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A SYNOPSIS OF *PHYLLANTHUS* SECTION *NOTHOCLEMA* (EUPHORBIACEAE)

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Abstract: *Phyllanthus* section *Nothoclema,* after revision, includes 10 species that are notable in the genus for their use as "barbascos" (fish poisons). The section is remarkable for its palynological diversity, which provides important diagnostic characters for distinguishing species. Two new species are described, both from Venezuela: **P. liesneri** from Falcón and Yaracuy; and **P. meridensis** from Mérida. Although pollen material is lacking for study, both species appear related to congeners with 3-colporate pollen having a vermiculate-reticulate exine. *Phyllanthus graveolens* is treated as a polytypic species, including *P. micrandrus* as a subspecies. Two subspecies are recognized within *P. brasiliensis,* the species most commonly used as a fish-poison; ssp. *brasiliensis* throughout most of its range includes mostly sterile semidomesticated clones.

Keywords: Euphorbiaceae, *Phyllanthus,* subgenus *Conami,* section *Nothoclema,* Venezuela, barbascos.

INTRODUCTION

Phyllanthus, the third largest genus of Euphorbiaceae, has not been revised at the species level on a worldwide basis since the monograph of Müller (1866). About a quarter of the 800 species of *Phyllanthus* are neotropical, but only the West Indian species have been revised monographically (Webster, 1956–58). In preparation for a synopsis of all of the neotropical species, a number of revisions have appeared (Webster, 1970, 1991, 1999, 2001a, 2001b, 2002).

Phyllanthus section *Nothoclema* G. L. Webster was described (Webster, 1957) to include woody plants having compound (bipinnatiform) deciduous branchlets with axillary cymules of flowers mostly on the lateral (ultimate) axes (Fig. 1). The hexamerous flowers have a well-developed disk, and the androecia each consist of 3 connate stamens dehiscing more or less horizontally. With 10 species and 5 subspecies, it is the largest of the three sections of the neotropical subgenus *Conami* (Aubl.) Webster.

The species of section *Nothoclema* are of ethnobotanical interest because of their widespread use as fish-poisons in South America, where they are commonly referred to as "barbascos," they also have many indigenous names (Radlkofer, 1886; Acevedo-Rodriguez, 1990). Uses as a fish-poison have been recorded for three species: *Phyllanthus acuminatus, P. anisolobus,* and *P. brasiliensis* but in the Amazon region all reports of use as barbascos are based on *P. brasiliensis.* References to piscicidal species of *Phyllanthus* in the literature are confused because species delimitations and nomenclature have remained unclear. It is not surprising that a large percentage of the specimens of section *Nothoclema* in all herbaria are misidentified, because the morphological variations in foliar and floral morphology are rather subtle, and it is often difficult to identify species without flowers or fruit. Preparatory to a monographic revision of the section (Webster, ined.), this synopsis is presented here with validation of new taxa and new combinations. As treated in this new revision, 10 species are recognized, in addition to several subspecific taxa.

A notable aspect of taxonomic diversity within sect. *Nothoclema* is the striking variation in pollen morphology. As dem-

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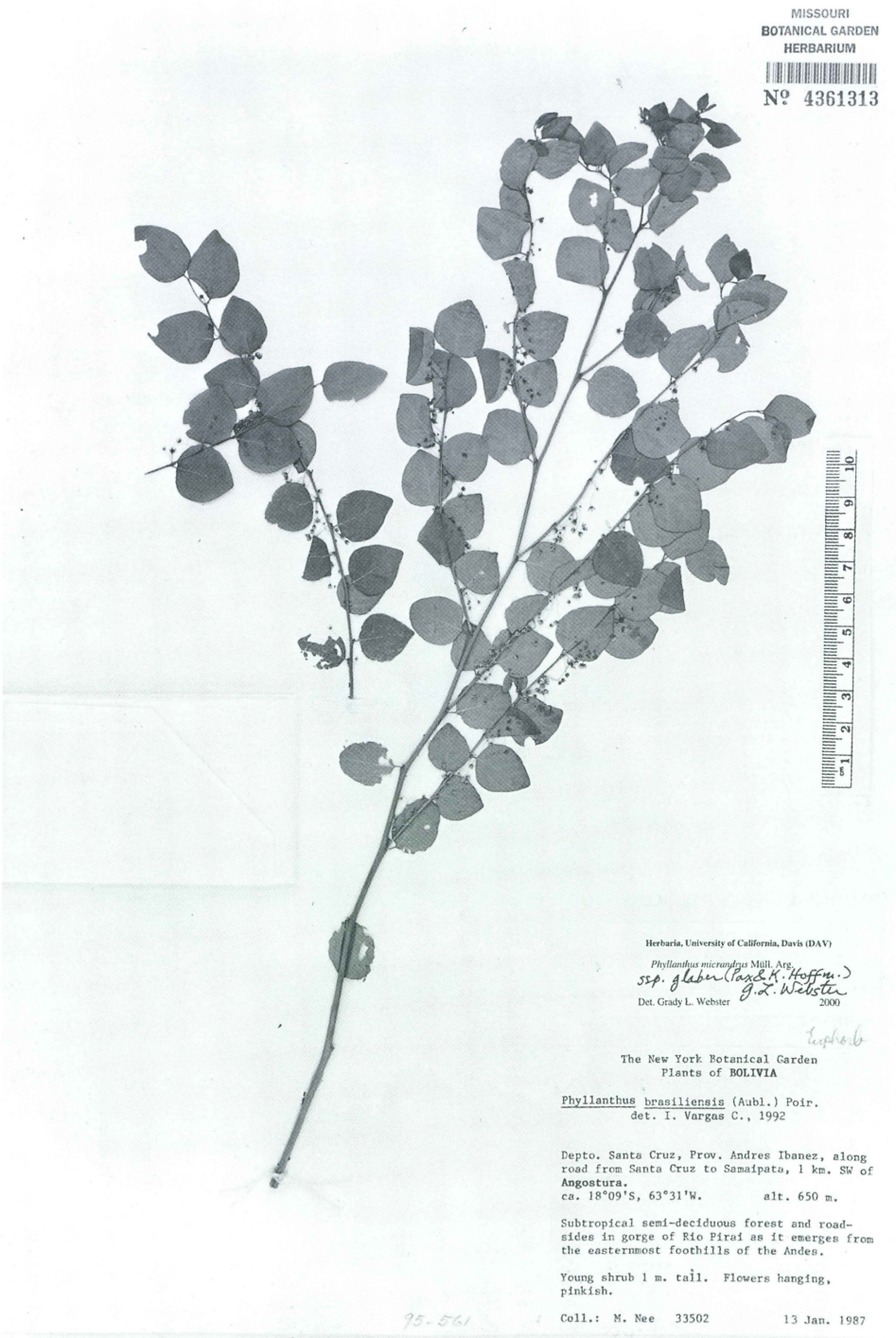


FIG. 1. Habit of *Phyllanthus brasiliensis* ssp. *glaber* (*Nee 33502,* MO).

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onstrated by Webster and Carpenter (2002), pollen grains of several species (*Phyllanthus anisolobus, P. graveolens,* and *P. mocinianus*) have tricolporate pollen grains with elongated colpi and exine sculpturing that varies from reticulate to vermiculate; two species (*P. acuminatus* and *P. mcvaughii*) have crassimarginate colpi and pilate exines; and in two species (*P. brasiliensis* and *P. pavonianus*) the pollen grains are pantoporate with pilate exines. These three palynological groups appear to be diagnostic in recognizing three clades within sect. *Nothoclema.* However, because pollen morphology has not been determined for all taxa, and the floral and palynological characters appear imperfectly correlated, formal subsections are not proposed here.

Systematic Treatment

Phyllanthus section **Nothoclema** G. L. Webster, Contr. Gray Herb. 176: 56. 1955; J. Arnold Arb. 38: 363. 1957.—Type: *Phyllanthus acuminatus* Vahl.

Monoecious shrubs or trees with phyllanthoid branching: leaves of the permanent axes reduced to cataphylls; deciduous branchlets mostly compound (bipinnatiform). Leaves of the branchlets distichous; blades chartaceous, elliptic to orbicular, entire, pinnately veined. Flowers in axillary, mostly bisexual cymules, on lateral branchlet axes and sometimes on main axes. Staminate flowers distinctly pedicellate; sepals 6, ± biseriate; disk entire to dissected; stamens 3, filaments connate, anthers dehiscing horizontally. Pollen grains spheroidal, 3-colporate or pantoporate, exine reticulate or vermiculate to pilate. Pistillate flowers pedicellate; sepals similar to the staminate; disk usually cupular; ovary 3-locular; styles mostly free or basally connate, bifid or bipartite. Fruits capsular; columella persistent; seeds trigonous, smooth or puncticulate.

Key to the Species of Section *Nothoclema*

1. Branchlets and leaves glabrous (petioles rarely sparsely scabrid or hirtellous).
   2. Branchlets simple or occasionally with 1 or 2 lateral axes; seeds smooth or nearly so.
      3. Branchlets strongly compressed-ribbed; leaf blades narrowly elliptic to obovate, cuneate at base, mostly < 1 cm broad; fruiting pedicel winged-angled, 5–7 mm long; pollen grains pantoporate, exine pilate . . . . . 10. *P. pavonianus*
      3. Branchlets angled, not ribbed; leaves ovate, rounded at base, mostly > 1 cm broad; fruiting pedicel terete, 8–12 mm long; pollen grains colporate, exine reticulate. . . . . 6. *P. caymanensis*
   2. Branchlets with 2 to 20 or more lateral axes (rarely unbranched); seeds puncticulate.
      4. Styles emarginate, erect, coherent into a column; pistillate sepals 2.5–4 mm long . . . . . 5. *P. meridensis*
      4. Styles bifid, spreading or ascending, free or basally connate; pistillate sepals 1–2.5 mm long.
         5. Bracts of cymules inconspicuous, not scarious-indurate; leaf blades obtuse or rounded at apex, mostly 1–4 × 1–3 cm.
            6. Staminal column 0.7–1.2 mm long; anthers distinctly deflexed; styles 0.7–1.1 mm long; branchlets with 5 to 10 lateral axes; veinlets of leaf blade abaxially prominulous . . . . . 1. *P. anisolobus*
            6. Staminal column < 0.7 mm long; anthers not distinctly deflexed; styles not over 0.7 mm long; branchlets with 2 to 15 or more lateral axes; veinlets of leaf blade not abaxially prominulous (except in *P. mocinianus*).
               7. Branchlets with mostly 2 to 4(–10) lateral axes; fruiting sepals 1.5–2.5 mm long.
                  8. Staminate pedicels 5–15 mm long; sepals 1.7–2.2 mm long; anthers emarginate, not compressed; seeds 1.7–2.1 mm long; veinlets of leaf blades prominulous abaxially . . . . . 2. *P. mocinianus*
                  8. Staminate pedicels 1.5–4 mm long; sepals 0.8–1.7 mm long; anthers

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acute, compressed; seeds 2.1–2.5 mm long; veinlets of leaf blades not (or scarcely) prominulous abaxially . . . . . 7. *P. mcvaughii* (glabrous form)

7. Branchlets with mostly (10–) 15 to 20 lateral axes; fruiting sepals 0.8–1.3 mm long.
   9. Leaf blades mostly broadly elliptic to suborbicular, apically obtuse or rounded; fruiting pedicels 3–20 mm long . . 3. *P. graveolens*
   9. Leaf blades mostly broadly ovate, obtuse to acute at the apex; fruiting pedicels 3–7 mm long . . . . . 9. P. *brasiliensis* ssp. *glaber*

5. Bracts of cymules pale, scarious-indurate, persistent; leaf blades elliptic to ovate, acute to breviacuminate, mostly 3–6 × 2.5–3.5 cm . . . . . 4. *P. liesneri*

1. Branchlets and leaves (at least the petioles) usually scabridulous or hirtellous.
   10. Seeds puncticulate (rarely almost smooth); staminate disk segments 3, distinct; leaves glabrous or if hirtellous (in *P. mcvaughii*) then anthers compressed, acute.
      11. Leaf blades glabrous or hirtellous; anthers compressed, acute; pollen grains colporate, exine pilate; leaves often reddish . . . . . 7. *P. mcvaughii*
      11. Leaf blades glabrous (or hirtellus, not reddish); anthers not compressed, obtuse or emarginate; pollen exine vermiculate-reticulate . . . . . 3. *P. graveolens*
   10. Seeds smooth; staminate disk segments sometimes coalescent; leaf blades hirtellous or scabrid at least adaxially.
      12. Leaf blades distinctly and abruptly acuminate, scabridulous at least on midrib and petiole, and usually abaxially; staminate disk of 3 distinct ± bilobed segments; styles spreading, ± flattened and dilated; main axis of branchlet without staminate cymules . . 8. *P. acuminatus*
      12. Leaf blades acute or cuspidate, not distinctly acuminate, hirtellous rather than scabridulous; staminate disk annular or lobed; styles ascending, subulate; main axis of branchlet often with staminate cymules . . . . . 9. *P. brasiliensis* ssp. *brasiliensis*

1. PHYLLANTHUS ANISOLOBUS Müll. Arg., DC. Prodr. 15(2): 382. 1866; Webster, Ann. Missouri Bot. Gard. 54: 229. 1968. TYPE: "Peruvia," *J. A. Pavón* (HOLOTYPE: G!). The species has not been recorded from Peru, and Pavón's specimen was doubtless collected in Ecuador.

Phyllanthus pittieri Pax, Anal. Inst. Fis.-Geogr. Nac. Costa Rica 9: 1895; in Pittier, Prim. Fl. Costaric. 2(5): 327. 1900. TYPE: COSTA RICA. CARTAGO: Cantón Cartago, Aguacaliente, *H. F. Pittier 2505* (LECTOTYPE, chosen here: B!; ISOTYPES: BR!, US!).

Phyllanthus mexiae Croizat, J. Washington Acad. Sci. 33: 14. 1943. TYPE: ECUADOR. "León" [Cotopaxi]: Cantón Pujilí, near Santa Rosa, 1000 m, Nov. 1934, *Ynes Mexia 6718* (HOLOTYPE: US!).

DISTRIBUTION AND HABITAT: Costa Rica to western Ecuador, in lowland to upland rain forest or cloud forest, 100–1700 m.

PHENOLOGY: Collected in flower April to October; in fruit July to August, November to January.

REPRESENTATIVE SPECIMENS EXAMINED: NORTH AMERICA. **COSTA RICA. Alajuela:** Cantón Naranjo, *Austin Smith P2423* (A, UC). **Cartago:** Cantón Turrialba, 6 km SE of Tuis, *Webster & Raveret 22239* (CR, DAV, MO). **Puntarenas:** Cantón Coto Brus, Finca Las Cruces, *Webster 21946* (DAV); Cantón Golfito, Osa Peninsula, *Liesner 3118* (MO). **San José:** Cantón Turrubares, Cerro Turrubares, *Grayum et al. 10533* (DAV, MO). **NICARAGUA. Matagalpa:** Quebrada Santa Cruz, *Stevens & Moreno 22325* (DAV, MO). **PANAMA. Bocas del Toro:** Dto. Chaguinola, Río Teribe, *Kirkbride & Duke 553* (MO). **Chiriquí:** Dto. Gualaca, Fortuna Dam, *McPherson 11686* (DAV, TEX). **Coclé:** Dto. Antón, El Valle de Antón, *Allen 3626* (F, MO, NY). **Darién:** Dto. Chepigania, between Cerro Mali and Cerro Tacarcuna, *Gentry & Mori 13861*

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(DAV, MO). **Veraguas:** Dto. Santa Fé, *Hernández et al. 744* (F).

SOUTH AMERICA. **COLOMBIA. Risaralda:** Mistrato, *Franco et al. 3455* (MO). **Sucre:** Colosó, *Gentry & Cuadros 68123* (MO). **Valle del Cauca:** Mpio. Buenaventura, Timbiquí, *Lehmann 9016* (K). **ECUADOR. Carchi:** Cantón Chical, *Madison et al. 4679* (QCA). **Esmeraldas:** Cantón Quinindé, Bilsa Biological Station, *Clark 374* (US), *Pitman 1148* (DAV, QCNE). **Imbabura:** Cantón Ibarra, Lita to Cachaco, *Boyle et al. 3693* (DAV, MO). **Los Ríos:** Cantón Quevedo, Rio Palenque Station, *Gentry 9918* (MO, US), *9977* (DAV, MO, Q). **Pichincha:** Cantón Quito, Bosque Protector Maquipucuna, *Webster et al. 32940* (DAV, GH, QCNE, TEX).

This species was combined with *Phyllanthus mocinianus* by Burger and Huft (1995), but is retained here as a separate species because of its morphological distinctiveness, with larger flowers, the staminal column to 1 mm high, and anthers deflexed and distinctly emarginate.

2. PHYLLANTHUS MOCINIANUS Baillon, Adansonia I. 1: 35. 1860; Müll. Arg., DC. Prodr. 15(2): 382. 1866; McVaugh, Bot. Results Sessé and Moçiño Exped. 243. 2000; Webster, Contr. Univ. Michigan Herb. 23: 383. 2001. TYPE: MEXICO. *M. Sessé & J. M. Moçiño* (HOLOTYPE: G, Delessert; *n.v.*).

Phyllanthus pringlei S. Wats., Proc. Amer. Acad. 26: 147. 1891. TYPE: MEXICO. SAN LUIS POTOSÍ: June 1890, *C. G. Pringle 3532* (HOLOTYPE: GH!).

DISTRIBUTION AND HABITAT: Western Mexico to Belize, Guatemala, and western El Salvador, in tropical deciduous or semideciduous forests or woodlands, often on limestone, 0–1200 m.

PHENOLOGY: Collected in flower May to August; in fruit August to January.

REPRESENTATIVE SPECIMENS EXAMINED: **BELIZE. Corozal:** Lowry's Bight, *Crane 202, 370, 486* (LL), *543* (TEX). **EL SALVADOR. Ahuachapán:** El Imposible, San Benito, *Sandoval JBL 1337* (MO). **GUATEMALA. Escuintla:** 2 km N of San José, *Morrison 8834* (UC). **Huehuetenango:** Quen Santo, *Seler 3088* (GH, NY, US). **Quetzaltenango:** Río Ocosito, *Donnell Smith 2622* (F, GH, US). **Retalhuleu:** 4 km W of Retalhuleu, *Standley 87448* (A, F). **Suchitepéquez:** 2–3 km N of La Máquina, *Proctor 27452* (DAV). **MEXICO. Campeche:** Mpio. Champotón, Tuxpeña, *Lundell 821* (GH, MO, UC, US, WIS). **Chiapas:** Mpio. Ocozocuautla, 8 km S of Berriozabal, *Breedlove 23071* (MICH). **Chihuahua:** Mpio. Batopilas, Batopilillas, *H. S. Gentry 2619* (A, MO, UC, US). **Colima:** Manzanillo, *Ferris 6066* (A, DS, US). **Guanajuato:** Mpio. Atarjea, Mangas Cuatas, *Ventura & López 8739* (DAV). **Guerrero:** Mpio. La Unión, El Cedral, *Langlassé 304* (GH, US). **Jalisco:** Mpio. Autlán de Navarro, 9–10 mi SW of Autlán, *McVaugh 14201* (MICH, US); Mpio. La Huerta, Estación Chamela, *Lott 534* (DAV), *1661* (US), *3671* (DAV). **México:** Mpio. Apatzingo, Sierra Nanchititla, *Hinton et al. 5330* (GH, MO, TEX, US, WIS). **Michoacán:** Mpio. Coahuayano, 8 km NW of Aquila, *Rzedowski 17923* (ENCB, MICH). **Morelos:** Mpio. Yautepec, Cañón de Lobos, *Rzedowski 12571* (ENCB), *Webster & Armbruster 20673* (DAV, MEXU). **Nayarit:** Islas Tres Marías, María Madre, *Ferris 5569* (A, DS, US); Mpio. Compostela, La Cucaracha, *McVaugh 19218* (MICH). **Oaxaca:** Mpio. San Miguel Puerto, 3 km SW of Copalita, *Torres et al. 5226* (DAV, MEXU). **Puebla:** Mpio. Tepexi de Rodríguez, 15.5 km S of Molcaxac, *Chiang & Valiente 2007* (DAV, MEXU). **Querétaro:** Mpio. Pinal de Amoles, Las Adjuntas, *Zamudio et al. 9045* (DAV). **Quintana Roo:** Isla Mujeres, *Webster & Lynch 17621* (DAV); Isla Cozumel, *Gaumer 68* (GH). **San Luis Potosí:** Mpio. Valles, 9 mi E of Valles, *Webster & Breckon 15475* (DAV, MEXU). **Sinaloa:** Mpio. Rosario, Colomos,

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Rose 1774 (GH, US). **Tamaulipas:** Mpio. Mante, Cañón del Abra, *Moore & Wood 3634* (MICH, UC, US), *Sharp 50#509* (MEXU). **Veracruz:** Mpio. Zacualpan, *Dorantes et al. 1501* (MO), *Purpus 8445* (MO, US), **Yucatán:** Mpio. Valladolid, Kanxoc, *Lundell 7609* (F, GH, TEX, US).

This is the most common species of sect. *Nothoclema* in Mexico, and tends to occur at lower and drier sites than *Phyllanthus acuminatus.*

3. PHYLLANTHUS GRAVEOLENS Kunth in H.B.K., Nov. Gen. Sp. 2: 112. 1817; Müll. Arg., DC. Prodr. 15(2): 383. 1866; Macbride, Field Mus. Nat. Hist., Bot. 13 (3A, 1): 40. 1951; Madsen et al., Fl. Puná Isl. 178. 2001. TYPE: PERU. [CAJAMARCA:] "in exustis ad ripam Chamayae et fluminis Amazonum juxta Tomependam Bracamorensium," *A. Bonpland* (HOLOTYPE: Herb. Humboldt, P!).

Phyllanthus graveolens is here delimited in a much broader sense than in the previous literature. After considerable study, it has become obvious that *P. graveolens* and *P. micrandrus* Müll. Arg. are not separable, except for a difference in indumentum. It is necessary, therefore, to reduce *P. micrandrus* to a subspecies of *P. graveolens* (the name with priority). *Phyllanthus graveolens* emerges as distinctly polytypic, with four subspecies extending from western Mexico to northwestern South America. However, it must be noted that sampling is still inadequate, and subspecific delimitations require further testing.

KEY TO THE SUBSPECIES OF *PHYLLANTHUS GRAVEOLENS*

1. Branchlets and leaves glabrous.
   2. Staminate pedicels mostly 10–15 mm long; fruiting pedicels 9–22 mm long; seeds 1.8–2.5 mm long . . . . . 3a. ssp. *micrandrus*
   2. Staminate pedicels mostly 2–4 mm long; fruiting pedicels 3–18 mm long.
      3. Seeds 1.8–2.4(–2.7) mm long; fruiting pedicels mostly 10–18 mm long; staminate sepals 0.5–1 mm long . . . . . 3b. ssp. *novogalicianus*
      3. Seeds 1.3–1.7 mm long; fruiting pedicels 4–8 mm long; staminate sepals 0.8–1.2 mm long . . . . . 3c. ssp. *benthamianus*
1. Branchlets and leaves hirtellous (rarely glabrous); staminate pedicels 5–10(–20) mm long; seeds 1.8–2.4 mm long . . . . . 3d. ssp. *graveolens*

3a. PHYLLANTHUS GRAVEOLENS ssp. **micrandrus** (Müll. Arg.) G. L. Webster, comb. & stat. nov.

Phyllanthus micrandrus Müll. Arg., Linnaea 32: 27. 1863; DC. Prodr. 15(2): 383. 1866. TYPE: VENEZUELA. [ARAGUA, Dto. Ricaurte:] Colonia Tovar, 1854–55, *A. Fendler 1195* (LECTOTYPE, designated here: G!; ISOLECTOTYPES: K!, MICH!, MO!).

DISTRIBUTION AND HABITAT: Coastal Cordillera of Venezuela, in seasonal tropical woodlands, often in gallery forests, 900–1300 m.

PHENOLOGY: Collected in flower and fruit June, July.

REPRESENTATIVE SPECIMENS EXAMINED: **VENEZUELA. Aragua:** Dto. Girardot, Parque Nacional Henri Pittier, *Steyermark 100527* (VEN); Dto. Ricaurte, SE of Colonia Tovar, *Steyermark & Liesner 131957A* (MO). **Distrito Federal:** Dto. Libertador: Las Adjuntas, *Eggers 13357* (A, F, US); Dto. Vargas, Bosque de Catuche, *Pittier 6295* (F, MO, US). **Miranda:** Dto. Sucre, Río Guarita, *Steyermark & Berry 112019* (VEN); Turgua, *Meier et al. 8618* (DAV). **Monagas:** Dto. Caripe, Cerro de la Cueva de Doña Anita, *Steyermark 61872* (US, VEN).

Subspecies *micrandrus,* as delimited here, is confined to the coastal sierras of Venezuela. In its elongated pedicels and large seeds, it approaches ssp. *graveolens,*

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from which it differs mainly in lack of pubescence.

3b. PHYLLANTHUS GRAVEOLENS ssp. **novogalicianus** G. L. Webster, subsp. nov.

TYPE: MEXICO. JALISCO: Mpio. Guadalajara, Barranca de Huentitán el Alto, 1350 m, 4 July 1990, *B. Cházaro 6260* (HOLOTYPE: MEXU; ISOTYPES: DAV!, TEX!, WIS!).

Frutex glaber, a subspeciei *benthamiano* differt pedicelis ♀ seminibusve longioribus, a subspeciei *micrandro* differt pedicelis ♂ brevioribus, a subspeciei *graveolente* differt ramulis glabris, pedicelis ♂ brevioribus.

GLABROUS SHRUB to 4 m; branchlets with mostly 10 to 15 lateral axes 7–15 cm long, with 10–20 leaves. LEAF BLADES elliptic to ovate, obtuse to acute at tip, cuneate to rounded at base, 1–3 × 2–2.5 cm. STAMINATE pedicels 2–3 mm long; sepals 6, 0.6–0.8 × 0.5–0.7 mm; disk segments 3, duplex; staminal column up to 1 mm high; anthers emarginate, ca. 0.25 mm broad. PISTILLATE pedicel 10–20 mm long in fruit; sepals 6, subequal, ca. 0.8 mm long; disk pitted, 0.7–0.8 mm across; styles bifid, 0.3–0.4 mm long. SEEDS brownish, smoothish (finely striolate), 1.8–2.4(–2.7) mm long.

DISTRIBUTION AND HABITAT: Western Mexico, tropical deciduous or semideciduous forest, 1300–1800 m.

PHENOLOGY: Collected in flower June, July; in fruit September to November.

ADDITIONAL SPECIMENS EXAMINED: **MEXICO. Jalisco:** Mpio. Guadalajara, Barranca de Huentitán el Alto, *Acevedo & Hernández 1625* (TEX), *Flores & Reynoso 1106* (WIS); Mpio. Zapopan, *Carvajal & Casillas 3365* (WIS). **Nayarit:** Islas Tres Marías, María Madre, *Ferris 5647* (DS), *5669* (A), *Howell 10452* (A, CAS); Mpio. Compostela, 4 mi N of San Juan Caxstle, *Norris & Taranto 13668* (MICH); Mpio. Tepic, 6.5 mi E of Jalcocotán, *McVaugh et al. 8929* (MICH).

Subspecies *novogalicianus* was earlier referred to *Phyllanthus micrandrus* (Webster, 2001a), and it does seem to be most similar to ssp. *micrandrus,* from which it differs in its shorter staminate pedicels.

3c. PHYLLANTHUS GRAVEOLENS ssp. **benthamianus** (Müll. Arg.) G. L. Webster, stat. & comb. nov.

Phyllanthus benthamianus Müll. Arg., Linnaea 32: 29. 1863; based on *Phyllanthus tenellus* Benth., Bot. Voy. Sulphur 165. 1846 (*nom. illeg.,* non *P. tenellus* Roxb., 1832). *Phyllanthus graveolens* var. *tenellus* Müll. Arg., DC. Prodr. 15(2): 383. 1866. TYPE: COLOMBIA. [Nariño ?], *R. B. Hinds (ex A. Sinclair) s.n.* (HOLOTYPE: K!). It seems preferable not to use the epithet *tenellus,* which is illegitimate, and rather to follow Müller in honoring the author of the name, George Bentham.

DISTRIBUTION AND HABITAT: Costa Rica to northwestern Colombia, in rain forests or seasonal forests, 0–1300 m.

PHENOLOGY: Collected in flower June to August, in fruit July to August.

REPRESENTATIVE SPECIMENS EXAMINED: **COLOMBIA. Cundinamarca:** Mpio. La Mesa, *Fernández & Mora 1383* (US); Mpio. Sasaima, *Barclay et al. 3674* (DAV). **Magdalena:** Santa Marta, *H. H. Smith 373* (F, US). **Sucre:** Mpio. Colosó, Estación de Primatos, *Gentry & Cuadros 68123* (MO). **COSTA RICA. Puntarenas:** Cantón Golfito, Osa Peninsula, Parque Nac. Corcovado, *Liesner 3118* (MO); Sirena, *Kernan 360* (MO). **San José:** Cantón San Isidro de Tarrazú, San Isidro, *Zamora et al. 1426* (DAV, MO).

Subspecies *benthamianus* is distinguished from the other three subspecies by its smaller seeds, but this character needs confirmation by additional sampling.

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3d. PHYLLANTHUS GRAVEOLENS ssp. GRAVEOLENS.

Phyllanthus millei Standl., Field Mus. Nat. Hist., Bot. 22: 87. 1940. TYPE: ECUADOR. MANABÍ: Cantón Sucre, Bahía de Caráquez, Jan. 1938, *L. Mille 1061* (HOLOTYPE: F!; photograph, AAU).

DISTRIBUTION AND HABITAT: Southern Ecuador to northern Peru, mostly in semideciduous woodlands or scrub, 100–2400 m.

PHENOLOGY: Collected in flower January, February, May, August to October; in fruit March.

REPRESENTATIVE SPECIMENS EXAMINED: **ECUADOR. Guayas:** Cantón Guayaquil, 24 km W of Guayaquil, *Dodson & Gentry 9639* (AAU, MO); Isla Puná, *Madsen 63552, 63993* (AAU), *63847* (AAU, MO). **Loja:** Cantón Gonzanamá, Gerinoma, *Pasaca 1656* (LOJA); Macará, Tambo Negro, *Harling & Andersson 18382* (AAU), *Kessler 2724* (DAV); Cantón Paltas, Catacocha to Macará, *Klitgaard et al. 399* (QCNE). **Manabí:** Cantón Jipijapa, Cerro Cabeza de Vaca, *Cornejo & Bonifaz 833* (DAV); Cantón Montecristi, Montecristi Hill, *Fagerlind & Wibom 609* (S); Cantón Sucre, Bahía de Caráquez, *Cornejo & Bonifaz 1737* (DAV). **PERU. Cajamarca:** Prov. Contumazá, Chiletes, *Brandbyge & Astholm 145* (AAU), *Sánchez Vega 197* (F), Prov. Jaén, Pucará, *Sagástegui 880, 5851* (US). **Lambayeque:** Prov. Chiclayo, Cahuageno, *Llatas 777* (MO); Prov. Lambayeque, Purculla ad Olmos, *Woytkowski 6780* (CTES, MO). **Piura:** Prov. Huancabamba, Quebrada Beatita de Humay, *López et al. 8998* (AAU, MO). **Tumbés:** Prov. Tumbés, E of Hacienda Chicama, *Weberbauer 7644* (NY, US).

Subspecies *graveolens* diverges from the other three subspecies in its hirtellous axes, but otherwise appears morphologically similar; however, in Ecuador at least it appears to occur in drier habitats than the other subspecies. In Cajamarca, Peru, both glabrous (*Sánchez 197*) and hirtellous (*Brandbyge 145*) forms occur, and the pointed leaf blades are similar to those of Peruvian populations of *P. brasiliensis.*

4. **Phyllanthus liesneri** G. L. Webster, sp. nov. (Fig. 2a, b).

TYPE: VENEZUELA. FALCÓN: Dto. Acosta, Parque Nacional de la Cueva El Toro, trail to La Piedra, 10°N, 69°07′W, 600–900 m, 22 June 1979, *R. Liesner, A. González, & R. Wingfield 7802* (HOLOTYPE: MO!; ISOTYPE: DAV!).

Frutex vel arbor 4–5 m alto, caulibus foliisve glabris laevis, ramulis lateralibus plerumque 7 ad 10; ab aliis speciebus sectionis differt foliis majoribus ovatis acutis subacuminatisve, bracteis floralibus scariosis insigniter persistentibus.

GLABROUS TREES OR SHRUBS to 5 m high; branchlets bipinnatiform, mostly 20–30 cm long; main axis 1.5–3 mm in diameter, with 5 to 10 nodes; lateral axes smooth, subterete-angled, 8–20 cm long, 1–2 mm in diameter, with mostly 8 to 10 leaves. LEAF BLADES mostly ovate (occasionally suborbicular), acute or breviacuminate, 2.5–5.5 × 2–3.5 cm; veins and veinlets slightly prominulous adaxially and abaxially; petioles 2–2.5 mm long, smooth or obscurely papillate; stipules on branchlets 1–1.5 mm long, persistent. FLOWERS in axillary bisexual cymules on branchlet lateral axes, each cymule with 1 central pistillate and 10 to 15 lateral staminate flowers; bracts scarious-indurate, pale, persistent, forming nodules 1–4 mm in diameter. STAMINATE pedicel ca. 4 mm long; sepals 6, biseriate, 1–1.5 mm long; staminal column ca. 0.5 mm high; anthers ca. 0.3 mm long. PISTILLATE pedicel 13–17 mm long in fruit; sepals ca. 1–1.5 mm long; styles free, bifid, 0.3 mm long. FRUIT capsular, ca. 4 mm in diameter; columella 2 mm long; seeds trigonous, 2.2–2.4 mm long, puncticulate.

DISTRIBUTION AND HABITAT: Northern Venezuela, semideciduous forests on limestone hills, 10–600 m.

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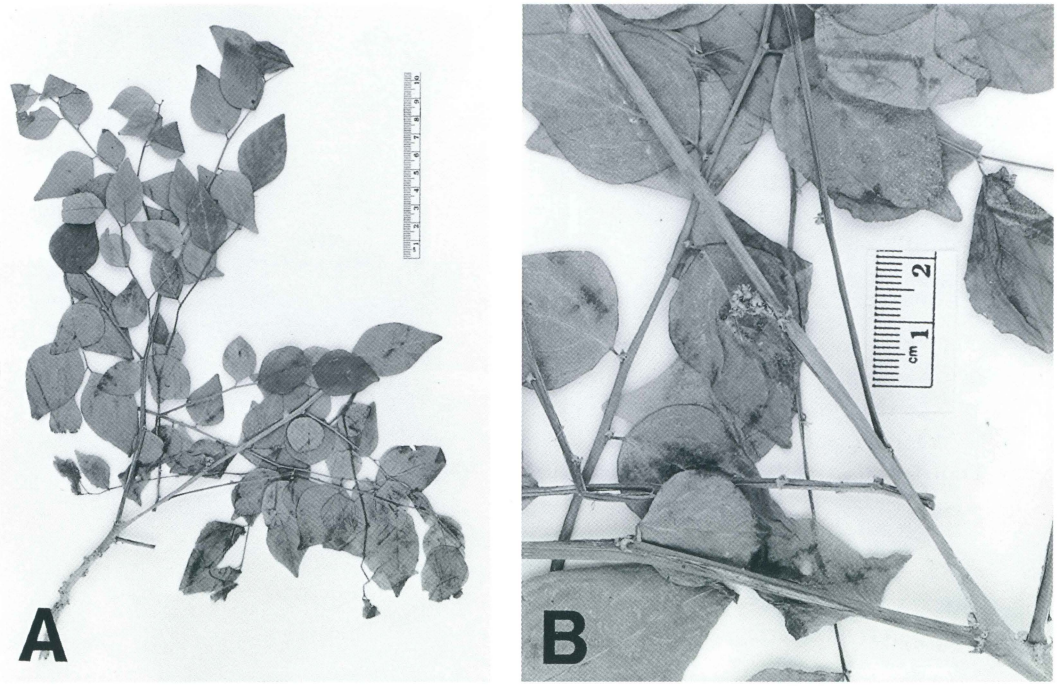


FIG. 2. Habit of *Phyllanthus liesneri* (*Liesner et al. 7780,* DAV). 2a, Branch with branchlets. 2b. Part of branchlet with node of indurated floral bracts.

PHENOLOGY: Collected in flower April, June; in fruit July.

ADDITIONAL SPECIMENS EXAMINED: **VENEZUELA. Falcón:** Dto. Acosta, Parque Nacional Quebrada de la Cueva El Toro, *Liesner et al. 7780* (DAV, MO); Dto. Silva, La Soledad, *Steyermark & Manara 110825* (VEN); Lizarde, *R. Smith V8338* (VEN); Lizarde to Mallorquines, 10–25 m, *Steyermark 110744* (VEN); Sanare, 10 m, *Webster 23576* (DAV). **Yaracuy:** Prov. Bolívar, zona El Charal, *R. Smith V9899* (MO).

This species is named for the collector of the type, Ronald Liesner, who has made many interesting collections of *Phyllanthus* in Venezuela. It appears to be closely related to *P. graveolens,* but the habit of *Phyllanthus liesneri* appears strikingly different due to its larger pointed leaves and to the persistent indurate floral bracts.

5. **Phyllanthus meridensis** G. L. Webster, sp. nov. (Fig. 3a, b).

TYPE: VENEZUELA. MÉRIDA: Dto. Arzobispo Chacón, between La Cumbre, San José, and Mucutuy, 1820–2590 m, 3 May 1944, *J. A. Steyermark 56256* (HOLOTYPE: F 1245696!).

Frutex glaber monoicus, ab aliis speciebus sectionis differt stylis subintegris erectis coherentibus, sepalis grandioribus.

MONOECIOUS SHRUBS to 3 m high; branchlets bipinnatiform; lateral axes 7 to 10, subterete, hirsutulous, 8–10 cm long, 0.7–1 mm thick, bearing ca. 10 to 15 leaves. LEAF BLADES glabrous, slightly ovate to mostly obovate or orbicular, obtuse to rounded at apex and base, 1.5–2.5 × 1.2–2.2 cm; midrib and major lateral veins 5 to 7 on a side, straightish but irregular, prominulous adaxially and abaxially; tertiary veinlets slender, not raised; petiole smooth,

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FIG. 3. Habit of *Phyllanthus meridensis* (*Steyermark 56256,* F). 3a, Type specimen. 3b. Part of branchlet with flowers.

1.5–2 mm long; stipules lanceolate-acuminate, scarious, brownish, 2.5–3 mm long. FLOWERS in mostly bisexual cymules on lateral branchlet axes; staminate flowers 5 to 10 per cymule, subtended by inconspicuous bracts. STAMINATE pedicel 4–5 mm long; sepals oblong, the larger ca. 1.7 mm long, the shorter 1.2–1.3 mm long; staminal column ca. 0.5 mm high; anthers deflexed, obtuse, ca. 0.8 mm long; disk segments 3, obcuneate, c. 0.7 mm long. PISTILLATE pedicel 10–12 mm long at anthesis; sepals broadly elliptic, the larger 3.5–4 × 2–2.5 mm, the shorter ca. 2.5 × 1.5 mm; disk cupular, pitted, rim irregularly dentate, c. 0.7 mm high, 1.7–2 mm broad; ovary smooth; styles erect, subentire (emarginate to slightly bifid distally), cohering in a column 1.3–1.5 mm high. FRUITS and seeds not seen.

DISTRIBUTION AND HABITAT: Known only from the type collection in the Venezuelan Sierra Nevada. It appears to occur at the highest elevation of any species in section *Nothoclema,* and is perhaps the only species to extend into the Matorral Andino (Ceja).

In its general facies, *Phyllanthus meridensis* appears quite similar to *P. graveolens* ssp. *micrandrus.* However, it is clearly distinct in its larger flowers, and especially in its remarkable gynoecium, quite different from that of any other species in the section.

6. PHYLLANTHUS CAYMANENSIS G. L. Webster & G. R. Proctor, Rhodora 86: 121, figs. 1, 2. 1984; Proctor, Kew Bull. Add. Ser. 11: 524. 1984. TYPE: CAYMAN ISLANDS. Cayman Brac, Foster Land District, 0.7 mi. NW of Portland Bay, ca. 30 m, 7 Aug. 1975, *G. R. Proctor 35151* (HOLOTYPE: JAM; ISOTYPES: DAV!, US!).

DISTRIBUTION AND HABITAT: Endemic to the Cayman Islands, in woodlands on rocky substrate, near sea level.

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PHENOLOGY: Collected in flower and fruit August.

ADDITIONAL SPECIMENS EXAMINED: **CAYMAN ISLANDS. Little Cayman:** N of W end of airstrip, *Proctor 35145* (JAM, US).

This is the only endemic West Indian species in section *Nothoclema,* and its relationships are unclear. Although similar to *Phyllanthus mocinianus* in its habit, prominulous leaf venation, and pollen type, it is closer to *P. mcvaughii* in its pointed anthers and it approaches *P. acuminatus* in anther form and smooth seeds.

7. PHYLLANTHUS MCVAUGHII G. L. Webster, Brittonia 18: 339, figs. 1, 7. 1966. TYPE: MEXICO. CHIAPAS: Mpio. Ixtapa, 30 mi by road E of Tuxtla Gutiérrez, 1400 m, 24 June 1962, *G. L. Webster, W. P. Adams, K. Miller, & L. Miller 11698* (HOLOTYPE: DAV!; ISOTYPES: GH!, MEXU!, MICH!, TEX!).

DISTRIBUTION AND HABITAT: Eastern Mexico (Chiapas) to Guatemala and El Salvador, mainly in oak/pine forest on limestone, 850–1800 m.

PHENOLOGY: Collected in flower July to September, in fruit September to February.

REPRESENTATIVE SPECIMENS EXAMINED: **EL SALVADOR. Morazán:** Mt. Cacaguatique, *Tucker 679* (DAV, F, UC, US). **GUATEMALA. Chimaltenango:** between Chimaltenango and San Martín Jilotepeque, *Standley 64499* (A, F, US). **Huehuetenango:** between Las Palmas and Chaculá, *Steyermark 51756* (F, GH). **Jalapa:** 2 mi E of San Pedro Pinula, *Steyermark 32993* (F). **Sololá:** Lago Atitlán, Panajachel, *Molina et al. 16264* (NY), *Webster et al. 11817* (DAV, MEXU, TEX), *Williams et al. 25333* (GH, US). **MEXICO. Chiapas:** Mpio. Chiapa de Corzo, 5.6 mi E of Chiapa, *Breedlove 10680* (MICH, US); Mpio. Cintalapa de Figueroa, 5 km W Rizo de Oro, *Breedlove 24645* (MICH, MO); Mpio. Teopisca, 5 km SW of Teopisca, *Sousa & Magallanes 6697* (UC); Mpio. Zinacantán, *Laughlin 1216* (US).

8. PHYLLANTHUS ACUMINATUS Vahl, Symb. Bot. 95. 1791; Müll. Arg., DC. Prodr. 15(2): 381. 1866; Fl. Brasil. 11(2): 42, t. 7 fig. 2. 1873; Webster, J. Arnold Arb. 38: 364, t. 23 figs. C–F. 1957; Ann. Missouri Bot. Gard. 54: 228. 1968; Fl. Nicaragua 1: 896. 2001; Burger & Huft, Fl. Costaricensis 113 (Fieldiana Bot. II 36): 142. 1995. TYPE: TRINIDAD. *J. Ryan* (HOLOTYPE: C!).

Phyllanthus lycioides Kunth in H.B.K., Nov. Gen. Sp. 2: 112. 1817. TYPE: COLOMBIA. [Bolívar] Mompox [Mompós], *F. W. H. A. Humboldt & A. J. A. Bonpland* (HOLOTYPE: P!).

Phyllanthus mucronatus Kunth in H.B.K., Nov. Gen. Sp. 2: 112. 1817. TYPE: VENEZUELA. "Provincia Caracasana," *F. W. H. A. Humboldt & A. J. A. Bonpland* (HOLOTYPE: P!).

Phyllanthus ruscoides Kunth in H.B.K., Nov. Gen. Sp. 2: 113. 1817. TYPE: VENEZUELA. [Monagas] "in sylvis prope Caripe et in devexis montis Cocollar," *F. W. H. A. Humboldt & A. J. A. Bonpland* (HOLOTYPE: P!).

DISTRIBUTION AND HABITAT: Northern Mexico and Cuba south to northern Argentina, Paraguay, and Brazil; mostly in secondary moist woodlands, gallery forests, or montane rain forests, 0–2250 m.

PHENOLOGY: Collected (Northern Hemisphere) in flower mainly May to November; in fruit July to December; (Southern Hemisphere) in flower and fruit mainly November to March.

REPRESENTATIVE SPECIMENS EXAMINED: NORTH AMERICA. **BELIZE. Belize:** Gracie Rock, *Liesner & Dwyer 1529* (GH, MO). **Cayo:** Vaca, *Gentle 2520* (MO). **Orange Walk:** Orange Walk, *Lundell 4901* (UC, US). **COSTA RICA. Alajuela:** Orotina, *Holway 327* (US). **Cartago:** Cantón Turrialba, Juan Viñas, *Pittier 3655* (US).

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Guanacaste: Cantón Liberia, 11.5 mi SE of Liberia, *Webster & Millers 12443* (DAV). **Heredia:** Universidad Nacional campus, *Unander & Poveda 1520* (DAV). **Limón:** Cantón Guácimo, 7 km NW of Siquirres, *Wilbur 20751* (GH). **Puntarenas:** Cantón Osa, 5 km E of Puerto Cortez, *Wilbur 20980* (GH, MO, US). **San José:** Cantón Turrubares, Reserva Biológica Carara, *Zúñiga & Jiménez 152* (DAV). **EL SALVADOR. Cuscatlán:** Las Pavas, *Hernández 211* (US). **San Salvador:** Tonacatepeque, *Standley 19520* (US). **GUATEMALA. Escuintla:** Finca El Baúl, *Tonduz & Rojas 74* (MO). **Izabal:** Los Amates, *Blake 7733* (US). **Petén:** Tikal, *Ortiz 478* (MO). **Retalhuleu:** San Felipe, *Donell Smith 2620* (US). **Zacapa:** Gualán, *Deam 6301* (GH). **HONDURAS. Atlántida:** Cerro Puerto Arturo, *Saunders 1056* (MO). **Comayagua:** Talauba, *Molina 13017* (US, WIS). **Copán:** Hacienda Grande to Ostuman, *Molina 24760* (US, WIS). **Lempira:** Lepaera, *Hazlett 774* (GH, MO). **Santa Bárbara:** San Pedro Sula, *Kamb 3165* (US). **Valle:** Amapala, *Rodríguez 3371* (GH). **Yoro:** Quebrada Olotillo, *Molina 6828* (GH, US). **MEXICO. Baja California Sur:** La Burrera, 27 km E of Todos Santos, *Tenorio & Romero 10506* (DAV, MEXU). **Campeche:** Mpio. Champotón, Tuxpeña, *Lundell 805* (MO, US, WIS). **Chiapas:** Mpio. Villa Corzo, *Breedlove 52041* (CAS). **Colima:** Mpio. Manzanillo, Playa Santiago, *McVaugh 15593* (MICH, US). **Guerrero:** Atoyac de Alvarez, *Hinton 14606* (US). **Jalisco:** Mpio. La Huerta, Rancho Cuixmala, *Lott et al. 3565* (DAV). **Michoacán:** Aquila, *Hinton 25965, 16109* (MICH, US), **Nayarit:** Acaponeta, *Rose 1906* (NY, US). **Oaxaca:** Mpio. San Juan Guichicovi, Mogoñe, *Orcutt 5214* (DAV). **Quintana Roo:** Cobá, *Lundell 7614* (MICH, US). **San Luis Potosí:** Tamasopo Canyon, *Pringle 3708* (UC, US). **Tabasco:** Tenosique, *Cowan & Magaña 3226* (DAV). **Tamaulipas:** Mpio. Gómez Farias, 3 km NW of Gómez Farias, *Diggs & Nee 2430* (DAV, MICH). **Yucatán:** Mayapán, *Cabrera & Cabrera 9121* (MO). **NICARAGUA. Atlántico Norte:** Siuna, *Narvaez 3180* (MO). **Atlántico Sur:** NW of Caño Angostura, *Sandino 4628B* (DAV, MO). **Carazo:** Diriamba, *Reyes 77* (MO). **Chinandega:** Los Balcones, *Moreno 11515* (DAV, MO). **Chontales:** Hac. San Martín, *Stevens 21823* (DAV, MO). **Jinotega:** Cerro Peñas Blancas, *Grijalva & Moreno 1046* (DAV, MO). **Masaya:** Volcán Masaya, *Neill 2810* (MO). **Matagalpa:** 5–10 km W of Matagalpa, *Williams et al. 23791* (MO, US). **Rivas:** Isla Ometepe, *Robleto 1014* (DAV). **PANAMA. Bocas del Toro:** Dto. Bocas del Toro, Cayo Agua, *von Wedel 870* (GH, MO). **Chiriquí:** Dto. Barú, Progreso, *Cooper & Slater 222* (US). **Coclé:** 12 mi NE of Penonomé, *Lewis et al. 1522* (DAV, MO, UC, US). **Colón:** Portobelo, *Correa & Dressler 1751* (DUKE). **Panamá:** Dto. Capira, Cerro Campana, *Duke 5978* (US), *Webster & Breckon 16522* (DAV). **Veraguas:** Dto. Santiago, between Atalaya and Santiago, *Dwyer & Kirkbride 7421* (UC).

WEST INDIES. **CUBA. Cienfuegos:** Pico Sombrero, *Webster 4769* (GH). **Habana:** Santiago de las Vegas (cult. ?), *Baker 104* (UC). **Pinar del Río:** Viñales, Palmarito, *Ekman 16624* (S). **JAMAICA. St. Mary:** Wag Water Valley, *Harris 11147* (F, JAM, NY). **TRINIDAD & TOBAGO. Tobago:** St. George, Easterfield, *Broadway 4555* (US). **Trinidad:** Chaguaramas naval base, *Webster & Miller 9957* (DAV).

SOUTH AMERICA. **ARGENTINA. Jujuy:** Dto. Ledesma, Parque Nacional Calilegua, *Bartlett 20354* (MICH, US), *Múlgara et al. 1376* (MO). **Salta:** Dto. San Ramón, Río Blanco, *Venturi 5561* (MO, UC, US). **BOLIVIA. Beni:** Prov. Vaca Díez, Cachuela Esperanza, *White 533* (A, US). **Chuquisaca:** Prov. Tomina, between Monteagudo and Sucre, *Beck 6346, Moretti 1502* (DAV). **La Paz:** Prov. Nor Yungas, Coripata, *Bang 2086* (MO). **Santa Cruz:** Prov. Florida, 6 km SW of Angostura, *Nee 48145* (MO). **Tarija:** Prov. Arce, N of Sidras, *Solomon 10141* (MO). **BRAZIL. Alagoas:** Serra Pão de Açucar, *de Lyra et al. 287* (MBM). **Bahia:** Mun. Feira de Santana, Ipiraçu, *Pedra de Cavalho 741* (BAH). **Ceará:** Mun. Pacoti,

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Serrinha, *Fernandes & Matos EAC 12061* (DAV). **Distrito Federal:** Corrego Landim, *Irwin & Wasshausen 19444* (M, MO). **Goiás:** 35 km NE of Formosa, *Irwin et al. 15697* (UB, US). **Maranhão:** Ilha São Luis, *Fróes 11816* (MICH). **Minas Gerais:** Mun. Curvelo, Gruta do Maquiné, *Heringer 7397* (U). **Pará:** Mun. Alenquer, *Ducke 4946* (RB). **Paraiba:** Areia, *Coelho de Moraes 733, 923* (US). **Pernambuco:** Mun. Vitória de Santo Antão, Tapera, *Pickel 1274* (US, WIS). **Rio de Janeiro:** Rio de Janeiro, São Cristóvão, *Glaziou 7820* (US). **Rondônia:** 100 km SW of Ariquemes, *Zarucchi et al. 2711* (DAV). **Roraima:** Porto Alegre, Rio Amajary, *Fróes 23085* (RB). **São Paulo:** Mun. Campinas, Reserva Santa Genebra, *Leitão Filho & Morellato 22894* (UEC). **COLOMBIA. Antioquia:** Mun. Anorí, Toná to Liberia, *Callejas et al. 4561* (MO, US). **Bolívar:** Cartagena, *Heriberto 375* (US). **Boyacá:** Mt. Chapon, *Lawrence 189* (MICH, US). **Caldas:** Mun. Manizales, *Zuluaga 6* (HUA). **Cauca:** La Manuelita, near Palmira, *Pittier 812* (MO, US). **Chocó:** Mun. Istmina, below Andagoya, *Forero et al. 5077* (MO). **Cundinamarca:** Mun. San Francisco, Guaduas, *Garca-Barriga 10961, 11703* (US). **Guajira:** Mun. Barrancas, Río Ranchería, *Roldán et al. 908* (MO). **Huila:** Mun. Algeciras, *Little 7511* (US). **Magdalena:** Santa Marta, 8 km E of Banda, *H. H. Smith 375* (UC). **Norte de Santander:** Sarare, La Cabuya, *Cuatrecasas et al. 12071* (US). **Putomayo:** Puerto Limón, *Plowman 2152* (US). **Risaraldo:** Mun. Mistrato, between Geguadas and San Antonio de Chami, *Fernández et al. 10018* (MO, US). **Santander:** Mun. Betulia, between Lebrija and San Vicente, *Langenheim 3170* (UC, US). **Tolima:** Mun. Espinal, Chicoral, *Haught 6343* (UC, US). **Valle del Cauca:** Mun. Buenaventura, El Papayo, *Cuatrecasas 15999* (F). **ECUADOR. Carchi:** Cantón Mira, between Ibarra and San Lorenzo, *Dodson & Thien 1566* (MO). **El Oro:** Palo Solo, *Vivar & Merino 3018* (LOJA). **Esmeraldas:** Cantón Eloy Alfaro, Comuna de Calle Mansa, *Yánez et al. 1487* (DAV, MO, QCNE). **Guayas:** Cantón Guayaquil, Reserva Faunística Churute, *Cornejo 1132* (MO, QCNE). **Loja:** Bosque Petrificado Puyango, *Cornejo & Bonifaz 5034* (LOJA). **Manabí:** Cantón Pajjón, Guale, *Haught 3063* (US). **Pastaza:** Mera, *Asplund 18602* (B, US). **Tungurahua:** Baños, *Fagerlind & Wibom s.n.* (MICH, MO). **Zamora-Chinchipe:** Cantón Chinchipe, Zumba, *Vivar & Merino 3018* (LOJA). **GUYANA. Rupununi:** between Kato and Paramakatoi, *Gillespie & Persaud 879* (US). **PARAGUAY. Amambay:** Sierra Amambay, *Hassler 11435* (MICH, MO, UC). **Gran Chaco:** Loma Clavel, *Hassler 6699* (MICH, MO). **PERU. Ayacucho:** Prov. La Mar, Ayna, *Killip & Smith 22822* (US). **Cajamarca:** Prov. San Ignacio, Mandriga, *Campos & Díaz 2423* (DAV, MO). **Cuzco:** Prov. Calca, La Quebrada, *van der Hoogte & Roersch 1819* (MO). **Junín:** Prov. Chanchamayo, La Merced, *Killip & Smith 23417* (US). **San Martín:** Tarapoto to Yurimaguas, *Rimachi 4091* (F), *5177* (MO). **SURINAME.** Suriname River, *Kappler 1688* (MO). **VENEZUELA. Aragua:** Dto. San Sebastián, Baños de San Juan de Los Morros, *Pittier 12296* (MO, US). **Barinas:** Dto. Bolívar, Barinitas, *Breteler 4238* (MO, US). **Carabobo:** Dto. Bejuma, Canoabo, *Meier & Flauger 8790, 8805* (DAV). **Cojedes:** Dto. Girardot, El Baúl, *Trujillo et al. 16589* (MO). **Distrito Federal:** Dto. Vargas, La Guaira, *Curran & Hamman 978* (US). **Guárico:** Dto. Roscio, San Juan de los Morros, *Meier & Elsner 6145* (DAV). **Lara:** Dto. Palavecino, Sanare, *Div. Ejuc. Progr. 5* (MY). **Miranda:** Dto. Acevedo, E of Caucagua, *Berry 920* (MO). **Monagas:** Dto. Maturín, W of Jusepin, *Seigler 1110* (DAV). **Portugesa:** Dto. Araure, Camburito, *Ortega & Aymard 1722* (MO). **Táchira:** San Cristóbal, *Archer 3210* (US). **Trujillo:** Dto. Boconó, SW Agua Fría, 550 m, *Dorr et al. 8503* (DAV, US). **Zulia:** Dto. Mara, Destacamento Guasare, *Bunting & León 12574* (MO).

Phyllanthus acuminatus is the commonest and most widespread species of sect. *Nothoclema,* but it shows remarkably little

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geographic variation in morphological characters. Although it has been confused by collectors with *P. brasiliensis,* pollen characters indicate a closer relationship with the Central American *P. mcvaughii* (Webster & Carpenter, 2002).

9. PHYLLANTHUS BRASILIENSIS (Aubl.) Poir. in Lam., Encycl. 5: 296. 1804; Müll. Arg., DC. Prodr. 15(3): 383; Fl. Brasil. 11(2): 44. 1873. *Conami brasiliensis* Aubl., Hist. Pl. Guiane 2: 926, t. 354. 1775. *Phyllanthus conami* Sw., Prodr. 28. 1788 (as to type only). *Conami conami* (Sw.) Britton, Bot. Porto Rico 5: 475. 1924. TYPE: GUIANE FRANÇAISE. *Aublet* (HOLOTYPE: BM!).

The delimitation of *Phyllanthus brasiliensis* in botanical literature has been difficult for both taxonomic and nomenclatural reasons. Swartz (1788, 1800) introduced confusion that lasted for two centuries by describing *P. conami,* derived from Aublet's name but based on a description of *P. acuminatus.* As a consequence, the name *P. brasiliensis* has been misapplied to specimens of *P. acuminatus* by authors into the 20th century (e.g., Standley & Steyermark, 1949). Müller (1866, 1873) avoided that confusion but recognized three species, *P. brasiliensis, P. piscatorum,* and *P. pseudoconami,* for populations in the Brazilian Amazon, where only a single species is accepted in the present treatment.

The delimitation of *Phyllanthus brasiliensis* is further complicated as far as populations from Bolivia are concerned. The Bolivian highland populations have been assigned to *P. graveolens* by Pax and Hoffmann, but except for lack of indumentum appear to have many of the characteristics (especially in pollen morphology) of *P. brasiliensis.* Consequently two subspecies of *P. brasiliensis* are recognized here.

KEY TO THE SUBSPECIES OF *PHYLLANTHUS BRASILIENSIS*

1. Branchlets and flowers mostly hirtellous; ovary glabrous to hirtellous; main branchlet axis with or without staminate cymules; seeds rarely produced; widespread in Amazon lowlands . . ssp. *brasiliensis*
1. Branchlets and flowers (including ovary) glabrous; main branchlet axis usually lacking staminate cymules; seeds commonly produced; uplands of Bolivia . . . . . ssp. *glaber*

9a. PHYLLANTHUS BRASILIENSIS ssp. BRASILIENSIS.

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: 90, 113. 1817. TYPE: VENEZUELA. [Amazonas] "cataractum Aturensium," *F. W. H. A. Humboldt & A. J. A. Bonpland* (HOLOTYPE: Herb. Humboldt, P!).

Phyllanthus pseudo-conami Müll. Arg., Fl. Brasil. 11(2): 43. 1873; var. *glaber* Müll. Arg., ibid. TYPE: VENEZUELA. AMAZONAS: San Carlos, *R. Spruce 3016* (HOLOTYPE: Herb. Martius, M).

Phyllanthus pseudo-conami var. *pubescens* Müll. Arg., Fl. Brasil. 11(2): 43. 1873. TYPE: PERU. [LORETO]: Yurimaguas, *Poeppig 2758* (LECTOTYPE, selected here: W!).

DISTRIBUTION AND HABITAT: Amazonian lowland forests from Colombia and Venezuela south to Peru, Brazil, and northern Bolivia, 10–500(–1000) m; introduced to the West Indies from Trinidad to Guadaloupe (Webster, 1957, 1991).

PHENOLOGY: Collected in flower throughout the year; in fruit (rare) April, June, July, October.

REPRESENTATIVE SPECIMENS EXAMINED: WEST INDIES. **LESSER ANTILLES. Dominica:** Grand Bay, *Eggers 662* (GH, GOET, L, US, W), *Imray s.n.* (GOET). **Guadeloupe:** Matouba, *Duss 212* (P), *2446* (GH, MO, US); Grande Terre, *L'Herminier s.n.* (A, P); St. Claude, *Quentin 527* (F), *Stehlé 63* (A); Trois-Rivières, *Quentin 671* (P). **Martinique:** Ajoupa-Bouillon, *Duss 2047*

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(NH); St. Pierre, *Belanger 294* (G, P). **Tobago:** Valencia Road, *Baker* (TRIN 14864). **Trinidad:** without locality, *Ryan* (C).

SOUTH AMERICA. **BOLIVIA. Beni:** Prov. Gral. José Ballivian, NE San Borja, *Oviedo 41* (DAV). **BRAZIL. Acre:** Mun. Cruzeiro do Sul, *Penereiro 11063* (UEC); Mun. Manoel Urbano, *Silveira 1520* (DAV, NY); Mun. Santa Rosa, *Daly et al. 9913* (MO); Mun. Tarauacá, *Ehringhaus et al. 378* (DAV). **Amapá:** Amapá, *Ducke* (MG 4840). **Amazonas:** Mun. Barcelos, *Prance & Ramos 23616* (MO, U); Mun. Boca do Acre, Bom Lugar, *Goeldi* (MG 3978); Mun. Manaus, *Fróes 20521* (US); Mun. Sta. Isabel do Rio Negro, *Prance et al. 15556* (F, MG, U, US); Mun. Umarituba, Rio Xió, *Fróes 20521* (F). **Pará:** Mun. Belém, Jardim Botânico, *Ducke 1261* (MG, RB, US); Mun. Breves, *Black 48-3019* (NY). **Roraima:** Mun. Boa Vista, Auaris, *Prance et al. 21351* (MG, U). **COLOMBIA. Amazonas:** La Chorrera, *Schultes 3898* (AAU, GH). **Boyacá:** Mun. Chiscas, *Cuatrecasas 13030* (US). **Caquetá:** La María, *Hermann 11233* (COL, US). **Putumayo:** Mocoa, *Archer 3416* (COL); between Puerto Asís and Puerto Leguízamo, *García-Barriga et al. 18702* (US). **Vaupés:** Jinogojé, *Schultes & Cabrera 16832* (GH); confluence of Río Vaupés and Río Kubiyú, *Soejarto & Lockwood 2432* (F, HUA). **ECUADOR. Napo:** Cantón Archidona, *Mexia 7246* (U, US); Cantón La Hoya de los Sachas, *Baker et al. 5981* (MO); Cantón Tena, Ahuano, *Rios & Vivanco 375* (QCA); Jatun Sacha, *Cerón 1140* (QCA); E of Puerto Napo, *Webster & Richerson 28494* (DAV, MO, QCA, QCNE). **Orellana:** Cantón Aguarico, Nuevo Roacafuerte, *Alarcón 101* (QCA); Cantón Orellana, San Pablo de los Secoyas, *Brandbyge & Asanza 32853, 32941* (AAU). **Pastaza:** Cantón Pastaza, near Puyo, *Skutch 4441* (MO, US), *Webster 23170* (DAV, MO, Q, TEX, WIS). **Sucumbíos:** Cantón Lago Agrio, Shushufindi, *Vickers 45* (F); Cantón Putumayo, Puerto El Carmen, *Andrade 33115* (AAU). **GUIANE FRANÇAISE:** Dégrad Kaw, rivière Cainama, *Oldeman B-775* (NY, U); Rivière Orapu, *Moretti CM1046* (U). **GUYANA. Essequibo:** Kabakaburi, *Hoffman & Roberts 2466* (DAV, TEX). **Northwest:** Koriabo River, *Archer 2355* (US); Moruka River, Mora Landing, *de la Cruz 962* (US). **PERU: Huánuco:** Prov. Huánuco, Cerros del Sira, *Wolfe 17193* (F); Tingo María, *Belshaw 3068* (F, LL, MICH, MO, UC, US); Prov. Leoncio Prado, Dto. Rupa Rupa, *King & Ramírez 350* (F, MO); Dto. Puerto Inco, *Seiderschwarz 3774* (F). **Loreto:** Prov. Alto Amazonas, Balsapuerto, *Klug 2913* (MO, US); Yurimaguas, *Poeppig 2758* (W); Pongo de Manseriche, *Mexia 6253* (TEX, UC, US); Prov. Maynas, Intuto, *McDaniel 10841* (DAV, MO); Prov. Coronel Portillo, Bosque Nacional von Humboldt, *Díaz & Aronson 736* (DAV, F, MO); Pongo de Canarachi, *Ule 6408* (MG, RB). **Madre de Díos:** Prov. Manú, Cocha Cashu Station, *Foster 9847* (MO); Prov. Tambopata, Barosola, *Vargas 18704* (MO, US). **San Martín:** Prov. Lamas, Distr. Alonso de Alvarado, *Schunke 9725* (AAU, DAV, F, MO); Prov. Mariscal Cáceres, Juan Jui, *Klug 3806* (F, MO, US); Prov. Moyobamba, Rioja, *Woytkowski 6063* (MO); Rioja to Pedro Ruíz, *van der Werff et al. 15480* (DAV, MO); Prov. San Martín, Pucacaca, *Zegarra 9* (NY); Tarapoto, *Spruce 4939* (NY). **SURINAME. Nickerie:** Sipaliwini, *Oldenburger et al. 1275* (BBS, MG, NY, U). **Saramacca:** between Voltzberg and Ralegh Vallen, *Webster 24145* (DAV, U). **VENEZUELA. Amazonas:** Dto. Atabapo, Culebra, *Pérez & Sosa JPB-602* (MO), *Steyermark & Delascio 129155* (MO); base of Duida near Culebra, *Liesner 17878* (DAV); S of San Juan de Manapiare, *Berry 1605* (MO); Dto. Casaquiare, Río Guainía, *Williams 14800* (F); Dto. Río Negro, San Carlos de Río Negro, *Spruce 3016* (W); Tamatama, *Williams 15865* (F, RB, US). **Anzoátegui:** Dto. Cedeño, Sta. Marìa de Erebato, *Steyermark et al. 109862* (F); Dto. Freites, Bajos del Rìo Tigre, Cristovero, *Pittier 14822* (UC, US). **Bolívar:** Dto. Roscio, Mata Negra, S de El Tigre, *Williams 13392* (F, US).

Subspecies *brasiliensis* is the most widespread taxon in sect. *Nothoclema* after *P.*

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acuminatus, and is the main plant used in South America as a fish poison. Examination of specimens across the Amazon basin has shown that except for southern Ecuador and northern Peru, nearly 100% of the plants in the rest of the distribution produce no fruits and seeds. Apparently most populations of ssp. *brasiliensis* represent sterile clones that have been cultivated by indigenous peoples in a semi-domesticated state.

9b. PHYLLANTHUS BRASILIENSIS ssp. **glaber** (Pax & K. Hoffm.) G. L. Webster, stat. & comb. nov. (Fig. 1).

Phyllanthus graveolens var. *glaber* Pax & K. Hoffm., Meded. Rijksherb. Leiden 40: 18. 1921. TYPE: BOLIVIA. SANTA CRUZ: between Santa Cruz and Río Piraí, *T.K.J. Herzog 1338* (LECTOTYPE: W!; chosen here to replace destroyed holotype at B).

Phyllanthus ichthyomethius Rusby, Mem. N. Y. Bot. Gard. 7: 282. 1927. TYPE: BOLIVIA. EL BENI: Prov. Gral. José Ballivian, Rurrenabaque, *White 886 ex p.* (HOLOTYPE: NY!; ISOTYPES: K!, MICH!, US!).

DISTRIBUTION AND HABITAT: Bolivia, upland subtropical forests from southern Dpto. El Beni to Dptos. Santa Cruz and Tarija, 300–700 m.

PHENOLOGY: Collected in flower and fruit October, November.

REPRESENTATIVE SPECIMENS EXAMINED: **BOLIVIA. La Paz:** Prov. Sud Yungas, Alto Beni, San Miguel de Huachi, *White 886 ex p.* (US); Sapecho, *Seidel 2788* (DAV); Santa Ana de los Mosetenes, *Hinojosa & Bozo 1056, Hinojosa & Huasang 1146* (DAV). **Santa Cruz:** Prov. Andrés Ibañez, 1 km SW Angostura, *Nee 33502* (MO); Río Salado, *Nee 38047* (U); Río Pirai, Jardín Botánico, *Nee 30480, Zuloaga et al. 1425* (MO); 6 km NW Santa Cruz, *Solomon 13841* (MO); Prov. Florida, 4.5 km ENE La Guardia, *Nee 45943* (TEX); Pro. Ichilo, Río Surutú, *Steinbach 7315 bis* (MO); 4 km NW Buena Vista, *Nee 39061* (MO). **Tarija:** Prov. Arce, 2 km NW Bermejo, *Nee 46166* (TEX).

The resemblance of Bolivian specimens of ssp. *glaber* to the glabrous populations of *Phyllanthus graveolens* is so apparent that Pax and Hoffmann's attribution was not unreasonaable. However, the discovery that the pantoporate pollen grains with pilate exine are nearly indistinguishable from those of ssp. *brasiliensis* (Webster & Carpenter, ined.) justifies the taxonomic disposition made here.

The choice of *glaber* as subspecific epithet is undesirable because of the prior var. *glaber* used by Müller (1873) for his *Phyllanthus pseudoconami* var. *glaber*; even though Müller's name is illegitimate, it could lead to confusion. However, use of Rusby's *P. ichthyomethius* as the basis of a name is also undesirable. Specimens from El Beni and La Paz have a distinctly different leaf shape from those in Santa Cruz and Tarija departments, and furthermore, it appears that *P. ichthyomethius* is apparently founded on a mixed collection. The description and the holotype at NY cited Rurrenabaque, in El Beni, as the location; but the label on the sheet at US indicates Huachi in La Paz as the locality. It appears possible that *White 886* may include plants collected at two locations over 100 kilometers apart! Although it would be acceptable to create an entirely new epithet at the subspecific rank, it appears that the least unsatisfactory alternative is to use Pax and Hoffmann's epithet as the basionym of the subspecies.

The differences between the northern and southern populations of ssp. *glaber* suggest that the taxon might eventually be subdivided even further. However, until further sampling can be done, it appears best to refer all of the non-Amazonian Bolivian specimens to ssp. *glaber.*

10. PHYLLANTHUS PAVONIANUS Baill., Adansonia I. 1: 30. 1860; Müll. Arg., DC.

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Prodr. 15(2): 380. 1866; Macbride, Field Mus. Nat. Hist., Bot. 13 (3A, 1): 44. 1951. TYPE: PERU. *J. A. Pavon 314* (LECTOTYPE, designated here: Herb. Lessert, G!).

Phyllanthus oxycladus Müll. Arg., Linnaea 32: 26. 1863. TYPE: *Herb. Pavon* (LECTOTYPE, designated here: G-Boiss.). The data provided by the *Flora Huayaquilensis* (Estrella, 1989) suggest that the type specimens for both species names were collected at Colonche, Prov. Guayas, Ecuador, by Juan Tafalla, in 1801 (not far from the type locality of *P. haughtii*). However, the illustration in *Flora Huayaquilensis* (lamina CLXXI) appears more similar to *P. anisolobus.* Apparently the type locality of *P. pavonianus,* as suggested by Estrella (and verified by L. Holm-Nielsen) is correct, but was mistakenly associated with a different illustration.

Phyllanthus haughtii Croizat, Caldasia 3: 22. 1944. TYPE: ECUADOR. GUAYAS: Cantón Pedro Carbo, 15 km W of Pedro Carbo, 17 Jan. 1940, *O. Haught* (HOLOTYPE: GH!; ISOTYPES: K!, US!; photograph, AAU).

DISTRIBUTION AND HABITAT: Southern Ecuador and northwestern Peru, in deciduous shrubbery along banks of intermittent streams, 200–1500 m.

PHENOLOGY: Collected in flower January, February, April; in fruit January, August.

ADDITIONAL SPECIMENS EXAMINED: **ECUADOR. El Oro:** Cantón Arenillas, Quebrada Los Zábalos, 330 m, *Cornejo & Bonifaz 4077* (DAV); Cantón Zaruma, between Guishahuina and Curtincapa, Río Luis, 850 m, *Steyermark 5381* (AAU, NY). **Loja:** Cantón Catamayo, Quebrada Grande, Gerinoma, 1500 m, *Pasaca 1656* (LOJA); Cantón Puyango, Mercadillo, between Celica and Alamor, *J. F. Smith 1971* (MO). **PERU. Piura:** Prov. Huancabamba, 900–1000 m, *Weberbauer 6019* (GH, US). **Tumbés:** Prov. Contralmirante Villar, mountains E of Hacienda Chicama, 700–800 m, *Weberbauer 7664* (NY, US).

Because of its elongated leaf blades and ribbed-compressed branchlet axes, *Phyllanthus pavonianus* is one of the most morphologically distinctive species in sect. *Nothoclema.* However, the pantoporate, pollen grains with pilate exine are very similar to those of *P. brasiliensis.*

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