

Outline of the neotropical infrageneric taxa of *Phyllanthus* (Euphorbiaceae)

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ABSTRACT. The 220 described neotropical species of *Phyllanthus* (Euphorbiaceae) are arranged in 33 sections belonging to 8 subgenera. Descriptions are given for one new subgenus, *Cyclanthera*, and five new sections – *Antipodanthus*, *Salviniopsis*, *Pityrocladus*, *Hylaeanthus*, and *Sellowianthus*. Three new subsections are described: sect. *Phyllanthus* subsect. *Almadenses*, sect. *Phyllanthus* subsect. *Clausseniani*; and sect. *Choretropsis* subsect. *Choretropsis*. Keys to species, and enumerations of them, are provided for new or revised sections and subsections.

The 800-odd species of *Phyllanthus*, one of the larger genera of Euphorbiaceae, have recently been tabulated by Govaerts et al. (2000), but the subgenera and sections are not indicated. The first comprehensive arrangements of sections in *Phyllanthus* were published by Baillon (1858) and by Grisebach (1859). Jean Müller (1863, 1866, 1873) presented a much more sophisticated system involving sections and subsections; his arrangement was followed, almost unaltered, by Pax and Hoffmann (1931). Since then, the infrageneric taxa have been summarized by Webster (1956-58; 1967a) and by Webster and Airy Shaw 1971; for taxa in Australasia). Pollen characters have proved to be very important indicators of relationship (Webster, 1956, 1988; Punt, 1967, 1987). The outline proposed here reflects changes due to ongoing revision of the neotropical species of *Phyllanthus* (Webster, 1967b, 1968, 1970, 1978, 1984, 1988, 1991, 1999, 2001; and ined.). In addition to a key to the subgenera and sections, the 9 subgenera and their constituent sections are enumerated. Species are enumerated for most sections except for the West Indian taxa previously treated (Webster, 1956, 1957, 1958, 1991). Only native taxa are included, hence characters used in the key may not apply to Old World taxa introduced into the neotropics.

Key to the neotropical subgenera and sections of *Phyllanthus*

- 1a. Branching unspecialized (not phyllanthoid), the axes all persistent; leaves on main axes spiral
stamens 3, filaments free; pollen grains colpate or porate; seeds verruculose or smooth.

subg. I. **ISOCLADUS**

2a. Phyllotaxy spiral; stipules not strongly auriculate.

3a. Pistillate disk usually dissected; pollen grains finely reticulate. sect. I.1. **Paraphyllanthus**

3b. Pistillate disk entire; pollen grains coarsely reticulate. sect. I.2 **Antipodanthus**

2b. Phyllotaxy distichous; stipules often strongly auriculate.

4a. Plants annual or perennial, rooted in substrate; leaves not inflated; fruiting

pedicels ± recurved; pollen grains 4-colporate; pollen grains 4-colporate, finely reticulate.

sect. I.3. **Loxopodium**

4b. Floating aquatics; leaves inflated; pollen grains 3-colporate, coarsely reticulate.

sect. I.4. **Salviniopsis**

1b. Branching phyllanthoid (except in sect. *Elutanthos*); leaves on main axes spiral and (at least distally) reduced to cataphylls; stamens mostly 2—6 (1—15), free or connate; pollen grains colporate, porate, or clypeate; seeds smooth, striate, ribbed, or verruculose.

5a. Fruits drupaceous (unknown in sect. *Ciccopsis*); stamens 3 or 4, filaments free; sepals 4 or 6; pollen grains 3-colporate, reticulate; trees or shrubs, often ramiflorous or with fascicled branchlets.

subg. II. **CICCA**

6a. Dioecious; flowers ramiflorous; sepals and stamens mostly 4; pollen grains not

angulaperturate. sect. II.1. **Cicca**

6b. Monoecious; flowers not ramiflorous; sepals 6, stamens 3; pollen grains

angulaperturate. sect. II.2. **Ciccopsis**

5b. Fruits mostly capsular (indehiscent in sect. *Hylaeanthus*); stamens free or connate; sepals mostly 5 or 6; pollen grains 3—8 colporate or porate; trees, shrubs, or herbs.

7a. Pollen grains 4—8 colporate, colpi monorate or diorate; exine reticulate; stamens 2 or 3,

filaments connate; trees or shrubs. subg. III. **EMBLICA**

8a. Pollen grains 4- or 5-colporate, monorate, globose to oblate; leaves without subapical

laminar glands; indumentum sometimes scurfy; anthers not apiculate, dehiscing

horizontally to obliquely; styles free, bifid, slender sect. III.1. **Pityrocladus**

8b. Pollen grains 5—8-colporate, diorate, subprolate; leaves sometimes with subapical laminar

glands; indumentum never scurfy; anthers often apiculate and dehiscing longitudinally;

styles free or connate, tips bifid to unlobed. sect. III.2. **Microglochidion**

7b. Pollen grains various (3-4-colporate, zonoporate, or pantoporate), colpi monorate or diorate; exine reticulate to vermiculate; stamens (1) 2—6 (-15), filaments free or connate; trees, shrubs, or herbs.

9a. Pollen grains globose to prolate, exine shields not developed; stamens

mostly 2 or 3, filaments free or connate; trees, shrubs, or herbs.

10a. Perianth 5-merous; Pollen grains globose, 3-syncolporate, exine coarsely rugose;

stamens 3, free, anthers dehiscing vertically; staminate disk of 3 segments; styles

connate into a long column...subgenus IV. **GOMPHIDIUM**, sect. IV.1. **Calodictyon**

10b. Perianth 6-merous; pollen grains not 3-syncolporate; exine not coarsely rugose;

styles usually not connate into a column.

11a. Pollen grains globose, brevicolporate and diorate, or porate, exine vermiculate to

pilate; staminate disk entire to dissected; monoecious or dioecious trees, shrubs or

herbs, branchlets simple (pinnatifid) or ramified (bipinnatifid).

subg. V. **CONAMI**

12a. Branchlets mostly bipinnatifid; pollen grains colporate to porate, exine

vermiculate to pilate; pistillate disk entire; seeds smooth; trees or shrubs.

sect. V.1. **Nothoclema**

12b. Branchlets pinnatifid; pollen grains porate, exine pilate; pistillate disk

entire or dissected; seeds smooth or verruculose.

13a. Fruit indehiscent, fleshy; seeds smooth; filaments usually connate;

pistillate disk entire; trees or shrubs with acuminate leaves.

sect. V.2. **Hylaeanthus**

13b. Fruit capsular; seeds verruculose; filaments free; pistillate disk

dissected; herbs with leaves rounded to acute. sect. V.3. **Apolepis**

11b. Pollen grains subprolate to prolate, 3- or 4-colporate, colpi monorate, exine

reticulate; seeds mostly ribbed, striate, or verruculose (rarely smooth); shrub or

herbs, branchlets pinnatifid; seeds striate, ribbed, or verruculose.....

subg. VI. **PHYLLANTHUS**

14a. Branchlets with well-developed leaves, terete or angled, not modified into phylloclades.

15a. Leaves on main axes tardily (or not at all) reduced to cataphylls; stamens 3, filaments free, connective enlarged; pistillate disk ± dissected

sect. VI.1. **Lysiandra**

15b. Leaves on main axes reduced to cataphylls; stamens 2—5, filaments free or connate; pistillate disk entire to angled.

16a. Ovary smooth; staminate flowers proximal on branchlet; leaf blades smooth on margins; seeds verruculose, striate, or horizontally ribbed

sect. VI.2. **Phyllanthus**

16b. Ovary bullate or rugose; pistillate flowers proximal on branchlet; leaves hispidulous on margins; seeds transversely ribbed.

sect. VI.3. **Urinaria**

14b. Branchlets lacking well-developed leaves, or modified to phylloclades.

sect. VI.4. **Choretropsis**

9b. Pollen grains globose, polyporate, with exine shields; stamens 2—15, filaments connate.

17a. Pollen exine shields elongated or if round with only 1 pila; herbs with solitary flowers, calyx and disk usually with purplish pigment; stamens 2 or 3, filaments connate; pistillate disk dissected.

Subgenus VII. **CYCLANTHERA**

18a. Anthers 2, discrete; pollen shields elongated (banded); leaves crisply succulent; branchlets unramified, rooting at nodes.

sect. VII.1. **Callitrichoides**

18b. Anthers 3, completely confluent into a circumscissile synandrium; pollen shields isodiametric, each with a central pila surrounded by a murus; leaves not succulent; branchlets often with 1 or 2 lateral branches, not rooting at nodes.

sect. VII.2. **Cyclanthera**

17b. Pollen shields pentagonal or hexagonal, with several to many brochi, ornamentation

± vermiculate; shrubs or small trees; staminate flowers usually several per glomerule; purplish pigment uncommon in disk or calyx (except in species of sect. *Orbicularia*); stamens (2) 3—6 (-15 in sect. *Williamia*), pistillate disk entire.

Subg. VIII. **Orbicularia**

19a. Branching phyllanthoid (branchlets deciduous); flowers in axillary cymes.

20a. Leaves on branchlets not reduced; branchlet axes not expanded into phylloclades.

21a. Leaves on main stems not reduced to cataphylls; dioecious; stamens 3, filaments free; seeds smooth (minutely striate).

sect. VIII.2. **Sellowianthus**

21b. Leaves on main stems reduced to cataphylls; monoecious.

22a. Branchlets pinnatifid.

23a. Styles bifid or unlobed, but not dilated or lacerate.

24a. Staminate disk dissected; branchlets mostly with > 10 leaves.

25a. Styles bifid; anthers not apiculate.

26a. Capsule somewhat fleshy, tardily dehiscent; stamens 3; leaves without mesophyllar sclereids.

sect. VIII.1. **Omphacodes**

26b. Capsule dry, readily dehiscent; stamens 2—6; leaves with mesophyllar sclereids.

27a. Filaments equalling or shorter than anthers; stipules caducous; leaves > 2 cm long.

sect. VIII.2. **Thamnocharis**

27b. Filaments longer than anthers; stipules caducous; leaves mostly 1—2 cm long.

sect. VIII.3. **Orbicularia**

25b. Styles entire or emarginate; stamens 3, filaments

connate, anthers apiculate, dehiscent vertically;
pistillate sepals deciduous.

sect. VIII.4 **Ciccastrum**

24b. Staminate disk not dissected; stamens 3, filaments
free or connate, branchlets mostly with 5—10
leaves. sect. VIII.5. **Brachycladus**

23b. Styles distinctly dilated, ± lacerate; stamens 2—15.

28a. Staminate disk dissected.

29a. Stamens 4 or more; flowers strictly axillary, not
cauliflorous; styles elongated, abruptly dilated distally;

30a. Leaves obtuse, usually with mesophyllar
sclereids; stamens 3—15; seeds colliculose or
verruculose. sect. VIII.3. **Orbicularia**

30b. Leaves obtuse to acuminate, without prominent
mesophyllar sclereids; seeds ± smooth.

31a. Pistillate flowers solitary; leaves glabrous;
seeds verruculose. sect. VIII.6. **Williamia**

31a. Pistillate flowers several per node;
leaves often pubescent; seeds smooth.

sect. VIII.7. **Oxalistyliis**

29b. Stamens 2 or 3; flowers in cauliflorous

thy rses; styles calyptriform. sect. VIII.8. **Epistylum**

28b. Staminate disk not dissected; stamens 2—7,
anthers dehiscent horizontally.

32a. Staminate sepals 5; stamens 3—7; seeds
smooth; leaves chartaceous, acuminate,
greenish beneath. sect. VIII.9. **Asterandra**

32a. Staminate sepals 4; stamens 2; seeds
with fissured testa; leaves coriaceous,
revolute, yellowish beneath.

sect. VIII.10. **Glyptothamnus**

23b. Branchlets bipinnatifid; axes incrustate or hirsutulous; stamens 2—6.

sect. VIII.11. **Hemiphyllanthus**

20b. Branchlet axes modified into phylloclades, leaves usually reduced; stamens
mostly 3; seeds verruculose.

sect. VIII.12. **Xylophylla**

19b. Branching not phyllanthoid, the axes not deciduous; stamens 3, filaments
usually connate; styles connate, bifid or unlobed; seeds smooth.

33a. Stamens 1—3; anthers extrorse (except *P. tequilensis*); pistillate flower
with 5 or 6 sepals.

sect. VIII.14. **Elutanthos**

33b. Stamens (3-) 4; anthers introrse, dehiscing longitudinally; pistillate
flowers with 8 (-10) sepals.

sect. VIII.15. **Diplocicca**

ENUMERATION OF TAXA

Subgenus I. **ISOCLADUS** G. L. Webster, J. Arnold Arb. 37: 345. 1956. TYPE: *Phyllanthus maderaspatensis* L.

About 60 species in 9 sections, 2 (*Loxopodium* and *Salviniopsis*) restricted to the neotropics.

Section I.1. **Paraphyllanthus** Müll. Arg., Linnaea 32: 3. 1863; DC. Prodr. 15(2): 1866. TYPE: *Phyllanthus maderaspatensis* L. (lectotypified by Webster, 1957).

Maschalanthus Nutt., Trans. Amer. Philos. Soc. 5: 175. 1837 (nom. illeg., non Sprengel, 1826). TYPE:

Maschalanthus polygonoides Nutt. (\equiv *Phyllanthus polygonoides* Nutt. ex Spreng.).

10 North American species, centered in the southwestern U.S. and Mexico, with 1 species,

Phyllanthus liebmannianus Müll. Arg., extending to Guatemala and Belize.

Key to the neotropical species of sect. *Paraphyllanthus*

1a. Styles distinctly bifid (or else less than 0.5 mm long).

2a. Branches smooth.

3a. Leaves broadly elliptic to suborbicular; styles 0.7—1 mm long;

filaments completely connate, staminal column 0.7—1.5 mm high;

seeds 2—2.3 mm long.

I.6. *P. gypsicola*

3b. Leaves elliptic to obovate; styles 0.3—1 mm long; staminal column

0.3—0.6 mm high; seeds 1.1—2.3 mm long.

4a. Herbs with often whip-like stems clustered on a caudex.

5a. Caudex not rhizome-like; filaments united $\frac{2}{3}$ or more;

fruiting pedicel 2.5—7 mm long; seeds 1.1—1.5 mm long. I.2. *P. polygonoides*

5b. Caudex rhizome-like; filaments united $\frac{1}{2}$ way; fruiting

pedicel 6—13 mm long; seeds 1.8—2 mm long.

I.3. *P. neoleonensis*

4b. Herbs or shrubs, not with whip-like clustered stems.

6a. Herbs, usually not over 0.5 m high; leaves obtuse to rounded

at base; stipules conspicuously auriculate; seeds 1.3—1.7 mm

long.

I.1. *P. liebmannianus*

6b. Shrub, often more than 0.5 m high; leaves cuneate at base;

stipules scarcely auriculate; seeds 1.9—2.4 mm long.

P. peninsularis ssp. *pen insularis*

2b. Branches papillate or scabridulous.

7a. Leaves distinctly obovate-cuneate, rounded to emarginate at apex, margins

± revolute; styles 0.3—0.7 mm long; seeds 1.5—2 mm long. I.5. *P. barbarae*

7b. Leaves oblong to ovate, obtuse and often apiculate at apex, margins not

revolute; styles 0.5—1.3 mm long; seeds 1.7—2.1 mm long.

I.4b. *P. peninsularis* ssp. *novogalicianus*

1b. Styles entire or emarginate at apex, sometimes dilated; filaments connate; branches smooth.

8a. Leaves broadly elliptic, apiculate at apex, rounded to emarginate at base, mostly 15—30 mm

long; styles 1—1.5 mm long, connate 1/3-1/2 way; staminal column mostly 1—2 mm high; seeds 2—2.3 mm long.

I.7. *P. galeottianus*

8b. Leaves linear to obovate, rounded to apiculate at apex, acute to obtuse at base, < 15 mm long; styles not over 1 mm long, ± free; staminal column < 1.5 mm long.

9a. Shrub mostly 1—2 m high; leaves obovate, neither pungently tipped nor falcate, 3—5 mm broad; seeds c. 2 mm long.

I.8. *P. subcuneatus*

9b. Subshrubs or perennial herbs not over 0.5 m high; leaves pungently tipped or falcate, not over 2 mm broad; seeds < 2 mm long.

10a. Leaves pungently tipped, not falcate, 0.7—1.5 mm broad; styles 0.3—0.5 mm long; seeds 0.9—1 mm long.

I.9. *P. ericoides*

10b. Leaves falcate, not pungently tipped, not over 0.8 mm broad; styles 0.9—1 mm long; seeds 1.4—1.5 mm long.

I.10. *P. fraguensis*

I.1.1. *Phyllanthus liebmannianus* Müll. Arg., DC. Prodr. 15(2): 366; Webster, Brittonia 23: 57. 1970.

TYPE: Mexico, *Liebmann* (syntypes, C!).:

The species includes 2 subspecies:

I.1.1a. *Phyllanthus liebmannianus* ssp. *liebmannianus* . .

Phyllanthus ferax Standl., Publ. Field Mus. Nat. Hist. Bot. 11: 134. 1932. TYPE: Guatemala, Petén, Uaxactun, *Bartlett 12157* (holotype, F 652466!).

Stems unbranched or sparsely branched at base, annual or perennial flowering first year; seeds 1.4—1.6 mm long.

Gulf coastal plain, 50—1000 m, Mexico (Tamaulipas to Chiapas and Quintana Roo) and Belize.

I.1.1b. *Phyllanthus liebmannianus* ssp. *platylepis* (Small) G. L. Webster, Brittonia 22: 57. 1970.

Phyllanthus platylepis Small, Fl. S.E. United States, ed. 2, 1347. 1913. TYPE: United States, Florida, Levy Co., Rosewood, 1876, *Garber* (holotype, NY!; isotype, F!).

Perennial herbs, stems clustered on a rhizome-like caudex; seeds 1.7—1.8 mm long.

Northwestern Florida, < 50 m, near Gulf coast of Florida..

I.1.2. *Phyllanthus polygonoides* Nutt. ex Spreng., Syst. Veg. 3:23. 1826. *Maschalanthus polygonoides*

- Nutt., Trans. Amer. Phil. Soc. II. 5: 175. 1837. TYPE: “Arkansas,” *Nuttall* (holotype, presumably at BM, not seen; isotype, NY!).
- Common, mostly on limestone substrates, 20—1500 m, from Missouri to New Mexico, south to Querétero, Aguascalientes, and Sonora.
- I.1.3. *Phyllanthus neoleonensis* Croizat, J. Wash. Acad. Sci. 33: 14. 1943. TYPE: Mexico, Nuevo León, Monterrey, *Pringle 1388bis* (holotype, GH!; isotype, US!).
- Locally common on Chipinque Mesa and adjacent limestone peaks, 800—1200 m, near Monterrey, Nuevo León, Mexico.
- I.1.4. *Phyllanthus peninsularis* Brandegee, Erythea 7: 8. 1899; Webster, Contr. Univ. Mich. Herb. 2001. TYPE: Mexico, Baja California Sur, San José del Cabo, *Anthony 264* (lectotype, [Webster, 2001], UC 178059!; isotype, US 313821!).
- I.1.4a. *Phyllanthus peninsularis* ssp. *peninsularis*.
- Tropical deciduous forest to oak forest, 0—1700 m, Baja California Sur.
- I.1.,4b. *Phyllanthus peninsularis* ssp. *novogalicianus* G. L. Webster, Contr. Univ. Mich. Herb. 2001. TYPE: Mexico, Jalisco, Mpio. Talpa de Allende, 11—12 mi S of Talpa, *McVaugh 20390* (holotype, MICH!).
- Tropical montane moist or subdeciduous forests, 1200—1900 m, western Mexico (Nayarit and Jalisco).
- I.1.5. *Phyllanthus barbarae* M. C. Johnston, Syst. Bot. 11: 35, fig. 1. 1986. TYPE: Mexico, Tamaulipas, Mpio. Gómez Farias, Sierra de Guatemala, Casa Piedras, *Johnston et al. 12851* (holotype, TEX!; isotype, DAV!).
- Oak, oak/pine, or cloud forests on limestone, 1100-2200 m, Sierra Madre Oriental from Tamaulipas to Hidalgo.
- I.1.6. *Phyllanthus gypsicola* McVaugh, Britton 13: 194. 1961; Webster, Contr. Univ. Mich. Herb. 2001. TYPE: Mexico, Colima, 11 mi SSW of Cd.Colima, *McVaugh & Koelz 1573* (holotype, MICH!; isotypes, DAV!, US!).
- Tropical deciduous woodland, 0—500 (1400) m, Baja California Sur, Jalisco, and Colima.
- I.1.7. *Phyllanthus galeottianus* Baillon, Adansonia I. 1: 32. 1860; Webster, Contr. Univ. Mich. Herb.

2001. TYPE: Mexico, Michoacán, Morelia, *Galeotti 7215* (lectotype: P!).

Phyllanthus americanus Sessé & Moçño, Pl. Nov. Hisp. 159. 1890. TYPE: Mexico, Guerrero, Mazatlán, *Sessé & Moçño 4561* (M).

Pine/oak and tropical deciduous forests, often in barrancas, 1100—2200 m, Sierra Madre Occidental (Jalisco) through transverse ranges to Chiapas.

I.1.8. *Phyllanthus subcuneatus* Greenm., Proc. Amer. Acad. Arts 33: 478. 1898. TYPE: Mexico, Puebla, Tehuacán, *Pringle 6753* (holotype, GH!; isotypes, UC!, US!).

Xeric scrub on limestone, 1500—1850 m; Tehuacán Desert, southeastern Puebla and adjacent Oaxaca.

I.1.9. *Phyllanthus fraguensis* M. C. Johnston, Syst. Bot. 10: 300. 1985. TYPE: Mexico, Coahuila, Mpio. Cuatrociénegas, Sierra de la Fragua, *I. M. Johnston 8768* (holotype, TEX!; isotype, GH!).

Known only from the type collection, from a pine forest on limestone, c. 1100 m.

I.1.10. *Phyllanthus ericoides* Torr., in Emory, Rep. U. S. Mex. Bound. 2(1): 193. 1858; Webster, Brittonia 22: 58. 1970.. TYPE: Mexico, Chihuahua, “high mountains near the Rio Grande,” *Parry* (holotype, US!).

Canyons in limestone areas, 550--650 m, west Texas and adjacent Chihuahua.

Section I.2. **Antipodanthus** G. L. Webster, Novon [in press]. TYPE: *Phyllanthus calycinus* Labill.

Frutices suffruticesve; folia spiraliter inserta; ramuli non decidui; flore ♂ laciniis calycis 5 vel 6; stamina 3, libera vel connata, antheris horizontaliter vel verticaliter dehiscentibus; pollinis grana subglobosa, 3- vel 4-colporata, reticulata; flore ♀ laciniis calycis 5 vel 6; discus integer; ovario 3-loculare; styli liberi bifidi; capsula in coccis 3 dehiscentibus; semina laevia vel verruculosa.

Shrubs or subshrubs with spiral phyllotaxy, branches not deciduous; staminate sepals 5 or 6; stamens 3, filaments free or connate; anthers horizontally or vertically dehiscent; pollen grains subglobose, 3- vel 4-colporatis, reticulatis; pistillate sepals 5 or 6; disk entire; fruits capsular; seeds smooth or verruculose.

This new section of about 15 species appears to be the southern hemisphere vicariant of the primarily holarctic sect. *Paraphyllanthus*. About 10 of the species are native to Australia (nos. 25—32 and

35—37 in Bentham, Fl. Austral. 6: 95. 1873) and the remainder to South America. Although the species of sect. *Antipodanthus* are similar in habit to plants of sect. *Paraphyllanthus*, they differ in their more coarsely reticulate pollen grains and the undivided pistillate disk.

Key to the species

- 1a. Filaments connate; stems \pm terete; seeds 2—2.7 mm long.
- 2a. Stipules 3—6 mm long; stems smooth; leaves on main stems > 5 mm long; dioecious.
- 3a. Leaves on main stems > 5 mm broad; seeds reticulate or irregularly verruculose. 1. *P. dictyospermus*
- 3b. Leaves on main stems 5 mm broad or less; seeds foveolate-punctate. 2. *P. pinifolius*
- 2b. Stipules 1—2.5 mm long; stems smooth or papillose; leaves on main stems mostly < 5 mm long; monoecious or dioecious.
- 4a. Dioecious; stems papillose; pistillate sepals 5; leaves strongly revolute, apically blunt with abruptly reflexed acumen. 3. *P. ramillosus*
- 4b. Monoecious; stems smooth; leaves concave but not revolute, tapering to a straight acumen.
- 5a. Staminate flower subsessile, pedicel < 1 mm long; staminal column 1—1.2 mm long; anthers deflexed or dehiscent horizontally. 4. *P. dawsonii*
- 5b. Staminate pedicel > 1 mm long; staminal column 0.5—0.6 mm high, anthers dehiscent obliquely. 5. *P. allemii*
- 1a. Filaments free; stems decurrent-angled from nodes; stipules 2 mm long or less; dioecious; seeds 1.4—1.7 mm long. 6. *P. rosmarinifolius*

I.2.1. *Phyllanthus dictyospermus* Müll. Arg., DC. Prodr. 15(2): 394. 1866; Fl. Brasil. 11(2): 58. 1873.

TYPE: Brazil, Minas Gerais, *Widgren 1003* (holotype: G!).

Phyllanthus regnellianus Müll. Arg., Fl. Brasil. 11(2): 58. 1873. TYPE: Brazil, Minas Gerais, Caldas,

Regnell II 48 (lectotype [designated here], S!).

Montane scrublands, c. 1000—1500 m, Minas Gerais. *Phyllanthus regnellianus*, which was distinguished by Müller only on the basis of a questionable difference in seed sculpturing, is here reduced to synonymy.

I.2.2. *Phyllanthus pinifolius* Baillon, Adansonia I. 5: 353. 1865; Müll. Arg., DC. Prodr. 15(2): 395.

1866; Fl. Brasil. 11(2): 59. 1873. TYPE: Brazil, Paraná, Curitiba, *St. Hilaire 1559o* (holotype, P!; isotype, K!).

Scrublands, 1500—2800 m, Minas Gerais, Espírito Santo, and Paraná.

I.2.3. *Phyllanthus ramillosus* Müll. Arg., Linnaea 32: 36. 1863; DC. Prodr. 15(2): 394. 1866;

Fl. Brasil. 11(2): 59. 1873; Webster, Sellowia 11: 165. 1959; L. B. Smith et al., Fl. Ilustr.

Catarinense EUFO 29. 1988.. TYPE: Brazil, Santa Catarina, *Herb. Franqueville* (syntype, G);

“Brasilia meridionali”, *Sello* (syntype, B, destroyed). Since the *Sello* syntype is presumably destroyed, the *Herb. Franqueville* specimen logically should become the lectotype; however, that specimen could not be located in the Prodr. Herbarium at Geneva.

15—2700 m, Bolivia, northern Argentina, and Brazil (Santa Catarina and Rio Grande do Sul)..

I.2.4. *Phyllanthus dawsonii* Steyerl., Los Angeles Co. Mus. Contr. Sci. 21: 13. 1958. TYPE: Brazil,

Goiás, Chapada dos Veadeiros, *Dawson 14776* (holotype, R!).

Campos rupestres, 1200—1500 m, Goiás.

I.2.5. *Phyllanthus allemii* G. L. Webster, **sp. nov.** TYPE: Brazil, Goiás, Mun. Alto Paraiso,

44 km S de Cavalcante rumo a Alto Paraiso, campo cerrado con *Vochysia*, *Vellozia*,

1525 m, 22 XI 1984, A. Allem, W. L. Werneck, G. L. Webster 3103 (holotype, DAV!;

isotype, CEN!).

Ab affine *Phyllanthus dawsonii* differt foliis minoribus, pedicello ♂ longior, columna staminalis brevior, antheris oblique dehiscentibus.

Dioecious subshrub 0.5—1 m high, glabrous; stems terete, smooth; cymules axillary, unisexual; staminate pedicel 1.4—1.8 mm long; sepals 6, biseriate, the smaller 1.2—1.3 × 0.8—1 mm, the larger 1.5—1.6 × 0.8—1.3 mm; filaments completely connate, staminal column 0.5—0.6 mm high; anthers muticous, oblique, dehiscing longitudinally, 0.3—0.4 mm long; disk-segments 6, round, smooth, 0.4—0.4 mm broad; pistillate pedicel 2.5—5 mm long in fruit ; sepals 6, subequal, 1.7—1.8 × 1.1—1.2 mm; ovary

3-locular; styles free, erect or ascending, bifid, tips slender and ± deflexed; mature fruits and seeds not seen.

Known with certainty only from the type locality in the Brazilian planalto in Goiás. A specimen from Minas Gerais (*Glaziou, 18478a*, K) has larger leaves (7—10 × 5—7 mm), but may be conspecific.

I.2.6. *Phyllanthus rosmarinifolius* Müll. Arg., Fl. Brasil. 11(2): 60. 1873. TYPE: Brazil, Rio de Janeiro, Serra dos Orgãos, *Gardner 5852* (holotype, G).

Recorded only from rocky slopes, c. 2000—2250 m, Rio de Janeiro, Brazil.

Section I.3. **Loxopodium** G. L. Webster, Contr. Gray Herb. 176: 46. 1955; J. Arnold Arb. 37: 346. 1956.

Brittonia 22: 59. 1970. *Geminaria* Raf., First Cat. Circ. Bot. Gard. Transylv. Univ. 14. 1824.

Synexemia Raf., Neogenyton 2. 1825. TYPE: *Phyllanthus caroliniensis* Walt.

This American section of 12 species is mostly neotropical, only *Phyllanthus caroliniensis* and *P. evanescens* entering the United States.

Key to the species

1a. Monoecious; smooth or verruculose.

2a. Filaments free; seeds minutely verruculose.

3a. Stems terete (or glabrous, if narrowly winged); capsules less than 2.7 mm broad.

4a. Leaf blades blunt; staminate flowers in glomerules. 1. *P. caroliniensis*

4b. Leaf blades sharply acute; staminate flowers in racemiform cymules.

2. *P. leptocaulos*

3b. Stems narrowly winged, distally compressed and hirtellous; capsules 2.7 mm

broad, or more. 3. *P. evanescens*

2b. Filaments connate, or if free then seeds smooth.

5a. Seeds smooth; filaments free or connate below; stems compressed, not sharply angled. 4. *P. hyssopifolioides*

5b. Seeds verruculose; stems terete or compressed.

6a. Stems terete, not winged.

7a. Styles bifid; leaf blades foveolate-punctate beneath. 5. *P. fallax*

- 7b. Styles dilated; leaf blades smooth beneath. 6. *P. brandegei*
- 6b. Stems compressed and winged. 7. *P. compressus*
- 1b. Dioecious; seeds [where known] verruculose.
- 8a. Perennials (or if annual then stems compressed); staminate pedicels 1 mm long or more; leaves elliptic to oblong or lanceolate.
- 9a. Filaments free; stems strongly compressed.
- 10a. Leaves thin, lanceolate; stipules lacerate, hastate at base. 8. *P. avicularis*
- 10b. Stipules auriculate at base but not hastate.
- 11a. Seeds 1.3—1.6 mm long; leaves subcoriaceous, blade mucronate at apex; 9. *P. heliotropus*
- 11b. Seeds 0.9—1.3 (1.4) mm long; leaves thin, not mucronate. 10. *P. montevidensis*
- 9b. Filaments connate; stems terete or slightly compressed. 11. *P. pohlianus*
- 8b. Annuals, stems terete; staminate flowers subsessile; leaves suborbicular; filaments ± connate. 12. *P. simplicicaulis*

I.2.1. *Phyllanthus caroliniensis* Walter, Fl. Carol. 228. 1788; Müll. Arg., DC. Prodr. 15(2): 399.

1866; Webster, J. Arnold Arb. 37: 347. 1956; Brittonia 22: 59. 1970. TYPE: United States, Carolina, *Herb. Walter* 83 (holotype, BM).

The most widely distributed American species of *Phyllanthus*: Pennsylvania and Illinois south to Argentina and Paraguay. Three subspecies were recognized by Webster (1956).

I.2.1a. *Phyllanthus caroliniensis* ssp. *caroliniensis*.

For synonyms see Webster (1970). Tropics and subtropics, 0—1000 m, throughout most of the range of the species; however, in much of its range it has probably been introduced.

I.2.1b. *Phyllanthus caroliniensis* ssp. *saxicola* (Small) G. L. Webster, Contr. Gray Herb. 176: 46. 1955; J.

Arnold Arb. 37: 350. 1956; Brittonia 22: 60. 1970. *Phyllanthus saxicola* Small, Bull. N. Y. Bot. Gard. 3: 428. 1905. TYPE: Florida, Dade Co., between Coconut Grove and Cutler, *Small & Carter* 775 (holotype, NY!).

Pinelands and scrublands on limestone, 0—400 m, southern Florida, Bahamas, Cuba, and Hispaniola.

I.2.1c. *Phyllanthus caroliniensis* ssp. *guianensis* (Klotzsch) G. L. Webster, Contr. Gray Herb. 176: 46. 1955; J. Arnold Arb. 37: 349. 1956. *P. guianensis* Klotzsch, Lond. Jour. Bot. 2: 51. 1843. *P. schomburgkianus* and *P. schomburgkianus* var. *guianensis* (Klotzsch) Müll. Arg., DC. Prodr. 15(2): 387. 1866. TYPE: Guayana, Essequibo and Rupununi Rivers, *Robert Schomburgk* 529 (lectotype [selected here], G!).

Phyllanthus guianensis var. *acuminatus* Müll. Arg., Linnaea 32: 29. 1863. *P. schomburgkianus* var. *acuminatus* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 387. 1866. TYPE: Suriname, Miq. Stirp. Surinam. t. 31B.

? *Phyllanthus guianensis* var. *anceps* Müll. Arg., Linnaea 32: 29. 1863. *P. schomburgkianus* var. *anceps* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 387. 1866. TYPE: Brazil, São Paulo, *Riedel* (holotype, B, destroyed).

Swamps and savannas, 0—500 m, Nicaragua and Hispaniola south to Brazil and Paraguay. Müller's variety *acuminatus* is probably a synonym of ssp. *guianensis*, but the disposition of var. *anceps* remains uncertain—it could be some other species of sect. *Loxopodium*. The status of this taxon remains equivocal. It could be recognized as a distinct species because of its perennial habit; on the other hand, it approaches *P. montevidensis* except for its monoecious flower production.

I.2.1d. *Phyllanthus caroliniensis* ssp. *stenopterus* (Müll. Arg.) G. L. Webster, J. Arnold Arb. 37: 348. 1956; Ann. Missouri Bot. Gard. 54: 222. 1968. *P. stenopterus* Müll. Arg., DC. Prodr. 15(2): 399. 1866.: TYPE: Colombia, Magdalena River, *Holton* 870 (holotype, G!).

Wet savannas, 0—700 m, Nicaragua, Panama, Colombia, and Venezuela. A distinctive subspecies, possibly deserving status of a distinct species.

I.2.2. *Phyllanthus leptocaulos* Müll. Arg., Fl. Brasil. 11(2): 47. 1873. TYPE: Brazil, Minas Gerais, Lagoa Santa, *Warming* 1582 (holotype, C!).

Known only from the type collection in cerrado, c. 750 m, Minas Gerais.

I.2.3. *Phyllanthus evanescens* Brandegee, Zoe 5: 207. 1905. TYPE: Mexico, Sinaloa, Culiacán, *Brandegee* (holotype, UC!).

Phyllanthus pudens L. C. Wheeler, Contr. Gray Herb. 127: 50. 1939. *P. avicularia* Small, Bull.

Torrey Bot. Club 27: 278. 1900 (nom. illeg.; non *P. avicularis* Müll. Arg., 1863). TYPE: Texas, Austin Co., Columbus, *Bush 263* (holotype: NY).

Sporadic in intermittently moist depressions, 0—1900 m, Mexico (Sonora to Tamaulipas), Texas, and Louisiana, south to Nicaragua. In the United States, this plant has generally gone under the name *Phyllanthus pudens*

I.2.4. *Phyllanthus hyssopifolioides* Kunth in H.B.K., Nov. Gen. Sp. 2: 108. 1817; Müll. Arg., DC.

Prodr. 15(2): 390. 1866; Fl. Brasil. 11(2): 50. 1873; Webster, J. Arnold Arb, 37: 353. 1956;

Fl. Venez. Guayana 5: 197. 1999; Fl. Nicaragua 2000. TYPE: “in sylvis Orinocensibus prope cataractum Maypurensium,” *Humboldt & Bonpland* (holotype, P!).

Phyllanthus monocladius Urb., Repert. Sp. Nov. 15: 404. 1919. TYPE: Trinidad, Piarco Savanna, *Broadway 2130* (holotype, B, destroyed).

Swamps, 0—200 m, Nicaragua to Venezuela, Brazil, and Paraguay; disjunct in Hispaniola.

I.2.5. *Phyllanthus fallax* Müll. Arg., Linnaea 32: 29. 1863; 34: 73. 1865; DC. Prodr. 15(2): 388. 1866; Fl.

Brasil. 11(2): 48. 1873. TYPE: Brazil, Minas Gerais, Serra do Lapa, *Riedel 1115* (holotype, B, destroyed; photograph, UC!). Müller apparently described this species again, two years later; Govaerts et al. (2000) give the later citation.

Known only from Minas Gerais.

I.2.6. *Phyllanthus brandegei* Millsp., Proc. Cal. Acad. Sci. II. 2: 218. 1889; Webster, Contr. Univ.

. TYPE: Mexico, Baja California Sur, Comondú, 1889, *Brandegee 19* (holotype, UC!).

Rare in Sonoran Desert, c. 500 m, Baja California Sur and possibly Sonora.

I.2.7. *Phyllanthus compressus* Kunth in H.B.K., Nov. Gen. Sp. 2: 109. 1817; Müll. Arg., DC. Prodr.

15(2): 390. 1866; Fl. Bras. 11(2): 50. 1873; Macbride, Field Mus. Nat. Hist., Bot. 13 (3A, 1): 38. 1951. TYPE: Mexico, Veracruz, *Humboldt & Bonpland* (holotype, P!).

Along streams, rain forest areas, 50—1300 m, Mexico to Peru.

I.2.8. *Phyllanthus avicularis* Müll. Arg., Linnaea 32: 32. 1863; DC. Prodr. 15(2): 389. 1866;

Fl. Brasil. 11(2): 49. 1873. TYPE: Brazil, Minas Gerais, *Claussen 792* (lectotype [chosen here], G!).

Along streams, Brazil (Minas Gerais) and Paraguay.

I.2.9. *Phyllanthus heliotropus* Wright ex Griseb., Goett. Nachr. 1865: 167. 1865; Müll. Arg.,

DC. Prodr. 15(2): 388. 1866; Webster, J. Arnold Arb. 37: 354. 1956. TYPE: Cuba, Pinar del Rio, *Wright 1945* (holotype, GOET; isotypes, F, G, GH, NY, S, US).

Moist savannas and pinelands, 50—100 m, western Cuba (Pinar del Río).

I.2.10. *Phyllanthus montevidensis* Müll. Arg., Linnaea 32: 37, 1863; DC. Prodr. 15(2): 397.

1866; Fl. Brasil. 11(2): 46. 1873; Allem, Iheringia Bot. 22: 6. 1977; L. B. Smith et al.,

Fl. Ilustr. Catarin. EUFO: 56. 1988.. TYPE: Uruguay, Montevideo, *Sello 1414* (holotype, B, destroyed; isotype perhaps at L).

? *P. pseudoguayanensis* Herter & Mansf., Rev. Sudamer. Bot. 5: 33. 1937. TYPE: Uruguay, frontier with Brazil, Rivera/Santana do Livramento, *Herter 1807* (holotype, G).

Streambanks and forests, c. 100—200 m, Argentina, Uruguay, Paraguay, and Brazil. Similar to some forms of *Phyllanthus carolinensis*, and reduced to that species by Allem (1977).

I.2.11. *Phyllanthus pohlianus* Müll. Arg., Fl. Brasil. 11(2): 49. 1873. TYPE: Brazil, Minas Gerais,

Salto Grande, *Pohl 3893* (holotype, W).

Cerrado, c. 1000 m, Minas Gerais. Closely related to *Phyllanthus avicularis*, and perhaps not distinct.

I.2.12. *Phyllanthus simplicicaulis* Müll. Arg., Linnaea 32: 38. 1863; DC. Prodr. 15(2): 400. 1866;

Fl. Brasil. 11(2): 67. 1873. TYPE: Brazil, Minas Gerais, *Weddell 1858* (holotype, S; isotype, G!).

Brazil, Minas Gerais; according to Müller (1873), related to *Phyllanthus submarginatus* in sect. *Phyllanthus*; its affinities need to be verified.

Section I.4. **Salviniopsis** G. L. Webster & Holm-Nielsen, **sect. nov.** Herbae monoicae aquaticae, habitus ut *Salvinia*, foliis distichis inflatis; flores axillares; sepala florem ♂ 5, segmenta disci 5, stamina 3 libera, antherae horizontaliter dehiscentes, pollinis grana subglobosa 3-colporata, reticulata; sepala florem ♀ 5, disco cupuliforme, ovario laeve loculis 3; styli liberi bifidi ramis subcapitatis; semini laevia. TYPE: *Phyllanthus fluitans* Müll. Arg.

Floating aquatics with habit of *Salvinia*; leaves distichous, blade inflat; flowers solitary, axillary; staminate sepals and disk segments 5; stamens 3, filaments free, anthers horizontally dehiscent; pollen grains subglobose, 3-colporate, exine reticulate; pistillate sepals 5; disk patelliform; ovary smooth, 3-locular; styles free, bifid, tips subcapitate; fruits capsular; seeds smooth.

This monotypic section, endemic to the Amazonian region of South America, is ecologically the most highly specialized taxon of *Phyllanthus*. The leaves are modified as floating organs, and the plant overall is certainly the most extreme aquatic of any Euphorbiaceae. The relationships of sect. *Salviniopsis* are rather difficult to determine because of its reduced and highly specialized morphology. The flowers resemble those in sect. *Phyllanthus*, especially subsect. *Niruri*, but are also similar to those of sect. *Loxopodium*, and its closest affinity appears to be with the latter. The unusual characteristics of *P. fluitans* in Argentina were studied by Holm-Nielsen (in an unpublished manuscript), who believed that the Argentine specimens, which develop elongated stems, might be a distinct species. Further investigation is needed to determine whether the Argentine specimens represent a growth stage or possibly a geographically defined subspecies or species.

I.4.1. *Phyllanthus fluitans* Benth ex Müll. Arg., *Linnaea* 32: 36. 1863; DC. Prodr. 15(2): 400. 1866; Fl. Brasil. 11(2): 48. 1873; Chodat, Bull. Herb. Boissier II. 6: 143. 1906; Lourteig, Ark. Bot. II. 3(5): 73. 1954; Lot et al., Bol. Soc. Bot. Mex. 39: 83. 1980; Webster, Fl. Venez. Guayana 5: 197. 1999. TYPE: Brazil, Pará, Santarem, *Spruce* (holotype, G!; isotype, US!). Streams and ponds, 50—200 m, Colombia and Brazil to Argentina and Paraguay; recently discovered in Mexico, where it may possibly have been introduced.

Subgenus II. **CICCA** (L.) G. L. Webster, J. Arnold Arb. 37: 344. 1956. *Cicca* L., Mant. Pl. 124. 1767.

TYPE: *Cicca disticha* L. (= *Phyllanthus acidus* [L.] Skeels).

This small subgenus of only 4 species could be included within subg. *Kirganelia* (Juss.) G. L. Webster, to which it shows many similarities. However, the studies of pollen diversity in the African species of subg. *Kirganelia* by Brunel and Roux (1977) and Meewis and Punt (1983) show such a great diversity that it seems quite possible that subg. *Kirganelia* will be subdivided. In that event, it is possible

that additional African species might appropriately be transferred to subg. *Cicca*, so it seems premature to combine the two subgenera.

Section II.1. **Cicca** (L.) Müll. Arg., *Linnaea* 32: 50. 1863; DC. Prodr. 15(2): 413. 1866; Webster, J. Arnold.

Arb. 38: 65. 1957. TYPE: *Cicca disticha* L. (= *Phyllanthus acidus* [L.] Skeels).

Tricarium Lour., Fl. Coch. 557. 1790. TYPE: *Tricarium cochinchinensis* Lour. (= *Phyllanthus acidus* [L.] Skeels).

Staurothyra Griff., Notul. 4: 476. 1854. TYPE: not stated (by inference, *Phyllanthus acidus* (L.) Skeels).

In contrast to my treatment of 1957, further consideration has led to the decision to include *Aporosella* as a coordinate subsection with *Cicca*. This involves a biogeographic conundrum, since subsect. *Cicca* is now interpreted to be African in origin, and subsect. *Aporosella* to be neotropical. In view of the many trans-Atlantic vicariant links in *Phyllanthus* (and other Euphorbiaceae), this arrangement does not seem unreasonable.

Subsect. II.1a. **Cicca** (L.) Müll. Arg., DC. Prodr. 15 (2): 413. 1866 (as subsect. *Eucicca*). TYPE: *Cicca disticha* L. (= *Phyllanthus acidus* [L.] Skeels).

Ovary 3- or 4-locular; fruit fleshy; monoecious.

One species, *Phyllanthus acidus*, the “grosella”, widely cultivated circumtropically. The origin of the species has always been problematic because it has been known only from cultivated plants. In an earlier review of this problem (Webster, 1957), it was noted that there were no authentic reports of wild *P. acidus*, but the relationship with subsect. *Aporosella* pointed towards an American origin. I cited a collection of Poeppig from Isla Colares, in Brazil (Pará) at the mouth of the Amazon as probably the only collection that represented a wild population. Unfortunately, Prof. João Murça Pires (in lit., 1965) informed me that he was certain the plant was not native in Pará. Subsequently, I discovered that *Phyllanthus wildemanni* Beille, described from “Conakry et îles de Los” in what is now Guinea. It is notable that in his description Beille noted that *P. wildemanni* was close to *P. acidus*. However, Hutchinson and Dalziel (Fl. W. Trop. Afr., ed. 1, 290. 1928) mistakenly treated *P. wildemanni* as a synonym of *P. profusus* N. E. Br., an error repeated by Govaerts et al. (2000). Further exploration in the coastal forests of Guinea and adjoining areas

is needed to determine whether any extensive wild populations of *P. wildemannii* remain. The existence of *P. acidus* in coastal forests of west tropical Africa would explain its early historical occurrence in India, Ceylon, and Java.

II.1a.1. *Phyllanthus acidus* (L.) Skeels, USDA Bur.Pl. Ind. Bull. 148: 17. 1909. *Averrhoa acida* L., Sp. Pl. 428. 1753. *Cicca acida* (L.) Merr., Interpr. Rumph. Herb. 17. 1917. TYPE: "India," Hermann ? (holotype, LINN 592.3!).

Cicca disticha L., Mant. 1: 124. 1767. *Phyllanthus distichus* (L.) Müll. Arg., DC. Prodr. 15(2): 413. 1866. TYPE: "India," (holotype, LINN).

Phyllanthus wildemannii Beille, Bull. Soc. Bot. France 61(*): 293. 1917. TYPE: Guinée Française [Guinea], Conakry et îles Los, *Wildemann 12721, 13305* (syntypes, P!).

Apparently native to lowland rainforests, Guinea; cultivated throughout the tropics. A more extensive synonymy is provided in Webster (1957: 66)/

Subsect. II.1b. **Aporosella** (Chodat) G. L. Webster, Contr. Univ. Mich. Herb. 23: 381. 2001. *Aporosella* Chodat, Bull. Herb. Boissier II. 5: 488. 1905. *Phyllanthus* sect. *Aporosella* (Chodat) Webster, J. Arnold Arb. 38: 72. 1957. TYPE: *Phyllanthus chacoensis* Morong.

Ovary 2- or 3-locular; drupe with corky rather than fleshy exocarp; dioecious.

Although subsect. *Aporosella* is separated from subsect. *Cicca* by distinct "key characters", the two taxa are clearly closely related and adapted to similar lowland coastal forests. The 2 species of subsect. *Aporosella* are classic vicariants: *P. elsiae* Urb. in the Caribbean, from Mexico to Colombia and Venezuela, and *P. chacoensis* Morong in the pantanal region of Bolivia, Argentina, Paraguay, and Brazil.

II.1b.1. *Phyllanthus elsiae* Urb., Repert. Sp. Nov. 15: 405. 1919; Webster, J. Arnold Arb. 38: 73. 1957; Contr. Univ. Mich. Herb. 23: 381. 2001. TYPE: Tobago, Auchenskeoch Beach, *Broadway 4789* (holotype, B, destroyed; lectotype [designated by Webster, 1957], US 759650!).

Woods along lagoons and rivers near sea level, often behind mangroves, Mexico south through Central America to Colombia, Venezuela, and Tobago.

II.1b.2. *Phyllanthus chacoensis* Morong, Ann. N. Y. Acad. Sci. 7: 218. 1893. *Aporosella chacoensis* (Morong) Speg., Cat. Mad. Argent. 349. 1910; Pax & K. Hoffm., Med. Rijksherb. Leiden 40:

2. 1921. TYPE: Paraguay, Central, Asunción, *Morong 355* (holotype, NY; isotype, US!).

Aporosella hassleriana Chodat, Bull. Herb. Boissier II. 5: 489. 1905. TYPE: Paraguay, Concepción, *Hassler7161* (holotype, G).

Swampy lowlands of the *pantanal* and Chaco regions, 20—100 m, Bolivia, Paraguay, Brazil, and Argentina.

Sect. II.2. **Ciccopsis** Webster, Contr. Gray Herb. 176: 57. 1955; J. Arnold Arb. 38: 61. 1957. TYPE:

Phyllanthus pseudocicca Griseb.

This section includes only a single rare species from eastern Cuba. Because the fruit is still unknown, the position of sect. *Ciccopsis* within subg. *Cicca* must be considered as uncertain.

II.2.1. **Phyllanthus pseudocicca** Griseb., Goett. Nachr. 1865(7): 166. 1865; Müll. Arg., DC. Prodr.

15(2): 384. 1866; Webster, J. Arnold Arb. 38: 62. 1957. TYPE: Cuba, Oriente [Guantánamo], Cuchillas de Baracoa, *Wright 1940* (holotype, GOET; isotypes, G!, GH!, MO!).

Phyllanthus brevistipulus Urb., Symb. Antill. 9: 183. 1924. TYPE: Cuba, Oriente [Guantánamo],

Baracoa, valley of Río Macaguanigua, *Ekman 4323* (lectotype [selected here];, S!).

Phyllanthus punctulatus Urb., *ibid.* 1924. TYPE: Sierra de Nipe, Río Piedra, *Ekman 9825* (lectotype, S!).

Evergreen forests and pinelands, to 600 m, eastern Cuba.

Subgenus III. **EMBLICA** (Gaertn.) Kurz, As. Soc. Bengal 42(2): 238. 1874. *Embllica* Gaertn., Fruct. Sem.

2: 122. 1790. TYPE: *Embllica officinalis* Gaertn. (nom. illeg.; = *Phyllanthus emblica* L.).

As delimited here, subg. *Embllica* includes 40—50 species of both the Old World and New World. Typically, species of subg. *Embllica* differ from subg. *Gomphidium* in their stephanocolporate (4—8 colpi) pollen, androecium of only 2 or 3 connate stamens, and bifid connate styles. The boundaries between subgenera *Kirganelia*, *Cicca*, and *Gomphidium* still remain to be determined more precisely.

Sect. III.1. **Pityrocladus** G. L. Webster, **sect. nov.** Frutices arborescentes dioeci; rami plusminusve furfuracei; ramuli simplici; folia eglandulosa; flores axillares; sepala 5 imbricata; segmenta disci ♂ 5;

stamina 2 vel 3, filamenta connata; pollinis grana 4—5-colporata, reticulata; ovario 3-loculare; styli liberi bifidi; fructus dehiscentes; semina laevia. TYPE: *Phyllanthus ruscifolius* Kunth.

Monoecious (rarely dioecious) shrubs, often scandent; branches and branchlets more or less scabridulous or scurfy; deciduous branchlets pinnatifid (not ramified), with c. 10—50 leaves; leaf blades chartaceous, lacking a subapical laminar gland; stipules persistent; flowers pedicellate, in axillary unisexual or bisexual cymes; staminate sepals 5 or 6, subequal, free, imbricate; disk-segments 5; stamens 2—5 (-7), filaments connate (rarely free); anthers dehiscent obliquely or horizontally; pollen grains subprolate, 4- or 5-colporate, colpi monorate and lacking borders, exine reticulate; pistillate sepals 5, imbricate; disk crateriform or dissected; ovary 3-locular; styles free, spreading, bifid to unlobed; fruits dehiscent or indehiscent, seeds smooth.

This new section includes 6 species mainly of South America, but extending to Costa Rica; several additional species appear to be undescribed. The 4—5-colporate reticulate pollen grains suggest placement in subg. *Emblica*, even though the shape of the grains is not typically prolate. Section *Pityrocladus*, named for the characteristic scurfy indumentum, is similar to sect. *Microglochidion* but differs in its tendency to a scandent habit, eglandular leaves, scurfy indumentum, and less prolate pollen grains with fewer monorate colpi.

Key to the species

1a. Leaves glabrous (or nearly so) on both faces, veins distinctly prominulous abaxially; branchlets 0.8—1.8 mm thick, 10-30 cm long with 20—35 leaves; staminate pedicels 3—7 mm long; stamens 3—6; sepals 5.

2a. Monoecious; branchlets not winged; leaf blades elliptic, 1.5—2.5 cm long, rounded-apiculate at apex; stamens (3) 4—6; styles unlobed or apically bifid. fruits indehiscent.

1. *P. symphoricarpoides*

2b. Dioecious; branchlets winged; leaf blades ovate-lanceolate, 3—6 cm long, acuminate; stamens 3; styles bifid; fruits dehiscent.

2. *P. sponiifolius*

1b. Leaf blades glabrous or hirsutulous adaxially; veins not prominulous (or if so, then blades distinctly

hirsutulous abaxially); branchlets 5—25 cm long with 5—75 leaves; staminate pedicels < 1 mm long; stamens 2 or 3; sepals 5 or 6.

3a. Leaf blades abaxially copiously hirsutulous, lateral veins prominent; stamens 2.

4a. Monoecious; branchlets 0.6—0.9 mm thick, with 5—11 leaves; leaf blades 1.5—3.5 cm long; petioles 1—2 mm long; stipules 3—5 mm long; styles unlobed. 3. *P. popayanensis*

4b. Dioecious; branchlets 0.4—0.6 mm thick, with 20—45 leaves; leaf blades 1—1.5 cm long; petioles c. 0.5 mm long; stipules 1.5—2 mm long; styles bifid. 4. *P. ruscifolius*

3b. Leaf blades abaxially glabrous or minutely scabridulous; veins not prominent; stamens 2 (rarely 3).

5a. Leaf blades elliptic, alveolate-reticulate abaxially, 5—7 mm broad; branchlets 0.4—0.7 mm thick; stipules 1—1.5 mm long; staminate disk segments discrete, flat.

5. *P. cuatrecasanus*

5b. Leaf blades oblong, smooth abaxially, 2—5 mm broad; branchlets 0.7—1 mm thick; stipules 2—3.5 mm long; staminate disk segments massive, ± confluent. 6. *P. valerii*

III.1.1. *Phyllanthus symphoricarpoides* Kunth in H.B.K., Nov. Gen. Sp. 2: 114. 1817. *Glochidion*

symphoricarpoides (Kunth) Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 58. 1931. TYPE: Ecuador, “Loxa” [Loja], *Humboldt & Bonpland* (holotype, P!; isotype, B!).

Montane thickets and cloud forest, 1500-2750 m, Colombia to Peru.

III.1.2. *Phyllanthus sponiifolius* Müll. Arg., Linnaea 32: 25. 1863; DC. Prodr. 15(2): 378. 1866. TYPE:

Ecuador, *Fraser* (holotype, G!).

Montane thickets and cloud forest, 1000—2000 m, Colombia and Ecuador.

III.1.3. *Phyllanthus popayanensis* Pax, Bot. Jahrb. 26: 503. 1899. TYPE: Colombia, Popayán, Páramo de

Guanacas, *Lehmann 4708* (holotype, B, destroyed; lectotype [chosen here], K!).

Montane thickets and cloud forest, 2000-2800 m, Colombia (Cauca).

III.1.4. *Phyllanthus ruscifolius* Müll. Arg., DC. Prodr. 15(2): 358. 1866. TYPE: Colombia, Prov. Cauca,

Triana 3659 (holotype, P).

Montane thickets and cloud forest, 1900-2200 m, Colombia (Valle del Cauca).

III.1.5. *Phyllanthus bahiensis* Müll. Arg., Linnaea 32: 20. 1863; DC. Prodr. 15(2): 367. 1866. TYPE:

Brazil, Bahia, *Blanchet 1842* (holotype, G!).

Coastal forests (Mata Atlántica), eastern Brazil (Bahia and Sergipe).

III.1.5. *Phyllanthus cuatrecasanus* G. L. Webster, **sp. nov.** TYPE: Colombia, Caquetá, Quebrada del Río

Hacha, 2100-2250 m, *Cuatrecasas 8533* (holotype, US).

Frutex ramis glabris, ramulis deciduis hirtellis; differt ab *P. valerio* foliis ellipticis, infra alveolato-reticulatis; ramulis tenuioribus, stipulis minoribus, segmentis disci liberis.

Known only from the type collection.

III.1.6. *Phyllanthus valerii* Standl., Field Mus. Bot. 18: 619. 1937; Burger & Huft, Fieldiana Bot. n.s. 36:

147. 1995. TYPE: Costa Rica, Heredia, Yerba Buena, NE of San Isidro de Heredia, 2000 m,

Standley & Valerio 49814 (holotype, F).

Montane forests, Costa Rica, 1200-2100 m; very similar plants have been collected in Bolivia.

Sect. III.2. **Microglochidion** (Müll. Arg.) Müll. Arg., Flora 1865: 370. 1865; DC. Prodr. 15(2): 322. 1866;

Jablonski, Mem. N. Y. Bot. Gard. 17: 89. 1967. *Glochidion* sect. *Microglochidion* Müll. Arg.,

Linnaea 32: 58. 1863; Pax & K. Hoffman, Natürl. Pflanzenfam. ed. 2, 19c: 58. 1931. TYPE:

Glochidion vacciniifolium Müll. Arg. (\equiv *Phyllanthus vacciniifolius* (Müll. Arg.) Müll. Arg.).

This large section of c. 40 species is the most characteristic group of *Phyllanthus* in the montane scrub on the *tepui*s of the Guayana highlands (Webster, 1999). Although species of sect. *Microglochidion* are readily distinguished by their relatively small coriaceous leaves, the prolate, diorate pollen grains furnish one of the most important synapomorphies for recognition of the group. The diorate colpi of sect. *Microglochidion* point towards a possible affinity with subg. *Conami*, since that is the only other group of neotropical *Phyllanthus* in which the feature occurs. On the other hand, the common occurrence of laminar glands, apiculate anthers, and stylar columns in sect. *Microglochidion* distinguishes it from nearly all other neotropical species of *Phyllanthus*. Since the revisions of Jablonski (1967) and Webster (1999) have not yet reached the monographic level, no attempt to recognize subsections is made here.

Provisional key to the species

1a. Leaf blades > 5 mm broad; laminar glands present or absent.

- 2a. Leaves without laminar glands; anthers muticous or emarginate.
- 3a. Leaf blades obovate, cuneate at base; anthers deeply emarginate, \pm horizontally
dehiscent; styles bifid; fruiting pedicel 3—7 mm long. 1. *P. jablonskianus*
- 3b. Leaf blades \pm orbicular, rounded at base; anthers muticous, vertically dehiscent;
styles unlobed; fruiting pedicel 14—20 mm long. 2. *P. neblinae*
- 2b. Leaf blades with laminar glands (at least 0.2 mm broad); anthers mostly apiculate.
- 4a. Styles free, unlobed; leaves narrowly elliptic, revolute; laminar gland subapical; seeds 3.5 mm
long; branchlets with 4—8 leaves. 3. *P. lediformis*
- 4b. Styles connate, or else laminar gland usually at least 1 mm from tip; leaves not
revolute; branchlets with 5—20 leaves.
- 5a. Filaments free; staminate pedicels < 6 mm long.
- 6a. Pistillate pedicel > 1 mm long; styles bifid or unlobed.
- 7a. Styles free, bifid; free; fruiting pedicel 18—20 mm long; leaf blades obovate,
cuneate at base, c. 1—2.5 \times 0.8—2 cm..... 4. *P. myrsinites*
- 7b. Styles connate, unlobed or stigmatiform.
- 8a. Styles elongated (not stigmatiform).
- 9a. Leaves opposite on branchlet; leaf blades round, mostly broader than;
5. *P. paraqueensis*
- 9b. Leaves alternate on branchlet; leaf blades obovate to round, usually
not broader than long.
- 10a. Leaf blades reniform-cordate, \pm clasping stems; styles
4—5 mm long; filaments < 1 mm long... 6. *P. duidae*
- 10a. Leaf blades shallowly cordate to truncate at base; styles
0.3--0.5 mm long; filaments > 2 mm long. 7. *P. jauaensis*
- 8b. Styles stigmatiform
- 11a. Leaf blades obovate, cuneate at base, c. 1.5—2 \times 0.8—1.2 cm;
staminate disk segments 6; fruiting pedicel 20—25 mm long.
P. ventuarii

11b. Leaf blades reniform, broader than long, c. 2.5—3 × 3.5-4 cm;
staminate disk segments 3; fruiting pedicel < 5 mm long.

9. *P. strobilaceus*

6b. Pistillate pedicel < 1 mm long; styles connate, unlobed.

12a. Styler column 1—1.3 mm high; fruiting pedicels 3—9 mm long;
leaves c. 1 cm long and broad, chartaceous; branchlets terete, mostly
with > 10 leaves.....10. *P. vacciniifolius*

12b. Styler column < 1 mm high; fruiting pedicels 10—25 mm long;
leaf blades mostly > 1 cm long, ± coriaceous; branchlets angled, with
≤ 10 leaves.....11. *P. majus*

5b. Filaments connate; staminate pedicels 6—8 mm long; styles connate.

13a. Leaf blades coriaceous; styler column not longer than pedicel.

14a. Ovary sessile; styles completely connate; leaf blades rounded at
tip.12. *P. longistylus*

14b. Ovary stipitate; styles free distally; leaf blades emarginate.

13. *P. chimantae*

13b. Leaf blades chartaceous; styler column longer than pedicel.

.....14. *P. websterianus*

1b. Leaf blades 1—5 (6) mm wide; laminar gland absent or minute (≤ 0.2 mm dm); staminate
filaments and styles free or connate..

15a. Leaf blades not falcate; laminar gland minute.

16a. Styles bifid, free.

17a. Filaments free, staminate disk segments 6; fruiting pedicel

18a. Leaf blades narrowly elliptic, 3-6 mm broad; staminate pedicel 1—2 mm
long.14. *P. tepuicola*

18b. Leaf blades linear, 1—2 mm broad; staminate pedicel 4—5 mm long.

.....15. *P. maguirei*

17b. Filaments connate; staminate disk segments 3.16. *P. minutifolius*

- 16b. Styles unlobed, connate.
- 19a. Leaf blades oblong to linear, lateral veins obscure; branchlets with 50—60 leaves; filament longer than anther.....17.*P. subapicalis*
- 19b. Leaf blades obovate, emarginate, lateral veins prominent; branchlets with 5—15 leaves.....18.*P. carrenoi*
- 15b. Leaf blades falcate, subapical laminar glands 0.1`--0.2 mm broad; staminate filaments free, anthers apiculate; styles connate, unlobed.
- 20a. Leaf blades > 2 mm broad; branchlets with 20—35 leaves; seeds c. 3 mm long.
.....19.*P. pycnophyllus*
- 20b. Leaf blades 1—2 mm broad; branchlets with > 40 leaves; seeds 2.3—2.7 mm long.
.....20..*P. obfalcatus*

III.2.1. *Phyllanthus jablonskianus* Steyrm. & Luteyn, Ann. Missouri Bot. Gard. 71: 317. 1984;

Webster, Fl. Venez. Guayana 5: 197. 1999.

TYPE: Venezuela, Amazonas, Cerro de la Neblina, *Steyermark 129816* (holotype, VEN; isotype, NY!).

Montane scrub, 1800—2300 m, Cerro de la Neblina.

III.2.2. *Phyllanthus neblinae* Jabl., Mem. N. Y. Bot. Gard. 17:: 107. 1967; TYPE: Venezuela,

Amazonas, Cerro de la Neblina, *Maguire et al. 42256* (holotype, NY!; isotype, US!).

Montane scrub, 1700—2100 m, Amazonas, Cerro de la Neblina..

III.2.3 *Phyllanthus lediformis* Jabl., Mem. N. Y. Bot. Gard. 17: 103. 1967. TYPE: Venezuela,

Amazonas, Cerro Yutaje, *B. & C. K. Maguire 35110* (holotype, NY!; isotype, US!).

Montane thickets and savanna, 1300—1500 m, Amazonas, Serranía Yutaje.

III.2.4. *Phyllanthus myrsinites* Kunth in H.B.K., Nov. Gen. Sp. 2: 111. 1817; Müll. Arg., DC. Prodr.

15(2): Müll. Arg., DC. Prodr. 15(2): 355. 1866; Jablonski, Mem. N. Y. Bot. Gard. 17: 107.

1967; Webster, Fl. Venez. Guayana 5: 198. 1999. TYPE: Venezuela, “in umbrosis

Tuamini prope pagum San Antonio de Javita,” *Humboldt & Bonpland* (holotype, P!).

This species is treated by Webster (1999) as comprising two subspecies:

III.2.4a. *Phyllanthus myrsinites* ssp. *myrsinites*.

Phyllanthus adenophyllus Müll. Arg., *Linnaea* 32: 24. 1863. TYPE: Brazil, Rio Negro, between Barcellos and San Gabriel, *Spruce 2072* (holotype, G!; isotype).

Phyllanthus dinizii Huber, *Bull. Soc. Bot. Genève* II. 6: 182. 1915. TYPE: Brazil, Pará, basin of Rio Arirambe, *Ducke 8018* (holotype, MG).

Phyllanthus gallinetae Jabl., *Mem. N.Y. Bot. Gard.* 17(1): 111. 1967. TYPE: Venezuela, Amazonas, Rio Siapo below Gallineta, *Wurdack & Adderley 43550* (holotype, NY!; isotype, US!).

Phyllanthus glaucoviridis Jabl., *Mem. N. Y. Bot. Garad.* 17(1): 101. 1967. TYPE: Venezuela, Ríó Atabapo, *Wurdack & Adderley 42943* (holotype, NY!; isotype, US!).

Widespread on white-sand savannas, 50—600 m, eastern Colombia, northeastern Peru, Brazil, and Venezuela.

III.2.4b. *Phyllanthus myrsinites* ssp. *francavillanus* (Müll. Arg.) G. L. Webster, *Fl. Venez. Guayana*

5: 198. 1999, fig. 190. *Phyllanthus francavillanus* Müll. Arg., *Linnaea* 32: 20. 1863. TYPE: Venezuela, Amazonas, Caño Pimichín, *Spruce 3713* (holotype, G!; isotype, K!).

Phyllanthus pimichinianus Jabl., *Mem. N. Y. Bot. Garad.* 17: 111. 1967. TYPE: Venezuela, Amazonas, Cano San Miguel, *Wurdack & Adderley 43233* (holotype, NY).

White-sand savannas and banks of blackwater rivers, 50—200 m, Venezuela and Brazil.

III.2.5. *Phyllanthus paraqueensis* Jabl., *Mem. N. Y. Bot. Gard.* 17: 104. 1967; Webster, *Fl.*

Venez. Guayana 5: 199. 1999.. TYPE: Venezuela, Amazonas, Cerro Sipapo, *Maguire & Politi 27519* (holotype, NY!; isotype, US!).

Montane scrub, 1500—1800 m; endemic to Cerro Sipapo; very close to *Phyllanthus duidae*.

III.2.6. *Phyllanthus duidae* Gleason, *Bull. Torrey Bot. Club* 58: 382. 1931; Jablonski, *Mem. N. Y. Bot.*

Gard. 17: 103. 1967; Webster, *Fl. Venez. Guayana* 5: 197, fig. 188.. 1999. TYPE: Venezuela, Amazonas, summit of Duida, *Tate 629* (holotype, NY!; isotype, US!).

Tepui meadows and montane scrub, 1000--2300 m; endemic to Cerro Duida.

III.2.7. *Phyllanthus jauaensis* Jabl., *Mem. N. Y. Bot. Gard.* 23: 865. 1972; Webster, *Fl. Venez. Guayana*

5: 197. 1999. TYPE: Venezuela, Bolívar, Cerro Jaua, *Steyermark 97877* (holotype, NY!; isotypes, US!, VEN).

- Montane scrub, 1900—2200 m; endemic to Cerro Jaua; very similar to *P. paraqueensis*.
- III.2.8. *Phyllanthus ventuarii* Jabl., Mem. N. Y. Bot. Gard. 17(1): 104. 1976; Webster, Fl. Venez. Guayana 5: 200. 1999. TYPE: Venezuela, Amazonas, Serranía Parú, Cano Asisa, Rio Ventuari, *Cowan & Wurdack 31155* (holotype, NY!).
.Montane thickets, c. 2000 m; endemic to Serranía Parú. This species is closely related to *Phyllanthus duidae*, *P. jauaensis*, and *P. paraqueensis*; the four species in ensemble form a “superspecies.”
- III.2.9. *Phyllanthus strobilaceus* Jabl., Mem. N. Y. Bot. Gard. 17(1): 96. 1967; Webster, Fl. Venez. Guayana 5: 200. 1999. TYPE: Venezuela, Amazonas, Cerro de la Neblina, Rio Yatua, *Wurdack & C. K. Maguire 42476* (holotype, NY!; isotype, US!).
Montane scrub, 1000—1800 m, Bolívar (Macizo de Chimantá) and Amazonas (Cerro Marahuaka, Cerro de la Neblina).
- III.2.10. *Phyllanthus vacciniifolius* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 322. 1866; Jablonski, Mem. N. Y. Bot. Gard. 17(1): 98. 1967; Webster, Fl. Venez. Guayana 5: 200, fig. 191.. 1999.
Glochidion vacciniifolium Müll. Arg., Linnaea 32: 63. 1863. TYPE: Guayana, Roraima, *Richard Schomburgk 1007* (holotype, B, destroyed; lectotype [selected here], K!).
Phyllanthus vacciniifolius ssp. *vinillaensis* Steyerl., Ann. Missouri Bot. Gard. 71: 317. 1984. TYPE: Venezuela, Amazonas, Serranía Vinilla, *Steyerl, Berry, & Velascio 130328* (holotype, VEN).
Widespread in savannas, 400—2400 m, Bolívar (Gran Sabana) and Amazonas in Venezuela, extending to Guayana and northern Brazil. The species is somewhat variable, but the proposed ssp. *vinillaensis* does not appear to merit formal recognition.
- III.2.11. *Phyllanthus majus* Steyerl., Fieldiana Bot. 28: 318. 1952; Jablonski, Mem. N. Y. Bot. Gard. 17(1): 99. 1967; Webster, Fl. Venez. Guayana 5: 198, fig. 58.. 1999. TYPE: Venezuela, Bolívar, Ptari-tepui, *Steyerl 59482* (holotype, F; isotype, US!).
Montane scrub and savannas, 1000-2300 m, Bolívar (Gran Sabana), Amazonas (Duida and adjacent massifs), Guayana.
- III.2.12. *Phyllanthus longistylus* Jabl., Mem. N. Y. Bot. Gard. 17(1): 100. 1967; Webster, Fl. Venez. Guayana 5: 197. 1999. TYPE: Venezuela: Bolívar, Auyan-tepui, *Tate 1181* (holotype, NY!).
Montane scrub, 1100—2200 m, Bolívar (Auyán-tepui, Chimantá), Amazonas (Cerro Parú,

Sipapo). The species appears very close to *Phyllanthus chimantae*, and may not be separable.

III.2.13. *Phyllanthus chimantae* Jabl., Mem. N. Y. Bot. Gard. 17(1): 100. 1967; Webster, Fl. Venez.

Guayana 5: 196. 1999. TYPE: Venezuela, Bolívar, Churi-tepui (Muru-tepui), *Wurdack 34176* (holotype, NY!).

Tepui meadows and scrub, 2000—2500 m; endemic to the Macizo de Chimantá, Bolívar.

III.2. 14. *Phyllanthus tepuicola* Steyerm., Acta Bot. Venez. 10: 236. 1975; Webster, Fl. Venez. Guayana

5: 200. 1999. TYPE: Venezuela, Amazonas, Cerro Duida, *Fariñas, Velásquez, & Medina 433* (holotype, VEN; isotype, DAV!).

Montane scrub, c. 1000 m; endemic to Cerro Duida. Closely related to *P. maguirei*.

III. 2.15. *Phyllanthus maguirei* Jabl., Mem. N. Y. Bot. Gard. 17(1): 105. 1967; Webster, Fl. Venez.

Guayana 5: 198. 1999. TYPE: Venezuela, Amazonas, Cerro de la Neblina, Cañon Grande, *Maguire & Wurdack 42360* (holotype, NY!; isotype, US!).

Along streams in montane woodlands, 1000-2000 m, Amazonas (Cerro Duida, Cerro de la Neblina).

III.2.16. *Phyllanthus minutifolius* Jabl., Mem. N. Y. Bot. Gard. 17(1): 115. 1967; Webster, Fl.

Venez. Guayana 5: 198, fig. 178. 1999. TYPE: Venezuela, Amazonas, Cerro Sipapo, *Maguire & Politi 27648* (holotype, NY!; isotype, US!).

Endemic to tepui meadows, Cerro Sipapo.

III.2.17. *Phyllanthus subapicalis* Jabl., Mem. N. Y. Bot. Gard. 17(1): 101. 1967; Webster, Fl. Venez.

Guayana 5: 200, fig. 193. 1999. TYPE: Venezuela, Amazonas, Cerro Sipapo, *Maguire & Politi 27549* (holotype, NY!).

Riparian scrub, and tepui meadows, 1000—1900 m. Three subspecies can be recognized (key in Webster, 1999).

III.2.17a. *Phyllanthus subapicalis* ssp. *subapicalis*.

Phyllanthus anadenus Jabl., Mem. N. Y. Bot. Gard. 17(1): 93. 1967. TYPE: Venezuela, Amazonas, Cerro Sipapo, *Maguire & Politi 27922* (holotype, NY!; isotype, US!).

Widespread in tepuis in Amazonas, and in Brazil (Roraima, Serra Parima).

III.2.17b. *Phyllanthus subapicalis* ssp. *sequoiifolius* (Jabl.) G. L. Webster, Fl. Venez. Guayana 5: 200.

1999. *Phyllanthus sequoiifolius* Jabl., Mem. N. Y. Bot. Gard. 17(1): 93. 1967. TYPE: Venezuela, Bolívar, Macizo de Chimantá, Sarvén-tepui, *Wurdack 34159* (holotype, NY!).

Montane forests, 1700—1900 m, Macizo de Chimantá.

III.2.17c. *Phyllanthus subapicalis* ssp. *holstii* G. L. Webster, ssp. nov.

Ab aliis subspeciebus *P. subapicalis* differt foliis vix imbricatis; stylis bifidis; ab ssp.

sequoiifolio antheris c. 1 mm longis. TYPE: Venezuela, Amazonas, Dpto. Atures, along stream through sandstone, valley of Río Coro-Coro, W of Serranía de Yutaje, 1250—1300 m; shrub 1.5 m high, branches arching, flowers pale green with reddish tinge, *B. K. Holst & R. L. Liesner 3339* (holotype, DAV!; isotype, MO!). Known from the type locality and from another site in Dpto. Atures: Caño Piedra, 15 km SE of Puerto Ayacucho, 1500 m, 04° 54' N, 66° 54' W, *Fernández Elio & Manuel Yáñez 5944* (MO).

III.2.18. *Phyllanthus carrenoi* Steyerl., Bol. Soc. Venez. Cienc. Nat. 32: 343. 1976; Webster, Fl.

Venez. Guayana 5: 196. 1999. TYPE: Venezuela, Bolívar, Cerro Jaua, *Steyerl., Carreño E. & Brewer-Carias 109596* (holotype, VEN).

Endemic to Cerro Jaua, in tepui meadows and savanna, 1900—2300 m.

III.2.19. *Phyllanthus pycnophyllus* Müll. Arg., DC. Prodr. 15(2): 322. 1866; Jablonski, Mem. N. Y. Bot.

Gard. 17(1): 102. 1967; Webster, Fl. Venez. Guayana 5: 199, fig. 191. 1999. *Glochidion microphyllum* Müll. Arg., Linnaea 32: 69. 1863. TYPE: Guayana, Roraima, *Richard Schomburgk 1006* (holotype, B, destroyed; lectotype [selected here], K!).

Montane scrub, 1900—2400 m, Bolívar (Cerro El Sol, Ilú-tepui) and Guayana (Roraima).

III.2.20. *Phyllanthus obfalcatus* Lasser & Maguire, Brittonia 7: 79. 1950.; Webster, Fl. Venez. Guayana

5: 199, fig. 192. 1999. TYPE: Venezuela, Amazonas, Cerro Yaví, *Phelps & Hitchcock 45* (holotype, NY).

Montane scrub, 1300—2200 m, northeastern Amazonas and adjacent Bolívar.

Subgenus IV. **GOMPHIDIUM** (Baillon) G. L. Webster, J. Arnold Arb. 48: 338. 1967; Kew Bull. 26:

92. 1971. *Phyllanthus* sect. *Gomphidium* Baillon, Adansonia I. 2: 234. 1862. LECTOTYPE:

Phyllanthus chamaecerasus Baillon (designated by Webster, 1967).

A primarily Old World group of about 100 described species, mainly in southeast Asia and the Pacific islands; the majority of the species are endemic to New Caledonia (Schmid, 1991). Only one section is known from the Americas.

Section IV.1. **Calodictyon** G. L. Webster, Ann. Missouri Bot. Gard. 54: 194. 1967. TYPE: *Phyllanthus tuerckheimii* G. L. Webster.

The only species of this section, *Phyllanthus tuerckheimii*, is confined to montane forests in Guatemala and Chiapas. The plant resembles Australian and Melanesian species of subg. *Gomphidium*, which appear to be most similar. There is also a resemblance to sect. *Nothoclema* (subg. *Conami*) in the androecium and staminate disk, but this is contradicted by the pinnatifid branchlets with large firm leaves, elongated stylar column, and very different pollen. Evidently sect. *Calodictyon* is a relict disjunct, and it is possible that other species in the section may be discovered in Central or South America.

IV.1.1. *Phyllanthus tuerckheimii* G. L. Webster, Ann. Missouri Bot. Gard. 54: 195, fig. 1. 1967.

TYPE: Guatemala, Alta Verapaz, Pansamalá, *von Tuerckheim 1085* (holotype, US 931347!; istotypes, GH!, US!).

Evergreen forests, 400--1500 m, Chiapas and Guatemala.

Subgenus V. **CONAMI** (Aubl.) G. L. Webster, J. Arnold Arb. 37: 345. 1956; 38: 363. 1957.

Conami Aubl., Hist. Pl. Guiane Fr. 926, t. 354. 1775. TYPE: *Conami brasiliensis* Aubl. (≡ *Phyllanthus brasiliensis* (Aubl.) Müll. Arg.).

This entirely tropical American subgenus includes 3 sections with a total of c. 20 species. The subgenus is distinguished from most taxa of subg. *Kirganelia* by the common occurrence of bipinnatifid branchlets, pollen grains with pores or diorate colpi (Webster, 1966; Webster and Proctor, 1984), an androecium of 3 connate stamens with horizontally dehiscent anthers, and a staminate disk usually of 3 duplex segments. However, subg. *Conami* is much more difficult to separate from subg. *Gomphidium*, in which bipinnatifid branchlets and a similar staminate disk may occur; only the diorate colpi furnish a

diagnostic feature. This character of diorate colpi is shared by sect. *Microglochidion*, but as noted above that group in many other respects has little in common with subg. *Conami*.

Sect. V.1. *Nothoclema* G. L. Webster, Contr. Gray Herb. 176: 56. 1955; J. Arnold Arb. 38: 363. 1957.

TYPE: *Phyllanthus acuminatus* Vahl.

Pollen studies (Webster & Carpenter, ined.) indicate that sect. *Nothoclema* is the basal group in subg. *Conami*; some species have colporate pollen with vermiculate exine sculpturing, whereas other species in sect. *Nothoclema* and in sects. *Hylaeanthus* and *Apolepis* have porate pollen with pilate exine sculpturing. In a revision of sect. *Nothoclema* (Webster, ined.) 9 species, ranging throughout the neotropics from Mexico to Argentina, are recognized.

Key to the species

- 1a. Branchlets and leaves glabrous (petioles rarely sparsely scabrid or hirtellous).
 - 2a. Branchlets bipinnatifid, with 2—20 or more lateral axes (occasional proximal branchlets on early year's growth unramified); seeds punctulate.
 - 3a. Staminal column 0.7—1.2 mm high; anthers distinctly deflexed; styles 0.7—1.1 mm long; branchlets with 5—10 lateral axes. 1. *P. anisobus*
 - 3b. Staminal column < 0.7 mm high; anthers not distinctly deflexed; styles ≤ 0.7 mm long; branchlets with 2—20 lateral axes.
 - 4a. Branchlets with mostly 2—4 (-10) lateral axes; sepals in fruit 1.5—2.5 mm long.
 - 5a. Staminate pedicels 5—15 mm long, sepals 1.7—2.2 mm long; anthers emarginate, not compressed; seeds 1.7—2.1 mm long. 2. *P. mocinianus*
 - 5b. Staminate pedicels 1.5—4 mm long, sepals 0.8—1.7 mm long; anthers acute, compressed.....5. *P. mcvaughii*
 - 4b. Branchlets mostly with 15—20 lateral axes; staminate sepals 1—1.5 mm long; sepals in fruit 1—1.3 mm long. 3. *P. micrandrus*
 - 2b. Branchlets simple (occasionally with 1 or 2 lateral axes); seeds smooth or nearly so.
 - 6a. Branchlets angled but not ribbed; leaves ovate, rounded at base, mostly > 1 cm broad;

fruiting pedicel terete, 8—12 mm long; pistillate disk 3-lobed, not crenulate.

6. *P. caymanensis*

6a. Branchlets strongly compressed and ribbed; leaves narrowly elliptic to obovate, cuneate at base, mostly < 1 cm broad; fruiting pedicel wing-angled, 5—7 mm long; pistillate disk cupular with crenulate rim.7. *P. pavonianus*

1b. Branchlet axes and leaves (at least the petioles) usually scabridulous or hirtellous; seeds smooth or punctulate.

7a. Staminate disk of 3 discrete segments; main axis of branchlet usually without staminate cymules; leaf blades glabrous, hirtellous, or scabridulous; plants always producing seeds.

8a. Leaves and branchlet axes glabrous or hirtellous, but not scabridulous; leaf blades obtuse to acute; styles bifid, branches slender; seeds punctulate..

9a. Leaf blades glabrous (except petiole and adjacent midrib); anthers not flattened, obtuse or emarginate; leaves not reddish.....4. *P. graveolens*

9b. Leaf blades hirtellous; anthers flattened, acute; leaves often reddish. 5. *P. mcvaughii*

8b. Leaves and branchlet axes scabridulous or scabrous (at least on midrib and petiole); leaf blades acuminate; styles flattened and dilated; seeds smooth. 8. *P. acuminatus*

7a. Staminate disk segments ± coalesced. disk annular or lobed; main axis of branchlet often with staminate cymules; leaf blades hirtellous at least adaxially; plants mostly not producing seeds.....9. *P. brasiliensis*

V.1.1.1. *Phyllanthus anisobus* Müll. Arg., DC. Prodr. 15(2): 382. 1866; Webster, Ann. Missouri Bot. Gard.

54. 229. 1968; Fl. Nicaragua 2000. TYPE: “Peru,” [probably collected in Ecuador], *Pavón* (holotype, G).

Phyllanthus pittieri Pax, Anal. Inst. Fis.-Geogr. Nac. Costa Rica 8: 327. 1895. TYPE: Costa Rica,

Aguacaliente, *Pittier 2505* (lectotype [designated here], B!; isotype, BR!, US!).

Phyllanthus mexiae Croizat, J. Wash. Acad. Sci. 33: 14. 1943. TYPE: Ecuador, El Oro, Cantón Pajilí, near Santa Rosa, *Mexia 6718* (holotype, US 1663544!)

Lowland to upland rain forest, 100-1700 m, Costa Rica to western slopes of Ecuadorian Andes. Burger and Huft (1995) reduce *Phyllanthus anisolobus* to a synonym of *P. mocinianus*. However, although similar morphologically, the two species appear clear distinguishable; a conservative interpretation would be to treat them as allopatric subspecies.

V.1.2 *Phyllanthus mocinianus* Baillon, Adansonia I. 1: 35. 1860; Müll. Arg., DC. Prodr. 15(2): 382.

1866; Burger & Huft, Fieldiana Bot. 36: 144. 1995; Webster, Contr. Univ. Mich. Herb.

2001. TYPE: Mexico, *Sessé & Moçino* (lectotype, G!; isotype, M).

Phyllanthus pringlei S. Wats., Proc. Amer. Acad. 26: 147. 1891. TYPE: Mexico, San Luis

Potosí, *Pringle 3532* (holotype, GH!).

Deciduous or semideciduous woodlands, often on limestone, 20—1700 m, Mexico to Belize and Guatemala. Specimens have often been incorrectly determined as *Phyllanthus micrandrus*.

V.1.3. *Phyllanthus micrandrus* Müll. Arg., Linnaea 32: 27. 1863; DC. Prodr. 15(2): 383. 1866; Webster,

Contr. Univ. Michigan Herb. 2001. TYPE: Venezuela, Aragua, Colonia Tovar, *Fendler 1195* (lectotype [designated here]: G!; isotypes, K!, MICH!, MO!).

Phyllanthus tenellus Benth., Bot. Voy. Sulphur 165. 1846 (nom. illeg., non *P. tenellus* Roxb., 1832).

Phyllanthus benthamianus Müll. Arg., Linnaea 32: 29. 1863. *Phyllanthus graveolens* var.

tenellus Müll. Arg., DC. Prodr. 15(2): 383. 1866. TYPE: Colombia, [Nariño, Valle del Cauca ?]

Hinds (ex Sinclair) (holotype, K!).

Deciduous and evergreen forests, 400—1800 m, western Mexico, Costa Rica, Colombia, and Venezuela. The Colombian and Costa Rican populations, as suggested by Müller (1866, may prove to be separable at the subspecific level.

V.1.4. *Phyllanthus graveolens* Kunth in H.B.K., Nov. Gen. Sp. 2: 112. 1817; Müll. Arg., DC. Prodr.

15(2): 383. 1866; Macbride, Publ. Field Mus. Nat. Hist. 13 (3A, 1): 40. 1951.. TYPE: Peru,

Cajamarca, “in exustis ad ripam Chamayae et fluminis Amazonum juxta Tomependam

Bracamorensium,” *Bonpland* (holotype, Herb. Humboldt, P!).

Phyllanthus millei Standl., Field Mus. Nat. Hist. Bot. 22: 87. 1940. TYPE: Ecuador, Manabí, Bahia de

Caráquez, *Mille 1061* (holotype, F).

Seasonal woodlands, 100—2400 m, southern Ecuador to northern Peru.

- V.1.5. *Phyllanthus pavonianus* Baillon, Adansonia I. 1: 30. 1860; Müll. Arg., DC. Prodr. 15(2): 380. 1866; Macbride, Field Mus. Nat. Hist. Bot. 13 (3A,1): 44. 1951. TYPE: Peru, *Pavon* (holotype, G-Del!).
- Phyllanthus oxycladus* Müll. Arg., Linnaea 32: 26. 1863. TYPE: Peru, *Pavon* (holotype, G-Boiss.) [Apparently Müller described *P. oxycladus* from a different *Pavon* specimen that might be an isotype of *P. pavonianus*].
- Phyllanthus haughtii* Croizat, Caldasia 3: 22. 1944. TYPE: Ecuador, Guayas, 15 km W of Pedro Carbo, *Haught 3042* (holotype, GH!; isotype, K!).
- Deciduous thickets along intermittent streams, 200—1000 m, southern Ecuador and northern Peru.
- V.1.6. *Phyllanthus mcvaughii* G. L. Webster, Brittonia 18: 339. 1966. TYPE: Mexico, Chiapas, Mpio. Ixtapa, 30 mi by road E of Tuxtla Gutiérrez, *Webster et al. 11698* (holotype, DAV!; isotypes: GH!, MEXU!, MICH!, TEX!).
- Oak/pine forests on limestone, 850—1800 m, eastern Mexico (Chiapas) to Guatemala and El Salvador. Sometimes confused with *Phyllanthus mocinianus*, but the pollen is very different.
- V.1.7. *Phyllanthus caymanensis* G. L. Webster & Proctor, Rhodora 86: 121. 1984; Proctor, Kew Bull. Add. Ser. 11: 524. 1984. TYPE: Cayman Islands, Cayman Brac, Forster Land Distr., *Proctor 35151* (holotype, JAM; isotypes, DAV!, US!).
- Endemic to the Cayman Islands (Little Cayman, Cayman Brac)..
- V.1.8. *Phyllanthus acuminatus* Vahl, Symb. Bot. 95. 1791; Müll. Arg., DC. Prodr. 15(2): 381. 1866; Fl. Brasil. 11(2): 42. 1873; Fawc. & Rendle, Fl. Jamaica 4: 254. 1820; Croizat, Caldasia 2: 129. 1943; Webster, J. Arnold Arb. 38: 364. 1957; Burger & Huft, Fieldiana Bot. 36: 142. 1995. TYPE: Tinidad, *Ryan* (holotype, C!).
- Phyllanthus lycioides* Kunth in H.B.K., Nov. Gen. Sp. 2: 112. 1817. TYPE: Colombia, Bolívar, Mompox [Mompós], *Humboldt & Bonpland* (holotype, P!).
- Phyllanthus mucronatus* Kunth, loc. cit. TYPE: Venezuela, “Provincia Caracasana,” *Humboldt & Bonpland* (holotype, P!).
- Phyllanthus ruscooides* Kunth, op. cit. 113. TYPE: Venezuela, “in sylvis prope Caripe et in devexis montis Cocollar,” *Humboldt & Bonpland* (holotype, P!).

Phyllanthus acuminatus var. *paraguariensis* Chodat, Bull. Herb. Boissier II. 5: 488. 1905. TYPE:

Paraguay, Cordillera de Piribebuy, *Hassler 6699* (G).

Secondary moist woodlands, gallery forests, or montane forests, 0—2250 m, northern Mexico (Baja California Sur, Tamaulipas) east to Cuba and the Lesser Antilles, south to northern Argentina, Paraguay, and Brazil. Collections of the species have often been incorrectly named *Phyllanthus conami* Sw. or *P. brasiliensis* (Aubl.) Poir.

V.1.9. ***Phyllanthus brasiliensis*** (Aubl.) Poir., in Lam., Encycl. Method. 5: 296. 1804; Müll. Arg.,

DC. Prodr. 15(2): 383. 1866; Fl. Brasil. 11(2): 44. 1873; Webster, Fl. Venez. Guayana 5: 196.

1999. *Conami brasiliensis* Aubl., Hist. Pl. Guiane 2: 926. 1775. *Phyllanthus conami* Sw., Prodr.

28. 1788 (nom. illeg.). *Conami conami* (Sw.) Britton, Bot. Porto Rico 5: 475. 1924. TYPE:

Guyane Française, *Aublet* (holotype, BM!).

Phyllanthus subglomeratus Poir., Encycl. Method. 5: 304. 1805. TYPE: Martinique, *Herb. Lamarck*

(holotype, P!).

Phyllanthus piscatorum Kunth in H.B.K., Nov. Gen. Sp. 2: 113. 1817. TYPE: Venezuela, Amazonas,

“cataractam Aturensium,” *Humboldt & Bonpland* (holotype, P!).

Phyllanthus pseudo-conami Müll. Arg., Fl. Brasil. 11(2): 43. 1873, var. *glaber* Müll. Arg., *ibid.*

TYPE: Venezuela, Amazonas, San Carlos, *Spruce 3016* (holotype, Herb. Martius, M!; isotype, W!).

Phyllanthus pseudo-conami var. *pubescens* Müll. Arg., *loc. cit.* TYPE: Peru, Loreto, Yumimaguas,

Poeppig (lectotype [selected here], W!).

? *Phyllanthus ichthyomethius* Rusby, Mem. N. Y. Bot. Gard. 7: 282. 1927. TYPE: Bolivia, Benf,

Rurrenabaque, *White 886* (holotype, NY!; isotype, US!).

Riparian forests and clearings, often cultivated, 100—500 (-1000) m, Colombia and Venezuela south to Peru and Brazil; also in the Lesser Antilles (Guadeloupe, Dominica, Martinique). This widespread species is quite variable, despite the fact that sexual reproduction appears lacking in most populations.

Although *Phyllanthus piscatorum* was recently accepted as distinct (Webster, 1999), further study shows that it is not distinguishable at the species level. Plants from Bolivia, including the type of *Phyllanthus*

ichthyomethius, are divergent in a number of characters (especially lack of indumentum); their status is still under investigation.

Sect. V.2. **Hylaeanthus** G. L. Webster, **sect. nov.** TYPE: *Phyllanthus attenuatus* Miq.

Arbores fruticesve monoicae vel dioicae; ramuli simplici; cymulae axillares; sepala 6 (5); stamina 3, libera vel connata, pollinis grana globosa, porata, pilata; ovarium 3—5-loculare; styli liberi vel connatis, bifidi vel simplici; fructus indehiscens, ± baccatus; semina laevia.

Monoecious or dioecious trees or shrubs; branchlets pinnatifid, usually subtended by reduced leaves (but generally not by cataphylls); flowers in axillary unisexual or bisexual cymes borne on brachyblasts; sepals 6 (rarely 5), usually biseriate; disk of discrete or confluent segments; stamens 3, filaments free or connate, anthers mucous, dehiscing horizontally or obliquely; pollen grains globose, lacking distinct colpi, porate, exine pilate; pistillate sepals persistent in fruit; ovary 3—5-locular, styles free or connate, bifid or unlobed; fruits baccate, indehiscent; seeds smooth, ± compressed.

This new section of *Phyllanthus* subg. *Conami*, named for the prevalent distribution of its species in the lowland Brazilian rain forest, has escaped recognition partly because the vegetative resemblance with sect. *Brachycladus* (in subg. *Xylophylla*) has led to confusion and failure to recognize the significance of the diagnostic characters. Müller (1866, 1873) also created confusion when he mistakenly identified the type species, *Phyllanthus attenuatus* Miq., with Aublet's *Meborea guianensis*; Lanjouw (1931) indicated *P. attenuatus* is very distinct from *Meborea*. The pollen grains with pilate ornamentation separate sect. *Hylaeanthus* from sect. *Brachycladus*, to which *Meborea* apparently belongs.

Key to the species

1a. Ovary 3-locular; styles bifid; filaments connate.

2a. Leaves completely glabrous; dioecious.

3a. Leaf blades lanceolate, abruptly acuminate; styles connate.

1. *P. skutchii*

- 3b. Leaf blades usually ovate, blunt; styles free 2. *P. manausensis*
- 2b. Leaves hirtellous at least on petiole; monoecious or dioecious.
- 4a. Fruiting pedicels 2—4 mm long; styles free, bifid or unlobed; leaf blades lanceolate, < 5 cm broad.
- 5a. Dioecious; styles bifid, free; seeds > 2 mm long; ♂ disk entire 3. *P. attenuatus*
- 5b. Monoecious; styles unlobed, free; ♂ disk of 5 segments 4. *P. bernardii*
- 4b. Fruiting pedicels 6—7 mm long; styles connate into a column, twice bifid; leaf blades elliptic, cuspidate, at least 5 cm broad. 5. *P. callejasianus*
- 1b. Styles unlobed; ovary 4—5-locular; branchlets glabrous. *P. madeirensis*

V.2.1. *Phyllanthus skutchii* Standl., Publ. Field Mus. Nat. Hist., Bot. 22: 346. 1940; Burger & Huft, Fieldiana II. 36: 146, fig. 25. 1995.. TYPE: Costa Rica, *Skutch 4375* (holotype, F).
Evergreen forest, 20—900 m, southern Costa Rica (Pacific slope).

V.2.2. *Phyllanthus manausensis* W. A. Rodrigues, Acta Amazonica 1: 17, fig. 1. 1971; Ribeiro et al., Flora da Reserva Ducke 393. 1999. TYPE: Brazil, Amazonas, Manaus, *Rodrigues 7520* (holotype, INPA 16822).
Lowland Amazonian rain forest, mostly on terra firma, 100—200 m, Brazil (Amazonas, Pará, Roraima, Amapá).

V.2.3. *Phyllanthus attenuatus* Miq., Linnaea 21: 479. 1848; Stirp. Surinam. 100, t. 31. 1850; Lanjouw, Euphorb. Surinam 101. 1931; Webster, Fl. Venez. Guayana 5: 196. 1999. TYPE: Suriname, *Hostman & Kappler 305* (holotype, L; isotype, W!).
Terra firme or seasonally inundated rain forests, 0—1000 m, Colombia, Venezuela, Guayanas, Brazil, and Peru.

V.2.4. *Phyllanthus bernardii* Jabl., Mem. N. Y. Bot. Gard. 17: 112. 1967. TYPE: Venezuela, Mérida, Aricagua, *Bernardi 6258* (holotype, NY).
Andean forests, > 2000 m, western Venezuela (Mérida). The species deviates from others in sect. *Hylaeanthus* in its monoecious flower production, winged pedicels, and small smalls (< 2 mm long); the pollen has not been examined, and it may prove not to belong to the section.

V.2.5. *Phyllanthus callejasii* G. L. Webster, sp. nov., ab aliis speciebus sectionis differt stylis connatis

bis bifidis, sepalis fructiferis majoris, ramulis crassioribus. TYPE (pistillate): COLOMBIA.

ANTIOQUIA: Mun. Frontino, Corr. La Blanquita, región de Murrí, Alto de Cuevas, 1850 m,

14.VII.1988, R. Callejas, A. L. Arbeláez, J. Betancur, I. D. Castaño 6864 (holotype, HUA

52926!; isotype, DAV!). PARATYPE (staminate): COLOMBIA. ANTIOQUIA: Mun. Frontino,

Corr. Nutibara, zona de Murrí, 5—8 km S de Alto de Cuevas, 1000-1850 m, 14.II.1991, R.

Callejas, F. J. Roldán, M. V. Arbeláez 9940 (paratype: HUA 79857).

Dioecious tree 6—8 high; branchlets terete, smooth (minutely papillate), 15—25 cm long, 1.5—2.5 mm thick, with 6—9 leaves; leaf blades ovate to elliptic, 7—12 cm long, 3.5—7 cm broad, glabrous except for the incised midrib adaxially and midrib and major lateral veins abaxially, veins 5—7 pairs, curving; veinlet reticulum prominulous beneath; petiole 5—7 × 1—1.5 mm, copiously scabrid-hirtellous; stipules blackish, triangular, 2—3 mm long. Flowers in axillary glomerules, the pistillate mostly 2—5 per axil; bracts and bractlets blackish, persistent. Staminate flowers seen only in bud; sepals 6; disk undivided; stamens 3, filaments connate, anthers dehiscing horizontally. Pistillate flowers with pedicel glabrous or sparsely and minutely hirtellous, 5.5—7 mm long in fruit; fruiting sepals (5) 6, 3—3.8 mm long, 2—2.2 mm broad; disk patelliform, c. 1.5 mm broad; ovary 3-locular; styles connate into a column c. 1.5 × 0.7 mm; style branches 0.5—0.7 mm long, ± twice-bifid. Fruits baccate, 7—9 mm (dried); seeds somewhat compressed, acute, truncate at base, 2.5—3 × 2—2.7 mm; testa smooth, brownish.

Phyllanthus callejasii clearly is related to *Phyllanthus attenuatus* Miq., but is easily distinguished by its larger leaf blades and longer petioles, thicker branchlet axes, and longer fruiting pedicels and sepals. It differs from *P. attenuatus* and *P. manausensis* in its upper montane cloud forest habitats. *Phyllanthus bernardii*, the only other upland species of sect. *Hylaeanthus*, differs in its hirtellous branchlet axes, winged pedicels, and smaller seeds.

Additional Paratype: COLOMBIA. **Nariño**: Mun. Piedraancha, Correg. Chucunéz, Reserva La Planada, 1650—1800 m, 18.V.1991, J. Betancur, S. Churchill, F. J. Roldán 2576 (HUA).

V.2.6. *Phyllanthus madeirensis* Croizat, Trop. Woods 78: 7. 1944. TYPE: Brazil, Amazonas,

Mun. Humayta, between Rio Livramento and Rio Ipixuna, *Krukoff 7163* (holotype, A!; isotype, NY!).

Although *Phyllanthus madeirensis* is exceptional with sect. *Hylaeanthus* in its 4- or 5-locular ovary with unlobed styles, it has pollen grains with pilate exine sculpturing and typical staminate flowers.

Sect. V.3. **Apolepis** G. L. Webster, J. Arnold Arb. 38: 371. 1957. TYPE: *Phyllanthus orbiculatus* Rich.

A monotypic section; the single species occurring in South America. The pollen characters of sect. *Apolepis* link it to those species of sect. *Nothoclema* with pilate exine sculpturing.

V.3.1. ***Phyllanthus orbiculatus*** Rich., Act. Soc. Hist. Nat. Paris 1: 113. 1792; Müll. Arg., DC. Prodr.

15(2): 401. 1866; Fl. Brasil. 11(2): 62. 1873; Webster, J. Arnold Arb. 38: 371. 1957; Fl. Venez. Guayana 5: 199. 1999; Cordeiro, Bol. Bot. Univ. São Paulo 13: 183, figs. 52-56. 1992. *P. poiretianus* Müll. Arg., Linnaea 32: 39. 1863. TYPE: Guyane Française, *Leblond* (holotype, P!; isotype, C!).

:*Phyllanthus orbiculatus* var. *acutifolius* (Müll. Arg.) Müll. Arg., Fl. Brasiliensis 11(2): 62. 1873.

P. poiretianus Müll. Arg. var. *acutifolius* Müll. Arg., Linnaea 32: 39. 1863. TYPE: Brazil, Minas Gerais, Serra do Lapa, *Riedel* (holotype, B, destroyed).

Phyllanthus orbiculatus var. *intermedius* Müll. Arg., Fl. Brasil. 11(2): 62. 1873. TYPE: Brazil, Goiás, Rio Bocaina, *Pohl 2476* (holotype, W!).

Phyllanthus orbiculatus var. *lignescens* Müll. Arg., ibid. TYPE: Brazil, Amazonas, Ega, *Martius* (holotype, presumably at M).

Phyllanthus orbiculatus var. *rupestris* Chodat & Hassl., Bull. Herb. Boissier II. 5: 488. 1905. TYPE: Paraguay, “in cacumine collinum prope Tobaty,” *Hassler 4034, 6132* (syntypes, G, W!).

Common in savannas and cerrado, 20—1000 m, Colombia to Venezuela and Trinidad, south to Bolivia, Paraguay, and Brazil. There are no critical studies of geographic variation within *Phyllanthus orbiculatus*, but except possibly for var. *acutifolius*, there seems little justification for recognizing subspecific taxa.

Subgenus VI. **PHYLLANTHUS**. TYPE: *Phyllanthus niruri* L..

This subgenus, which includes the vast majority of the herbaceous species of *Phyllanthus*, is probably unnatural; there are affinities with subg. *Isocladus* and subg. *Kirganelia*. Section *Pentandra*, an

exotic group with one species (*P. tenellus* Roxb.) widely introduced in the Americas (Webster, 1970), seems related to African taxa of subg. *Kirganelia*.

Sect. VI.1. **Lysiandra** (F. Mueller) G. L. Webster, *Rhodora* 80: 573. 1978. *Phyllanthus* subg.

Lysiandra F. Mueller, *Frag. Phyt. Austral.* 1: 108. 1859. TYPE: *Phyllanthus subcrenulatus* F. Mueller.

This small section of about 10 species appears isolated and may have an independent origin from the other sections in subg. *Phyllanthus*. Its distribution is curiously disjunct between Australia and the single Mexican species *P. harrimanii*. However, the pollen of *P. harrimanii* resembles the Brazilian *P. websterianus* Steyrm. of sect. *Microglochidion*, so it is not at all certain that the Mexican species really belongs in sect. *Lysiandra*. It is possible that Mueller may prove to be right after all, and *Lysiandra* might be recognized as a distinct subgenus.

VI.1.1. ***Phyllanthus harrimanii*** G. L. Webster, *Rhodora* 80: 570. 1978. TYPE: Mexico, Tamaulipas,

scrub on limestone slopes, 6 mi W of Palmillas, *Webster & Armbruster 20496* (holotype, DAV!; isotypes MEXU!, TEX!).

Endemic to slopes above the Jaumave Desert in Tamaulipas.

Sect. VI.2. **Phyllanthus**. TYPE: *Phyllanthus niruri* L.

This very heterogeneous section of c. 80 species is circumtropical, and almost surely not monophyletic. In the neotropics there are 4 subsections, one of which is here defined as new.

Key to the subsections

1a. Anther connectives not enlarged, the thecae not widely separated; filaments free or connate.

2a. Cataphyllary stipules thin and scarious, not indurate, scarcely if at all auriculate at base.

3a. Cataphyllary stipules linear-lanceolate; branchlet stipules narrow, \pm involute; leaf blades obliquely unequal at base; stamens 3, filaments free or connate; pollen grains prolate,

4-colporate, tectate-perforate; seeds verruculose.

subsect. a. **Niruri**

- 3b. Cataphyllary stipules broader; branchlet stipules not involute; leaf blades scarcely oblique at base; stamens 2 or 3, filaments usually connate; pollen grains subprolate, 3-colporate; seeds striate or longitudinally ribbed. subsect. b. **Swartziani**
- 2b. Cataphyllary stipules ± indurate, dark reddish or black; seeds finely striate; mostly perennials. subsect. c. **Pentaphylli**
- 1b. Anther connectives enlarged or bifurcate, thecae widely separated; filaments free; seeds striate; perennials, often shrubby. subsect. d. **Clausseniani**

Subsect. VI.2a. **Niruri** G. L. Webster, *Contr. Gray Herb.* 176: 52. 1955; *J. Arnold Arb.* 38: 299.

1957. TYPE: *Phyllanthus niruri* L.

The widespread species *Phyllanthus niruri* is highly variable, but so far subspecies have not been satisfactorily defined. At least two other taxa in South America, *P. mimicus* G. L. Webster and *P. rosellus* (Müll. Arg.) Müll. Arg., appear separable (with some difficulty). Three other South American species, *P. augustinii* Baillon, *P. bolivianus* Pax & K. Hoffm., and *P. perpusillus* Baillon, may belong to subsec. *Niruri*, but their status needs to be evaluated.

Key to the species

- 1a. Branchlets smooth; fruiting sepals 1.3—2.7 mm long.
- 2a. Staminate sepals 1.9—2.4 mm long. 1. *P. augustinii*
- 2b. Staminate sepals not over 1.5 mm long.
- 3a. Leaf blades mostly distinctly inaequilateral at base; branchlets with c. 15—30 leaves; staminate flowers 3—7 per cymule; sepals 1.2—1.5 mm long; filaments 0.6—0.9 mm long, usually connate below; seeds 1.4—1.6 mm long. 2. *P. niruri*
- 3b. Leaf blades not distinctly inaequilateral at base; branchlets with c. 35—45 leaves; staminate flowers mostly solitary, sepals 0.6—0.8 mm long; seeds 0.9—1 mm long. 3. *P. mimicus*
- 1b. Branchlets distinctly scabridulous; fruiting sepals 3.5—4.5 mm long. 4. *P. bolivianus*

VI.2a.1. *Phyllanthus augustinii* Baillon, *Adansonia* I. 5: 354. 1865; Müll. Arg., DC. *Prodr.* 15(2): 433.

1866; *Fl. Brasil.* 11(2): 65. 1873.. TYPE: Brazil, Rio de Janeiro, “montagne de S. Diogo,” *St. Hil.*

cat. AI 743 (holotype, P!).

This species remains poorly known; Müller stated that he had never seen Baillon's specimen. A collection from Rio de Janeiro at Kew (*Glaziou 17757*) has unusually large flowers for *Phyllanthus niruri* and might represent Baillon's species.

VI.2a.2. *Phyllanthus niruri* L., Sp. Pl. 981. 1753; Webster, J. Arnold Arb. 37: 300. 1957; Ann. Missouri Bot. Gard. 54: 225. 1968; Brittonia 22: 66. 1970; Allem, Rev. Brasil. Biol. 37: 103. 1977; L. B. Smith et al., Fl. Ilustr. Catarin. EUFO 43. 1988; . TYPE: Hortus Cliffortianus Herbarium (holotype, BM!). Detailed synonymy is given in Webster (1957, 1970) and Govaerts et al. (1970).

This very widespread American species many years was known under the name *Phyllanthus lathyroides* Kunth, due to the misinterpretation of Linnaeus's species by Müller (1866, 1873). Earlier (Webster, 1957, 1970), *P. lathyroides* was accepted at the subspecies level, with ssp. *niruri* being confined to the West Indies. As more collections have become available for study, it no longer appears expedient to recognize two subspecies, because *P. niruri* consists of a number of populations of varying distinctness. Müller (1873) described a number of forms from Brazil, and he elevated one of these to a distinct species, *P. rosellus* (Müll. Arg.) Müll. Arg.. However, as pointed out by Allem (1977), *P. rosellus* as described by Müller was characterized by distinctly larger flowers, which does not agree with the flowers of the small-leaved specimens that have been annotated by various botanists. Nevertheless, the specimens from the Brazilian cerrado appear distinctive because of their small, often reddish leaves and flowers, and long staminate pedicels. Pending a critical revision of subsect. *Niruri*, it seems expedient to recognize two subspecies within *P. niruri*.

VI.2a.1a. *Phyllanthus niruri* ssp. *niruri*.

Phyllanthus lathyroides Kunth in HBK., Nov. Gen. Sp. 2: 110. 1817; Lourteig & O'Donell, Lilloa 9: 84.

1943. *P. lathyroides* var. *genuinus* Müll. Arg., Linnaea 32: 42. 1863 (nom. illeg.). TYPE: Venezuela, Monagas, Caripe, *Humboldt & Bonpland* (holotype, P!).

Phyllanthus purpurascens Kunth in H.B.K., Nov. Gen. Sp. 2: 110. 1817. *P. lathyroides* * *purpurascens*

(Kunth) Müll. Arg., DC. Prodr. 15(2): 404. 1866. TYPE: Venezuela, Cumaná, *Humboldt & Bonpland* (holotype, P!).

Phyllanthus chlorophaeus Baillon, Adansonia .I. 1: 27. 1861. TYPE: Mexico, Sierra San Pedro

Nolasco, *Jurgensen* 858 (holotype, P).

Phyllanthus ellipticus Buckley, Proc. Acad. Nat. Sci. Philadelphia 1862: 7. 1863. TYPE: (holotype, west Texas, *Wright* (not seen).

Phyllanthus williamsii Standley, Publ. Field Mus. Nat. Hist. Bot. 17: 266. 1937. TYPE: Mexico, Veracruz, *Williams* 8433 (holotype, F).

Leaves mostly 7—15 mm long, not reddish-tinged; branchlets mostly with 15—30 leaves; staminate pedicel 1—2 (-3) mm long; seeds mostly 1.4—1.8 mm long.

Various habitats, mostly in tropical moist forests, 0—2000 m, United States (Texas only), Mexico and West Indies south to Argentina and Brazil. Müller (1863, 1866, 1873) recognized a number of forms indicated by the sign <*> which are listed by Govaerts et al. (2000), but no attempt is made here at typifying all of them.

VI.2a.2b. *Phyllanthus niruri* ssp. *rosellus* (Müll. Arg.) G. L. Webster, **comb. & stat. nov.** *Phyllanthus lathyroides* ** *rosellus* Müll. Arg., *Linnaea* 32: 42. 1863. *P. rosellus* (Müll. Arg.) Müll. Arg., Fl. Brasil. 11(2): 53. 1873. TYPE: Brazil, Minas Gerais, Ouro Preto, *Vauthier* 83 (lectotype [selected here], G!).

Branchlets mostly with 25—50 leaves; leaf blades mostly 3—5 mm long, often reddish-tinged; staminate pedicel mostly 4—6 mm long.

Campos rupestres and woodlands, 800—1300 m, Brazil (mainly Minas Gerais, but extending to lower elevations in São Paulo and Paraná).

VI.2a.3. *Phyllanthus mimicus* G. L. Webster, Contr. Gray Herb. 176: 52. 1955; J. Arnold Arb. 38: 303. 1957. TYPE: Tobago, Mason Hall, *Broadway* 3038 (holotype, G!; iostypes, F!, MO!, NY!).

Rain forest, Tobago; plants with small seeds from Venezuela, Brazil, and Paraguay are similar to *Phyllanthus mimicus*, but it is not clear whether they are conspecific.

VI.2a.4. *Phyllanthus bolivianus* Pax & K. Hoffm., Meded. Rijks Herb. Leiden 40: 18. 1921. TYPE: Bolivia, [Santa Cruz] Comarapa, 2600 m, *Herzog* 1950 (holotype, B, destroyed; lectotype [selected here], W!; isotype, S!).

VI.2a.5. *Phyllanthus perpusillus* Baillon, *Adansonia* I. 5: 358. 1865; Müll. Arg., DC. Prodr. 15(2): 410. 1866; Fl. Brasil. 11(2): 55. 1873; Webster, in Smith & Downs, *Sellowia*. TYPE: Brazil, Minas

Gerai, Ponte Alta, *St. Hilaire 301d* (holotype, P!).

Subsect. VI.2b. **Swartziani** G. L. Webster, *Contr. Gray Herb.* 176: 53. 1955; *J. Arnold Arb.* 38: 306. 1957; *Brittonia* 22: 68. 1970. TYPE: *Phyllanthus swartzii* Kostel. (= *P. amarus* Schumach. & Thonn.).

About 20 species native to America, Africa, and India, but several species (especially *Phyllanthus amarus*) have become widely distributed across the tropics.

Key to the species

1a. Cymules bisexual (at least at distal nodes of branchlet).

2a. Sepals 5, distinctly acute; distal cymes with only 1 staminate flower; seeds finely ribbed on back, 0.9—1 mm long; leaves ± oblong.....1. *P. amarus*

2b. Sepals 6, obtuse or subacute; distal cymules with 1—3 staminate flowers; seeds striate on back, 1.2—1.5 mm long.2. *P. hexadactylus*

1b. Cymules unisexual; staminate flowers at proximal nodes of branchlet..

3a. Leaves membranous to chartaceous; branchlets smooth (or nearly so); monoecious or dioecious; seeds longitudinally striate or ribbed.

4a. Stamens 3 (rarely some flowers with 2).

5a. Stamens partially to completely connate; stems herbaceous.

6a. Plants monoecious; anthers dehiscing horizontally or obliquely..

7a. Stems often with conspicuous basal aerenchyma; leaf margins often reddish; pistillate disk 5-angled or -lobed; filaments completely connate. 3. *P. stipulatus*

7b. Stems without basal aerenchyma; leaf margins not reddish; pistillate disk asymmetrically 3-lobed; filaments connate halfway. 4. *P. caribaeus*

6b. Plants dioecious or subdioecious; anthers dehiscing vertically or obliquely.

8a. Anthers dehiscing vertically; staminate sepals 1.5—2.3 mm long; staminal column ≥ 0.5 mm high; seeds 1.8—2 mm long. 5. *P. lindbergi*

8b. Anthers dehiscing horizontally or obliquely; floral parts and seeds smaller.

- 9a. Seeds striate, 1.1—1.3 mm long; style branches not capitate.
6. *P. microphyllus*
- 9b. Seeds verruculose; style branches capitate. 7. *P. leptophyllus*
- . 5b. Filaments free; fruiting pedicel 3—3.5 mm long; stems woody. 12. *P. fadyenii*
- 4b. Stamens 2 (rarely occasional flowers with 3).
- 10a. Style branches slender; branchlets mostly with 15—30 leaves; pistillate sepals \geq 1.2 mm
 in fruit..
- 11a. Staminate sepals mostly 5; leaf blade narrowed to tip. 8. *P. minutulus*
- 11b. Staminate sepals 4; leaf blade obtuse at tip. 9. *P. standleyi*
- 10b. Style branches thickened as in a Maltese cross; branches mostly with 30—60 leaves;
 pistillate sepals 0.7—1 mm long;10. *P. procerus*
- 3b. Leaves subcoriaceous, \pm concave; branchlets scabridulous; dioecious; seeds verruculose.
 11. *P. fastigiatus*

VI.2b.1. *Phyllanthus amarus* Schumach. & Thonn., Kongl. Danske Vidensk. Selsk. Skr. 4: 195. 1829;
 Webster, J. Arnold Arb. 38: 313. 1957; Ann. Missouri Bot. Gard. 54: 226. 1968; Brittonia 22:
 69. 1970; Correll, Fl. Bahama Archipelago 837. 1982.. *Phyllanthus niruri* var. *amarus* (Schumach.
 & Thonn.) Leandri, Fl. Madag. 111(1): 73. 1958. TYPE: Guinea, *Schumacher & Thonning*
 (holotype, C!). Additional synonyms are cited in Webster (1957: 313).

The most widespread species of *Phyllanthus* in the world; circumtropical, including remote Pacific
 islands. Its close morphological similarity with the temperate North American species *P. abnormis* Baillon
 indicates that it was a neotropical species in origin.

VI.2b.2. *Phyllanthus hexadactylus* McVaugh, Brittonia 13: 195. 1961; Webster, Contr. Univ. Mich. Herb.
 2001. TYPE: Mexico, Michoacán, 4 mi NW of Apatzingás, *McVaugh 17945* (holotype,
 MICH!; isotype, DAV!).

Lowland deciduous forests, 240—320 m, Sonora and Michoacán.

VI.2b.3. *Phyllanthus stipulatus* (Raf.) Webster, Contr. Gray Herb. 176: 53. 1955; J. Arnold Arb. 38: 315.
 1957; Ann. Missouri Bot. Gard. 54: 227. 1968; Burger & Huft, Fieldiana 36: 146. 1995. *Moeroris*
stipulata Raf., Sylva Tellur. 91. 1838. TYPE: Jamaica, *Swartz* (lectotype [designated by Webster,

1955], S!).

Phyllanthus diffusus Klotzsch, Bot. Voy. Herald. 105. 1853. TYPE: Panama, *Seemann* (holotype, BM).

Phyllanthus hoffmannseggii Müll. Arg., Linnaea 32: 45.. 1863. TYPE: Brazil, Pará, *Hoffmannsegg*
(lectotype [selected here], Herb. Willdenow 17983, B!).

? *Phyllanthus hoffmannseggii* var. *oblongifolius* Müll. Arg., Linnaea 32: 45. 1863. *P. diffusus*
var. *oblongifolius* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 410. 1866. TYPE: Brazil,
Pará, Santarem, *Spruce 797* (lectotype [selected here]),

Phyllanthus aquaticus C. Wright ex Sauvalle, Anal. Acad. Ci. Habana 7: 110. 1870. TYPE: Cuba,
Pinar del Rio, *Wright 3683* (lectotype [designated here], GH!; isotypes, F!, NY!, P!, S!, US!).

? *Phyllanthus paraguayensis* Parodi, Anal. Soc. Cient. Argentina 11: 50. 1881. TYPE: Paraguay,
“Cordillera in fossis acquosis,” *Parodi ?* (holotype possibly at BAF).

Widespread in moist or aquatic lowland habitats, 0—1500 m, Mexico and Cuba south to Bolivia,
Paraguay, and southern Brazil. The disposition of *Phyllanthus diffusus* var. *oblongifolius* requires further
investigation.

VI.2b.4. *Phyllanthus caribaeus* Urb., Symb. Antill. 5: 382. 1908; Webster, J. Arnold Arb. 38: 318. 1957;
Ann. Missouri Bot. Gard. 54: 227. 1968. TYPE: Tobago, *Eggers 5733* (lectotype [selected by
Webster, 1957], F!; isotype, NY!).

Very similar morphologically to *Phyllanthus stipulatus*, but occurring in better drained evergreen
forest habitats, 100—1500 m, Mexico and Lesser Antilles south to Peru and Brazil.

VI.2b.5. *Phyllanthus lindbergii* Müll. Arg., Fl. Brasil. 11(2): 35. 1873; Webster, Sellowia 11: 168.
1959; Fl. Venez. Guayana 5: 197. 1999; L. B. Smith et al., Fl. Ilustr. Catarin. EUFO 43. 1988..
TYPE: Brazil, Minas Geraes, Caldas, *Lindberg 438*
(lectotype, S).

Swamps and wet savannas, 50—200 m, Colombia and Venezuela to Paraguay and Brazil. This
species and *Phyllanthus microphyllus* form a seemingly intergrading complex that needs careful study.

VI.2b.6. *Phyllanthus microphyllus* Kunth in H.B.K., Nov. Gen. Sp. 2: 109. 1817; Müll. Arg., DC. Prodr.
15(2): 410. 1866; Fl. Brasil. 11(2): 56. 1873; Webster, Fl. Venez. Guayana 5: 198. 1999. TYPE:
Venezuela, “in ripa Orinoci ?,” *Humboldt & Bonpland* (holotype: P!).

Phyllanthus microphyllus var. *orbignyanus* Müll. Arg., *Linnaea* 32: 45. 1863. TYPE: Bolivia,

Chiquitos, *D'Orbigny 734* (holotype, G!).

Phyllanthus microphyllus var. *radicans* Müll. Arg., *Fl. Brasil.* 11(2): 56. 1873. TYPE: Brazil, Minas

Gerais, Ouro Preto, *Riedel 2810* (holotype, G ?; not seen).

Swamps and wet savannas, 50—300 m, Venezuela and Brazil. The status of Müller's varieties *orbignyanus* and *radicans* is not clear.

V.2b.7. *Phyllanthus leptophyllus* Müll. Arg., *DC. Prodr.* 15(2): 411. 1866; *Fl. Brasil.* 11(2): 57. 1873.

TYPE: Brazil, Minas Geraes, Serra da Lapa, *Riedel 1008* (holotype, B, destroyed; photograph, ex Field Mus.).

Cerrado, c. 1000 m, Distrito Federal and Minas Geraes. Closely related to *P. microphyllus*.

V.2b.8. *Phyllanthus minutulus* Müll. Arg., *Fl. Brasil.* 11(2): 54. 1873; Cordeiro, *Bol. Bot. Univ. São*

Paulo 13: 180. 1992. TYPE: Goiás, Porto Imperial; Minas Gerais, *Langsdorff* (syntypes; not seen).

Wet areas in savanna and forests, 50—1200 m, Venezuela and Guayanas south to central Brazil.

VI.2b.9. *Phyllanthus standleyi* McVaugh, *Brittonia* 13: 199. 1961; Webster, *Contr. Univ. Mich. Herb.*

2001. *Phyllanthus perpusillus* Standl., *Amer. Midl. Nat.* 36: 178. 1946 (nom. illeg.; non *P. perpusillus* Baillon, 1865). TYPE: Mexico, Michoacán, 2 mi W of Uruapan, *Leasvenworth & Hoogstraal 1282* (holotype, F).

Oak/pine forests and deciduous woodlands, 300-1200 m, western Mexico (Nayarit to Guerrero).

VI.2b.10. *Phyllanthus procerus* C. Wright, in Sauvalle, *Anal. Acad. Ci. Habana* 7: 149. 1870; Webster, *J.*

Arn. Arb. 38: 320. 1957. TYPE: Cuba, Pinar del Río, *Wright 3684 ex p.* (lectotype [selected by Webster, 1957], GH; isotypes, NY, P, S, US).

Savannas, pinelands, and serpentine barrens, 50—100 m, Cuba (Pinar del Río to Oriente).

VI.2b.11. *Phyllanthus fastigiatus* Mart. ex Müll. Arg., *Linnaea* 32: 45. 1863; *DC. Prodr.* 15(2): 411.

1866; *Fl. Brasil.* 11(2): 57. 1873. TYPE: Brazil, Minas Gerais, Serra Itacolomi, Morro de Villa Rica, *Martius* (holotype, B, destroyed; lectotype [selected here], M!). The typification of this species is somewhat problematic because Müller in 1863 ascribed the species to “Mart. mss. in herb. Berol.” but cited only collections by Riedel and Sellow; however, the manuscript label of the specimen at Munich (annotated by Müller!) indicates that the collection was made by Martius.

Montane scrub, c. 800—1000 m or more, Serra do Espinaço, Minas Gerais, Brazil. *Phyllanthus fastigiatus* is unusual within subsect. *Swartziani*, since it vegetatively seems to have more in common with subsect. *Clausseniani*. However, the androecium with connate filaments and narrow anther connectives points toward subsect. *Swartziani*.

VI.2b.12. *Phyllanthus fadyenii* Urb., Symb. Antill. 6: 13, 1909; Fawc. & Rendle, Fl. Jam. 4: 255. 1920; Webster, J. Arnold Arb. 38: 323. 1957. TYPE: Jamaica, *McFadyen* (holotype, K).

Known only from the type collection, and now possibly extinct. Because of its shrubby habit and androecium of 3 free stamens with vertically dehiscent anthers, the species fits poorly into both subsect. *Swartziani* and subsect. *Pentaphylli*, and may not belong to either.

Subsect. VI.2c. **Pentaphylli** G. L. Webster, Contr. Gray Herb. 176: 54. 1955; J. Arnold Arb. 38: 11 325. 1957; Brittonia 22:72. 1970. TYPE: *Phyllanthus pentaphyllus* Wright ex Griseb.

This section of 14 species is confined to the Greater Antilles except for the type species, *Phyllanthus pentaphyllus* (one subspecies of which reaches southern Florida and Curaçao); 7 species are endemic to Cuba, and 6 to Hispaniola. No species occur on Jamaica, unless the poorly-known (and probably extinct) *P. fadyenii* belongs to this subsection. All of the species are enumerated in Webster (1957).

Subsect. VI.2d. **Clausseniani** G. L. Webster, subsect. nov. TYPE: *Phyllanthus claussenii* Baill.

Frutices vel suffrutices; monoicae vel dioicae; sepalis 6; segmentis disci ♂ 6; stamina 3, filamentis liberis vel infra connatis; anthers profunde emarginatis; pollinis grana 3-colporatis; discus ♀ patelliformis; ovarium 3-locularis; stylis liberis, bifidis; semina striatula vel verrucosa.

Monoecious or dioecious shrubs or subshrubs; branchlets pinnatifid, but sometimes appearing as though bipinnatifid (occasionally branching not clearly phyllanthoid); sepals 6, imbricate; staminate disk segments 6; stamens 2 or 3, filaments free or nearly so; anther connectives deeply emarginate, anther thecae sometimes appearing stipitate; pollen grains 3-colporate, exine reticulate (rarely tectate-perforate); pistillate disk patelliform; ovary 3-locular; styles free, bifid; seeds striate or if verruculose then the verrucae in lines..

Subsection *Clausseniani* is a Brazilian group of species especially common in the *cerrado*. The reticulate pollen grains and deeply emarginate anthers. It probably has a common origin with the phylloclade-bearing species of sect. *Choretropsis*.

Key to the species

1a. Monoecious; branching clearly phyllanthoid, leaves on main (penultimate) axes reduced to cataphylls; branchlets smooth or papillose..

2a. Branchlets smooth; anthers deeply emarginate to thecae stipitate.

3a. Leaf blades mostly 3—6 cm long,; stipules 4—5 mm long; fruiting pedicels 1.5—2 cm long; sepals free; seeds dotted-striate, 1.5—1.8 mm long. 1. *P. glaziovii*

3b. Leaf blades, stipules, and fruiting pedicels shorter.

4a. Leaf blade abaxially without a whitish or yellowish coat of minute papillae; fruiting sepals c. 1 mm long; 2. *P. claussenii*

4b. Leaf blades whitish or yellowish and minutely papillate beneath; fruiting sepals c. 2 mm long. 3. *P. hypoleucus*

2b. Branchlets papillose; anthers slightly to deeply emarginate.

7a. Branchlets terete, not sharply angled.

8a. Fruiting pedicels > 15 mm long; leaf blades distinctly falcate, strongly asymmetrical at base; staminate sepals c. 2 mm long. 4. *P. carvalhoi*

8b. Fruiting pedicels < 15 mm long; leaf blades not distinctly falcate nor strongly asymmetrical at base (slightly so in *P. itatiaiensis*).

9a. Leaf blades rigid, papillose beneath; ovary papillose; stamens usually 2. 5. *P. arenicola*

9b. Leaf blades thin, smooth or indistinctly papillose beneath; ovary smooth; stamens 2 or 3.

10a. Stamens 2; staminate pedicel not over 1 mm long; fruiting pedicel 2—2.5 mm long. 6. *P. bradeanus*

10b. Stamens 3; staminate pedicel 1.5—6 mm long; fruiting pedicel 3—9 mm long.

- 11a. Leaf blades ovate or elliptic, not falcate, mostly 8—12 mm long; staminate sepals < 1 mm long; . 7. *P. lagoensis*
- 11b. Leaf blades oblong-elliptic, ± falcate, 2—8 mm long; staminate sepals 1—1.5 mm long. 8. *P. itatiaiensis*
- 7b. Branchlets sharply angled or winged .
- 11a. Leaf blades acuminate, mostly 10-20 mm long. 9. *P. acutifolius*
- 11b. Leaf blades emarginate, mostly 3—5 mm long. . ssp. *P. caparaoensis*
- 1b. Monoecious or dioecious; leaf blades on main axes not regularly reduced; branchlets smooth..
- 11a. Monoecious; branching clearly phyllanthoid, branchlets not ramified; fruiting pedicel 1—2.5 mm long. 10. *P. atalaianus*
- 12a. Bracts of staminate cymules glandular-lobed or –dissected; staminate pedicels 2--3 mm long; staminate disk-segments asymmetrically caudate; seeds c. 1.7 mm long. 11. *P. heteradenius*
- 12b. Bracts of staminate cymules neither glandular nor lobed/dissected; staminate pedicels 0.1—0.5 mm long; staminate disk segments rounded; seeds 1.1—1.4 mm long. 12. *P. submarginatus*
- 11b. Dioecious; branching not clearly phyllanthoid, branchlets often ramified; fruiting pedicel 2.5—4 mm long. 13. *P. piranii*
- 1b. Branches persistent, axes mostly with distichous phyllotaxy; axes and leaves copiously hirsutulous with multicellular hairs; stamens 2, free, anthers dehiscing horizontally. 13. *P. piranii*
- VI.2d.1. *Phyllanthus glaziovii* Müll. Arg., Fl. Brasil. 11(2): 41, t. 8. 1873. TYPE: Brazil, Rio de Janeiro, *Glaziou 2892* (holotype, G!; isotype, BR!).
Rainforests of Serra do Mar, 50—1100 m, Brazil (Paraná and Rio de Janeiro).
- VI.2d.2. *Phyllanthus claussenii* Müll. Arg., Linnaea 32: 40. 1863; DC. Prodr. 15(2): 401. 1866; Fl. Brasil. 11(2): 61. 1873. TYPE: Brazil, Minas Gerais, *Claussen 7891* (holotype, G).
Phyllanthus claussenii var. *oblongifolius* Müll. Arg., Fl. Brasil. 11(2): 61. 1873. TYPE: Brazil, Minas Gerais, Riacho Fundo, *Riedel 1364* (holotype, presumably LE).

Thickets and gallery woods, 650—1150 m, Brazil (Minas Gerais and Bahia). Müller lectotypified the species when he removed the only other specimen cited (in 1863) to a separate variety. Since var. *oblongifolius* is known only from the type specimen, which has not been examined, its status cannot at present be evaluated.

VI.2d.3. *Phyllanthus hypoleucus* Müll. Arg., *Linnaea* 32: 40. 1863. *Phyllanthus lacteus* Müll. Arg., DC. Prodr. 15(2): 63. 1866 (nom. illeg.). TYPE: Brazil, Bahia, Nazaret, *Sello* (holotype, B, destroyed; photograph of holotype, UC; lectotype, G).

Mata de cipó, 900—1000 m, and restinga, 20—50 m, Bahia, Brazil.

VI.2d.4. *Phyllanthus carvalhoi* G. L. Webster, **sp. nov.** TYPE: Brazil, Bahia, Mun. Itamarajú, Fazenda Pau-Brasil, mata higrófila, 160 m, 3 XI 1983, A. M. Carvalho *et al.* 2022 (holotype, DAV; isotype, CEPEC).

Species ab aliis speciebus subsectionis differt foliis rhomboido-falcatis; sepalis ♂ majoribus (c. 2 mm longis); pedicellis fructiferis > 20 mm longis.

Monoecious subshrub 2—3 dm high; stems unbranched, distally reddish-brown and scabridulous; branchlets 6—14 cm long, with 20—35 leaves; branchlet axis ± terete but distinctly winged, 0.7—1 mm wide (including wings), scabridulous; leaf blades broadly rhomboid-obovate, rounded to truncate at apex, falcate and asymmetrically cuneate at base, adaxially with veins obscure, epidermis minutely foveolate, abaxially smooth to minutely scabridulous.. Staminate flowers in brachyblasts 2—2.5 mm long at proximal axils of branchlet; pistillate flowers solitary in reduced brachyblasts at distal nodes, accompanied by 1 or 2 staminate flowers. Staminate pedicel 5—7 mm long; sepals 5, c. 2 mm long; disk segments 5, glandular-punctatae, c. 0.4 mm wide; stamens 3, filaments free, anthers 0.5—0.6 mm long, mucous, dehiscing ± horizontally. Pistillate pedicel in fruit 14—27 × 0.2 mm; sepals 5, elliptic to obovate, ± persistent in fruit, 2—2.5 × 0.8—2 mm; disk thin, entire, c. 1.5 mm broad; ovary smooth, 3-locular; styles c. 0.8 mm long, bifid. Capsule not seen entire; seeds trigonous, c. 2 mm long, testa thin, with rows of small scarcely raised dots.

This new species from Bahia is strikingly different from its congeners in its rhombic-falcate leaves with distinctly asymmetric base. The only other species that has (much less pronounced) falcate leaf blades,

Phyllanthus itatiaiensis Brade, has much smaller leaves (3—5 mm long), and very much shorter fruiting pedicels (1.5—3.5 mm long).

VI.2d.5. *Phyllanthus arenicola* Casar., Nov. Stirp. Bras. Dec. 88. 1824; Müll. Arg., DC. Prodr. 15(2):

402. 1866; Fl. Brasil. 11(2): 64. 1873; Cordeiro, Bol. Bot. Univ. São Paulo 13: 182. 1992.. TYPE: Brazil, Rio de Janeiro, Taipú, *Casaretto 1793* (holotype: G).

Cordeiro (1992) has shown that *Phyllanthus arenicola* has a rather remarkable disjunct distribution. It was originally known from sandy beaches and restingas near sea level, Espírito Santo and Rio de Janeiro, but it has recently been found in gallery woodlands, at c. 800—900 m, in Minas Gerais.

VI.2d.6. *Phyllanthus bradeanus* G. L. Webster, **sp. nov.** TYPE: Brazil, Espírito Santo, Mun. Itaguassú,

Alto Limeiro, 11 V 1946, A.C. Brade, Altamiro, & Aparicio 18154 (holotype, RB 56141).

Species ab congeneribus subsectionis differt staminibus 2, sepalis ♂marginatis 1.3—1.5 mm longis.

VI.2d.7. *Phyllanthus itatiaiensis* Brade, Arch. Jard. Bot. Rio de Jan. 15: 9. 1957. TYPE: Brazil, Rio de

Janeiro, Serra do Itatiaia, Pedra do Altar, *Brade 15575* (holotype, RB).

Montane scrubland, 2400—2600 m, Brazil (Rio de Janeiro).

A distinctive high-elevation species with small rather falcate leaves somewhat suggesting those of *Phyllanthus carvalho*.

VI.2d.8. *Phyllanthus lagoensis* Müll. Arg., Fl. Brasil. 11(2): 65. 1873. TYPE: Brazil, Minas Geraes,

Lagoa Santa, *Warming 1586* (holotype, G).

Wooded areas, 150—750 m, Minas Gerais, Espírito Santo, Pernambuco..Müller (1873) noted its resemblance in habit to *Phyllanthus submarginatus* and *P. clausenii*, but it differs from the first in its clearly phyllanthoid branching and from both in its papillate/scabridulous stems.

VI.2d.9. *Phyllanthus acutifolius* Poir. ex Spreng., Syst. Veg. 3: 21. 1821; Müll. Arg., DC. Prodr. 15(2):

402. 1866; Fl. Brasil. 11(2): 64. 1873. TYPE: *Herb. Poiret* (holotype, P).

Phyllanthus oxyphyllus Müll. Arg., Linnaea 32: 40: 1863. TYPE: “Brasilis meridionali, *Sello* (holotype, B, destroyed

VI.2d.9a. *Phyllanthus acutifolius* ssp. *acutifolius*

Montane areas, 1000—1200 m, Rio de Janeiro, Minas Gerais, and perhaps Bahia. The relatively long (10—20 mm) acuminate leaf blades suggest a possible relationship with *Phyllanthus glaziovii*. However, it differs from that species in its smaller stipules (1—2 mm long), shorter pedicels, and smaller seeds.

VI.2d.9b. *Phyllanthus acutifolius* ssp. *caparaoensis* ssp. nov. TYPE: Brazil, Minas Gerais/Espírito Santo, Serra do Caparaó, *Wawra 1039* (holotype, US 1234018!).

Ab ssp. *acutifolius* differt foliis minoribus (3—5 mm longis) emarginatis.

Montane rock fields, c. 2000—2500 m, Serra do Caparaó, on the border of Minas Gerais and Espírito Santo. Although this plant looks very different from ssp. *acutifolius* because of its much smaller leaves, the flowers appear quite similar; it appears to be an “alpine” ecotype.

VI.2d.10. *Phyllanthus atalaianus* G. L. Webster, sp. nov. TYPE: Brazil, Goiás, Serrada Atalaia, 25 km by road SW of Monte Alegre de Goiás, granitic slope, 600—800 m, 12 III 1973, *W.R. Anderson et al. 6911* (holotype, US!).

Species ab aliis subsectionis differt bracteis glanduloso-lobatis, glandulis disci ♂ falcato-acuminatis.

Annual herbs 1—3 dm high; leaves on main axes equal in size to those on branchlets; branchlets terete, smooth, stramineous, 5—9 cm long, 0.25—0.4 mm thick, with mostly 8—12 leaves; leaf blades 5—10 × 5—8 mm, obovate-orbicular, rounded at apex, cuneate at base, margins reflexed and scabrous; veins 4 or 5 on a side, arching, slightly prominulous abaxially; petiole 1—1.5 mm long; stipules 0.5—1 mm long, glandular-dentate; flowers axillary on branchlets, subtended by glandular-toothed bracts, the staminate 3—5 per node proximally, the pistillate solitary distally; staminate pedicel 2—3 mm long; sepals 5, obovate, 1—1.2 × 0.9—1.2 mm; disk-segments 5, massive, c. 0.3 mm broad; stamens 3, filaments free, anthers deeply emarginate; pistillatae pedicel 2—2.5 mm in fruit; sepals 5, obovate, 1-veined, 2.7—3 × 2.5—2.7 mm; ovary 3-locular; styles bifid, c. 0.3—0.4 mm long; seeds 1.7 mm long, longitudinally 5—6 striate with very fine cross striae.

Known only from the type collection. The species appears to be unique in its glandular-dissected stipules and bracts, but the rounded scabrous-margined leaves are also distinctive.

VI.2d.11. *Phyllanthus heteradenius* Müll. Arg., Fl. Brasil. 11(2): 63. 1873. TYPE: Brazil, *Herb.*

Reg. Monac. (holotype, M!; photograph, DAV).

Seasonal woodlands, c. 500 m, Bahia and Paraiba. This species is remarkable for the highly modified staminate disk segments; it sometimes resembles plants of sect. *Loxopodium*, but has phyllanthoid branching and except for the staminate disk its characters agree with those of subsect. *Clausseniani*.

VI.2d.12.. *Phyllanthus submarginatus* Müll. Arg., *Linnaea* 32: 39. 1863; DC. *Prodr.* 15(2): 400. 1866;

Fl. Brasil. 11(2): 66. 1873; Webster, *Sellowia* 11: 166. 1959; L. B. Smith et al., *Fl. Ilustr. Catarin.*

EUFO 34. 1988.. TYPE: Brazil, Rio de Janeiro, *Weddell 308* (lectotype [selected here], G).

? *Phyllanthua amoenus* Müll. Arg., *Fl. Brasil.* 11(2): 66. 1873. TYPE: Brazil, Minas Gerais, Serra da Piedade, *Warming 1585* (lectotype [selected here], C).

Phyllanthus retroflexus Brade, *Arq. Jard. Bot. Rio Janeiro* 15: 8. 1957. TYPE: Brazil, Espírito Santo,

Mun. Cachoeiro do Tapemerim, Vargem Alto, Morro de Sal, 700 m, *Brade 19768* (holotype, RB).

Common in woodlands, often along streams, 80-1000 m, Minas Geraes and Rio de Janeiro to Santa Catarina. This species is unusual in its variability in branching pattern; some specimens appear to have typical phyllanthoid branching (except for the unreduced leaves subtending branchlets), but in others the branchlet axes branch and even rebranch. *Phyllanthus retroflexus* appears to be an extreme form in which the axes are strongly zig-zag.

VI.2d.13. *Phyllanthus piranii* G. L. Webster, **sp. nov.** TYPE: Brazil, Espírito Santo, Mun. Conceição de

Castelo, na base de rochedo, 24 XI 1982, *J. R. Pirani, O. Yano, D. F. Santos 230* (holotype, SP 183289!).

Species insigniter; axes foliisve hirsutulis pilis multicellularibus; stamina 2, libera, antheris horizontaliter dehiscentibus; ovarium hirtellum.

Monoecious herb or subshrub c. 3 dm high; stems and foliage hirsutulous with multicellular hairs; branches terete, zigzag, 1—5 dm long; leaves distichous, those not main axes not reduced; leaf blades broadly ovate to orbicular, 1—2 × 0.8—1.7 cm, obtuse or subacute at apex, rounded at base, hirtellous on both faces; midrib and lateral veins (4 or 5 per side) prominulous abaxially; petiole 1—1.5 mm long; stipules subulate-lanceolate, hirsutulous, 2—3.5 mm long. Flowers axillary, solitary; staminate pedicel c. 3 m long; sepals 5, sparsely hirtellous, 1.4—1.5 mm long; disk-segments 5, smooth, c. 0.25 mm in diam.; stamens 2, filaments free, c. 0.5 mm long; anthers c. 0.2 mm broad, dehiscing

horizontally; pistillate pedicel hirtellous, 1.5—1.7 mm long in fruit; sepals 1.8—2.2 mm long; disk patelliform, 1.2—1.5 mm broad; ovary 3-locular; styles free, bifid, branches reflexed and capitate; seeds trigonous, verruculose in lines, c. 1.2 mm long.

Known only from the type collection. This is a very puzzling species. It has the non-phylloid branching and zigzag stems of *Phyllanthus submarginatus*; however, it can immediately be distinguished from that species by the unique indumentum of multicellular hairs. The flowers are similar (except for the pubescence) to those of *P. submarginatus* and related species, so that it seems most reasonable to include *P. piranii* in subsect. *Clausseniani*.

Subsect. VI.2e. **Almadenses** G., L. Webster, subsect. nov. TYPE: *Phyllanthus almadensis* Müll.

Arg.

Herbae glabrae perennes, monoicae; ramulis foliis oppositis; thyrses terminales; sepalis 5, liberis; stamina 3, libera; antherae muticae; stylis bifidis.

Glabrous perennial herbs, monoecious; branchlets with a single pair of opposite acuminate leaves; terminating in slender spiciform thyrses; sepals 5; disk segments 5, massive, stipitate; stamens 3, filaments free; anthers muticous (connective not emarginate), dehiscing horizontally; pollen grains prolate, 3-colporate, tectum smooth, minutely perforate; pistillate disk patelliform; ovary smooth, styles bifid.

1. *Phyllanthus almadensis* Müll. Arg., Fl. Brasil. 11(2): 38. 1873. TYPE: Brazil, Bahia, “in sylvis ad lacum da Almada,” *Martius* (holotype, M!; isotype, G!)

Evergreen forests (Mata Atlántica), c. 100 m, vicinity of Ilhéus, Bahia. The unique habit of *Phyllanthus almadensis*, with branchlets bearing only a single pair of leaves and terminating in a thyrsoid inflorescence, sets it apart from all other neotropical species. It differs strongly from subsect. *Clausseniani* in its anthers lacking an emarginate connective, and in its pollen grains with tectate-perforate exine. The pollen is compatible with that found in subg. *Phyllanthus*, but the plant does not resemble any other taxon in the subgenus.

Section VI.3. **Choretropsis** Müll. Arg., Linnaea 32: 4. 1863; DC. Prodr. 15(2): 427. 1866; Fl. Brasil. 11(2): 70. 1873; Santiago, Bradea 5(2): 44. 1988.

70. 1873. TYPE: *Phyllanthus choretroides* Müll. Arg.

This distinctive section of 10 species is endemic to Brazil, and is common in the *cerrado* and *catinga*. Müller (1873) included the Brazilian species with phylloclades in sect. *Xylophylla*, but pollen characters (Webster, 1958; Webster & Carpenter, 2001) clearly show that those species do not belong in sect. *Xylophylla* (in which the exine is organized into pollen shields). The present treatment follows Santiago (1988), who recognizes two subsections that differ mainly in vegetative morphology. There may be little point in maintaining these two subsections, because there is a gradient vegetatively between the platyclade species of subsect. *Applanata* and the “scoparioid” species of subsect. *Choretropsis*; two species, *Phyllanthus angustissimus* and *P. coradinii*, are juxtaposed just across the dividing line.

Subsect. VI.3a. **Choretropsis** Santiago ex G. L. Webster, subsect. nov. TYPE: *Phyllanthus choretroides* Müll. Arg.

Suffrutices; ramis ramulisve teretes; stamina 2 vel 3, filamenta connata; semina reticulata.

Monoecious or dioecious shrubs or subshrubs; axes terete or nearly so; stamens 2 or 3, filaments connate; anthers dehiscing horizontally to vertically; seeds reticulate.

This subsection was automatically created by Santiago (1988), but without validating description, which appears to be required by the INC. Most of the species can be considered “subdioecious”, as the majority of specimens are unisexual, but with occasional flowers of the opposite sex.

Key to the species

1a. Stamens 2 (sometimes 3), anthers dehiscing horizontally; staminate flowers sessile

(pedicel 0.2—0.5 mm long).

1. *P. choretroides*

1b. Stamens 3, anthers dehiscing horizontally or vertically; staminate flowers distinctly

pedicellate (pedicel 0.5—1.2 mm long)..

2a. Anthers dehiscing vertically; stipules strongly asymmetric at base; leaf blades 1—2 mm long..

3a. Staminate sepals 1.5—1.7 mm long; staminal column 0.5—0.6 mm high;

branchlets 0.5—0.6 mm thick.

2. *P. goianensis*

3b. Staminate sepals 2.0—2.5 mm long; staminal column 0.9—1 mm high;

branchlets 0.9—1 mm thick.

3. *P. coradinii*

2b. Anthers dehiscing horizontally or obliquely; stipules not strongly asymmetric at base;
horizontally or obliquely.

4a. Sepals mostly 6; fruiting pedicel 2.5—3 mm long. 4. *P. sarothamnoides*

4b. Sepals mostly 5; fruiting pedicel c. 1 mm long.. 5. *P. spartioides*

VI.3a.1. *Phyllanthus choretroides* Müll. Arg., Linnaea 32: 52. 1863; DC. Prodr. 15(2): 427. 1866;
Fl. Brasil. 11(2): 70. 1873; Cordeiro, Bol. Bot. Univ. São Paulo 13: 177. 1992.. TYPE: Brazil,
Minas Gerais, Serra da Lapa, *Riedel 923* (holotype, G).

Campos rupestres, sandstone peaks, to 1200 m, Minas Gerics. Müller (1873) characterized this
species as dioecious, but Cordeiro (1992) describes it as monoecious; apparently the sexual expression is
variable.

VI.3a.2. *Phyllanthus goianensis* Santiago, Bradea 5: 45. 1988. TYPE: Brazil, Goiás, Chapada Vargem
Grande, Tocantins Superior, *Ule 52* (holotype, R).

If Ule's Chapada Vargem Grande is the one listed by the IBGE (Índice dos topônimos da carta do
Brasil ao milionésimo), the type was collected in cerrado or campo rupestre at c. 1100—1200 m..

VI.3a.3. *Phyllanthus sarothamnoides* Govaerts & Radcl.-Sm., Kew Bull. 51: 177. 1996. *Phyllanthus*
scoparius Müll. Arg., Fl. Brasil. 11(2): 74. 1873 (nom. illeg.; non *P. scoparius* Welw., 1859).
TYPE: Brazil, Minas Gerais (?), Rio dos Pedras, Serra da Lapa, *Riedel 1353* (holotype, LE ?; a
sheet at K, *Riedel 1393*, may be an isotype despite the difference in number).

Montane fields, probably above 1000 m, Serra da Lapa, Brazil. This species is very close to
Phyllanthus spartioides and *P. choretroides*, especially the latter; it may be significant that Riedel collected
the types of both *P. choretroides* and *P. scoparius* in the Serra da Lappa..

VI.3a.4. *Phyllanthus spartioides* Pax & K. Hoffm., Repert. Sp. Nov. 19: 174. 1923; Cordeiro, Fl. Pico das
Almas, 312. 1995. TYPE: Brazil, Bahia, Pico das Almas, *von Lützelberg 258* (holotype, B,
destroyed; lectotype [selected here], M!).

Montane scrub and grassland, 1000—1700 m, Pico das Almas, Bahia, Brazil.

Subsect. **Applanata** Santiago, Bradea 5: 45. 1988. TYPE: *Phyllanthus edmundoi* Santiago.

Shrubs or subshrubs; branchlet axes dilated into phylloclades, leaf blades often reduced; stamens 3 or 4, free or connate, dehiscent vertically or obliquely.

Key to the species

1a. Phylloclades spirally inserted on terete axes, 250—400 × (5-) 20—35 mm; filaments free; styles twice bifid. 5. *P. gladius*

1b. Phylloclades mostly distichous on ± angled branches, 50—200 × 2—12 mm; filaments free or connate; styles bifid to multifid.

2a. Filaments connate (or pistillate pedicel angled).

3a. Phylloclades mostly 5 mm broad or more; styles deeply bifid.

5a. Pistillate pedicel terete, < 2 mm long; seeds verruculose.

2. *P. klotzschianus*

5b. Pistillate pedicel angled, > 2 mm long; seeds reticulate.

3. *P. edmundoi*

3b. Phylloclades 1—2 (-4) mm broad.; styles bifid to emarginate.

1. *P. angustissimus*

2b. Filaments free; pistillate pedicel terete; phylloclades caudate-acuminate.

4. *P. flagelliformis*

VI.3b.1. *Phyllanthus gladius* Müll. Arg., Linnaea 32: 52. 1863; DC. Prodr. 15(2): 428. 1866;

Fl. Brasil. 11(2): 71. 1873. TYPE: Brazil, Bahia, between Salvador and Vitoria, *Sello 814* (holotype, B, destroyed; photograph CNHM 5045, DAV, UC).

Restingas, coastal lowlands (< 100 m), Bahia, Brazil; apparently rare.

VI.3b.2. *Phyllanthus klotzschianus* Müll. Arg., Linnaea 32: 53. 1863; DC. Prodr. 15(2): 76. 1873;

Cordeiro, Bol. Bot. Univ. São Paulo 13: 177. 1992; **nom. cons. prop.** *Phyllanthus klotzschianus* var. *robustus* Müll. Arg., Linnaea 32: 53. 1863. TYPE: Brazil, Minas Gerais, Tejuco, Ouro Preto, *Vauthier 81* (lectotype [chosen here], G!; isotype, W!). Müller did not designate a type variety, but var. *robustus* is the logical choice, since it was listed first, had the most citations of specimens, and the specific epithet appears to have been taken on the basis of an annotation by Klotzsch at B.

Phyllanthus obtusatus (Thunb.) Müll. Arg., DC. Prodr. 15(2): 433. 1866. *Xylophylla obtusata* Thunb.,

Pl. Brasil. 1. 1817. TYPE: Brazil, *Freyreiss* (holotype, UPS). *Phyllanthus obtusatus* clearly has

priority over *P. klotzschianus*, but since Thunberg's name has never been used by any subsequent botanist, it is desirable to conserve the name of this common Brazilian species.

Phyllanthus klotzschianus var. *gardneri* Müll. Arg., *Linnaea* 32: 53. 1863. TYPE: Brazil, Minas Gerais, 1846, *Gardner 5174 ex p.* (holotype, G!).

Phyllanthus klotzschianus var. *major* Müll. Arg., *ibid.* TYPE: "Brasilia meridionali," *Sello 2101* (holotype, B, destroyed).

Phyllanthus klotzschianus var. *minor* Müll. Arg., *Linnaea* 32: 54. 1863. TYPE: "Brasilia meridionali," *Sellow 2101* (holotype, B, destroyed; lectotype [selected here], W!).

Phyllanthus klotzschianus var. *racemosus* Müll. Arg., *ibid.* TYPE: Brazil, Bahia [Mun. Campo Formoso], São Tomé, *Blanchet 3814* (holotype, G!).

Phyllanthus klotzschianus var. *pallidiflorus* Müll. Arg., *Linnaea* 32: 54. 1863. TYPE: Brazil, "in montibus Jacobinae prope Bahiam," *Blanchet 2543* (holotype, G!; isotypes, K!, W!).

Phyllanthus klotzschianus var. *linearis* Müll. Arg., *ibid.* TYPE: Brazil, Minas Gerais, *Claussen* (holotype, G!).

Phyllanthus klotzschianus var. *brachycladus* Müll. Arg., *Fl. Brasil.* 11(2): 72. 1873. TYPE: Brazil, Bahia, *Martius, Reinhardt* (syntypes presumably at M).

Phyllanthus klotzschianus var. *elongatus* Müll. Arg., *op. cit.* 73. TYPE: Brazil, Bahia, "in camporum marginibus ad fluvium Peruaguam," *Martius* (holotype, M).

Campos rupestres and scrublands, Minas Geraes, Espírito Santo, and Bahia. The species shows considerable vegetative variability, which Müller (unconvincingly) tried to encompass by describing an excessive number of varieties. Cordeiro (1992, 1995) does not recognize any of these, and except possibly for var. *pallidiflorus*, it does not appear worthwhile to try to distinguish them.

VI.3b.3 *Phyllanthus edmundoi* Santiago, *Bradea* 5: 46. 1988. TYPE: Brazil, Bahia, Mun. Lençóis, *Lewis, Carvalho, & Hage 923* (holotype, CEPEC).

Known only from the type collection.

VI.3b.4. *Phyllanthus coradinii* G. L. Webster, **sp. nov.** TYPE: Brazil, Bahia, campo rupestre near Lençóis, *Coradin et al. 6531* (holotype, DAV)..

Ab aliis speciebus sectionis differt antheris verticaliter dehiscentibus, stylis dilatatis crenulatis (non bifidis)

Glabrous shrub 1.5 m high; branchlet axes somewhat compressed, \pm ridged or channelled, 10—14 mm long, 0.9—1.1 mm thick, with 8—13 nodes; leaf blades elliptic, blunt, apex \pm glandular; petiole c. 0.5 mm long; stipules blackish, cordate, aristate, auriculate on basipetal side, 0.5—0.7 mm long; dioecious, staminate flowers axillary on branchlets, 1 or 2 per cymule, buds often coated with resin; pistillate flowers solitary, often near tips of branchlets; staminate pedicel 0.5—1 mm long; sepals 6, biseriate, 2—2.5 \times 1.1—1.4 mm; disk-segments 0.25—0.3 mm long; stamens 3, filaments connate, staminal column c. 1 mm high; anthers discrete, mucous, dehiscing vertically, c. 0.5 mm long; pistillate flowers subsessile, fruiting pedicel up to 1.2 mm long; sepals 6, 3—3.2 \times 1.7—2 mm; disk cupular, c. 0.7 mm high, 1.8 mm broad; ovary 3-locular, styles distally dilated and crenulate (not bifid), c. 1 mm long; capsule 3.7 mm broad; mature seeds not observed.

Campo rupestre; known only from the type collection.

VI.3b.5. *Phyllanthus angustissimus* Müll. Arg., Linnaea 32: 55. 19863; DC. Prodr. 15(2): 430. 1866;

Fl. Brasil. 11(2): 73. 1873. TYPE: “Brasilia meridionali,” *Sellow 1294* (holotype, B, destroyed; lectotype [selected here]. G!; isotype, K!).

Campos rupestres, 900—1100 m (Minas Geraes) and restingas, <100 m (Bahia).

VI.3b.6. *Phyllanthus flagelliformis* Müll. Arg., Linnaea 32: 54. 1863; DC. Prodr. 15(2): 432. 1866;

Fl. Brasil. 11(2): 74. 1873. TYPE: Brazil, Bahia, Salvador, *Blanchet 2093 ex p.* (holotype, G).

Phyllanthus flagelliformis var. *demonstrans* Müll. Arg., Linnaea 32: 55. 1863. TYPE: Brazil, Bahia, *Blanchet 2093 ex p.* (holotype, G!; isotype, K!).

Campos rupestres and mata do cipó, c. 600--1000 m, Eastern Bahia. Forms that produce leaves with well-developed lamina have been named var. *demonstrans* Müll. Arg. (also based on *Blanchet 2093*), but do not merit formal recognition..

Subgenus VII. **CYCLANTHERA** G. L. Webster, **subg. nov.** TYPE: *Phyllanthus lindenianus* Baillon.

Herbae vel suffrutices, ramificatione more sectionis *Phyllanthi*; flores solitarii vel paucis, axillares; sepalis 5 vel 6, imbricatis; segmentis disci ♂ purpureis; stamina 2 vel 3, filamentis coalitis;

antherae extrorsae; horizontaliter dehiscentibus; pollinis grana globosa, exinium fasciatum vel clypeatum; discus ♀ dissectus vel lobatus; ovarium triloculare; stylis emarginatis vel bifidis; fructus capsularis; semina verruculosa.

This small section includes two sections with only 5 species endemic to Cuba and Hispaniola. In Webster (1957) these were included in subg. *Phyllanthus*, but with serious reservations. The pollen grains have unique exine sculpturing patterns different from that in all other subgenera (Webster, 1956; Webster & Carpenter, 2001). The occasional production of ramified branchlets in sect. *Cyclanthera* suggests a possible relationship to subg. *Conami*, but that group has totally different pollen grains. The remarkable clypeate pollen grains in sect. *Cyclanthera* are most similar, perhaps, to the clypeate grains in subg. *Xylophylla*, but presumably are derived from the “banded” exine sculpturing of sect. *Callitrichoides*, and the resemblance therefore appears superficial. The creation of a separate subgenus for sections *Callitrichoides* and *Cyclanthera* therefore seems unavoidable.

Section VII.1 **Callitrichoides** G. L. Webster, Contr. Gray Herb. 176: 47. 1955.; J. Arnold Arb. 38: 171. 1957. TYPE: *Phyllanthus carnosulus* Müll. Arg.

Only the type species from eastern Cuba is known.

Section VII.2. **Cyclanthera** G. L. Webster, Contr. Gray Herb. 176: 47. 1955; J. Arnold Arb. 38: 177. 1957; Borhidi, Bot. Közlem. 58: 176. 1971. TYPE: *Phyllanthus lindenianus* Baillon

Four species from Cuba and Hispaniola: *Phyllanthus abditus* G. L. Webster, *P. berterioanus* Müll. Arg., *P. lindenianus* Baillon, and *P. tenuicaulis* Müll. Arg. Several subspecies have been recognized in *P. lindenianus* and *P. tenuicaulis* (Borhidi, 1971).

Subgenus VIII. **XYLOPHYLLA** (L.) Pers., Syn. Pl. 591. 1807; Webster, J. Arnold Arb. 39: 66. 1958.

Xylophylla L., Mant. Pl. 2: 147. 1771. TYPE: *Xylophylla latifolia* L. (nom. illeg., = *Phyllanthus epiphyllanthus* L.).

Subgenus *Xylophylla* is the largest group endemic to the New World, with 16 sections and about 80 species. It is definitely centered in the West Indies, where there are 10 sections (7 endemic) with 42 species (40 endemic). In South America, there are also 10 sections, but with less than 30 species. The circumscription of subg. *Xylophylla* has been broadened since the treatment of Webster (1958) by the inclusion of subg. *Botryanthus*. West Indian specimens are cited in Webster (1958).

Section VIII.1. **Omphacodes** G. L. Webster, Contr. Gray Herb. 176: 59. 1955; J. Arnold Arb. 39: 142.

1958. TYPE: *Phyllanthus subcarnosus* C. Wright ex Müll. Arg.

This section includes only the poorly known type species from Cuba and Hispaniola. In many respects, it resembles another rare Cuban species, *Phyllanthus pseudocicca* Griseb. of subgenus *Cicca*. If this putative relationship can be substantiated, then it would strongly argue for an origin of subg. *Xylophylla* from subgenus *Cicca*, and a sister-group relationship of sect. *Omphacodes* with the other sections of subg. *Xylophylla*. Synonymy and specimen citations for *P. subcarnosus* are provided in Webster (1958).

Section VIII.2. **Sellowianthus** G. L. Webster, **sect. nov.** TYPE: *Phyllanthus sellowianus* Müll. Arg.

Frutices dioecae, glabrae; ramificatione more sectionis *Phyllanthi* sed foliis axium penultimorum not reducti; sepala 5 libera; discus ♂ et ♀ segmenti 5, stamina 3, discreta; pollinis grana clypeata; ovarium 3-loculare; stylis bifidis; semina laevia.

Dioecious, glabrous shrubs; branching phyllanthoid (branchlets deciduous), but leaves on main axes scarcely reduced; leaves chartaceous; sepals and disk-segments 5; stamens 3, filaments free; anthers deflexed, emarginate, dehiscing obliquely; pollen grains pantoporate, clypeate; ovary 3-locular; styles free, bifid; fruit capsular, seeds smooth (minutely striate).

This monotypic section includes only the type species, *Phyllanthus sellowianus* Müll. Arg., which is native to the basin of the Río Paraná and Río Uruguay from Argentina and Paraguay to Uruguay and southern Brazil. The lack of reduction of leaves subtending branchlets is not necessarily a “primitive” condition.

VIII.2.1. *Phyllanthus sellowianus* Müll. Arg., Linnaea 32: 37. 1863; DC. Prodr. 15(2): 397. 1866; Fl.

Brasil. 11(2): 39. 1873; Lourteig & O'Donnell, Lilloa 9: 89. 1943; Webster, Sellowia 11: 167. 1959; L. B. Smith et al., Fl. Ilustr. Catar. EUFO: 39. 1988. TYPE: Brazil, Matto Grosso, “ad flum. Cujaba,” *Riedel 1130* (lectotype [selected here; syntype of Sellow, B, destroyed], LE ?).

? *Phyllanthus pulcherrimus* Herter ex Arech., Anal. Mus. Nac. Montevideo II. 1: 72. 1911. TYPE:

Uruguay, orillas del Río Negro, *Araecheveleta 25* (holotype, B, destroyed); Dep. Durazno, *Herter 2725* (“cotype”, B, destroyed).

Riparian woodlands, Argentina, 50—250 m, Paraguay, Uruguay, and southern Brazil.

Although Herter (1935) insisted that his *Phyllanthus pulcherrimus* is not synonymous with *P. sellowianus*, his denial is not convincing.

Section VIII.3. **Thamnocharis** G. L. Webster, Contr. Gray Herb. 176: 59. 1955; J. Arnold Arb. 39: 91.

1958. TYPE: *Phyllanthus cinctus* Urb.

A section of 3 species endemic to Cuba: *Phyllanthus comptus* G. L. Webster in Pinar del Rio; and *P. cinctus* Urb. and *P. ekmanii* G. L. Webster in eastern Cuba.

Section VIII.4. **Orbicularia** (Baillon) Griseb., Fl. Br. W. Ind. 34. 1859; Müll. Arg., DC. Prodr. 15(2); 331.

1866; Webster, J. Arnold Arb. 39: 111. 1958. *Orbicularia* Baillon, Étude Gen. Euphorb. 616.

1858. TYPE: *Orbicularia phyllanthoides* Baillon (= *Phyllanthus orbicularis* Kunth in H.B.K.).

Roigia Britton, Mem. Torrey Bot. Club 16: 73. 1920. TYPE: *Phyllanthus comosus* Urb.

Dimorphocladium Britton, op. cit. 74. 1920. *Phyllanthus* sect. *Dimorphocladium* (Britton) Pax & K.

Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 63. 1931. TYPE: *Phyllanthus formosus* Urb.

This section includes 9 species of the Greater Antilles, mostly occurring in pinelands and microphyllous scrub on serpentine. Most of the species (some with several subspecies) are endemic to Cuba: *Phyllanthus chamaecristoides* Urb., *P. comosus* Urb., *P. formosus* Urb., *P. myrtilloides* Griseb., *P. orbicularis* Kunth, *P. phlebocarpus* Urb., and *P. scopulorum* Urb. There is one species in Hispaniola, *P. nummularioides* Müll. Arg., occurring in serpentine matorral similar to that in Cuba. One species in Puerto Rico, *P. cuneifolius* (Britton) Croizat, was omitted from the original treatment; since it was incorrectly placed in the synonymy of *P. orbicularis* by Govaerts et al. (2000), it is listed here.

VIII.4.1. *Phyllanthus cuneifolius* (Britton) Croizat, J. Wash. Acad. Sci. 33: 12. 1943; Liogier, Descr.

Fl. Puerto Rico 2: 418. 1988. *Andrachne ? cuneifolia* Britton, Mem. Torrey Bot. Club 16: 72.

1920. TYPE: Puerto Rico, Coamo Springs, *Underwood & Griggs 545* (holotype, NY!).

Xeromorphic thickets on both limestone and serpentine, 10—250 m, eastern Cuba, Hispaniola, and Puerto Rico. This is an isolated species within sect. *Orbicularia* because of its suppression of typical phyllanthoid branching and dioecious flower production. Its is perhaps closest to *Phyllanthus phlebocarpus* Urb.

Section VIII.5. *Ciccastrum* Müll. Arg., Fl. Brasil. 11(2); 26. 1873. *Glochidion* sect. *Ciccastrum* (Müll.

Arg.) Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 58. 1931. TYPE: *Phyllanthus riedelianus* Müll. Arg.

This section of 2 species is curiously disjunct, with *P. purpusii* Brandege in Central America and *P. riedelianus* in eastern Brazil.

Key to the species.

1a. Sepals biseriate, the larger 4—5 mm long; cymules unisexual. 1. *P. purpusii*

1b. Sepals subequal, the larger < 2 mm long; cymules mostly bisexual. 2. *P. riedelianus*

V.1. *Phyllanthus purpusii* Brandege, Univ. Cal. Publ. Bot. 6: 55. 1914. TYPE: Mexico, Chiapas, Cerro del Boquerón, *Purpus 6960* (holotype, UC 173007).

Phyllanthus minarum Standl. & Steyerl., Field Mus. Bot. 23: 125. 1944. TYPE: Guatemala, El Progreso, Sierra de las Minas, *Steyermark 43385* (holotype, F).

Phyllanthus petaloideus P. G. Wilson, Hook. Ic. Pl. 36: t. 3589. 1962. TYPE: Mexico, México, Temascaltepec, Cajones, *Hinton 2376* (holotype, K).

Montane forests, 1600—2500 m, Mexico (México, Chiapas) and Guatemala.

V.2. *Phyllanthus riedelianus* Müll. Arg., Linnaea 32: 16; DC. Prodr. 15(2): 357. 1866; Fl. Brasil.

11(2): 26, 1873; L. B. Smith et al., Fl. Illustr. Catarin. EUFO: 55. 1988. *Glochidion riedelianum* (Müll. Arg.) Pax & K. Hoffm., Natürl. Pflanzenfam. ed. 2, 19c: 58. 1931. TYPE: Brazil, São Paulo, Sebastianópolis, *Riedel 1621* (holotype, presumably LE; isotype fragment, G).

Eastern Brazil, coastal rain forest (mata atlántica), 30—750 m, Santa Catarina and Paraná to Minas Gerais and Bahia.

Section VIII.6. **Brachycladus** G. L. Webster, Contr. Univ. Mich. Herb.

TYPE: *Phyllanthus rupestris* Kunth in H.B.K.

Monoecious shrubs; branchlets fasciculate, pinnatifid, leaves 5—10; sepals 6, free; ♂ and ♀ disk patelliform; stamens 3, filaments free or connate; anthers mucous; pollen grains clypeate; ovary 3-locular, styles free, bifid; fruits capsular; seeds smooth.

This section of 8 species includes mainly shrubs of riparian habitats. All of the species are South American except *Phyllanthus mickelii* McVaugh, which is disjunct in western Mexico. Plants of this section are often confused with species of sect. *Hylaeanthus* (in subg. *Conami*), but have very different pollen grains typical of subg. *Xylophylla*.

Key to the species

- 1a. Styles distinctly bifid, not dilated, 0.3—0.5 mm long; filaments free or connate, anthers dehiscing vertically or horizontally.
 - 2a. Filaments free.
 - 3a. Dioecious; anthers dehiscing vertically.. 1. *P. duckeanus*
 - 3b. Monoecious; anthers dehiscing vertically or horizontally..
 - 4a. Leaves coriaceous, (4-) 7—14 cm long; anthers dehiscing vertically; branchlet axes hirtellous. 2. *P. atabapoensis*
 - 4b. Leaves chartaceous, < 4 cm long; anthers dehiscing ± horizontally; branchlet axes glabrous.
 - 5a. Branchlets with 10—15 leaves; leaf blades suborbicular, rounded to retuse at apex; fruiting pedicel capillary, 25—30 mm long. 3. *P. spruceanus*
 - 5b. Branchlets with 3—5 (-8) leaves; leaf blades elliptic to obovate, obtuse or rounded to acute or apiculate at apex; fruiting pedicel < 20 mm long.
 - 6a. Leaf blades with prominulous venation, rounded or obtuse at apex, completely glabrous. 4. *P. rupestris*

- 6b. Leaves blades with venation not prominulous, obtuse to subacute and apiculate at apex, irtellous on midrib abaxially. 5. *P. mickelii*
- 2b. Filaments connate; anthers dehiscing vertically; branchlets hirtellous..
- 7a. Leaf blades 3—7 cm long; pedicels 10—18 mm long; anthers apiculate.. 6. *P. adianthoides*
- 7b. Leaf blades 2—2.5 (4) cm long; pedicels 4—8 mm long; anthers muticous 7. *P. paezensis*
- 1a. Styles dilated, apically crenulate, 0.7—1 mm long; filaments connate, anthers dehiscing horizontally. 8. *P. manabianus*
- VIII.6.1. *Phyllanthus duckeanus* G. L. Webster, **sp. nov.** TYPE: Brazil, Amazonas, Manaus, 1932, *Ducke* (holotype, RB 24928)
- Frutex (?) glabra, dioecius; ramuli decidui (?); folia chartacea, 5.5—8.5 cm longa, petiolo corrugato, 3—4 mm longo;
- VIII.6.2. *Phyllanthus atabapoensis* Jabl., Mem. N. Y. Bot. Gard. 17: 110. 1967; Webster, Fl. Venez. Guayana 5: 195. 1999. TYPE: Venezuela, Río Orinoco, mouth of Río Atabapo, *Wurdack & Bunting 37552* (holotype, NY).
- Riparian woodlands, 50—200 m, Colombia to Venezuela and Brazil.
- VIII.6.3. *Phyllanthus spruceanus* Müll. Arg., Linnaea 32: 40. 1863; DC. Prodr. 15(2): 401. 1866; Fl. Brasil. 11(2): 60, t. 9. 1873. TYPE: Brazil, “prope Barra” [Amazonas, Manaus], *Spruce 1247* (lectotype [selected here], G!; isotype, K!).
- Phyllanthus borjaensis* Jabl., Mem. N. Y. Bot. Gard. 17: 108. 1967. TYPE: Venezuela, Bolívar, Cerro San Borja, *Wurdack & Monachino 41424* (holotype, NY).
- Riparian woodlands, 100—200 m, Orinoco and Amazon basins, Venezuela and Brazil.
- VIII.6.4. *Phyllanthus rupestris* Kunth in H.B.K., Nov. Gen. Sp. Pl. 2: 110. 1817; Müll. Arg., DC. Prodr. 15(2): 395. 1866; Fl. Brasil. 11(2): 40: 1873; Jablonski, Mem. N. Y. Bot. Gard. 17: 110. 1967; Webster, Fl. Venez. Guayana 5: 199. 1999. TYPE: Venezuela, “in ripa obumbrata fluvii Orinoci inter Maypure et San Fernando de Atabapo,” *Humboldt & Bonpland* (holotype, P!).
- Phyllanthus brachycladus* Müll. Arg., Linnaea 32: 35. 1863. TYPE: Brazil, Rio Negro, San Carlos, *Spruce 3044* (holotype, G!; isotype, W!).

Phyllanthus rupestris var. *oblongifolius* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 395. 1866. *Phyllanthus brachycladus* var. *oblongifolius* Müll. Arg., Linnaea 32: 35. 1863. TYPE: Brazil, Rio Negro, San Gabriel de Cachoeira, *Spruce 2270* (lectotype, G!).

Phyllanthus microcarpoides Croizat, Trop. Woods 78: 6. 1944. TYPE: Venezuela, Amazonas, mouth of Río Sanariapo, *L. Williams 13054* (holotype, US 1800060!).

Phyllanthus delicatissimus Jabl., Mem. N. Y. Bot. Gard. 17: 107. 1967. TYPE: Venezuela, Amazonas, between Santa Barbara and Sabana Huachapana, *Maguire et al. 41462* (holotype, NY; isotype, US).

Riparian vegetation, 50—300 m, Amazonian Colombia, Venezuela, and Brazil.

VIII.6.5. *Phyllanthus mickelii* McVaugh, Brittonia 13: 196. 1961; Webster, Contr. Univ. Mich. Herb. 2001. TYPE: Mexico, Colima, 8 mi WNW of Santiago, *McVaugh 15763* (holotype, MICH!). Tropical deciduous woodlands, c. 50--100 m, Jalisco and Colima.

VIII.6.6. *Phyllanthus adianthoides* Klotzsch, Hook. London J. Bot. 2: 51. 1843; Müll. Arg., DC. Prodr. 15(2): 356. 1866; Lanjouw, Euphorb. Surinam 101. 1931 TYPE: British Guayana, *Schomburgk 78* (holotype, K!).

Along streams in lowland rain forest, 50—250 m, Suriname and Guayana.

VIII.6.7. *Phyllanthus paezensis* Jabl., Mem. N. Y. Bot. Gard. 17: 113. 1967; Webster, Fl. Venez. Guayana 5: 199. 1999. TYPE: Venezuela, Bolívar, island in Río Orinoco between Puerto Paez and Orupe, *Wurdack & Monachino 39970* (holotype: NY; isotype, UC!).

Lowland riparian rain forest, 50—100 m, Venezuela and eastern Colombia; very similar to *P.*

adianthoides and perhaps distinguishable only at the subspecific level.

VIII.6.8. *Phyllanthus manabianus* G. L. Webster, **sp. nov.** TYPE: Ecuador, Manabí, Parque Nacional Machelilla, San Vicente, 1°35' S, 80°41' W, 120—180 m, 8 I 1992, *C. Josse & B.*

Ølgaard 742 (holotype, AAU!). Paratype collection: Ecuador, Manabí, Río Pitalat,

Puerto Lopez, *Holm-Nielsen et al. 27845* (AAU!).

Ab aliis speciebus sectionis *Brachyclado* differt stylis obtruncatis-crenulatis; androecio filamentis connatis, antheris muticis horizontaliter dehiscentibus.

Glabrous monoecious shrub c. 2 m high; branchlets 2—7 (-10) cm long, with 4—9 leaves; branchlet axis terete, smooth, 0.5-0.8 mm in diam.; leaves elliptic, 2—4 × 1.5—3 cm, acute or obtuse at the tip, rounded at base; petiole 1.3—1.7 mm long; stipules acuminate, 1.5—2 mm long, deciduous; flowers in axillary clusters on branchlet; staminate pedicel to 20 mm long, sepals 6, 1.7—2 mm long; disk cupular, c. 0.5 × 1-1.5 mm; stamens 3, filaments connate, column c. 0.3 mm high; anthers 0.5—0.6 mm long, dehiscent horizontally; pistillate pedicel 25—33 mm long in fruit; sepals 6, biseriata, the larger 1.8—2.3 mm long, smaller 1.5—1.8 mm long; disk cupular, rim crenulate, 0.3—0.4 × 1—1.5 mm; ovary 3-locular; styles 0.7—0.9 mm long, dilated, tip lacerate-crenulate; fruits and seeds not seen.

Wet to semideciduous forest, 10—180 m, coastal Ecuador. This species appears isolated within sect. *Brachycladus* by its dilated truncate-crenulate styles. The elongated fruiting pedicels are approached by some specimens of *P. rupestris*, but that species has free stamens and normal bifid styles. There are some similarities with *P. spruceanus*, but it has fruiting pedicels only 8—11 mm long, and smaller leaves and flowers.

Section VIII.6a. **Diplocicca** Müll. Arg., Fl. Brasil. 11(2): 30. 1873. TYPE: *Phyllanthus octomerus*

Müll. Arg.

This monotypic section is very similar to sect. *Brachycladus*, differing mainly by its 2- or 4-merous flowers. The type species, known only from Bahia, Brazil, is very similar to a possibly unnamed taxon in Bolivia.

Section VIII.7. **Williamia** (Baillon) Müll. Arg., Linnaea 32: 4. 1863; DC. Prodr. 15(2): 328. 1866;

Webster, J. Arnold Arb. 39: 69. 1958. *Williamia* Baillon, Étude Gen. Euphorb. 559. 1858. TYPE: *Williamia pruinosa* Baillon (= *Phyllanthus discolor* Poepp. ex Spreng.).

Of the 7 species of this section endemic to Cuba, one (*P. discolor*) occurs in the western end of the island and the others in the old province of Oriente. In Webster (1958), sect. *Williamia* was placed at the beginning of subg. *Xylophylla*, and *Phyllanthus discolor* was regarded as the closest species to the “ancestral” condition., mainly because of its higher stamen number. Further study suggests, however, that

the pleiandrous condition is probably secondary. Section *Williamia* is diverse for a relatively small group, and three subsections have been proposed (Webster, 1958): subsect. *Discolores* G. L. Webster, including *Phyllanthus discolor* Poepp. ex Spreng. and *P. microdictyus* Urb.; subsect. *Incrustati* G. L. Webster, including *P. incrustatus* Urb. and *P. williamioides* Griseb.; and subsect. *Mirifici* G. L. Webster, including only *P. mirificus* G. L. Webster. In addition, one intersectional hybrid, *Phyllanthus* × *pallidus* (*P. discolor* × *P. comptus*), is known from the Cajálbana area in Pinar del Río.

Sect. VIII.8. **Oxalistyli** Baillon, Étude Gen. Euphorb. 628. 1858; Müll. Arg., DC. Prodr. 15(2): 330. 1866.

TYPE: *Phyllanthus kunthianus* (as *Oxalistyli kunthiana*) Baillon (= *Phyllanthus salviifolius* Kunth in H.B.K.).

Although this section contains only the type species *Phyllanthus salviifolius*, it is very common in the Andes from Colombia and Venezuela to Ecuador and Peru. Its habit is very different from the Antillean species of sect. *Williamia*, but is very similar to *P. microdictyus* in floral morphology. The two sections appear closely related, and it seems probable that sect. *Williamia*, and perhaps sect. *Orbicularia*, represent West Indian colonists of a montane South American group.

VIII.8.1. **Phyllanthus salviifolius** Kunth in H.B.K., Nov. Gen. Sp. 2: 116. 1817; Müll. Arg., DC.

Prodromus 15(2): 330. 1866; Macbr., Fieldiana Bot. 13 (3A, 1): 46. 1951. *Kirganelia salviifolia* (Kunth) Spreng., Syst. Veg. 3: 48. 1826. TYPE: Colombia, Cauca, La Vega de San Lorenzo, between Popayán and Pasto, *Humboldt & Bonpland* (holotype, P!).

Phyllanthus floribundus Kunth in H.B.K., Nov. Gen. Sp. 2: 116. 1817. *Kirganelia floribunda* (Kunth)

Spreng., Syst. Veg. 3: 48. 1826. *Phyllanthus salviifolius* γ *floribundus* (Kunth) Müll. Arg., DC. Prodr. 15(2): 330. 1866. TYPE: Ecuador, between Chillo and Turubamba, *Humboldt & Bonpland* (holotype, P!).

Andean forests, 1500—3500 m, Colombia and Venezuela to Ecuador and Peru.

Section VIII.9 **Asterandra** (Klotzsch) Müll. Arg., Linnaea 32: 5. 1863; DC. Prodr. 15(2): 329. 1866;

Webster, J. Arnold Arb. 39: 146. 1958. *Asterandra* Klotzsch, Arch. Naturgesch. 7: 200. 1841.

TYPE: *Asterandra cornifolia* (Kunth in H.B.K.) Klotzsch (= *Phyllanthus cornifolius* Kunth).

This section of 2 or 3 species is widespread in the neotropics, but variation patterns have made species definitions problematic. In Webster (1958), the original type species, *Phyllanthus cornifolius*, was reduced to a subspecies of *Phyllanthus juglandifolius* Willd. However, with the more recent publication of *Phyllanthus gentryi* G. L. Webster, the situation has become more complicated. Provisionally, it now appears most reasonable to recognize 3 species.

Key to the species.

1a. Seeds 6.5—7 mm long, floral disk not pitted; styles nearly free; larger leaf blades at least 6 cm broad, minutely alveolate abaxially. 1. *P. gentryi*

1b. Seeds 4.5—6 mm long; floral disk distinctly pitted; styles connate c. halfway; larger leaves 3—5 (rarely to 6) cm broad, not minutely alveolate abaxially.

2a. Leaves elliptic-lanceolate, 5—11 (-15) cm long, glabrous abaxially; stamens 3—5; fruiting pedicel 6—11 (-14) mm long; capsule (9-) 10—12.5 mm broad. 2. *P. juglandifolius*

2b. Leaves oblong-lanceolate, (9-) 12-20 cm long, often pubescent abaxially; stamens mostly 6 (5—7); fruiting pedicel 15—30 mm long; capsule 12—15 (-17) mm broad.

3. *P. cornifolius*

VIII.9.1 *Phyllanthus gentryi* G. L. Webster, Ann. Missouri Bot. Gard. 75: 1096, t. 1. 1988. TYPE:

Panama. Darién, Cerro Pirre, *Gentry & Clewell 7017* (holotype, F; isotypes, DAV!, MO!).

Known only from evergreen forests, 300—750 m, eastern Panama (Darién).

VIII.9.2 *Phyllanthus cornifolius* Kunth in H.B.K., Nov. Gen. Sp. Pl. 2: 115. 1817; Urban, Repert. Sp.

15: 404. 1919. *Asterandra cornifolia* (Kunth) Klotzsch, Arch. Naturgesch. 7: 200. 1841.

Phyllanthus juglandifolius ssp. *cornifolius* (Kunth) G. L. Webster, J. Arnold Arb. 39: 151. 1958.

(additional synonymy in Webster, 1958). TYPE: Ecuador, Guayaquil, *Humboldt & Bonpland* (holotype, P!).

Widespread in South America from Colombia, Venezuela, and Trinidad to Amazonian Brazil; specimens from eastern Brazil are atypical, some resembling *P. juglandifolius*. It remains uncertain whether or not *P. cornifolius* and *P. juglandifolius* can be maintained as distinct species.

VIII.9.3 *Phyllanthus juglandifolius* Willd., Enum. Hort. Berol. Suppl. 64. 1813; Webster, J. Arnold Arb.

39: 146. 1958. *Phyllanthus grandifolius* var. *genuinus* Müll. Arg., DC. Prodr. 15(2): 329. (non *P.*

grandifolius L.). TYPE: cultivated, Berlin Botanical Garden, *Herb. Willdenow 17995* (holotype, B!).

Agyneia berterii Spreng., Syst. Veg. 3: 19. 1826. TYPE: Santo Domingo [Dominican Republic], *Bertero* (lectotype, P!).

Phyllanthus quinquefidus Sessé & Moçño, Flora Mex. ed. 2, 212. 1894; McVaugh, Bot. Res. Sessé & Moçño Exped. VII, 244. 2000. TYPE: Puerto Rico, Toa Alta, *Sessé* (G).

Phyllanthus petenensis Lundell, Phytologia 57: 367. 1985. TYPE: Guataemala, Petén, La Cumbre, *Contreras 8778* (holotype, LL!).

Moist to wet forests, 100—1000 m, Greater Antilles (except Jamaica) and Virgin Islands, also in Central America (Guatemala, Belize, and Honduras).

Section VIII.10. **Glyptothamnus** G. L. Webster, J. Arnold Arb. 39: 68, 160. 1958. TYPE: *Phyllanthus chryseus* R. A. Howard.

This monotype section includes only the type species, endemic to pinelands on serpentine at 50—400 m in eastern Cuba (Oriente, now Guantánamo province).

Section VIII11. **Epistylum** (Sw.) Griseb., Fl. Br. W. Ind. 33. 1859; Webster, J. Arnold Arb. 39: 153. 1958.

Epistylum Sw., Fl. Ind. Occid. 1100. 1800. TYPE: *Omphalea axillaris* Sw. (= *Phyllanthus axillaris* [Sw.] Müll. Arg.).

Phyllanthus sect. *Catastylum* Griseb., Fl. Br. W. Ind. 33. 1859. TYPE: *Phyllanthus cladanthus* Müll. Arg.

The three species of sect. *Epistylum*, found on limestone outcrops in Jamaica, are distinguished by their racemoid sometimes cauliflorous inflorescences. Biogeographic relationships—the absence of sect. *Asterandra* from Jamaica—and morphological similarities suggest that sect. *Epistylum* may be a vicariant of sect. *Asterandra*.

Species included: *Phyllanthus axillaris* (Sw.) Müll. Arg., *P. cauliflorus* (Sw.) Griseb., *P. cladanthus* Müll. Arg.

Sect. VIII.12. **Hemiphyllanthus** (Müll. Arg.) Müll. Arg., Flora 1865: 370. 1865; DC. Prodr. 15(2): 323.

1866; Webster, Contr. Gray Herb. 176: 62. 1955; J. Arnold Arb. 39: 163. 1958. *Glochidion* sect.

Hemiphyllanthus Müll. Arg., Linnaea 32: 59. 1863. TYPE: *Phyllanthus ovatus* Poir.

Six species, 2 from Haiti and the others from the Lesser Antilles (Antigua to Tobago). The section may be a vicariant of sect. *Epistylum* and—because of the bipinnatifid branchlets—the sister group of the phylloclade-bearing species of sect. *Xylophylla*.

Species included: *Phyllanthus acacioides* Urb. (Tobago), *P. maleolens* Urb. & Ekm. and *P. myriophyllus* (Haiti), *P. megapodus* G. L. Webster (Dominica), *P. mimosoides* Sw. (Antigua to Martinique), and *P. ovatus* Poir. (Martinique).

Section VIII.13. **Xylophylla** (L.) Baillon, Étude Gen. Euphorb. 623. 1858; Müll. Arg., DC. Prodr. 15(2):

427. 1866; Webster, J. Arnold Arb. 39: 179. 1958. *Xylophylla* L., Mant. Pl. 2: 147. 1771. TYPE:

Xylophylla latifolia L. (nom. illeg., = *Phyllanthus epiphyllanthus* L.).

Genesiphylla L'Her., Sert. Angl. 29. 1778. *Phyllanthus* sect. *Typophyllanthus* subsect. *Genesiphylla*

(L'Her.) Kuntze, Lex. Gen. Phan. 434. 1904. TYPE: *Genesiphylla aspleniifolia* L'Her. (=

Phyllanthus latifolius Sw.).

Hexadena Raf., Sylva Tellur. 92. 1838. TYPE: *Hexadena angustifolia* Raf. (= *Phyllanthus*

angustifolius [Sw.] Sw).

Lomanthes Raf., Sylva Tellur. 92. 1838. TYPE: *Lomanthes latifolia* Raf. (= *Phyllanthus latifolius* Sw.).

This section of 8 species is the most distinctive and well-known group of neotropical *Phyllanthus* because of its phylloclades. Because of the primitively bipinnatifid branchlets and other characters, it appears to have been derived from sect. *Hemiphyllanthus*. Primarily on the basis of pollen evidence, the section was redefined by Webster (1958) to exclude South American phylloclade-bearing species that were included by Müller (1873). Since one additional species was described since the revision by Webster (1958), a new key is offered here. A horticultural form, *Phyllanthus* 'Elongatus', is listed at the end of the section but not included in the key.

Key to the species

1a. Phylloclades bipinnatifid, borne distichously on main axis of deciduous branchlet.

- 2a. Primary axis of branchlet developing slowly, main axis greyish or brownish, different in color from lateral phylloclades; pedicel of pistillate flower 0.5—1.5 mm long; pistillate disk dissected. 1. *P. montanus*
- 2b. Primary axis of branchlet expanding more rapidly, main axis greenish and with similar consistency to lateral axes (phylloclades).
- 3a. Pedicel of pistillate flower only 0.5—1.5 mm long; pistillate disk dissected; phylloclades ± rhombic-lanceolate, with mostly 20—50 nodes; cataphylls glabrous or very sparsely ciliate, apical cone 10—15 mm broad. 2. *P. latifolius*
- 3b. Pedicel of pistillate flower mostly 2 mm long or more; pistillate disk unlobed; phylloclades elliptic- to obovate-lanceolate.
- 4a. Cataphylls of main stem remaining brown or grey, glabrous or ciliate only at base; phylloclades mostly 1—2 cm broad, with 20—40 nodes; ovary smooth. 3. *P. arbuscula*
- 4b. Cataphylls of main stem becoming dark brown or blackish, copiously ciliate on margins (at least when young); phylloclades mostly 1 cm broad or less, with 10—25 nodes, often subopposite at ends of branchlet axis.
- 5a. Phylloclades (floriferous axes) lanceolate, mostly well over 3 mm broad, with mostly 10—20 nodes; ovary rugulose; styles not dilated, 3-5 fid into slender tips. 5. *P. angustifolius*
- 5b. Phylloclades narrowly linear, only 1—3 mm broad, with mostly 7—10 nodes; ovary smooth; styles dilated, tips merely crenulate, forming a calyptra over the ovary. 6. *P. proctoris*
- 1b. Phylloclades simple, borne spirally on main axis.
- 6a. Cataphylls on main stem more or less deciduous, stipules free from blade; lateral veins of phylloclades prominulous, conspicuous; filaments united only at base; pistillate disk flat, not enclosing any of the ovary. 4. *P. eximius*
- 6b. Cataphylls on main stem persistent, stipules (at least basally) adnate to blade; lateral veins of phylloclades inconspicuous; filaments united at least halfway; pistillate disk enclosing

at least ¼ of ovary.

7. P. epiphyllanthus

VIII.13.1. *Phyllanthus montanus* (Sw.) Sw., Fl. Ind. Occid. 2: 1117. 1800; Müll. Arg., DC. Prodr. 15(2):

429. 1866; Fawc. & Rendle, Fl. Jam. 4: 261. 1920; Webster, J. Arnold Arb. 39: 183. 1958;

Adams, Fl. Pls. Jamaica 409. 1972. *Xylophylla montana* Sw., Prodr. 28. 1788. TYPE: Jamaica, Swartz (holotype, S).

Woods on limestone, 300—1000 m, western and central Jamaica (Clarendon, St. Ann, St.

Elizabeth, Trelawny).

VIII.13.2 *Phyllanthus latifolius* Sw., Fl. Ind. Occid. 2: 1109. 1800 (non *Xylophylla latifolia* L.); Webster, .

J. Arnold Arb. 39: 185. 1958; Adams, Fl. Pl. Jamaica 409. 1972. TYPE: Jamaica, Browne

(lectotype, LINN 1105-1).

Thickets on limestone, 0—300 m, southern Jamaica (St. Andrew, St. Catherine).

VIII.13.3. *Phyllanthus arbuscula* (Sw.) Gmel., Syst. Pl. 2: 204. 1791; Webster, J. Arnold Arb. 39: 188.

1985; Adams, Fl. Pls. Jamaica 409. 1972. TYPE: Jamaica, St. Andrew, St. Catherine Hill, Swartz

(holotype, BM; isotype, S).

Montane forests, 400--900 m, central and western Jamaica. The species is quite variable, and has a lengthy synonymy (summarized by Webster, 1958: 188, 189).

VIII.13.4. *Phyllanthus eximius* G. L. Webster & Proctor, J. Arnold Arb. 41: 283. 1960; Adams, Fl. Pls.

Jamaica 409. 1972. TYPE: Jamaica, Portland, John Crow Mountains, 2—2.5 mi SW of

Ecclesdown, Webster *et al.* 8320 (holotype, PUR; isotypes, DAV, GH, JAM, NY).

Rainforest on dogtooth limestone, 400—800 m, eastern Jamaica,

VIII.13.5. *Phyllanthus angustifolius* (Sw.) Sw., Fl. Ind. Occid. 2: 1111. 1800; Fawc. & Rendle, Fl. Jam. 4:

262. 1920; Webster, J. Arnold Arb. 39: 193. 1958; Adams, Fl. Pls. Jam.410. 1972; Proctor, Kew

Bull. add. ser. 11: 525. 1984. *Xylophylla angustifolia* Sw., Prodr. 28. 1788. *Hexadena angustifolia*

Raf., Sylva Tellur. 92. 1838. TYPE: Jamaica, Browne (holotype, LINN!).

Phyllanthus cognatus Spreng., Syst. Veg. 3: 23. 1826. TYPE: Jamaica, Bertero (lectotype, MO!).

Xylophylla contorta Britton, Bull. Torrey Bot. Club 37: 353. 1910. TYPE: Jamaica, St. Ann, St. Ann's Bay,

Britton 2515 (holotype, NY!).

Thickets and woodlands, mainly on limestone, 0—500 m; widespread in Jamaica, and also in the

Cayman Islands and Swan Islands.

VIII.13.6 *Phyllanthus proctoris* G. L. Webster, J. Arnold Arb. 39: 195. 1958; Adams, Fl. Pls. Jam. 410.

1972. TYPE: Jamaica, Westmoreland, seaacoast, *Purdie* (holotype, K!).

Scattered in western Jamaica at low elevations (Hanover, Manchester, St. Elizabeth, St. James).

This species was confused with *Phyllanthus linearis* (Sw.) Sw. by Grisebach (1859), Müller (1866), Fawc. & Rendle (1920), and others. However, the plant collected by Swartz, to which the binomial *P. linearis* properly applies, may be a narrow-leaved form of *P. arbuscula*.

VIII.13.7. *Phyllanthus epiphyllanthus* L., Sp. Pl. 981. 1753; Müll. Arg., DC. Prodr. 15(2): 428. 1866;

Webster, J. Arnold Arb. 39: 197. 1958; Correll, Fl. Bahama Arch. 838, fig. 348. 1982; Howard, Fl.

Lesser Antilles 5: 76. 1989. *Xylophylla epiphyllanthus* (L.) Hornem., Hort. Bot. Hafn. 961. 1815.

TYPE: Hort. Clifortianus 439.1 (BM; fide Howard, 1989).

The commonest and most widespread species of sect. *Xylophylla*, occurring over most of the West Indies, but never collected wild on the mainland of North or South America. Webster (1958) recognized 3 subspecies:

VIII.13.7a. *Phyllanthus epiphyllanthus* ssp. *epiphyllanthus*. *Xylophylla epiphyllanthus* (L.) Britton, in

Small, Fl. Florida Keys 76. 1913. .

Xylophylla falcata Sw., Prodr. 28. 1788. *Phyllanthus falcatus* (Sw.) Gmel., Syst. Nat. ed. 13, 2: 204. 1791.

TYPE: Herb. Sloane 97: 100; 101: 106 (syntypes, BM!).

Lowland scrub, 0—50 m, Bahamas, Cuba, Hispaniola, Puerto Rico, Lesser Antilles (Virgin Islands to Barbados); absent from Jamaica.

VIII.13.7b. *Phyllanthus epiphyllanthus* ssp. *domingensis* G. L. Webster, J. Arnold Arb. 39: 202. 1958;

Liogier, Fl. Española 4: 197. 1986. TYPE: Dominican Republic, Santiago, Monción, Río Magua, *Ekman H12642* (holotype, S!; isotype, US!).

Wooded hillsides, 200—800 m, Hispaniola.

VIII.13.7c. *Phyllanthus epiphyllanthus* ssp. *dilatatus* (Müll. Arg.) G. L. Webster, J. Arnold Arb. 39: 203.

1958; *Phyllanthus epiphyllanthus* var. *dilatatus* Müll. Arg., DC. Prodr. 15(2): 428. 1866. TYPE: Cuba, Oriente, cliffs at Monteverde, *Wright 1951* (holotype, G!; isotypes, GOET, MO!, NY!, P!, US!).

Pinelands and evergreen woods on calcareous uplands, 500—600 m, eastern Cuba.

VIII.13.8. *Phyllanthus x elongatus* (Jacq.) Steud., Nom. Bot. ed. 1, 615. 1821 (pro. sp.; =

Phyllanthus arbuscula × *P. epiphyllanthus* ssp. *epiphyllanthus*); Webster, Brittonia 11: 178.

1959. TYPE: Cult., Schönbrunn Gardens, Vienna, *Jacquin* (holotype, G!).

This common ornamental is strictly a horticultural entity; no interspecific hybridization in the wild has been observed in sect. *Xylophylla*. The origin of the hybrid, and the synonymy of the names applied, is given in Webster (1959). Because it is a strictly cultivated plant, Govaerts et al. (2000) refer to it as *Phyllanthus* ‘Elongatus.’

Section VIII. 14. **Elutanthos** Croizat, J. Wash. Acad. Sci. 33: 12. 1943; Webster, J. Arnold Arb. 39: 50.

1958. *Phyllanthus* subg. *Botryanthus* Webster, J. Arnold Arb. 37: 345. 1956. TYPE: *Phyllanthus glaucescens* Kunth in H.B.K. (= *P. grandifolius* L.).

This section of 13 neotropical species was placed in a subgenus separate from *Xylophylla* by Webster (1958), primarily because of the unspecialized branching (no deciduous branchlets). However, since the sister group of subg. *Xylophylla* is almost surely subg. *Emblica* or subg. *Conami*, which share the synapomorphy of phyllanthoid branching, the lack of deciduous branchlets in sect. *Elutanthos* must be interpreted as a reversion. The distribution of sect. *Elutanthos* is centered in three areas: Mexico, the Greater Antilles, and Brazil.

Key to the species

1a. Flowers in axillary or terminal glomerules (or brachyblasts < 3 mm long).

2a. Stamens 3.

3a. Staminate disk dissected.

4a. Staminate sepals at least 1.5 mm long.

5a. Staminal column without appendages; leaf blades glabrous or sparsely hirsutulous abaxially; styles bifid.

6a. Seeds less than 5 mm long; fruit not over 10 mm broad; leaf blades with smooth epidermis abaxially (not reticulate).

7a. Fruiting pedicel > 5 mm long.

- 8a. Styles bifid; monoecious.
- 9a. Leaf blades chartaceous, veins not sunken adaxially; stipules not indurate;
 styler column distinctly narrower than ovary. 1. *P. nutans*
- 9b. Leaf blades coriaceous, main veins distinctly sunken adaxially; stipules
 indurate; styler column nearly as broad as ovary. 2. *P. pachystylus*
- 8b. Styles unlobed; dioecious.*P. aripuanensis*
- 7b. Fruiting pedicel < 5 mm long; 3. *P. huallagensis*
- 6b. Seeds (5-) 6—10 mm long; fruit usually well over 10 mm broad; leaf blades
 smooth or reticulate abaxially.
- 10a. Leaf blades distinctly whitish-reticulate abaxially. 4. *P. grandifolius*
- 10b. Leaf blades smooth and green abaxially. 5. *P. coalcomanensis*
- 5b. Staminal column with 3 apical appendages; leaf blades densely hirsutulous beneath;
 styles entire or emarginate. 6. *P. urbanianus*
- 4b. Staminate sepals < 1.5 mm long.
- 11a. Leaf blades acuminate; pistillate flowers several to many per axil. 7. *P. umbratus*
- 11b. Leaf blades rounded to acute; pistillate flowers one/axil.
- 12a. Styles bifid, tips reflexed; pistillate disk tenuous; branches and inflorescence
 axes hirsutulous. 8. *P. anderssonii*
- 12b. Styles truncate or emarginate, erect and connivent; pistillate disk massive;
 plants glabrous. 9. *P. botryanthus*
- 3a. Staminate disk not dissected, entire or crenulate.
- 13a. Staminal column slender, > 1 mm. high; styles unlobed; dioecious.
 10. *P. poeppgianus*
- 13b. Staminal column < 1 mm high; monoecious.
- 14a. Styles bifid, free; staminal column inflated. 11. *P. vincentae*
- 14b. Styles entire, connate into a column; staminal column slender. 12. *P. harlingii*
- 1b. Stamens 1 or 2.
- 15a. Staminate sepals and disk-segments 5 or 6.

- 16a. Seeds > 5 mm long; staminate sepals usually 6; stamen solitary. 13. *P. tequilensis*
- 16b. Seeds < than 5 mm long; staminate sepals 5.
- 17a. Pistillate pedicels 30—50 mm long; stipules entire. 14. *P. cladotrichus*
- 17b. Pistillate pedicels < 20 mm long; stipules lacerate. 15. *P. morianus*
- 15b. Staminate sepals and disk-segments 4. 16. *P. biantherifer*

VIII.12.1. *Phyllanthus nutans* Sw., Prodr. 27. 1788; Fl. Ind. Occid. 1103. 1800; Müll. Arg., DC.

Prodr. 15(2): 375. 1866; Fawc. & Rendle, Fl. Jamaica 4: 253. 1920; Webster, J. Arnold Arb.

39: 56. 1958; Proctor, Kew Bull. add. ser. 11: 524. 1984. TYPE: Jamaica, Swartz

(holotype, S!; isotypes, A!, C!, G!, P!).

Dry to moist forests, 0—750 m; Jamaica (ssp. *nutans*) and in Cuba and the Cayman Islands (ssp. *grisebachianus* [Müll. Arg.] G. L. Webster); synonymy and specimen citations are provided in Webster (1958).

VIII.12.2. *Phyllanthus pachystylus* Urb., Symb. Ant. 3: 286. 1902; Webster, J. Arnold Arb. 39: 62. 1958.

TYPE: Cuba, Oriente, savannas near Sagua de Tánamo, Wright 1947 (lectotype, GH!; isotypes, G!, GOET!).

Savannas and woodlands on serpentine, below 500 m, eastern Cuba.

VIII.12.3. *Phyllanthus huallagensis* Standl. ex Croizat, J. Wash. Acad. Sci. 33: 13. 1943.

TYPE: Peru, San Martín, Juan Juí, Klug 4240 (holotype, A; isotype, US!).

Deciduous forests, 400--800 m, southern Ecuador and northern Peru.

VIII.12.4. *Phyllanthus grandifolius* L., Sp. Pl. 981. 1753. TYPE: probably from Campeche, Mexico,

Houston (holotype, Herb. Hort. Cliffort., BM!).

Andrachne arborea Miller, Gard. Dict. Ed. 8. 1768. TYPE: Mexico, Campeche, Houston (holotype, Herb.

Miller, BM; possibly part of the same collection as *Phyllanthus grandifolius*).

Phyllanthus glaucescens Kunth in H.B.K., Nov. Gen. Sp. 2: 115. 1817. TYPE: Mexico, Campeche,

Humboldt & Bonpland (holotype, P!; photograph of isotype, UC!).

Phyllanthus adenodiscus Müll. Arg., Linnaea 32: 23. 1863. TYPE: Mexico, Veracruz, Papantla,

Schiede 1134 (holotype, B, destroyed; photograph, UC).

Widespread in Mexico, usually on limestone, 50—1400 m, Tamaulipas to San Luis Potosí, Campeche, and Oaxaca.

VIII.12.5. *Phyllanthus laxiflorus* Benth., Pl. Hartweg. 90. 1840. TYPE: Guatemala, *Hartweg 612*

(holotype, K; isotype, G).

Phyllanthus chiapensis Sprague, Kew Bull. 1909: 264. 1909. TYPE: Mexico, Chiapas, Cacate, *Linden 1634* (holotype, K).

Highlands of Guatemala and Chiapas; very similar to *Phyllanthus grandifolius* but lacking the characteristic cuticular reticulum of that species.

VIII.12.6. *Phyllanthus coalcomanensis* Croizat, J. Wash. Acad. Sci. 33: 13. 1943. TYPE: Mexico,

Michoacán, Coalcomán, Aquila, *Hinton et al. 15857* (holotype, A!; isotypes, NY!, UC!, US!).

Seasonal forests, 20—500 m, Western Mexico (Jalisco and Michoacán); perhaps also represented by incomplete specimens in Nicaragua.

VIII.12.7. *Phyllanthus urbanianus* Mansf., Repert. Sp. Nov. 32: 86. 1933; Webster, J. Arnold Arb.

39: 65. 1958. TYPE: Haiti, Dept. Sud, Massif de la Hotte, Les Roseaux, *Ekman H10435*

(holotype, S!; isotypes, A!, US!).

Known only from the type collection; possibly now extinct.

VIII.12.8. *Phyllanthus anderssonii* Müll. Arg., DC. Prodr. 15(2): 395. 1866; Webster, J. Arnold Arb.

39: 53. 1958; Howard, Fl. Lesser Antilles 5: 74. 1989. TYPE: “Caracas, Herb. Holm. 288,”

Andersson (holotype, G!).

Phyllanthus barbadensis Urb., Symb. Ant. 3: 287. 1902. TYPE: Barbados, Forsteer Hall Wood,

Eggers 7130 (lectotype [designated by Webster, 1958], US!; isotypes, A!, GOET!).

Seasonal woodlands, c. 100 m; earlier thought to be endemic to Barbados, but specimens from Colombia (e.g., Magdalena Valley, Tolima, Melgar, *Goudot* (K, P) appear conspecific, so that contrary to Webster (1958), it no longer appears unlikely that Andersson’s collection could have been made in Venezuela.. Problems in typification are discussed by Webster (1958) and Howard (1989).

VIII.12.9. *Phyllanthus botryanthus* Müll. Arg., DC. Prodr. 15(2): 323. 1866; Webster, J. Arnold Arb. 39:

51. 1958; Contr. Univ. Mich. Herb. 2001. *Glochidion botryanthum* (Müll. Arg.) Pax &

K. Hoffm., Natürl. Pflanzenfam. Ed. 2, 19c: 58. 1931. 2001. TYPE: Colombia, Cartagena,

- Triana 3664* (lectotype, P; isotypes, K!, W!).
- Phyllanthus euwensii* Bold., Fl. Dutch W. Ind. Isl. 2: 50. 1914. TYPE: Curaçao, *Boldingh 5279* (isotype, NY 83521!).
- ? *Phyllanthus larensis* Croizat, Fieldiana Bot. 28(2): 318. 1952. TYPE: Venezuela, Lara, between Carora and boundary with Trujillo, *Staeyermark 56813* (holotype, F).
- Seasonal woodlands, 50—900 m; disjunct between western Mexico (Jalisco) and the southern Caribbean (Aruba, Bonaire, Curaçao, Colombia, and Venezuela). West Indian specimens are cited in Webster (1958) and Mexican in Webster (2001).
- VIII.12.10. *Phyllanthus poeppigianus* (Müll. Arg.) Müll. Arg., DC. Prodr. 15(2): 323. 1866; Fl. Brasil. 11(2): 27. 1873. *Glochidion poeppigianum* Müll. Arg., Linnaea 32: 71. 1863. TYPE: Brazil, Amazonas, Ega [Tefé], *Poeppig 2758* (holotype, G!; isotype, W!).
- Phyllanthus martii* Müll. Arg., Fl. Brasil. 11(2): 27. 1873. TYPE: Brazil, Amazonas, “Rio Negro in sylvis Japurensibus,” *Martius* (lectotype [selected here], M!).
- Widespread in lowland Amazonian forests, often in várzea or igapó, 100—250 m, Peru and Brazil. Müller (1873) distinguished *Phyllanthus martii* on the basis of its smaller leaves and flowers, as well as its longer inflorescence. Only the latter character seems impressive, and even here there is more or less continuous intergradation with *P. poeppigianus*.
- VIII.12. 11. *Phyllanthus vincentae* J. F. Macbr. Publ. Field Mus. Nat. Hist., Bot. 13(3A): 47. 1951.
- Xylosma minutiflora* J. F. Macbr., Candollea 5: 392. 1934 (not *Phyllanthus minutiflorus* F. Muell., 1865). TYPE: Peru, Loreto, Yurimaguas, Puerto Arturo, *Williams 4970* (holotype, F!).
- Phyllanthus ventricosus* G. L. Webster, Ann. Missouri Bot. Gard. 54: 198. 1967. TYPE: Peru, Loreto, Iquitos, Rancho Indiana, *Mexia 6414* (holotype, MO; isotypes, GH, UC, US, WIS).
- Amazonian rain forests, c. 100-200 m, northeastern Peru.
- VIII.12.12. *Phyllanthus harlingii* G. L. Webster, **sp. nov.** TYPE: Ecuador, Loja, 5 km E of Celica, seasonal evergreen forest, 1500 m, 11 IV 1980, *G. Harling & L. Andersson 18185* (holotype, AAU).

Frutex monoicus glaber, ab affine *Phyllanthi poeppigiani* differt foliis emarginatis, sepalis majoribus, stylis connatis dilatatis.

Glabrous monoecious shrub; leaves elliptic, rounded or emarginate at apex, veinlets pale and \pm prominulous adaxially, 2.5—4 cm long, 1.8—2.5 cm broad; petiole 1—2 mm long, fluted; stipules reflexed, acuminate, 1.8—2.5 mm long; flowers in axillary glomerules, the pistillate solitary; staminate pedicel 8—9 mm long; sepals 6, elliptic, 1.7—2.2 mm long; disk flat, angled, 1.8—2 mm broad; stamens 3, filaments connate, staminal column c. 0.3 mm high; anthers muticous, dehiscing horizontally, 0.5—0.6 mm long; pistillate sepals 6, 2—2 mm long; disk patelliform, c. 1.5 mm broad; ovary 3-locular; styles c. 0.5 mm long, erect, connate; fruits and seeds not seen.

Known only from the type collection.

VIII.12.13. *Phyllanthus tequilensis* Robinson & Greenm., Proc. Amer. Acad. 29: 392. 1894; Webster,.

Contr. Univ. Mich. Herb. 2001. TYPE: Mexico, Jalisco, Tequila, *Pringle 5490* (holotype, GH; isotype, UC).

Phyllanthus micromalus McVaugh, Brittonia 13: 198. 1961. TYPE: Mexico, Nayarit, 10 mi SE of Tepic, *McVaugh 16569* (holotype, MICH!; isotype, DAV!).

Seasonal woodlands, 300—1500 m, western Mexico (Nayarit to Guerrero).

VIII.12.14. *Phyllanthus cladotrichus* Müll. Arg., Linnaea 32: 25. 1863; DC. Prodr. 15(2): 380. 1866;

Fl. Brasil. 11(2): 41. 1873. TYPE: Brazil, Rio de Janeiro, Mandioca, *Riedel* (holotype, G; photograph of isotype at B, UC).

? *Phyllanthus ramosus* Vell., Fl. Flumin. 10: t. 17. 1832. TYPE: No specimen appears to be extant, hence Vellozo's plate must serve as holotype.

Coastal rain forests (Mata Atlántica), 50—150 m, Brazil (Ceará to Rio de Janeiro). Govaerts et al. (2000) treat *Phyllanthus cladotrichus* as a synonym of *P. ramosus*, but in the absence of a type specimen the identity of the latter cannot be established with certainty.

VIII.12.15. *Phyllanthus morianus* G. L. Webster, *sp. nov.* TYPE: Brazil, Bahia, Mun. Maracás,

Fazenda do Pássaros, 24 km E of Maracás, *Mori & King 12176* (holotype, DAV; isotype, NY).

Frutex monoica glabra, ab *Phyllantho cladotricho* differt pedicellis fructiferus brevioribus, stipulis laceratis; ab *P. umbrato* staminibus 2.

Monoecious, glabrous shrub; branchlets c. 10—15 cm long with c. 13—15 leaves; stipules lacerate, c. 1.5 mm long; flowers in axillary glomerules; staminate pedicels c. 4 mm long; sepals 5, c. 1.2 mm long; disk massive, entire (3-angled), c. 0.5 mm broad; stamens 2, filaments very short (c. 0.1 mm long); anthers mucous, dehiscing horizontally, c. 0.5 mm long; pistillate flowers 2 or 3 per axil; pedicel 8—17 mm long in fruit; sepals 5, c. 1.3--1.4 mm long; disk massive, entire (angled), c. 1 mm broad; ovary smooth; seeds c. 2.9 mm long, testa smooth, with carunculate appendage.

Mata de cipó, c. 1000 m, Bahia, Brazil.

VIII.12.16. *Phyllanthus biantherifer* Croizat, Trop. Woods 78: 7. 1944. TYPE: Brazil, Amazonas, Humayta, Livramento, *Krukoff 6691* (holotype, A; isotypes, NY!, US!).

Lowland rain forest, 100--200 m, western Amazonian Brazil.

VIII.12.17. *Phyllanthus racemigerus* Müll. Arg., Linnaea 32: 23. 1863; DC. Prodr. 15(2): 375. 1866; Fl. Brasil. 11(2): 34. 1873. TYPE: Brazil, between Santarem and Barra do Rio Negro, Oct. 1850, *Spruce 1097* (lectotype [selected here], K!; isotype, G!).

Riparian forests, 100--200 m, Amazonian Brazil.

VIII.12.18. *Phyllanthus umbratus* Müll. Arg., DC. Prodr. 15(2): 356. 1866; Fl. Brasil. 11(2): 32. 1873. TYPE: Brazil, Rio de Janeiro, *Riedel* (holotype, B, destroyed; photograph, CNMH 5041, DAV).

Coastal rain forests (Mata Atlántica), Rio de Janeiro, Brazil.

Sect. VIII.15. **Diplocicca** Müll. Arg., Fl. Brasil. 11(2): 30. 1873. TYPE: *Phyllanthus octomerus* Müll. Arg.

This monotypic section is still poorly known, and its placement remains doubtful. The clypeate pollen grains indicate that it belongs in subg. *Xylophylla*, but it is not clear that it is closely related to sect. *Elutanthos*. Apparently due to its very dry habitat, the branchlets, leaves, and flowers expand concurrently, and it is difficult to determine whether it has phyllanthoid branching. The pleiomerous perianth and androecium is unusual, but probably trivial; however, the introrse anthers (emphasized by Müller) are rare in *Phyllanthus*.

VIII.15.1. *Phyllanthus octomerus* Müll. Arg., Fl. Brasil. 11(2):30. 1873. TYPE: Brazil, Bahia, Villa de Caiteté, *Martius 2987-2989* (holotype, M!).

This species from the caatinga of Bahia has also been collected in xeric scrub in Bolivia.

EXCLUDED SPECIES

1. *Phyllanthus bolivarensis* Steyerl., Fieldiana Bot. 28: 317. 1952. TYPE: Venezuela, Bolívar, 1—10 km NW of Uputa, 700 m, *Steyermark 57688* (holotype, F; photograph, DAV!).

This plant, described from a fruiting specimen, does not belong to *Phyllanthus*. As noted by Jablonski (1967), the locules of the capsule have single seeds. Vegetatively, the type specimen appears very similar to species of *Sebastiania*, such as *Sebastiania larensis* Croizat & Tamayo.

2. *Phyllanthus croizatii* Steyerl., Fieldiana Bot. 28: 317. 1952. TYPE: Venezuela, Yaracuy, near Taria, *Steyermark 56854* (holotype, F; isotype, US!).

The type collection represents the common weed *Phyllanthus urinaria* L., introduced from the Old World.

3. *Phyllanthus lacerilobus* Croizat, Caldasia 3: 21. 1944; Macbride, Field Mus. Nat. Hist., Bot. 13(3A,1): 41. 1951. TYPE: Peru, Loreto, Caballo-Cocha, *Ll. Williams 2378* (holotype, F).

This is a synonym of *Phyllanthus pulcher* Wall. ex Müll. Arg., an Asiatic ornamental that is occasionally planted in tropical American gardens; it has become naturalized to some extent in the West Indies (Trinidad and St. Vincent; Webster, 1958).

4. *Phyllanthus orinocensis* Steyerl., Fieldiana Bot. 28: 321. 1952. TYPE: Venezuela, Amazonas, Cerro Duida, *Steyermark 57891* (holotype, F). Probably not a *Phyllanthus*; cf. *Sebastiania*.

4. *Phyllanthus zanthoxyloides* Steyerl., Fieldiana Bot. 28: 321. 1952. TYPE: Venezuela, Monagas, Montaña de Aguacate, between Caripe and Caripito, *Steyermark 62189* (holotype, F). Perhaps a species of sect. *Hylaeanthus*.

Literature cited.

- Allem, A. A. 1977. Notas sistemáticas y nuevos sinónimos en Euphorbiaceae de América del Sur—III. Rev. Brasil. Biol. 37: 103—109.
- Baillon, H. 1858. Étude générale du groupe des Euphorbiacées. Victor Masson, Paris.
- Cordeiro, I. 1992. *Phyllanthus*, in Flora da Serra do Cipó, Minas Gerais: Euphorbiaceae. Bol. Bot. Univ. São Paulo 13: 176—183.

- Govaerts, R., D.G. Frodin, & A. Radcliffe-Smith. 2000. World Checklist and Bibliography of Euphorbiaceae. Royal Botanic Gardens, Kew.
- Grisebach, A.H.R. 1859. *Phyllanthus*. Pp. 33—35 in Flora of the British West Indian Islands. Lovell Reeve & Co., London.
- Herter,
- Howard, R. A. 1989. *Phyllanthus*. Flora of the Lesser Antilles 5: 70—81.
- Jablonski, E. 1967. Euphorbiaceae, in Botany of Guayana Highland—Part VII. Mem. N. Y. Bot. Gard. 17: 80—190.
- Lourteig, A., & C. A. O'Donnell. 1943. Euphorbiaceae Argentinae: Phyllantheae, Dalechamptiae, Couytiae, Manihoteae. Lilloa 9: 77—173.
- Müller, J. 1863. Euphorbiaceae. Vorläufige Mitteilungen aus dem für De Candolle's Prodrromus bestimmten Manuscript über diese Familie. Linnaea 32: 1—126.
- , 1866. Euphorbiaceae [except Euphorbieae] , in A. De Candolle, Prodrromus systematis naturalis regni vewgetabilis 15(2): 189—1286. Victor Masson, Paris.
- , 1873. *Phyllanthus*, in F. von Martius (ed.), Flora Brasiliensis 11(2): 23—76.
- Pax, F., & K. Hoffmann. Euphorbiaceae. Natürl. Pflanzenfam., ed. 2, 19c: 11—233.
- Punt, W. 1967. Pollen morphology of the genus *Phyllanthus* (Euphorbiaceae). Rev. Palaeobot. Palynol. 39: 131—160.
- Punt, W. 1987. A survey of pollen morphology in Euphorbiaceae with special reference to *Phyllanthus*. Bot. J. Linn. Soc. 94: 127—142.
- Santiago, L. J. M. 1988. Estudos preliminares da seção *Choretropsis* Müll. Arg., gênero *Phyllanthus* L. (Euphorbiaceae). Bradea 5(2): 44—49.
- Smith, L. B., R. J. Downs, & R. M. Klein. 1988. Monografia as Plantas Euforbiáceas. Flora Ilustrada Catarinense I Parte (EUFO). Herbário “Barbosa Rodriques,” Itajaí, Brazil.
- Webster, G. L. 1956. A monographic study of the West Indian species of *Phyllanthus*. J. Arnold Arb. 37: 91—122, 217—268, 340—359.
- , 1957. [continuation] per. cit. 38: 51—80, 170—198, 295—373.
- , 1958. [conclusion] per. cit. 39: 49—100, 111-212.

- , 1960., Supplement to a monographic study of the West Indian species of *Phyllanthus*.
J. Arnold Arb. 41: 279—286.
- , 1966. A new species of *Phyllanthus* (Euphorbiaceae) from Central America. Brittonia 18:
336—342.
- , 1967a. Tahe genera of Euphorbiaceae in the southeastern United States. J. Arnold Arb.
48: 303--430.
- , 1967b. A remarkable new *Phyllanthus* (Euphorbiaceae) from Central America. Ann.
Missouri Bot. Gard. 54: 194—198.
- , 1988. A revision of *Phyllanthus* (Euphorbiaceae) in eastern Melanesia. Pacific Science
40: 88—105.
- _____. 1991. Euphorbiaceae, Pp. 79—89 in D. H. Nicolson, Flora of Dominica, Part 2: Dicotyledoneae.
Smithsonian Contributions to Botany 77. Smithsonian Institution Press, Washington. .
- _____. 1999. *Phyllanthus*, Pp. 191—205 in P. E. Berry, K. Yatskievych, & B.K. Holst, Flora of the
Venezuelan Guayana, vol. 5. Missouri Botanical Garden Press, St. Louis.
- , 2001. A review of *Croton* and *Phyllanthus* in western tropical Mexico. Contr. Univ.
Mich. Herb.
- _____, and H. K. Airy Shaw. 1971. A provisional synopsis of the New Guinea taxa of
Phyllanthus (Euphorbiaceae). Kew Bulletin 26: 85—109.
- _____, and K. Carpenter. 2001. Pollen morphology and phylogenetic relationships in
neotropical *Phyllanthus* (Euphorbiaceae). Bot. J. Linn. Soc. (ined.).
- _____, and G. R. Proctor. 1984. A new species of *Phyllanthus* (Euphorbiaceae) from the
Cayman Islands. Rhodora 86: 121—125.