobes 5 or 6 (rarely 4), entire or less commonly toothed or lacerate; disk various: cupuliform or plane, entire or lobed or divided into segments, absent in a few species; staminodia absent (except in P. acidus); ovary usually of 3 carpels, in a few species of 4 up to 12 (only 2 in P. chacoensis), smooth or less commonly roughened, bullate, or hairy; ovules always two in each locule, usually collateral (at least at first), anatropous or amphitropous, with two integuments; nucellus usually projecting beyond exostome as a beak in contact with the obturator; embryo-sac the normal 8-nucleate type; styles erect or spreading, free or united into a column, bifid, multifid, or dilated into an entire or lacerate stigma. Fruit mostly a dehiscent capsule (the cocci explosively dehiscent in many species), less commonly baccate or drupaceous, the carpels normally separating as crustaceous cocci from a persistent columella. Seeds usually two in each locule, sometimes unequal, rarely only one developing to maturity; seed-coat dry, crustaceous, smooth or variously ornamented; endosperm whitish, cartilaginous; embryo straight or slightly curved, the cotyledons usually considerably broader than the radicle.
**Type species:** *Phyllanthus niruri* L.

As delimited in this work, *Phyllanthus* is primarily an Old World genus, only about 200 of the 650 species being native to the New World. The West Indian region, however, harbors a disproportionately high percentage of the native American species; in the western hemisphere only southern Brazil appears to be a comparably important center of speciation.

A detailed analysis of the generic relationships of *Phyllanthus* is beyond the scope of the present treatment. Here it must suffice to say that of the other West Indian genera of Phyllanthaceae, a close affinity is shown only by *Margaritaria*, which is well distinguished by its very different fruit structure. Still more closely related but evidently generically distinct are a series of Old World genera with phyllanthoid branching: *Glochidion*, *Breynia*, *Sauropus*, and *Phyllanthodendron*.

The generic limits of *Phyllanthus*, as here interpreted, correspond rather closely to those earlier held by Pax (Naturl. Pflanzenfam. ed. 1. 3(5): 18–23, 1890), with the exception that *Margaritaria* is here recognized as a distinct genus. The subgeneric divisions, on the other hand, are very different from those in the interpretations of Mueller and of Pax. The most radical innovations are the grouping of the sections into subgenera and the breaking up of the Muellerian sect. *Euphyl-lanthus* into a number of small sections, some of which belong to different subgenera. These changes in concept, which are now undertaken only after study of representatives of all sections of the genus (whether West Indian or not), are due largely to the application of new criteria — in particular, the branching and pollen types. Since, however, examination of the small pollen grains of *Phyllanthus* is very inconvenient for making routine identifications, the reader may prefer to use the artificial key to the subgeneric groups (Appendix I).

### SYNOPSIS OF THE SUBGENERA

1. Branching not phyllanthoid; herbs or subshrubs with spiral or distichous leaves; stamens 3, filaments (in ours) free; pollen grains (in ours) colporate. 
   1. *Isocladus*
2. Pollen grains colporate, or if not then plants shrubby and filaments connate.
   2. *Kirganelia* ¹
3. Stamens 5; pollen grains colporate; carpels 3–10  III. *Cicca* ²
5. Trees with drupaceous or pithy fruits; carpels 3 or 4; pollen grains colporate  IV. *Phyllanthus*
6. Herbs or low shrubs with capsular fruits; carpels 3; pollen grains colporate, striate, or foveolate

¹ The keys and descriptions are in most cases based solely on West Indian material, and do not take into account exceptional species outside our limits.
² Apparently acolpate in an anomalous species of subg. *Phyllanthus*.
⁴ Subgenus *Cicca* (L.), stat. nov. *Cicca* L. Mant. 17. 1767.
2. Pollen grains otherwise; entirely woody; stamens 2–15, filaments usually connate; fruit capsular, dry or rarely somewhat fleshy.

3. Pollen grains porate; perianth segments lacerate; stamens 3

4. Pollen grains echinulose, with short colpi; stamens 3; branching phyllanthoid, branchlets bipinnatifid

5. Branching not phyllanthoid; stamens 3

VI. Conami

7. Branching phyllanthoid; stamens 2–15

VIII. Xylophylla

Subgenus I. Isocladus, subg. nov.

Herbs or shrubs with unspecialized branching, the leaves spirally or distichously arranged. Monoecious or dioecious. Male flower: calyx-lobes 5; disk-segments 5; stamens 3, the filaments free or united, anthers dehiscing vertically or horizontally; pollen grains colporate or areolate with ora midway between the angles. Female flower: calyx-lobes 5; disk cupuliform or of 5 segments, the segments often bifid; ovary 3-celled, styles free or united. Fruit a dehiscent capsule; seeds trigonous, smooth or verruculose.

This subgenus is typified by sect. Paraphyllanthus, which does not occur in the West Indies; our representatives all belong to sect. Loxopodium. Subgenus Isocladus includes the species which vegetatively appear to be the least specialized within the genus. The species of sect. Paraphyllanthus, in particular, are similar in aspect to some species of Andrachne; but the male flower is so different in the two groups that a direct relationship appears unlikely.

In addition to sects. Paraphyllanthus and Loxopodium, subg. Isocladus also includes sects. Macraca and Anisolobium, these last being primarily Old World groups. The subgenus as a whole is thus circumtropical in distribution and comprises about 60 species of diverse habit.


Subgenus Botryanthus, subg. nov. Frutices vel arbores monoicae ramulis distichis, glabris vel hirsutulis, foliis nonnihil magnis; floribus axillaris vel in fructibus; flor masculo laciniosis calycis plerumque 6, staminibus 3, filamentis connatis, antheris plusminusve horizontaliter dehiscentibus, granis pollinis globosis, areolatis; flor feminine laciniosis calycis 6, disco integro vel crenato, ovario loculis 3, stylis erectis, connatis, ad apicem reflexis; capsula sicca, seminibus laevibus. — Species typica Phyllanthus grandi-jolius L.

Subgenus Isocladus, subg. nov. Herbae fruticosae, ramificacione disticha vel spirale; flore masculo staminibus 3, filamentis liberi vel connatis, granis, pollinis oblongis vel globosis, sulpatis vel areolatis; flore feminine disco integro vel disco dissecto, ovario laevo loculis 3, stylis bifidis; capsula in cocciis 3 dehiscentia; seminibus trigonis verruculosis vel laevibus — Species typica Phyllanthus maderaspatensis L.

The type of sect. Paraphyllanthus (Muell. Arg. Linnaea 32: 5. 1863; DC. Prodr. 15(2): 355. 1866) is hereby designated as P. maderaspatensis L.; and the section is redefined so as to exclude all species with phyllanthoid branching, such as P. urinaria L.

Gentinaria Raf. Western Minerva 42. 1821.

Annual or perennial herbs, sometimes suffruticose; primary axis or axes erect, bearing distichous leaves and axillary flowers; branches terete, compressed, or winged. Stipules acuminate, more or less auriculate or appearing peltate at the base, entire or denticulate. Leaf-blade membranous or chartaceous, not over 3 cm. long.

Monoecious, subdioecious, or dioecious, the flowers present on all orders of branching in contracted unisexual or bisexual cymes. Male flower: pedicel slender, articulate near the middle; calyx-lobes 5 or 6; disk of 5 or 6 distinct segments; stamens 3, filaments free or rarely connate at base; anthers subglobose or flattened, the connective enlarged adaxially; anther-sacs opening horizontally; pollen grains oblong, 4-colporate, the ora transversely elongate, reticulation obscure. Female flower: pedicel straight at anthesis, becoming geniculate-reflexed in fruit, usually 1 mm. long or less; calyx-lobes 5 or 6; disk cupuliform, lobed, or parted into 5 or 6 segments; ovary smooth; styles free or somewhat fused basally, usually bifid. Capsule green or reddish, not strongly nervèd; seeds trigonous, brown to fuscous, not over c. 1.7 mm. long, verruculose or smooth.

Type species: P. caroliniensis Walt.

This strictly New World group of perhaps a half dozen species (and a number of subspecies) is well defined by the completely distichous phyllotaxy, flowers on all orders of branching, and colporate pollen grains. Some of the species of the Old World sect. Macraea are very similar to the West Indian plants both in aspect and in floral morphology, but they have very different areolate pollen grains. A very close similarity in many details is also shown by the species of sect. Uroaria, which however have phyllanthoid branching. Members of sect. Loxopodium are as a rule small and inconspicuous plants; they tend to be mesophytes growing in wet savannas and along stream-beds, but some varieties of P. caroliniensis are found on dry limestone areas.

KEY TO THE SPECIES

1. Capsule 2 mm. or less in diameter, the seed 0.7–1 mm. long; stem and branches terete or flattened, not winged; strictly monoecious, the cymes bisexual. 1. P. caroliniensis

1. Capsule about 3 mm. in diameter, the seed 1.3–1.7 mm. long; stems and branches flattened, sharply angled or winged; male and female flowers at separate axils.

2. Seed smooth; capsule olivaceous; annual with subsimple stems; styles appressed, horizontal. 2. P. hyssopifoilioides

2. Seed verruculose; capsule reddish; perennial with stems clustered on a caudex; styles erect-ascending. 3. P. heliotropus


Annual or short-lived perennial herbs, usually erect, mostly 1–3 dm. high, the base never becoming more than softly woody; taproot usually simple, with filiform lateral roots. Primary stem straight with pinnately arranged branches (branches of tertiary order sometimes developing), or replaced above by few to several erect secondary branches. Branches terete or somewhat flattened, never winged (in West Indian forms), greenish, brownish, or reddish-tinged, smooth or papillate-scabridulous, the internodes quite variable in length (2–15 mm.). Stipules ovate-triangular to lanceolate, acute or more often acuminate, usually more or less auriculate at the base, nearly entire to conspicuously dentate, thin and papery or becoming slightly toughened, pale brown or reddish-brown, 0.7–2 mm. long, 0.4–0.6 mm. broad. Petioles smooth, 0.5–1 mm. long. Leaf-blades obovate, elliptic, or oblong, obtuse or rounded and apiculate (rarely sharply acute), acute at the base, c. 5–20 mm. long, 2–10 mm. broad, membranous to rather firm; above bright green or olivaceous, usually smooth, the nerves only slightly raised; beneath green, pruinose, or rubescent, smooth to papillate, midrib prominently raised, lateral veins often somewhat raised, tertiary veinlets anastomosing to form a delicate reticulum, or not visible; margin scarcely to conspicuously thickened, smooth or scabridulous.

Monoecious, all axils except the lowest on the primary stem normally floriferous; cymules axillary, greatly reduced: male flowers 1 or 2, followed by 1 or 2 (rarely 3) female flowers.

Male flower: pedicel c. 0.6–1 mm. long. Calyx-lobes (5) 6, oblong to suborbicular, rounded or obtuse, more or less entire, 0.5–0.7 mm. long, 0.5–0.8 mm. broad, thin and scarious, pale yellowish (rarely pink-tinged), 1-nerved. Disk of (5) 6 elliptic to broadly cuneate entire or crenulate segments. Stamens 3, filaments free, obliquely ascending; anthers emarginate, anther-sacs parallel, inserted on the adaxially broadened connective, opening horizontally, not confluent.

Female flower: pedicel sharply reflexed, usually geniculate, smooth, terete, often reddish-tinged, 1 mm. long or shorter. Calyx-lobes 6 (rarely 5 or 7), linear-oblanceolate to oblong, rounded to acute, 0.6–1.4 mm. long, with a narrow to broad whitish or yellowish often reddish margin and a thicker convex herbaceous midrib area, red-tinged at the base or sometimes entirely reddish, 1-nerved, the midrib plane without, saliently raised within. Disk entire or lobed or dissected into roundish or cuneate segments, rather thin, not glandular. Ovary smooth; styles free and sharply ascending or somewhat fused at the base and more or less horizontally spreading, not over c. 0.3 mm. long, bifid (sometimes shallowly so), the arms slender or thickened, spreading apart or recurved, rounded or subcapitate at the tip.

Capsule c. 1.6–2 mm. in diameter when mature but often precociously dehiscent; valves thin, smooth, olivaceous or reddish-tinged, nervation obscure. Seeds 0.7–1 mm. long, 0.6–0.75 mm. radially and tangentially,
usually dull greyish-brown when mature, verruculose, i.e., covered with evenly or rather irregularly spaced dark raised points.

This is the most widespread and — with the possible exception of *P. niruri* — most variable of the New World species of *Phyllanthus*. It occurs from Illinois and Pennsylvania south throughout most of tropical America to Argentina and Paraguay, although in parts of this range it may be an introduced weed, and has also colonized the Galapagos Islands. Its true limits have not been understood owing to the rather confused treatment by Mueller Argoviensis in the “Prodromus” (1866), where the different populations are distributed among no less than four different species: *P. pruinosis*, *P. schomburgkianus*, *P. caroliniensis*, and *P. stenopterus*, these last two placed considerably distant from the first two. Although the systematic elaboration of *P. caroliniensis* will itself require a special monograph, it is already evident that the species includes some distinctive subordinate taxa with well-defined ranges. In the West Indies these are three:

**KEY TO THE WEST INDIAN SUBSPECIES**

1. Branches scabridulous with papillae scattered or in striae; disk of female flower lobed or parted into segments; calyx-lobes of female flower broadly oblong or spathulate, usually rounded or obtuse, often reddish-tinged to the tip, 0.6-0.9 (-1) mm. long; styles appressed; leaves firm, the tertiary veinlets usually very obscure or invisible. ssp. *saxicola* (1c)

1. Branches quite smooth; disk of female flower entire or obscurely angled; calyx-lobes of female flower narrower, more acute, usually not red-tinged except at base; styles more or less ascending; leaves thinner, margin scarcely thickened, tertiary veinlets usually forming an evident reticulum beneath.

2. Stipules 0.8-1.2 mm. long; disk-segments of male flower cuneate-squarish or roundish, as broad as or broader than long; leaves obovate, tapering from above middle to base; calyx-lobes of female flower mostly linear-spathulate. (0.9) 1-1.2 (-1.4) mm. long ssp. *caroliniensis* (1a)

2. Stipules 1.5-2 mm. long; disk-segments of male flower ovate or elliptic, mostly longer than broad; leaves more often elliptic, tapering at or below middle toward base; calyx-lobes of female flower oblong or spathulate, mostly 0.7-0.9 mm. long ssp. *guianensis* (1b)

Another subspecies from Panama, Colombia, and perhaps other parts of South America may eventually be found in the West Indies. It is distinguished at once by its narrowly winged stems and is here designated as *Phyllanthus caroliniensis* ssp. *stenopterus* (Muell. Arg.) comb. nov. (*P. stenopterus* Muell. Arg. Prodr. 15[2]: 399. 1866).

1a. **Phyllanthus caroliniensis** ssp. *caroliniensis*.

(PLATE XIII, figs. A, B).

*Phyllanthus caroliniensis* Walt. Fl. Car. 228. 1788.
Synexemia obovata Raf. ibid.
Synexemia pumila Raf. ibid.
Synexemia cuneifolia Raf. New Fl. N. Amer. 4: 100. 1838.

Erect annual herb 1–3 dm. high, primary stem with several to many lateral branches; branches smooth or furrowed, not scabridulous; stipules triangular-lanceolate, denticulate especially toward the base, thin and scarios, (0.8–) 1–1.2 mm. long, 0.5–0.6 mm. broad. Leaves obovate or elliptic, rounded and apiculate or obtuse at the tip, 6–13 mm. long, 4–7 mm. broad, smooth on both sides and margins; midrib above plane, beneath conspicuously raised (at least proximally), the laterals (4 or 5 on a side) forming with the tertiaries a delicate reticulum. Male flowers solitary, each associated with 2 or 3 females in the cymule, calyx-lobes 6, segments of the disk cuneate or squarish, as broad as or broader than long. Female flower: calyx-lobes 6, linear-lanceolate or narrowly spatulate, acute, green, (0.9–) 1–1.2 (–1.4) mm. long, 0.2–0.3 mm. broad; disk cupular, enclosing $\frac{1}{2}$ to $\frac{3}{4}$ the ovary at anthesis, entire. Capsule c. 1.7 mm. in diameter, green; seeds light greyish brown, 0.8 mm. long, 0.65 mm. radially (in West Indian specimens).

**Type:** Herb. Thomas Walter, sheet 83 (holotype in BM not seen, but photograph in GH library examined).

**DISTRIBUTION:** more or less coextensive with the range of the species (Map 1).

JAMAICA: St. Mary: Castleton grounds, alt. 500 ft., Harris 12143 (F, GH, JAM, MO, US).

LESSER ANTILLES: SWAN ISLANDS: Eastern Swan Is., 17.22° N., growing in sand, Lord Moyne 4 (NY). MARTINIQUE: Bélanger 222 (P), 203 (G, P), 670 (P), 782 (P); Duss 48 (ex p., mixed with ssp. guianensis, F, NY); cultures, Balata, Mouret 113 (P). TOBAGO: The Widow, near Easterfield, on banks of the main road, Broadway 3515 (F). TRINIDAD: hb. Hooker (P); Woodbrook, wild in garden, Broadway 6675 (S); coastal plain, grassy roadside, Carenage, Britton & Hazen 12 (NY, HOLOTYPE of P. graminicola; GH, US, ISOTYPES); swale, O'Meara Savanna, N. L. & E. G. Britton 2502 (GH, TRIN).

The West Indian specimens of ssp. caroliniensis represent heterogeneous and sporadic populations; the specimens at least from Jamaica and Martinique have probably been introduced. The Trinidad form, made a separate species P. graminicola by Britton, has very narrow calyx lobes and small seeds but represents at most a rather unimportant variant of ssp. caroliniensis.

1b. Phyllanthus caroliniensis ssp. guianensis (Klotzsch) Webster\textsuperscript{10} var. antillanus Muell. Arg. Linnaea 32: 36. 1863.

\textsuperscript{10} Contr. Gray Herb. 176: 46. 1955.
Phyllanthus schomburgkianus var. antillanus Muell. Arg. in DC. Prodr. 15(2): 387. 1866.

Erect sparsely branched herb becoming 2–4.5 dm. high; branches smooth, often quite flattened above. Stipules rather narrowly triangular-lanceolate, acuminate, denticulate or entire, mostly 1.5–2 mm. long, c. 0.5–0.6 mm. broad. Leaf-blades elliptic to oblong or obovate, often broadest at or slightly below the middle, 8–22 mm. long, 4–10 mm. broad, smooth on both sides and on margins, thin, the reticulum of tertiary veinlets visible beneath. Male flowers paired (sometimes single?); calyx-lobes 6, disk-segments ovate or elliptic, definitely longer than broad, obscurely glandular at the tip. Female flowers 1 or 2 per axil; calyx-lobes 6, oblong to spatulate, acute or obtuse, green or reddish-tinged only at the base, 0.7–0.9 (–1) mm. long, (0.2–) 0.25–0.4 (–0.5) mm. broad; disk entire or roundly angled; styles free, ascending. Capsule c. 1.7–2 mm. in diameter; seed 0.9–1 mm. long, 0.75–0.8 mm. broad.

Type: Martinique, Sieber Herb. Martin, Suppl. 10.

Distribution: var. antillanus is endemic to the Lesser Antilles (Map I).

Lesser Antilles. Antigua: Wüllschlagel 496, 497 (GOET); Fig Tree Hill, a weed in the S.W. (volcanic) district, Box 1226 (F, US). Montserrat: weed in provision lands, alt. 1200 ft., Shaffer 178 (NY, US). Guadeloupe: 1839, Beaupérier (P); dans les champs cultivés, Camp Jacob, Duss 2447b (F, NY, US); Quentin 254 (P). Dominica: woodlands on the western slopes of Morne Brule, Portsmouth, Hodge 5734 (NY); Montpelier, Lloyd 582 (NY). Martinique: 1858, Bélanger 220 (P); 1867–70, Haun (P); herb. Vaillant (P); S. Marie, Bordas 7 (P); abondant le long des routes, Fonds St. Denis, Camp-Balata, &c., Duss 48 (ex p., mixed with ssp. caroliniensis, F, NY, US); Herb. Martin, Suppl. 10, Sieber (L, W, syntypes).

This plant is the Antillean representative of the South American ssp. guianensis, agreeing with var. guianensis in the stipules and male flowers and hardly differing in anything more than leaf shape. On Martinique var. antillanus occurs together with ssp. caroliniensis, which has presumably been introduced; there is no evidence that intergradation has occurred, but no careful field studies have been made. By virtue of its large stipules and elliptic disk segments in the male flower, ssp. guianensis is a very well-characterized group; but when the entire range of variation of P. caroliniensis is taken into account, it does not appear to warrant the rank of a separate species.


Erect annual or short-lived perennial, the primary stem either bearing pinnately arranged secondary branches or with few to several erect secondary branches clustered near its top; branches with minute papillae
either in discontinuous striae or densely arranged. Stipules triangular, acuminate, obscurely to conspicuously denticulate, (0.7–) 1–1.2 (–1.5) mm. long, 0.4–0.6 mm. broad. Leaf-blades narrowly elliptic to obovate, acute or more commonly obtuse or rounded-apiculate at the tip, acute at the base, 5–12 (–18) mm. long, 2–8 mm. broad, usually rather firm, bright green to olivaceous above, green to pallid beneath, secondary veins obscure above, usually evident and often raised beneath, tertiary veinlets ordinarily very obscure or quite invisible. Male flowers 1 or 2 per axil; calyx-lobes 6, olivaceous or infrequently reddish-tinged, c. 0.6–0.7 mm. long; disk-segments squarish or cuneate, about as broad as long. Female flowers 1 or 2 per axil; calyx-lobes 6 (rarely 5 or 7), mostly oblong to rather broadly spatulate and rounded to subacute at the tip, 0.6–0.9 (–1) mm. long, 0.2–0.3–0.5 (–0.6) mm. broad, green with pink-tinged scarious margins or often brilliantly red-stained, rarely lacking reddish color; disk usually lobed to irregularly or regularly divided into 6 cuneate or spatulate segments; styles more or less horizontally spreading. Capsule (1.5–) 1.6–1.75

Map I. Distribution of the Caribbean representatives of Phyllanthus carolinensis Walt.: black dots, ssp. carolinensis; vertical lines, ssp. saxicola; stippling, ssp. guianensis (var. antillanus); fine horizontal lines, ssp. stenopterus.

(-1.9) mm. in diameter, green or red-stained. Seeds (0.7–) 0.75–0.9 mm. long, 0.6–0.75 mm. radially and tangentially, dark-fuscous or light greyish brown.

Type: Florida, Dade County, everglades between Cocoanut Grove and Cutler, November 1903, Small & Carter 775 (NY, holotype).

Distribution: southern Florida to Greater Antilles (Map I).

CUBA: Without definite locality, Poeppig (P); Wright 500 (BR, F, GH GOET, MO, NY, P, S, US), 391 (S). PINAR DEL RIO: Las Martinas to the coast, Shafer 11095 (NY, US); banks of San Diego River not far from San Diego de los Baños, León & Hieram 4519 (NY), León 4411, 4553 (NY), Roig 2330 (SV). ISLA DE PINOS: Blain 174 (F); Caleta Cocodriros, coastal limestone, Britton, Wilson, & León 15293 (F, GH, MO, NY, US). HABANA: cerca de Kincón, Wilson 1055 (NY); coastal sands between Río Cojimar and Playa de Bacunarao, P. Wilson 9529 (NY); valley of Cuente Blanca River near Guanabacoa, León 500 (NY); banks of Qubú River, Mariano, León 3674 (NY, SV); inter Campo Florido et Loma de Coca, Ekman 1242 (S). MATANZAS: along railroad near Ibarra, Britton, Britton, & Shafer 340 (NY); prope Matanzas, Rugel 292 (NY); in graminos humides, in pratis salsis ad Matanzas, Poeppig (BR, MO, P, W).

LAS VILLAS: Ciénaga de Zapata, montes, Santo Tomas, Acuña 4333 (SV); a orillas río Caibarién, Fernando 482 (NY). CAMAGÜEY: savanna north of La Gloria, in grass, Shafer 360 (NY, US); Santa Cruz del Sur ad Río Najassa, Ekman 8612 (S). ORIENTE: Bayate, border of Río Cauto, Ekman 1094, 2442 (S); Sierra Maestra, León 10748 (NY); Sevilla Estate near Santiago, upper Guama River, alt. 550 ft., N. Taylor 164 (NY); steep banks of the Río Jojo c. 7 km. north of Cajovavo, Webster 4000 (MICH); stone banks of Jauco River, Jauco, León 11685 (NY); gorge of the Río Yamurí, in sandy crevices of rock near the river, Shafer 7853 (NY); vicinity of Baracoa, in yard, Shafer 3906 (NY); playa de Mata, Baracoa, Acuña & Díaz Barreto 18615 (SV); Baracoa, between Yumuri and Mata, on shady limestone rock, Ekman 3646 (S).


Paix, limestone terraces west of Saline-Michel, quite rare, *Ekman H3948* (S).


**DOMINICAN REPUBLIC:** Barrabas [province not indicated], *Raunkiaer 784* (C).

This subspecies of southern Florida, the Bahamas, and the Greater Antilles is perplexingly variable and eventually may be divided into several varieties. It grows in a wide variety of habitats including pinelands on limestone, salty meadows, sandy wastes, abandoned fields, etc., with perhaps an overall preference for rocky, shaded streambeds. The plants from southern Florida (at the type locality) and from Great Bahama Cay comprise a geographic race which differs from most of the rest of the subspecies by virtue of darker seeds, red-tinged male flowers, and more depauperate habit. These characters can scarcely be defined well enough for purposes of identification, however. Moreover, since there are in Cuba and Haiti a number of aberrant types, it does not seem practicable to describe outlying segments of the main population as varieties. Some collections, particularly those from Haiti, have scarcely scabridulous stems (even with close inspection under a lens!) and are thus hardly separable from ssp. *carolinensis*.


*Phyllanthus hyssopifolius* Muell. Arg. in DC. Prodr. 15(2): 390. 1866, sphaun.


Erect annual herb, completely smooth and glabrous; main stem unbranched or with very few laterals, 1–2.5 dm. high, 0.5–1 mm. in diameter, light brown, below terete, above becoming flattened and with a thin narrow wing c. 0.1–0.15 mm. broad at the margins; internodes 5–9 mm. long. Leaves: stipules ovate-lanceolate, acuminate, auriculate, more or less denticate, midrib area as in *P. heliotropus*, 1.2–1.5 mm. long, 0.6–0.7 mm. broad. Petioles 0.5–0.8 mm. long, plano-convex, adaxially grooved. Leaf-blades ovate, oblong, or elliptic, obtuse-apiculate at the tip, obtuse to rounded at the base, 6–12 mm. long, 2.5–5 mm. broad; above olivaceous, beneath pallid, green, or dull reddish; midrib raised above and beneath, laterals 4 or 5 on a side, obscure but usually visible above, beneath visible or obsolete; margin smooth.

Monoecious (sometimes dioecious?), the male and female flowers at separate axils, the male in few-flowered clusters (sometimes apparently solitary at branch-tips), the female solitary; male and female flowers irregularly alternating, with occasional axils barren.

Male flower: pedicel c. 0.5 mm. long. Calyx-lobes 5, obovate to orbicular or broader than long, rounded, entire, 0.6–0.7 mm. long, 0.6–0.9 mm. broad, scarious-hyaline, pale yellowish, the midrib unbranched, no herbace-
ous midstrip developed. Disk-segments 5, cuneate to orbicular, inconspicuously crenulate, rather thin, not evidently glandular, c. 0.2 mm. in diameter. Stamens 3, filaments free, c. 0.15 mm. long, obliquely ascending; anthers subglobose, 0.25–0.3 mm. broad, the slits confluent.

Female flower: pedicel 1 mm. long or less, geniculate. Calyx-lobes 6, oblong to obovate-oblong, obtuse or subacute, (0.8–) 1–1.2 mm. long, 0.4–0.7 mm. broad. Disk of 6 cuneate entire segments. Ovary smooth; styles horizontal, bifid, the greatly dilated and thickened branches spreading and appressed on the top of the ovary, less than 0.2 mm. long.

Capsule subglobose, c. 1.9 mm. high and 3 mm. broad, olivaceous, not veined. Seed bluntly trigonous, 1.6–1.7 mm. long, 1.4–1.5 mm. radially and tangentially, dull chestnut-brown with a thin easily rubbed-off yellowish coating, quite smooth, the ornamentation due to the outlines of the wavy rows of longitudinally elongated cells; hilum circular, purplish-black.

Type: Venezuela, Orinoco region, Santa Barbara, Maypure, Humboldt (Herb. Humboldt, P).

Distribution: savannas, Hispaniola and northern South America (Map II).


Trinidad: Piarco Savanna, Crueger (GH), Baker (TRIN 14854); O'Meara Savanna, Britton & Hazen 1573 (TRIN), Broadway (TRIN 9341).

The identification of the specimens from Hispaniola as this characteristically South American species is one of the more surprising phytogeographic discoveries made during this study. The material collected by Ekman and the Howards matches Mueller's description in the "Prodromus" (1866: 390) in all essential details. The very characteristic seeds, present in the mature condition in both Ekman collections, establish the identity of the Hispaniolan plant beyond doubt. The type specimen in Humboldt's herbarium in Paris differs from the West Indian plants in the small capsule (c. 2.5 mm. in diameter) and calyx-lobes only 0.7–0.8 mm. long, but nevertheless appears clearly to be conspecific.

Although Broadway 2130 from Piarco Savanna, Trinidad — the type collection of *P. monocladus* Urb. — has not been examined, the Crueger specimen from the same locality surely represents the same population. The Trinidad plants differ from the Hispaniolan ones only in their somewhat smaller size, while they correspond in all the technical characters. *Phyllanthus monocladus* may therefore be relegated to synonymy with confidence.

Erect perennial (but flowering the first year), entirely smooth and glabrous, the primary axis becoming a thickened, dark-brown caudex up to 1–2 cm. long and 5 mm. thick, with few to many somewhat thick sub-simple or branched dark brown lateral roots. Stems clustered atop the caudex, unbranched or with one or very few laterals, becoming mostly 3–5 (–7) dm. high, c. 1–1.5 mm. thick, greenish brown to deep chestnut brown, more or less terete at the very base but above soon flattened and with a narrow sharp wing 0.1–0.2 mm. wide, or merely acute-angled near ends of branches; internodes variable, decreasing in length from c. 7–15 mm. at base of large stems to c. 3–5 mm. at tips and on smaller stems. Stipules ovate-lanceolate, acuminate, auriculate, obscurely to conspicuously dentate, the midvein of the thickened dark basal median area extending as a conspicuous rib through the light to dark brown scarious margins, (1–) 1.3–1.7 (–2) mm. long, 0.5–0.9 mm. broad. Leaves: petioles plano-convex, grooved above, 0.7–1 mm. long, dark brown. Blades mostly oblong or sometimes ovate or elliptic, obtuse and mucronate at the tip, obtuse or rounded at the base, those on main stems mostly 5–12 mm. long and 2.5–6 mm. broad (somewhat smaller at tips and on smaller branches), subcoriaceous, bright to dull olivaceous above, olivaceous to reddish-bronzen or silvery beneath, the midrib depressed but visible above, salient and running to the mucro beneath; margin thickened, smooth or with irregular thickenings.

 Dioecious or subdioecious (rarely monoecious), sporadic female flowers occasionally appearing on otherwise male plants, the female and male flowers always at different axils; female flowers solitary (rarely paired):
male flowers in densely bracteolate monochasia eventually becoming 1–2 mm. long (but appearing as if in clusters of 2 or 3 at tips of branches or on plants flowering the first year).

Male flower: pedicel slender, 0.6–0.8 mm. long above the articulation. Calyx-lobes 5 or 6, oblong to obovate or suborbicular, rounded-obtuse to subtruncate, entire, (0.6–) 0.7–0.8 (–1) mm. long, 0.6–0.9 (–1) mm. broad, the yellowish scarious margins broader than the narrow to obsolete greenish midstrip; midrib unbranched, running to the tip. Disk-segments 5 or 6, orbicular to cuneate, 0.25–0.35 mm. long, entire or obscurely wavy, not evidently glandular. Stamens 3, completely free (very rarely united halfway), 0.3–0.5 mm. long, obliquely ascending; anthers swollen adaxially at the top of the filament (thus appearing globose from behind), 0.2–0.25 mm. long. 0.25–0.4 mm. broad; anther-sacs discrete, opening horizontally and transversely.

Female flower: pedicel geniculate, becoming c. 1 mm. long, reddish. Calyx reddish-tinged, massive at the base; calyx-lobes 5 or 6, ovate to oblong in flower, oblong to oblong-ovate in fruit, rounded or obtuse, entire, (0.9–) 1–1.3 mm. long, (0.5–) 0.6–0.75 (–0.9) mm. broad, spreading or reflexed, midstrip dark green but usually deeply reddish-stained, scarious margins broad; midrib plane without, salient within. Disk cut to the base into 5 or 6 squarish or cuneate more or less emarginate segments c. 0.35–0.4 mm. in diameter, these yellowish, rather thick, smooth and nearly entire, not evidently glandular. Ovary smooth, deeply sulcate; styles free, erect-ascending, c. ⅓–fid, c. 0.35 mm. long, 0.2 mm. wide across the thick and fleshy divericate and recurved branches.

Capsule depressed-globose, c. 1.7 mm. high, (2.7–) 2.8–3 mm. broad, deep lavender-reddish, no nervation visible on sides. Seeds trigonous, (1.3–) 1.35–1.55 mm. long, (1–) 1.2–1.3 (–1.4) mm. radially, 1–1.3 mm. tangentially, chestnut-brown to fuscous, lucid becoming dull, with scattered raised black points; hilum dark purplish-brown, triangular or round-ish.

TYPE: Cuba, Pinar del Río, Wright 1945 (GOET, HOLOTYPE; F, G, GH, NY, P, S, US, ISOTYPES). The collection in the Gray Herbarium has in a packet manuscript notes by Wright indicating the localities as: “savannas, Vueltabajo”, and “Pinales Hatequemado”. “Vueltabajo”, however, is merely a general name for a large stretch of tobacco-growing country in Pinar del Río; and the Pinales Hatequemado have not been identified.

DISTRIBUTION: endemic to Cuba and the Isle of Pines (Map II).

CUBA: PINAR DEL RÍO: Wright 1945 (GOET, HOLOTYPE; F, G, GH, NY, P, S, US, ISOTYPES); Laguna Santa Maria, wet sand, Britton, Britton, & Gager 7184 (NY); Laguna Jovero, dry sand, Shafer 10708 (F, NY, US); Laguna Los Indios and vicinity, in water, Shafer 10804 (NY); between Guane and Remates, sabanas near El Payuco, Killip 32363 (GH, US); savanes de San Luis, Marie-Victorin & Alain 326, 354 (MT); Laguna Redonda, between Pinar del Río City and La Coloma, fairly common in white sand, Webester 4672 (GH, MICH); between Pinar del Río and Coloma, Colpothrinax savanna, Britton et al. 6608.
This plant, characteristic of savannas and pinelands of western Cuba, takes its specific epithet from Wright’s manuscript notes that the plant “spreads its leaves to the morning sun”. It is related on the one hand to *P. pudens* Wheeler of Texas, but also to *P. hyssopifolioides*. In seed characters it agrees with the former but in the male flower and in fruit size it approaches more closely to the latter. It is also related to the widespread *P. compressus* which, however, is monoecious and has monadelphous stamens. These species, together with a few others of South America, comprise a complex whose distribution pattern parallels that of the subspecies of *P. carolinensis*; but in this case the differentiation between the groups is so pronounced that they certainly represent distinct species.

(To be continued)

EXPLANATION OF PLATES

PLATE XIII

Figs. A–B. *Phyllanthus carolinensis* ssp. *carolinensis* (*Harris 12143 [GH]*): A. branch, × 4; B. female flower, × 10.


Figs. E–G. *Phyllanthus hyssopifolioides* (*Baker 14854 [TRIN]*): E. branch, × 4; F. female flower, × 10; G. fruiting calyx, × 10.

PLATE XIV

*Phyllanthus heliotropus* Wright ex Griseb. (*Killip 32363 [GH]*, Figs. A–B, D–E; *Webster 4672 [GH]*, Fig. C): A. habit, c. ½ natural size; B. branch, × 5; C. male flower, × 20; D. female flower, after fertilization, × 10; E. seed, × 8.
Webster, West Indian Phyllanthus
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