

**COMPOSITAE OF CENTRAL AMERICA–VI.
PERYMENIUM HONDURENSE, PODACHAENIUM SALVADORENSE, AND VERBESINA
MONTEVERDENSIS, THREE NEW WOODY SPECIES OF HELIANTHEAE**

JOHN F. PRUSKI

Missouri Botanical Garden
P.O. Box 299
St. Louis, Missouri 63166

ABSTRACT

Yellow-rayed ***Perymenium hondurense*** Pruski, **sp. nov.** (Compositae: Heliantheae: Ecliptinae) from Honduras is described. By its arborescent habit and winged fruits it resembles *Perymenium grande* Hemsl., but differs by its pinnately-veined finely serrulate-denticulate leaves, pyriform outer phyllaries, and narrow-tipped inner phyllaries. A key to the ten Mesoamerican species of *Perymenium* is provided. White-rayed ***Podachaenium salvadoreense*** Pruski, **sp. nov.** (Compositae: Heliantheae: Verbesininae) is validated, and *Podachaenium* Benth. is accepted now as containing six species. By woody habit and densely persistent-hirtellous obgraduate phyllaries, *Podachaenium salvadoreense* is most similar to *Podachaenium chiapanum*, but differs by its cypselae with usually four(–five) slightly to moderately unequal elongate scales without intermediate small squamellae. A distribution map and a key distinguishing *Podachaenium salvadoreense* from regional congeners are given. Alternate-leaved yellow-rayed ***Verbesina monteverdensis*** Pruski, **sp. nov.** (Compositae: Heliantheae: Verbesininae) is described. It is most distinctive in its obgraduate phyllaries and subsquarrose outer phyllaries, but differs from other similar regional species by pilosulose corolla tubes, glabrous to weakly pubescent herbage with straight trichomes, and by relatively small leaves, capitulescences, and capitula. As fruit characters help diagnose each genus here treated, SEM micrographs of cypselae of each new species are provided.

Study of recent collections of the Central American Heliantheae (Compositae) for Flora Mesoamericana has resulted in discovery of three new woody species of *Perymenium* Schrad., *Podachaenium* Benth., and *Verbesina* L. Plants from Honduras, based on their pistillate yellow-rays and caducous-pluriaristate pappus, are placed *Perymenium* (subtribe Ecliptinae sensu Panero 2007), where they are most distinctive by their pinnately veined leaves. The five collections with pinnately veined leaves known to me have been identified previously as one of four names: *Perymenium ghiesbreghtii* B.L. Rob. & Greenm., *P. grande* Hemsl., *P. nicaraguense* S.F. Blake, and *P. purpusii* Brandege. This *Perymenium* with pinnately veined leaves is described here as *Perymenium hondurense* Pruski, a species typical of Ecliptinae by its disk corolla throats with fibers embedded in the nerves.

Also described here are species of *Podachaenium* and *Verbesina* of Verbesininae, a subtribe with a checkered past. Although Robinson (1981) recognized Ecliptinae as including *Verbesina* and Bremer (1994) recognized Verbesininae but treated *Eclipta* L. as incertae sedis, I follow Panero (2007), who recognized Ecliptinae and Verbesininae as distinct. A white-rayed Compositae from El Salvador is named as *Podachaenium salvadoreense* Pruski, and *Podachaenium* (Compositae: Heliantheae: subtribe Verbesininae) is now accepted as containing six species. *Podachaenium salvadoreense* is most similar to *P. chiapanum* B.L. Turner & Panero, but differs most strikingly by its disk cypselae with a nearly *Tetrachyron*-like pappus usually of four(–five) only slightly to moderately unequal long scales (the lateral two–three technically represent elongated squamellae and are more fimbriate than the two true radial scales) without intermediate reduced squamellae. Lastly, *Verbesina monteverdensis* Pruski, also of subtribe Verbesininae, is described. It is most distinctive by its obgraduate phyllaries and subsquarrose outer phyllaries. In the involucre character it resembles

Guatemalan endemic *V. eperetma* S.F. Blake, which differs by capitula twice the size of the Costa Rican species. *Verbesina monteverdensis* is compared to the other 15 alternate-leaved yellow-rayed Central American Verbesinas and involucre differences notwithstanding, the new species seems moderately similar to *V. oerstediana* Benth., but would key in D'Arcy (1975) to *V. lanata* B.L. Rob. & Greenm.

Perymenium was monographed by Robinson and Greenman (1899a) as containing 26 species, treated by Fay (1978) as containing 33 species in Mexico and Central America, and cited as having between about 36–50 total species by Strother (1999), Panero (2007), and Turner (2014). Most species of *Perymenium* are found in Mexico and Central America, and only a handful occur in the northern Andes. Among American genera of Ecliptinae, *Perymenium* by its caducous pluriaristate pappus perhaps is most similar to widespread *Melanthera* Rohr and northern Andean *Steiractinia* S.F. Blake, but it differs from *Melanthera* by yellow-flowered radiate (vs. typically white-flowered discoid) capitula and from *Steiractinia* by pistillate (vs. sterile) ray florets. Amazonian-centered *Tilesia* G. Mey. (syn.: *Wulffia* Neck. ex Cass.) is similar in gestalt to *Perymenium*, but differs from it by sterile ray florets in addition to its strange fleshy berry-like epappose fruits (Pruski 1996; Panero 2007).

Perymenium hondurensis differs from each of the four aforementioned species of *Perymenium* (as well as from the entire core of this genus of 36–50 species) by its pinnately-veined finely serrulate-denticulate leaves. By the technical character of winged fruits the Honduran plant resembles the species of the *P. grande* group, the only species group present from El Salvador and Honduras south to Costa Rica. Although *P. nelsonii* was treated by Fay (1978) as a variety of *P. grande*, it differs quite noticeably from the nominant variety by its capitula about twice as large and by apically broadly rounded inner phyllaries that contrast strongly to the paleae. On the other hand, the other taxa of the group have much smaller capitula than does *P. grande*. Even though capitula size is used taxonomically as the most facile feature distinguishing the previously described species of the *P. grande* group and capitula size quite naturally may vary ecologically, the species of this group nevertheless seems distinct from each other, and by the trinerved leaves reasonably different from the newly described *P. hondurensis*.

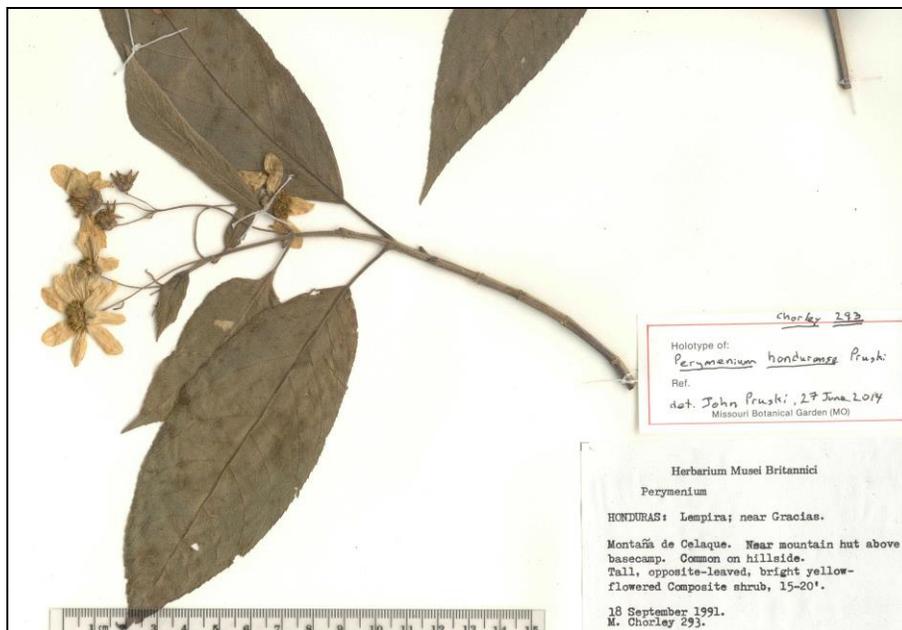


Figure 1. Holotype of *Perymenium hondurensis*. (Chorley 293, MO).

Among wing-fruited species *Perymenium hondurense* appears to most closely resemble woody *P. grande* (Figs. 6–7), especially in size of capitula and by inner phyllaries that are more or less transition in shape and texture to the paleae. The new species from Honduras differs from *P. grande*, however, by consistently pyriform (vs. ovate to lanceolate-ovate) outer phyllaries and apically acuminate to attenuate (vs. obtuse and oblong) inner phyllaries. Although Fay (1978) in his monograph interpreted similar variation in phyllary features as found within *P. ghiesbreghtii* B.L. Rob. & Greenm., I do not find such extreme variation elsewhere in the genus. Thus, phyllary characters and leaf venation are used here to distinguish taxa. A key to the ten Mesoamerican species of *Perymenium*, each with a more or less graduated involucre, follows the description.

PERYMENIUM HONDURENSE Pruski, *sp. nov.* **TYPE: HONDURAS. Lempira.** Near Gracias, Montaña de Celaque, sin. elev., 18 Sep 1991, *M. Chorley 293* (holotype: MO; isotype: BM). Figs. 1–5.

Frutex vel arbor 2.5–8 m alta; caules subhexagoni distale hispidulosa vel substrigosa; folia opposita petiolata, lamina 7–14 × 1.5–5 cm anguste elliptica pinnatim venosa serrulata-denticulata subtus glandulosa et hirsuto-pilosa; capitulescentia 6–22 cm diam. corymbiforma vel corymbiformi-paniculata; pedunculi 10–40 mm longi; capitula radiata; involucrum 5–7 × 4–7 mm campanulatum; phyllaria circiter 3-seriata, externa pyriformia interna lanceolata; flosculi radiati 8 pistillati, corollis luteolis, limbo 10–14 × 3–6 mm obovato 13–15-nervio; flosculi disci 30–40, corollis 4.8–5.5 mm longis infundibuliformis luteolis; cypselae 3–4 mm longae alatae; aristae pappo 10–15, 0.6–3.2 mm longae.



Figure 2. Close-up from Figure 1 of capitula of holotype of *Perymenium hondurense* showing involucre with outer pyriform phyllaries about half as long as to 2/3 or more as long as the inner phyllaries (*Chorley 293*, MO).

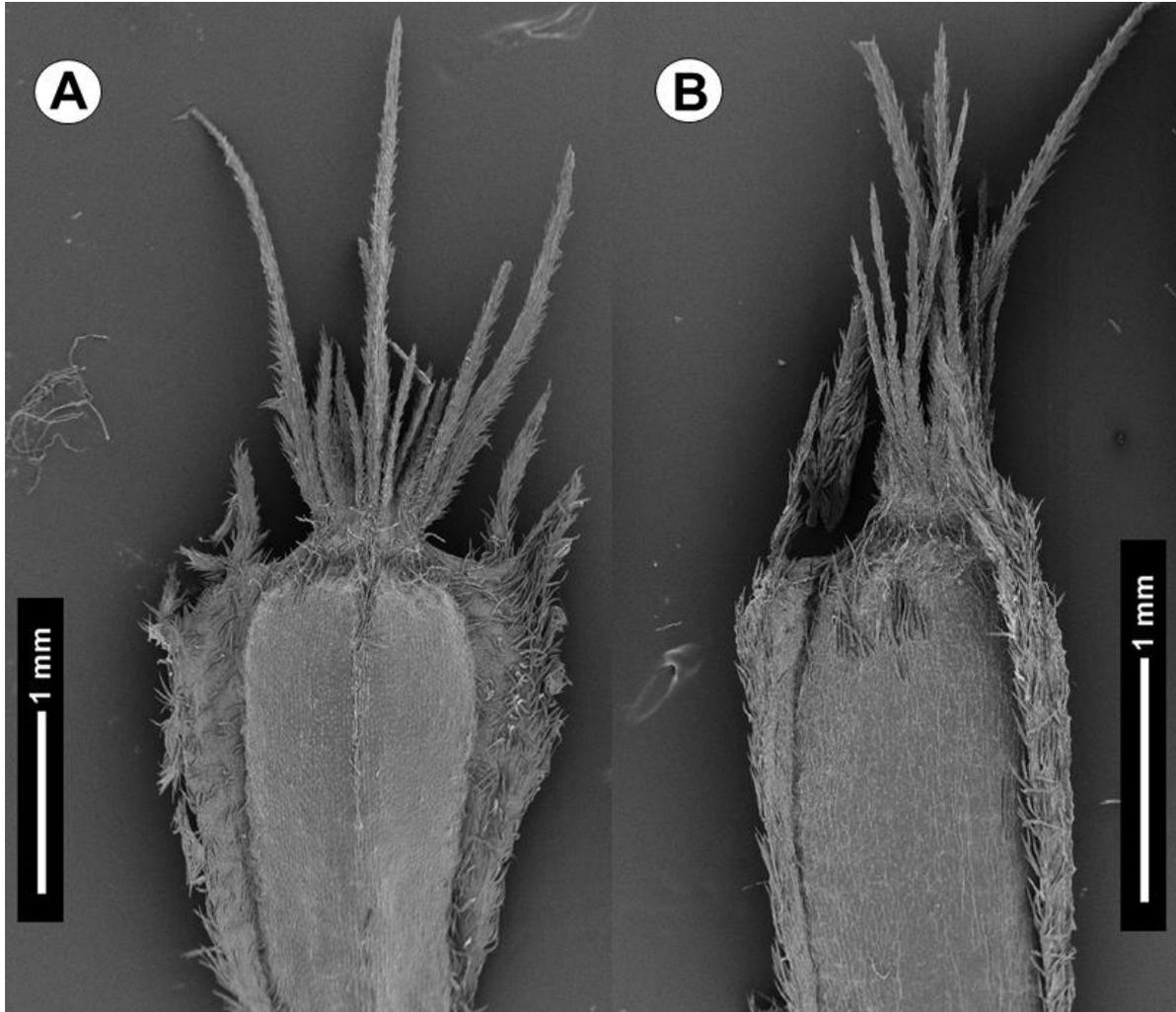


Figure 3. SEM micrographs of cypselae from holotype of *Perymenium hondurensense* showing narrow marginal wings (from base to apex), rostra, and pluriaristate pappus of fragile awns. Each wing extends distally from the shoulders into a pappus-like appendage. The short central rostrum is topped by several short and a few elongate pappus awns. A. Abaxial (inner) face of slightly obcompressed triquetrous ray cypsel showing lateral margin wings. B. Biconvex disk cypsel (lateral face) showing radial margin wings (Chorley 293, MO).

Shrubs or trees 2.5–8 m tall; stems with branches ascending, straight, exalate, sulcate-costate and subhexagonal, hispidulous or substrigose with antrorse(–subappressed) trichomes; herbage never stipitate-glandular. **Leaves** opposite, petiolate; blade 7–14 × 1.5–5 cm, narrowly elliptic, broadest near mid-blade, stiff-chartaceous, venation more or less evenly and regularly pinnate, never clearly trinerved from above base, secondary veins 9–13 per side, equally spaced and equally thickened, ascending at about 45 ° from stems, sometimes a pair of mid-leaf slightly more forward directed and hinting at the trinerved condition that very nearly characterizes the genus, the occasionally slightly more arching pair of veins not thicker than the other secondaries, tertiary reticulations moderately well-defined, surfaces more or less concolorous, adaxial surface scabrous-hirtellous, abaxial surface glandular, also hirsute-pilose to densely so with antrorse trichomes, base cuneate to obtuse but never with a clearly defined basal acumen, margins finely and evenly serrulate-denticulate with about 30–40 teeth per side, teeth ca. 0.2 mm long, apex acuminate to attenuate; petiole 1–2 cm long, hispidulous or substrigose. **Capitulescence** terminal, 6–22 cm diam., somewhat openly corymbiform to corymbiform-paniculate, (7–)17–50+–capitulate; peduncles mostly 10–40 mm long, filiform, ebracteolate. **Capitula** radiate; involucre 5–7 × 4–7 mm, campanulate; phyllaries

ca. 3-seriate, unequal with 1–2 outer phyllaries about half as long as inner to nearly subequal with most outer phyllaries usually more than $\frac{2}{3}$ as long as the inner, 2–3 mm diam., stiff, the pale indurate base appressed, the green-subherbaceous apex spreading; outer phyllaries pyriform, moderately to densely strigillose or strigose, apex acute to obtuse; inner phyllaries lanceolate, progressively less pubescent, more or less transitional in shape and texture to paleae, apex acuminate to attenuate; clinanthium paleate, convex; paleae 5–6 mm long, conduplicate, midrib hispidulous, herbaceous and carinate distally, apex acute to sometimes apiculate. **Ray florets** 8, pistillate; corolla golden-yellow, tube ca. 1.5 mm long, limb 10–14 × 3–6 mm, obovate, 13–15-nerved, abaxially minutely glandular and setulose, apex rounded, 2–3-denticulate. **Disk florets** 30–40, bisexual; corolla 4.8–5.5 mm long, funnellform, golden-yellow, tube 1.2–1.3 mm long, throat slightly longer than tube with thin fibers embedded in the nerves, lobes 0.6–1 mm long, hirtellous; anthers 2–2.5 mm long, black, appendage ca. 0.3 mm long, lanceolate, stramineous; style short-appendiculate, branches ca. 1.2 mm long, spreading, stigmatic surfaces 2-banded. **Cypselae** somewhat dimorphic, the rays triquetrous, the disks biconvex, 3–4 mm long (excluding wings), body black, smooth, eglandular, broadly rounded distally and short-rostrate, sparsely strigillose-setulose distally, narrowed apex ca. 0.3 mm tall, margins mostly thinly winged to near base, wings 0.2–0.5 mm diam., wings prolonged distally into pappus-like lateral appendages, base without elaiosomes, carpodium not prominent; ray cypselae slightly obcompressed and triquetrous, winged on lateral margins, adaxial margins typically merely strigillose-setulose; disk cypselae somewhat radially compressed, biconvex, winged on radial margins, wings narrower than in rays; pappus pluriaristate, of 10–15 unequal caducous awns set in from margins, 0.6–3.2 mm long.

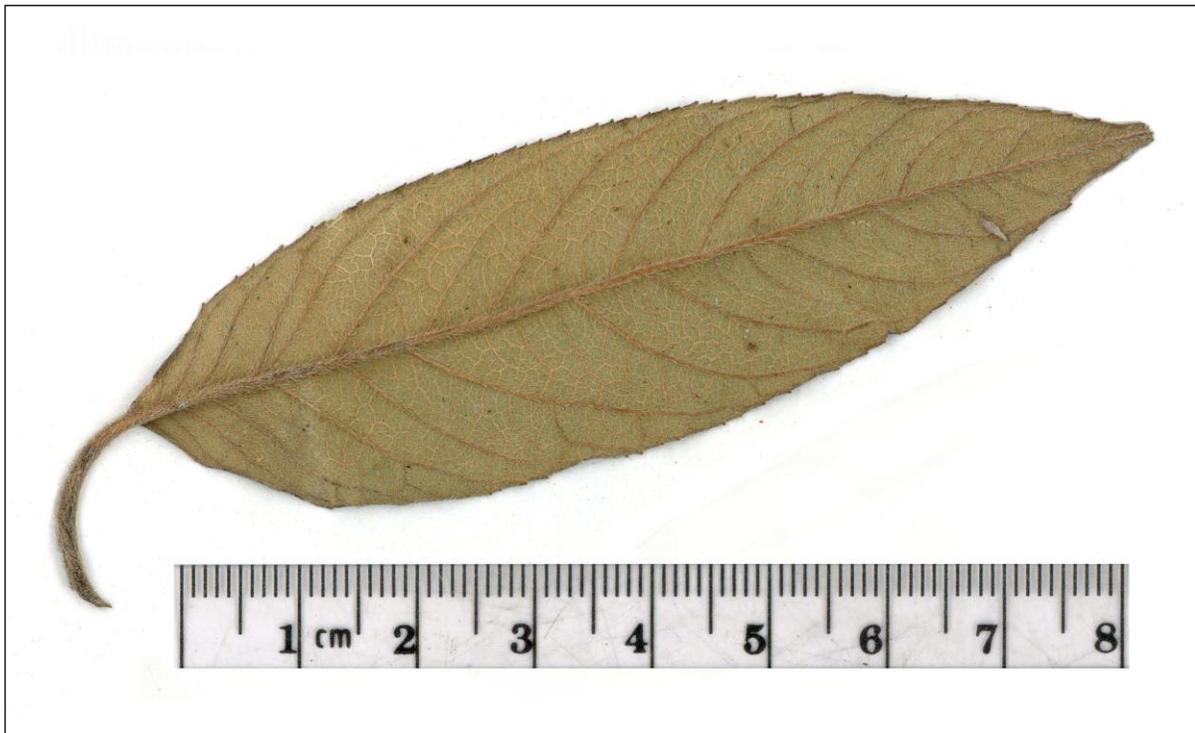


Figure 4. Abaxial view of leaf from a paratype of *Perymenium hondurensis* showing pinnate blade venation with lateral veins more or less equally thick (House 1040, MO).

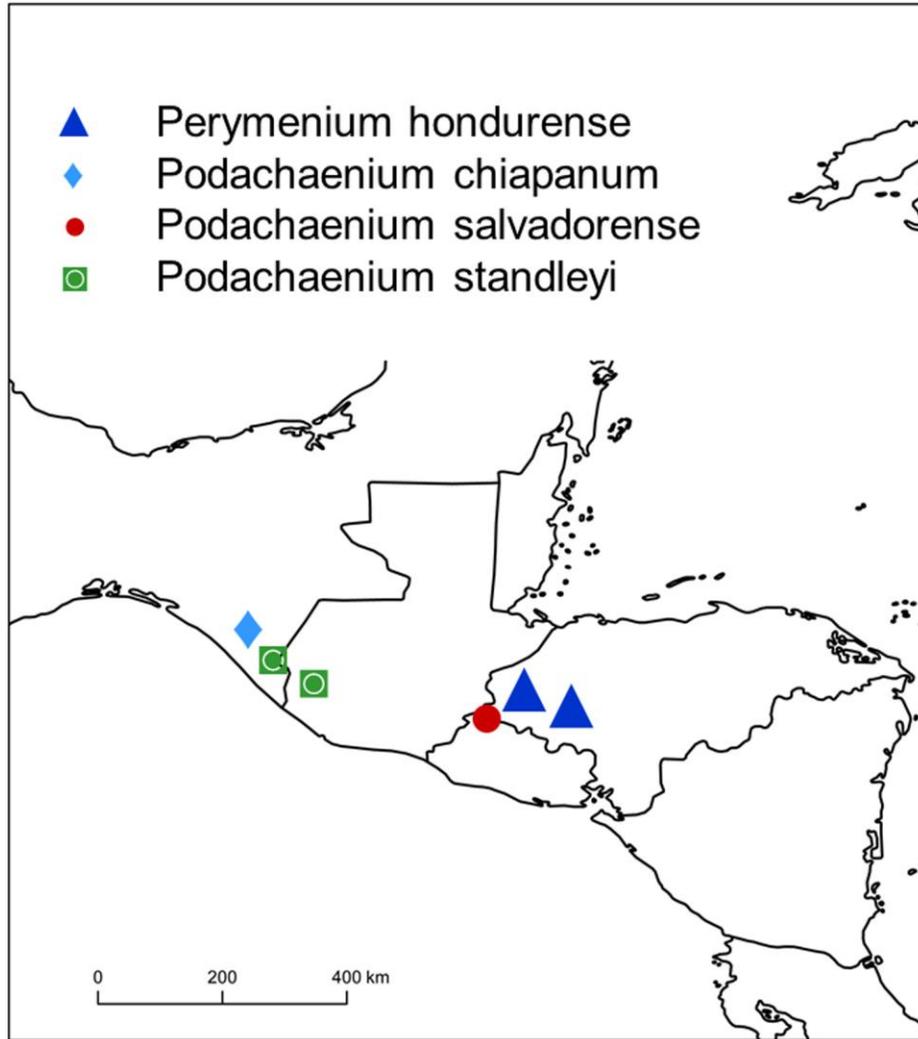


Figure 5. Distributions of *Perymenium hondurense*, *Podachaenium chiapanum*, *Podachaenium salvadorensis*, and *Podachaenium standleyi*.

Paratypes. **HONDURAS. Intibucá.** Cerro San Cristobal, La Esperanza, 2000 m, 12 Sep 1981, *T. Mejía* 70 (MO); Cerro Pelanariz, 1.5 km al NE de La Esperanza, 2000 m, 13 Sep 1981, *Sosa* 37 (MO). **Lempira.** Parque Nacional de Celaque, cerca del Campamento de Don Tomás, 2000 m, 10 Jul 1991, *Paul House* 1040 (EAP, MO, TEFH); Al noreste del Campamento Naranjo, 11 km al suroeste de Gracias, Parque Nacional de Celaque, 2530 m, 7 Aug 1992, *D. Mejía* 206 (EAP, HEH, MO, TEFH).

Etymology, distribution, and ecology. *Perymenium hondurense* is endemic to western Honduras (whence the epithet). It occurs in wet premontane forests, secondary forests, and cloud forests from about 2000–2530 meters elevation, and flowers from July until November.

Perymenium hondurense is reminiscent of Central America *Lundellianthus steyermarkii* (S.F. Blake) Strother, South American *Oyedaea wedelioides* (Klatt) S.F. Blake, South American *Steiractinia ocanensis* S.F. Blake, and South American *Wedelia penninervia* S.F. Blake in that each is a penninerved species belonging to genera of Heliantheae-Ecliptinae that are predominantly characterized by trinerved-leaved species. The penninerved vs. trinerved leaf venation character is much used in characterizing taxa in Heliantheae Alliance (sensu Panero 2007), and although perhaps sometimes environmentally influenced it generally seems to be useful and trustworthy taxonomically.



Figure 6. Representative specimen of *Perymenium grande* var. *grande* showing trinerved leaf blades broadest in proximal third (Pruski et al. 4450, MO).

At one point I had considered using the epithet "penninervium" for the new species, but given that the generic boundaries in Ecliptinae often waver and that *Wedelia* Jacq., the oldest generic name in the group, includes *W. penninervia*, it seems preferable to use an epithet less likely to be blocked amid possible generic restructuring. Among Heliantheae sensu lato I find only *Desmanthodium hondurensis* Ant. Molina (tribe Millerieae) and *Tithonia hondurensis* La Duke (Heliantheae subtribe Helianthinae) using this adjectival geographic epithet, clearing the path for the use of "hondurensis" in the moderately distantly related *Perymenium* of Heliantheae subtribe Ecliptinae.

Key to the Mesoamerican species of *Perymenium*

1. Cypselae often winged to the base or nearly so, wings typically prolonged distally into pappus-like appendages; leaf blade abaxial surfaces typically glandular.
 2. Involucres 3.5–5 × 3–5 mm.
 3. Perennial herbs to sprawling soft-wooded shrubs; leaf blades widest near the base, adaxial surface substrigillose to hispidulous, abaxial surface hirsute-pilose, trichomes antrorse to patent; phyllaries often moderately glandular, apices broadly obtuse to rounded; (Mexico, Guatemala) ***Perymenium gymnomoides*** (Less.) DC.
 3. Erect shrubs or small trees; leaf blades widest near the middle, surfaces strigillose, trichomes appressed; phyllaries eglandular or sparsely glandular, apices usually acute to obtuse; (Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica) ***Perymenium nicaraguense*** S.F. Blake
 2. Involucres 4.5–13 × 4–10 mm.
 4. Leaf blades pinnately-veined, broadest near middle; outer phyllaries consistently pyriform; inner phyllaries lanceolate, apically acuminate to attenuate; (Honduras) ***Perymenium hondurensis*** Pruski
 4. Leaf blades trinerved, broadest in proximal third; outer phyllaries ovate to lanceolate-ovate; inner phyllaries oblong, apically obtuse.
 5. Inner phyllaries typically appressed, typically transitional to paleae, apices acute to obtuse; involucres 4.5–6 × 5–6.5 mm; (syns.: *P. grande* var. *strigillosum* B.L. Rob. & Greenm., *P. tuerckheimii* Klatt); (Mexico, Guatemala, Honduras, El Salvador) ***Perymenium grande*** Hemsl. var. ***grande***
 5. Inner phyllaries spreading distally, contrasting with paleae, apices mostly rounded; involucres 7–13.5 × 6–10 mm; (syn.: *P. latisquamum* S.F. Blake); (Mexico, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica) ***Perymenium grande*** var. ***nelsonii*** (B.L. Rob. & Greenm.) J.J. Fay
1. Cypselae exalate although sometimes sharp-edged, cypselae shoulders rounded and typically not prolonging into pappus-like appendages or very rarely with ray cypselae short marginal setae coalescing into stout structures; leaf blade abaxial surfaces eglandular or glandular.
 6. Inner phyllaries with broadly obtuse to rounded ciliate membranous apex, either much broader than paleae or contrasting texturally with paleae.
 7. Leaf surfaces discoloured, abaxial surfaces densely white-strigillose or matted white-tomentulose; disk florets 40–60; (Mexico) ***Perymenium klattianum*** J.J. Fay
 7. Leaf surfaces concolorous, abaxial surfaces sparsely strigillose; disk florets 9–25.

- 8. Capitulescences corymbiform or corymbiform-paniculate, pluricapitulate; capitula small; involucre 4.5–5.5 mm long, turbinate or narrowly campanulate; disk florets 9–13(–19); paleae 4.2–4.5 mm long; (Mexico, Guatemala) **Perymenium gracile** Hemsl.
- 8. Capitulescences open cymose, 3–15-capitulate; capitula mid-sized; involucre 6.5–8.5 mm long, campanulate; disk florets ca. 25+; paleae 7–7.5 mm long; (Guatemala) **Perymenium jalapanum** Standl. & Steyerf.

- 6. Inner phyllaries transitional to paleae, stiffly herbaceous-tipped, apex usually acute to obtuse, not ciliate.

- 9. Ray florets 4–5, corolla limbs 3–4 mm long; disk florets 6–8; (Mexico) **Perymenium pinetorum** Brandegee
- 9. Ray florets 6–12, corolla limbs 4–13 mm long; disk florets 15–50.

- 10. Leaf blades ovate or oval-ovate, veins often more or less immersed abaxially, surfaces eglandular; corollas eglandular; (Mexico, Guatemala) **Perymenium chloroleucum** S.F. Blake
- 10. Leaf blades lanceolate to lanceolate-ovate, veins often prominent abaxially, abaxial surface usually glandular, corollas sometimes glandular; (Mexico, Guatemala) **Perymenium ghiesbreghtii** B.L. Rob. & Greenm.



Figure 7. Woody trunk of a representative tree of *Perymenium grande* var. *grande* (Pruski et al. 4479).

An arborescent Composite from El Salvador with white ray corollas, large capitula, biconvex somewhat compressed to subquadrangular cuneate-based disk cypselae, and a pappus of usually four(–five) slightly to moderately unequal pappus scales is described here as *Podachaenium salvadorensis*. The genus *Podachaenium* (Verbesininae) was described by Bentham (1853) and now contains six species, but was thought of historically as monotypic, being represented solely from the well-known white-flowered *P. eminens* (Lag.) Sch. Bip. (Fig. 8).



Figure 8. *Podachaenium eminens* (reproduced from Bot. Mag., ser. 4, 9: tab. 8502. 1913).

Podachaenium eminens is distinctive in its discolorous abaxially glandular 5-angled maple-like leaves, white rays, and attenuate-stipitate cypselae (Fig. 9A–B), and although it contains the generitype, by intermediate pappus squamellae it is atypical in *Podachaenium* and Verbesininae. *Podachaenium eminens* is occasionally cultivated in tropical America as well as in the western United States, but I have seen also a collection (NY) of it made in Florida a century ago by John K. Small. By white ray corollas (Fig. 8) and biconvex(–subquadrangular) cypselae (Fig. 9, 11), *Podachaenium* is accepted as enlarged by Jansen et al. (1982) and as redefined by Turner and Panero (1992). As opposed to *P. eminens*, however, none of other species *Podachaenium* are well-known, nor have any merited much attention outside of synantherology. The species recently added to *Podachaenium* are mostly unlobed concolorous-leaved, have glabrous disk corolla tubes, and cuneate-based disk cypselae (Fig. 9C–D). They appear to be more closely related to each other than to *P. eminens*.

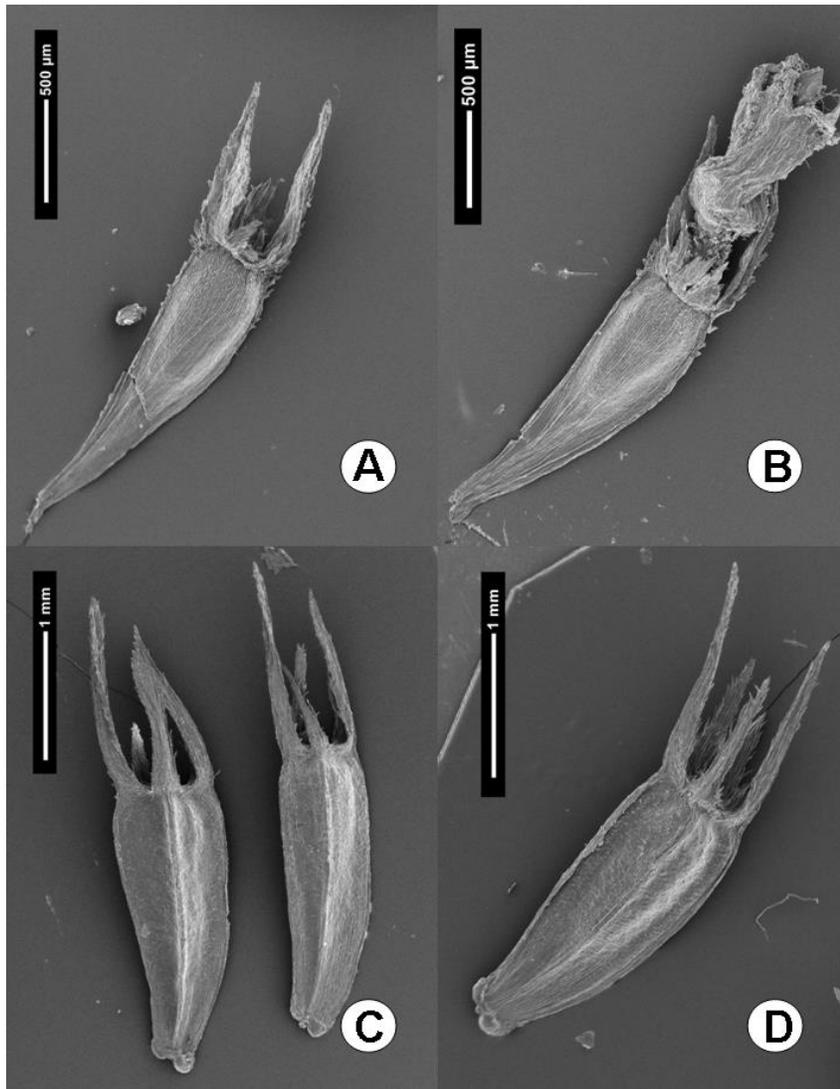


Figure 9. SEM micrographs of disk cypselae (in B a disk floret) of *Podachaenium*. A–B. Representative cypselae of *Podachaenium eminens*, which includes in synonymy the generitype, showing long-tapering fruit base (whence the generic name), two long radial pappus scales, and several small intermediate lateral squamellae. C–D. Cypselae from holotype of *Podachaenium salvadorensis*, showing merely cuneate fruit bases, four(–five) unequal pappus scales, and no small intermediate squamellae; the lateral scales represent elongated squamellae and are shorter and more fimbriate than are the radial scales (A–B *Pena 1032*, MO; C–D *Villacorta & Puig 2420*, MO).

PODACHAENIUM SALVADORENSE Pruski, *sp. nov.* **TYPE: EL SALVADOR. Santa Ana.** Parque Nacional Montecristo, Metapán, orilla del bosque nebuloso, 2230 m, 16 Aug 1996, R. Villacorta & G. Puig 2420 (holotype: MO; isotype: LAGU). Figs. 5, 9C–D, 10–11.



Figure 10. Holotype of *Podachaenium salvadorensis* (Villacorta & Puig 2420, MO). A metric scale bar is on upper left.

Arbor a 4 m alta; caules dense hirsuto-pilosa; folia opposita petiolata, lamina 6–14 × 2–5 cm elliptico-ovata eglandulosa et glabrata vel subglabrata; capitulescentia cymosa; pedunculi dense pilosuli vel dense villosopilosi (2–)3–8 cm longi; capitula radiata; involucrium 11–15 × 10–17 mm late campanulatum vel hemisphaericum; phyllaria obgradata, 3(–4)-seriata, externa dense hirtella; flosculi radiati 13–16 pistillati, corollis albis, limbo 15–20 × 2–4 mm oblongo 11–13-nervio, glanduloso; flosculi disci circiter 200, corollis circiter 3 mm longis late infundibuliformis luteolis; cypselae 2–2.5 mm longae; aristae pappo (3–)4(–5), 1–1.5 mm longae, squamellae nullae.

Small trees to 4 m tall, branches sometimes vining; stems densely and persistently hirsute-pilose distally; herbage with trichomes brownish. **Leaves** opposite, petiolate; blade 6–14 × 2–5 cm, elliptic-ovate, unlobed, venation arching plinerved from well above base with 2 pairs of thick secondary veins reaching past mid-blade, tertiary venation not well-developed, adaxial surface glabrous, abaxial surface eglandular, mostly glabrous but with larger veins sometimes substrigose, base narrow-cuneate, margins serrate, apex acuminate; petiole 0.5–1.5 cm long, unwinged. **Capitulescence** open-cymose, 3–6-capitulate; peduncle (2–)3–8 cm long, densely pilosulose to densely villous-pilose. **Capitula** to ca. 15 mm long, hemispherical post-anthesis; involucre 11–15 × 10–17 mm, broadly campanulate or hemispherical; phyllaries erect through anthesis, obgraduate, ca. 3(–4)-seriate, loosely imbricate, flat; outer phyllaries 10–15 × 1–2 mm, herbaceous, densely persistent-hirtellous, oblong-lanceolate, apex obtuse, typically spreading or reflexed; inner phyllaries subtending ray florets usually much smaller and paler than the outer, resembling paleae in color and texture; clinanthium paleate, to 5 mm tall, conical, fistulose post anthesis; paleae ca. 4 mm long, pale with midrib darker and finely glandular from apex to base. **Ray florets** 13–16, pistillate; corolla white, limb 15–20 × 2–4 mm, oblong, 11–13-nerved, glandular abaxially. **Disk florets** ca. 200; corolla ca. 3 mm long, broadly funnellform, yellow, tube ca. 0.7 mm long, glabrous, lobes ca. 0.5 mm long, sometimes sparsely setulose; style exappendiculate, branches with stigmatic surfaces 2-banded. **Cypselae** 2–2.5 mm long, glabrous, black with paler margins and base, the rays triquetrous, the disks somewhat compressed and biconvex to subquadrangular, base cuneate; ray pappus scales 3; disk pappus scales (3–)4(–5), extremely persistent, slightly–moderately unequal, the longer 2 usually ca. 1.5 mm long, the shorter (1–)2(–3) intermediate ones between the longer scales usually ca. 1 mm long and fimbriate-tipped, without intermediate minute fragile squamellae.

Etymology, distribution, and ecology. *Podachaenium salvadorensis* is endemic to cloud forests in Parque Nacional Montecristo, El Salvador (whence the epithet) only a few kilometers from the Guatemala–Honduras border. It occurs at about 2200–2300 meters elevation, and flowers in August. It is known only with certainty from the type collection, but from near the type locality I have seen two budding collections (*V. Martínez* 927 and 964, both MO) that may be *Podachaenium salvadorensis*.

By its stems and obgraduate herbaceous phyllaries persistently brown-pubescent, large capitula in open-cymose capitulescences, and leaves with venation arching plinerved from well above base, *Podachaenium salvadorensis* is most similar to *P. chiapanum* B.L. Turner & Panero (Fig. 5). *Podachaenium salvadorensis* differs most strikingly by its disk pappus usually of four(–five) slightly to moderately unequal long scales (Figs. 9C–D, 11). It appears that in *P. salvadorensis* the lateral two(–three) moderately elongated scales represent modified squamellae, and are more fimbriate than are the two true elongated radial scales. The disk cypselae pappus scales in *P. salvadorensis* are more or less constant in number, not greatly unequal, and the lateral ones are persistent.

Although intermediates in lateral squamellae elongation between the new species and the very-different-in-pappus-characters *Podachaenium chiapanum* are indeed possible, in the material in front of me no hint of intermediacy has been found, and the new species apparently merits recognition. The pappus characters of *P. salvadorensis* nearly bridge the gap (albeit falsely so) in

pappus characters between *Podachaenium* and the earlier yellow-rayed *Tetrachyron* Schldl. (described in 1847), but *Podachaenium* differs by two true always equally long radial pappus scales, ray corollas always white, and biconvex to subquadrangular cypselae that are never obviously quadrangular.

Also similar to *Podachaenium chiapanum* and *P. salvadorensis* is subequally and glabrous-phyllaried *P. standleyi* (Steerm.) B.L. Turner & Panero (Chiapas and Guatemala, Fig. 5). Wussow and Urbatsch (1978) and Jansen et al. (1982) treated *P. standleyi* in synonymy of *P. pachyphyllum* (Klatt) R.K. Jansen, N.A. Harriman, & Urbatsch, but I follow Turner and Panero (1992) who resurrected *P. standleyi* from synonymy. *Podachaenium salvadorensis* is less similar to true *P. pachyphyllum* and the presumably distinct *P. chimalapanum* B.L. Turner, which each occur from Oaxaca northwards and differ by thicker pinnately veined leaves and relatively short outer phyllaries. Lastly, a distribution map (Fig. 5) is given for the similar regional *P. chiapanum*, *P. salvadorensis*, and *P. standleyi*, and a key to species of *Podachaenium* in Mesoamerica is included.



Figure 11. Disk cypselae and florets from holotype of *Podachaenium salvadorensis*. (Villacorta & Puig 2420, MO). [Scale bar increments are 1 mm].

Key to the Mesoamerican species of *Podachaenium*

1. Leaf blades mostly (3–)5(–7)-angled, palmately 3-veined from near basal acumen, abaxial surfaces tomentose, glandular; disk corolla tubes glandular; cypselae base attenuate-stipitate; (syn.: *P. paniculatum* Benth.); (Mexico to Colombia) **Podachaenium eminens** (Lag.) Sch. Bip.
1. Leaf blades unlobed, venation arching plinerved from well above base, abaxial surfaces mostly glabrous, eglandular; disk corolla tubes glabrous; cypselae base cuneate.
2. Capitulescences corymbiform-paniculate; phyllaries usually subequal to very slightly obgraduate; outer phyllaries stiff-chartaceous, typically glabrous; (Chiapas and Guatemala) **Podachaenium standleyi** (Steyerm.) B.L. Turner & Panero
2. Capitulescences open-cymose; phyllaries obgraduate; outer phyllaries herbaceous, densely persistent-hirtellous.
3. Capitula to ca. 11 mm tall, involucre 6–10 mm long; ray florets ca. 21; disk pappus scales 2, equal, 1–4 minute squamellae between the longer scales; (Chiapas) **Podachaenium chiapanum** B.L. Turner & Panero
3. Capitula to ca. 15 mm tall, involucre 11–15 mm long; ray florets 13–16; disk pappus scales (3–)4(–5), slightly to moderately unequal, without intermediate small squamellae which are represented instead by the 2(–3) elongated lateral relatively fimbriate scales; (El Salvador) **Podachaenium salvadorensis** Pruski

A second new species of Heliantheae subtribe Verbesininae is described below as *Verbesina monteverdensis*. In Chiapas and Central America, there are nearly 40 species of *Verbesina*, of which about 22 are either white-rayed or opposite-leaved. The remaining 16 species are alternate-leaved yellow-rayed species as is the new species, which is distinctive in its obgraduate phyllaries and subsquarrose outer phyllaries (Fig. 14).

Because various species of our four regional genera of Verbesininae have been shuffled about, it seems fitting here to provide the below key to the Central American genera of subtribe Verbesininae.

1. Cypselae alate, bases not stipitate; pappus mostly 2–3-awned on margins, faces without intermediate squamellae; (38 regional species from Chiapas into Central America) **Verbesina** L.
1. Cypselae exalate, bases narrowed and stipitate or sometimes cuneate; pappus of 2–10 awns or scales on angles, faces sometimes with intermediate shorter squamellae.
2. Disk cypselae quadrangular; pappus usually of only 4 equal scales; (one regional species from Chiapas into Central America) **Tetrachyron** Schldl.
2. Disk cypselae somewhat compressed and biconvex(–subquadrangular); pappus of 2–4(–5) awns or of unequally developed scales.
3. Capitula globose or broadly campanulate; ray corollas white; cypselae base stipitate-tapered or cuneate; (four regional species from Chiapas into Central America) **Podachaenium** Benth.
3. Capitula turbinate to narrow-campanulate; ray corollas yellow and cypselae base stipitate-tapered; pappus of 4–10 unequal lacerate aristate scales; (monotypic / unispecific) **Squamopappus** R.K. Jansen, N.A. Harriman, & Urbatsch

VERBESINA MONTEVERDENSIS Pruski, **sp. nov.** TYPE: **COSTA RICA. Puntarenas.** Monteverde, road to TV Tower, 1700 m, 24 Aug 1985, *W. Haber 2373* (holotype: MO; isotype: CR). Figs. 12–15.

Frutex vel arbor 2–8 m alta; caules exalata piloso-hirsuta vel glabrata; folia alterna petiolata, lamina 5–10(–15) × 1.5–3.5 cm lanceolata vel anguste elliptico-ovata pinnatim venosa glabrata vel parce pilosulo-hirsutula; capitulescentia 5–15 cm diam. corymbiformi-paniculata, pedunculi 0.5–3 cm longi; capitula radiata; involucrum 4–5.5 × 4–5(–6) mm campanulatum; phyllaria obgradata 2–3-seriata, externa 5–10 spatulata subsquarrosa; flosculi radiati 8–10 pistillati, corollis luteolis, limbo 5–9 × 2–4 mm ovato vel obovato 5(–7)-nervio; flosculi disci 25–40, corollis 4.5–5.5 mm longis infundibuliformis luteolis; cypselae 2.7–3.7 mm longae; aristae pappo 2, 2.5–3 mm longae.



Figure 12. Holotype of *Verbesina monteverdensis*. (*Haber 2373*, MO).

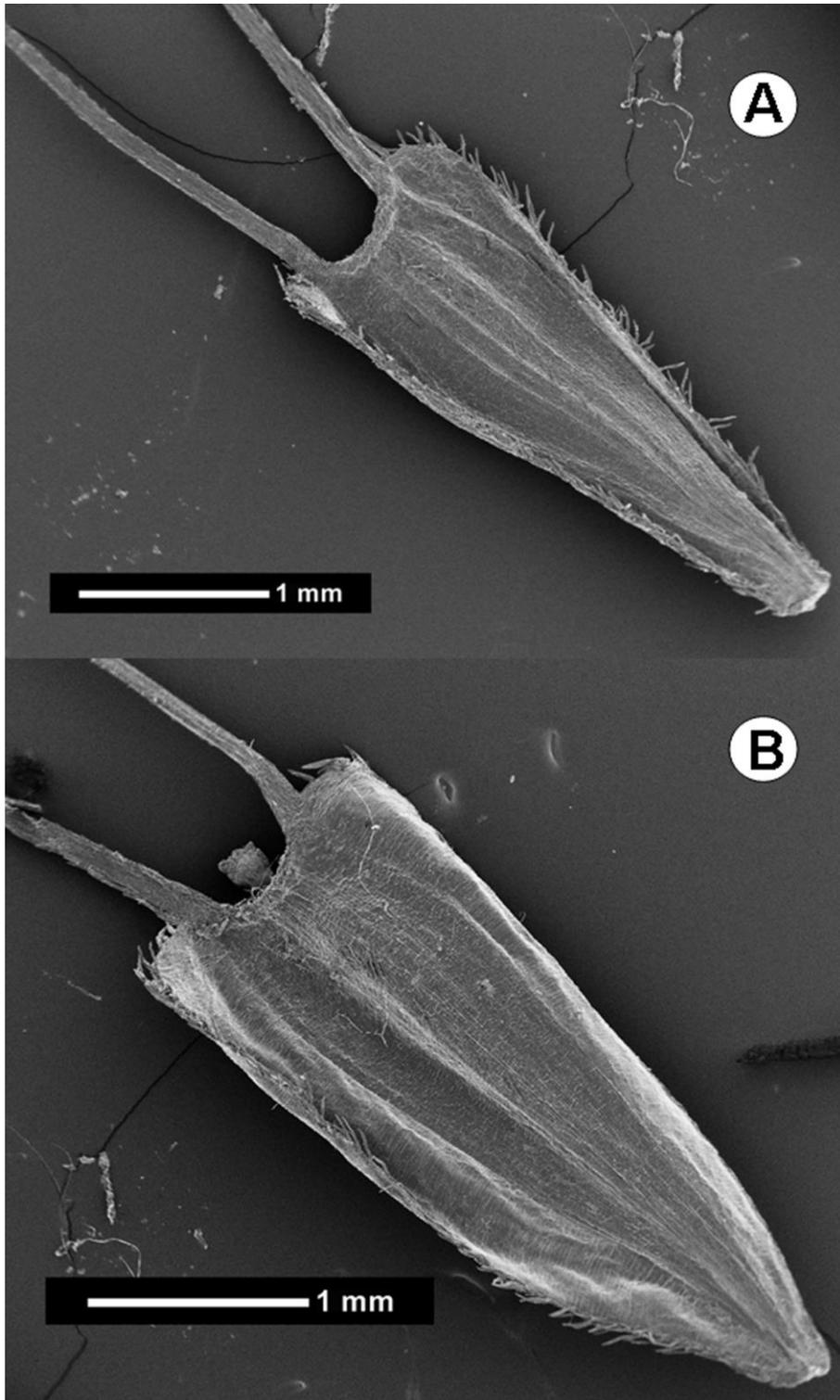


Figure 13. SEM micrographs of narrowly winged immature cypselae of *Verbesina monteverdensis*. (Gentry *et al.* 48721, MO).

Shrubs to trees 2–8 m tall; stems brittle, subangulate proximally to striate-subterete distally, exalate, brownish, sparsely to moderately pilose-hirsute distally to glabrate, trichomes straight, not crisped; herbage mostly glabrous to sparsely pubescent, eglandular. **Leaves** alternate, unlobed,

petiolate; blade 5–10(–15) × 1.5–3.5 cm, lanceolate or narrowly elliptic-ovate, chartaceous, venation pinnate, finely reticulate, secondary nerves 4–6 per side, directed forward, prominulous abaxially, surfaces concolorous, adaxial surface basically glabrous, abaxial surface glabrous or often with larger veins subappressed pilosulose-hirsutulous, base narrowly cuneate to attenuate, sometimes slightly decurrent onto distal portions of the petiole, margins entire to remotely denticulate, apex acuminate to attenuate; petiole 0.5–1.5 cm long. **Capitulescence** terminal 5–15 cm diam., not exerted well above subtending leaves, weakly convex to nearly flat-topped, corymbiform-paniculate, pluricapitulate, proximal branchlets strongly ascending, pilose-hirsute, internal bracteate leaves usually much smaller than main stem leaves; peduncles 0.5–3 cm long, moderately pilose-hirsute. **Capitula** 7–8.5 mm long, 33–50-flowered, radiate; involucre 4–5.5 × 4–5(–6) mm, double with the outer phyllaries resembling the 0–3 distal loosely inserted bracteoles of peduncle, campanulate but phyllaries spreading in fruit, 2–3-seriate; phyllaries obgraduate (infrequently merely subequal); outer phyllaries 5–10, herbaceous, subsquarrose with distal half reflexed, spatulate, (4–)5–6 × 1–1.5 mm, dark-veined, glabrous to sparsely pilosulose, apex acute to narrowly obtuse; inner phyllaries ca. 4 × 1 mm, chartaceous, shorter than both the outer phyllaries and the paleae; clinanthium paleate, flat to weakly convex, ca. 1.5 mm diam.; paleae 5–6 mm long, oblong, conduplicate, sparsely pilose along the midvein, apex acute, often outwardly directed. **Ray florets** 8–10, pistillate; corolla yellow, tube 1–1.5 mm long, sparsely pilosulose, limb 5–9 × 2–4 mm, ovate to obovate, 5(–7)-nerved. **Disk florets** 25–40; corolla 4.5–5.5 mm long, funnellform, yellow, tube 1–1.5 mm long, sparsely pilosulose, lobes 0.5–0.7 mm long, deltate; anthers ca. 1.8 mm long, thecae black but connectives pale; style exappendiculate, branches 1–1.2 mm long, stigmatic surfaces 2-banded. **Cypselae** 2.7–3.7 mm long, body black, with pale narrow wings, faces weakly setose distally but otherwise usually glabrous; pappus awns 2, 2.5–3 mm long.

Paratypes. COSTA RICA. Border of Alajuela, Guanacaste, and Puntarenas. Reserva de Monteverde, Cordillera de Tilarán, bosque enano en cumbre de Divis Continental, 1550–1580 m, 31 Jul 1976, *Dryer 530* (CR, MO). **Puntarenas.** Monteverde Reserve, area around TV towers, lower montane rain forest, 1600 m, 11 Oct 1985, *Bello 3043* (MO); Monteverde Reserva Forestal, sendero nubloso, 1550–1600 m, 21 Aug 1984 (fr), *Gentry & Haber 48721* (CR, MO, UC); Monteverde Cloud Forest Res., secondary thickets along continental divide near radio towers atop Cerro Los Amigos, 1550–1840 m, [label coordinates perhaps incorrect], 27 Feb 1992, *Grayum et al. 10189* (CR, MO, TEX); Monteverde, road to TV tower, 1700 m, 24 Aug 1985, *Haber 2342* (MO, TEX); Reserva Biológica Monteverde, area around TV towers and access road, 10° 19' N, 84° 48' W, 1600–1800 m, 20 Dec 1990, *Haber & Zuchowski 10248* (CR, MO, TEX, UC); Monteverde Reserva Biológica, sin. elev., 8 Aug 1975, *Poveda 1127* (CR, MO); Monteverde Cloud Forest Reserve, Cordillera de Tilarán, Pacific slope of continental divide, 1500–1620 m, 10 Aug 1984, *Pounds 299* (MO).

Etymology, distribution, and ecology. *Verbesina monteverdensis* is known only from montane forests in Monteverde Reserve (whence the epithet) in Costa Rica on the Pacific watershed. It occurs from about 1500–1840 meters elevation, and has been collected in flower in February, July, August, October, and December. The one fruiting only collection in front of me was made in August, which together with the flowing material suggests that this species has a broad flowering period, perhaps only out of flower in the driest months (i.e., March–June) of the year.

Verbesina monteverdensis by its yellow-flowered radiate capitula seems best placed in the *Verbesina* sect. *Saubinetia* sensu Robinson and Greenman (1899b) and Olsen (1985). *Verbesina monteverdensis* stands out in the loosely defined *Verbesina* sect. *Saubinetia* by its obgraduate phyllaries and subsquarrose outer phyllaries. Standley (1938) listed six species in Costa Rica, of which only *V. oerstediana* is alternate-leaved and yellow-rayed. Indeed, specimens of *V. monteverdensis* have generally passed under either *V. lanata* or *V. oerstediana*, and would key to *V. lanata* in D'Arcy (1975).



Figure 14. *Verbesina monteverdensis*, capitulum showing obgraduate phyllaries and subsquarrose outer phyllaries. (From the holotype, *Haber 2373*, MO).

Verbesina lanata was described by Robinson and Greenman (1899b) in *Verbesina* sect. *Saubinetia* and as yellow-flowered, but instead this species has white ray corollas and is a member of *Verbesina* sect. *Ochractinia* (Olsen 1985). *Verbesina lanata* does not seem very closely related to the new species. Yellow-rayed Panamanian material called *V. lanata* by D'Arcy (1975) has mostly been referred instead to a broadly defined *V. oerstediana*, which is centered in Costa Rica and Panama, but which perhaps includes in synonymy Honduran *V. vicina* S.F. Blake. *Verbesina oerstediana* has a graduate involucre with non-squarrose phyllaries, as do nearly all Central American species, much unlike *V. monteverdensis*. Further distinguishing *V. monteverdensis* from *V. oerstediana*, but less taxonomically significant, are merely pilosulose (vs. pilose) corolla tubes, and herbage glabrous to weakly pubescent with straight trichomes (vs. mostly tomentulose to tomentose with crisped trichomes), smaller leaves, and smaller capitulescences with fewer, smaller capitula. While the pubescence character seems striking, Blake (1938) noted Costa Rican *V. oerstediana* var. *glabrior* S.F. Blake is unusually glabrous to weakly pubescent. However, in technical feature Blake's variety matches *V. oerstediana* and lacks the obgraduate phyllaries and subsquarrose outer phyllaries that distinguishes the new species.

Costa Rican and Panamanian alternate-leaved yellow-rayed species described since Standley (1938) but not sufficiently distinct from *Verbesina monteverdensis* include: *V. baruensis* Hammel & D'Arcy, which has ovate, truncate-based leaves and capitula twice the size of the new species; and *V. fuscasicans* (D'Arcy) D'Arcy and *V. tapantiana* Poveda & Hammel, each of which are winged-petiolate nearly to stem and subsessile-leaved. Costa Rican *V. trichantha* (Kuntze) S.F. Blake is yellow-flowered but discoid-capitulate, otherwise distinguished by its disk corolla lobes longer than throat, and is unlike any other regional species. *Verbesina trichantha* is known only from the type. Among other regional alternate-leaved yellow-rayed species, *V. monteverdensis* is similar to *V.*

eperetma in the subsquarrose involucre character, and by narrow leaves to *V. chiapensis* B.L. Rob. & Greenm. and *V. perymenioides* Sch. Bip. ex Klatt, but these three species occur only from Guatemala northwards into Mexico (Nash 1976; Strother 1999), and otherwise do not seem too similar to *V. monteverdensis*. Finally, a few regional alternate-leaved yellow-rayed Verbesinas are variously annuals, winged-stemmed, large-leaved, discoloured-leaved, winged petiolate, large-capitulate, long-rayed, or sterile-rayed, and each seems distant to *V. monteverdensis*.

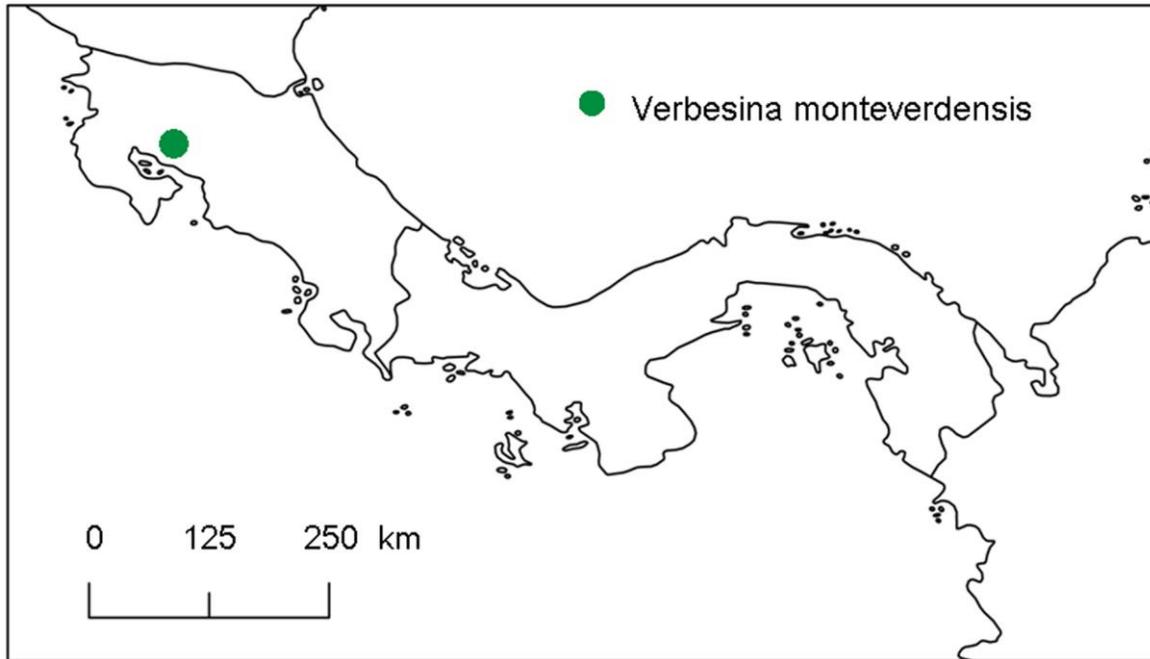


Figure 15. Distribution of *Verbesina monteverdensis*.

ACKNOWLEDGEMENTS

I would like to thank Guy Nesom and Rosa Ortiz for helpful comments on an earlier draft of this paper, Rosa Ortiz for providing the base maps, and Stephanie Keil and Wendy Westmoreland for their photograph of the *Perymenium grande* herbarium specimen.

LITERATURE CITED

- Benthams, G. 1853. *Compositae centroamericanae*. Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 65–121.
- Blake, S.F. 1938. *Verbesina oerstediana* var. *glabrior* S.F. Blake. Pp. 404–405, in T.G. Yuncker, A contribution to the flora of Honduras. Publ. Field Mus. Nat. Hist., Bot. Ser. 17: 289–407.
- Bremer, K. 1994. *Asteraceae: Cladistics & Classification*. Timber Press, Portland, Oregon.
- D'Arcy, W.G. 1975 [1976]. *Flora of Panama, Part IX. Family 184. Compositae*. Ann. Missouri Bot. Gard. 62: 835–1321.
- Fay, J.J. 1978. Revision of *Perymenium* (Asteraceae-Heliantheae) in Mexico and Central America. *Allertonia* 1: 235–296.
- Jansen, R.K., N.A. Harriman, and L.E. Urbatsch. 1982. *Squamopappus* gen. nov. and redefinition of *Podachaenium* (Compositae: Heliantheae). *Syst. Bot.* 7: 476–483.
- Nash, D.L. 1976. Tribe V. Heliantheae. Pp. 181–361, 503–570, in D.L. Nash and L.O. Williams, *Flora of Guatemala: Compositae*. Fieldiana, Bot. 24(12): x + 1–603.
- Olsen, J. 1985. Synopsis of *Verbesina* sect. *Ochraetinia* (Asteraceae). *Pl. Syst. Evol.* 149: 47–63.
- Panero, J.L. 2007 [2006]. Tribe Heliantheae Cass. (1819). Pp. 440–477, in K. Kubitzki (ed.), *Fam. Gen. Vasc. Pl.*, Vol. 8. Springer, Berlin.

- Pruski, J.F. 1996. Compositae of the Guayana Highland—XI. *Tuberculocarpus* gen. nov. and some other Ecliptinae (Heliantheae). *Novon* 6: 404–418.
- Robinson, B.L. and J.M. Greenman. 1899a. Revision of the genera *Montanoa*, *Perymenium*, and *Zaluzania*. *Proc. Amer. Acad. Arts* 34: 507–534.
- Robinson, B.L. and J.M. Greenman. 1899b. Synopsis of the genus *Verbesina*, with an analytical key to the species. *Proc. Amer. Acad. Arts* 34: 534–566.
- Robinson, H. 1981. A revision of the tribal and subtribal limits of the Heliantheae (Asteraceae). *Smithsonian Contr. Bot.* 51: iv + 1–102.
- Standley, P.C. 1938. Flora of Costa Rica. Compositae. Composite Family. *Publ. Field Mus. Nat. Hist., Bot. Ser.* 18: 1418–1538.
- Strother, J.L. 1999. Compositae-Heliantheae s.l. Flora of Chiapas, Vol. 5: 1–232. California Academy of Sciences, San Francisco.
- Turner, B.L. 2014. The Comps of Mexico. A systematic account of the family Asteraceae, chapter 16, subtribe Ecliptinae [Part 2], genera: *Perymenium*, *Plagiolophus*, *Rensonia*, *Sphagneticola*, *Synedrella*, *Tuxtla*, *Wamalchitamia*, *Wedelia*, *Zexmenia*, *Zyzyxia*. *Phytologia Mem.* 21: 1–165.
- Turner, B.L. and J.L. Panero. 1992. New species and combinations in *Podachaenium* (Asteraceae, Heliantheae). *Phytologia* 73: 143–148.
- Wussow, J.R. and L.E. Urbatsch. 1978. A taxonomic study of the *Calea orizabensis* complex and its bearing on the nomenclature of *Verbesina standleyi* (Asteraceae). *Brittonia* 30: 477–482.