

**COMPOSITAE OF CENTRAL AMERICA—VIII.
THE GENUS *LEPIDAPLOA* (VERNONIEAE)**

JOHN F. PRUSKI

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

ABSTRACT

The genus *Lepidaploa* (Compositae: Vernonieae), a segregate of *Vernonia*, is revised in Central America, where ten species are reported. New combinations are ***Lepidaploa acilepis* (Benth.) Pruski, comb. nov.**, ***Lepidaploa argyropappa* (H. Buek) Pruski, comb. nov.**, ***Lepidaploa ovata* (Less.) Pruski, comb. nov.**, and ***Lepidaploa vernicosa* (Klatt) Pruski, comb. nov.** The name of a widespread neotropical weed previously misidentified as *L. salzmannii* (a narrow Brazilian endemic) is here corrected to *L. argyropappa*. *Lepidaploa acilepis* is documented in Costa Rica and excluded from Mexico; *L. canescens* is recognized as distinct from *L. arborescens*; *L. chiriquiensis* is newly reported in Costa Rica; and *L. argyropappa* is newly reported in Panama. *Lepidaploa lehmannii*, formerly considered a South American endemic, is documented from Panama along the border with Colombia and is a new record for Central America. *Lepidaploa boquerona* is treated in synonymy of *L. tenella*, which is consequently a new record of the latter for Mexico. *Lepidaploa polypleura* is newly reported in El Salvador and Honduras, albeit from imperfect specimens. Lectotypes are designated for *Conyza uniflora* Mill. and *Vernonia lehmannii* Hieron. *Lepidaploa arborescens* is endemic to the West Indies, and both *L. remotiflora* and *L. salzmannii* are endemic to South America; each of the latter has been attributed previously to Central America but are here excluded.

The American genus *Lepidaploa* Cass. (Compositae: Vernonieae) is a segregate of *Vernonia* and contains about 150 Neotropical species. *Lepidaploa* as recognized currently is the largest genus of tribe Vernonieae, far outnumbering *Vernonia sensu stricto* in species. Similarly, Candolle (1836) recognized 290 species of *Vernonia*, with species numbers 64 (*V. zeylanica* (L.) Less.) to 259 (*V. tragiaefolia* DC.) treated in *Vernonia* sect. *Lepidaploa*, which as circumscribed by Candolle, however, contained both neotropical as well as paleotropical species.

Robinson (1990, 1999) resurrected *Lepidaploa* from synonymy with *Vernonia*, where most of its species were treated traditionally as *Vernonia* subgen. *Vernonia* sect. *Lepidaploa*, mostly there either without infrasectional placement or positioned variously in either subsect. *Graciles*, subsect. *Arborescentes*, subsect. *Scorpioideae*, ser. *Canescentes*, ser. *Foliatae*, or the informal *Lepidaploae Axiliflorae* etc. (viz Candolle 1836; Bentham 1853; Baker 1873; Bentham & Hooker 1873; Hoffmann 1890–1894; Gleason 1906, 1922, 1923; Ekman 1914; Keeley & Jones 1977; Keeley 1978; Jones 1979). Regarding *Vernonia* sect. *Lepidaploa*, Gleason (1906) stated that "the close relationship of the *Scorpioideae foliatae* and *Scorpioideae aphyllae* is obvious" and that a "migration route through ... Central America has been followed mostly by *Scorpioideae aphyllae*." It is perhaps noteworthy that in Central America 5 of our species are axillary-flowered and 5 are terminal-flowered and that Jones (1979) typified his *Vernonia* ser. *Canescentes* by *V. canescens* and his ser. *Foliatae* by *V. argyropappa*.

The segregate *Lepidaploa* most consistently differs from true *Vernonia* Schreb. (as well as from the large neotropical segregate *Vernonanthura* H. Rob.) by having echinolophate pollen (Robinson 1990, 1999, types C, D, and G; Keeley & Jones 1977, types B and C; Jones 1979, types B and C), generally sessile capitula (Figs. 1–2), and elongate-hexagonal (vs. quadrangular) pericarp raphide crystals (Fig. 3).

As mentioned above, *Lepidaploa* contains species often with capitula remote and sessile in the leaf axils forming interrupted leafy capitulescences (Figs. 1–2). These axillary-flowered species of *Lepidaploa* resemble many species of *Lessingianthus*, which differs by its sometimes quadrangular to elongate-hexagonal (vs. always elongate hexagonal) pericarp raphide crystals (Angulo et al. 2015) and simple (vs. nodular in *Lepidaploa*) style bases. A large number of *Lepidaploa* species, however, may have obviously terminal, aphyllous, seriated-cymose (not truly scorpioid) capitulescences (Figs. 9–10, 13; see Robinson 1990). The species of *Lepidaploa* with terminal capitulescences may resemble somewhat the genera *Cyrtocymura* H. Rob. and *Eirmocephala* H. Rob., each having only a single species in Central America. These two genera, however, differ from *Lepidaploa* by their densely truly scorpioid cymose capitulescence with curved apices and by pollen not always lophate.

Robinson (1999) treated *Cyrtocymura*, *Eirmocephala*, *Lepidaploa*, and *Lessingianthus* together in Vernoniae subtribe Vernoniinae. More recently, Keeley and Robinson (2009) described Lepidaploinae to include about a dozen genera (including the four genera aforementioned). In either subtribal system, *Lepidaploa* may be recognized by its capitulescence type and sessile capitula. The three other Central American genera of the Lepidaploinae (*Harleya* S.F. Blake, *Stenocephalum* Sch. Bip., and *Struchium* P. Browne; viz Pruski 2013), as well as the remaining South American genera do not seem overly similar to *Lepidaploa*. Although Central American *Lepidaploa acilepis* is so named for its resemblance in phyllary features to Asian *Acilepis* D. Don, which is not closely related and which differs from *Lepidaploa* by "unequal deeply separated cells" of the cypselar duplex trichomes and by usually "totally deciduous pappus" (Robinson & Skvarla 2009).



Figure 1. Field photograph of *Lepidaploa argyropappa* showing erect leafy flowering branches, sessile axillary capitula, outer phyllaries spreading and subulate-spinose, and the inner phyllaries more or less appressed and acuminate apically. The individual florets have lavender corollas and the pappus bristles are white. (Pruski & Ortiz 4144).



Figure 2. Field (roadside) photograph of *Lepidaploa tortuosa* showing an arching leafy flowering branch, sessile capitula, involucre of tightly appressed broad-tipped phyllaries, and white well-exserted corollas spreading laterally from the involucre. (Pruski *et al.* 4239).

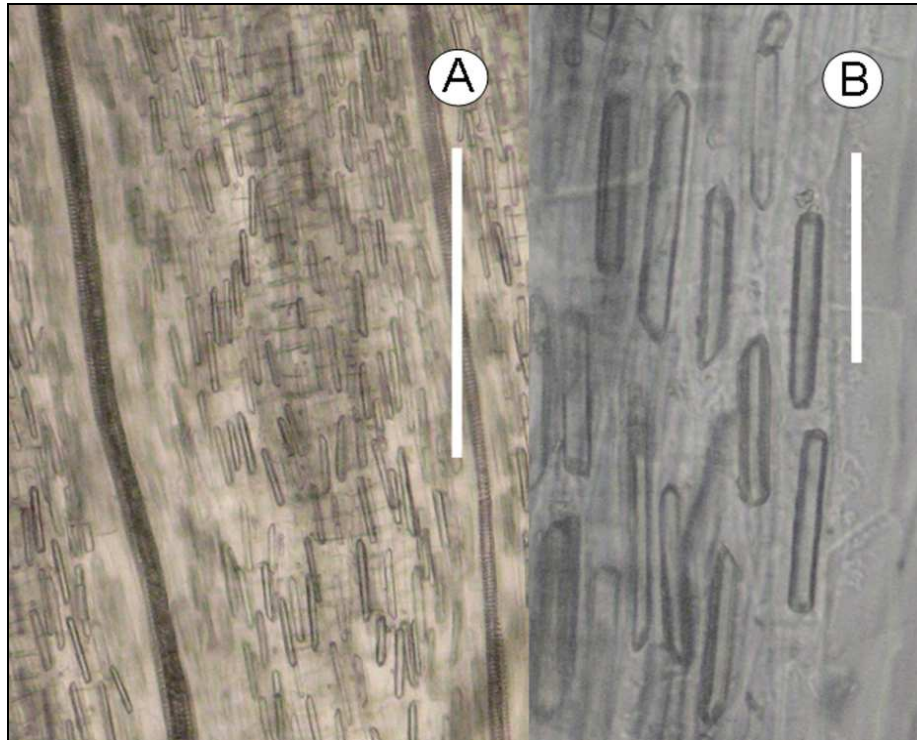


Figure 3. Elongate hexagonal pericarp raphide crystals in *Lepidaploa tortuosa*, typical of *Lepidaploa*. (Both from Pruski *et al.* 4239, MO; reprinted from Pruski 2016). [Scale bars: A 50 μ m; B 10 μ m].

In the discussion above and in what follows, species are generally referred to as *Lepidaploa* when nomenclatural combinations exist for them, even though called *Vernonia* in for example Gleason (1906, 1922, 1923), Keeley (2001), Nash (1976), and Turner (2007).

LEPIDAPLOA (Cass.) Cass., Dict. Sci. Nat. (ed. 2) 36: 20. 1825. *Vernonia* subgen. *Lepidaploa* Cass., Bull. Sci. Soc. Philom. Paris 1817: 66. 1817. *Vernonia* sect. *Lepidaploa* (Cass.) DC., Prodr. 5: 26. 1836. **LECTOTYPE** (viz Robinson 1990): *Vernonia albicaulis* Vahl ex Pers. (= *Lepidaploa glabra* (Willd.) H. Rob.).

Annual or perennial herbs to subshrubs, vining shrubs, or trees to 7(–20) m; stems erect, often branched, leafy, mostly pubescent, usually eglandular; herbage sessile-glandular or with simple trichomes, trichomes never stellate or T-shaped. **Leaves** alternate(-opposite), sessile or petiolate; blade usually elliptic to ovate, mostly (stiffly) chartaceous, pinnately veined, never lobed, surfaces usually concolorous. **Capitulescence** axillary of 1–few sessile capitula on leafy stems, or terminal and held above leaves, seriated-cymose with repeated axillary-lateral branching overtopping-displacing the more mature sessile (rarely pedunculate) previous capitulum, branch apices slightly curved and somewhat arcuate, sometimes fractiflex, the maturation indeterminate (as is characteristic of Compositae) but appearing determinate, capitula single or clustered, typically subtended by reduced bracteate leaves, when obviously exerted and held above the axis unbranched for 5+ nodes, the flowering branchlet main axis one per node. **Capitula** homogamous, discoid, mostly 8–60-flowered, characteristically sessile or nearly so, very rarely obviously long-pedunculate (in Mesoamerica only in *L. chiriquiensis*); involucre usually campanulate, terete in cross-section; phyllaries usually more numerous than the florets, spirally imbricate, persistent but spreading laterally post-fruit, graduate to merely slightly so with outer phyllaries sometimes more than half as long as the inner, 3–6(–9+)-seriate, lanceolate (acicular to oblong), mostly green or purplish-tipped, margins sometimes hyaline, often dimorphic, never long-appendiculate nor strongly colored throughout, the outer phyllaries often spreading, commonly slender with aristate apices, the inner phyllaries commonly erect with acute (acuminate-rounded) apices; clinanthium epaleate, commonly flat and foveolate at anthesis, becoming convex and smooth post-fruit. **Florets** bisexual, 5-merous; corolla actinomorphic or nearly so, never discoid-subligulate, pre-anthesis usually relatively narrowly funnelliform with a tube much longer than the limb to salverform with lobes spreading (coiling when dried) near anthesis, throat usually much shorter than either the tube or the lobes (corolla infrequently gradually and broadly funnelliform short-tubed with and elongate throat), mostly violet throughout, violet with a white tube, or white throughout, often papillose-setulose or glandular (but never stipitate-glandular), especially so apically on the 5 elongate lobes, the tube generally glabrous, the pair of marginal veins in the lobes usually relatively broadly fused apically; anthers with appendages characteristically eglandular, infrequently glandular, spurred at base, the spurs polleniferous and longer than collar; pollen echinolophate; styles branches ascending-elongate, filiform-subulate, stigmatic surface continuous, shaft papillose distally, base with glabrous node. **Cypselae** monomorphic, never carbonized, prismatic, commonly (5–)8–10-ribbed, generally setose with antrorse duplex trichomes of equal appressed (infrequently divergent at apex) paired cells, often also glandular, rarely solely glandular with no duplex trichomes, pericarp surface cells usually with elongate hexagonal raphide crystals (Fig. 3; Robinson 1999; Pruski 2016); carpodium well-developed, symmetric, several cell layers tall; pappus double, never coroniform, white or dull white to less commonly brown, persistent or inner bristles fragile with age, outer series of several distinct short scales, inner series of many long straight bristles. $n = 10, 16, 17$ (but published miscounts apparently frequent).

Characters. The often used key character of the capitulescences being terminal and held well above leaves vs. the capitulescences being leafy and axillary is a convenient and generally trustworthy character. The terminal vs. axillary character is usually diagnostic, but sometimes aphyllous terminal flowered *L. canescens* may initiate flowering on extremely foreshortened axillary branches (viz *Cándido* 7; and *King* 5256 cited by Robinson 1990) and seems axillary-flowered. Conversely, axillary-flowered *L. tortuosa* may have some leaves deciduous, thereby falsely appearing terminal-flowered. Gleason (1906, 1922) treated usually terminal-flowered *L. canescens* in a group

apart from most species now referred to *Lepidaploa*. Similarly, Jones (1979) cited *Vernonia salzmannii* within ser. *Canescentes* and *V. argyropappa* as belonging to ser. *Foliatae*, but he subsequently (Jones 1980) treated them together as *V. salzmannii*, characterized by capitulescences "sparingly branched." Although inner phyllaries in *L. tortuosa* may vary from narrow to broad, they are always broad-tipped. The outer phyllary lengths relative to that of the inner phyllaries may vary in several species (e.g., *L. argyropappa*, *L. canescens*), but the outer phyllary shape is not very variable.

The corollas of *Lepidaploa acilepis*, *L. argyropappa*, and *L. uniflora* are distinctly tubular-funnelform, and those of *L. tortuosa* and *L. vernicosa* are relatively narrowly funnelform becoming slightly salverform. Those of *L. canescens* and *L. lehmannii* are short, obviously salverform, and basically without a throat. In each of the seven aforementioned species, the tube is as long as limb to much longer than limb. This is in contrast to the gradually broadly funnelform, moderately short-tubed *L. polypleura* and *L. tenella*. *Lepidaploa polypleura*, *L. tenella*, and *L. uniflora* are similar in having hairy corolla limbs, and in this regard stand apart from the other species. The most noteworthy species in corolla form is perhaps short-tubed gradually broad-funnelform or campanulate glabrous flowered *L. chiriquiensis*, which nevertheless has floral microfeatures (i.e., nodular style, and elongate-hexagonal pericarp raphide crystals) consistent with its placement in *Lepidaploa*. The corolla color of our species is mostly lavender to violet; *L. tortuosa* is odd in its white corollas. The five axillary-flowered species are those with the relatively long tubed-flowers, whereas the salverform and broad-flowered species are terminal-flowered.

Of our species, *Lepidaploa acilepis* and *L. uniflora* are the smallest herbs and *L. polypleura* is the tallest tree. *Lepidaploa uniflora* is totally different from all species by its glandular cypselae and adaxially obviously glandular leaves. *Lepidaploa tortuosa* and *L. vernicosa* are recognized by their unusually large capitula. Only *L. lehmannii* consistently displays glomerulate capitula. The most distinctive leaf venation and darkest pappus are those of plurinerved *L. polypleura*. *Lepidaploa argyropappa* and *L. canescens* are similar in their pilose leaves and commonly impressed-veined adaxial leaf surfaces, but mostly *L. argyropappa* is an axillary-flowered herb and *L. canescens* a terminal-flowered shrub. Further distinctions follow in the key below.

Distributions. The three most widespread species with nearly continuous distributions from Mexico to Panama are *Lepidaploa argyropappa*, *L. canescens*, and *L. tortuosa* (Pruski 2013). On rare occasions plants of *L. canescens* (especially in northern South America) have glabrous (not papillose-setulose or glandular) corolla tubes, and glandular-leaved *L. argyropappa* in the middle of Central America has longer outer phyllaries than does the type from Huánuco, but both are treated broadly here with no segregates used. However, *L. vernicosa* is pulled from synonymy of *L. tortuosa*, even though *L. tortuosa* occurs on all sides of the range of the narrowly endemic *L. vernicosa*.

I follow Ekman (1914), who noted that beginning with Baker (1873) the name *Lepidaploa salzmannii* has generally been misapplied (e.g., Jones 1980; Robinson 1990, 1999) to the widespread neotropical weed that occurs mostly from western Brazil and Peru northeastwards near continuously into Mexico. This weed is usually moderately pilose-leaved, nodally single-capitulate, and white-pappose: its name is changed here from *L. salzmannii* back to *L. argyropappa*. Moreover, Ekman (1914), in his summary of the *L. argyropappa* group, did not consider *L. salzmannii* as closely related to the *L. argyropappa* species group. Rather, *L. salzmannii* proves to have weakly pubescent leaves, mostly 2–3 small capitula per node, a tawny pappus, and is endemic to Brazil. The redefined *L. argyropappa* is among Brazilian species similar to *L. aurea* (Mart. ex DC.) H. Rob., which is a different, much more pubescent plant with adaxially glandular leaf blades.

Lepidaploa canescens is usually recognized by its small capitula, narrow inner phyllary apices, papillose-setulose or glandular corolla tubes, and terminal flowers. *Lepidaploa canescens* has a near continuous distribution from Central America into South America, so much so that although corolla tube papillosity varies in northern South America, segregates are hard to envision. West Indian *L. arborescens* (L.) H. Rob., however, appears geographically and morphologically distinct from it. On the other hand, a large geographic break occurs between morphologically similar sparsely pubescent *L. remotiflora* and more densely pubescent *L. acilepis*, and in this case the narrow species concepts used here are supported partly by allopatry. Other relatively narrowly endemics are *L. acilepis*, *L. chiriquiensis*, *L. polypleura*, *L. tenella*, *L. uniflora*, and *L. vernicosa*. *Lepidaploa lehmannii* is common in Colombia and Venezuela and newly reported here in Central America. In summary, Central American *Lepidaploa* more or less resembles most groups with about ten species, i.e., composed mostly of one to few widespread neotropical weeds (some of which are admittedly arbitrarily circumscribed and need further study), but the bulk of the group consists of narrowly defined regional endemics.

1. Capitulescence axillary and leafy; corolla tubes relatively long.
 2. Cypselae glandular; leaves obviously glandular adaxially **9. *Lepidaploa uniflora***
 2. Cypselae rarely glandular; leaves not obviously glandular adaxially.
 3. Inner series of phyllaries constricted then distally dilated and cucullate, obtuse to rounded at apex **8. *Lepidaploa tortuosa***
 3. Inner series of phyllaries never dilated, not cucullate, acute at apex.
 4. Capitula 12–18 mm long **10. *Lepidaploa vernicosa***
 4. Capitula 7–12 mm long.
 5. Erect annual or short-lived perennial herbs 0.12–1 m tall; leaves widest at or above the middle of blade, eglandular abaxially **1. *Lepidaploa acilepis***
 5. Perennial herbs or subshrubs 0.5–2 m tall; leaves widest in proximal 1/3 of blade, glandular abaxially **2. *Lepidaploa argyropappa***
2. Capitulescence terminal and held above stem leaves; corollas salverform or broad.
 6. Capitula often obviously pedunculate; corollas gradually broad-funnelform or campanulate **4. *Lepidaploa chiriquiensis***
 6. Capitula sessile; corollas more or less broadly funnelform, but not campanulate.
 7. Shrubs to trees 3–19 m tall; stems angled; inner phyllaries broad-tipped **6. *Lepidaploa polypleura***
 7. Subshrubs, shrubs, or vines 1–8 m tall; stems subterete; inner phyllaries narrow-tipped.
 8. Corolla tube papillose-setulose or glandular **3. *Lepidaploa canescens***
 8. Corolla tube glabrous.
 9. Terminal capitula glomerate **5. *Lepidaploa lehmannii***
 9. Terminal capitula usually 1–2 cm apart **7. *Lepidaploa tenella***

1. LEPIDAPLOA ACILEPIS (Benth.) Pruski, **comb. nov.** *Vernonia acilepis* Benth., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1852: 68. 1853. **TYPE: NICARAGUA. Masaya.** Volcán Masaya, 2000 ft., Dec 1847, *Oersted 2/8528* (holotype: K-BENTH; isotypes: C, F, US). The holotype is numbered as 2 [perhaps a species number], but the isotypes are numbered "8528." The isotype in C was photographed as Macbride number 22654, but was not seen on microfiche of the Copenhagen types (IDC microfiche 2204, card 214). Figs. 4, 5B.

Erect annual or short-lived perennial herbs 0.12–1 m tall; stems simple to few-branched, striate distally, thinly to moderately strigillose-villosulous, eglandular, somewhat sparsely leafy, internodes about 1/2+ as long as leaves. **Leaves** short-petiolate; blade 2.5–11 × 1–5 cm, elliptic to characteristically obovate (widest at or above the middle), thinly chartaceous, secondary veins 4–5 per side, often curving towards apex, both surfaces eglandular, adaxial surface smooth, thinly and sparsely to moderately villous-pilose adaxially and more densely so abaxially, trichomes 0.5–1+ mm long, basal cell of trichomes sometimes dark and leaves falsely appearing glandular, base cuneate to attenuate, margins subentire to serrulate, apex acute to acuminate; petiole 0.1–0.5 cm long. **Capitulescence** of axillary, remote, single(–3) capitula per node in smaller plants, in larger plants of (1–)3–5+ leafy seriated cymose branchlets in distal 1/2–2/3 of stem, each cymose branchlet 4–9+ capitulate, nodes usually 2–3 cm long, capitula single(–3) per node. **Capitula** 7–10 mm long, 12–19-flowered; involucre 7–9 × 4–8 mm long, turbinate-campanulate, nearly as long as florets; phyllaries 3–4-seriate, erect or outer ones somewhat spreading, villous-strigillose, eglandular; outer series of phyllaries 2–4 × 0.3–0.7 mm long, linear-lanceolate, about half as long as inner, 1-costate in distal 1/2, apex long-subulate with apical mucro 1–2 mm long; inner phyllaries 7–9 × 1.2–1.8 mm long, elliptic-lanceolate, margins scarious, purplish distally, apex acuminate. **Florets:** corolla 4–6 mm long, tubular-funnelform, pale pink to lavender, glabrous, tube often elongate, to ca. 4 mm long and obviously longer than the sometimes short limb, throat and lobes often nearly subequal, lobes ca. 1.1 mm long, eglandular. **Cypselae** 1.3–3 mm long, substrigose, trichomes to ca. 0.4 mm long, eglandular; pappus white or dull white or sometimes brown; outer squamellae 0.5–0.8 mm long; inner bristles 4–5 mm long, reaching to middle of corolla lobes.

Distribution and Ecology. *Lepidaploa acilepis* is an occasional regional Central American endemic known to me from only El Salvador, Nicaragua, and Costa Rica, where it is centered in the drier Pacific watershed. It was not reported in Honduras by Clewell (1975). The species should be looked for in Guatemala and Mexico, to where it has been attributed, but all collections from there examined by me are misdeterminations. *Lepidaploa acilepis* occurs from 100–700(–1500) meters elevation and has been collected in flower from September to December. Although long-known from Costa Rica based on B.L. Robinson's determination of *Tonduz 13595* (cited by Gleason 1906), *L. acilepis* was not treated by Standley (1938). The Gleason (1922) citation of the type locality as Costa Rican was erroneous, as Volcán Masaya instead is in Nicaragua. Vouchers cited by Gleason (1906) and those here, however, document the species in Costa Rica.

Representative collections. COSTA RICA. *Chavarria 887* (MO); *Chavarria 1324* (MO); *Chavarria 1968* (MO); *Grayum 12349* (MO); *Heithaus 482* (MO); *Opler 1579* (MO); *Tonduz 13595* (US). **EL SALVADOR.** *Calderón 1373* (US); *Castillo ISF00496* (B, K, LAGU, MO); *Rodríguez & Tejada 2152* (B, LAGU, MO); *Sandoval ES-01704* (B, EAP, K, LAGU, MO); *Tucker 440* (US). **NICARAGUA.** *Moreno 11715* (MO); *Neill 2856* (MO-2); *Neill 2925* (MO-3); *Stevens 10882* (MO).

Lepidaploa acilepis (as *Vernonia*) was recognized by Hemsley (1881), Gleason (1906, 1922), Nash (1976), Villaseñor (1989), and Keeley (2001) but reduced to synonymy with *L. remotiflora* (Rich.) H. Rob. by Robinson (1990), who was followed by Redonda-Martínez and Villaseñor (2011) and Pruski (2013). Here, Central American *L. acilepis* is resurrected from synonymy with South

American *L. remotiflora* as lectotypified by Pruski (1998). *Lepidaploa acilepis* differs from *L. remotiflora* by its corolla tube relatively longer, shorter eglandular corolla lobes, and more densely pubescent stems, adaxial leaf surfaces, and phyllaries. *Lepidaploa remotiflora* is thus excluded from Central America, with the collections from Costa Rica northwest into El Salvador proving instead to be *L. acilepis*. Material from Guatemala and Mexico previously identified as either *L. acilepis* or *L. remotiflora* are mostly redetermined as either *L. argyropappa* or *L. uniflora*.



Figure 4. Representative specimen of *Lepidaploa acilepis* showing leaves widest at or above the middle. (Grayum 12349, MO).

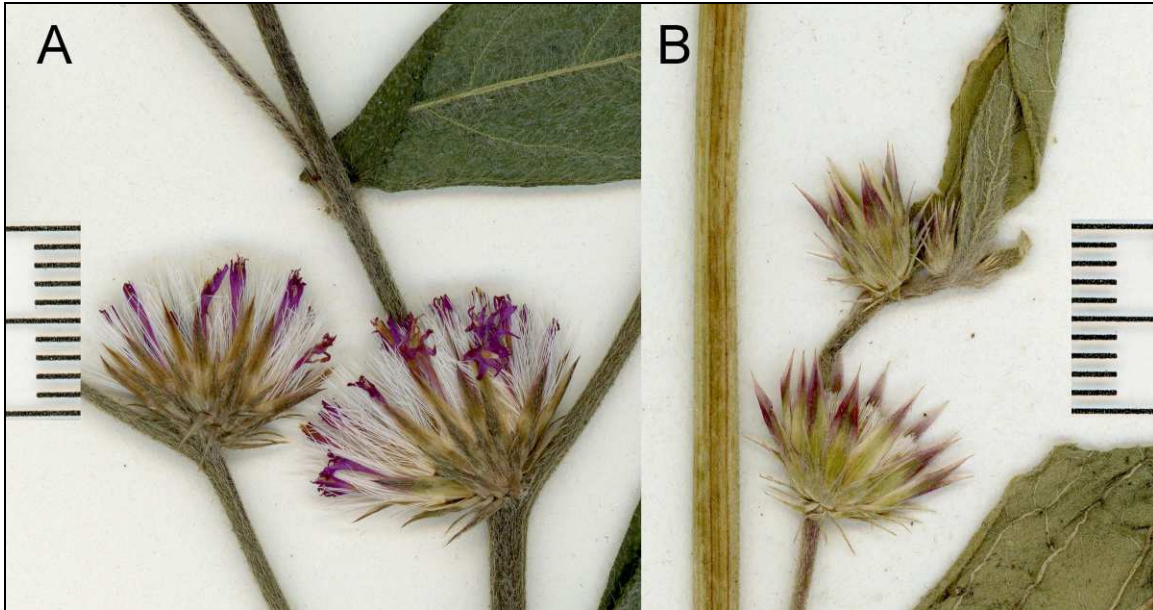


Figure 5. Involucres of (A) *Lepidaploa argyropappa* and (B) *Lepidaploa acilepis*. In each species the outer phyllaries are acicular, and the apices of the inner phyllaries acute to acuminate. At anthesis the pappus bristles of *Lepidaploa argyropappa* (A) are about as long as the tubular-funnelform corollas. A metric scale is positioned vertically in each image. (A Pruski & Ortiz 4144, MO; B Neill 2856, MO, a topotype).

By its short stature and apically narrowed inner phyllaries, *Lepidaploa acilepis* among Central American *Lepidaploa*s seems most similar to *L. uniflora* (Mill.) H. Rob. *Lepidaploa uniflora*, basically a Yucatán Peninsula endemic, differs from *L. acilepis*, however, by setose corollas limbs and by entire leaves glandular on both surfaces. By its small herbaceous habit and broad, thinly chartaceous leaves, *L. acilepis* is similar to Brazilian ***Lepidaploa ovata*** (Less.) Pruski, **comb. nov.** (basonym: *Vernonia ovata* Less., *Linnaea* 4: 294. 1829), which differs from *L. acilepis* by larger campanulate capitula, obtuse inner phyllaries, weakly pubescent leaves. Other similarly aristate-phyllaried regional species are *L. canescens* and *L. argyropappa*, but they are much taller plants.

Reports of the species in Guatemala and Mexico were not verified by me. Collections determined earlier as either *Lepidaploa acilepis* or *L. remotiflora* but here redetermined as other species include: (1) Cowan 2773 from Tabasco cited by Cowan (1983) as *L. acilepis* is a misdetermination of the similar *L. argyropappa*; (2) Croat 47502 from Chiapas cited by Redonda-Martínez and Villaseñor (2011) as *L. remotiflora* proves instead to be *L. tortuosa*; (3) Orellana 50 from Guatemala distributed from BIGU as *L. acilepis* is determined here as *L. argyropappa*; (4) Contreras 9347 (US) from Guatemala annotated *in sched.* in 1983 by Keeley as *V. acilepis* is *L. argyropappa*. Standley and Steyermark (1940: 394) reported *Standley 59631* (F) from Fiscal as *L. acilepis*, and commented that only a single plant was found. Guatemalan collections also determined *in sched.* by Jones and Keeley as *V. acilepis* include *Steyermark 31195* (NY) and *Standley 59192* (NY). Nash (1976: 21) also reported *L. acilepis* in both Guatemala and Chiapas, but I do not have at hand the collections seen by her. Her report of *L. acilepis* in Jutiapa is not based on the above Standley or Steyermark material. Although I do not have at hand *Standley 59192*, *Standley 59631*, *Steyermark 31195*, and all Chiapas collections, *L. acilepis* should nevertheless be looked for in Guatemala, especially given that Samuel Jones, Sterling Keeley, Rosario Redonda-Martínez, Dorothy Nash, Paul Standley, Julian Steyermark, and José Luis Villaseñor are renowned specialists and their determinations can be trusted. On the other hand, I cannot verify that *L. acilepis* occurs in Chiapas, and the species is excluded provisionally from Mexico.

2. **LEPIDAPLOA ARGYRO-PAPPA** (H. Buek) Pruski, **comb. nov.** *Vernonia argyropappa* H. Buek, Gen. Sp. Synon. Cand. 2: v. 1840. [this is a nom. nov. in the preface and numbered using the Roman numeral v; the page numbered page 5 using Arabic numerals is a different page having some of the index to genera that begin with the letter A]. *Vernonia poeppigiana* DC., Prodr. 5: 55. 1836 (non DC. 5: 20. 1836). *Vernonia geminiflora* Poepp., Nov. Gen. Sp. Pl. 3: 42. 1843, nom. superfl. **TYPE: PERU. Huánuco.** Prope Cuchero, Jul 1829, *Poeppig* pl. exs. n. 1204 [species number 31] (holotype: G-DC, as Macbride neg. 8135, as IDC microfiche 800. 774.III.8; isotypes: F, HAL, NY, W). Pruski (2012) gave the Ruiz and Pavón and Poeppig locality of Cuchero (abandoned when visited by Poeppig) as "near modern day San Juan, and about 4–8 km SW of the boca del Río Chinchao at the Río Huallaga, 9° 30–31' S, 75° 56–59' W." Poeppig (1843) gives the locality more precisely as at Pompayaco [aka Pompayacu], which is at 9° 33' 28" S, 75° 54' 35" W or about 6 km SE of Cuchero and just across (east of) río Huallaga. Figs. 1, 5A, 6–8.

Cacalia argyropappa (H. Buek) Kuntze, *Cacalia virens* (Sch. Bip. ex Baker) Kuntze, *Vernonia friedrichsthalii* Sch. Bip. ex Ekman, *Vernonia guianensis* V.M. Badillo, *Vernonia miersiana* Gardner, *Vernonia virens* Sch. Bip. ex Baker

Perennial herbs (less commonly perhaps subshrubs) 0.5–2 m tall; stems erect, simple or few-branched, striate, hirsute to pilose with appressed or ascending trichomes. **Leaves** subsessile or short-petiolate; blade 3–14(–18) × 0.7–3.5(–8) cm, lanceolate to elliptic-lanceolate or rarely oblanceolate, usually widest in proximal 1/3 of blade, chartaceous, secondary veins usually 4–6 per side, sometimes obviously impressed adaxially, prominent abaxially, strongly arching toward apex, surfaces concolorous to sometimes somewhat discolored, adaxial surface puberulent to hispid or strigose, eglandular, veins often impressed with surface appearing rugulose, abaxial surface strigose to pilose-villous with trichomes to ca. 1+ mm long, typically patent-antrorse, also glandular, base cuneate or obtuse to sometimes rounded, margins usually entire or sometimes minutely serrulate, sometimes subrevolute, apex acute to acuminate; petiole 0.1–0.5 cm long. **Capitulescence** of leafy few-branched weak seriate-cymes, ultimate branches usually 10–15 cm long, 5–12-capitulate, capitula sessile, remotely spaced (internodes 1–3 cm long) and capitula at anthesis always subtended by a leaf much larger than capitulum, capitulescence leaves similar to vegetative leaves but slightly smaller. **Capitula** 9–12 mm long, 21–35(–40)-flowered; involucre 6–10 × 9–14 mm, campanulate to nearly hemispheric, phyllaries moderately graduate with outer usually at least about half as long as inner, 4–6-seriate, outer and mid-series phyllaries pilose to inner series only sparsely pilose; outer and mid-series phyllaries 3–6 × 0.3–0.8 mm, linear-lanceolate, sometimes recurved, outer series with somewhat thickened pale midrib extending into subulate-subspinose apex, mid-series narrowly attenuate, not spinulose, without midrib prominulous distally; inner series of phyllaries 6–10 × 1–1.5 mm, lanceolate, the thin midrib pale sometimes purplish, apex acuminate; clinanthium to 3 mm diam., often dome-shaped. **Florets:** corolla 5–8 mm long, sometimes those of the marginal florets noticeably longer than those of the central florets, tubular-funnelform, reddish-purple, glabrous, or apex of lobes sometimes papillose-glandular, tube elongate, 3.5–4.5 mm long, gradually widening into throat, often noticeably longer than limb, lobes 1–1.6 mm long. **Cypselae** 1.5–2.8 mm long, densely substrigose to hirsutulous, usually eglandular or sometimes at maturity glandular especially proximally (sometimes with resiniferous idioblasts prominent throughout); pappus white or dull white, outer squamellae 1–1.5 mm long, inner bristles 6–8 mm long, usually slightly exerted from involucre.



Figure 6. *Lepidaploa argyropappa* line drawing showing impressed secondary veins. Reproduced from Pruski 1997, Fig. 256.

Distribution and Ecology. *Lepidaploa argyropappa* is widespread in the Neotropics, occurring in Mexico, Central America, Colombia, Venezuela, Guyana, Ecuador, Peru, Bolivia, and western Brazil. In Central America it occurs from near sea level to 1800 meters elevation, flowers mostly from December to May, and seems only to have not been collected in flower in July. It is noteworthy, however, that this widespread moderately common species was not cited by Elias (1975), Correa et al. (2004), or Pruski (2013) for Panama, where it represents a new record.

Representative collections. **BELIZE.** *Bartlett 11340* (MO, US); *Davidse & Brant 32472* (MO, US); *Gentle 3889* (MO, NY); *Gentle 8144* (MO, NY, TEX); *Schipp 85* (MO, NY). **COSTA RICA.** *Haber & Zuchowski 10478* (CR, MO, TEX); *Pittier 3252* (US; cited by Klatt 1892 as *Vernonia remotiflora* var. *tricholepis*); *Pittier 12159* (US); *Skutch 2385* (MO, US); *Skutch 4176* (MO, US); *Tonduz 13268* (US); *Wilbur & Stone 10098* (MO, US). **EL SALVADOR.** *Standley 21565* (US); *Tucker 771* (US). **GUATEMALA.** *Contreras 9347* (MO, US; cited in Villaseñor 1989: 108 sub *Vernonia argyropappa*; US annotated by Keeley 1983 as *V. acilepis*); *Orellana 50* (BIGU, MO; distributed to MO as *V. acilepis*); *Véliz 95.4360* (BIGU, MO); *Williams et al. 42204* (F, NY, US). **HONDURAS.** *Blackmore & Heath 1602* (BM, MO); *Croat & Hannon 64442* (MO, US); *Nelson et al. 7905* (MO, UC, US). **MEXICO. Chiapas.** *Matuda 1914* (MEXU, MO, TEX, US); *Méndez Ton (Shilom Ton) 5733* (IEB MEXU, MO). **Tabasco.** *Cowan 2773* (CAS, ENCB, MEXU, MO, NY). **Veracruz.** *Pruski & Ortiz 4144* (MO, XAL). **NICARAGUA.** *Atwood 4018* (BM, F, GH, MO); *Proctor 27397* (NY, US); *Rueda 15806* (MO, US); *Stevens 7367* (MO). **PANAMA.** *Correa et al. 4786* (MO, PMA); *Correa et al. 10492* (PMA, US); *Galdames & Stapf 5391* (US).



Figure 7. Isotype of *Vernonia poeppigiana* [\equiv *Lepidaploa argyropappa*] showing the somewhat discolored leaves and axillary capitula. (Poeppig pl. exs. n. 1204, NY).

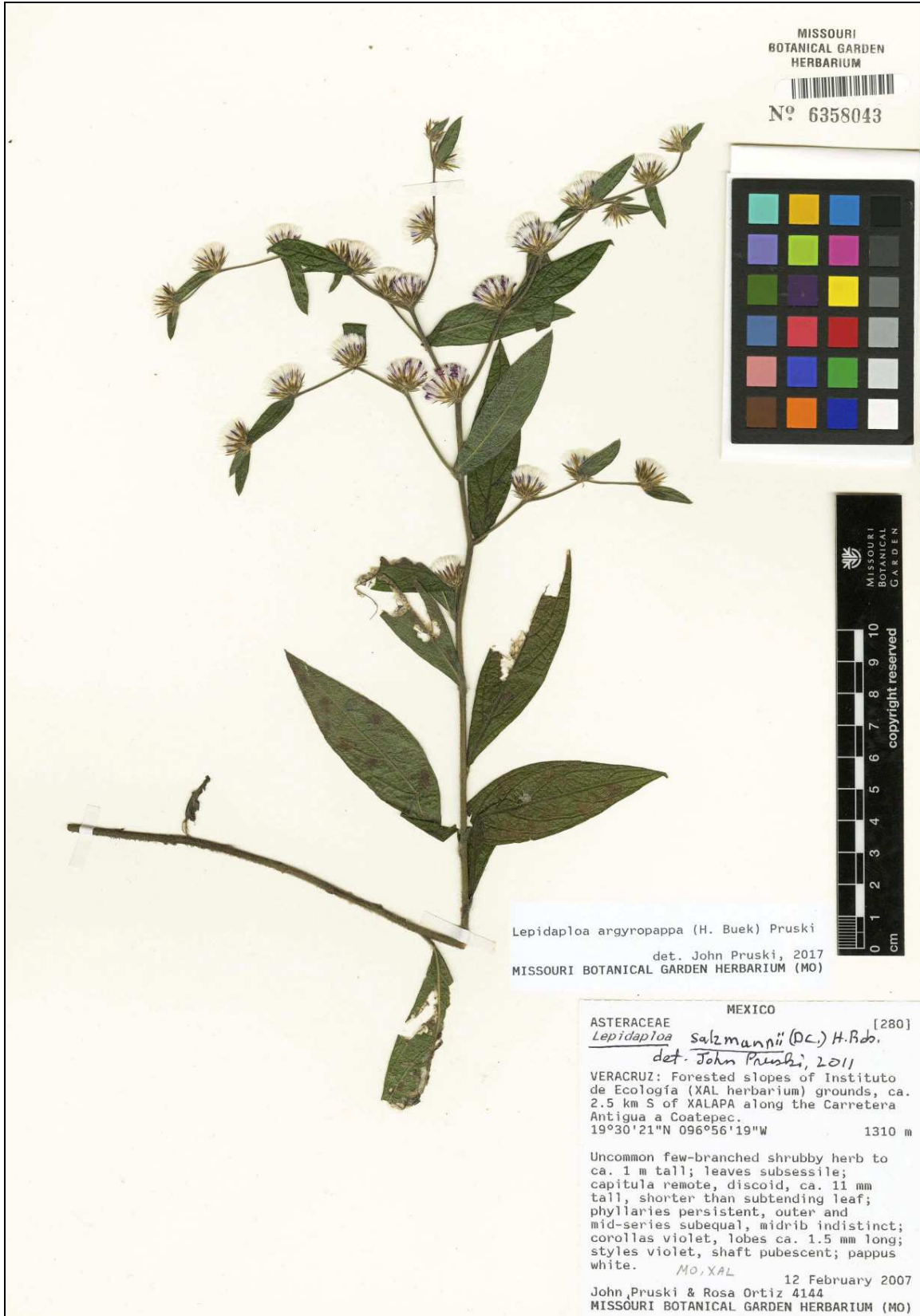


Figure 8. Representative specimen of *Lepidaploa argyropappa* showing the relatively large, axillary capitula. (Pruski & Ortiz 4144, MO).

In Central America, the name *Lepidaploa argyropappa* has usually been used for our plants (e.g., Gleason 1906, 1922; Standley 1938; Clewell 1975; Nash 1976; Jones 1979; Villaseñor 1989; Rzedowski & Calderón de Rzedowski 1995; Keeley 2001). Ekman (1914) in his key to "The allies of *Vernonia argyropappa* H. Buek," recognized *V. argyropappa*, *V. hirsutivena* from the Yucatán (= *L. canescens*), and *V. miersiana* Gardner [which included fide Ekman 1914 *V. salzmännii* DC. sensu Baker (1873) non DC. 1836]. Ekman (1914) segregated from *L. argyropappa* more strongly cuspidate-phyllaried *V. friedrichsthalii* Sch. Bip. ex Ekman, which is based presumably on material from either Nicaragua or Costa Rica. Nash (1976) gave *V. friedrichsthalii* as a nomen and in synonymy with *L. argyropappa*. *Vernonia miersiana* Gardner was treated in synonymy with *L. salzmännii* by Robinson (1990, 1999), but I do not have material of it at hand and leave it unplaced. Material from Costa Rica and Nicaragua often has longer outer series of phyllaries than, for example, Andean and Mexican plants, but across the species range there seems to be a continuum in outer phyllary lengths relative to that of involucre and segregates are not recognized here.

After Jones (1980) in Flora of Peru treated *Lepidaploa argyropappa* in synonymy with *L. salzmännii* and Robinson (1990, 1999) resurrected *Lepidaploa*, however, the name *L. salzmännii* has been adopted uncritically (e.g., Pruski 1997, 2013; Turner 2007; Nelson 2008; Redonda-Martínez & Villaseñor 2011). Here, too, the common Neotropical species is interpreted broadly but excludes the type of *V. salzmännii* from Bahia, which is a very different plant that is weakly pubescent leaved, mostly 2–3 nodally capitulate, and has a tawny pappus. The name *Vernonia velutina* Hieron. from Rio de Janeiro has occasionally been treated in synonymy of *L. salzmännii* sensu auct., but by its terminal capitulescence is excluded here from synonymy of each *L. argyropappa* and *L. salzmännii*.

By similar glandular leaves axillary-flowered *Lepidaploa argyropappa* recalls *L. canescens*, which differs usually by its terminal flowers and papillose-setulose corolla tubes. By relatively large capitula *L. argyropappa* is somewhat similar to *L. tortuosa*, but *L. argyropappa* differs by basically sessile chartaceous leaves, by corolla lobes only 1–1.6 mm long, by outer and mid-series phyllaries often more pubescent than inner phyllaries, and by subequal outer and mid-series phyllaries with midrib indistinct or merely prominulous. The corolla tube of *L. argyropappa* often noticeably elongates during flower. The citation by Sousa and Cabrera (1983) and Martínez et al. (2001) of *L. argyropappa* in Quintana Roo and Campeche, respectively, are based on misdeterminations of vouchers referred here to *L. uniflora*.

3. LEPIDAPLOA CANESCENS (Kunth) H. Rob., Proc. Biol. Soc. Wash. 103: 483. 1990. *Vernonia canescens* Kunth, Nov. Gen. Sp. (folio ed.) 4: 27, tab. 317. 1820 [1818]. **TYPE: PERU. Piura.** Prope Huancabamba (as "Guancabamba"), 127 hex, (?Apr–?Aug) 1802, *Humboldt & Bonpland 3529* (holotype: P-HBK, as IDC microfiche 6209 91.II.5; isotype: P, as Macbride neg. 37320). Sandwith (1968) gave as Aug 1802 the date of the Huancabamba collections, but the protologue noted the flowering epoch as April, conflicting with Sandwith. Humboldt material in B-W and HAL may be type material of other Kunth species, i.e., of synonymous *V. micrantha* Kunth, or *V. mollis*. Figs. 9–10.

Cacalia bullata (Benth.) Kuntze, *Cacalia canescens* (Kunth) Kuntze, ?*Lepidaploa aristata* Cass., *Vernonia arborescens* var. *cuneifolia* Britton, *Vernonia bullata* Benth., *Vernonia canescens* var. *pilata* S.F. Blake, *Vernonia cuneifolia* (Britton) Gleason, *Vernonia hirsutivena* Gleason, *Vernonia medialis* Standl. & Steyerl., ?*Vernonia micradenia* DC., *Vernonia micrantha* Kunth, *Vernonia patuliflora* Rusby, *Vernonia pseudomollis* Gleason, *Vernonia purpusii* Brandegees, *Vernonia rusbyi* Gleason, *Vernonia sodiroi* Hieron., *Vernonia unillensis* Cuatr., *Vernonia volubilis* Hieron.



Figure 9. Representative specimen of *Lepidaploa canescens* showing single capitulescence branch per node, each of which then branches distally. (Pruski et al. 1319, MO).

Subshrubs to shrubs 1–5(–8) m tall; stems erect to scandent, laxly branched, sprawling, subterete, striate distally, villous or densely puberulent, glabrate proximally, leaves usually well-spaced. **Leaves** alternate, petiolate; blade (3–)5–14(–20) × (1.5–)2.5–5(–7) cm, lanceolate to ovate-elliptic, rarely ovate or oblong, typically broadest in basal third of blade, secondary veins typically 6–11 per side, often impressed adaxially, prominent abaxially, diverging from midrib at about a 50° angle and thereafter strongly arching towards apex, surfaces occasionally slightly discoloured, adaxial surface sometimes rugulose or bullate with secondary veins deeply impressed, eglandular, scabrid with short erect trichomes to substrigose or pilose with elongate trichomes, trichome base sometimes prominent, abaxial surface typically glandular, pilosulose or pilose to densely sericeous, trichomes to ca. 1+ mm long, typically patent-antrorse, base cuneate to broadly obtuse or rounded, margins entire to remotely serrulate, sometimes revolute, apex acute to long-acuminate; petiole 0.3–1.7 cm long, villous. **Capitulescence** terminal from distal most nodes (very rarely axillary as in type of *V. hirsutivena* but then corolla tube papillose-setulose), typically very well-exserted, non-leafy, of (1–)few–many sparsely but usually repeatedly branched (-simple) seriated cymes (with the sessile capitula moderately well-spaced) typically 4–10 cm long, cymes often arranged in large spreading panicles to 20 × 15 cm, ultimate branchlets with several typically sessile (rarely short-pedunculate) and ebracteolate (seldom inconspicuously linear bracteolate, then typically the bracteate leaf is on the same side of the stem) capitula moderately remote and occurring singly (not in terminal glomerules), branchlets much less commonly shortened with capitula somewhat congested but not in well-defined terminal glomerules. **Capitula** 5–8 mm long, 18–27-flowered; involucre usually 4–6(–7.5) × 4–5 mm, campanulate; phyllaries 0.5–1 mm diam., 4–6-seriate, graduate, frequently tinged with violet; the outer series 1–2.5 mm long, narrowly lanceolate, somewhat spreading, sericeous to laxly arachnoid-tomentose, these and mid-series phyllaries typically strongly 1-costate to apex, apex typically spinose-aristate; inner series 4–6 mm long, lanceolate, subappressed, sericeous or only apically so, apex occasionally slightly glandular, typically obtuse, frequently short-apiculate, less much commonly aristate. **Florets** not greatly exserted from involucre; corolla 3.8–5.3 mm long, usually becoming obviously salverform, lavender (rarely white), tube 2.1–2.7 mm long, papillose-setulose or glandular (sometimes subglabrous in *V. medialis*, putative hybrids, and some South America plants), lobes (1–)1.5–2.2 mm long, usually very much longer than the short throat, usually sparsely setose and/or sparsely glandular (sometimes subglabrous in South America); anthers 1.5–2.3 mm long, tails 0.2–0.4 mm long, appendage rarely glandular; style branches 1.5–2.1 mm long. **Cypselae** 1.2–2(–2.5) mm long, turbinate, ribbed, sericeous or strigillose, eglandular but often with resiniferous idioblasts; pappus stramineous to white or dull white, the outer series of fimbriate scales 0.6–1 mm long, the inner series of bristles, usually 3.5–5 mm long. $2n = 32, 34$.

Distribution and Ecology. *Lepidaploa canescens*, presumably a diploid, is a common Neotropical species that occurs from Mexico and Central America southward to Colombia, Venezuela, Ecuador, Peru, Bolivia, and Brazil. In Central America is sometimes common enough to form large thickets. It also occurs on Trinidad and Tobago but not in the Antilles. The species flowers year-round and in Central America it has been collected from sea level to 2500 meters elevation.

Representative collections. **COSTA RICA.** *Cooper 5839* (MO, US); *Croat 47092* (MO, UC); *Grayum 10482* (MO); *King 6773* (MO, US); *Örsted 4/8540* (C-2 as IDC microfiche 2204 214.II.6–7, one sheet as Macbride neg. 22662, K-BENTH; type of *V. bullata*); *Rodríguez et al. 9762* (MO, NY); *Skutch 3446* (MO, NY, US). **EL SALVADOR.** *Calderón 58* (NY, US); *Calderón 1445* (MO, US); *Carlson 37* (F, MO); *Sandoval & Rivera 1481* (B, K, LAGU, MO); *Standley 20301* (NY, US). **GUATEMALA.** *Keeley & Keeley 3176* (MO); *King 7241* (NY, US); *King 7250* (MO, NY, US); *Nelson 3691* (F, US); *Skutch 1993* (F, GH, NY, TEX, US; type of *V. canescens* var. *pilata*); *Standley 63945* (F); *Standley 87473* (F; type of *V. medialis*). **HONDURAS.** *Clewell 3015* (MO); *Croat & Hannon 63877* (MO, US); *Edwards P-7855* (F, MO, NY, US); *Molina 815* (MO, US);

Williams & Molina 23248 (F, MO, US). **MEXICO. Chiapas.** *Breedlove & Almeda* 47686 (CAS, MO); *Matuda* 2784 (MEXU, MO, TEX); *Purpus* 7189 (MO, NY, UC, US; type of *V. purpusii*); *Ventura & López* 2976 (IEB, MEXU, MO, TEX); *Ventura & López* 2992 (IEB, MO, XAL). **Quintana Roo.** *Soto et al.* 22593 (MO). **Yucatán.** *Gaumer* 1325 (F, NY; type of *V. hirsutivena*; cited by Millspaugh and Chase 1904 as *L. arborescens*); *Gaumer* 23540 (MO, NY, US). **NICARAGUA.** *Coronado et al.* 482 (MO, USM); *Greenman & Greenman* 5800 (MO). **PANAMA.** *Allen* 187 (MO, US); *Allen* 1344 (MO, NY); *Bernal* 17 (MO); *Cándido* 7 (PMA, MO; axillary flowered but corolla tube setose); *D'Arcy & McPherson* 16087 (MO); *Darwin* 2831 (MO, NO); *Dwyer et al.* 522 (F, GH, K, MO, NY, UC, US); *Fendler* 160 (K, MO, US); *Gentry & Mori* 13582 (MO, US); *Greenman & Greenman* 5202 (MO); *Kennedy* 2280 (MO, US); *King* 6773 (MO, US); *Nee* 9310 (MO, NY); *Standley* 29314 (MO, US); *Valdespino* 53 (MO, NY, PMA); *Wilbur et al.* 13260 (DUKE, MO).

Lepidaploa canescens may be recognized most readily by its typically terminal capitulescence composed of many small sessile capitula with acicular outer phyllaries and narrow-tipped inner phyllaries. It commonly also has broad-based abaxially densely pubescent leaf blades with curved secondary veins. The synonyms *V. canescens* var. *pilata*, *V. medialis*, and *V. hirsutivena* from Guatemala and the Yucatán were named for more weakly pubescent-leaved, axillary capitulate, or larger capitulate populations. Nash (1976) recognized *V. medialis* as distinct, keying it by the nearly double the average involucre size of typical *L. canescens*, but Keeley (1982) reduced *V. medialis* to synonymy with *L. arborescens*. In Central America, *L. canescens* is perhaps most similar *L. lehmannii* (Hieron.) H. Rob., which differs by its capitula consistently clustered at the tips of its branchlets. By terminal capitulescences it is somewhat similar to *L. polypleura*, which otherwise is totally different, arborescent, has larger capitula, obtuse-tipped inner phyllaries, and a (usually) fulvous or tawny pappus.

Blake et al. (1926), Standley (1938), Clewell (1975), Elias (1975), Nash (1976), and McVaugh (1984) recognized *Lepidaploa canescens* (as *Vernonia*) in Central American, but Millspaugh and Chase (1904), Rzedowski and Calderón de Rzedowski (1995), and Turner (2007) cited *L. arborescens* in the Yucatán. Keeley (1982) treated *L. canescens* as a synonym of a broadly defined *L. arborescens*. Recently, Robinson (1990, 1999) recognized *L. arborescens* as a West Indian endemic and referred South American and Central American material to *L. canescens*. Robinson (1990) noted that *L. canescens* usually differs from West Indian material by having larger leaves, smaller involucre, more densely pubescent phyllaries, and by generally lacking capitulescence bracts, or in the infrequent cases when with foliar bracts then these are attached "on the opposite side of the stem" from the capitula (Robinson 1990). Indeed, by its characteristic aphyllous terminal capitulescence *L. canescens* was placed by Gleason (1906; viz also 1923: 195, Fig. 2b) in *Vernonia* sect. *Lepidaploa* "Scorpioideae Aphyllae" nearer to *Vernonanthura patens* than to species now placed in *Lepidaploa*.

Pruski (2010, 2013) applied the name *Lepidaploa canescens* to South American material, which he characterized as typically having usually setose but eglandular corolla lobes. He noted that that Antillean *L. arborescens* has glabrous corolla tubes, densely glandular corolla lobes, and eglandular cypselae often with resiniferous idioblasts. The Mesoamerican (and most South American) material of *L. canescens* has characteristically papillose-setulose or glandular corolla tubes. Some South American materials called *L. canescens* seem to have subglabrous corolla tubes and may belong to cryptic species currently treated in synonymy.

Grayum 10482 has long, simple-flowering seriated-cymose branches resembling those of sympatric *Eirmocephala* H. Rob., but *L. canescens* may be generally diagnosed by corollas with papillose-setulose or glandular tubes and short throats. *Eirmocephala* H. Rob. has broader corollas

with a glabrous tube and a moderately elongate throat. The common widespread *Vernonanthura patens* lacks spinose-aristate outer phyllaries and has leaves abaxially short-strigillose with short, broad, appressed, solid, white, L-shaped trichomes ca. 0.1 mm long but is nevertheless often misdetermined as *L. canescens*.



Figure 10. Protologue illustration of *Vernonia canescens* [\equiv *Lepidaploa canescens*] showing the spreading corolla lobes. (Reprinted from Kunth, Nov. Gen. Sp. 4: tab. 317 1820 [1818]).

Many records of *Lepidaploa canescens* from the Yucatán (but not of *Gaumer 1325*, the type of *V. hirsutivena*) may be based on misdeterminations. *Gaumer 23540* from Yucatán has both axillary and subterminal capitula but by papillose-setulose or glandular corolla tubes proves to be *L. canescens* rather than *L. argyropappa*. Cowan (1983) cited *Cowan 1986* and *Cowan 1997* from Tabasco as *L. canescens*, but both are redetermined here as *Vernonanthura patens*, as is material from Campeche as well. Villaseñor (1989: 108) cited *L. canescens* in Tabasco, but it was not cited there by Turner (2007) or by Redonda-Martínez and Villaseñor (2011). The species has apparently not been collected in Belize, albeit cited by Villaseñor (1989) as occurring there.

I am uncertain of the identity of the non-typical variety, Colombian *Lepidaploa canescens* var. *opposita* (H. Rob.) H. Rob., which is provisionally excluded. Thus albeit a segregate of *L. arborescens*, I treat *L. canescens* broadly and without infraspecies. However, in South America the species is admittedly variable as to corolla tube papillosity, and much material there is misdetermined as *L. costata* (Rusby) H. Rob., *L. lehmannii*, and *L. myriocephala* (DC.) H. Rob.

4. **LEPIDAPLOA CHIRIQUIENSIS** (S.C. Keeley) H. Rob., *Phytologia* 78: 385. 1995. *Vernonia chiriquiensis* S.C. Keeley, *Brittonia* 39: 45, fig. 2. 1987. **TYPE: PANAMA.** Chiriquí, Cerro Hornito, 1400–1750 m, 27 Dec 1977, *Folsom et al. 7212* (holotype: MO; isotypes: BM, MEXU, PMA, US). Fig. 11.

Shrubs 1–2 m tall, sometimes vining; stems glabrous to strigose or hispid. **Leaves** short-petiolate; blade 6–16 × 1.5–3.5 cm, lanceolate to elliptic-lanceolate, chartaceous, secondary veins 5–10 per side, not prominent abaxially, surfaces subglabrous to sparsely substrigillose, both surfaces also pustulate-punctate glandular, base cuneate, margins entire, apex acuminate; petiole 0.6–1 cm long. **Capitulescence** 5–15 cm diam., open corymbiform in Panama and open seriate-cymose in Costa Rica, non-leafy, held above stem leaves; peduncles 0.5–20 mm long. **Capitula** 10–12 mm long, 19–21-flowered; involucre 8–9.5 × 6–8 mm, campanulate; phyllaries 5–6-seriate, extremely strongly graduated, substrigillose to subsericeous more or less throughout, never apiculate or strongly 1-costate; outer phyllaries small to minute, 1–1.8 × ca. 0.6 mm, triangular, apex acute to acuminate, often broadly spreading and slightly decurrent onto peduncle; mid-series and inner series phyllaries with apex obtuse or sometimes with mid-series obtuse and the inner ones broadly acute; inner phyllaries 6–7 × 1–1.5 mm, lanceolate or oblanceolate. **Florets:** corolla 6.5–7.5 mm long, white to pinkish, gradually broad-funnelform or campanulate, glabrous but with cells of tube sometimes bulbous and glistening, tube short, 1–1.5 mm long and never narrowly elongate, throat unusually elongate, about as long as lobes, lobes 2.5–3 mm long; anther thecae ca. 3 mm long, filaments ca. 2.5 mm long; pollen echinolphate; style base nodular. **Cypselae** ca. 2 mm long, ca. 8+ lines of pubescence visible in immature cypselae but otherwise costae not prominent at all when cypselae mature, sericeous (duplex trichome apical cells appressed or sometimes somewhat divergent), eglandular, pericarp raphide crystals ca. 30 µm long, elongate-quadrangular; pappus white or dull white to stramineous, outer squamellae ca. 1 mm long, inner bristles 6–7 mm long and nearly as long as corolla.

Distribution and Ecology. *Lepidaploa chiriquiensis* is a rare southeastern Central American endemic described from Panama but here reported as also occurring in Costa Rica. The species grows in montane forests from 900–2100 meters elevation, flowers from December to March, and has been collected in late fruit in May. In Panama it is known to me to have been collected from 1977–1989 and only from near Chiriquí, but in Costa Rica it is known not only from the somewhat distant Talamanca Mountains near Cerro de la Muerte (a 2001 collection) but also much further to the northwest near Alajuela in the central part of the country, where it was collected in 1982.



Figure 11. Holotype of *Vernonia chiriquiensis* [= *Lepidaploa chiriquiensis*] showing the pedunculate capitula and broadly tipped inner phyllaries. A metric ruler is in the upper left of the image. (Folsom *et al.* 7212, MO).

Specimens examined. **COSTA RICA.** Carvajal 83 (CR, MO); Rodríguez *et al.* 7200 (INB, MO). **PANAMA.** Hammel 3059 (MO); Hammel 6194 (MO); Knapp *et al.* 4227 (MO); McPherson 11839 (MO); McPherson 13561 (MO, US).

By its often pedunculate capitula in open corymbiform capitulescences and its gradually broadening short-tubed long-limbed corollas, *Lepidaploa chiriquiensis* is anomalous in *Lepidaploa*. In other species of *Lepidaploa* where the corolla throats may be about as long as the lobes, the tube is very elongated (e.g., *L. acilepis*, *L. argyropappa*) and the corolla more typical Lepidaploan in its structure. The moderately broad corollas with an elongate throat in *L. chiriquiensis* bring to mind those of *Eirmocephala*. The strange capitulescence form, echinolophate pollen, and slightly decurrent

outer phyllaries are characters shared by *L. chiriquiensis* and several South American species of *Lessingianthus* H. Rob., e.g. Bolivian *L. laurifolius* (DC.) H. Rob.

Some species of *Lessingianthus* are similar to *Lepidaploa* in having elongate-hexagonal pericarp raphide crystals, but most *Lessingianthus* species differ by quadrate raphide-crystals. *Lepidaploa chiriquiensis* has elongate-quadrangular pericarp raphide crystals and does not conflict with either genus. But *L. chiriquiensis* has nodular style bases, a character that conflicts with *Lessingianthus* (viz Robinson 1999, 2007) but which is typical of *Lepidaploa*.

While the two recent collections from Costa Rica have corollas, leaves, and phyllaries typical of *Lepidaploa chiriquiensis*, they have sessile capitula and open seriated-cymose capitulescences atypical of the species but typical of the genus. This suggests that the type material from Panama may actually be atypical of the species and conversely that the newly detected Costa Rican populations could be the most characteristic *Lepidaploa* form.

As part of ongoing studies, further material of *Lepidaploa chiriquiensis* from Costa Rica and Panama will be sought, which when in hand I anticipate could help show trends in morphological variation, phylogenetic affinities, and may shine light towards its correct generic placement. Given the paucity of collections (and inconclusive micromorphology), *L. chiriquiensis* seems best retained at present in *Lepidaploa*, albeit atypical there.

5. **LEPIDAPLOA LEHMANNII** (Hieron.) H. Rob., Proc. Biol. Soc. Washington 103: 489. 1990. *Vernonia lehmannii* Hieron., Bot. Jahrb. Syst. 19: 44. 1894. **TYPE: COLOMBIA. Cundinamarca.** Prope Pacho, 1600–2200 m, Jan 1892, *Lehmann 7482* (holotype: B†, Macbride neg. 14557; lectotype (designated here): US-1420448; isotypes: F, K n.v., S). The handwriting style of Hieronymus on the B sheet is not a perfect match for the handwriting on either the F, S, or US sheets, which Hieronymus may not have seen, but nevertheless the US lectotype matches *Lepidaploa lehmannii* as applied currently. Fig. 12.

Cacalia lehmannii (Hieron.) Kuntze, *Vernonia larensis* V.M. Badillo

Shrubs to vines 1–7 m tall; stems erect to scandent or sprawling, subterete, striate distally, crisped puberulent to griseous villous-pilose. **Leaves** alternate, short-petiolate; blade 5–13 × 2–3.5 cm, lanceolate to ovate-lanceolate, secondary veins typically 5–6(–8) per side, sometimes impressed adaxially, moderately prominent abaxially, moderately arching towards apex, surfaces concolorous, adaxial surface smooth or sometimes rugulose, eglandular, strigillose to subglabrous, abaxial surface glandular, hirtellous-pilose to strigillose, base cuneate to obtuse(–rounded), margins entire, sometimes revolute, apex narrowly acute to long-attenuate; petiole 0.2–0.6 cm long, hirtellous. **Capitulescence** terminal on short lateral branchlets from distal most nodes, somewhat exserted, non-leafy and ebracteolate, of few–several densely-capitulate, densely branched seriate-cymes typically 3–7 cm long, cymes arranged in tightly held panicles at apex of main stems, ultimate branchlets with several small capitula subglomerate at apex, sometimes longer branchlets less compact-capitulate proximal to apex, then with a very few capitula occurring singly and ca. 0.5 cm from each other. **Capitula** 6–8 mm long, (13–)19–23-flowered; involucre usually 4–5.5 × 3–4.5 mm, campanulate, without outer elongate acicular phyllaries; phyllaries 4–5-seriate, strongly graduate, strigillose to villous; the outer series 1–1.5 × ca. 0.5 mm, narrowly lanceolate, appressed, these and mid-series phyllaries moderately 1-costate towards apex, but apex not obviously long-aristate at all; inner series 4–5 × ca. 1 mm, lanceolate, appressed, typically broadly acute to subobtuse, slightly apiculate. **Florets** exserted from involucre; corolla 3.8–6 mm long, becoming salverform, lavender to violet, glabrous or lobe apex few-glandular, tube 2–3 mm long, glabrous, throat short, lobes 1.5–2 mm long, longer than the throat, usually lightly glandular; anthers ca. 2 mm long, often fully exserted.

Cypselae 1–2 mm long, turbinate, ribbed, sericeous, eglandular; pappus white or dull white, the outer series of fimbriate scales 1–1.5 mm long, the inner series of bristles 4–4.5 mm long.

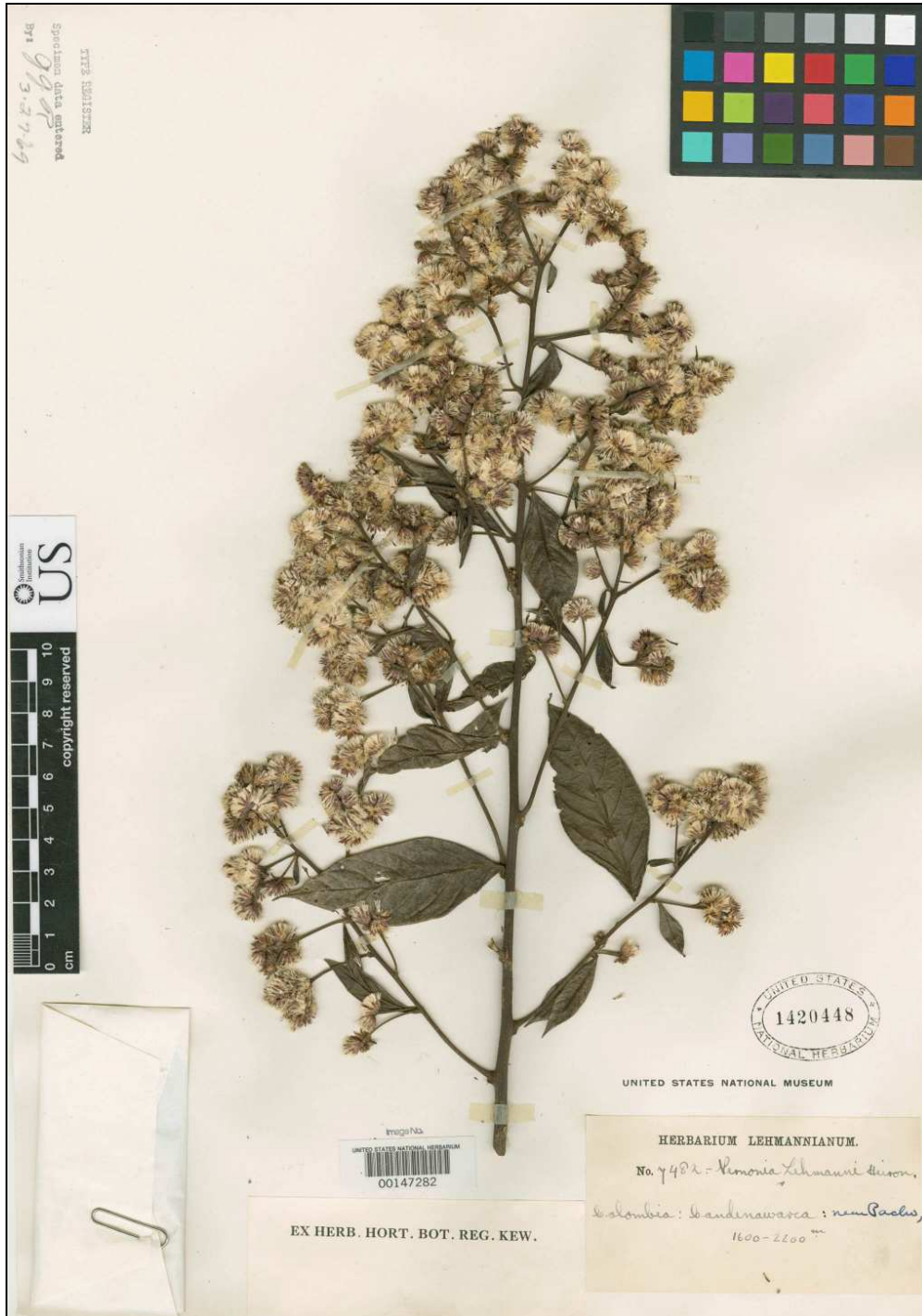


Figure 12. Lectotype of *Vernonia lehmannii* Hieron. showing branchlets tips subglomerate-flowered. [= *Lepidaploa lehmannii* (Hieron.) H. Rob.]. (Lehmann 7482, US).

Distribution and ecology. *Lepidaploa lehmannii* is a new record for Central America (not reported in Panama by Pruski 2013) and the species is now known in Panama, Colombia, Venezuela, and Ecuador. It is known in Central America only from a single collection made in Panama along the

border with Choco, Colombia, where it was collected as a vine over branches in a primary forest at 850 meters elevation, flowering in October.

Collection examined. PANAMA. Darién. Parque Nacional del Darién, ridge between Río Topalisa and Río Pucuro, ca. 17 km E of Pucuro, La Laguna area, 08° 03' 30" N, 77° 17' 00" W, 850 m, 16 Oct 1987, *de Nevers, Cuadros, Hammel & Herrera 8371* (MO, US).

The Klatt (1886) treatment of Lehmann collections mentioned only three collections but not the type collection of our species, which post-dated the Klatt work. Although Klatt was still publishing his treatments for *Florae Costaricensis* (viz Klatt 1892, 1896), by 1892 when the *L. lehmannii* type was collected Klatt was in his mid-60s, and determinations of Lehmann Compositae mostly fell into the hands of Hieronymus (viz Hieronymus 1894, 1901), who was 21 years Klatt's junior.

Lepidaploa lehmannii has been moderately well collected in South America. Pruski and Funston (2011) noted *L. lehmannii* to be moderately widespread in Antioquia Colombia, occurring there from near sea level to 2500+ meters elevation. Thus, the 1987 collection along the Choco-Darién frontier was a to-be-expected minor range extension. The species is similar to *L. canescens* but differs by sparser short leaf pubescence, dense terminal cymes, glabrous corolla tubes, and a relatively long outer series of pappus scales.

- 6. LEPIDAPLOA POLYPLEURA** (S.F. Blake) H. Rob., *Smithsonian Contr. Bot.* 89: 72. 1999. *Vernonia polypleura* S.F. Blake, *J. Wash. Acad. Sci.* 28: 478. 1938. **TYPE: MEXICO. Chiapas.** Mt. Orando [possibly on labels in error for Ovando], 23 Dec 1936, *Matuda 730* (holotype: US; isotypes: MEXU, MICH, TEX). Figs. 13–14.

Shrubs to trees 3–19 m tall; stems densely tomentulose to tomentose, trichomes patent, mostly 0.2–0.4 mm long, distal internodes much shorter than leaves. **Leaves** petiolate; blade 10–22 × 2–5–7.5 cm, lanceolate or elliptic-lanceolate to oblanceolate or rarely obovate, typically broadest near middle of blade, stiff-chartaceous, secondary veins 8–12(–17) per side, prominent abaxially, diverging from midrib at about 45° then near margins becoming arcuate, adaxial surface eglandular, pilose-hirsute to only so on veins with areolae subglabrous, trichomes patent or subappressed, often deciduous above prominulous base, abaxial surface (moderately–) densely pilose-villous to tomentose, also glandular, base acuminate, margins entire or subentire, apex acute to acuminate; petiole 1–3 cm long. **Capitulescence** terminal, non-leafy, held above stem leaves (infrequently a few proximal capitula bracteate), seriate-cymose or a diffuse panicle, capitula usually 1–1.5(–2) cm apart, sessile, ultimate branches relatively (5–25 cm) long, densely tomentulose. **Capitula** 7–10 mm long, 17–25-flowered; involucre 6–7 × 5–8 mm, campanulate, sometimes subtended by a pilose-tomentose bracteole 0.2–0.8 cm long; phyllaries graduated, 5–6(–7)-seriate, erect, villosulous to strigillose-sericeous; outer series 1–2 × ca. 0.5 mm, triangular-lanceolate, apex acute to acuminate but never long-subulate; mid-series and inner series with apex usually obtuse to rounded, albeit often mucronulate; inner series 6–7 × 0.8–1.3 mm, elliptic-lanceolate, sometimes slightly constricted below the relatively broad apex. **Florets:** corolla 5–6 mm long, broadly funnellform, pink to lavender (rarely white), tube relatively short, glabrous, limb and especially lobes obviously setose, lobes ca. 2 mm long. **Cypselae** 1.6–2.5 mm long, substrigose, eglandular; pappus commonly fulvous or tawny, infrequently stramineous; outer squamellae 0.5–0.8 mm long; inner bristles 4–5 mm long.

Distribution and ecology. *Lepidaploa polypleura* was known previously from only southern Mexico (Chiapas and Oaxaca) and Guatemala, but is newly reported in (P.N. Montecristo in extreme NW) El Salvador and (west-central) Honduras from woody, angle-stemmed specimens, albeit each

imperfect. The species is occasional and has been collected at about (700–)1300–2400 meters elevation, in flower from December to March.

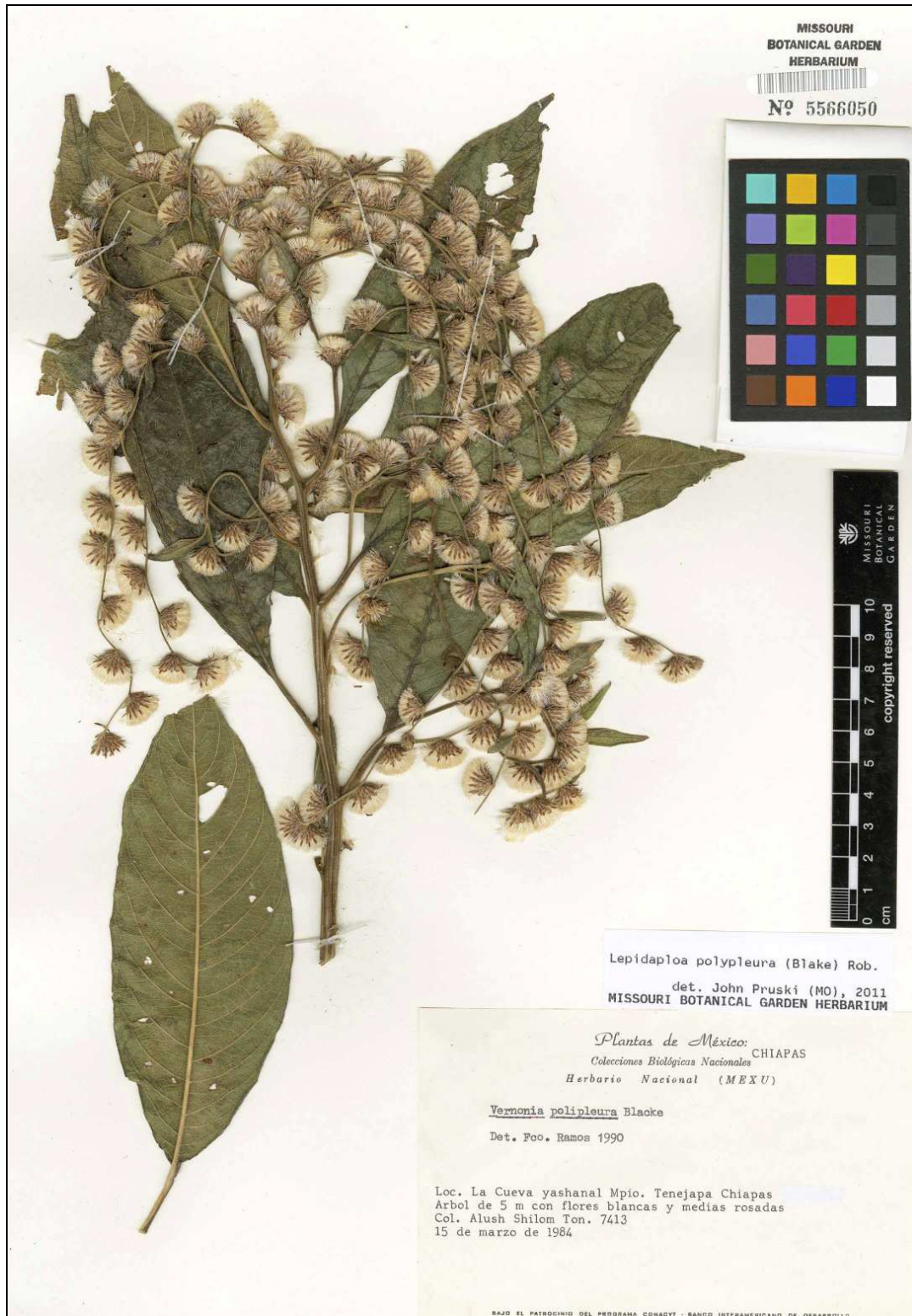


Figure 13. Representative specimen of *Lepidaploa polypleura* showing the pluriveined leaves and terminal capitulescence. (Shilom Ton 7413, MO).



Figure 14. Close-up of *Lepidaploa polypleura* from figure 13 showing the angled-stems, tawny pappus bristles, and relatively broad-tipped phyllaries. (*Shilom Ton 7413*, MO).

Representative specimens. **EL SALVADOR.** *Martínez 528* (MO). **GUATEMALA.** *Rodríguez 433* (P, US). **HONDURAS.** *Evans 1116* (MO). **MEXICO. Chiapas.** *Breedlove 24117* (CAS, MO); *Breedlove 33475* (CAS, MO); *Breedlove & Almeda 58096* (CAS, MEXU, MO, TEX); *Breedlove & Almeda 58310* (CAS, MEXU, MO); *Croat 47629* (MO, UC); *N. Martínez 1432* (HEM, MO); *Matuda 2067* (MEXU, US); *Shilom Ton 7413* (IEB, MEXU, MO); *Stafford et al. 331* (BM, MEXU, MO; 20-flowered but pappus paler than usual). **Oaxaca.** *Maya 4198* (MEXU, MO, TEX).

Lepidaploa polypleura may be recognized by its woody habit, angled stems, relatively narrow leaf blades with several–many prominent secondary veins, terminal capitulescences, broad-tipped inner phyllaries, broad hairy corollas, and its fulvous or tawny pappus. It is quite distinctive among Central American species and brings to mind Colombian *L. cordifolia* (Kunth) H. Rob., which seems to differ by acute mid-series and inner phyllaries and by a more densely branched capitulescence with much short terminal branchlets. The fine illustration of *L. polypleura* provided by Redonda-Martínez and Villaseñor (2011) shows the characteristic long narrow leaf blades with many prominent secondary veins but depicts the mid-series phyllaries as much more acute than usual. The narrower tipped mid-series condition is found only occasionally in material from Oaxaca.

By similar elongate leaf trichomes and terminal capitulescences, Robinson (1990) reduced *L. polypleura* to synonymy with *L. canescens*, but Robinson (1999) reinstated the species. Nash (1976), Redonda-Martínez and Villaseñor (2011), and Pruski (2013) also recognized the species as distinct. Turner (2007) recognized *L. polypleura* as endemic to Chiapas and Guatemala, but Redonda-Martínez and Villaseñor (2011) and Pruski (2013) noted its occurrence also in Oaxaca.

The single specimen seen from Honduras was described by the collector as white-flowered, and indeed in the dried specimen in front of me not only are the corollas pale but the pappus is much lighter in color than other collections seen. By the stems, leaves, terminal capitulescence, and setose corolla lobes, however, this collection matches the species. The single specimen seen from El Salvador is in bud (but labeled as white-flowered) but similarly is woody and has angled stems. These pale-pappose(-flowered) plants (from El Salvador, Honduras, and Stafford *et al.* 331 from Chiapas) are fairly pubescent-leaved and ca. 20-flowered but nevertheless recall partly sympatric *L. tenella*, a similar albeit much less pubescent, few-flowered relative.

7. LEPIDAPLOA TENELLA (D.L. Nash) H. Rob., *Proc. Biol. Soc. Wash.* 1032: 495. 1990. *Vernonia tenella* D.L. Nash, *Fieldiana, Bot.* 369: 74. 1974. **TYPE: GUATEMALA. San Marcos.** Tajumulco Volcano, 8–10 km W San Marcos, 2300 m, 31 Dec 1964–1 Jan 1965, *Williams et al.* 26876 (holotype: F).

Lepidaploa boquerona (B.L. Turner) H. Rob., *Vernonia boquerona* B.L. Turner

Shrubs or vines 2–3 m tall; stems arching to scandent, subterete, striate, puberulent to substrigillose or glabrate, trichomes often appressed, distal internodes about 1/2 as long as leaves. **Leaves** petiolate; blade 5–12 × 1.5–3 cm, lanceolate to ovate-lanceolate, broadest near the middle, chartaceous, secondary veins usually 5–7 per side, adaxial surface smooth or sometimes veins somewhat impressed, prominulous abaxially, diverging from midrib at about 45°, surfaces eglandular, adaxial surface glabrous or costa puberulent, abaxial surface puberulent especially on the veins, never densely tomentose, base narrowly cuneate to attenuate, margins entire, apex acute to acuminate; petiole 0.3–1.5 cm long. **Capitulescence** a terminal non-leafy diffuse panicle with individual branchlets seriate-cymose, capitula usually 1–2 cm apart, sessile, ultimate branches 5–10 cm long, appressed-pubescent to tomentulose. **Capitula** 8–10 mm long, 8–15-flowered; involucre 6–8 mm long, turbinate-campanulate or campanulate, sometimes subtended by a reduced bracteole; phyllaries moderately to strongly graduated, 4–5(–8)-seriate, erect, villosulous to strigose-sericeous; outer series 1–2 × ca. 0.5 mm, triangular-lanceolate, never acicular, apex acute to acuminate but never long-subulate; inner series 6–8 × 0.9–1.3 mm, lanceolate or oblanceolate, apex obtuse or sometimes acute. **Florets** slightly exerted or in fruit well-exserted; corolla 6–7 mm long, somewhat broadly funnelform, purplish, lobes 2–3 mm long, setose. **Cypselae** 2–3 mm long, substrigose or pilose; pappus white or dull white; outer squamellae ca. 1 mm; inner bristles ca. 6 mm long.

Distribution and Ecology. *Lepidaploa tenella* is a rare montane (pine or oak) forest shrub endemic to Guatemala (San Marcos in the southwest) and Mexico (southernmost Chiapas) and occurs only near Volcán Tacaná, Volcán Tajumulco, and the Sierra Madre on the Pacific watershed. It has been collected from about 1800–2600 meters elevation and flowers between November and January. Both Turner (2007) and Redonda-Martínez and Villaseñor (2011) used the name *L. boquerona* for our species. *Lepidaploa tenella* was described and long-known from only Guatemala, but here *L. boquerona* is treated in synonymy with *L. tenella*, which is consequently a new record for Mexico. The respective type localities, albeit each in a different country, are only 60 km distant from each other.

Representative specimens. GUATEMALA. *Williams et al.* 26094 (F, NY); *Williams et al.* 26246 (F, US). **MEXICO. Chiapas.** *Breedlove* 42791 (MEXU); *Breedlove & Sigg* 66118 (CAS, MEXU, TEX); *Breedlove & Sigg* 66139 (CAS; type of *V. boquerona*).

Pruski (2013) keyed *Lepidaploa boquerona* as 8–9-flowered and *L. tenella* as ca. 15-flowered, but further study has convinced me that these two weakly pubescent plants are a single species. *Lepidaploa boquerona* is thus reduced to synonymy with *L. tenella*. By similar terminal capitulescences, broad-tipped phyllaries, and setose corolla lobes, *L. tenella* is envisioned as a subglabrous to less densely pubescent-leaved, fewer-flowered, and paler-pappose relative of *L. polypleura*. But the two species seem sufficiently distinct and each is recognized. The occasional plants that are pale-pappose and have abaxially merely moderately pilose-villous leaves, thus especially recalling *L. tenella* (e.g., *Stafford et al.* 331 from Chiapas), are ca. 20-flowered and referred, albeit with some reservations, to the much more common *L. polypleura*. The aspect of *L. tenella* much resembles that of *Vernonanthura patens* (Kunth) H. Rob., a common widespread neotropical weed characterized by its strange, solid small trichomes (?T-shaped) on its abaxial leaf surfaces.

8. LEPIDAPLOA TORTUOSA (L.) H. Rob., *Proc. Biol. Soc. Wash.* 103: 495. 1990. *Conyza tortuosa* L., *Sp. Pl.* 862. 1753. **LECTOTYPE:** (designated by Britten 1898): **MEXICO.** Veracruz, *Houstoun s.n.* (BM-CLIFF 405 *Conyza* 5). Figs. 2–3, 15–16.

Cacalia schiedeana (Less.) Kuntze, *Cacalia seemanniana* (Steetz) Kuntze, *Conyza scandens* Mill., *Vernonia schiedeana* Less., *Vernonia seemanniana* Steetz, *Vernonia tortuosa* (L.) S.F. Blake, *Vernonia vernicosa* var. *comosa* Greenm.

Shrubs 1–5 m tall; stems usually scandent or climbing, striate, villosulous or pilosulose to more typically densely tomentulose (rarely glabrous). **Leaves** petiolate or short-petiolate; blade (5–)8–17 × 2–6(–9.5) cm, elliptic-lanceolate to ovate, stiffly chartaceous, secondary veins usually prominent, 6–10 per side, spreading to slightly ascending, adaxial surface strigillose or hirsute throughout or at least along proximal portion of midrib, veins sometimes impressed, abaxial surface weakly sericeous or strigillose to villous-tomentose, not glabrous, trichomes mostly 0.1–0.5 mm long, patent to appressed, sometimes also slightly glandular, base cuneate to rounded (rarely subcordate), margins usually entire, sometimes subrevolute, apex acuminate to broadly obtuse; petiole 0.3–1.6 cm long, often tomentulose. **Capitulescence** of bracteate-leafy seriate-cymes to weakly leafy freely branched panicles with ultimate paniculate branchlets usually 7–15 cm long, capitula remotely spaced (internodes 1–4 cm long), sessile or subsessile, bracteate leaves similar to vegetative leaves but much smaller; peduncles 0–2(–3) mm long. **Capitula** (9–)11–15 mm long, (18–)25–40(–50)-flowered; involucre (7–)9–12 × (5–)7–11 mm, campanulate; phyllaries strongly graduate (rarely merely moderately graduate in specimens from Olancho, Honduras), 5–8(–10)-seriate, dull-green tinted distally or inner ones pale brown, substrigillose or subsericeous especially medially in mid-series, in bud covered by dense arachnoid pubescence mostly derived from cilia from the distal mid-series and inner series phyllary margins; outer phyllaries spreading; outer and mid-series phyllaries 1–6 × 0.5–1.5 mm, triangular to lanceolate, midrib thick and raised in distal 1/2–1/3, apex gradually and stoutly cuspidate; inner 1–2 series of phyllaries (6–)8–12 × 2–3 mm, oblanceolate to oblong, nerves indistinct, margins often distally villous-ciliate, apex typically constricted then distally dilated and cucullate, usually membranous-scarious, obtuse to rounded, clinanthium to 6 mm diam., usually flat. **Florets:** corolla (6–)8–11 mm long, relatively narrowly funnelform becoming slightly salverform, often widely spreading laterally from top of the involucre, white, infrequently faint violet, usually glabrous throughout or lobes sometimes setulose or glandular, tube and limb nearly subequal, throat very short, lobes (2.2–)3.5–4 mm long, often fully exerted from involucre; anther thecae longer than filaments, nearly as long as corolla lobes. **Cypselae** (1.5–)2–2.5 mm long, densely substrigose to

hirsutulous, eglandular; pappus white or dull white to stramineous, outer squamellae 1–2 mm long, inner bristles (5–)6–8 mm long, reaching to about top of involucre and to about base of corolla lobes.



Figure 15. *Lepidaploa tortuosa*. Sessé and Mociño expedition illustration labeled in Candolle's hand as the non-published *Conyza? secunda*. The faint number "19-1" on the upper portion of the plate refers to the Linnaean sexual system Class XIX Syngenesia: Polygamia Aequalis. Neither the species nor this illustration appears to be cited in either Sessé and Mociño (1887) or McVaugh (1980, 2000). In the Madrid Herbarium I find one sheet only of *Lepidaploa tortuosa*: Sessé & Mociño 4147 (Field neg. 42898, IDC microfiche BT-13 card 267-A4) originally labeled as "dubia." This figure was drawn between 1787–1803 and is figure 1045 in the Torner collection (Illustr. Hunt Institute (Torner) 6331.1045).

Distribution and Ecology. *Lepidaploa tortuosa* is widespread, occurring from southern Mexico southeastwards into Panama. The species flowers mostly in (November–)December–April(–August) from sea level to 1900 meters elevation. There is a general north-south trend not taken by me as taxonomically significant, from Mexican plants with very broad phyllaries and eglandular long-pubescent leaves to Panamanian plants with narrower phyllaries and glandular short-pubescent leaves. In Panama, *L. chiriquiensis* has glandular short-pubescent leaves and is similar (to the type of *V. seemanniana*) but lacks spinose phyllaries.

Representative specimens. **BELIZE.** *Arvigo et al.* 122 (MO, NY, US); *Bartlett* 12885 (MO, US); *Davidse & Brant* 32375 (LP, MO, US); *Gentle* 1920 (MICH, MO, NY); *Proctor* 35807 (IJ, MO); *Schipp* 12 (MO, NY, US). **COSTA RICA.** *Davidse et al.* 23364 (MO, US); *Dodge & Thomas* 6284 (MO, US); *Morales et al.* 1234 (INB, MO); *Pittier* 3727 (US; cited by Klatt 1892: 184 as *Vernonia schiedeana*); *Rodríguez et al.* 3399 (INB, MO); *Skutch* 4112 (MO, US); *Williams et al.* 24221 (F, MO); *Williams et al.* 26474 (MO, US). **EL SALVADOR.** *Calderón* 1509 (NY, US); *Carbollo et al.* 1124 (B, LAGU, MO); *Munro et al.* 2275 (B, BM, LAGU, MO); *Standley* 19992 (MO, US). **GUATEMALA.** *Blake* 7712 (US); *Contreras* 726 (MO, TEX, US); *Contreras* 3478 (MO, TEX, US); *Tuerckheim* 1346 (MO, US); *Türkheim II* 1627 (MO, US). **HONDURAS.** *Blackmore & Heath* 2146 (BM, MO); *Croat & Hannon* 64287 (MO, US); *Evans* 1344 (EAP, MO, NO, UC); *Nelson & Clewell* 404 (MO); *Nelson & Vargas* 2674 (MO); *Thieme* 5307 (US); *Williams & Molina* 17943 (US). **MEXICO. Campeche.** *Flores* 10428 (CICY n.v.; cited by Redonda-Martínez and Villaseñor 2011). **Chiapas.** *Breedlove* 50441 (CAS, MO, TEX); *Croat* 47502 (MEXU, MO; cited by Redonda-Martínez and Villaseñor 2011 as *L. remotiflora*); *Matuda* 736 (MEXU, MO); *Pruski et al.* 4191 (HEM, K, MEXU, MO, TEX, UC); *Pruski et al.* 4239 (HEM, MO); *Ventura* 880 (MEXU, MO, XAL). **Tabasco.** *Cowan* 2772 (CAS, MEXU, MO, NY, TEX); *Cowan* 2800 (CAS, ENCB, MEXU, MO, NY); *Fernández* 1430 (IEB, MO); *Johnson* 15 (K). **Veracruz.** *Houstoun s.n.* (BM-Banks (NYBG neg. 577, BH neg. 5224), BM-Sloane 292, 65/67 [sic]; type of *Conyza scandens*); *Pruski & Ortiz* 4125 (GH, K, MEXU, MO, NY, TEX, UC, XAL; distributed as *Vernonia patens*); *Schiede* 1237 (HAL-2; type of *V. schiedeana*). **NICARAGUA.** *Araquistain & Moreno* 1748b (MO); *Nelson* 4914 (BM, F, GH, MO); *Pipoly* 4430 (MO). **PANAMA.** *Allen* 4179 (MO); *Folsom* 15997 (MO); *Hamilton & Dressler* 2993 (MO, UC); *Seemann* 1589 (BM, K-Hook; type of *V. seemanniana*); *Sytsma* 4040 (MO, US).

The common and widespread *Lepidaploa tortuosa* can be recognized by its moderately large axillary capitula, an arachnoid involucre in bud, and pubescent phyllaries, the inner series of which are dilated distally and broad-tipped at apex. Only in few areas with steep rocky river banks in Olancho, Honduras, is the involucre arachnoid-pubescent but with acute inner phyllaries and outer phyllaries strongly spreading-decurrent onto peduncle (e.g., *Blackmore & Heath* 2146; *Croat & Hannon* 64287; *Nelson & Vargas* 2674), which I suspect are ecological variants.

Gleason (1922) recognized each *Vernonia schiedeana*, *V. seemanniana*, and *V. vernicosa* as distinct, but Blake (1926) recognized *V. tortuosa* and placed *V. schiedeana* in synonymy of it. Elias (1975) recognized *V. seemanniana* in Panama and Standley (1938) recognized *L. vernicosa* in Costa Rica as distinct. Robinson (1999) expanded Blake's synonymy by also treating *V. seemanniana* and *V. vernicosa* in synonymy with *L. tortuosa*. As circumscribed by Robinson (1999), *L. tortuosa* is broadly defined but here slightly less broadly so with *L. vernicosa* reinstated below and circumscribed more or less as in Gleason (1906, 1922). As circumscribed here, there is in *L. tortuosa* a distinct (but not absolute) trend from northern populations (the typical forms) often having hairier leaves and broad-tipped nearly cucullate inner phyllaries to southern populations (described as *Vernonia seemanniana*) in Costa Rica and Panama often having more weakly pubescent but glandular leaves and narrow-tipped inner phyllaries.

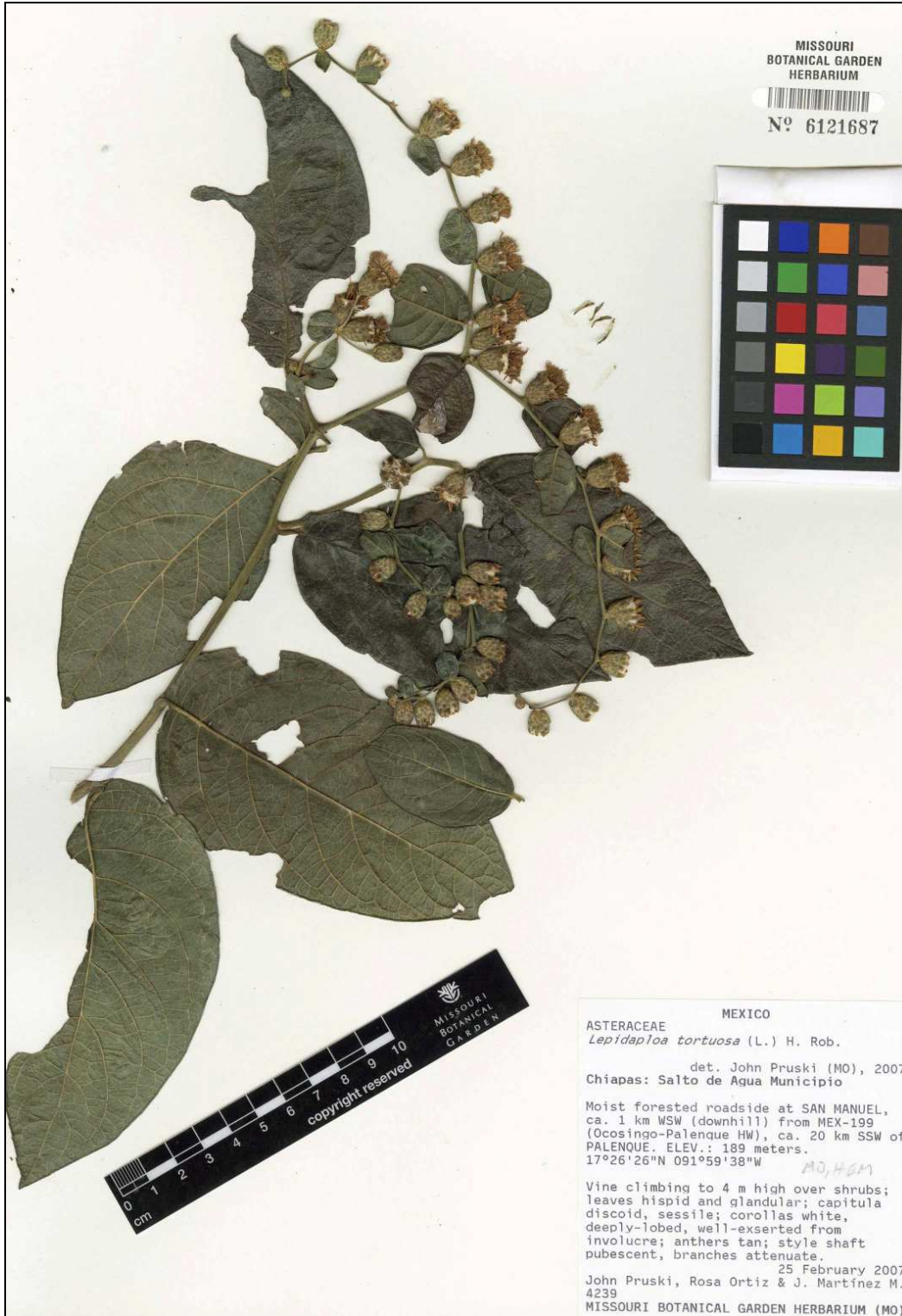


Figure 16. Representative specimen of *Lepidaploa tortuosa* showing the leafy capitulescence with large axillary capitula. (Pruski et al. 4239, MO).

The citation by Hemsley (1881: 74) of *Vernonia schiedeana* in "Yucatan and Tabasco" vouchered by Johnson 15 (K) is in reference to a collection I presume to be from Tabasco. I know of no Johnson collections from Edo. Yucatán, where this species remains undocumented.

9. **LEPIDAPLOA UNIFLORA** (Mill.) H. Rob., Proc. Biol. Soc. Wash. 103: 496. 1990. *Conyza uniflora* Mill., Gard. Dict. (ed. 8), *Conyza* no. 13. 1768. **LECTOTYPE** (designated here): **MEXICO**. ?Campeche, Anon., possibly *Houstoun* (lectotype: BM-*Conyza Americana frutescens* ... (BH negative 5226, as photograph in E, MO, NY). Possible syntype or possible isotype: BM-Sloane vol. 5 sheet 17, specimen on right. The lectotype contains the *Houstoun* binomial cited in the protologue by Miller (1768), and is presumably a *Houstoun* sheet collected pre-1733 (the year *Houstoun* died in Jamaica). The protologue (as *Conyza* no. 13) included the *Houstoun* polynomial, and also mentioned other materials coming from the same source as *Conyza* no. 12, i.e., "from Carthagea Mr. Robert Millar." Blake (1915) gave the Millar material as collected about 1736. Although the lectotype may be a *Houstoun* collection, the species is unknown in Veracruz, where most *Houstoun* material originated. The Millar locality "Carthagea" is possibly in reference to Cartago, Costa Rica [Blake 1915 stated that Millar's Carthagea to "eighteenth century collectors ... is ... Cartago, not Carthagea, Columbia"], but the species is not known from either Costa Rica or Colombia either. If indeed original material was received by Philip Miller from Robert Millar, most likely the actual locality is instead "Campeachy" from where some Millar material originates and from where the species is known. The Sloane herbarium sheet is not clearly the same collection as the lectotype sheet, and perhaps instead it is the Robert Millar syntype material. The BM Sloane herbarium sheet from folio 5 is a later continental American addition to the otherwise mostly West Indian folios 1–7, and *Houstoun* collections are occasional in the Sloane folios (Dandy 1958). Fig.17.

Cacalia uniflora (Mill.) Kuntze, non Schumach. & Thonn., *Vernonia ctenophora* Gleason

Perennial herbs 1–1.5(–2) m tall, apparently brittle-stemmed and sometimes labeled as a shrub, but perhaps never truly woody based; stems few-branched, weakly striatulate distally, villosulous, also glandular. **Leaves** short-petiolate; blade 2.5–5.5 × 0.8–2.5 cm, lanceolate to elliptic-lanceolate (widest below the middle), chartaceous, secondary veins 4–6 per side, both surfaces glandular, adaxial surface also thinly and sparsely villosulous-strigillose, smooth, abaxial surface villosulous-strigillose to villous-strigose with antrorse, sometimes griseous trichomes to ca. 0.5 mm long, base rounded or obtuse, margins entire, apex acuminate; petiole 0.1–0.4 cm long. **Capitulescence** leafy, with a single sessile axillary capitulum (whence the epithet) in each of the 5–10+ distal well-spaced nodes, the capitula remote but nevertheless the arching branch tips often more or less unifacial and thus loosely seriate-cymose, branches sometimes pressing very weakly bifacial and fractiflex. **Capitula** 7–10 mm long, 18–23-flowered; involucre 6–7(–8) × 4–6(–7) mm, turbinate to campanulate, reaching to about base of corolla lobes; phyllaries graduate or sometimes weakly graduate with outer phyllaries more than half as long as the inner, 0.2–1.5 mm diam., substrigillose to subsericeous and glandular distally, ca. 4-seriate; outer 1–2 series of phyllaries linear-lanceolate, 1-costate distally, apex long-subulate with apical mucro 1–2 mm; the mid-series often abruptly cuspidate and purplish in the middle; inner 1–2 series of phyllaries elliptic-lanceolate, purplish distally, apex acuminate. **Florets**: corolla 6–7 mm long, tubular-funnelform, reddish to pinkish, tube glabrous, slightly longer to much longer than limb, throat short, lobes ca. 2.5 mm long, sparsely to moderately setose distally to sometimes proximally to near throat, glandular distally. **Cypselae** 1.3–1.5 mm long, strigillose, intercostae glandular; pappus outer squamellae 0.6–1 mm long, inner bristles 4–5 mm long, reaching to proximal 1/3 of corolla lobes.

Distribution and Ecology. *Lepidaploa uniflora* is basically a Yucatán peninsula endemic — Belize, Guatemala (Petén), and Yucatán peninsular Mexico — where it is moderately common and occurs in and near open low forest, pastizal, and tinal from 10–300 meters elevation, flowering mostly from November to May.



Figure 17. Representative specimen of *Lepidaploa uniflora*. (Lundell 1221, MO).

Representative collections. **BELIZE.** Bartlett 11530 (US); Davidse & Brant 32784 (MEXU, MO, NY); Davidse & Brant 32829 (BM, MO, US). **GUATEMALA.** Contreras 484 (MO,

US); *Contreras* 8545 (MO, US). **MEXICO. Campeche.** *Goldman* 508 (US; holotype of *V. ctenophora*); *Lundell* 1221 (MO, US; cited by Martínez et al. 2001 as *L. argyropappa*; cited by Carnevali et al. 2010 as *L. salzmannii*); *Martínez et al.* 2955 (CICY, IEB, MEXU, MO). **Quintana Roo.** *Cabrera* 1277 (MEXU; cited by Sousa and Cabrera 1983 as *L. argyropappa*; cited by Carnevali et al. 2010 as *L. salzmannii*); *Carnevali et al.* 5437 (CICY, MEXU, MO); *Hernández* 303 (CICY, MO). **Tabasco.** *Fernández & Guadarrama-Zamudio* 1336 (MO); *Matuda* 3112 (MEXU, MICH, MO; cited by Cowan 1983 as *V. ctenophora*).

Lepidaploa uniflora may be recognized by its obviously glandular cypselae, leaf blades glandular on both surfaces, and tubular-funnelform (not as drawn in Redonda-Martínez and Villaseñor 2011, where all species are depicted as similarly salverform). *Lepidaploa uniflora* was recognized by Nash (1976), Villaseñor (1989), and Turner (2007) as *V. ctenophora* Gleason. Pruski (2016) noted that *Vernonia uniflora* Sch. Bip. blocked use of the Miller name in *Vernonia*. The plant was called *L. uniflora* by Robinson (1990, 1999), Redonda-Martínez and Villaseñor (2011), and Pruski (2013). By the unusual characters of strongly glandular cypselae and leaves obviously glandular adaxially, *L. uniflora* is reminiscent of Guayana Highland endemic *L. bolivarensis* (V.M. Badillo) H. Rob. (Pruski 1997). The report by Carnevali et al. (2010) of *L. uniflora* in Chiapas is apparently based on a misdetermination. Redonda-Martínez and Villaseñor (2011) erroneously gave Brazilian *Lessingianthus varroniifolius* (DC.) H. Rob. in synonymy with *L. uniflora*. Britten (1898) and Aristeguieta (1964) gave *Conyza uniflora* in synonymy with similarly aristate-phyllaried *V. remotiflora* Rich., which in the strict sense is South American and has narrower capitula. Pruski (2016) recognized *L. uniflora* as one of six Miller (1768) species described in *Conyza*. Miller (1768) described well the axillary capitula, but (mis)stated that the plant is "eight or ten feet high," whereas material I have seen is herbaceous and less than 1.5(–2) meters tall.

10. LEPIDAPLOA VERNICOSA (Klatt) Pruski, **comb. nov.** *Vernonia vernicosa* Klatt, Bull. Soc. Roy. Bot. Belgique 35(1): 294. 1896. **TYPE: COSTA RICA.** Bord du Río Virilla, Jan 1896, *Tonduz* 7065 [= 9860 herb. nat. Cost.] (holotype: BR; isotypes: CR, F, GH p.p., MO, US). The BR sheet is complete, but a fragment of it is on the left of the GH sheet. Figs. 18–19.

Vernonia vernicosa var. *comosa* Greenm.

Shrubs, sometimes vines 0.3–3 m tall; stems erect to scandent, striate, glabrous to puberulent. **Leaves** blade 3–11 × 1–4 cm, lanceolate to ovate-lanceolate, chartaceous, secondary veins thin, usually 3–5 per side, directed forward, adaxial surface smooth and sometimes nitidous, veins sometimes weakly impressed, glabrous to strigillose, trichomes (when present) appressed, sometimes punctate, abaxial surface weakly strigose, trichomes mostly 0.1–0.3 mm long, appressed, also glandular, base broadly obtuse or rounded to rarely subcordate, margins entire, apex acute to attenuate; petiole 0.3–0.4 cm long, glabrous to puberulent. **Capitulescence** of lax sparsely branched leafy elongate branches (taking up much of individual herbarium sheets) with large axillary capitula solitary in distal nodes, flowering branchlets nodally deflected-fractiflex distally (not obviously seriate-cymose), capitula remote, well-spaced, nodes 2–5 cm long, sessile to very short-pedunculate, bracteate leaves similar to vegetative leaves but slightly smaller; peduncles to 3 mm long. **Capitula** 12–18 mm long, 50–62+-flowered; involucre 10–14 × 9–12 mm, campanulate; phyllaries strongly graduate, all gradually narrow-acuminate or sometimes the mid-series broader and abruptly narrowed apically from broad apex, 7–9-seriate, outer and mid-series stiff-coriaceous nitidous green distally with pale midrib and pale very thin margins, grading to inner ones thin and pale brown in distal 1/3, glabrous to sometimes minutely and weakly puberulent or ciliate, in bud all phyllaries glabrous or mid-series loosely arachnoid pubescent; outer phyllaries 2–5 × ca. 0.5 mm, triangular to lanceolate, midrib thick and raised in distal 1/3, apex stoutly cuspidate; mid-series to ca. 2 mm wide, stoutly cuspidate to sometimes only slightly so; inner-series of phyllaries 10–14 × ca. 1.5

mm, lanceolate, nerves indistinct, apex narrow-acuminate but not stoutly cuspidate, membranous-scarious, neither obviously dilated nor cucullate. **Florets:** corolla 10–11.2 mm long, relatively narrowly funnellform becoming slightly salverform, white, usually glabrous throughout or lobes sometimes minutely setulose, tube 6–8 mm long, tube gradually widening into throat and together tube and throat much longer than the lobes, throat proper usually shorter than the lobes, lobes 2.5–3.2 mm long. **Cypselae** 1–1.5 mm long, densely substrigose to hirsutulous, eglandular; pappus white or dull white, outer squamellae 1–1.5 mm long, inner bristles 7–8.5 mm long, reaching to about top of involucre and to about base of corolla lobes.

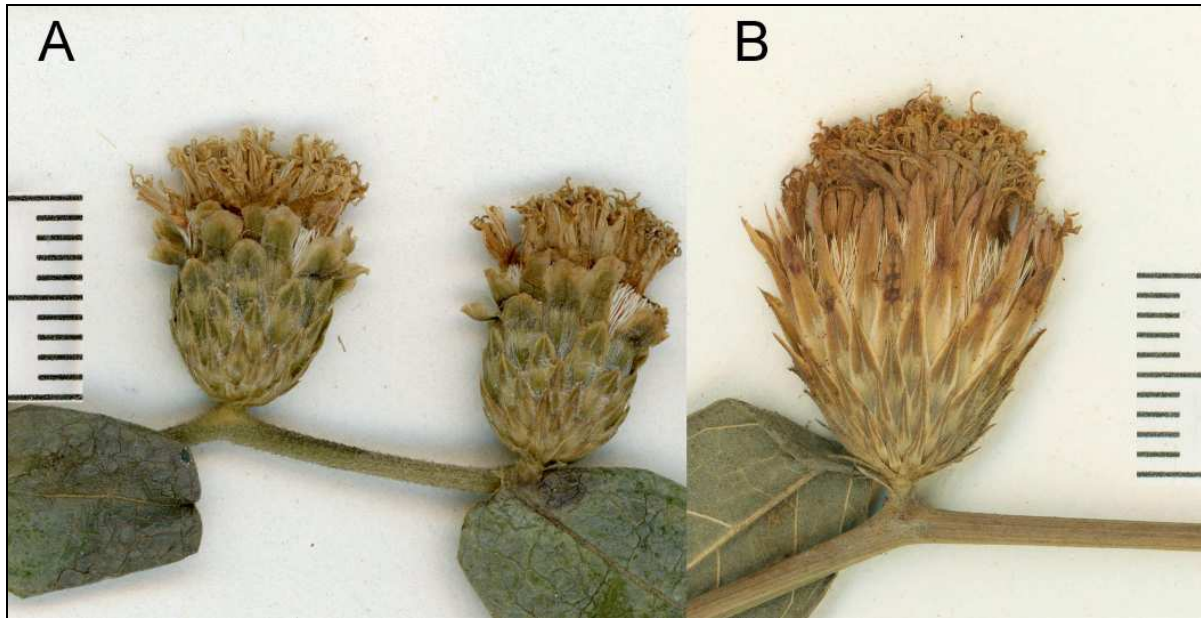


Figure 18. Involucres of (A) *Lepidaploa tortuosa* and (B) *Lepidaploa vernicosa*. In each species the pappus is held within the involucre and reaches only about to the base of the corolla lobes. A. Two capitula of *Lepidaploa tortuosa* showing the arachnoid-margined mid-series phyllaries and the obtuse to rounded apices of the mid-series and inner phyllaries. B. Capitulum of *Lepidaploa vernicosa* showing the subglabrous nitidous phyllaries, and the acute to acuminate tipped mid-series and inner-series of phyllaries. A metric scale is positioned vertically in each image. (A Pruski *et al.* 4239, MO; B Weston 4160, MO).

Distribution and Ecology. *Lepidaploa vernicosa* is endemic to Costa Rica, where it is occasional from 200–1100 meters elevation, and flowers mostly from December to April. The note by Standley (1938) of *L. vernicosa* being "frequent" I believe is partly in reference to plants that I would mostly determine as *L. tortuosa*. *Lepidaploa tortuosa*, however, was specifically excluded from Costa Rica by Standley.

Representative specimens. COSTA RICA. *Biolley* 7013 (GH p.p., US; cited by Klatt 1892 as *V. schiedeana*); *Carvajal* 115 (CR, MO); *González & González* 2489 (INB, MO); *González et al.* 201 (INB, MO, TEX); *Hammel et al.* 18690 (INB, MO, TEX); *Hoffmann* 305 (B, GH; Beaman color slide 5768; distributed from B as *V. hoffmanni* Vatke); *Khan et al.* 275 (BM, MO); *Morales* 6165 (INB, MO); *Pittier* 16341 (US); *Scherzer s.n.* (W); *Standley* 44905 (US); *Tonduz* 13189 (US); *Tonduz* 13607 (GH-2, NY, US; type of *V. vernicosa* var. *comosa*); *Weston* 4160 (MO, UC).

By its large axillary capitula and white corollas much longer than pappus bristles, *L. vernicosa* is similar to *L. tortuosa* and was placed adjacent to it by Gleason (1906, 1922). *Lepidaploa vernicosa* (Klatt) Pruski was recognized by Standley (1938), treated in synonymy of *L. tortuosa* by Robinson (1999), and here is reinstated from synonymy. *Lepidaploa vernicosa* (Klatt) Pruski differs

from *L. tortuosa* most obviously by adaxial glabrous to strigillose (vs. strigillose or hirsute throughout or at least proximally on midrib, never glabrous) leaf blade surfaces, larger capitula, involucre glabrous or loosely arachnoid-pubescent (vs. strongly arachnoid pubescent) in bud, glabrous nitidous (vs. dull, substrigillose or subsericeous) phyllaries, the inner series of which are narrow-acuminate and neither obviously dilated nor cucullate (vs. typically constricted then dilated and cucullate and obtuse to rounded) at apex. *Lepidaploa vernicosa* is more similar to *L. tortuosa* than it is to other Central American species but these are no more similar to each other than are other the regional species pairs.



Figure 19. Fraxtiflex, large-capitulate flowering branch of *Lepidaploa vernicosa*. A metric ruler is in the lower right of the image. (Weston 4160, MO).

Excluded species.

Lepidaploa arborescens (L.) H. Rob., Proc. Biol. Soc. Washington 103: 481. 1990. *Conyza arborescens* L., Syst. Nat. (ed. 10) 2: 1213. 1759. *Vernonia arborescens* (L.) Sw., Fl. Ind. Occid. 3: 1320. 1806. **LECTOTYPE** (designated by Keeley 1982): Plumier in Burman, Pl. Amer., 122, t. 130, tab. 2, *Conyza foliis ovatis*. 1757. This species has been reported (e.g., Keeley 1982, 2001; Nelson 2008; Turner 2007) in Central America, with *L. canescens* in synonymy. Here, following Clewell (1975), Elias (1975), Nash (1976), and Robinson (1990, 1999), I recognize *L. canescens* (characterized in part by its usually papillose-setulose or glandular corolla tube) as distinct from *L. arborescens* (characterized in part by its glandular corolla lobe apices), the latter being interpreted as endemic to the West Indies.

Lepidaploa remotiflora (Rich.) H. Rob., Proc. Biol. Soc. Washington 103: 491. 1990. *Vernonia remotiflora* Rich., Actes Soc. Hist. Nat. Paris 1: 112 (as page "105"). 1792. **LECTOTYPE** (designated by Pruski 1998): **FRENCH GUIANA**. Cayenne, 1792, *LeBlond* 336 (lectotype: G; isolectotypes: C, P-3, US). *Lepidaploa remotiflora* is endemic to South America, and has been

misapplied (e.g., Robinson 1990, 1999; Redonda-Martínez and Villaseñor 2011; Pruski 2013) to Central American material of *L. acilepis*. Some other Central American materials determined earlier as *L. remotiflora* are determined here variously as *L. argyropappa*, *L. tortuosa*, or *L. uniflora*. Similarly, *L. remotiflora* (as *Vernonia remotiflora*) was erroneously attributed by Grisebach (1863, 1866) to the West Indies but was excluded subsequently by Ekman (1914). South American *L. remotiflora* is distinguished by its gland-tipped, relatively long corolla lobes. Nevertheless, in its spinulose outer phyllaries, *L. remotiflora* is similar *L. acilepis* as well as to a larger group of species centering around *L. gracilis* (Kunth) H. Rob., each species having aristate-spinulose outer phyllary tips (Pruski 1997).

Lepidaploa salzmännii (DC.) H. Rob., *Proc. Biol. Soc. Wash.* 1032: 492. 1990. *Vernonia salzmännii* DC., *Prodr.* 5: 55. 1836, as "salzmänni." **TYPE: BRAZIL.** In umbrosis circa Bahiam, 1830, *Salzmann s.n.* (holotype: G-DC, as Macbride neg. 8134, as IDC microfiche 800. 774.III.4; isotype: MPU). The numbers on the sheets are taxon numbers rather than collection numbers. As mentioned in the discussion above, *L. argyropappa* is the correct name for the Mexican, Central American, and northern South American species once called *L. salzmännii* (sensu Baker 1873, non DC. 1836). *Lepidaploa salzmännii* s. str. is thus excluded from Central America and proves instead to be endemic to Brazil.

Vernonia punctata Sw. ex Wikstr., *Kongl. Vetensk. Acad. Handl.* 1827: 72. 1828 [in Robinson 1990, 1999 as a synonym of West Indian **Lepidaploa glabra** (Willd.) H. Rob.] was cited by Hemsley (1881: 73) as in Belize based on a Temple collection, which presumably I would determine as *L. uniflora*.

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