SYNOPSIS OF THE NEOTROPICAL TAXA OF *PHYLLANTHUS* (EUPHORBIACEAE)

Introduction

Phyllanthus, the largest and most diversified genus of the subfamily Phyllanthoideae (sensu Webster, 1975, 1994), includes about 200 American species, somewhat less than half the number found in the Old World. Since the revision of Müller (1866, 1873), there has been no worldwide review of the subegenera and sections, although partial treatments for the U. S. and the West Indies have been published (Webster, 1956-58, 1967, 1970).

Six of the ten subgenera of *Phyllanthus* are represented in the New World by native species, and four of the subgenera (*Cyclanthera, Conami, Botryanthus,* and *Xylophylla*) are endemic to America. In contrast, Africa has only four subgenera, none of which are restricted to that continent, while only two (*Emblica* and *Eriococcus*) of the six Asiatic subgenera are endemic. The American taxa are thus relatively more diverse at the infrageneric, rather than the species, level.

As pointed out by Bentham (1878), taxa of *Phyllanthus* show some remarkable geogrpahical distributions. Bentham noted some resemblances between West Indian and Madagascar species, which in some instances appear to reflect phylogenetic affinities. Perhaps the most striking group is the South American sect. *Gomphidium*, which appears to be related to species of subg. *Gomphidium* in Madagascar and New Caledonia. In the Mesoamerica, there are two relict taxa with extraordinary ties to the Old World: *Phyllanthus tuerckheimii* of the monotypic section *Calodictyon*, with resemblances to subgenera *Emblica* and *Gomphidium*, and *Phyllanthus harrimanii*, which belongs to the primarily Southern Hemisphere section *Lysiandra*. It seems evident that the geographical distribution patterns in *Phyllanthus* reflect a long and complex history, and much more detailed monographic work needs to be done in order to provide a credible explanation for these geographic and taxonomic relationships.

The vegetative and floral morphology in American *Phyllanthus* was discussed in detail for the West Indian species (Webster, 1956-58), and need not be repeated at length here. As in earlier works (including Webster, 1967, 1970; Bancilhon, 1971, 1985), considerable emphasis is placed on the distinction between unspecialized branching patterns (as found in subg. *Isocladus*) and *phyllanthoid branching*-- in which flowers and functional leaves are borne on deciduous branchlets. After four decades of additional study, this distinction still seems crucial in phylogenetic studies, even though there are some transitional or intermediate situations. The variations in branching pattern are succinctly described and illustrated by Bancilhon (1985).

Since the original work on the West Indian taxa, further investigations of pollen morphology (e.g. Punt, 1987) have further strengthened evidence for the systematic value of exinal and apertural structural diversity. Photographs of characteristic

pollen types are therefore included for at least one species in each of the supraspecific taxa.

In my opinion, the morphological and palynological evidence by and large supports the system of sections and subgenera proposed in 1956, in which 8 subgenera (7 native) were recognized for the West Indies. In additional to subg. *Eriococcus*, which is introduced in the neotropics, there is 1 mainly Old World subgenus found in South America (*Gomphidium*), plus 2 not represented in the New World by native or naturalized species (*Emblica, Phyllanthodendron*). This system of 11 subgenera is somewhat arbitrary and is almost certain to require modification when tested by cladistic studies using molecular data; however, at our present state of knowledge it is convenient for arranging sections and species according to their presumed closeness of affinity.

Actually, a greater problem is presented by the interrelationships between *Phyllanthus* and other genera of subtribe Flueggeinae as delimited by Webster (1994). In 1956 I commented on the artificiality of generic boundaries in this subtribe, and later (Webster, 1967) stated: "It seems fairly clear that *Glochidion* and the smaller Old World genera *Breynia*, *Sauropus*, and *Synostemon* have arisen from *Phyllanthus* subg. *Kirganelia*..." I would not now state the case in precisely those words, but it does seem evident that in the modern sense (since Bentham, 1880; Pax, 1890), *Phyllanthus* is a flagrantly paraphyletic taxon. In cladistic terms, the treatment of Müller (1866) was more defensible, since he included *Glochidion* within *Phyllanthus*; however, he left *Breynia* and *Sauropus* as independent genera. An extreme solution to this problem would be to expand the limits of *Phyllanthus* to include all of the Flueggeinae with the synapomorphy of phyllanthoid branching; however, this would result in an extraordinarily diverse genus of over 1,000 species, in many respects paralleling *Euphorbia* in degree of internal heterogeneity. The other cladistically respectable solution (not taking into account proposed alternatives of non-Linnaean nomenclature) would be to revert to the narrow generic concepts of the early and mid 19th century (such as Baillon, 1858) and recognize *Cicca, Emblica, Kirganelia*, et al., as distinct genera. Judging from the modern tendencies in generic delimitation in Cyperaceae and Poaceae, this may well be the direction of systematics of the Flueggeinae in the 21st century.

Systematic treatment

In the following synopsis, keys are provided to subgenera, sections, subsections, and species. Although species descriptions are brief and telegraphic, the detailed deads in the keys provide a reasonable amount of morphological data. Complete synonmy is given for all native American species, and is representative for introduced Old World species. Types are cited for all taxa, and new lectotypifications are indicated as such. Only a relatively small number of representative specimens are cited for each species, but at least one specimen is indicated for each major geographic entity

(contry, province, department, state, or island).
A complete list of exsiccatae is available electronically. A list of names published in *Phyllanthus* that actually belong in other genera is given at the end of the synopsis.

Synoptic key to the subgenera

1. Branching not phyllanthoid; herbs or shrubs with spiral or distichous phyllotaxy; stamens 3 (rarely 2), anthers not apiculate; pollen grains 3- or 4-colporate, or pancolporate to areolate; fruits capsular; seeds smooth or verruculose, not longitudinally ribbed..... 2.

1. Branching phyllanthoid, persistent axes with spiral phyllotaxy, lateral deciduous axes (branchlets) with distichous phyllotaxy, flowers produced only on deciduous branchlets; stamens 2-20; pollen grains various; fruits capsular, baccate, or drupaceous; seeds smooth, verruculose or ribbed..... 3.

2. Herbs or undershrubs, phyllotaxy distichous or spiral, leaves less than 2 cm long; stamens free or connate; pollen grains subglobose to prolate, 3-4-colporate or areolate; styles mostly free, bifid; seeds smooth or verrculose..... **I. ISOCLADUS**

2. Shrubs or trees, phyllotaxy spiral, leaves over 2 cm long; stamens mostly connate; pollen grains subglobose, areolate; styles connate, bifid or entire; seeds smooth.. **II. BOTRYANTHUS**

3. Pollen grains 3-colporate; stamens 3-5, free or united, ovary 2-10 locular; fruits capsular, baccate, or drupaceous; trees or shrubs, monoecious or dioecious..... **III. CICCA**

3. Pollen grains various; stamens 2-15, free or united, ovary 3-locular; fruits capsular; trees, shrubs, or herbs, mostly monoecious (rarely dioecious)..... 4.

4. Pollen grains 3-colporate, oblate or globose, rugulose, colpi often marginate or with 2 ori; mostly trees or shrubs... 5.

4. Pollen grains, if 3-colporate, globose to prolate, often tectate or areolate, usually unicolpate; trees, shrubs, or herbs..... 6.

5. Styles entire (less commonly bifid); branchlets mostly pinnatiform; leaves sometimes with apical gland.. **IV. GOMPHIDIUM**

5. Styles bifid; branchlets mostly bipinnatiform; leaves never with apical gland..... **V. CONAMI**

6. Pollen grains tricolporate, mostly prolate; anthers sometimes deeply emarginate; herbs or shrubs; seeds smooth, striate, or

ribbed..... **VI. PHYLLANTHUS**

6. Pollen grains areolate or panporate, globose; anthers not deeply emarginate; trees, shrubs, or (less commonly) herbs; seeds usually smooth..... 7

7. Pollen grains panporate; sepals lacerate [in ours]..... ..... **VII. ERIOCOCCUS**

7. Pollen grains areolate; sepals entire..... **VIII. XYLOPHYLLA**

Artificial Key to Subgenera and Distinctive Sections

1. Leaves normally developed, phylloclades not present..... 3.

1. Leaves reduced to bract-like structures, stem axes photosynthetic, expanded into phylloclades..... 2.

2. Pollen grains tricolporate; anthers sometimes deeply emarginate; branching not distinctly phyllanthoid, the phyloclades irregularly ramifying... **Subg. Phyllanthus, sect. Choretropsis.**

2. Pollen grains areolate; anthers not deeply emarginate; branching phyllanthoid..... **Subg. Xylophylla, sect. Xylophylla.**

3. Branching not phyllanthoid, the axes all persistent, leaves distichous or spiral..... 4.

1. Branching phyllanthoid, flowers and photosynthetic leaves borne on deciduous branchlets..... 5.

4. Herbs; pollen grains prolate, 3- or 4-colporate..... .....**Subg. Isocladus**

4. Shrubs or trees; pollen grains globose, areolate..... ..... **Subg. Xyllophylla sect. Botryanthus**

5. Fruits baccate or drupaceous; stamens 4 or 5, free or partially connate; pollen grains 3-colporate..... **Subg. Cicca**

5. Fruits capsular; stamens 2-15, free or connate; pollen grains various..... 6

6. Anthers completely united into a circumscissile (horizontally dehiscing) synandrium; herbs..... 7

6. Anthers not completely confluent into synandrium; trees, shrubs, or herbs..... 8

7. Dioecious; stipules indurate; column of synandrium 1 mm high or more..... *P. dimorphus* (**Subg. Phyllanthus**)

7. Monoecious; stipules not indurate; column less than 1 mm high. ..... **Subg. Conami sect. Cyclanthera**

8. Branchlets bipinnatiform (at least in part); shrubs or trees. 9

8. Branchlets pinnatiform; trees, shrubs, or herbs..... 10

9. Sepals 6; indumentum not reddish; pollen grains tricolporate... ..... **Subg. Conami**

9. Sepals 5; indumentum ± reddish; pollen grains areolate..... ..... **Subg. Xylophylla sect. Hemiphyllanthus**

10. Shrubs or trees; seeds usually more than 1.5 mm long..... 11

10. Herbs or subshrubs; seeds usually no more than 1.5 mm long.. 13

11. Sepals 4, dark red and lacerate; pollen grains panporate..... ..... **Subg. Eriococcus**

11. Sepals mostly 5-6, not lacerate; pollen grains 3-colporate or areolate..... 12

12. Leaves subtending branchlets not reduced to scales; pollen grains 3-colporate; anthers often emarginate..... ..... **Subg. Phyllanthus sect. Lysiandra**

12. Leaves subtending branchlets reduced to scales; pollen grains areolate; anthers not distinctly emarginate. **Subg. Xylophylla**

13. Annual herb; pedicels long and capillary; stamens 5, free; pistillate disk ..... **Subg. Phyllanthus sect. Pentandra**

13. Annual or perennial herbs; pedicels not long and capillary; stamens not 5 and free..... 14

14. Pollen grains areolate-banded or porate (foveolate); pistillate disk of 6-8 distinct segments..... **Subg. Cyclanthera**

14. Pollen grains 3- or 4-colporate; pistillate disk entire or

lobed, not dissected into 6-8 segments... **Subg. Phyllanthus**

Systematic treatment

Phyllanthus L., Sp. Pl. 981. 1753; Gen. Pl. LT: *P. niruri* (J. K. Small in N. L. Britton & A. Brown, Illus. Fl. N. U. S. ed. 2, 2: 453).

Niruri Adans., Fam. Pl. 2: 356. 1763. T.: *P. niruri* L.
Urinaria Medic., Malvenfam. 80. 1787. T.: *Urinaria erecta* Medicus, Malven-Fam. 80 (≡ *Phyllanthus urinaria* L.)

Diasperus Kuntze, Rev. Gen. 2: 596. 1891.

Trees, shrubs (sometimes clambering), or herbs; axes all equivalent (and phyllotaxy spiral or distichous) or differentiated into persistent orthotropic stems with spiral phyllotaxy, the axillary deciduous branchlets bearing the flowers. Leaves 0.1-50 cm long, variable in shape but always unlobed and entire, pinnately veined or triplinerved, short-petiolate, stipulate; lamina on orthotropic stems usually reduced to a cataphyll. Plants monoecious or dioecious; flowers unisexual, usually in axillary clusters (cymules), but sometimes aggregated in thyrses or panicles; cymules sometimes bisexual, with 1 ♂ and usually 2 or more ♀ flowers, but often unisexual (♀ flowers then appearing at the proximal nodes of the branchlet, ♂ flowers distal); bracts usually small, scarious. Staminate flower pedicellate or rarely subsessile; sepals mostly 5 or 6 (but sometimes 4), connate at base, entire or (in subg. *Eriococcus*) toothed or lacerate; disk nearly always extrastaminal, usually dissected into the same number of segments as the sepals, but sometimes connate in pairs or replaced by a cupular disk; stamens central, mostly 2-5 (rarely to 10 or more), filaments free or connate; anthers round to linear in outline, the connective sometimes indented or apiculate, dehiscing horizontally to vertically; pollen grains 2-nucleate, colpi mostly 3 but sometimes 4 or more, sometimes syncolpate, polyrugate, or porate; pistillode absent; pistillate flowers sessile to long-pedicellate; sepals mostly 5 or 6, usually entire, persistent in fruit; fruits capsular or less commonly indehiscent (baccate or drupate), dehiscing to leave a usually persistent columella; seeds with smooth to ornamented, dry or fleshy testa; endosperm copious, embryo with cotyledons usually broader than the radicle.

According to the tabulation of Frodin (1999), 832 species are recorded in *Phyllanthus*; it is the third largest genus of Euphorbiaceae, after *Croton* and *Euphorbia*. Infrageneric classification remains unsatisfactory, but at present the 10 genera recognized earlier (Webster, 1956) include 43 sections, of which 7 subgenera and 23 sections have native species in the New World.

Subg. I. **ISOCLADUS** Webster, J. Arnold Arb. 37: 345. 1956. T: *Phyllanthus maderaspatensis* L.

Monoecious or dioecious herbs or shrubs with spiral or distichous phyllotaxy, not producing deciduous floriferous branchlets. Calyx 5- or 6-merous; disk dissected in ♂ flowers, annular to dissected in ♀ flowers; stamens usually 3, filaments free or connate, anthers dehiscing vertically or horizontally; pollen grains 3-4-colporate (in ours); ovary 3-locular, styles bifid, free or united. Fruit a dehiscent capsule; seeds trigonous, smooth or verruculose.

Key to the neotropical sections

1. Leaves spirally arranged; stipules not conspicuously auriculate at base; fruiting pedicels not curved or deflexed. 2

1. Leaves distichous; stipules mostly auriculate at base; ovary glabrous; seeds smooth or verruculose; fruiting pedicels often bent and deflexed. **Loxopodium**

2. Pistillate disk usually dissected; seeds verruculose; pollen grains prolate, 3-colporate; ovary glabrous; style-branches ± capitate. **Paraphyllanthus**

2. Pistillate disk undivided; seeds smooth, striate, or reticulate; pollen grains subglobose, coarsely reticulate, 3- or 4-colporate; ovary glabrous or pubescent; style-branches slender. **Antipodanthus**

Sect. 1. **PARAPHYLLANTHUS** Müll. Arg., Linnaea 32: 3. 1863; Webster, Brittonia 22: 55. 1970. T: *Phyllanthus maderaspatensis* L.

Subshrubs or annual or perennial herbs; phyllotaxy spiral; stipules ± auriculate at base; sepals usually 6; ♂ flower with 6 disk-segments; stamens 3, filaments free or united, anthers dehiscing vertically; pollen grains ± prolate, 3-colporate, finely reticulate; ♀ flower pedicellate, disk dissected into 6 spathulate to obcuneate segments; ovary smooth, styles bifid to emarginate or entire; seeds verruculose.

This section is Holarctic, with 15 species mainly concentrated in Mexico and the U.S., but also occurring in Africa and India, where *Phyllanthus maderaspatensis* L. is very widespread. As here circumscribed, sect. *Paraphyllanthus* is more narrowly defined than in the artificial concept of Müller (1866), who included most species of *Phyllanthus* having 3 carpels, bifid styles, and vertically dehiscent anthers.

Species distinctions among the neotropical species of sect.

Paraphyllanthus are rather weak, and additional field observations in Mexico are needed to resolve some difficult problems.

Key to the neotropical species

1. Styles distinctly bifid (or else less than 0.5 mm long); filaments free or connate; branches smooth or scabridulous/ papillate. 2

1. Styles entire or dilated or emarginate at tip; filaments of stamens usually completely connate; branches smooth. 8

2. Branches smooth. 3

2. Branches papillate or scabridulous. 7

3. 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; stipules 0.5--1.5 mm long. 6. *P. gypsicola*

3. Leaves elliptic to obovate; styles 0.3-1 mm long; filaments 1/2 to 3/4 connate, staminal column 0.3-0.6 mm high; stipules (1-) 1.5--2.5 (-3) mm long; seeds 1.1--2.3 mm long. 4

4. Herbs with often whip-like stems clustered on a caudex. 5

4. Herbs or shrubs, not with many clustered stems. 6

5. Caudex not rhizome-like; filaments united 2/3 or more; fruiting pedicel 2.5-7 mm long; seeds 1.1-1.5 mm long. 2. *P. polygonoides*

5. Caudex rhizome-like; filaments united 1/2 way; fruiting pedicel 6--13 mm long; seeds 1.8--2 mm long. 3. *P. neoleonensis*

6. Herbaceous, usually not over 0.5 m high; leaves obtuse to rounded at base; stipules conspicuously auriculate; seeds 1.3-1.7 mm long. 1. *P. liebmannianus*

6. Shrub, often more than 0.5 m high; leaves cuneate at base; stipules scarcely auriculate; seeds 1.9-2.4 mm long. 4a. *P. peninsularis* ssp. *peninsularis*

7(2). Leaves distinctly obovate-cuneate, rounded to emarginate at apex, margins ± revolute; styles 0.3--0.7 mm long; seeds 1.5--2 mm long. 5. *P. barbarae*

7. 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. 4b. *P. peninsularis* ssp. *novogalicianus*

8(1). Leaves broadly elliptic, apiculate at apex and 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. 7. *P. galeottianus*

8. Leaves linear to obovate, rounded to apiculate at apex, acute to obtuse at base, less than 15 mm long; styles not over 1 mm long, ± free; staminal column < 1.5 mm long. 9

9. Shrub mostly 1--2 m high; leaves obovate, neither pungently tipped or falcate, 3--5 mm broad; seeds 2 mm long. 8. *P. subcuneatus*

9. Subshrubs or perennial herbs not over 0.5 m high; leaves pungently tipped or falcate, not over 2 mm broad; seeds < 2 mm long. 10

10. Leaves pungently tipped, not falcate, 0.7--1.5 mm broad; styles 0.3--0.5 mm long; seeds 0.9--1 mm long. 9. *P. ericoides*

10. Leaves falcate, not pungently tipped, not over 0.8 mm broad; styles 0.9--1 mm long; seeds 1.4--1.5 mm long. 10. *P. fraguensis*

1. **Phyllanthus liebmannianus** Müll. Arg., DC. Prodr. 15(2): 366. 1866; Webster, Brittonia 23: 57. 1970. The species includes two subspecies:

1a. **Phyllanthus liebmannianus** ssp. **liebmannianus**

Type: Mexico, *Liebmann* (C, syntypes). *Phyllanthus ferax* Standl., Publ. Field Mus. Nat. Hist. Bot. 11: 134. 1932. Type: GUATEMALA. Petén, Uacactun, *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.

Widespread in the Gulf coastal plain of Mexico, from Tamaulipas south to Oaxaca, Chiapas, and Quintana Roo; also in Belize, Guatemala; from near sea level to 1900 m, often on limestone.

Representative specimens: BELIZE. Belize Distr.: Burrel Boom, at Ferry, *Dwyer 12807* (MO); Cayo Distr.: Benque Viejo, *Dwyer et al. 258* (MO); Cohune Ridge, *Lundell 6432* (TEX); Cuevas, S of Millionario, *Croat 23548* (MO); 5 mi S of Georgeville, *Croat 23365* (MO); Macaal River, 10 mi SW of San Ignacio, *Arvigo 1987-16*

(MO). GUATEMALA. Petén: Gringo Perdido, *Walker 1166* (MO); Santa Elena, *Tún Ortiz 1763* (MO). MEXICO. Chiapas: Mpio. Pueblo Nuevo Solistahuacán, *Clarke 435* (MO); Mpio. San Fernando, Cañon del Sumidero, *Koch & Soderstrom 77289* (DAV). Hidalgo: Mpio. Huejutla, *Seler 665* (GH); Mpio. Jacala, *Chase 7068* (MO). Oaxaca: Mpio. Acatlán, Cerro Buenos Aires, Presa Temazcal, *Cortes et al. 216* (DAV); Mpio. Sta. María Chimalapa, Rio Negro, 7 km S of Santa María, *Hernández G. 998* (CAS); Mpio. Tuxtepec, Chiltepec, *Calderón 159* (MEXU). Querétaro: Mpio. Jalpan, 17 km SE of Tancoyol, *Fernández N. 2696* (NY). Quintana Roo: Mpio. Cozumel, Coba, *Lundell 7779* (MICH). San Luís Potosí: Mpio. Ciudad del Maíz, *Croat & Hannon 63051* (MO); Mpio. San Antonio, El Lejen, *Alcorn 2259* (TEX). Tabasco: Mpio. Tacotalpa, Tapijulapa, *Cowan & Zamudio et al. 3460* (DAV); Mpio. Tenosique, Retiro, *Matuda 3471A* (MICH). Tamaulipas: Mpio. Aldama, Rancho Las Yucas, 40 km NNW of Aldama, *Dressler 1936* (MICH). Veracruz: Mpio. Dos Ríos, Rinconada, *Ventura 11756* (CAS, MO); Mpio. El Palmar, *Cházaro Dorantes 158* (DAV); Mpio. Zacuapan, *Purpus 2076* (GH). Yucatán: Mpio. Hoctún, 4.5 mi SE of Tahmek, *Webster & Lynch 17575* (DAV, MEXU, TEX); Mpio. Izamal, *Gaumer 508 ex p.* (MO); Mpio. Timun, 15 km NW of Valladolid, *Cabrera 11240* (DAV).

1b. **Phyllanthus liebmannianus** ssp. **platylepis** (Small) G. L. Webster, Brittonia 22: 57. 1970. *Phyllanthus platylepis* Small, Flora S. E. United States, ed. 2, 1347. 1913. Type: UNITED STATES. Florida: Levy Co., Rosewood, 1876, *Garber* (holotype: NY!; isotype: F!).

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

This taxon restricted to a small area in northwestern Florida, although greatly disjunct from the Mexican populations of *Phyllanthus liebmannianus*, is very similar in all respects.

Representative specimens (in addition to those cited in Webster, 1970): UNITED STATES. Florida: Levy Co., 5.8-6.2 mi SW of Otter Creek, *Hansen 9649* (WIS).

2. **Phyllanthus polygonoides** Nutt. ex Spreng., Syst. Veg. 3: 23. 1826. *Maschalanthus polygonoides* Nutt., Trans. Amer. Philos. Soc. II. 5: 175. 1837. Type: "Arkansas", *Nuttall s.n.* (holotype: n.v.; isotype: NY!).

Widespread and common on limestone from Texas and Louisiana northward to Missouri, west to New Mexico; in Mexico, south to Querétaro and west to Aguascalientes and Sonora. Representative specimens from the United States are cited in Webster (1970).

Representative specimens. MEXICO. Aguascalientes: Mpio. Rincón de Romos, 6 km E of Tepezalá, *Rzedowski & McVaugh 1230* (DAV). Chihuahua: Mpio. Praxedis Guerrero: 9 mi S of El Porvenir, *Worthington & Diaz 11619* (NY); Esperanza, *Worthington & Diaz 9736* (NY). Coahuila: Mpio. Cuatrociénegas, Sierra de la Madera, *Mayfield et al. 1373* (DAV, TEX); Mpio. Melchior Muzquiz, 15 km NW of Babia, *Mayfield et al. 1415* (DAV, TEX); Hacienda La Rosita, *Wynd & Mueller 290* (NY), Rancho Agua Dulce, *Wynd & Mueller 325* (NY). Nuevo Leon: Mpio. Aramberri, 5.5 mi by road WSW of Los Caballos, *Mayfield et al. 2068* (DAV, TEX);

Mpio. Monterrey, *Palmer 1229* (NY); Mpio. Sabinas Hidalgo, 5 km S of Sabinas, *Frye & Frye 2399* (NY).
Querétaro: Mpio. Cadereyta, 4 km S of Vizarrón de Montes, *Steinmann et al. 701* (RSA); Mpio. Landa de Matamoros, 11 mi by road NE of Landa, *Webster & Breckon 16325* (DAV) San Luis Potosí: Mpio. Charcas, Minas San Rafael, *Purpus 5471* (NY). Tamaulipas: Mpio. Ciudad Victoria: 12, 14 mi S of Victoria, *Webster et al. 11245, 11259* (DAV); Mpio. Santander de Jiménez, 30 km SW of Santander, Lago Vicente Guerrero, *Nee & Diggs 24424* (DAV). Zacatecas: Mpio. Sain Alto: 40 km NW of Fresnillo, *Iltis & Lasseigne 280* (WIS).

3. **Phyllanthus neoleonensis** Croizat, J. Washington Acad. Sci. 33: 14. 1943. Type: MEXICO. Nuevo León: Monterrey, *Pringle 1388bis* (holotype: GH!).

Although of very restricted distribution in the pine and oak forests at 800-1200 m on limestone peaks above Monterrey, this species has been collected frequently, especially on Chipinque Mesa.

Representative specimens: MEXICO. Nuevo León: Mpio. Monterrey, Chipinque Mesa, *Barkley et al. 7124* (TEX), *L. I. Davis s.n.* (TEX), *Poole & Watson 1401* (TEX), *Webster & Aguirre Pequeño 2943* (TEX), *Webster et al. 11198* (DAV); La Ventana, *Smith M168* (TEX); Mpio. Santa Catarina, Sierra Anahuac, *Hinton 16908* (GH); Mpio. Santiago, Cola de Caballo, Cola de Caballo (Horsetail Falls), *Thompson 278* (TEX); Diente Canyon, *Muller 251* (TEX), *2685* (GH, UC).

4. **Phyllanthus peninsularis** Brandegee, Erythea 7: 8. 1899. Type: MEXICO. Baja California Sur: San José del Cabo, *Anthony 264* (lectotype: UC 178059!; isotype: US 313821!).

The lectotypification of *Phyllanthus peninsularis* is necessary because of confusion of specimens cited in the protologue (Webster, 2000). Two subspecies have been distinguished:

4a. **Phyllanthus peninsularis** ssp. **peninsularis**

Branches smooth; fruiting sepals 3--4.5 mm long; styles 0.5--1 (-1.3) mm. long; seeds 1.9-2.4 mm long.

Tropical deciduous forest to oak forest, near sea level to 1700 m; endemic to Baja California.

Representative specimens: MEXICO. Baja California Sur: Isla Espiritu Santo, canyon 2 km inland from Bahís Candelero, *Wiggins 16121* (MICH, US); La Laguna Mountains, *Breedlove & Axelrod 43234* (MICH), *H. S. Gentry 4374* (MO, US), *M. E. Jones 27501* (UC, US), *Moran 7340* (UC), *Nelson & Goldman 7460* (US); San Dionisio Canyon, near La Laguna, *Hrusa 8390* (DAV); La Burrera, 27 km E of Todos Santos, *Tenorio et al. 10516* (MEXU); Saucito, 1893, *Brandegee s.n.* (UC); San José del Cabo, 1891, *Brandegee 540* (UC 110167; paratype?); 1902, *Brandegee s.n.* (US 398015); *Dawson 1178* (MICH).

4b. **Phyllanthus penisularis** ssp. **novogalicianus** G. L. Webster, Sida xx: 2000. Type: MEXICO. Jalisco: Mpio. Talpa de Allende, 11--12 mi S of Talpa, 1200--1700 m, in subtropical mixed forest, *McVaugh 20390* (holotype: MICH!).

Branches papillate; fruiting sepals 2--3 mm long; styles 0.5--0.7 mm long; seeds 1.7--2 mm long.

Confined to Nayarit and Jalisco, in tropical montane moist or subdeciduous forest, 1200-1900 m. In contrast to ssp. *peninsularis*, there are no lowland records of ssp. *novogalicianus*; lowland specimens from Sinaloa resembling ssp. *novogalicianus* appear better placed in *P. gypsicola*.

Representative specimens: MEXICO. Nayarit: Mpio. Tepic, c. 15 km (airline) W of Tepic, *Steinmann & Varela 1076* (DAV). Jalisco: Mpio. Cihuatlán, Sierra de Manantlán, 30--35 km SE of Autlan, *McVaugh 23228* (MICH); 1--2.5 km SW of Rincón de Manantlán, *Judziewicz & Guzmán 5062* (MICH); Mpio. Talpa de Allende, 10--12 km N of La Cuesta, *McVaugh 23368* (MICH); 5-8 mi N of La Cuesta, *McVaugh 21307* (MICH).

5. **Phyllanthus barbarae** M. C. Johnston, Syst. Bot. 11: 35, fig. 1. 1986. Type: MEXICO. Tamaulipas: Mpio. Gómez Farias, Sierra de Guatemala, Casa Piedras, 1400-1500 m, 24 Aug. 1984, *Johnston et al. 12851* (holotype: TEX!; isotype DAV!).

Widespread on limestone, eastern slopes of the Sierra Madre Oriental, in moist oak or oak/pine forests or cloud forest, 1100--2200 m. This species has been confused with *P. subcuneatus*, but differs in its larger leaf blades (mostly 1-3 cm long), papillate branches, and distinctly bifid styles.

Representative specimens: MEXICO. Hidalgo: Mpio. Jacala, 5.2 mi S of Jacala, *Wiggins 13332* (US). Querétaro: Mpio. Jalpan, 17 km SE of Tancoyol, *Fernández 2696* (IEB); Mpio. Landa de Matamoros, 3-4 km N of Encino Solo, *Carranza 1128* (DAV); Mpio. Pinal de Amoles, 3 km S of Escanelilla, *Fernández 2382* (IEB), 1.5 km SE of San Pedro Escanela, *Fernández 2487* (IEB); 23.5 mi SW of Xilitla, *Webster & Breckon 16362* (DAV, MEX, TEX). Tamaulipas: Mpio. Gómez Farias, waterfall at Casa Piedra, 6 km NW of Gómez, *Johnston 7400* (DAV, TEX), *12769* (TEX, paratype); Rancho El Cielo, *Sharp et al. 52209* (MO); 6 mi WNW of Gómez Farias, *Johnston 12769* (TEX; paratype).

6. **Phyllanthus gypsicola** McVaugh, Brittonia 13: 194. 1961. Type: MEXICO. Colima: 11 mi SSW of Colima, in deciduous woodland with *Bursera, Juliania*, et al., 400--500 m, *McVaugh & Koelz 1573* (holotype: MICH!; isotype: DAV!).

Tropical deciduous woodland, sea level to 500 m, with one station at 1400 m, Baja California, Jalisco, and Colima.

In some ways, the distribution pattern of *Phyllanthus gypsicola*-- disjunction between Baja California and Jalisco/Colima-- parallels that of *P. peninsularis*. However, except for one station, *P. gypsicola* occurs at low elevations (500 m or less), whereas *P. peninsularis* on the mainland is recorded only from upland sites (> 1000 m). Although Brandegee confused these two species where they are sympatric near Cabo San Lucas, *P. gypsicola* seems closer to *P. galeottianus*, which it resembles in leaf shape, filaments united into a long column, and long styles.

Representative specimens: MEXICO. Baja California Sur: 14 mi by road E of Cabo San Lucas, *Hastings & Turner 64-345* (DS); San José

del Cabo, 1902, *Brandegee* (US), *Brandegee 540* (UC, US). Colima: Mpio. Colima, 15 mi SW of Colima, *McVaugh 15542* (DAV, MICH); Mpio. Comala, 19--20 km NW of Colima, *Santana et al. 5269* (WIS); Jalisco: Mpio. La Huerta, Cerro Maderas, *Lott 1823* (TEX). Sinaloa: Mpio. Los Mochis, Bahía Topolobampo, Cerros de Navachiste, *H. S. Gentry 14330* (LL, MICH, US).

7. **Phyllanthus galeottianus** Baill., Adansonia I. 1: 32. 1860. Type: MEXICO. Michoacán: Morelia, *Galeotti 7215* (lectotype: P!).
Phyllanthus americanus Sessé & Moç/. Pl. Nov. Hisp. 159. 1890. Type: MEXICO. Michoacán: Mazatlán, *Sessé & Moçiño* (lectotype: G-Del.).

Upland forests (pine-oak, tropical deciduous) and in barrancas, 1100--2200 m, transverse ranges from Jalisco to Chiapas.

Typically, *Phyllanthus galeottianus* is readily distinguished from other Mexican taxa of sect. *Paraphyllanthus* by its large leaves apiculate at the tip and emarginate at the base, by its androecium with filaments completely united into a column mostly 1-1.5 mm high, and its erect, connate, unlobed or apically dilated styles. Vegetatively it is similar to *P. gypsicola*, but occurs at much higher elevations, and clearly differs in its larger flowers and connate unlobed styles. Even at higher elevations, there are specimens that are questionably referable to *P. galeottianus*; notable among these is *Crutchfield & Johnston 6000* (MICH, TEX) from Guerrero (Mpio. Chilpancingo), which has small flowers and leaves narrowed at base. In many respects this collection resembles *P. peninsularis* ssp. *peninsularis*.

Specimens from Chiapas are distinctive in having stiff leaves and somewhat smaller reddish flowers, and could possibly be recognized as a distinct subspecies.

Representative specimens: MEXICO. Chiapas: Mpio. Amatenango del Valle, Yochib Ja', 5--7 km N of Amatenango, *Gómez López 418, 477* (TEX); Mpio. Ixtapa, near Aztlán, *Breedlove 9601* (DS); Mpio. Jitotol, road to waterfall, *Breedlove 26400* (CAS); Mpio. Las Rosas, 3 km S of Aguacatenango, *Breedlove 51396* (CAS); Mpio. San Cristóbal de las Casas, Cerro San Cristóbal, *Breedlove & Raven 13308* (DAV, MICH); Guerrero: Mpio. Coyuca, Carriceras, *Hinton 10482* (LL, MICH); Jalisco: Mpio. Guadalajara, barrancas near Guadalajara, *Holway 537* (NY), *Pringle 4443* (MICH); Mpio. Tuxcacuesco, 5--6 km ENE of Zezontla, *Santana & Benz 5922* (WIS). México: Santo Tomás, *Matuda 27115* (DAV); Mpio. Tehupilco, Luvianos, *Hinton 4497* (LL), Chorrera, *Hinton 1285* (GH, LL). Oaxaca: Mpio. Ejutla, km 71 carr. Oaxaca to Sola la Vega, *Rzedowski 21275* (TEX); Mpio. San Juan Mixtepec, 2 km S of San Juan, *Reyes Santiago 389* (MEXU).

8. **Phyllanthus subcuneatus** Greenm., Proc. Amer. Acad. Arts 33: 478. 1898. Type: MEXICO. Puebla: Tehuacán, *Pringle 6753* (holotype: GH!; isotype: UC!).

Xeric scrub on limestone, 1500--1850 m; apparently endemic to the Tehuacan Desert of southeastern Puebla and northern Oaxaca.

Representative specimens: MEXICO. Oaxaca: Mpio. Jocotipac, 6

km N of Cuicatlán and 10 km W towards Jocotipac, *Salinas & García 4856* (DAV); Nacaltepec, 6 km SE of Nacaltepec, *Salinas & Martínez Correa 6170* (CAS). Puebla: Mpio. Caltepec, Cerro de Coatepe [Santiaago Cuautepec], July 1907, *Purpus 3437* (UC); San Luis Tultilanapa, July 1908, *Purpus 3437* (NY); Mpio. Tehuacán, El Riego, *Purpus s.n.* (UC); Tehuacán, *Pringle 9389* (CAS, NY, US); Mpio. Totoltepec: 4 km N of Santa Cruz Nuevo, *Medrano et al. F-1222* (CAS).

9. **Phyllanthus fraguensis** M. C. Johnst., Syst. Bot. 10: 300. 1985.
Type: MEXICO. Coahuila, Mpio. Cuatrociénegas, SW end of Sierra de la Fragua, 1--2 km N of Puerto Colorado, *I. M. Johnston 8768* (holotype: TEX!; isotype: GH!).
This species is known only from the type collection, from a pine forest on limeston, at an elevation of > 1000 m. Johnston compared it with *Phyllanthus ericoides*, which has a similar habit but differs in its non-falcate leaves. Until _ flowers are collected, little more can be said about its relationships.

10. **Phyllanthus ericoides** Torr. in W. H. Emory, Rep. U. S. Mex. Bound. 2(1): 193. 1858. Type: MEXICO. Chihuahua: "high mountains near the Rio Grande", *Parry s.n.* (holotype: US!).
Canyons in limestone areas, west Texas and adjacent Chihuahua, c. 1000 m elevation. The species resembles *P. fraguensis* in its ericoid suffrutescent habit, and also *P. polygonoides*; however, it differs from the latter in its pungently tipped leaf blades and androecium with the filaments completely united.
Representative specimens: UNITED STATES: Texas: Brewster Co., Bullis Range, *Butterwick & Lott 3568* (TEX); Terrell Co.: San Francisco Creek, *Warnock 9849* (DAV, TEX). No additional specimens have been recorded from Mexico.

Sect. 2. **ANTIPODANTHUS** G. L. Webster, sect. nov. Ab aliis sectiones subg. *Paraphyllanthus* differt granis pollinis subglobosis, exino reticulata; disco _ integro, stylis gracilis.
T.: *Phyllanthus calycinus* Labill.
Perennial herbs or subshrubs; phyllotaxy spiral; stipules scarcely auriculate at base; sepals usually 6; _ flower with 6 disk-segments; stamens 3, filaments free or connate, anthers dehiscing vertically or horizontally; pollen grains subglobose, reticulate, 3--4-colporate; _ flowers pedicellate, disk unlobed; ovary smooth and glabrous; styles free, bifid; seeds smooth, reticulate, or verruculose.
This section of approximately 15 species is represented in the New World by 5 South American species; the other species are Australian. Section *Antipodanthus* appears to be the austral vicariant of the holarctic sect. *Paraphyllanthus*; the type species, *Phyllanthus calycinus*, from Australia, appears vegetatively similar to the North American *P. polygonoides*.

Key to the species of sect. *Antipodanthus*

1. Filaments connate; stems ± terete; seeds 2-2.6 mm. long. 2

1. Filaments free; stems decurrent-alate; stipules 2 mm long or less; dioecious; seeds 1.4-1.7 mm long. 12. *P. rosmarinifolius*

2. Stipules 3--6 mm long; dioecious; stems smooth. 3

2. Stipules 1--2.5 mm long; monoecious or dioecious; stems smooth or papillate; leaves often > 5 mm broad. 4

3. Leaves on main stems > 5 mm broad. 11. *P. dictyospermus*

3. Leaves mostly < 5 mm broad; seeds reticulate. 13. *P. pinifolius*

4. Dioecious; stems papillose; leaves strongly revolute, blunt at tip with abruptly relexed acumen; _ sepals 5. 14. *P. ramillosus*

4. Monoecious; stems smooth; leaves concave but not revolute, tapering to an acumen; _ sepals 6. 15. *P. dawsonii*

11. **Phyllanthus dictyospermus** Müll. Arg., DC. Prodr. 15(2): 394; 1866; Fl. Bras. 11(2): 58. 1873. Type: BRAZIL. Minas Geraes, *Widgren 1003* (holotype: G).
Upland vegetation, Minas Geraes.
Representative specimens: BRAZIL. Minas Geraes: Poços de Caldas, Veo da Noiva, *Santos 5712* (RB); Serra de Ouro Branco, *Damazio s.n.* (RB 78678), *Campos Porto 480* (RB).

12. **Phyllanthus rosmarinifolius** Müll. Arg., Fl. Bras. 11(2): 60. 1873. Type: BRAZIL. Rio de Janeiro, Serra do Orgaos, *Gardner 5852* (holotype: K?).
Scrub on rocks, Serra dos Orgaos, c. 2000--2150 m.
Representative specimens: BRAZIL. Rio de Janeiro: Serra dos Orgaos, *Glaziou 16330* (NY); Campos dos Antas, 2140 m, *Kirkbride et al. 1719* (NY, RB).

13. **Phyllanthus pinifolius** Baill., Adansonia I. 5: 353. 1865; Müll. Arg., DC. Prodr. 15(2): 395. 1866; Fl. Bras. 11(2): 59. 1873. Type: BRAZIL. Paraná: Curitiba, *St. Hilaire 1559o* (holotype: P; isotype, K).
Montane scrub, Espirito Santo to Minaes Geraes and Sao Paulo, 1500-2850 m.
Representative specimens: BRAZIL. Espirito Santo: Pico de Bandeira, *Irwin 2787* (UC). Minas Geraes:

Sect. **LOXOPODIUM** G. L. Webster, Contr. Gray Herb. 176: 46. 1955; J. Arnold Arb. 37: 346. 1956. T.: *Phyllanthus caroliniensis* Walt. *Geminaria* Raf., Western Minerva 42. 1821. T.: *Geminaria obovata* Raf. *Synexemia* Raf., Neogenyton 2. 1825.

T.: *Synexemia caroliniana* Raf.

Monoecious or dioecious perennial or annual herbs, sometimes suffruticose; primary axis with distichous leaves and axillary flowers, sometimes alate; stipules acuminate, ± auriculate-cordate at base, entire or denticulate; _ flowers with articulate pedicels; sepals 5 or 6; disk of 5 or 6 segments; stamens 3, filaments free or connate at base, anthers dehiscing horizontally; pollen grains oblong, 4-colporate; _ pedicel becoming ± reflexed or geniculate in fruit; sepals 5 or 6; disk entire to lobed or segmented; styles free or basally connatae, usually bifid; seeds verruculose or smooth.

This New World section of about 10 species is distinctive in its distichous phyllotaxy and scarious, often prominently auriculate stipules. It appears to be a vicariant of the Old World sect. *Macraea*, which also has distichous phyllotaxy, but differs in its polyporate pollen grains.

Key to the neotropical species

1. Monoecious. 2

1. Dioecious. 8

2. Filaments free; seeds minutely verruculose. 3

2. Filaments connate, or else seeds smooth. 5

3. Stems terete or compressed but not winged, glabrous; capsules less than 2.7 mm broad. 4

3. Stems narrowly winged, hirsutulous or scabridulous; capsules 2.8-3.2 mm broad. *P. evanescens*

4. Leaves blunt (sometimes minutely apiculate); staminate flowers in sessile glomerules. *P. caroliniensis*

4. Leaves sharply acute; staminate flowers in racemiform cymules. *P. leptocaulos*

5. Seeds smooth; filaments free; stems compressed but not winged. *P. hyssopifolioides*

5. Seeds verruculose; filaments connate. 6

6. Stems terete, not winged. *P. fallax*

6. Stems compressed and winged. 7

7. Styles distinctly dilated; seeds 1.8--1.9 mm long. *P. brandegei*

7. Styles not dilated; seeds 0.9--1 mm long. *P. compressus*

P. compressus

8. Perennials; _ flowers pedicellate (pedicels mostly > 1 mm long. 9

8. Annuals; _ flowers subsessile; leaves suborbicular; stems terete. *P. simplicicaulis*

9. Filaments free; stems strongly compressed. 10

9. Filaments connate; stems ± terete. *P. pohlianus*

10. Stipules hastate, lacerate. *P. avicularis*

10. Stipules auriculate but not hastate, entire to dentate. *P. montevidensis*