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A REVISION OF *PHYLLANTHUS* SECTION *HYLAEANTHUS* (EUPHORBIACEAE)

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Abstract: A revision of *Phyllanthus* sect. *Hylaeanthus* (subg. *Conami*) treats seven species, mostly with a primarily Amazonian distribution, as well as one species of uncertain affinity. The section is characterized within subgenus *Conami* by a tendency to dioecy, unramified branchlets, distinctive pollen grains with pilate exine ornamentation, and indehiscent fruits with sarcotestal seeds. Two species are described as new: *Phyllanthus puntii* from western Brazil (Acre) and Bolivia, and *P. awaensis* from northern Ecuador. Two new subspecies of *Phyllanthus attenuatus* are described: *P. a. ssp. incarum* from western Amazonia in Ecuador, Peru, and Colombia; and *P. a. ssp. tucuruensis* from Amazonian Brazil. *Phyllanthus manausensis* is reduced to a synonym of *P. madeirensis*. A key is provided to help distinguish specimens of taxa in sect. *Hylaeanthus* from superficially similar but unrelated species of other subgenera of *Phyllanthus*.

Keywords: Euphorbiaceae, *Phyllanthus*, subgenus *Conami*, sect. *Hylaeanthus*, sect. *Nothoclema*, sect. *Pityrocladus*.

INTRODUCTION

Among the woody South American species of *Phyllanthus*, there is one distinctive group that has long failed to receive formal recognition. Müller (1866, 1873) assigned the most widespread species, *P. attenuatus* Miq., to his sect. *Euphyllanthus*, but considered the plant to represent Aublet's genus *Meborea*; he consequently incorrectly treated *P. attenuatus* as a synonym of *P. guianensis* (Aubl.) Müll. Arg. Lanjou (1931) convincingly demonstrated that Müller was mistaken, and Radcliffe-Smith (2001) has correctly observed that *Meborea guianensis* Aubl. is indeed a species of *Phyllanthus* (*P. aubletianus* Radcl.-Sm.). Section *Hylaeanthus* was finally described by Web-

ster (2002) as one of three sections of subg. *Conami* (Aubl.) G. L. Webster.

Most of the species of sect. *Hylaeanthus* are rain forest trees with tall slender trunks (up to 45 m high and 10–20 cm in diameter). The vegetative habit of unramified (pinnatifid) branchlets differs from most species of sect. *Nothoclema*, in which the branchlets are compound (bipinnatifid). In foliar characteristics, species of sect. *Hylaeanthus* are often extraordinarily similar to some species of sections *Pityrocladus* (subgenus *Emblia*) and *Elutanthos* (subgenus *Xylophylla*). The following key, emphasizing vegetative characters, may be helpful in distinguishing the superficially similar species of *Phyllanthus* in the Amazonian region.

KEY TO WOODY AMAZONIAN INTRAGENERIC TAXA OF *PHYLLANTHUS*

1. Branching phyllanthoid (leaf blades subtending branchlets reduced in size or scale-like), or apparently so; penultimate axes lacking flowers (or branchlets compound).
2. Branchlets mostly compound; fruits dehiscent, seed coat not fleshy. . . Subg. *Conami* sect. *Nothoclema*
2. Branchlets simple or paired; fruits dehiscent or indehiscent, seed coat dry or fleshy.
3. Foliar midrib incised; leaf blades acute to obtuse or rounded at base; plants not scandent.
4. Fruits indehiscent, columella not persistent; seed coat fleshy; flowers in glomerules, these sometimes pedunculate; leaf blades shiny and smooth adaxially; veinlets abaxially $\pm$ scalariform; trees commonly over 10 m high (to 45 m). Subg. *Conami* sect. *Hylaeanthus*

4. Fruits capsular, seed coat dry; flowers in clusters at several nodes of a brachyblast or thyrses; leaf blades adaxially rather dull or minutely roughened; veinlets abaxially not prominently scalariform; trees or shrubs, usually less than 10 m high. Subg. *Xylophylla*
5. Branchlets with 20 leaves or more; leaf blades acuminate. sect. *Asterandra*
5. Branchlets with 10 leaves or less; leaf blades obtuse to rounded at tip. sect. *Brachycladus*
3. Foliar midrib raised; leaf blades broadly rounded to truncate at base; fruits capsular; trees or shrubs, sometimes scandent, less than 10 m high. Subg. *Emblica* sect. *Pityrocladus*
1. Branching not phyllanthoid, leaves subtending ultimate axes not reduced to scales Subg. *Xylophylla* sect. *Elutanthos*

SYSTEMATIC TREATMENT OF SECT. *HYLAEANTHUS*

PHYLLANTHUS sect. *HYLAEANTHUS* G. L.
Webster, Novon 12: 293. 2002. TYPE:
Phyllanthus attenuatus Miq.

MONOECIOUS OR DIOECIOUS SHRUBS OR TREES up to 45 m high; branches $\pm$ lenticellate; branchlets pinnatifid, usually subtended by smaller leaves (but generally not reduced to cataphylls), axes terete, glabrous or pubescent, not (or scarcely) lenticellate, with distichous leaves. LEAF BLADES glabrous or pubescent, elliptic or ovate to lanceolate, mostly acute or acuminate, pinnately veined, brochidodromous; midrib incised adaxially; prominently raised abaxially; lateral veins arching, $\pm$ prominulous adaxially, distinctly prominulous abaxially; adaxial surface usually smooth and shiny; abaxial surface paler, often minutely punctulate; petiole terete, often rugulose; stipules lanceolate, persistent or deciduous. INFLORESCENCES glomerulate, axillary, unisexual (rarely bisexual); glomerules sessile or pedunculate; bracts indurate, persistent. STAMINATE flowers pedicellate; sepals 6 (rarely 5), usually in two whorls; disk-segments discrete or more often coalesced into a 6-lobed disk; stamens 3, filaments free (in *P. skutchii*), coherent or connate; anthers dehiscing horizontally to obliquely; pollen grains spheroidal, lacking distinct ectocolpi, exine heterogeneously pilate. PISTILLATE flowers pedicellate; sepals 6, discrete; disk patelliform to cupular; ovary 3- to 6-locular (2-locular in *P. awaensis*); styles free or connate, bifid or unlobed.

FRUITS indehiscent, exocarp fleshy or coriaceous; seeds with sarcoexotesta, exotegmen hard and smooth.

Sect. *Hylaeanthus* includes seven species of mainly South American distribution (with one species in Costa Rica); an additional Venezuelan species, *Phyllanthus bernardii* Jabl., may also belong to the section. Within subgenus *Conami* (Aubl.) G. L. Webster, sect. *Hylaeanthus* is distinguished by unramified branchlets and indehiscent fruits with sarcotestal seeds. The distinctive pilate exine ornamentation of the pollen grains (Webster and Carpenter, 2002, Figs. 9, 10) separates the species of sect. *Hylaeanthus* from most other woody taxa of *Phyllanthus*. Pollen grains of some taxa of sect. *Nothoclema* are similar, but in that section the fruits are dehiscent and the branchlets mostly bipinnatifid. Vegetatively, some of the species of sect. *Hylaeanthus* are similar to Amazonian species of the neotropical sect. *Elutanthos* (subg. *Xylophylla*). However, in that section the pollen grain exine is clypeate (synrugoidorate) and the fruits are dehiscent.

As noted by Meewis and Punt (1983), pilate pollen exines occur in other species of *Phyllanthus*, notably in the West African *P. dinklagei* Pax, which Brunel & Roux (1977) have referred to sect. *Brazzeani* in subg. *Conami*. Based on published descriptions, sect. *Brazzeani* morphologically resembles sect. *Hylaeanthus* in some respects, although it differs in its 5-merous perianth, discrete staminate disk-segments, and free stamens of unequal lengths. Because of these floral differences, it appears likely that

the similarities in pollen exine sculpturing between species of sects. *Hylaeanthus* and *Brazzeani* represent an instance of convergence rather than a close phylogenetic relationship, as suggested by Punt (1986).

The staminate flowers are so similar in most species of sect. *Hylaeanthus* that they offer few useful diagnostic characters; staminate specimens often can only be determined with certainty by using vegetative characteristics. The pistillate flowers, however, show considerable variation in stylar structure and number of carpels, although this morphological diversity can sometimes be erratic and difficult to interpret. The number of locules in the ovary, although often 3 or 4, may sometimes be 5 or 6; only *P. callejasii* G. L. Webster and *P. awaensis* G. L. Webster seem to be strictly 3-locular and 2-locular respectively (and that may reflect inadequate sampling). Unfortunately, the number of ovary locules is quite variable within species or even individuals, so that carpel number is sometimes of limited utility as a diagnostic character. Perhaps the most important diagnostic floral feature is that of the configuration of the styles, which are erect and subentire in *P. awaensis* and *mad-eirensis*; erect and bifid in *P. puntii* and *P. skutchii*; but bifid and more or less spreading in the other species. The indehiscent fruits and fleshy seeds are rather similar in all species, although there are some differences in size. The sarcotesta of the seed is usually elongated considerably beyond the hard ex-

otegmen. Because of the variability in size of the fleshy tissue, seed measurements have been limited to the exotegmen.

A characteristic feature of the inflorescence in sect. *Hylaeanthus* is its contraction into glomerules with scarious bracts that often become indurated in pistillate specimens. These glomerules terminate a stout peduncle that varies in length in different species. In the widespread *Phyllanthus attenuatus* ssp. *attenuatus*, the peduncle is usually contracted (1 mm or less in length) or even totally suppressed, but in *P. attenuatus* ssp. *incarum* and most other species, the peduncles may become as much as 4 mm long or more. However, the rather erratic variation in peduncle length is an obstacle to using the character for separating taxa.

The sectional epithet *Hylaeanthus* was chosen to indicate the prevalent distribution of the species in lowland Amazonian rain forest; only one species, *Phyllanthus skutchii* Standl., occurs in Mesoamerica (Costa Rica). However, two species, *P. awaensis* and *P. callejasii*, grow in montane forests mainly above 1,000 m. The distribution map of the taxa (Fig. 1) has been prepared from a data base (Microsoft Access) that includes geographical coordinates of more than 95% of the specimens cited. Many of the determinations of elevation have been obtained from the *Ornithological Gazetteer of Brazil* by Paynter and Traylor (1991, and earlier issues for other South American countries).

KEY TO THE SPECIES OF *PHYLLANTHUS* SECT. *HYLAEANTHUS*

1. Leaf blades acuminate to acute (acumen sometimes obtuse); branchlet axes glabrous to hirtellous; ovary 3- to 6-locular.
 2. Leaves completely glabrous (rarely with vestigial trichomes at base); plants often monoecious.
 3. Styles bifid; filaments of stamens free or basally connate; flowering glomerules sessile or subsessile (peduncle < 1 mm long); leaves acuminate or abruptly acute, not micropunctulate abaxially.
 4. Styles bifid, erect, coherent in a column that is persistent in fruit as a beak 1–1.5 mm long; filaments of stamens free; pistillate sepals 2.5–3.8 mm long in fruit; leaf blades lanceolate-acuminate (acumen c. 1 cm long), 8–10-veined. 1. *P. skutchii*
 4. Styles discrete, bipartite, not forming a beak in fruit; filaments of stamens basally connate; pistillate sepals < 2 mm long in fruit; leaf-blades elliptic, abruptly acute (acumen ≤ 0.5 cm long), 5–7-veined. 7. *P. valleanus*
 3. Styles unlobed, spreading, discrete, not persistent as a beak in fruit; staminate and pistillate glomerules

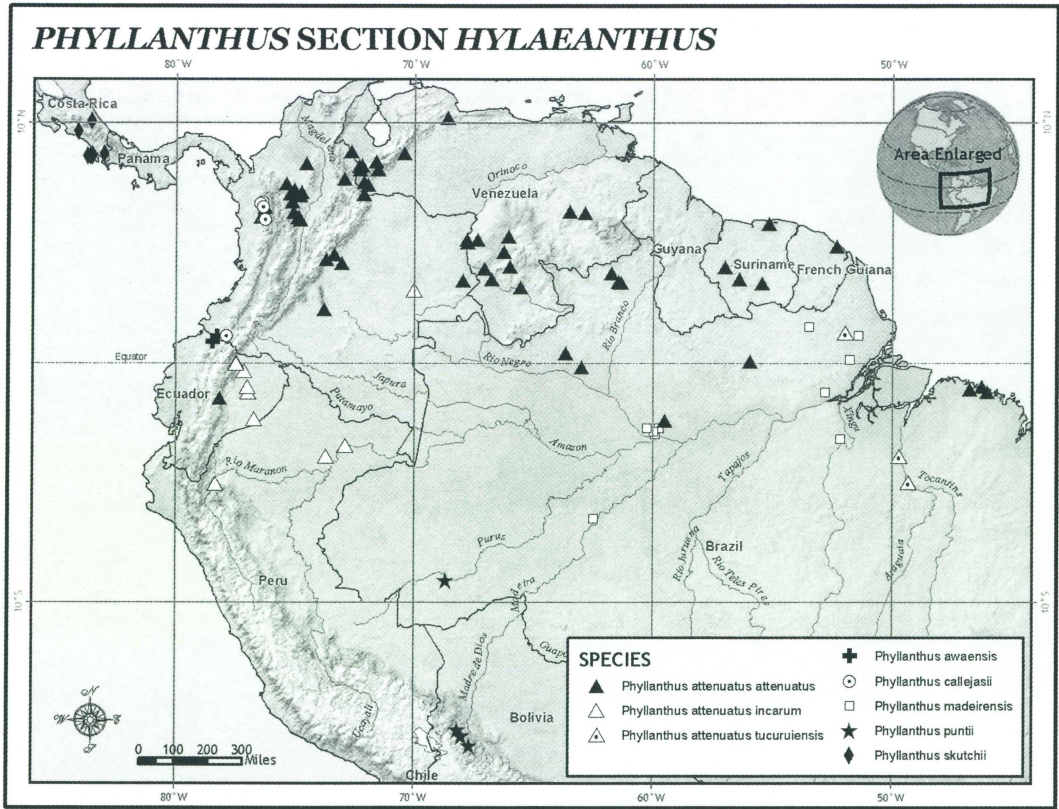


FIG. 1. Distribution of species of *Phyllanthus* sect. *Hylaeanthus*.

- pedunculate (1.5–3 mm long); filaments of stamens connate; pistillate sepals < 2 mm long in fruit; leaf blades obtuse to acute, mostly 3–6 cm long; abaxial leaf surface distinctly micropunctulate. 5. *P. madeirensis*
2. Leaves hirtellous at least adaxially on petiole and adjacent proximal midrib; plants mostly dioecious.
5. Branchlet axes and adaxial leaf surface glabrous (rarely sparsely hirtellous); leaf blade vein lets (tertiaries) prominulous adaxially, often irregular, not scalariform and perpendicular to midrib; fruiting pedicels glabrous, 3–10 mm long.
6. Styles bifid, spreading; plants monoecious or dioecious.
7. Fruiting pedicels 1.5–3 (–7) mm long, fruiting sepals not more than 2 mm long; styles bifid or bipartite, spreading, discrete; leaf blades lanceolate, prominently acuminate (acumen mostly 1–1.5 cm), mostly 5–8 cm long, abaxial surface not microreticulate. 2. *P. attenuatus*
7. Fruiting pedicels 3–10 mm long; fruiting sepals 2.5–4 mm long; styles twice-bifid; fruits 7–9 mm in diameter; styles connate into a distinct column c. 1.5 mm high; leaf blades ovate to elliptic, apiculate or breviacuminate, 7–13 cm long, abaxial leaf blade surface microreticulate/striate. 3. *P. callejasii*
6. Styles unlobed, erect or ascending; plants monoecious. 8. *P. bernardii*
5. Branchlet axes and abaxial leaf surfaces distinctly hirtellous; leaf blade veinlets (tertiaries) not prominulous adaxially, fruiting pedicels hirsutulous, 3–6 mm long. 4. *P. puntii*
1. Leaf blades rounded to obtuse at tip; branchlet axes finely scabridulous; ovary 2-locular. . . 6. *P. awaensis*
1. **PHYLLANTHUS SKUTCHII** Standl., Publ. 1940; Burger & Huft, Fieldiana II. 36: 146, Field Mus. Nat. Hist., Bot. Ser. 22: 346. fig. 25. 1995. TYPE: **COSTA RICA**. Prov.

San José, Valle del El General, June 1939, A. F. Skutch 4325 (HOLOTYPE: F!; ISOTYPES: K!, NY!, S!). (Figs. 1, 2a, 4a).

MONOECIOUS OR DIOECIOUS TREES, glabrous, 8–45 m high, trunk c. 0.2–1 m in diameter; bark fissured; branchlets mostly 15–30 cm long, 0.9–1.6 mm in diameter, with 10–20 leaves. LEAF BLADES elliptic-lanceolate, acuminate (acumen c. 1 cm long), $6\text{--}9 \times 2.5\text{--}3.5$ cm, with 8–10 lateral veins; petiole mostly 3–5 (6) mm long; stipules lanceolate-acuminate, 1–1.5 mm long, persistent. FLOWERS in axillary usually unisexual glomerules, the staminate sessile at proximal axils with 20–30 flowers; the pistillate short-pedunculate (1–1.5 mm), with (1–) 5–10 flowers, at distal axils. STAMINATE pedicel 2.5–5 mm long; sepals 6, broadly-ovate to elliptic, outer sepals $1.4\text{--}1.7$ mm $\times$ c. 1 mm, inner sepals $1.2\text{--}1.4 \times 1.1\text{--}1.2$ mm; disk cupular, ± 12 -lobed, c. 1 mm in diameter; stamens 3, filaments free, 0.3–0.4 mm long; anthers truncate-emarginate, broader than long, c. 0.25×0.30 mm. PISTILLATE pedicel (3–) 4–6 mm long; sepals $1.5\text{--}2.5 \times 1.2\text{--}1.7$ mm; disk crenulate, c. $0.3 \times 0.8\text{--}1$ mm; ovary 4- or 5-locular; styles erect, thickened and connivent, apically bifid, persisting in fruit as a beak 1–1.5 mm high. FRUITS 5–7 mm in diameter, greenish; seed tegmen basally $\pm$ truncate, reddish-brown, 3–5 mm long; hilum 1.2 mm long.

DISTRIBUTION AND HABITAT: Costa Rica, mainly in tropical rain forest, 20–900 m; possibly to be encountered in western Panama.

PHENOLOGY: Collected in flower May; in fruit January, June, October, November. The label of *Poveda* 709 indicates that the plant was completely leafless in October.

ADDITIONAL SPECIMENS EXAMINED: COSTA RICA. **Limón:** Cantón Guácimo, Moravia de Siquierres, c. 200 m, $10^{\circ} 05' \text{ N}$, $83^{\circ} 33' \text{ W}$, *Poveda* 709 (MO); Reserva Indígena Cocles Talamanca, 3–4 km SW of Pto. Viejo, 100 m, $9^{\circ} 38' \text{ N}$, $82^{\circ} 46' \text{ W}$, *Jiménez et al.* 799 (F). **Puntarenas:** Cantón Golfito, between Bahía Chal and Punta Camíbar, 100 m,

$8^{\circ} 44' \text{ N}$, $83^{\circ} 00' \text{ W}$, *Aguilar* 746 (DAV, F); Parque Nacional Corcovado, Quebrada Vaquedano, 500 m, $8^{\circ} 39' \text{ N}$, $83^{\circ} 35.5' \text{ W}$, *Herrera* 3993 (DAV); Cantón Osa, Osa Peninsula, Agua Buena Oeste, 50 m, $8^{\circ} 42' \text{ N}$, $83^{\circ} 31' \text{ W}$, *Aguilar* 1411 (DAV, TEX); Osa Peninsula opposite Golfito, 20–200 m, $8^{\circ} 38' \text{ N}$, $83^{\circ} 11' \text{ W}$, *Schmidt* 594 (DAV); Playa Campanario, Sierpe, 1–10 m, $8^{\circ} 39' \text{ N}$, $83^{\circ} 43' \text{ W}$, *Harmon* 189 (MO). **San José:** Valley of El General, 675–900 m, *Skutch* 5427 (F, US), 5491 (DAV, F).

Burger and Huft (1995) have provided an excellent description of *Phyllanthus skutchii*. Their reported dimensions of the seeds are much larger than those recorded here, apparently because they included the sarcotesta in their measurements. *Phyllanthus skutchii* differs from all the other species of sect. *Hylaeanthus* in its staminate flowers with discrete stamens and (except for *P. puntii*) its pistillate flowers with erect styles connate into a column.

2. *PHYLLANTHUS ATTENUATUS* Miq., *Linnaea* 21: 479. 1848; Stirp. Surinam. pl. 30. 1850. Lanjouw, *Euphorb. Suriname* 8, 107, t. II. 1931; Jablonski, *Mem. New York Bot. Gard.* 17: 113. 1967; Webster, *Fl. Venez. Guayana* 5: 196, fig. 182. 1999. TYPE: **SURINAME:** without locality, *F. W. R. Hostman & A. Kappler* 305 (HOLOTYPE: L; ISOTYPES: K, W!). (Fig. 1).

DIOECIOUS SHRUB OR TREE 5–12 m high; branches cylindrical, smooth and glabrous, lenticellate; branchlets 10–20 (–30) cm long, 0.8–1.5 mm in diameter, cylindrical, smooth and glabrous, sparingly lenticellate, with 8–15 (–20) leaves. LEAF BLADES ovate-oblong or elliptic, abruptly acuminate (acumen 0.5–1 cm long), pinnately veined, glabrous or hirtellous on base of midrib adaxially, often punctulate abaxially; petiole 2–4 mm long, hirtellous (very rarely glabrous); stipules lanceolate-acuminate, 1.3–2.2 mm long, deciduous or persistent. FLOWERS glabrous, greenish, in axillary subsessile or pedunculate glomerules, the staminate flowers 20–40 per node, the pistillate 3–10 (rarely 1 or 2 or up to

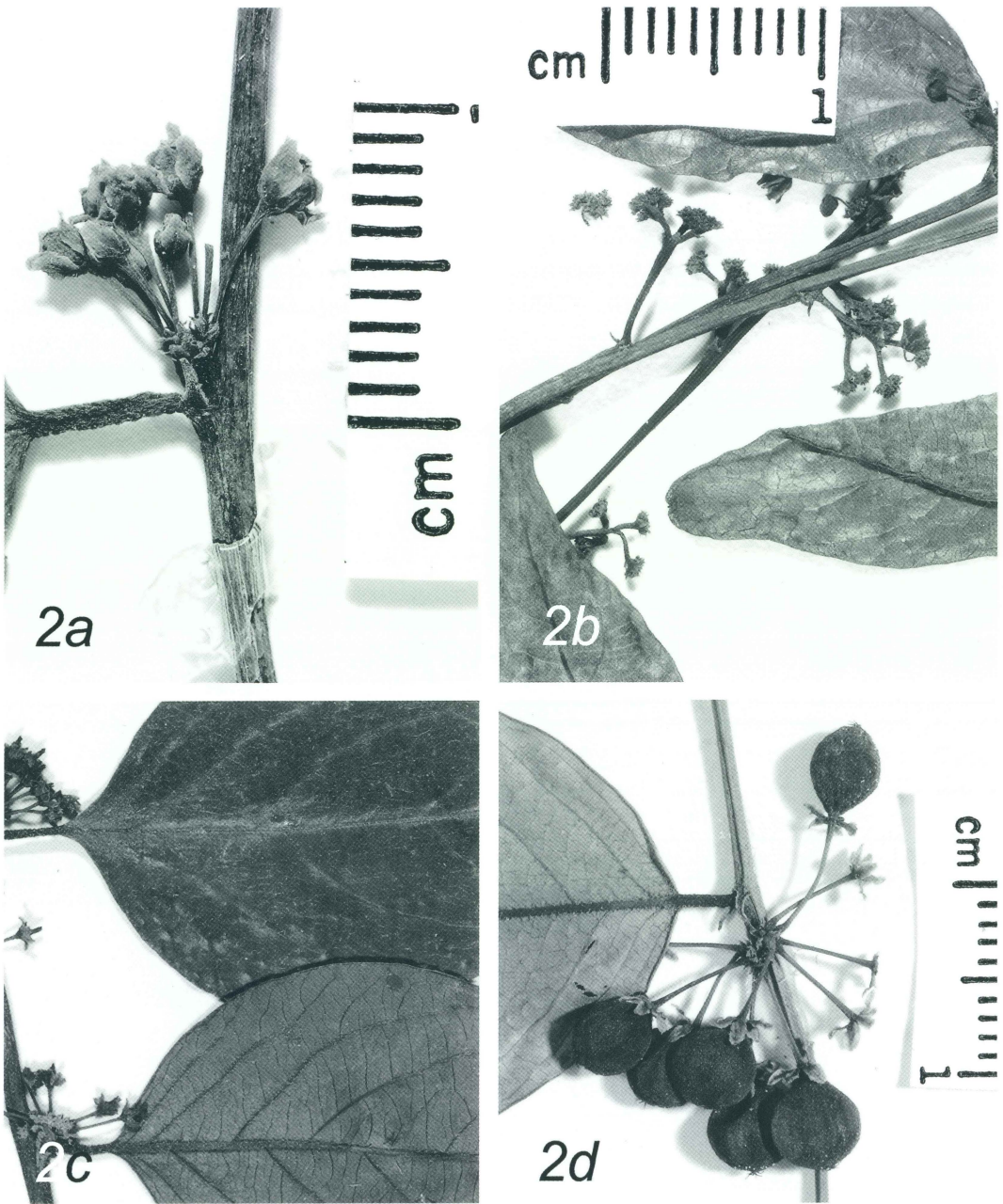


FIG. 2. Flowering and fruiting glomerules of species of *Phyllanthus* sect. *Hylaeanthus*. a–c. Flowering glomerules. a. *P. skutchii* (Skutch 5427), glomerules sessile; b. *P. attenuatus* ssp. *attenuatus* (Cárdenas & Ramírez 2577), variant with glomerules pedunculate; c. *P. punctii* (Prance et al. 7712); d. Fruiting glomerule: *P. attenuatus* ssp. *incarum* (Palacios 2095).

20) per node. STAMINATE pedicel (1.5–) 2–3 mm long; sepals 6, elliptic, acute, 0.8–1.5 × 0.3–0.6 mm; disk 6-lobed, 0.5–1 mm in diameter; stamens 3, filaments connate into a column 0.3–0.5 mm high; anthers muticous, dehiscent horizontally, 0.2–0.3 mm long, androecium 0.5–0.6 mm in diameter. PISTILLATE pedicel becoming 2.5–9 mm long in fruit; sepals elliptic, 0.8–1.7 × 0.8–1.3 mm; disk patelliform or cupular, 1–1.2 mm in diameter; ovary 3- to 6-locular; styles 1–1.3 mm long, basally connate, bifid, branches acute. FRUITS 4–7 mm in diameter; seed tegmen c. 3.5–5 mm long, hilum subterminal/lateral.

Phyllanthus attenuatus is the commonest and most widespread species in sect. *Hylaeanthus*, but due to a mistaken identification by Müller (1866, 1873) it was for

nearly a century erroneously considered to be the plant that Aublet described as *Meborea guianensis*. Lanjouw (1931) pointed out the error, but was undecided as to the affinities of *Meborea*. Radcliffe-Smith (2001) has correctly placed *Meborea guianensis* Aubl. in *Phyllanthus* as *P. aubletianus* Radcl.-Sm.; that species apparently belongs to *Phyllanthus* sect. *Elutanthos* (subgenus *Xylophylla*).

Three subspecies are recognized within *Phyllanthus attenuatus*, of which *P. a.* ssp. *attenuatus* is the most widespread—from northern Brazil and the Guianas to Colombia and northern Ecuador. It is replaced by *P. a.* ssp. *tucuruensis* in the Tocantins watershed in Pará and by *P. a.* ssp. *incarum* in Amazonian Colombia, Ecuador and Peru.

KEY TO THE SUBSPECIES OF *PHYLLANTHUS ATTENUATUS*

1. Branchlet axes glabrous (except sometimes for a few hairs near nodes); pistillate pedicels glabrous, 2.5–9 mm long.
 2. Leaf blades glabrous abaxially except for the midrib (rarely sparsely hirtellous on proximal part of blade); peduncles of glomerules mostly 1 mm long or less; fruiting pedicels 2–4 mm long; ovary mostly 3- or 4-locular. 2a. *P. a.* ssp. *attenuatus*
 2. Leaf blades abaxially hirtellous on midrib and secondary veins; peduncles of glomerules 1–3 mm long; fruiting pedicels 4–7 mm long; ovary mostly 5- or 6-locular. 2b. *P. a.* ssp. *incarum*
1. Branchlet axes hirsutulous; pistillate pedicels glabrous or hirsutulous, 1.5–3 mm long; ovary mostly 5- or 6-locular. 2c. *P. a.* ssp. *tucuruensis*

2a. *PHYLLANTHUS ATTENUATUS* ssp. *ATTENUATUS*. (Figs. 1, 2b, 3a).

Dioecious (rarely monoecious) TREES; branchlets glabrous; LEAF BLADES glabrous except abaxially near junction with petiole; STAMINATE GLOMERULES usually sessile or subsessile (peduncle mostly ≤ 1 mm long); staminate pedicels 2–4 mm long; pistillate flowers mostly 2–7 (–15) per node; fruiting pedicel glabrous (rarely hirtellous distally), 2–4 mm long; fruiting sepals (1.2–) 1.4–1.8 (–2.1) mm long; ovary 3- or 4- (rarely 5-) locular; seed tegmen (2–) 2.5–3.5 (–4) mm long.

DISTRIBUTION AND HABITAT: Northern South America and the Amazon basin, mostly 0–1000 (–1600) m in terra firma rainforests, sometimes in inundated forests (varzea).

PHENOLOGY: Collected in flower and fruit throughout the year, with a peak in July.

ADDITIONAL SPECIMENS EXAMINED. **BRAZIL.** **Amazonas:** Mun. Barcelos, margem do rio Aracá, poco abaixo da foz do Rio Jauari, 00° 25' N, 63° 25' W, *Cordeiro* 250 (DAV, MO, NY); Mun. Manaus, Dto. Agropecuario, 90 km NNE Manaus, 50–125 m, c. 2° 24.5' S, 59° 44' W, *Oliveira et al.* 269 (DAV); São Luís, 00° 10' S, 63° 00' W, *Alencar* 149 (NY), *Maia* 148 (MO). **Maranhão:** Mun. Carutapera, 5 m, 1° 13' S, 46° 01' W, *Froes* 2028 (A, NY). **Pará:** Mun.

Alenquer, Parque Indígena do Tumucumaque, Rio Pará do Oeste, Missão Tiriós, 450 m, 00° 05' N, 55° 58' W, *Cavalcante* 2572 (NY); Mun. Bragança, 13 km N of Bragança, 20 m, 0° 59' S, 46° 15' W, *Davidse et al.* 18022 (DAV); Quatipuru, 0–50 m, c. 1° 05' S, 46° 45' W, *Rosa* 2407 (NY). **Roraima:** Mun. Alto Alegre, Ilha do Maracá, 300 m, 3° 22' N, 61° 20' W, *Hopkins et al.* 564 (DAV, NY); SEMA Ecological Reserve, Ilha Maracá, 3° 23' N, 61° 27' W, *Milliken* 802 (NY); Mun. Boa Vista, Serra de Tepequém, 1600 m, 3° 45' N, 61° 45' W, *Silva et al.* 422 (DAV); Caracará, 100 m, 1° 50' N, 61° 08' W, *Kuhlmann* 1069 (RB 20285).

COLOMBIA. Antioquia: Mpio. Anorí, Río Anorí valley, near Planta Providencia, 350–600 m, c. 7° 15' N, 75° 00' W, *Shepherd* 531 (HUA), 792 (HUA, MO), 400–900 m, 733 (MO); Corr. Providencia, Valle del Río Anorí, entre Dos Bocas y Anorí, 400–900 m, 7° 05' N, 75° 10' W, *Soejarto et al.* 4101 (F), 4342 (HUA); Mpio. Gómez Plata (bordering Mpio. Yombé), Río Porce, 14 km via Amalfi, 1030 m, 6° 45' N, 75° 05' W, *Callejas et al.* 2349 (F, HUA, NY, TEX); Mpio. San Carlos, Corr. Alto Samaná, vereda Miraflores, 880–920 m, 6° 05' N, 74° 52' W, *Callejas et al.* 8553 (MO). Mpio. San Luis, Corr. Monteloro/el Prodigio, 600–950 m, 6° 04' N, 74° 50' W, *Cárdenas & Ramírez* 2577 (MO); Corr. Prodigio, 350 m, 6° 06' N, 74° 48' W, *Cárdenas & Ramírez* 2823 (MO); 350–580 m, *Cárdenas et al.* 2856 (MO), 500–630 m, 6° 06' N, 74° 48' W, *Cogollo et al.* 4576 (MO); Quebrada La Cristalina, 600–770 m, c. 6° 00' N, 74° 45' W, *Ramírez & Cárdenas López* 1291 (HUA); Vereda Maratejales, Cañón del Río Samaná, 300–800 m, 6° 06' N, 78° 48' W, *Cárdenas et al.* 3000 (MO); Mpio. San Rafael, 3 km E of San Rafael, 1110 m, 6° 18' N, 75° 02' W, *Brant & Roldán* 1519 (DAV, F, HUA, MO); Mpio. Segovia Antioquia, salida hacia Doña María, 750 m, c. 7° 05' N, 74° 45' W, *Renteria et al.* 1668 (HUA, MO); Mpio. Tarazá, Corr. El 12, vereda Barroblanco, 350 m, 7° 30' N, 75° 20' W, *Callejas & McAlpin* 1153 (HUA); Mpio. Urrao, vereda Calles, Parque Nacional Las Orquídeas, 1450 m, 6° 32' N, 76° 14' W, *Cogollo et al.* 6572 (DAV, HUA). **Bolívar:** Mpio. Achi, Ciénaga La Raya, 20–80 m, 8° 20' N, 74° 30' W, *Callejas et al.* 4405 (HUA, MO). **Cundinamarca:** Mpio. Medina, Mesa Calzón, 6 km NE of Medina, 850 m, 4° 32' N, 73° 20' W, *Grant* 10472 (US). **Guainía:** Mpio. Puerto Inírida, El Remanso, Cerro de Mavecuri, 300 m, 3° 27' N, 67° 58' W, *Franco et al.* 6130, *Rudas et al.* 7321 (MO). **Meta:** Mpio. La Macarena, 20 km NW on road to Conejos, 450 m, 2° 15' N, 73° 45' W, *Callejas & Marulanda* 6965 (HUA, MO); Puerto López, 240 m, 4° 10' N, 73° 40' W, *Little & Little* 8238 (DAV, US); Villaviciencia, 500 m, c. 4° 20' N, 73° 40' W, *Barclay et al.* 3616 (DAV, US), *Wijnnga* 524 (MO, NY). **Norte de Santander:** Mpio. Toledo, región Sarare, Río Cobugón, between Quebrada Gibraltar and La Palma,

320–400 m, c. 7° 03' N, 72° 05' W, *Cuatrecasas* 13238 (F, US).

ECUADOR. Pastaza: Cantón Mera, Mera, 1160 m, 1° 28' S, 78° 08' W, *Lugo* 244 (MO).

GUIANE FRANÇAISE. Cayenne: Cayenne, 0–50 m, 4° 00' N, 53° 00' W, *Broadway* 272 (NY, US), 429 (NY).

GUYANA. [without locality] *Schomburgk* 977 (US).

SURINAME. Commewijne: Paramaribo, 0–20 m, 5° 50' N, 55° 10' W, *Wullschlägel* 1072 (W). **Sipaliwini:** Bakhuis Mts., between Kabalebo R. and Coppename W., c. 4° 00' N, 57° 00' W, *Florschütz & Maas* 2748 (DAV); confluence of Paloemeu and Tapanahoni Rivers, 3° 20' N, 55° 27' W, *Wessels Boer* 1249 (F, NY, UC); Wilhelmina Gebergte, Lucie River, 2 km below confluence with Oost Rivier, 225 m, 3° 30' N, 56° 25' W, *Irwin et al.* 55435 (NY, US).

VENEZUELA. Amazonas: Dto. Atabapo, between Cerro Moriche and Las Mercedes, 100–150 m, c. 4° 40' N, 66° 15' W, *Foldats* 100A (US); Salto Yureba, 120–150 m, 4° 03' N, 66° 01' W, *Delascio & Guánchez* 10931 (MO); San Antonio, 120 m, 3° 30' N, 66° 45' W, *Williams* 15037 (US); San Juan de Manapiare, 150 m, 5° 18' N, 66° 03' W, *Huber* 1089 (NY); Santa Bárbara del Orinoco, 3° 57' N, 67° 04' W, *Berry* 652 (MO), *Maguire et al.* 32013 (MO, NY); Dto. Atures, Isla del Ratón, 100 m, 5° 02' N, 67° 46' W, *Breteler* 4696 (F, MO, NY, US); Pedra de Cataniapo, 50 km SE of Pto. Ayacucho, 100 m, c. 5° 10' N, 67° 20' W, *Guánchez* 180 (DAV); Raudal de Maypures, 100 m, 5° 10' N, 67° 47' W, *Spruce* 3592 (W); Dto. Río Negro, Esmeralda Ridge, 150–200 m, c. 3° 10' N, 65° 33' W, *Maguire & Maguire* 34638 (DAV, NY). **Barinas:** Dto. Bolívar, Barinitas, 8° 45' N, 70° 25' W, *Bernardi* 3326 (NY); Dto. Pedraza, 8° 31' N, 70° 35' W, *Dorr* 5765 (NY). **Bolívar:** Dto. Piar, Canaima, Río Caura, altura del caño Maskani, 6° 16' N, 62° 51' W, *Stergios & Delgado* 12830 (MO). **Mérida:** Dto. Arzobispo Chacón, km 50 de Sta. María de Chaparo, 350 m, c. 8° 05' N, 71° 30' W, *Aymard et al.* 4494 (MO, US); Dto. Tovar, Los Giros, near Empresa Río Unio, 700 m, 8° 26' N, 71° 35' W, *van der Werff & Ortiz* 5679 (MO, U). **Táchira:** Dto. Ayacucho, between San Juan de Colón and Las Cruces, 680 m, 8° 05' N, 72° 15' W, *Steyermark* 120285 (DAV, MO); Dto. García de Hevia, 4 km W of La Fría, 120 m, 8° 14' N, 72° 17' W, *Steyermark et al.* 120406 (MO, DAV); Dto. Libertador, Cerro La Espuma, 300–350 m, 7° 34' N, 72° 05' W, *Steyermark & Leisner* 119223 (F), 119289 (MO); 10 km S of El Piñal, 250 m, 7° 27' N, 71° 55' W, *Davidse & González* 21642 (DAV, F, MO); Dto. Panamericano, 10.5 km NE of La Fría, 90 m, 8° 16' N, 72° 10' W, *Steyermark et al.* 120547 (DAV, MO); Dto. San Cristóbal, Cava de Calizas, near Pericos, 7 km SW of San Cristóbal, 850–900 m, 7° 42' N, 72° 54' W, *Bono* 5128 (MO). **Yaracuy:** Dto. Nirgua, near boundary with Dto. San Felipe, 850–

990 m, 10° 13' 40" N, 68° 37' W, *Meier et al.* 8658 (DAV). **Zulia:** Dto. Catatumbo, Montaña El Mirador, 210 m, 8° 50' N, 72° 38' W, *Zambrano et al.* 1772 (MO); Dto. Colón, *Bunting* 9830 (NY).

Phyllanthus attenuatus ssp. *attenuatus* is usually readily distinguished from other taxa of sect. *Hylaeanthus* by its distinctly caudate-acuminate leaf blades and sessile or subsessile floral glomerules. However, occasional specimens, especially in Colombia, have distinctly pedunculate glomerules, e.g., *Callejas & Marulanda* 6965 from Meta and *Cogollo & Ramírez* 2577 from Antioquia. Another specimen from Antioquia (Mpio. San Carlos, *Callejas et al.* 8553) has completely glabrous leaves as in *P. skutchii*, but fruits typical for *P. attenuatus*.

2b. *PHYLLANTHUS ATTENUATUS* ssp. **incarum** G. L. Webster, ssp. nov.

TYPE: **ECUADOR.** Orellana: Cantón Orellana, Cañón los Monos-Sachas, árboles dejadas en potreros, 250 m, 0° 25' S, 76° 55' W, 8 Oct. 1987, *W. Palacios* 2095 (HOLOTYPE: QCNE!; ISOTYPE: MO!). (Figs. 1, 2d).

Differt ssp. *attenuato* plantis vulgo monoicis, foliis hirsutulis, glomerulis florum pedunculatis.

Monoecious (rarely dioecious) TREES; BRANCHLETS glabrous; leaf blades hirsutulous abaxially, especially along proximal parts of midrib and veins; FLORAL GLOMERULES mostly distinctly pedunculate (1–3 mm long); pistillate flowers 2–7 per glomerule, fruiting pedicel glabrous, 4–7 mm long, fruiting sepals 1.3–2 mm long; ovary (4-) 5- or 6-locular; seed tegmen 2.5–4 mm long.

DISTRIBUTION AND HABITAT: Lowland primary or secondary terra firme rain forests in Amazonian Colombia, Ecuador and adjacent northern Peru, 150–600 m.

PHENOLOGY: Collected in flower and fruit April to November.

ADDITIONAL SPECIMENS EXAMINED: **COLOMBIA. Amazonas:** Mpio. Tarapacá, Parque Nacional Natural Amaycayacu, 100 m, 3° 02' N, 70° 00' W, *Rudas et al.* 5215 (MO).

ECUADOR. Orellana: Cantón Orellana, Sector Huashito, 2 km N of Coca, 250 m, 00° 20' S, 77° 05' W, *Gudiño* 185 (MO, QCNE). **Pastaza:** Cantón Pastaza, Comuna Shuar (Kapawi), 250–300 m, 2° 31' S, 76° 41' W, *Cerón et al.* 4367 (DAV, MO); vía Auca, 115 km S of Coca, 5 km S of Río Tigüino, 320 m, 1° 15' S, 76° 55' W, *Rubio* 109 (DAV, QCNE), *Zak* 4045 (DAV). **Sucumbíos:** Cantón Gonzalo Pizarro, 8 km W of Tumbaque, 500 m, 0° 02' N, 77° 25' W, *Gentry & Miller* 54949 (DAV, MO).

PERU: Amazonas: Prov. Bagua, al lado de Quebrada Sasa, 600 m, 5° 03' S, 78° 18' W, *Kayap* 993 (DAV, US). **Loreto:** Prov. Maynas, Santa María de Nanay, Quebrada Yarina, 150 m, 3° 55' S, 73° 40' W, *Vásquez et al.* 12188 (MO); Indiana, Explorama Reserve, 105 m, 3° 28' S, 72° 50' W, *Vásquez & Jaramillo* 13158 (MO).

In Pastaza, Ecuador, *Phyllanthus attenuatus* ssp. *incarum* approaches the distribution of *P. a.* ssp. *attenuatus* but occurs at a lower elevation. Some specimens, especially *Cerón et al.* 4367 from Pastaza, have very sparsely hirtellous leaf blades, and are somewhat transitional to *P. a.* ssp. *attenuatus*. It is possible that contacts (or near-contacts) with *P. a.* ssp. *attenuatus* will be found in Pastaza and to the north in provinces Orellana and Napo.

2c. *PHYLLANTHUS ATTENUATUS* ssp. **tucuruensis** G. L. Webster, ssp. nov.

TYPE: **BRAZIL.** Pará: Mun. Tucuruí, Breu Branco, 40 km S of Represa Tucuruí, secondary forest on white sand, 90 m, 3° 55' S, 49° 44' W, 17 Mar. 1980, *T. Plowman*, *N. A. Rosa*, & *C. S. Rosário* 9692 (HOLOTYPE: NY!; ISOTYPES: FI, MO!). (Fig. 1)

Differt ssp. *attenuato* ramulis et pedicelis fructigeris pubescentibus, carpelibus saepe 5 vel 6.

Dioecious TREE; BRANCHLETS hirsutulous; FLORAL GLOMERULES subsessile to pedunculate (0.5–2 mm); pistillate glomerules with 1 to 5 (–7) flowers; fruiting pedicel 1.5–3 (–5) mm long, hirsutulous or some-

times glabrous; ovary (4-) 5- or 6-locular; seed endotesta (3-) 3.5–4.5 mm long.

GEOGRAPHICAL DISTRIBUTION: Eastern Brazil, in basin of Rio Tocantins (Pará), and probably also in Amapá, terra firme forest at elevations of < 100 m.

PHENOLOGY: Collected in fruit in March, November.

ADDITIONAL SPECIMENS EXAMINED: BRAZIL.

Amapá: Quadricula SB-22-VA Ponto 44 [location questionable], *Rosa et al.* 4155 (DAV, NY). **Pará:** Mun. Tucuruí, Tocantins, between Marabá and Tucuruí, c. 50 m, 5° 00' S, 49° 20' W, *Jangoux et al.* 1697 (NY); margem R. Tocantins, antiga estrada de ferro Alcobaca, *Lisboa et al.* 1370 (NY).

Subspecies *tucuruensis* seems much more similar to and less differentiated from *Phyllanthus attenuatus* ssp. *attenuatus* than is ssp. *incarum*. However, the pubescence observed on branchlets of *P. a* ssp. *tucuruensis* is rare or absent in populations of ssp. *attenuatus* in the Guayanas, Venezuela, and Colombia. It seems expedient to recognize *P. a* ssp. *tucuruensis* as a distinct entity pending more extensive sampling in eastern Amazonia.

3. **PHYLLANTHUS CALLEJASII** G. L. Webster, *Novon* 12: 295, fig. 2. 2002. **TYPE: COLOMBIA.** Prov. Antioquia, Mun. Frontino, Corr. La Blanquita, región de Murri, Alto de Cuevas, 1850 m, 14 July 1988, *R. Callejas, L. Arbeláez, J. Betancur, & L. D. Castaño* 6864 (HOLOTYPE: HUA 52926!; ISOTYPE: DAV!). (Fig. 1; see also Webster, 2002, fig. 2).

DIOECIOUS TREE 6–18 m high; axes glabrous; branchlets terete, smooth (minutely papillate), 15–25 × 1.5–2.5 cm, with 6–9 leaves. **LEAF BLADES** ovate to elliptic, abruptly apiculate, obtuse or rounded at base, 7–13 × 3.5–7 cm, glabrous except for incised midrib adaxially and prominulous midrib and major lateral veins abaxially; veins 5–7 pairs, veinlets prominulous and surface microreticulate abaxially; petiole 5–

7 × 1–1.5 mm, copiously scabrid-hirtellous; stipules blackish, triangular, 2–3 mm long. **FLOWERS** in axillary sessile or pedunculate (peduncles to 1.5 mm long) glomerules, the pistillate flowers mostly 2–5 per axil; bracts and bractlets blackish, persistent. **STAMINATE** flowers (known only in bud): pedicel c. 3 mm long; sepals 6, 1.4–2 × 0.8–1 mm; disk undivided, c. 0.7 mm in diameter; stamens 3, filaments connate into a column c. 0.5 mm high; anthers dehiscing horizontally, androecium c. 0.7 mm in diameter. **PISTILLATE** flowers: pedicel glabrous or sparsely and minutely hirtellous, 5.5–10 mm long in fruit; sepals 6 (rarely 5), 2.7–4 × 1.4–2.2 mm in fruit; disk patelliform, c. 1.5 mm in diameter; ovary 3-locular; styles connate into a column c. 1.5 × 0.7 mm; styles bifid, 0.5–0.7 mm long, ± twice-branched. **FRUITS** baccate, 7–9 mm in diameter when dried; seed tegmen somewhat compressed, acute, truncate at base, brownish, 2.5–4 × 2–2.8 mm.

DISTRIBUTION AND HABITAT: Endemic to montane rain forests, Colombian Andes, 1000–1850 m.

PHENOLOGY: Collected in flower February, July, August, and November; in fruit January, May, and August.

ADDITIONAL SPECIMENS EXAMINED: COLOM-

BIA. Antioquia: Mpio. Frontino, Corr. Nutibarra, 5–8 km S of Alto de Cuevas, 6° 39' N, 76° 25' W, 1000–1850 m. *Callejas et al.* 9940 (HUA); cuenca alta del Río Cuevas, 1630 m, *Sánchez et al.* 994 (M0); Mpio. Urrao, Parque Nacional “Las Orquídeas,” margen del Río Calles, 1450 m, 6° 32' N, 76° 19' W, *Cogollo et al.* 7472 (DAV); 1450 m, 6° 32' N, 76° 14' W, *Cogollo et al.* 6373, 6512 (DAV). **Nariño:** Mpio. Piedranca, Corr. Chucunéz, Reserva Nat. La Planado, camino hacia Pialapi, 1650–1800 m, 1° 08' N, 77° 55' W, *Betancur et al.* 2576 (HUA).

As noted in the original description (Webster, 2002), *Phyllanthus callejasii* replaces *P. attenuatus* at higher elevations (apparently > 1400 m) in the northern Andes of Colombia. It is easily distinguished by its larger broader leaves with a finely reticulate abaxial epidermis. In many ways, it

resembles *Phyllanthus valleanus* Croizat, which appears to be its lowland counterpart.

4. *Phyllanthus puntii* G. L. Webster, sp. nov.

TYPE: **BRAZIL**. Acre: Mun. Sena Madureira, trail to Rio Iaco from km 7 of Sena Madureira–Rio Branco road, 135 m, 9° 05' S, 68° 39' W, 1 Oct. 1968, G. T. Prance, D. F. Coelho, J. T. Ramos, & L. G. Farias 7712 (HOLOTYPE: U!; ISOTYPES: A, C, COL, FI, G, INPA, K, M, MG, MICH!, MO!, NY!, P, R, S, US!, VEN). (Figs. 1, 2c, 4b, 5).

Arbor monoica, differt ab aliis speciebus sectionis ramulis folisque hirtellis et venulis foliorum non prominulis, stylis erectis bifidis exsertis.

DIOECIOUS TREE 8–10 m high; branchlets c. 10–20 cm long, with 10–15 leaves, axis terete, hirsutulous, 0.8–1.5 mm in diameter. LEAF BLADES ovate to elliptic, acuminate, obtuse to rounded at base, copiously hirsutulous and micropunctulate abaxially, and sparsely pubescent adaxially, with 6–8 pairs of lateral veins, midrib and laterals $\pm$ incised adaxially and prominent abaxially, tertiaries $\pm$ scalariform and at right angles to midrib; petiole mostly 2–5 mm long, copiously hirsutulous both adaxially and abaxially; stipules lanceolate, c. 1.5–2 mm long, hirsutulous. FLOWERS in pedunculate glomerules, the peduncles 1–2.5 mm long. STAMINATE flowers unknown. PISTILLATE flowers 2–12 (rarely 1) per glomerule; pedicel hirsutulous, 3–5 mm long; sepals 6, abaxially hirtellous (especially at base), 1.3–2 mm long; disk patelliform, crenulate, c. 0.2 mm high and 0.8 mm in diam., ovary (3-) 4- (5-) locular; styles erect, bifid, c. 1–1.5 mm high, connate into a column. FRUITS 5–9 mm in diameter; seed tegmen 3–4.2 mm long.

DISTRIBUTION AND HABITAT: Presently recorded from the western Amazon (Acre) and lower Andean slopes in Bolivia (La Paz), 135–950 m.

PHENOLOGY: Collected in flower (Acre) in October, in fruit (Bolivia) from November to January.

ADDITIONAL SPECIMENS EXAMINED: **BOLIVIA. La Paz:** Prov. Larecaja, Copacabana, 10 km S of Mapi, 850–950 m, 15° 20' S, 68° 10' W, *Krukoff* 11281 (MO); 6.5 km W of Tipuani, 750 m, 15° 36' S, 68° 01' W, *Solomon* 17693 (DAV, MO); 3.2 km SW of Tipuani, 700 m, 15° 35' S, 68° 00' W, *Solomon* 17717 (DAV, MO); Prov. Sud Yungas, Alto Beni, Colonia San Pedro, 520 m, c. 16° 00' S, 67° 40' W, *Seidel & Vaquiata* 7532 (DAV, NY).

It is a great pleasure to dedicate this species to my colleague Willem Punt, who annotated the holotype as a possible new species. This is particularly appropriate in view of the significant contributions to the systematics of *Phyllanthus* that Dr. Punt has made with his many palynological studies at the Institute of Systematic Botany, Utrecht.

In the indumentum on the abaxial leaf blade surface, *Phyllanthus puntii* resembles *P. attenuatus* ssp. *incarum*; however, it is easily distinguished by its hirsutulous branchlet axes and gynoeceum with erect bifid styles, somewhat suggestive of *P. skutchii*. The type collection from Acre, at a much lower elevation, differs from the Bolivian specimens in a number of features (e.g., larger number of pistillate flowers per glomerule), but there seems little doubt that these disjunct populations are conspecific.

5. *PHYLLANTHUS MADEIRENSIS* Croizat, *Trop. Woods* 78: 7. 1944; Jablonski, *Mem. New York Bot. Gard.* 17: 108. 1967. TYPE: **BRAZIL**. Amazonas: Mun. Humaitá, plateau between Rio Livramento and Rio Ipixuna, 7–18 Nov. 1934, B. A. *Krukoff* 7163 (HOLOTYPE: A!; ISOTYPES: MO!, US!).

Phyllanthus manausensis W. A. Rodrigues, *Acta Amazonica* 1: 17, fig. 1. 1971. TYPE: **BRAZIL**. Amazonas: Reserva Forestal Ducke, 120 m, 2° 53' S, 59° 58' W, 18 Oct. 1963, W. A. *Rodrigues* 7520 (HO-



FIG. 3. Abaxial leaf surfaces. a. *Phyllanthus attenuatus* ssp. *attenuatus* (Callejas & Marulanda 6965); b. *Phyllanthus madeirensis* (Mori & Cardoso 17482).

LOTYPE: INPA 16822!; ISOTYPES: MO!, NY!). (Figs. 1, 3b).

MONOECIOUS or DIOECIOUS TREE 10–35 m high $\times$ 10–20 cm in diameter, glabrous throughout; inner bark reddish, aromatic; branches smooth, furrowed, not lenticellate; branchlets terete, smooth, not (or scarcely) lenticellate, 8–15 cm $\times$ 0.5–1 mm, with c. 10–15 leaves. LEAF BLADES ovate to elliptic, acute or apiculate to brevicauminate (acumen $\leq$ 0.5 cm), obtuse to rounded at base, 3–6 $\times$ 1.5–3 cm; abaxially

copiously puncticulate; midrib incised adaxially, prominently raised abaxially; lateral veins mostly 7–10, veinlets forming an irregular network, slightly prominulous on both faces; petiole 1.5–3 mm long; stipules lanceolate, 0.7–1.5 mm long. FLOWERS in axillary pedunculate unisexual glomerules (peduncle 1–3 mm long), staminate flowers 30–40 per axil, pistillate flowers 1–4 per axil. STAMINATE pedicel 2.5–4 mm long; sepals 6, elliptic-oblong, obtuse or subacute, 1.3–1.6 $\times$ 0.5–0.8 mm, midrib not prominent; disk 6-angled or $\pm$ dissected,



FIG. 4. Fruits and seeds: a. fruits of *Phyllanthus skutchii* (Herrera 3993); b. seeds of *P. puntii* (Solomon 17717).



FIG. 5. Branch and branchlets of *Phyllanthus punctii* (Prance et al. 7712).

0.7–0.8 mm across; stamens 3, filaments connate into a stout column 0.5–0.7 × 0.3–0.4 mm; anthers ovate, apiculate, dehiscent horizontally, androecium 0.6–0.7 mm in diameter. PISTILLATE pedicel slender, 4–7 × 0.1–0.2 mm; sepals 6, elliptic, 1.2–1.7 × 0.6–1 mm; disk patelliform, c. 1 mm in diameter; ovary (3-) 4- or 5-locular; styles erect, slender, unlobed, 0.3–0.5 mm long. FRUITS subspheroidal or slightly prolate, 5–8 mm in diameter; seed tegmen 3.5–4.5 mm long.

DISTRIBUTION AND HABITAT: Amazonian Brazil, from western Amazonas to Amapá, mostly in terra firme rain forests, 15–300 m.

PHENOLOGY: Collected in flower April, September–December, in fruit January, August.

ADDITIONAL SPECIMENS EXAMINED: BRAZIL.

Amapá: Mun. Macapá, 154 km NW of Porto Grande, 1° 30' N, 53° 30' W, *Rabelo et al.* 3089 (DAV, NY); Mun. Mazagão, 81 km WSW of Macapá, 0° 08' S, 51° 48' W, *Mori & Cardoso* 17482 (DAV, F, MO, NY); Mun. Porto Grande, Reserva INCRA, Rio Falsinho, 1° 08' N, 51° 27' W, *Campbell et al.* 10009 (MO). **Amazonas:** Mun. Humaitá, plateau between Rio Livramento and Rio Ipixuna, c. 50–100 m, 6° 30' S, 62° 30' W, *Krukoff* 7164 (MICH, MO); Mun. Manaus, Igarapé Leão, km 12 Manaus–Caracará road, 20 m, c. 3° 00' S, 59° 55' W, *Prance et al.* 3825 (DAV, NY); Rio Cuieras, just below mouth of Rio Brancinho, 20–30 m, c. 2° 45' S, 60° 15' W, *Coelho & Monteiro* 14935 (DAV); Reserva Florestal Ducke, 120 m, 2° 53' S, 59° 58' W, *Assunção* 276 (NY); 90 km NNE Manaus, Reserva 1501, Projeto Dinâmica Biológica de Fragmentos Florestais, 50–125 m, 2° 45' S, 59° 45' W, *Oliveira et al.* 269 (DAV). **Pará:** Mun. Almeirim, Monte Dourado, área do Felipe VI, c. 1° 15' S, 52° 50' W; *Pires & Silva* 1353 (MO); Mun. Altamira, Forte Altamira, Rio Xingú, 3° 12' S, 52° 12' W, *Kuhlmann* 2037 (RB 20293).

Comparison of the type specimens of *Phyllanthus madeirensis* Croizat, in western Amazonia, with specimens from the vicinity of Manaus to the mouth of the Amazon, suggests that the plants belong to a single species. Croizat (1944) described *P. madeirensis* as having 4 or 5 locules in the ovary, whereas Rodrigues (1971) illustrated *P. manausensis* as having 3 locules. In fact, locule number is variable; and specimens from western and eastern Amazonia agree in their rather small scarcely acuminate leaf blades conspicuously micropunctulate abaxially, as well as in their rather large seeds. Further sampling in western Amazonia might provide data to justify recognition of two subspecies.

6. *Phyllanthus awaensis* G. L. Webster, sp. nov.

TYPE: ECUADOR. Carchi: Cantón Tulcán, Parroquia Tobar Donoso, Reserva Indígena Awá, centro El Baboso, bosque premontano muy húmedo, 1800 m, 00° 53' N, 78° 25' W, 17–27 Aug. 1992, G. Tipaz, M. Tirado, G. Aulestia, N. Gale, & L. P. Ortiz 1830 (HOLOTYPE: QCNE!; ISOTYPES: DAV!, MO!). (Figs. 1, 6).

Differt ab aliis speciebus sectionis foliis ellipticis ad apicem obtusis vel rotundatis, ramulis pubescentibus, ovario 2-loculare.

DIOECIOUS SHRUB 1–6 m high; branches glabrous, terete; branchlets terete, axis densely hirtellous-scabridulous, 8–10 cm × 0.5–0.8 mm, with 10–15 leaves. **LEAF BLADES** broadly elliptic, obtuse to rounded at apex, obtuse at base, 2.5–6 × 2–3 cm; adaxial surface somewhat shiny, both adaxial and abaxial surfaces minutely scabridulous; midrib incised adaxially, prominently raised abaxially; lateral veins 6–10, veinlets mostly perpendicular to secondaries, not raised; petiole terete, rugulose, glabrous, 1.5–2.5 mm long; stipules lanceolate, 0.7–1 mm long, deciduous. **FLOWERS** in axillary sessile glomerules, the staminate flow-

ers not seen, pistillate flowers apparently solitary. **PISTILLATE** pedicel 8–9.5 mm long, slender (c. 0.1 mm in diameter), glabrous; fruiting sepals obovate-elliptic, 1.2–1.5 mm long; ovary 2-locular; styles connate, entire or emarginate. **FRUITS** broadly ellipsoidal, 5–8 mm in diameter, with stylar beak c. 1 mm long; seed tegmen 1.8–4 mm long.

DISTRIBUTION AND HABITAT: Known only from montane cloud forests of Carchi province, Ecuador, 900–1800 m.

ADDITIONAL SPECIMEN EXAMINED: ECUADOR. Carchi: Cantón Maldonado, Parroq. Tobar Donoso, Reserva Étnica Sabalera, 900 m, *Aulestia & Guanga* 715 (MO, NY); Cantón Tulcán, Parroquia El Chical, Reserva Étnica Awá, Centro San Marcos, 900–1000 m, 1° 06' N, 78° 14' W, Méndez *et al.* 349 (QCNE).

Phyllanthus awaensis is aberrant within sect. *Hylaeanthus* in a number of respects. It differs from all other species in the sect. by virtue of its scabridulous branchlet axes bearing completely glabrous leaves. In its small stature and leaf blades with rounded apices, it resembles species of sect. *Pityrocladus* such as *P. symphoricarpoides* H.B.K. (cf. synopsis in Webster, 2002). In fact, the venation of *P. symphoricarpoides* is very similar, especially in the prominulous abaxial midrib and secondaries, to that found in *P. awaensis* and other species of sect. *Hylaeanthus*. However, fruiting specimens of *P. symphoricarpoides*, like other species of sect. *Pityrocladus*, have a capsular fruit, persistent columella, and seeds lacking a sarcotesta. Furthermore, the pollen grains of *P. symphoricarpoides*, with 4 or 5 colpi and reticulate exine, are very different from the pollen of sect. *Hylaeanthus* (Webster & Carpenter, 2002). One can only conclude that there is a striking degree of vegetative convergence in Andean taxa of subgenera *Emblica* and *Conami*.

7. PHYLLANTHUS VALLEANUS Croizat, Ciencia (Mexico) 6: 354. 1946. **TYPE: COLOMBIA.** Valle: Veneral, Río Yurumanui, 2



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FIG. 6. Branch and branchlets of *Phyllanthus awaensis* (Tipaz et al. 1830).

Nov. 1944, *J. Cuatrecasas* 15868 (HOLOTYPE: A, not seen; ISOTYPE: F!).

MONOECIOUS TREE, glabrous throughout; bark fissured, reddish internally; branchlets 9–10 cm long, 0.8–1.1 mm in diameter, with 9 or 10 leaves. LEAF BLADES broadly elliptical, breviacuminate (acumen ≤ 0.5 cm long), $5\text{--}6 \times 2.5\text{--}3.3$ cm, with 5–7 lateral veins, not micropunctulate abaxially; petiole 3.5–4 mm long; stipules lanceolate, c. 1 mm long, subsistent. FLOWERS in sessile or subsessile staminate or bisexual glomerules. STAMINATE pedicel 2–3 mm long; sepals 6, elliptic; disk patelliform; stamens 3, filaments free or basally connate. PISTILLATE pedicel 2.5–6 mm long in fruit; sepals 6, obovate, $1.2\text{--}1.3 \times c. 1$ mm in fruit; disk patelliform; ovary 3-locular; styles discrete, bipartite. Fruits 5–7 mm in diameter.

DISTRIBUTION AND HABITAT: Colombia in lowland Chocó rain forest, below 100 m.

Phyllanthus valleanus, although known only from the single collection in extreme southwestern Colombia, appears to be a distinct species. It resembles *P. callejasii* in gross aspect due to the broad abruptly pointed leaf blades, but differs in its completely glabrous leaves, free stamens, and once-branched styles. Furthermore, it grows in Pacific lowland forests as opposed to the Andean rain forests where *P. callejasii* is found. The overall similarity in vegetative characters suggests that the two species may be related and perhaps derived from divergent ecotypes.

SPECIES INCERTAE SEDIS

8. *PHYLLANTHUS BERNARDII* Jabl., Mem. New York Bot. Gard. 17: 112, 1967. TYPE: VENEZUELA. Mérida, Aricagua, 1650 m, $8^{\circ} 13' N$, $71^{\circ} 08' W$, 18 Feb. 1957, *L. Bernardi* 6258 (HOLOTYPE: NY!).

MONOECIOUS SHRUB; branches glabrous, sulcate; deciduous branchlets 30–40 cm $\times$ 1–1.5 mm, with c. 20–30 leaves. LEAF BLADES ovate, acuminate, rounded at base, $5\text{--}7 \times c. 2.5$ cm; glabrous except for proximal midrib adaxially; petioles 2 mm long; stipules c. 1.5 mm long. FLOWERS in axillary unisexual glomerules, the staminate proximal and pistillate distal. STAMINATE pedicels c. 5 mm long; sepals 6; disk segments 5 or 6; stamens 3, filaments connate, anther sacs spheroidal, dehiscing $\pm$ horizontally. PISTILLATE pedicel c. 5 mm long; sepals 6, obtuse, c. 1.3 mm long; ovary 3-locular; styles slender, unlobed, ascending. FRUITS and seeds unknown.

This species so far is known only from the type collection, and the description has been adapted from that of Jablonski (1967). Until additional specimens are collected, it will be difficult to evaluate the relationships of *Phyllanthus bernardii*. Some characters in the description have been adapted from Croizat's account, and may have to be modified when additional collections are made.

Since *Phyllanthus bernardii* and *P. valleanus* are each known from unique localities, they have not been indicated on the distribution map.

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