COMPOSITAE OF CENTRAL AMERICA–IV. THE GENUS *EREMOSIS* (VERNONIEAE), NON-GLANDULAR TRICHOMES AND PERICARP CRYSTALS

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

ABSTRACT

The nine Central American species of the Mexican and Central American endemic genus Eremosis (Vernonieae) are revised. New combinations validated are these: Eremosis aristifera (S.F. Blake) Pruski, comb. nov., Eremosis baadii (McVaugh) Pruski, comb. nov., Eremosis corymbosa (Mill.) Pruski, comb. nov., Eremosis feddemae (McVaugh) Pruski, comb. nov., Eremosis macvaughii (S.B. Jones) Pruski, comb. nov., Eremosis mima (Standl. & Steyerm.) Pruski, comb. nov., Eremosis pugana (S.B. Jones & Stutts) Pruski, comb. nov., Eremosis solorzanoana (Rzed. & Calderón) Pruski, comb. nov., Eremosis standleyi (S.F. Blake) Pruski, comb. nov., Eremosis thomasii (H. Rob.) Pruski, comb. nov., and Eremosis villaregalis (Carvajal) Pruski, comb. nov. Illustrated features useful in characterizing *Eremosis* include typically simple or infrequently T-shaped non-glandular trichomes. narrow-based pappus bristles, and a slight trend towards moderately elongate hexagonal pericarp crystals (raphides). Photographs of types or representative specimens are given for half a dozen species including Conyza corymbosa (which includes in synonymy the type of Eremosis) and Turpinia tomentosa (the type of synonymous Turpinia). In the second part of the present work, an annotated nomenclator of the 27 recognized species in *Eremosis* is given, and nine informal species groups are outlined in tabular form. Lectotypes are chosen for Conyza corymbosa Mill., Eupatorium uniflorum Sessé & Moc., and Vernonia palmeri Rose, and the typification of Monosis salicifolia DC. is discussed.

Eremosis (DC.) Gleason (1906) (Compositae: Cichorioideae: Vernonieae) is a mostly midelevational genus endemic to Mexico and Central America. *Eremosis* may be generally recognized by its woody habit including trees to 15+ meters tall, large compound paniculate capitulescences, uniflorous to few-flowered discoid capitula, and deciduous inner phyllaries (Jones 1973; Robinson 1993). The earliest generic name for *Eremosis* is *Turpinia* Lex. (Lexarza 1824; viz Fig. 12), but that is an illegitimate later homonym of *Turpinia* Vent. (Ventenat 1807). *Eremosis* was described as *Monosis* sect. *Eremosis* DC. (Candolle 1836) and characterized as uniflorous (the sectional name was derived from the Greek "*eremos*") (viz Figure 1, an original element of the type of *Eremosis*). Gleason (1906, 1922) treated *Monosis* sect. *Eremosis* at the generic rank as *Eremosis*, into which he also accepted pauciflorous species. *Monosis* DC. sensu stricto proves to be endemic to southern Asian and differs by lophate pollen (Robinson and Skvarla 2006). Other early generic names associated with *Eremosis* are *Oliganthes* Cass., which Pruski (1996) listed as endemic to Madagascar and *Gymnanthemum* Cass., given by Robinson (1999b) as an African and Asian native.

Gleason (1922) listed as 18 the number of species of *Eremosis* in Mexico and Central America, and treated *Critoniopsis* Sch. Bip. as a possible synonym. Jones (1973) recognized *Eremosis* as *Vernonia* sect. *Eremosis* (DC.) Sch. Bip., gave *Critoniopsis* in synonymy, and treated 20 species in his regional revision. Historically, *Eremosis* has also usually been treated as *Vernonia* sect. *Eremosis* (e.g., Schultz Bipontinus 1847, 1856; Bentham and Hooker 1873; Hoffmann 1890–1894; Blake 1917; Jones 1977; Turner 2007). Jones (1979a), Keeley and Turner (1990), and Smith and Coile (2007) recognized the group as *Vernonia* subsect. *Eremosis* (DC.) S.B. Jones. Species of *Eremosis* were treated as *Vernonia* Schreb. sensu lato and without infrageneric distinction in floristic works of Hemsley (1881), Blake et al. (1926), Standley (1938), Clewell (1975), D'Arcy (1975), Nash (1976), Villaseñor (1989), Rzedowski and Calderón de Rzedowski (1995a), and Keeley (2001). When recognized as *Vernonia*,

however, four names with priority (i.e., *E. corymbosa*, *E. foliosa*, *E. ovata*, and *E. tomentosa*) are confusingly blocked nomenclaturally in *Vernonia*.



Figure 1. Uniflorous *Eremosis corymbosa* (Mill.) Pruski, a reproduction of Sessé and Mociño, Icon. Flora Mex. 164, drawn between 1787–1803 [Illustr. Hunt Institute (Torner) 6331.0241; redrawn in black and white as Candolle plate 526 = Field neg. 30707; viz Sprague 1926; McVaugh 1980, 2000]. Icon. Flora Mex. 164 is a protologue element of each *Monosis salicifolia* DC., Prodr. 5: 77. 1836 and *Eupatorium uniflorum* Sessé & Moc., Pl. Nov. Hisp. 132. 1887 [1890]; Pl. Nov. Hisp. (ed. 2) 123. 1893. The number "19" on the upper portion of the plate refers to the Linnaean sexual system Class XIX Syngenesia. *Seriphium corimbosum* is an unpublished Sessé and Mociño name and *Shawia corymbosa*, in Candolle's hand, is also unpublished.

Robinson et al. (1980: 426) positioned Eremosis in Vernonieae subtribe Vernoniinae and Critoniopsis in the newly described subtribe Piptocarphinae. Similarly, when Schultz Bipontinus (1863) described Critoniopsis as new he did not relate it to what he earlier called Vernonia sect. Eremosis (Schultz Bipontinus 1847). Cuatrecasas (1956) and Robinson (1980) recognized Vernonia sect. Critoniopsis (Sch. Bip.) Benth. & Hook. f. and Critoniopsis as endemic to South America. More recently, Robinson (1993, 1999a) added Eremosis to synonymy with Critoniopsis and placed it in subtribe Piptocarphinae. Robinson characterized Piptocarphinae by readily deciduous inner involucral bracts, thus distinguished from Vernonia sensu stricto (subtribe Vernoniinae). Robinson (1993, 1999a) recognized 76-85 species of Critoniopsis, with the genus distributed from South America northward into Mexico. Turner (2007) recognized as 24 the number of Mexican species and treated them as Vernonia sect. Eremosis. Keeley et al. (2007: Fig. 2) and Keeley and Robinson (2009: Fig. 28.2) showed (Keeley & Keeley 3161 determined as) E. shannonii (J.M. Coult.) Gleason in a clade containing Stokesia laevis (Hill) Greene and subtribe Leiboldiinae. At about the same time, Robinson (2007) and Haro-Carrión and Robinson (2008) suggested exclusion of Eremosis from synonymy with Critoniopsis. Keeley and Robinson (2009: Table 28.1) gave *Eremosis* as endemic to Mexico and *Critoniopsis* as found from Mexico to South America. Keeley and Robinson (2009) recognized 21 subtribes in Vernonieae. Eremosis was unplaced subtribally and as sister to a large clade containing most American genera including both Critoniopsis and Vernonia, the latter two treated in Piptocarphinae and Vernoniinae, respectively (Keeley and Robinson 2009). Nevertheless, Robinson et al. (1980) noted "some species of Piptocarphinae closely approach members of the Vernoniinae genus Eremosis in some characters."

Jones (1973) characterized Vernonia sect. Eremosis (i.e., Eremosis) as typically bearing only simple (rarely T-shaped) non-glandular trichomes (Figs. 2-3), supporting separation of *Eremosis* from Critoniopsis (Robinson 2009: 91; Mukherjee and Nordenstam 2012: 83). Robinson (2009: 91) gave Tshaped trichomes on herbage as characteristic of *Tephrothamnus* Sch. Bip., which has acute-tipped style branch sweeping papillae. This Venezuelan monotype seems recognizable by these trichome and papillae characters in combination with its glandular but never hirsute-pilose cypselae and its double pappus with the outer series of very short relatively membranous scales. The two species of *Eremosis* known to have T-shaped trichomes (E. angusta and E. thomasii) differ from Tephrothamnus by their combined characters (e.g., viz recommendation of Jones 1977) of eglandular setulose-substrigillose to pilose or pilose-hirsute cypselae with a simple pappus (Fig. 5A). These two species are provisionally maintained in Eremosis sensu Gleason (1922) and Jones (1973). Features other than kinds of nonglandular trichomes useful in distinguishing *Eremosis* from *Critoniopsis* include these: (1) relatively long, acute to obtuse-tipped style branch sweeping papillae (Robinson 1993: 607); (2) an isomorphic (vs. dimorphic with outer scales) pappus of relatively narrow-based bristles (Figs. 5-6); and (3) a slight trend towards moderately elongate hexagonal (vs. quadrangular or hexagonal) pericarp raphide crystals (Figs. 7-10). Critoniopsis and Piptocarpha of subtribe Piptocarphinae have short and blunt style branch sweeping papillae (Robinson 1993; Smith and Coile 2007: Fig. 7B).

Here, Mexican to Central American *Eremosis* is recognized as distinct from each American temperate-centered *Vernonia*, South American *Critoniopsis*, and Venezuelan *Tephrothamnus* Sch. Bip. The nine Central American species of *Eremosis* (basically those not treated by Turner 2007) are revised for Flora Mesoamericana project. Eleven new combinations are made for Mexican and Central American species, and the 27 recognized species of *Eremosis* (Table I places each species in one of nine somewhat arbitrarily defined informal species groups; viz similarly nearly throatless *E. leiocarpa* and *E. standleyi* being placed in different groups; as are T-shaped trichome-bearing *E. angusta* and *E. thomasii*) are enumerated with abbreviated typology and synonymy from among the suites of specimens mostly seen while working for about a decade each at NY, US, and MO.

Materials and Methods. Cypselae were boiled for one minute, dissected longitudinally into four pieces, and their ovaries and pappus removed. The pericarps were then bleached in a 5% aqueous hydrogen chloride solution for 20 minutes. Half of the pericarps were mounted on glass slides with their epidermis face-up and half were mounted with the epidermis face-down. Other preparations are basically those of Pruski (2012).

Non-glandular trichomes. Urbatsch (1972) and Faust and Jones (1973) reported both Lshaped and simple non-glandular trichomes in north temperate Vernonia Schreb. sensu stricto. Redonda-Martínez et al. (2012) showed that L-shaped, T-shaped, and simple non-glandular trichomes occur in Neotropical Vernonanthura H. Rob. And still elsewhere, another heterotrichous Vernonian group was noted by Wagner et al. (2014), who reported bladder-stellate, T-shaped, and simple nonglandular trichomes in Brazilian-centered Lychnophorinae. Andean Critoniopsis was also shown as very heterotrichous and was characterized in Haro-Carrión and Robinson (2008: Figs. 4-9) and Robinson and Keeley (2015: Fig. 3C; below viz also Fig. 4) by its "most often irregularly branched to stellate" non-glandular trichomes. Robinson (2009: Fig. 6:4) showed also goblet-shaped and basallyspurred non-glandular trichomes in Critoniopsis, T-shaped non-glandular trichomes in Venezuelan Tephrothamnus paradoxus Sch. Bip. (treated by Robinson 1993 in Critoniopsis), and simple trichomes in *E. leiocarpa*. Robinson (2009) suggested that by the presence of non-glandular trichome types Tephrothamnus and Eremosis could "be excluded" from Piptocarphinae. However, Haro-Carrión and Robinson (2008, Fig. 10A) also noted simple vermiform non-glandular trichomes in C. suaveolens (Kunth) H. Rob., and Robinson and Keeley (2015: Fig. 3F) noted T-shaped non-glandular trichomes in C. glandulata (Cuatr.) H. Rob. Apparently Piptocarphinae is not defined solely by kinds of trichomes as individual trichome types are known to co-occur in distinct subtribes.



Figure 2. Simple non-glandular trichomes characteristic of *Eremosis*. A. SEM micrograph of abaxial leaf surface of *Eremosis mima*. B. LM photograph of multicellular base of simple non-glandular abaxial surface foliar trichome of *Eremosis leiocarpa*. The terminal cells are elongated. (A *Véliz 94.3535*, MO; B *Breedlove 50060*, MO). [Scale bar: B 0.1 mm].



Figure 3. SEM micrograph (A) and LM photograph (B) of T-shaped non-glandular trichomes of *Eremosis thomasii*. Both from *Hawkins* 988 (MO). [Scale bar: B 100 µm].



Figure 4. SEM micrographs of non-glandular foliar trichomes in *Critoniopsis*. A. Unicellular, bladder-stellate trichomes in *Critoniopsis oblongifolia* Sagást. & M.O. Dillon. B. Irregularly ramified trichomes in *Critoniopsis lindenii* Sch. Bip., the generitype. (A *Sagástegui et al. 15798*, MO, an isotype; B *Triana 91*, MO).

Eremosis typically bears only simple non-glandular trichomes (viz Fig. 2), although Jones (1973) also noted T-shaped non-glandular trichomes in *E. angusta*. T-shaped non-glandular trichomes have subsequently also been observed in Honduran *E. thomasii* (Fig. 3). The "bilobed" trichomes of Vernonieae referred to in *Eremosis* by Jones (1973: viz Table II) and illustrated by Urbatsch (1972: Fig. 3A), Faust and Jones (1973: Figs. 1A–B, 2A), Robinson (2009: Fig. 6:4D), and Redonda-Martínez et al. (2012: Figs. 1D, 1H), are sessile globular glandular trichomes and occur widely throughout the tribe. The mention by Favi et al. (2008) of "peltate-glands" in *Vernonia* is in reference instead to short-stipitate biseriate glands; *Vernonia* lacks true peltate trichomes. In *Eremosis*, the sessile globular glandular trichomes (when present) in each species appear to be morphologically similar and are not further considered. Presence of similar simple, T-shaped, bladder-stellate non-glandular trichomes in *Eremosis, Critoniopsis*, and Lychnophorinae represent three of many Vernonian

groups where vestiture features are not at all diagnostic at higher taxonomic levels. Nevertheless, at lower taxonomic levels non-glandular trichome compliments may be a useful character and indeed, *Critoniopsis* mostly has non-glandular trichomes variously branched or armed, and *Eremosis* mostly simple non-glandular trichomes. Here, light microscope (LM) photographs and scanning electron microscope (SEM) micrographs of representative simple and T-shaped non-glandular trichomes in *Eremosis* (Figs. 2–3) and representative armed non-glandular trichomes in *Critoniopsis* (Fig. 4) are given.

Cypselae. Cypselae of *Eremosis* are obconical-prismatic, have 3–10 indistinct to obvious angles, striations, or costae and sometimes moderately developed apical callose zones (Fig. 5). Although the character extremes in cypselae that range from weakly few-striate to thickly 10-costate are noteworthy, species at each extreme are retained in *Eremosis*, as in Gleason (1922) and Jones (1973). For example, the first key lead in Gleason (1922) separated from remaining species *E. heydeana* and *E. leiocarpa* by their glabrous abaxially smooth cypselae. The cypselae surfaces of *Eremosis* may be solely pubescent with non-glandular trichomes, solely glandular, both glandular and pubescent, or glabrous throughout (Fig. 5). Bulbous idioblast cells are frequently present in the pericarp wall. When pubescent, the cypselae of *Eremosis* differ from those of basically non-setiferous *Critoniopsis* (Fig. 6B; Robinson 1993: 607) and *Tephrothamnus*. Although most species of *Eremosis* have unevenly few-angled cypselae, the Mesoamerican endemic *E. shannonii* has evenly strongly pluricostate cypselae (as keyed by Jones 1973), yet it falls within each of our concepts of *Eremosis*.



Figure 5. SEM micrographs of isomorphic simple pappus bristles and cypselae of *Eremosis*. A. *Eremosis thomasii*, showing the pilose, non-glandular, obviously costate cypselae with a glabrous slightly developed apical callose zone; most species of *Eremosis* have cypselae similarly setiferous. B. *Eremosis mima*, showing the basically glabrous cypselae with a narrow apical callose zone bearing narrow-based pappus bristles; the inner adaxial face (left) is weakly few-striate-costate and in mature cypselae the outer abaxial face (right) is more or less smooth and rounded. (A *Hawkins* 884, MO; B *Castillo & Vargas* 2765, MO).



Figure 6. SEM micrographs of double pappus of short broad outer scales and elongate inner bristles that are characteristic of cypselae of *Critoniopsis*. A. *Critoniopsis lindenii* Sch. Bip., the generitype. B. *Critoniopsis oblongifolia* Sagást. & M.O. Dillon, showing the non-setiferous cypselae typical of *Critoniopsis*. (A *Triana 91*, MO; B *Sagástegui et al. 15798*, MO, an isotype).

Elsewhere in Vernonieae, Pruski (1996) noted similar cypsela variations in Piptocoma Cass. (Piptocarphinae), where he recognized four sections. Similarly, it seems possible that infragenera stressing cypsela morphologies, and in turn the association of glabrous cypselae with a narrow apical callose zone giving rise to relatively narrow elongate slightly non-contiguous basally pappus bristles (viz Fig. 5B), could ultimately be recognized within Eremosis. At present, Eremosis itself is not divided, and more than being a convenient species residuum, Eremosis seems to be a natural group as defined by Gleason (1906, 1922) and Jones (1973). However, Robinson (1999b) noted that in many species groups of Gymnanthemum Cass. (albeit with some later removed to Decaneuropsis H. Rob. & Skvarla 2007 and elsewhere) members may have cypselae 5-costate or 10-costate, possibly devaluing infragenerically this character when used within related genera. The apical callose zone in Eremosis is sometimes slightly pronounced, but it is often poorly developed in glabrous-fruited species. A very large inflated apical callose zone characterizes subtribe Leiboldiinae, and some species of *Eremosis* begin slightly to approach this condition more so than do most taxa now placed in either Piptocarphinae or Vernoniinae. The pappus of *Eremosis* may be in a single series or in 2 series, often with all bristles elongate. However, several species of *Eremosis* have a shorter outer series of bristles, but then these shorter bristles are always as narrow as the inner and never broad and scale-like (Fig. 5). It is the isomorphic diameter of the pappus bristles in *Eremosis* that perhaps further distinguishes it from *Critoniopsis*, which typically has a double pappus of outer short broad scales and inner elongate bristles (Fig. 6).

Pericarp Crystals (raphides). The pericarps in *Eremosis* when bleached are seen to be littered with calcium oxalate crystals (raphides), which are moderately elongate and hexagonal (e.g., Figs. 7–8). The pericarp raphide crystals seen in *Critoniopsis* (Fig. 9B) are quadrangular or hexagonal and moderately similar to *Eremosis*. Robinson (1999a: viz Table 7) noted only quadrangular crystals in *Critoniopsis*, so further study of variation in crystal shapes is needed. *Piptocarpha triflora* has quadrangular pericarp crystals (Fig. 9A), but Robinson (1999a) noted a range from quadrangular to hexagonal crystals in the genus. Angulo et al. (2015) showed pericarp crystals in species of *Lessingianthus* H. Rob. (Vernoniinae) range from quadrangular to elongate hexagonal, and it is possible that similar variability may be present in *Eremosis* and *Critoniopsis*. At present, it appears that

Eremosis may be distinguished provisionally from *Critoniopsis* by its trend (albeit perhaps not a statistically noteworthy one) towards elongate hexagonal pericarp crystals. Figure 10 and Robinson (1999a: Tables 2–6) show wide variation but an overall trend toward elongate crystals in many Vernoniinae as opposed to those observed in *Eremosis*. Angulo et al. (2015) concluded that crystal types "may not be useful for generic segregation." Here, the trend towards having moderately elongate hexagonal pericarp crystals seems best used in tandem with other features to characterize *Eremosis*.



Figure 7. Moderately elongate hexagonal pericarp raphide crystals of *Eremosis corymbosa*. Both from *Pringle 6188* (MO), an isotype of synonymous *Eremosis leiophylla*. [Scale bars: A 30 µm; B 50 µm].



Figure 8. Moderately elongate hexagonal pericarp raphide crystals of *Eremosis leiocarpa*. Both from *Jones* 21675 (MO). [Scale bars: A 50 µm; B 10 µm].



Figure 9. Pericarp raphide crystals in two representative Piptocarphinae. A. *Piptocarpha triflora*, crystals quadrangular. B. *Critoniopsis jelskii*, crystals quadrangular and hexagonal; several surface bulbous idioblast cells are present. (A *Pruski et al. 3456*, NY; B *Vásquez et al. 26186*, MO). [Scale bars: A 15 µm; B 10 µm].



Figure 10. Elongate hexagonal pericarp raphide crystals of *Lepidaploa tortuosa* (Vernoniinae). (Both from *Pruski et al. 4239*, MO). [Scale bars: A 50 µm; B 10 µm].

EREMOSIS (DC.) Gleason, Bull. New York Bot. Gard. 4: 227. 1906. Monosis sect. Eremosis DC., Prodr. 5: 77. 1836. Vernonia sect. Eremosis (DC.) Sch. Bip., Linnaea 20: 506. 1847; Sch. Bip. in Seemann, Bot. Voy. Herald 297. 1856; Benth. & Hook. f., Gen. Pl. 2: 231. 1873. Vernonia subsect. Eremosis (DC.) S.B. Jones, Rhodora 81: 435. 1979. LECTOTYPE (Gleason 1906: 227): Monosis salicifolia DC. [= Eremosis corymbosa (Mill.) Pruski].

Turpinia Lex., Nov. Veg. Descr. 1: 24. 1824 (non *Turpinia* Vent., July 1807, Staphyleaceae, nom. cons.; non *Turpinia* Pers., April 1807, Fabaceae; non *Turpinia* Bonpl., April–June 1807, Barnadesieae). **Type:** *Turpinia tomentosa* Lex. [= *Eremosis tomentosa* (Lex.) Gleason].



Figure 11. Lectotype (*Houstoun s.n.*, BM) of uniflorous *Conyza corymbosa* Mill. [\equiv *Eremosis corymbosa* (Mill.) Pruski, which includes in synonymy *Monosis salicifolia* DC., the type of *Eremosis*].



Figure 12. Historical specimen of uniflorous *Turpinia tomentosa* Lex. (*Anon.*, NY). [\equiv *Eremosis tomentosa* (Lex.) Gleason], a name published in Nov. Veg. Descr. fascicle 1. *Turpinia tomentosa* is the generitype of *Turpinia* Lex., a synonym of *Eremosis*. Although this specimen is labeled as "Fascic. 1" and the handwriting on the rectangular label is of the Spanish School, I am uncertain if it was written by Lexarza. Perhaps instead it was written by La Llave, Sessé and Mociño (although not on longitudinally elongated labels), etc. This top-snatch specimen, although only a possibly authentic isotype is, nevertheless, used to confirm *Turpinia* as a generic synonym of *Eremosis*. A 15 cm ruler is at top.

Shrubs, vines, or trees to 15+ m, rarely collected flowering when seemingly a perennial herb: stems subterete to striate, sometimes angled; herbage usually with simple (infrequently T-shaped, seen only in E. angusta and E. thomasii) non-glandular trichomes, these never lepidote nor bladderstellate. Leaves alternate, petiolate or rarely sessile; blade lanceolate to ovate or obovate, chartaceous to subcoriaceous, pinnately veined, surfaces (even the adaxial) pubescent to tomentose, often glandular, infrequently completely glabrous, margins entire to serulate or denticulate. Capitulescence terminal (infrequently axillary), of many rounded corymbiform or umbellate, pluricephalous clusters forming a large compound panicle (viz Jones 1973: Figs. 1B, 1D), ultimate capitula sometimes subglomerate. Capitula discoid, 1-10(-16)-flowered, usually subsessile or shortpedunculate; involucre cylindrical to campanulate; phyllaries imbricate, graduate, 4-7+-seriate, usually tan-chartaceous often with a small apical herbaceous zone, outer phyllaries often closely inserted and densely imbricate, persistent, inner phyllaries somewhat loosely imbricate and moderately deciduous although sometimes only tardily so; clinanthium epaleate. Florets: corolla actinomorphic, funnelform to narrowly campanulate, infrequently salverform, 5-lobed, white to lavender, often glandular especially on the lobes; anther thecae sagittate to obtuse at base, without sclerified tails, apical appendage cell walls moderately thick; pollen tricolporate, echinate, sublophate (Type A; viz Jones 1979a: Fig 4A; Keeley and Turner 1990: Table 2); style with slightly enlarged basal node, trunk papillose distally, branches slender, sweeping papillae acute to obtuse (never blunt) Cypselae obconical-prismatic, 3–10-angled, 3–10-striate, or 3–10-costate, glabrous, at apex. glandular, or pubescent, apical callose zone slightly developed, rarely elongated as a membranous

skirt exterior to pappus bristles, apex truncate, base narrowed, pericarp with crystals moderately elongate hexagonal, carpopodium without distinct upper rim; pappus of many fragile white scabrid bristles, simple, uniseriate and typically most elongate (with innermost the longest) or sometimes with a distinct outer series of narrow bristles that are never broadened and scale-like. x = 17, 18, 19.

Eremosis is a Mexican and Central American genus of 27 recognized species (Table I), and is recognized as distinct from each Critoniopsis and Vernonia. Vernonia duncanii, V. macphersonii, and V. salicifolia/uniflora, each recognized by either Jones (1973) or Turner (2007), are treated here in synonymy; if shown to be distinct recognition of them could raise to 30 the number of species of Eremosis. Salient features of Eremosis are its woody habit, usually simple non-glandular trichomes, large and compound paniculate capitulescences, few-flowered capitula, deciduous inner phyllaries, relatively long, acute to obtuse-tipped style branch sweeping papillae, cypselae usually setiferous and with a slightly developed apical callose zone, an isomorphic pappus of relatively narrow-based bristles, and a slight trend towards moderately elongate hexagonal pericarp raphide crystals. The base chromosome numbers of *Eremosis* appear to be x = 17, 18, 19 (Jones 1973, 1979b), and the base numbers of "10, 17?" given for "Vernonia subsect. Eremosis" by Keeley and Turner (1990) seems aberrant. Robinson (1999a) gave as x = 17 the base number of *Critoniopsis* (then including Eremosis). Jones (1973) reported chromosome numbers of only five uniflorous species: E. aristifera, E. leiocarpa, and E. obtusa as diploids; and E. corymbosa and E. tomentosa as tetraploids. Eremosis was treated as a member of subtribe Vernoniinae by Robinson et al. (1980), in synonymy of Critoniopsis (subtribe Piptocarphinae) by Robinson (1993, 1999a), who stressed the character of deciduous inner phyllaries, and as unplaced to subtribe by Keeley and Robinson (2009). Although Robinson (1999b) noted that both American Piptocarphinae and Paleotropical Gymnantheminae share the character of deciduous inner phyllaries, this nevertheless remains a convenient character for recognizing Eremosis. Jones (1973), Harborne and Williams (1977), Jones (1979a), Seaman (1982), and Bohlmann and Jakupovic (1990) gave the secondary metabolite sesquiterpene lactone class glaucolide as found in species treated here as *Eremosis*, but they also noted that glaucolides are widespread in each Leiboldiinae, Piptocarphinae, and Vernoniinae. Another feature noted by Jones (1979a) as characteristic of *Eremosis* is the tricolporate echinate sublophate (Type A) pollen, also widespread elsewhere in Vernonieae. Eremosis is sister to Leiboldiinae but remains unplaced subtribally. Further study of phyllary persistence, cytology, glaucolide types, and pollen features, however, may help resolve ultimate placement of these taxa.

With regards to *Eremosis* species in Central American, it may be useful to note that Nash (1976) treated as Guatemalan seven of the nine species treated here in Mesoamerica, and only *E. oolepis* and *E. thomasii* remain unreported in Guatemala. The report by Sousa and Cabrera (1983: 81) of *E. barbinervis* (Sch. Bip.) H. Rob. in Quintana Roo is based on a misdetermination of *E. oolepis*. Breedlove (1986) cited *E. pallens* (Sch. Bip.) H. Rob. for Chiapas based on *Breedlove 24648* and *Ton 2073*. Turner (2007), however, listed this species as occurring only far to the NW of Chiapas, and pauciflorous *Breedlove 24648* is determined here as *E. triflosculosa*. Thus, each *E. barbinervis* and *E. pallens* are excluded from Mesoamerica. The citation by Turner (2007: 133) of *E. triflosculosa* in Quintana Roo, Mexico, is also presumably based on material of *E. oolepis*. *Vernonia mima* by its glabrous cypselae similar to *E. shannonii* is aligned with *Eremosis* and is one of six species endemic to Mesoamerica.

Of the six Mesoamerican endemics, only *E. standleyi* is moderately common; it can be distinguished by its long-lobed nearly throatless corollas (Fig. 14) and pilose-sericeous fruits. Five of nine Flora area species have been collected at or below 600 meters elevation (elevations here are rounded to nearest 100 meter intervals), but in general *Eremosis* is mid-elevational. *Eremosis heydeana*, described from Guatemala, is relatively widespread and occurs northwards into central Mexico but is nowhere common. On the other hand, *E. leiocarpa* and *E. triflosculosa* are widespread

and moderately common throughout much of southern Mexico and Central America. *Eremosis leiocarpa* and *E. triflosculosa* are often similarly tomentose-leaved and are best distinguished by corolla throat-lobe and fruit indumentum characters.

Seven of nine (78%) Mesoamerican species and four of six (67%) of Mesoamerican endemic species follow species key lead 1A or 6B; and in Table I fall into either the first or last morphologically-defined species group. Overall, only 11 of 27 (41%) species fall into either the first or last species group, showing a relative concentration of a few morphotypes (as delineated here in Table I) in Mesoamerica. On the other hand, only two of 27 species of *Eremosis*, each a Mesoamerican endemic (i.e., *E. angusta* and *E. thomasii*), are reported to have T-shaped non-glandular trichomes. Eleven of the total 27 (41%) species are primarily uniflorous and spread among species groups 2–5, but in Mesoamerica only *E. angusta* (one of nine species, 11%) is uniflorous. Should each of the following problem synonyms of uniflorous species [i.e., *V. duncanii* group two, *V. macphersonii* group four, and *V. uniflora* group five, viz Table I] be resurrected, the genus would expand to include 30 species; only 33% would then fall into either species group one or species group nine; and the count of primarily uniflorous species would increase from eleven (41%) to fourteen (47%).

Eremosis was recognized at the genus level by Gleason (1906, 1922), and Jones (1973) revised it recognizing 20 species. Robinson (1993) transferred most Mexican and Central American species to *Critoniopsis*. In the Flora del Bajio Rzedowski and Calderón de Rzedowski (1995a) treated six species of *Eremosis* as *Vernonia*, giving the names in *Eremosis* as synonyms, but not listing the then recently published (Robinson 1993) names in *Critoniopsis*. Turner (2007) revised Mexican *Eremosis* species also under the name *Vernonia*, and he updated Jones (1973) by including treatments of the species described after the Jones monograph. Redonda-Martínez and Villaseñor-Ríos (2009), Carnevali et al. (2010), and Villaseñor-Ríos (2011) recognized as *Critoniopsis* species of *Eremosis* in Flora del Valle de Tehuacán-Cuicatlán, the Yucatán peninsula, and Oaxaca, respectively. Berendsohn et al. (2009) treated as *Critoniopsis* three species of *Eremosis* in El Salvador.

For the present Flora Mesoamericana project treatment of *Eremosis*, I use a combination (nearly chronologically) of the taxonomies of Gleason (1906, 1922), Blake (1917), Blake et al. (1926), Jones (1973), Robinson (1993), and Turner (2007). The taxonomies of *E. obtusa*, *E. foliosa*, and *E. steetzii* groups, as noted by Blake et al. (1926) and McVaugh (1972a), are not satisfactorily worked out. Although Jones (1973) recognized *V. salicifolia* and *V. uniflora* as distinct, they are provisionally treated here in synonymy with *E. corymbosa*. Elsewhere too, the present treatment is conservative with broad species limits allowed; for example, six names previously proposed in *Eremosis* are treated in synonymy, and *V. duncanii* and *V. macphersonii* are not transferred to *Eremosis* but rather treated here in synonymy.

Following the Central American species treatments, the recognized species in *Eremosis* are briefly enumerated with new nomenclatural combinations made for eight Mexican endemics. I hope this abbreviated summary will supplement the fine revision of Jones (1973) and the thorough nomenclator of American Vernonieae in Robinson (1999a). In the discussion above and in what follow, species are generally referred to as *Eremosis* even though called *Vernonia* in Jones (1973) and Turner (2007) and even though 11 names in *Eremosis* have not been coined before today. Several names in *Vernonia* prove to be synonyms of *Eremosis* species, and those never treated nomenclaturally as *Eremosis* are still called *Vernonia* herein.

Key to Mesoamerican species of Eremosis

1. Cypselae glabrous or when sparsely glandular then either only distally so or with involucres 10–13 mm long.

Corollas nearly throatless with lobes cut to near tube; leaf blades discolorous, usually densely tomentose abaxially; mid-series phyllary apices usually broadly obtuse and tomentulose.
 Corollas with throat, lobes not cut to near tube; leaf blades more or less concolorous, glabrate to sparsely tomentulose abaxially; mid-series phyllary apices either acute or nontomentose.

- 3. Capitula 3-6(-7)-flowered.

4. Leaf blades pilose-hirsute to sometimes sparsely tomentulose; cypselae unequally 3–4-costate-angled with abaxial face often smooth and rounded, ca. 3 mm long; involucres 4–6 mm long; corollas glandular in distal half, tube infrequently glandular.
2. Eremosis heydeana
4. Leaf blades closely arachnoid-pubescent becoming glabrate; cypselae sometimes equally 10-costate, terete, 4–6.5 mm long; involucres 10–13 mm long; corollas glandular almost throughout.
6. Eremosis shannonii

1. Cypselae pubescent, sometimes also glandular; involucres 4–6.5 mm long.

5. Capitula 1-flowered; abaxial leaf surfaces tomentulose with T-shaped non-glandular trichomes.
5. Capitula 3–10-flowered; abaxial leaf surfaces (when pubescent) typically with simple non-glandular trichomes.

6. Capitulescences of axillary glomerules, glomerules usually sessile; corolla lobes about half the length of corollas, cut nearly to base of limb, throat nearly lacking.
6. Capitulescences variously paniculate, terminal or sometimes lateral; corolla lobes usually 1/3–1/4 length of corollas, throat present.

Non-glandular stem trichomes T-shaped; involucres narrowly campanulate, 2.5–3 mm diam.
 Non-glandular stem trichomes simple; involucres cylindrical, 1.3–2.5 mm diam.
 P. Eremosis triflosculosa

1. EREMOSIS ANGUSTA Gleason, N. Amer. Fl. 33: 98. 1922. TYPE: GUATEMALA. Zacapa. Gualan, 125 m, 21 Feb 1907, *Kellerman 6132* (holotype: F).

Critoniopsis angusta (Gleason) H. Rob., Vernonia angusta (Gleason) Standl.

Shrubs or small trees to 5 m tall; stems tomentulose. **Leaves** petiolate; blade $5-19(-6) \times 1.5-2(-3)$ cm, lanceolate to elliptic-lanceolate, usually widest above the middle, 2° veins usually 5 per side, adaxial surface scabrous, abaxial surface sparsely tomentulose with T-shaped (dolabriform)

non-glandular trichomes, also glandular, base cuneate, margins entire, revolute, apex acute to acuminate; petiole 0.5–1 cm long. **Capitulescences** ca. 10 cm diam., densely subglomerate-paniculate, rounded, terminal from distal-most nodes, capitula subsessile to short-pedunculate. **Capitula** 1-flowered; involucre $6-8 \times$ ca. 1.5 mm, narrowly cylindrical; phyllaries ca. 6-seriate, sparsely tomentulose, apical mucro to ca. 0.5 mm long; outer phyllaries ca. $1.7 \times$ ca. 1.1 mm, broadly ovate, apex obtuse; inner phyllaries $5.5-8 \times \le 1$ mm, oblanceolate, apex acute. **Florets**: corolla ca. 6.6 mm long, white. **Cypselae** 2–2.5 mm long, weakly costate, pilose-hirsute, non-glandular; pappus inner bristles ca. 6 mm long.

Distribution and Ecology. The rare Guatemalan endemic *E. angusta* flowers in February and March and has been collected between 100–1100 meters elevation.

Representative collection. GUATEMALA. Kellerman 7922 (F).

Jones (1973) noted the presence of T-shaped non-glandular trichomes in *E. angusta*. I have not seen any specimens collected in the past century.

 EREMOSIS HEYDEANA (J.M. Coult.) Gleason, Bull. New York Bot. Gard. 4: 234. 1906. Vernonia heydeana J.M. Coult., Bot. Gaz. 20: 4. 1895. TYPE: GUATEMALA. Quiché. San Miguel Uspantán, 6000–12000 ft., Apr 1892, Heyde & Lux 3392 (holotype: F; isotypes: GH, K, US).

Critoniopsis heydeana (J.M. Coult.) H. Rob.

Shrubs to trees to 8–15+ m tall; stems sometimes vining, finely tomentulose to hirsutulous, later glabrate. Leaves petiolate; blade $4-10(-14) \times 2.8-6(-7.5)$ cm, usually ovate and widest at or below the middle, 2° veins usually 5–7 per side, adaxial surface hirsutulous to glabrate, sometimes glandular, abaxial surface pilose-hirsute to sometimes sparsely tomentulose, pubescent with simple non-glandular trichomes, also glandular, base cuneate or obtuse, margins entire to remotely denticulate, apex acute to acuminate; petiole 0.9-2 cm long. Capitulescences 10-15 cm diam., loosely subglomerate-paniculate, rounded to long-pyramidal, terminal from distal-most nodes, capitula subsessile to distinctly short-pedunculate. Capitula 3–6-flowered; involucre $4-6 \times 3-4$ mm, campanulate, on bracteolate stipe; phyllaries 5–7-seriate; outer phyllaries many, $1-1.5 \times 0.4-0.6$ mm, triangular, sparsely tomentulose, apex usually narrowly acute; mid-series phyllary apices usually acute and subglabrous; inner phyllaries $4-6 \times 0.8-1.1$ mm, oblanceolate, subglabrous, apex obtuse. Florets: corolla 5.2–6.3 mm long, usually glandular mostly in distal half, tube infrequently glandular, throat present, lobes 1.4–2 mm long, about twice as long as throat, only ca. 1/3 length of corolla. Cypselae ca. 3 mm long, unequally 3-4-costate-angled, glabrous or sometimes sparsely glandular distally, never densely setiferous; pappus somewhat biseriate, outer bristles few, to ca. 1 mm long, inner bristles 5-6 mm long.

Distribution and Ecology. *Eremosis heydeana* is known from oak forests and selva caducifolia in Guatemala and Mexico (Chiapas, Jalisco, ?Oaxaca, Puebla, Querétaro, San Luis Potosí, Veracruz). It has been collected from about 900–1800 meters elevation and flowers from January to April. Jones (1973) cited *E. heydeana* in Mexico only in Veracruz, but Rzedowski and Calderón de Rzedowski (1995a) listed it for several other states on the Gulf watershed. In Querétaro *E. heydeana* occurs only at the extreme eastern frontier near the border with Hidalgo and San Luis Potosí. It is expected in Hidalgo and adjacent areas. Turner (2007) gave *E. heydeana* as expected in Oaxaca.

Representative collections. **GUATEMALA**. *Heyde & Lux 3392* (F, GH, K, US; the type). **MEXICO. Chiapas.** *Breedlove 32777* (CAS, LL, MO); *García et al. 1448* (CICY, MEXU, MO). **Querétaro.** *Rzedowski 42820* (ENCB, IEB). **Veracruz.** *Smith 1845* (F); *Ventura 16930* (MO); *Ventura 16968* (MO). The widespread but moderately uncommon *E. heydeana* may generally be distinguished from *E. leiocarpa* by its leaf blades abaxially less pubescent, but occasionally when this character begins to fail (e.g., *Breedlove 32777*) the narrower subglabrous mid-series phyllaries of the longer pedunculate capitula help to distinguish it from the much more common discolorous-leaved *E. leiocarpa*. *Eremosis heydeana*, *E. shannonii*, and *E. triflosculosa* have on occasion been collected as large-trunked 10+ meter tall trees; perhaps at least *E. heydeana* and *E. shannonii* are under-collected and more common than may be inferred from material poorly represented in herbaria.

3. EREMOSIS LEIOCARPA (DC.) Gleason, Bull. New York Bot. Gard. 4: 232. 1906. Vernonia leiocarpa DC., Prodr. 5: 34. 1836. TYPE: MEXICO. sin. loc., 1827–1832, Karwinski s.n. (holotype: M; isotype: G-DC, as IDC microfiche 800 769.I.4). Figures 2B, 8.

Cacalia leiocarpa (DC.) Kuntze, Critoniopsis leiocarpa (DC.) H. Rob., Eremosis melanocarpa Gleason, Vernonia melanocarpa (Gleason) S.F. Blake

Shrubs or trees 1-5+ m tall, crowns dense and rounded; stems densely tomentose to proximally glabrate. Leaves petiolate; blade $6-14(-18) \times 2-9$ cm, elliptic-ovate to ovate, usually widest below the middle, 2° veins usually 5-8 per side, adaxial surface villous-pilose or sparsely tomentulose to glabrate, abaxial surface usually densely tomentose, pubescent with simple nonglandular trichomes, base cuneate to obtuse or sometimes rounded, margins entire to obviously denticulate, apex acute to acuminate; petiole 1–3 cm long. Capitulescences 5–23 cm diam., densely subglomerate-paniculate, pyramidal, terminal from distal-most nodes, main lateral branches usually longer than subtending leaves, capitula subsessile to short-pedunculate. Capitula 3–5(–7)-flowered; involucre $3.5-7 \times 2.2-3$ mm, narrowly campanulate; phyllaries 5–6-seriate, sometimes in distinct vertical ranks, distally tomentose to tomentulose; outer phyllaries $1.3-2.2 \times 1-1.9$ mm, broadly triangular, apex broadly obtuse; mid-series phyllary apices usually broadly obtuse and tomentulose; inner phyllaries $3.5-6 \times 1-1.9$ mm, oblanceolate, subglabrous, apex obtuse or sometimes acute. Florets: corolla 6–6.7 mm long, white to pink, lobes sometimes distally glandular or setulose, throat nearly lacking, lobes cut to near tube, nearly 1/2 length of corolla, with the anthers thereby basically fully exserted and full exposed. Cypselae 2.5-3.2 mm long, broadly obconic-prismatic, unequally 3costate-angled, glabrous, never densely setiferous, non-glandular, apical callose zone narrow; pappus bristles 1-seriate, all bristles seemingly elongate without a hint of a shorter outer series, 5-6.5 mm long. 2*n* = 34 or 36 (Jones 1973).

Distribution and Ecology. *Eremosis leiocarpa* is widespread from southern Mexico (Chiapas, Guerrero, Oaxaca, Veracruz) southeastwards into Nicaragua where it occurs in open hills, pine forests, pine-oak forests, quebradas secas, rocky hillsides, selva caducifolia, selva perennifolia, and thickets. In Central America *E. leiocarpa* has been collected from about 600–2500 meters elevation and in flower from October to August, with an apparent peak from November to June.

Representative collections. BELIZE. Hicks 65 (MO). EL SALVADOR. Martínez 660 (B, LAGU, MO); Standley 20372 (GH, NY, US); Standley 21598 (NY); Williams 9 (B, K, LAGU, MO). GUATEMALA. Heyde & Lux 3416 (F, GH, MO, NY, US; type of synonymous Vernonia melanocarpa); King 7302 (MO, NY, US); Standley 61234 (F, GH); Standley 83233 (F); Türckheim II 1660 (MO); Williams & Molina 15408 (MO). HONDURAS. Clewell 3771 (MO, NY); Croat & Hannon 63927 (K, MEXU, MO, NO, NY); Keeley & Keeley 4039 (MO); Molina 23390 (NY); Nelson et al. 4058 (MO); Williams & Molina 12226 (MO). MEXICO. Chiapas. Breedlove 33434 (CAS, LL, MO, NY); Breedlove 50060 (CAS, MO); Breedlove 50280 (CAS, MO, NY, TEX); Breedlove 50799 (CAS, MO, TEX); Jones & Jones 21675 (GA, MO, TEX); Martínez et al. 22456 (MEXU, MO, XAL); Matuda 2776 (MO). Guerrero. Rzedowski 27052 (MICH, MO). Oaxaca. Camp 2481 (NY, US); Jones & Jones 21666 (GA, MO, NY); Liebmann 8548 (C, MO); Mexia 9119

(MO, NY). Veracruz. Purpus 14068 (F, US). NICARAGUA. Davidse et al. 30441 (MO); Moreno 23515 (MO); Standley 9604 (F); Stevens et al. 29390 (MO).



Figure 13. Representative specimen of Eremosis mima (Véliz 94.3535, MO).

The common *E. leiocarpa* is the most consistently discolorous broad-leaved species in Central America. A drawing of *E. leiocarpa* was given in Monro et al. (2001: 35, left), but there the non-glandular leaf trichomes were I believe incorrectly depicted as stellate. *Eremosis leiocarpa* is similar in gestalt to *E. triflosculosa*, which differs by its often narrower, less pubescent leaves, narrower involucres, and pubescent fruits. Jones (1973: 91) noted glaucolide F and G in *E. leiocarpa*.

4. EREMOSIS MIMA (Standl. & Steyerm.) Pruski, comb. nov. Vernonia mima Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 264. 1947. TYPE: GUATEMALA. Huehuetenango. East of San Rafael Pétzal, 1730 m, 9 Jan 1941, Standley 82871 (holotype: F; isotype: GH). Figures 2A, 5B, 13.

Shrubs 2-4 m tall; stems subscandent, striate, tomentulose to villosulous. Leaves petiolate; blade $5-12.5 \times 3-8$ cm, ovate or elliptic-ovate, widest at or below the middle, 2° veins 5-8 per side, adaxial surface sparsely puberulent to hirtellous or glabrate, abaxial surface tomentulose to villous, pubescent with simple non-glandular trichomes, base obtuse or rounded, sometimes with shortdecurrent acumen, margins subentire, apex acute; petiole 1-3 cm long. Capitulescences in distal 20-30 cm of larger stems, corymbiform-paniculate or subumbellate, of several broadly rounded somewhat congested clusters 5–10 cm diam. on lateral branches (3–)7–15 cm long from distal 3–7 nodes, lateral branching at about $45-80^{\circ}$ from larger stems; peduncles 2–6 mm long, tomentulose to villosulous, capitula infrequently subsessile. Capitula 10-13 mm long, ca. 10-flowered; involucre 8- $9 \times 4-5$ mm, turbinate-campanulate; phyllaries 5-6-seriate, ascending, sometimes the outer slightly decurrent onto peduncle, pale-greenish, margins sometimes ciliate-villous; outer phyllaries $0.1-2 \times$ 0.5–1 mm, triangular-lanceolate, villosulous, apex acute or acuminate; inner phyllaries $7-9 \times 1-1.4$ mm, about as high as pappus, lanceolate, distally slightly spreading and ultimately deciduous, subglabrous or sometimes villosulous, apex acute or sometimes obtuse. Florets: corolla 7-8 mm long, ochroleucous, glandular, tube ca. 5 mm long, longer than the limb, slender, throat campanulate, lobes 1.5–2.5 mm long, longer than throat, ca. 1/3 length of corollas. Cypselae 2.3–2.9 mm long, turbinate, unequally 3-4-costate-angled adaxially, abaxial (outer) face more or less rounded and smooth, glabrous, never densely setiferous, non-glandular, apical callose short or when mature with a welldeveloped (albeit perhaps simply unobstructed by setae and thereby more readily visible than in species with sericeous cypselae) bulbous subapical sclerified zone to 0.2+ mm long; pappus bristles 4.5–6 mm long, 1–2-seriate, sometimes when 1-seriate slightly non-contiguous at base.

Distribution and Ecology. *Eremosis mima* is endemic to Guatemala, where it occurs in Oak forests, thickets and on volcano slopes from about 1700–2100 meters elevation and flowers from January to March.

Representative collections. **GUATEMALA**. *Castillo & Vargas 2765* (MO, NY); *Steyermark 33990* (F); *Véliz 94.3535* (BIGU, MO); *Véliz 99.6954* (BIGU, MO); *Véliz 99.6984* (BIGU, MO).

Eremosis mima, endemic to (southwestern) Guatemala, by its leaves abaxially tomentulose and by cypselae glabrous and unequally 3–4-costate-angled is similar to *E. heydeana*, which was also described from Guatemala. *Eremosis mima* is distinguished *E. heydeana*, however, by ca. 10 (vs. 3–6) -flowered capitula and by villosulous (vs. glabrous) involucres that are 7–9 (vs. 4–6) mm long. In the protologue Standley and Steyermark (1947) noted its similarity to the common *E. leiocarpa*, but that generally *Eremosis* was 1–6-flowered. The very pubescent-leaved *E. mima* is in cypselae characters nevertheless also similar to weakly pubescent leaved *E. shannonii*.

EREMOSIS OOLEPIS (S.F. Blake) Gleason, N. Amer. Fl. 33: 97. 1922. Vernonia oolepis S.F. Blake, Contr. Gray Herb. 52: 20. 1917. TYPE: MEXICO. Yucatán. Izamal, 1888, Gaumer s.n. (holotype: GH; isotype: F).

Critoniopsis oolepis (S.F. Blake) H. Rob.

Vining shrubs to 3+ m tall; stems densely and finely tomentulose, sometimes glabrate proximally. Leaves petiolate; blade $6-10 \times 2-5$ cm, elliptic-ovate, widest at the middle, 2° veins usually 5–7 per side, surfaces nearly concolorous, adaxial surface glabrous, non-glandular, abaxial surface tomentulose, pubescent with simple non-glandular trichomes, also glandular, base cuneate, margins entire, subrevolute, apex acuminate; petiole 0.2–0.5 cm long. Capitulescences to ca. 40 cm long, cylindrical-paniculate, mostly terminating lateral branchlets 5–15 cm long that are found along length of elongate vining main stems, each lateral branchlet rounded apically with several 3-8capitulate glomerules, these lateral flowering branchlets about $1.5 \times$ as long as subtending leaves, capitula subsessile; peduncles 0-1(-2) mm long. Capitula 3–5-flowered; involucre $5-6 \times 2-3$ mm, narrowly campanulate; phyllaries 5–7-seriate, arachnoid-ciliate; outer phyllaries $1-1.8 \times 0.7-1.1$ mm, triangular-ovate, apex broadly acute; inner phyllaries $5-6.5 \times 1-1.4$ mm, oblong, apex obtuse. Florets: corolla 5.5–7 mm long, glabrous, lobes ca. 1.5 mm long, ca. 1/3 length of corolla. Cypselae 1.5–3 mm long, 6–7-costate, the 3 abaxial costae prominent, setulose-substrigillose throughout with the subappressed setae at apex typically longer than and somewhat obscuring the very small glabrous apical callose zone, in the few collections seen the callose zone not bulbous-inflated; pappus 2seriate, somewhat double, a few outer bristles usually distinctly shorter usually 1-2 mm long, inner bristles 5–6 mm long.

Distribution and Ecology. *Eremosis oolepis* is endemic to the Yucatán Peninsula (Campeche, Quintana Roo, and Yucatán), Mexico occurring in dry bush lands and selva subperennifolia from near sea level to 100 meters elevation, and flowering from December to April.

Representative collections. **MEXICO. Campeche.** *Chan 2009* (CICY). **Quintana Roo**. March 1917, *Gaumer 23648* (F, MO, NY, US); *Ucán & Poot 5102* (CICY, MO). **Yucatán.** *Carnevali & Tapia 6576* (CICY, MO); *Gaumer 23629* (F, K).

Jones (1973) gave the corollas as about "13 mm" long. Turner (2007) noted that *E. triflosculosa* is very similar to *E. oolepis*, which supposedly differs by corollas longer than 10 mm. The material of *E. oolepis* in my hands has corollas ≤ 7 mm long.

6. EREMOSIS SHANNONII (J.M. Coult.) Gleason, Bull. New York Bot. Gard. 4: 234. 1906. Vernonia shannonii J.M. Coult., Bot. Gaz. 20: 42. 1895. TYPE: GUATEMALA. San Marcos. continental divide, 9191 ft., Jan 1892, Shannon 605 (holotype: US). As noted in the protologue, the type "material is very scanty."

Critoniopsis shannonii (J.M. Coult.) H. Rob.

Shrubs to trees 3–10 m tall; stems sparse tomentulose to glabrate. **Leaves** petiolate; blade $(7-)10-17 \times (2.5-)4-7$ cm, usually elliptic-ovate, usually widest at the middle, 2° veins usually 7–9 per side (perhaps especially visible due to weak surface indumentum), surfaces non-glandular, glabrous or arachnoid-tomentulose with simple non-glandular trichomes, base cuneate to acuminate, margins entire, apex acute to acuminate; petiole 0.5–2 cm long. **Capitulescences** 5–10 cm diam., corymbiform, broadly rounded, terminal; peduncles 5–10 mm long. **Capitula** 5–6-flowered; involucre $10-13 \times 3-5$ mm, narrowly campanulate; phyllaries ca. 5-seriate, glabrous or apex very sparsely arachnoid-ciliate; outer phyllaries $2-4 \times 1.5-3$ mm, broadly ovate, apex acute; inner

phyllaries 8–11 \times 1.4–2.4 mm, oblong, apex obtuse to rounded. **Florets**: corolla 9–12 mm long, lavender, glandular almost throughout, lobes ca. 1/3 length of corolla. **Cypselae** 4–6.5 mm long, obconic-prismatic maturing elongate and terete; equally 10-costate or sometimes 3–4-angled with outer face rounded and smooth (my interpretation is that in this species, as in *E. littoralis*, cypsela position in the capitulum often determines cypselae shape, with the outer fruits round-faced abaxially and the inner fruits more evenly costate), glandular almost throughout or distally (I interpret the structures in the furrows as true glands, rather than as large idioblasts), otherwise glabrous, never densely setiferous, apical callose zone narrow; pappus 1-seriate, inner bristles 7–8.1 mm long.

Distribution and Ecology. *Eremosis shannonii* is endemic to Chiapas (Mexico) and Guatemala, where it occurs in mixed forest, mountain slopes, oak forest, pine-oak forest, and selva nublada from about 2500–3800 meters elevation and flowers from December to February.

Representative collections. **MEXICO. Chiapas.** *Breedlove 11493* (CAS, NY); *Breedlove & Thorne 31196* (CAS, MO, NY, TEX). **GUATEMALA**. *Keeley & Keeley 3161* (MO); *Williams et al. 22913* (NY); *Williams 25845* (NY).

Maturing fruits of *E. shannonii* have much in common with those of *E. mima*: both are obconicprismatic, and have a uniseriate pappus of bristles that are slightly non-contiguous at base. The cypselae may be several broad-ribbed in *E. shannonii*, which is further distinguished by its leaf blades abaxially glabrous arachnoid-tomentulose to glabrate, never with dense obvious patent indumentum found in *E. mima*.



Figure 14. *Eremosis standleyi*, florets (left and center) showing the nearly throatless corollas with lobes deeply cut to near tube, and on right an anther. Drawn by M. Pahl and reproduced from Nash (1976).

 EREMOSIS STANDLEYI (S.F. Blake) Pruski, comb. nov. Vernonia standleyi S.F. Blake, J. Wash. Acad. Sci. 13: 143. 1923. TYPE: EL SALVADOR. Near Santa Ana, 655–800 m, 8 Jan 1922, Standley 19703 (holotype: US; isotypes: GH, NY). Figures 14–15.

Critoniopsis standleyi (S.F. Blake) H. Rob., Vernonia calderonii S.F. Blake



Figure 15. Representative specimen of Eremosis standleyi (Renderos et al. 573, MO).

Shrubs 1–3 m tall; stems finely tomentulose and glandular becoming glabrate, sometimes slightly fractiflex. **Leaves** short-petiolate; blade 4–12 × 1.5–5 cm, elliptic to obovate, usually widest at or above the middle, 2° veins usually 5–9 per side, adaxial surface finely puberulent especially along the midrib and glandular, abaxial surface densely pilosulose to tomentose, pubescent with simple non-glandular trichomes, also glandular, base cuneate, margins entire to serrulate, apex acute to acuminate (infrequently obtuse); petiole 2–7 mm long. **Capitulescences** of sessile (infrequently on short stalks 1–2 cm long) rounded dense axillary glomerules 1–2.3(–3) cm diam., capitula subsessile on peduncles to 1 mm long. **Capitula** 4–5-flowered; involucre 4–5.5 × 2–3 mm, campanulate; phyllaries 5–7-seriate, distal 1/2 arachnoid to villous and also glandular, outer phyllaries 1–1.5 × 0.5–1 mm, ovate, apex acute to obtuse; inner phyllaries 4–5.5 × 1–1.4 mm, lanceolate, apex acute to acuminate. **Florets**: corolla 4–5 mm long, about 1/2 length of corolla, cut to base of the nearly absent throat, with the anthers thereby basically fully exserted and full exposed. **Cypselae** 2–3.5 mm long, strongly 5–8-costate, pilose to densely sericeous, apical callose zone to ca. 0.1–0.3 mm long but tardily elongated, glabrous, slightly constricted; pappus 2-seriate, inner bristles 3.7–5 mm long.

Distribution and Ecology. *Eremosis standleyi* is endemic to Central America (El Salvador, Guatemala, Honduras, Nicaragua), where it is moderately common and occurs in Acacia scrub, shrubby areas, pine forests, and pine-oak forests. It has been collected from about 600–1400 meters elevation and flowers from September to March.

Representative collections. **EL SALVADOR.** *Calderón 2499* (F-2, US; type of synonymous Vernonia calderonii); Monro et al. 2833 (B, BM, LAGU, MO); *Renderos et al. 573* (B, BM, K, LAGU, MO). **GUATEMALA.** *Standley 60489* (NY); *Standley 74968* (F, US). **HONDURAS.** *Standley 28221* (MO); *Williams 23262* (NY). **NICARAGUA.** *Molina & Williams 20186* (US); *Moreno 22601* (MO); *Moreno 22722* (MO).

Although Jones (1973) suggested that *Vernonia calderonii* is a hybrid between *E. leiocarpa* and *E. standleyi*, by its long corolla lobes, and pubescent cypselae it is synonymized with *E. standleyi*. *Eremosis standleyi* is similar by pubescent fruits to *E. triflosculosa*, which generally differs by its cylindrical involuce. A fine illustration was provided by Nash (1976) in the Flora of Guatemala series, and Figure 14 reproduces the deeply lobed corollas from that illustration.

EREMOSIS THOMASII (H. Rob.) Pruski, comb. nov. Critoniopsis thomasii H. Rob., Phytologia 78: 388. 1995. TYPE: HONDURAS. Comayagua. Azul Meambar National Park, 1740 m, 11 Mar 1993, T. Hawkins (as "Thomas") 571 (holotype: MO; isotypes: EAP, TEFH). Figures 3, 5A, 16.

Vining shrubs 4–10 m tall; stems tomentulose, non-glandular trichomes T-shaped, trichome stalk shorter than arms. **Leaves** short-petiolate; blade $2.5-9 \times 1-5$ cm, elliptic-ovate, usually widest at or above the middle, 2° veins usually 5–7 per side, surfaces hirtellous with simple non-glandular trichomes, adaxial surface sometimes also glandular, abaxial surface also glandular, base cuneate to obtuse, margins entire, apex acute to obtuse; petiole 0.4–0.7 cm long. **Capitulescences** terminal, pyramidal-paniculate, capitula subsessile in many clusters; peduncles 0–1.6 mm long, tomentulose with short-stalked T-shaped non-glandular trichomes. **Capitula** 3–4-flowered; involucre $4.5-6.5 \times 2.5-3$ mm, narrowly campanulate; phyllaries 5–6-seriate, glabrous or apex puberulent; outer phyllaries $0.6-1 \times 0.4-0.6$ mm, broadly ovate; inner phyllaries $4-5 \times 1-1.4$ mm, oblanceolate, apex acute. **Florets:** corolla 4.6–5.8 mm long, white, glandular distally, lobes ca. 1.5 mm long, ca. 1/3 length of corolla. **Cypselae** 2–2.3 mm long, ca. 3–7-costate, setulose-substrigillose to pilose, non-glandular, apical callose zone to ca. 0.1 mm long, glabrous; pappus bristles ca. 4.5 mm long, 1-2-seriate.



Figure 16. Representative specimen of Eremosis thomasii (Hawkins 884, MO).

Distribution and Ecology. *Eremosis thomasii* is endemic to Honduras, where it occurs in moist forests from about 1100–1700 meters elevation and flowers from March to April.

Representative collection. HONDURAS. Hawkins 884 (MO).

Eremosis thomasii is one of only two known species with T-shaped non-glandular trichomes. Robinson (1995) described the non-glandular trichomes as stellate, but the stellate or dendroid structures seen by me are mostly on mature leaves only, and are very thin, about an order of magnitude thinner than the T-shaped trichome stipe cells. It seems that the material seen by me is infected with fungal hyphae and that the species may not be stellate-pubescent.

 9. EREMOSIS TRIFLOSCULOSA (Kunth) Gleason, Bull. New York Bot. Gard. 4: 233. 1906. Vernonia triflosculosa Kunth, Nov. Gen. Sp. (folio ed.) 4: 31. 1820 [1818]. TYPE: MEXICO. Guerrero. Acaguisotla, Feb 1803 [the Sprague itinerary (1924: 21; 1968: 96) gave month as "April"], Humboldt & Bonpland 3909 (holotype: P-HBK, as IDC microfiche 6209 92.I.2, as Macbride neg. 37347; isotypes: B-W-15178 (as IDC microfiche 7440 card 1092), P-RICHARD, P-SCH-BIP).

Cacalia triantha (Schauer) Kuntze, Cacalia triflosculosa (Kunth) Kuntze, Critoniopsis triflosculosa (Kunth) H. Rob., Gymnanthemum congestum Cass., Vernonia dumeta Klatt, Vernonia luxensis J.M. Coult., Vernonia triantha Schauer

Shrubs or trees (2–)4–12 m, crowns dense and rounded; stems canescent or tomentose becoming glabrate, non-glandular trichomes simple. Leaves short-petiolate; blade $5-13 \times 1-3$ cm, oblanceolate to obovate, usually widest above the middle, 2° veins usually 5-7 per side, adaxial surface puberulent to commonly glabrate, abaxial surface glandular, otherwise glabrous to subtomentulose with simple non-glandular trichomes, base obtuse to more commonly acuminate to attenuate and subdecurrent, margins entire to serrulate or denticulate, apex acute to acuminate; petiole Capitulescences terminal rounded-paniculate, capitula subsessile in 0.4–1.2(–1.7) cm long. numerous clusters. **Capitula** 3(-4)-flowered; involucre $4.5-6.5 \times 1.3-2.5$ mm, cylindrical; phyllaries 4–6-seriate, mostly subglabrous, especially proximally; outer phyllaries $0.5-1 \times 0.7-1.4$ mm, broadly ovate, apex obtuse to rounded, often with midrib visible, somewhat greenish and glandular or puberulent; inner phyllaries $3.5-6.5 \times 1-1.6$ mm, oblanceolate, apex acute, seemingly more fragile than in many species. Florets: corolla 5-6 mm long, white, throat present, lobes to 1.5 mm long, usually 1/3–1/4 length of corolla. Cypselae 2–3 mm long, at maturity 3–6-striate-costate, setose, also glandular, the glabrous apical callose zone only moderately developed throughout much of fruiting and often obscured by cypsela body trichomes, infrequently collected in late fruit with tardily welldeveloped callose zone to ca. 0.2(-0.4) mm long; pappus 1-2-seriate, a few shorter outer bristles sometimes present but not as a well-defined ring and not imparting a double pappus appearance to fruit, inner bristles 4–5.5 mm long.

Distribution and Ecology. *Eremosis triflosculosa* is widespread from central Mexico (centered in Chiapas, Colima, Guerrero, Hidalgo, Jalisco, México, Morelos, Nayarit, Oaxaca, Veracruz) southeastwards into Panama, where it is known from a single collection. *Eremosis triflosculosa* occurs in deciduous forests, fields, forested rocky slopes, matorrales secos, pastizal, rocky hillsides, secondary vegetation, selva baja caducifolia, and thickets in Central America from about 100–1600 meters elevation and flowers from February to June. The citation by Turner (2007: 133) of *E. triflosculosa* in Quintana Roo, Mexico is presumably based on material of *E. oolepis*, and Carnevali et al. (2010) listed only *E. oolepis* in the Yucatán Peninsula.

Table I. Nine informal species groups (and 27 species) of *Eremosis* and some of their key characters. The relative placements of three synonyms, each perhaps meriting recognition, are indicated. [1–9 are morphotype group numbers; M = species present in Mesoamerica; ME = Mesoamerican endemic species].

1. Cypselae glabrous or subglabrous (or sometimes glandular, not densely setiferous) and capitula pauciflorous.	E. heydeana M E. leiocarpa M E. littoralis E. mima ME E. pugana E. shannonii ME
2. Capitula typically uniflorous; cypselae glandular and characteristically 7–10-ribbed, otherwise glabrous or sparsely setose; leaf blades typically discolorous, tomentose to sparsely so or even subglabrous abaxially.	E. macvaughii E. obtusa [?syn. V. duncanii]
3. Capitula typically uniflorous; cypselae obviously setiferous, sometimes also glandular; leaf blades discolorous, tomentose abaxially.	E. aristifera E. tomentosa
4. Capitula uniflorous; cypselae obviously setiferous, sometimes also glandular; leaf blades relatively large, not densely tomentose.	E. baadii E. solorzanoana E. steetzii [?syn. V. macphersonii]
5. Capitula typically uniflorous; cypselae obviously setiferous, sometimes also glandular; leaf blades relatively small, not densely tomentose.	E. angusta ME E. corymbosa [syn. V. salicifolia] [syn. V. uniflora] E. foliosa E. pallens
6. Capitula pauciflorous; cypselae setiferous, sometimes also glandular; corollas nearly throatless with lobes cut to near tube.	E. palmeri E. standleyi ME
7. Capitula pauciflorous; cypselae setiferous, sometimes also glandular; leaf blades discolorous, tomentose abaxially.	E. ovata E. tarchonanthifolia
8. Capitula pauciflorous; cypselae setiferous, sometimes also glandular; phyllaries decurrent onto peduncles.	E. feddemae
9. Capitula pauciflorous; cypselae setiferous, sometimes also glandular; corolla with throat; leaves concolorous to slightly discolorous, not densely tomentose abaxially.	E. barbinervis E. oolepis ME E. thomasii ME E. triflosculosa M E. villaregalis

Representative collections. COSTA RICA. Bello 824 (CR, MO, TEX); Brenes 1903 (NY); San Francisco de Guadalupe, 13 May 1894, Pittier 8767 (BR-2, F, G, GH; type of synonymous Vernonia dumeta); Golfo Dulce, May 1896, Tonduz 7076/8767 (MO, US); San Francisco de Guadalupe, 5 May 1896, Tonduz 8767 (P, presumably either the locality or the year is erroneous); Tonduz 13894 (MO). EL SALVADOR. González 20 (B, K, LAGU, MO); Standley 21810 (NY); Standley 23404 (GH, NY, US). GUATEMALA. Heyde & Lux 3421 (K, US); Rojas 267 (MO); Standley 64935 (NY); Standley 88043 (NY); Véliz 99.6942 (BIGU, MO). HONDURAS. Molina 2717 (F, GH); Valerio 2471 (MO); Williams & Molina 12115 (MO). MEXICO. Chiapas. Breedlove 24648 (CAS, MO); Breedlove 50984 (CAS, NY); Matuda 1561 (GH, MEXU, MO, NY); Ventura & López 1204 (MO, XAL); Ventura & López 1217 (MO, XAL). Jalisco. McVaugh 10208 (MEXU, MICH, NY). Oaxaca. Maya 3036 (CHAPA, MO). Veracruz. Purpus 8968 (MO, NY, US); Purpus 9016 (NY); Ventura 11132 (MO).

NICARAGUA. *Moreno* 243 (MO, NY); *Moreno* 8273 (MO); *Standley* 20342 (F); *Stevens* 16890 (MO). **PANAMA.** *Davidson* 642 (F, MO, US).

Eremosis triflosculosa is among the largest-trunked regional tree Compositae. A fine drawing of it was given in Zamora et al. (2000: 282). McVaugh (1972b) treated *E. barbinervis* and *E. palmeri* in synonymy with *E. triflosculosa*, whereas Jones (1973) recognized each, albeit with only two as species and the third as an infraspecies. Here I follow Gleason (1906, 1922) and recognize each at the specific rank. Thus, the northern lanceolate-leaved *V. triflosculosa* subsp. *palmeri* (Rose) S.B. Jones (1973), differing by nearly throatless corollas, is recognized here as *E. palmeri*, which I related more closely to *E. standleyi* than to either *E. barbinervis* or *E. triflosculosa*. In turn, I recognize *E. triflosculosa* in the restricted sense of *V. triflosculosa* subsp. *triflosculosa* sensu Jones (1973). Of the more common species in Central America, *E. triflosculosa* is characterized by its generally narrower less pubescent leaves and narrower capitula.

ANNOTATED NOMENCLATOR OF EREMOSIS.

- **EREMOSIS ANGUSTA** Gleason. **Type, distribution, and representative collection**. Guatemala; see species #1 above.
- **EREMOSIS ARISTIFERA** (S.F. Blake) Pruski, **comb. nov.** *Vernonia aristifera* S.F. Blake, Contr. U.S. Natl. Herb. 23: 1415. 1926. **TYPE: MEXICO. Jalisco.** Río Blanco, 1886, *Palmer 678* (holotype: US; isotypes: GH, K p.p., MEXU, MO, NY, NDG, YU).

Vernonia steetzii var. aristifera (S.F. Blake) McVaugh

Key features. Shrubs 1–2 m tall; leaf blades $3.5-6 \times 2.2-4.5$ cm, obviously discolorous, persistent tomentose abaxially; capitula usually 1-flowered; inner phyllaries often purplish, aristate; cypselae sericeous. 2n = 36 (Jones 1973; voucher *Jones et al. 20583* as *V. steetzii*).

Distribution and representative collections. Mexico (Jalisco, ?San Luis Potosí): *Jones et al.* 20583 (GA, MO); "chiefly in the region of San Luis Potosí" (but perhaps more to the SW and in Jalisco as in McVaugh 1984: 1035), *Parry & Palmer 332* (F, GH, MO, NY); *Pringle 1823* (F, GH, MO, NY, US); *Pringle 9993* (GH, MO).

Material of obviously discolorous-leaved *E. aristifera* (before it was described) was treated by Gleason (1906, 1922) as *E. callilepis*, but that is a less pubescent-leaved species recognized here as *E. foliosa*. Blake et al. (1926) commented on the presumed name misapplication of Gleason. Nevertheless, material of *E. aristifera* passed again as a broadly circumscribed *E. steetzii* in both Jones (1973) and Turner (2007) and as *E. foliosa* in Robinson (1999a), but *E. aristifera* is here resurrected from synonymy.

EREMOSIS BAADII (McVaugh) Pruski, comb. nov. Vernonia salicifolia var. baadii McVaugh, Contr. Univ. Michigan Herb. 9: 484. 1972. TYPE: MEXICO. Jalisco. 20 km SE Talpa de Allende, 2–3 Apr 1965, McVaugh 23473 (holotype: MICH; isotypes: CAS, DUKE, ENCB).

Critoniopsis baadii (McVaugh) H. Rob., Vernonia baadii (McVaugh) S.B. Jones

Key features. Shrubs to trees 3-5 m tall; leaves relatively long-petiolate, blades $11-20 \times 3-6$ cm, relatively long and narrow, surfaces nearly concolorous, glabrous adaxially, glandular abaxially; capitula 1-flowered; cypselae sericeous.

Distribution and representative collection. Mexico (Jalisco, Michoacán): *Mexia 1904* (F, MO, NY, US).

Eremosis baadii is similar to, and may be best considered a segregate of, short-petiolate *E. steetzii*.

EREMOSIS BARBINERVIS (Sch. Bip.) Gleason, Bull. New York Bot. Gard. 4: 232. 1906. Vernonia barbinervis Sch. Bip. in Seemann, Bot. Voy. Herald 297. 1856. TYPE: MEXICO. Nayarit. Sierra Madre, 1848–1850, Seemann 1998 (holotype: P-SCH-BIP; isotypes: GH, K).

Cacalia barbinervis (Sch. Bip.) Kuntze, Critoniopsis barbinervis (Sch. Bip.) H. Rob.

Key features. Shrubs 1–2 m tall; leaf blades $9-16 \times 3-10$ cm, surfaces concolorous; capitula usually 3-flowered; cypselae sericeous.

Distribution and representative collections. Mexico (Durango, Sinaloa, Zacatecas): *Gentry* 5305 (F, MO, NY, US); *Gentry* 5539 (GH, MEXU, MO, NY).

Schultz Bipontinus (1856) described *V. barbinervis* as a species of triflorous *Vernonia* sect. *Trianthaea* DC. At that time (1856) *Vernonia* sect. *Eremosis* was still considered to contain only uniflorous species.

- *EREMOSIS CALLILEPIS* (Sch. Bip.) Gleason, N. Amer. Fl. 33: 98. 1922. = **Eremosis foliosa** (Benth.) Gleason
- **EREMOSIS CORYMBOSA** (Mill.) Pruski, **comb. nov.** *Conyza corymbosa* Mill., Gard. Dict. (ed. 8) Conyza no. 7. 1768. **LECTOTYPE** (designated here): **MEXICO.** Probably western Veracruz ["Grows naturally at La Vera Cruz"], 1731, *Houstoun s.n.* (lectotype: BM [BH neg. 5267], photographs BH, E, MO, NY; possible isolectotype: BM-SLOANE 292.64, not seen). There does not appear to be any extant Chelsea garden material grown by Philip Miller (viz Pruski 2005). The lectotype bears the hand-written note "see also Herb. Sloane 292.64." Although the type locality was given as La Vera Cruz, the plants were presumably collected inland. Figures 1, 7, 11.

Cacalia baptizanda Kuntze (a nom. nov. for Vernonia uniflora Sch. Bip.), Critoniopsis salicifolia (DC.) H. Rob., Critoniopsis uniflora (Sch. Bip.) H. Rob., Eremosis leiophylla Gleason, Eremosis salicifolia (DC.) Gleason, Eupatorium uniflorum Sessé & Moc., Monosis salicifolia DC., Vernonia salicifolia (DC.) Sch. Bip. 1847 (non (Mart.) Less. 1829), Vernonia leiophylla (Gleason) S.F. Blake, Vernonia uniflora Sch. Bip.

Key features. Shrubs 1–3.5 m tall; leaf blades $4-9(-12) \times 1-3(-4.5)$ cm, surfaces nearly concolorous; capitula usually 1(-2)-flowered; inner phyllaries often evenly drying purplish and then strongly contrasting in color with the pappus; corollas purplish; pollen Type A (viz Robinson 1999a: Fig. 1A–B as *Critoniopsis uniflora*); cypselae sericeous. 2n = 74 + 2 as *V. salicifolia* (Jones 1973), tetraploid.

Distribution and representative collections. Mexico (Aguascalientes, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Veracruz, Zacatecas): *Arsène & Nicholas 5083* (GH, MO, US); 20 Oct 1827, *Berlandier 968* (G-DC p.p., LD, MO, NY, US, W; lectotype collection of synonymous *Monosis salicifolia*); 21 Oct 1827, *Berlandier 1047* (G-DC p.p., HAL, P, US; syntype collection of synonymous *Monosis salicifolia*); *Jones 21681* (GA, MO);

Matuda 30244 (NY, US); Mexia 9108 (F, GH, MO, NY, UC, US; neotype of Vernonia uniflora); Pringle 6188 (BR, F, GH, GOET, MICH, MO, NDG, NY, S, UC, US; type of synonymous Eremosis leiophylla); Pringle 13908 (MO, US); Rzedowski 36063 (MO); Sessé & Mociño 2735 (F-2, MA-2; lectotype of synonymous Eupatorium uniflorum Sessé & Moc.); Sessé & Mociño 3931 (MA, microfiche BT-13 267.A3, F neg. 42897; syntype of Eupatorium uniflorum Sessé & Moc.).

Typology of *Monosis salicifolia* **DC**. *Monosis salicifolia* DC., Prodr. 5: 77. 1836. *Vernonia salicifolia* (DC.) Sch. Bip., Linnaea 20: 507. 1847 [non (Mart.) Less. 1829]. *Eremosis salicifolia* (DC.) Gleason, Bull. New York Bot. Gard. 4: 231. 1906. *Critoniopsis salicifolia* (DC.) H. Rob., Proc. Biol. Soc. Washington 106: 621. 1993. **LECTOTYPE** (effected by Jones 1973: 112): **MEXICO. Morelos.** Ad Cuernavaca, 20 Oct 1827, *Berlandier 968* (lectotype: G-DC p.p., plant on the left, and likely also the plant in center of sheet, as IDC microfiche 800 781.I.5, as Macbride neg. #33568; isolectotypes: LD, MO, NY, P-2, US, W). Brazilian Cacalia salicifolia (Mart.) Less. was given incorrectly as a homotypic synonym by Redonda-Martínez and Villaseñor-Ríos (2009).

On the typification of *Monosis salicifolia* **DC**. The lectotype sheet of *Monosis salicifolia* has three twigs: that on far right is the syntype *Berlandier 1047* from Cordillera de Guchilaqua; and two others constitute the lectotype proper (*Berlandier 968*, G-DC) from Cuernavaca. The two twigs on the lectotype towards the left are considered here as of the same gathering, albeit having subtle label differences, and perhaps sent to Candolle at different times. The center twig is sub-labeled 6ex and dated "20/10 1827" and that on the far left sub-labeled 19ex (?in reference to the Linnaean sexual system?) and dated as "8bre," an early French shorthand for October sometimes misread as the 8th month (August). *Berlandier 1047* (G-DC p.p. twig on right, HAL, P, US) from Guchilaqua is dated 21 Oct 1827. A third original element of the Candolle name is the drawing of Sessé and Mociño collection cited as "fl. mex. mss. and now at CM [Illustr. Hunt Institute (Torner) 6331.0241 = Ic. Fl. Mex.164] (reproduced here as Fig. 1).

Lectotypification of *Eupatorium uniflorum* Sessé & Moc. *Eupatorium uniflorum* Sessé & Moc., Pl. Nov. Hisp. 132. 1887 [1890]; Pl. Nov. Hisp. (ed. 2) 123. 1893. *Critoniopsis uniflora* (Sch. Bip.) H. Rob., Proc. Biol. Soc. Washington 106: 625. 1993. LECTOTYPE (chosen here from among syntype elements): MEXICO. 1787–1790(–1803) [see Sprague 1926], "Xochixtlam and Mexicanorum Carmelitarum Eremo," *Sessé & Mociño 2735* (lectotype: MA (as microfiche BT-13 267.A2, F neg. 42893); presumed isolectotypes: F-2, MA (as microfiche BT-13 267.A1, F neg. 42896)).

On the typification of Eupatorium uniflorum Sessé & Moc. I have seen four sheets of Sessé & Mociño 2725 as numbered by Standley, and the short diagnosis of "calycibus unifloris foliis lanceolatis ... 8 ped" on the MA lectotype corresponds to the protologue. The isolectotype in MA, although presumed to be of the same gathering but perhaps from a shorter individual (as allowed by the ICBN) and reads "Eupatorium corymbosum N frutex sexpedalis ... folia oblonga" and perhaps also "No. 59." Each of the four lectotype collection sheets seen are robust, and Icon. Fl. Mex. 164 (Fig. 1) does not appear to have been drawn from them. Rather, Fl. Mex. 164 matches fairly well Sessé & Mociño 3931 (MA), which is labeled "Seriphium corimbosum," as is the color plate. Sessé & Mociño 3931 (MA) is intentionally not chosen as the lectotype. Thus as lectotypified V. uniflora and V. salicifolia are heterotypic. I do not know, however, which Sessé and Mociño collection is from which cited locality: Xochitlán (Morelos) and Carmelitarum aka Desierto de los Leones (Distrito Federal) (viz Sprague 1926; McVaugh 1980). Redonda-Martínez and Villaseñor-Ríos (2009) listed the black and white copy in G (Field neg. 30707) of Icon. Fl. Mex. 164 as the holotype of Eupatorium uniflorum. Although perhaps Mociño did see this black and white copy (McVaugh 2000: 158 suggested the annotation on it may be in Mociño's hand) of the original color plate, the citation of the copy illustration in G as holotype by Redonda-Martínez and Villaseñor-Ríos (2009) is

not followed here. Moreover, the type citation in Redonda-Martínez and Villaseñor-Ríos (2009) is post-2000 and does not effect typification (viz ICBN 7.10). Here, a lectotype of *Eupatorium uniflorum* is chosen from purple-phyllaried material collected by Sessé and Mociño deposited in MA. Even though I prefer basically to typify only recognized names, here I hope to fix application by proposing *Sessé & Mociño 2735* as lectotype for *Eupatorium uniflorum* (viz Sessé and Mociño 1887, 1893). This lectotype material has phyllaries drying the same color as in heterotypic *V. uniflora* Sch. Bip., and each is treated here in synonymy with *E. corymbosa*. Should the color forms prove specifically distinct, I would continue to equate taxonomically *Mexia 9108* (the neotype of *V. uniflora* 1847) and *Sessé & Mociño 2735* (the lectotype of *E. uniflorum* 1887 [1890]). The name *Eremosis uniflora* (Sch. Bip). ined. is available for the more purple-flowered segregate of *E. corymbosa*.

The available name *E. corymbosa* is adopted here, although long-blocked in *Vernonia* by *V. corymbosa* Schwein. Candolle (1836), Gleason (1906, 1922), Blake et al. (1926), and Turner (2007) each treated *V. uniflora* (or in the case of Candolle what was to become *V. uniflora*) in synonymy with *E. corymbosa*. I agree that there seems to be no great geographic separation of the (?drying influenced) color forms, and morphologies apparently grade into one another. Seaman (1982) gave the sesquiterpene lactones glaucolide D and glaucolide E as having been reported in *V. salicifolia* and *V. uniflora*, each treated here in synonymy of *E. corymbosa*. Elsewhere in *Eremosis*, differing glaucolide types within multiple exsiccate of a single species have also been noted. Schultz Bipontinus (1861) allied the two species, but it is not clear to me if he intended to treat them as the same. On the other hand, many authors recognized *E. corymbosa* (syn. *E. salicifolia*) and *V. uniflora* as distinct (Schultz Bipontinus 1847; Hemsley 1881; Jones 1973, 1979a; McVaugh 1984; Robinson 1993, 1999a; García 2004; Redonda-Martínez and Villaseñor-Ríos 2009).

As broadly circumscribed here, E. corymbosa is most distinctive by uniflorous capitula and its usually purplish phyllaries, as described in both the Sessé and Mociño (1887, 1893) and Schultz Bipontinus (1847) protologues, and as drawn clearly in Icon. Fl. Mex. 164 (Fig. 1). This commonly collected purple-phyllaried phase was called V. uniflora by Jones (1973) and McVaugh (1984), and the less frequent pale or faded acute-tipped phyllary form as E. salicifolia. The Miller (1768) protologue of *E. corymbosa* gives "floribus singulis" and "white," and the phyllaries of the lectotype collected in 1731 are not obviously purple (Fig. 11). Icon. Fl. Mex. 164 also is an original element of V. salicifolia, and Candolle (1836) took both color forms as a single species. The apex of outer few series of phyllaries of the drying pale color form are often thickly midribbed, broadly obtuse, arachnoid-pubescent, and glandular, more so in the purplish flower form. About 1/4 of material in front of me, however, has faded acute-tipped phyllaries as in what Jones (1973) called V. salicifolia, that grades into the more purplish-flower forms. *Eremosis corymbosa*, by its glandular weakly pubescent leaves, uniflorous capitula, and sericeous cypselae, however, is also clearly similar to E. barbinervis (Sch. Bip.) Gleason and E. pallens (Sch. Bip.) Gleason. Britten (1898) identified the lectotype of E. corymbosa as E. tarchonanthifolia, which differs by its abaxially tomentose leaves and pauciflorous capitula.

There are several recent examples (i.e., Blake 1930; Cabrera 1959; D'Arcy 1973; Robinson 1999a; Pruski 2005) of recognition in other genera of Miller (1768) species described in *Conyza*. Of the 18 Conyzas in Miller's Gard. Dict., ed. 8 (1768), seven are Linnaean names and 11 are Neotropical plants newly described by Miller (viz Miller 1768; Britten 1898). Five Miller (1768) Conyzas are either synonyms or blocked in currently recognized genera. The six Miller (1768) Conyzas currently recognized are placed in tribes Astereae, Inuleae, or Vernonieae and include dioecious, discoid, and disciform plants; i.e., *Baccharis pedunculata* (Mill.) Cabrera, *Eremosis corymbosa* (Mill.) Pruski, *Lepidaploa uniflora* (Mill.) H. Rob., *Pluchea baccharis* (Mill.) Pruski, *Pluchea salicifolia* (Mill.) S.F. Blake, *Pseudoconyza viscosa* (Mill.) D'Arcy.

EREMOSIS FEDDEMAE (McVaugh) Pruski, comb. nov. Vernonia feddemae McVaugh, Contr. Univ. Michigan Herb. 9: 480. 1972. TYPE: MEXICO. Nayarit. 5 km NE of Puga, 22 Aug 1959, Feddema 846A (holotype: MICH).

Critoniopsis feddemae (McVaugh) Redonda-Martínez & Villaseñor

Key features. Perennials to 1.5 m tall; leaf blades $5-12 \times 1.5-5$ cm, surfaces slightly discolorous, abaxial surfaces sparsely arachnoid-tomentose; phyllaries decurrent onto peduncles; capitula 3–5-flowered; cypselae pilose-sericeous. McVaugh (1972a: 481) provided a fine figure of this pauciflorous pluricephalous perennial.

Distribution and representative collection. Mexico (Nayarit): known only from the type.

Eremosis feddemae is unique in *Eremosis* by its phyllaries strongly decurrent onto peduncles, resembling in this regard *Critoniopsis jaramilloi* Pruski & H. Rob., the only species of *Critoniopsis* with this character.

EREMOSIS FOLIOSA (Benth.) Gleason, Bull. New York Bot. Gard. 4: 228. 1906. Monosis foliosa Benth., Pl. Hartw. 19. 1839. TYPE: MEXICO. Jalisco. Bolaños, 1837, Hartweg 133 (holotype: K; isotypes: BM, E, LD, NY-2, P, W). Figure 17.

Critoniopsis foliosa (Benth.) H. Rob., Eremosis callilepis (Sch. Bip.) Gleason, Eremosis steetzii var. callilepis (Sch. Bip.) Gleason, Vernonia foliosa (Benth.) Sch. Bip. 1861 (non Gardner 1846), Vernonia mucronata S.F. Blake (a nom. nov. for Monosis foliosa Benth.), Vernonia steetzii var. callilepis Sch. Bip.

Key features. Shrubs to 2 m tall; leaf blades relatively small, mostly 4–6 cm long, reticulate, glandular, tomentulose abaxially, but nevertheless more or less concolorous; capitula 1-flowered; cypselae sericeous.

Distribution and representative collections. Mexico (centered in Durango, Jalisco, Nayarit, Zacatecas; possibly also present in Aguascalientes, Guanajuato, and Nayarit as inferred from the wide distribution given by Rzedowski and Calderón de Rzedowski 1995a: 44 for a broadly circumscribed of *E. steetzii*): *Seemann 1997* (K, P-SCH-BIP dextrum, but P now cut and remounted on single sheet; type of synonymous Vernonia steetzii var. callilepis); *Tenorio & Flores 16721* (MEXU, MO).

Blake et al. (1926) commented that they thought Gleason (1922) misapplied names now recognized as *E. aristifera*, *E. foliosa*, and *E. steetzii*. Blake et al. (1926) used the homotypic new name *V. mucronata* (1917) for *Monosis foliosa*, and described *V. aristifera* as new. *Eremosis aristifera* was not recognized subsequently by Jones (1973), McVaugh (1984), Rzedowski and Calderón de Rzedowski (1995a), or Turner (2007), each of whom applied the name *E. steetzii* (non Brazilian *V. foliosa* Gardner) for this species much in the sense of Gleason (1922). Robinson (1993) treated each *E. aristifera* and *E. steetzii* as synonyms. About three decades ago (viz Fig. 17), however, while working on uniflorous species of *Piptocarpha* and *Piptocoma* for the Flora of the Guayana Highland (Pruski 1997), I noted that there appears to be several "kinds" of *E. foliosa*. I was working at NY with much of the same material Gleason used about a century ago, but the NY material was not annotated by Blake, and then-recent material was determined mostly as a broadly defined *E. steetzii*. It was not clear to me which taxonomic entity matched which name.



Figure 17. Isotype of *Monosis foliosa* Benth. [≡ *Eremosis foliosa* (Benth.) Gleason] (*Hartweg 133*, NY).

Now I feel more confident and apply the name *E. foliosa* to relatively small non-tomentose usually not obviously discolorous leaved uniflorous plants with sericeous cypselae. Following Blake et al. (1926), I treat *E. aristifera* as a relatively small tomentose discolorous-leaved uniflorous plant with mucronate-aristate often purplish inner phyllaries and sericeous cypselae. I restrict the concept of *E. steetzii* to relatively short-petiolate large-leaved non-tomentose uniflorous plants with sericeous cypselae. Small-denticulate-leaved uniflorous *E. callilepis* was treated in synonymy with *E. steetzii* by Jones (1973) and Turner (2007), but is here referred to *E. foliosa*. As circumscribed here, *E. foliosa* and *E. aristifera* are very similar in leaf and capitulescence size and shape to *E. obtusa*, which is a uniflorous species with glandular otherwise subglabrous cypselae. *Eremosis foliosa* was illustrated (as *V. steetzii*) in García (2004: 346), and his plants are the more or less concolorous leaved forms treated here as *E. foliosa*.

- **EREMOSIS HEYDEANA** (J.M. Coult.) Gleason. **Type, distribution, and representative collections**. Guatemala and Mexico; see species #2 above.
- **EREMOSIS LEIOCARPA** (DC.) Gleason. **Type, distribution, and representative collections**. Mexico and Central America; see species #3 above.
- *EREMOSIS LEIOPHYLLA* Gleason, Bull. New York Bot. Gard. 4: 231. 1906. = **Eremosis corymbosa** (Mill.) Pruski
- **EREMOSIS LITTORALIS** (Brandegee) Gleason, N. Amer. Fl. 33: 100. 1922. Vernonia littoralis Brandegee, Erythea 7: 3. 1899. **TYPE: MEXICO. Colima**. Socorro Island, Mar–Jun 1897, Anthony s.n. (holotype: UC; isotype: US).

Critoniopsis littoralis (Brandegee) H. Rob.

Key features. Scandent shrubs to trees to 7–15 m tall; leaf blades $6-12 \times 4-10$ cm, surfaces slightly discolorous, abaxial surfaces sparsely publicate except for main veins which are densely publicate and thereby obviously lighter in color than green adaxial surfaces; capitula ca. 8-flowered; cypselae glabrous, never densely setiferous, sometimes pluricostate.

Distribution and representative collection. Endemic to Socorro Island, Colima, Mexico; *Mason 1656* (MO, US).

EREMOSIS MACVAUGHII (S.B. Jones) Pruski, comb. nov. Vernonia macvaughii S.B. Jones, Brittonia 25: 105. 1973. TYPE: MEXICO. Oaxaca. 6 mi N of Huajuapan de León, 23 Mar 1972, Jones & Jones 21664 (holotype: GA; isotypes: F, GH, MEXU, MO, NY, TEX, US).

Critoniopsis macvaughii (S.B. Jones) H. Rob.

Key features. Shrubs 2–3 m tall; leaf blades $6-13 \times 2.5-6$ cm, extremely discolorous, tomentose abaxially; capitula 1-flowered; cypselae glandular, otherwise glabrous, obviously 8–10-ribbed.

Distribution and representative collections. Mexico (Guerrero, Oaxaca, adjacent Puebla): *McVaugh 22288* (MICH, MO); *Soule & Prather 3188* (MEXU, MO, TEX).

Although placed in different subtribes, *Eremosis macvaughii* immediately recalls Brazilian *Eremanthus crotonoides* (DC.) Sch. Bip. and Venezuelan *Piptocoma vernonioides* (Kunth) Pruski.

- *EREMOSIS MELANOCARPA* Gleason, Bull. New York Bot. Gard. 4: 232. 1906. = **Eremosis leiocarpa** (DC.) Gleason
- **EREMOSIS MIMA** (Standl. & Steyerm.) Pruski. **Type, distribution, and representative collections**. Guatemala; see species #4 above.
- **EREMOSIS OBTUSA** Gleason, N. Amer. Fl. 33: 99. 1922. **TYPE: MEXICO.** San Luis Potosí. San Rafael, Jul 1911, *Purpus 4811a* (as "4811") (holotype: NY; isotype: MEXU).

?Critoniopsis duncanii (S.B. Jones) H. Rob., Critoniopsis obtusa (Gleason) H. Rob., ?Vernonia duncanii S.B. Jones, ?Vernonia duncanii subsp. bartlettii S.B. Jones, Vernonia obtusa (Gleason) S.F. Blake, ?Vernonia obtusa var. bartlettii (S.B. Jones) B.L. Turner, ?Vernonia obtusa subsp. parkeri S.B. Jones, ?Vernonia obtusa var. parkeri (S.B. Jones) B.L. Turner

Key features. Shrubs to 2 m tall; leaf blades $3-15 \times 2-5.5(-7)$ cm, surfaces typically discolorous and moderately tomentose abaxially, but perhaps grading to subglabrous as in type of subsp. *parkeri*; capitula 1(-2)-flowered; cypselae glandular or idioblastic and characteristically 7–10-ribbed, otherwise glabrous or sparsely setose. 2n = 38 for subsp. *parkeri* (Jones 1973).

Distribution and representative collections. Mexico (Hidalgo, Nuevo León, ?Querétaro, San Luis Potosí, Tamaulipas): *Jones et al. 20559* (F, GA, GH, MEXU, MICH, MO, NY, P-2, TEX, US; type of possibly synonymous *Vernonia duncanii*); *Jones 20564* (F, GA, GH, MEXU, MO, TEX, UC, US; type of possibly synonymous *Vernonia obtusa* subsp. *parkeri*); Nov 1910, *Purpus 4811* (GH, MO).

Typical uniflorous *E. obtusa* is very similar in leaf and capitulescence size and shape to *E. aristifera* and *E. foliosa*, which each differ by their sericeous cypselae. Although typical *E. ovata* has glandular costate fruits, cypselae glands and costae are not always evident in *V. duncanii* subsp. *bartlettii* and *V. obtusa* subsp. *parkeri*. Rather, in some material the developing ovaries of these two subspecies are nearly ecostate and with only poorly manifest idioblasts. These subspecies at present cannot be matched with certainty. Nevertheless, these names are provisionally included here as in Turner (2007), who remarked that the leaves of these two subspecies are weakly pubescent. Each of these three possibly synonymous names may be deserving of recognition at some rank.

Although Jones (1973: 91) noted *V. duncanii* (*Jones 20559*) has glaucolide type B and *V. obtusa* subsp. *parkeri* (*Jones 20564*) has glaucolide type F, he also reported comparable infraspecific variation in each *E. leiocarpa* and *E. corymbosa*. Moreover, elsewhere in *Eremosis* Jones (1973) also noted individual glaucolide types may be shared among species. This suggests glaucolide kinds may not always be taxonomically significant. Similarly, chromosome numbers may not be useful in species-level taxonomy. Except for two tetraploids, all species of *Eremosis* appear to be consistently diploid. Variation in ploidy level within *E. obtusa* is unconfirmed. Jones (1973) reported *V. obtusa* subsp. *parkeri* as n = 19, but Turner (1981) gave a count of "n = 10 pairs" for *V. obtusa* subsp. *obtusa* and suggested that *V. obtusa* subsp. *parkeri* may be a tetraploid. Turner, however, commented that his count needs confirmation, as x = 9 and x = 10 are base numbers of African taxa. Turner (1981) noted that the count of "x = 10" would represent only the second such count for *Vernonia* s. lat. in the Americas. Nevertheless, it is anticipated that further chemical and cytological studies may be taxonomically helpful within *Eremosis*, and specifically could help resolve the limits of *E. obtusa*.

EREMOSIS OOLEPIS (S.F. Blake) Gleason. **Type, distribution, and representative collections**. Yucatán peninsula in Mexico; see species #5 above.

EREMOSIS OVATA Gleason, Bull. Torrey Bot. Club 40: 331. 1913. TYPE: MEXICO. Durango. San Ramón, 21 Apr-18 May 1906, *Palmer 139* (holotype NY; isotypes: F, GH, K, MO, UC, US).

Critoniopsis ovata (Gleason) H. Rob., *Vernonia durangensis* S.F. Blake 1924 (a legitimate nom. nov. for *Eremosis ovata*, non *Vernonia ovata* Less.), *Vernonia gleasonii* S.F. Blake 1917, non Ekman 1914 (an illegitimate nom. nov. for *Eremosis ovata*).

Key features. Shrubs; leaf blades $6-9 \times 3-5.5$ cm, surfaces moderately discolorous; capitula 4-flowered; cypselae sericeous.

Distribution and representative collection. Mexico (Durango, Nayarit): long known only from the type collection; Turner (2007) cited *Solis* 682 (TEX) from Nayarit.

Jones (1973) used the name *Vernonia durangensis*, because in *Vernonia* the Gleason name is blocked nomenclaturally. Pauciflorous *E. ovata* is very similar in gestalt to uniflorous *E. steetzii*. *Eremosis ovata* is known to me from only the type collection, yet for this taxon three (homotypic) names, each with a different epithet, have been variously applied.

EREMOSIS PALLENS (Sch. Bip.) Gleason, Bull. New York Bot. Gard. 4: 228. 1906. Vernonia pallens Sch. Bip., Jahresber. Pollichia 18/19: 161. 1861. TYPE: MEXICO. sin. loc., Buren s.n. (not seen). NEOTYPE (designated by Jones 1973: 112): MEXICO. Mexico. Pungarancho, dry hill, 1933, Hinton 3132 (neotype: MEXU; isoneotypes: GH, MO, NY, UC, US).

Critoniopsis pallens (Sch. Bip.) H. Rob., Vernonia michoacana McVaugh

Key features. Shrubs 3–4 m tall; leaf blades $5-12 \times 1.5-5$ cm, surfaces nearly concolorous; capitula 1-flowered; cypselae sericeous.

Distribution and representative collections. Mexico (Guerrero, Jalisco, México, Michoacán, Morelos): *Matuda 25973* (MEXU, NY); *Matuda 30473* (NY); *McVaugh 22668* (GA, MICH, NY).

As noted by McVaugh (1972a), this is clearly related to *E. steetzii* as circumscribed here, being basically a smaller leaved variant of it.

EREMOSIS PALMERI (Rose) Gleason, Bull. New York Bot. Gard. 4: 233. 1906. Vernonia palmeri Rose, Contr. U.S. Natl. Herb. 1: 101. 1891. **TYPE: MEXICO. Sonora.** Alamos, 16–30 Sep 1890, Palmer 387 (lectotype sheet designated here: US-49234; isotypes: ARIZ, CAS, GH, K, MEXU, MICH, US-2). There are three sheets of 387 in US, each annotated by Jones as a syntype. Jones (1973) cited US as the lectotype, but it is not clear from either the literature or annotations which sheet was intended as lectotype. One sheet of 387 is from the J.D. Smith herbarium transferred apparently to US post-1891. Of the two USDA sheets in US, the lectotype 49234 has two annotations each clearly in Rose's hand. The other sheets are taken as isotypes (not isolectotypes) in the spirit of earlier versions of the ICBN indicating that only a single type gathering (*Palmer 387*) was cited in the protologue.

Vernonia chacalana S.F. Blake, Vernonia triflosculosa subsp. palmeri (Rose) S.B. Jones, Vernonia triflosculosa var. palmeri (Rose) B.L. Turner

Key features. Shrubs 1–2.5 m tall; leaf blades $10-18 \times 2-3$ cm, surfaces nearly concolorous; capitula 1-flowered; cypselae sericeous.

Distribution and representative collections. Mexico (Chihuahua, Durango, Nayarit, Sinaloa, Sonora): *Gentry 1443* (F, GH, MO, NY); *Goldman 333* (GH, NY, US; type of synonymous Vernonia chacalana).

Plants called *V. triflosculosa* subsp. *palmeri* by Jones (1973) differ from *E. triflosculosa* sensu stricto by their nearly throatless corollas with an elongate tube and shorter corolla lobes deeply cut (albeit asymmetrically so) to near tube and by their double pappus.

EREMOSIS PUGANA (S.B. Jones & Stutts) Pruski, comb. nov. Vernonia pugana S.B. Jones & Stutts, Brittonia 33: 544. 1981. TYPE: MEXICO. Jalisco. 16–22 km S El Chante, 3–6 Feb 1975, McVaugh 26172 (holotype: MICH; isotypes: IEB, MEXU, MICH, TEX).

Critoniopsis pugana (S.B. Jones & Stutts) H. Rob.

Key features. Scandent shrubs with branches to 10 m long; leaf blades $8-10 \times 3.5-4.5$ cm, surfaces nearly concolorous; capitula 6–8-flowered; cypselae glandular, never densely setiferous.

Distribution and representative collection. Mexico (Jalisco); known only from the type collection.

By non-setiferous albeit glandular cypselae, *E. pugana* is similar to *E. heydeana* on one hand, but on the other hand seems similar to *E. villaregalis*, as noted by Turner (2007).

- *EREMOSIS PURPURASCENS* (Sch. Bip.) Gleason, Bull. New York Bot. Gard. 4: 233. 1906. = **Eremosis** tarchonanthifolia (DC.) Gleason
- *EREMOSIS SALICIFOLIA* (DC.) Gleason, Bull. New York Bot. Gard. 4: 231. 1906. = **Eremosis** corymbosa (Mill.) Pruski
- **EREMOSIS SHANNONII** (J.M. Coult.) Gleason. **Type, distribution, and representative collections**. Chiapas (Mexico) and Guatemala; see species #6 above.
- EREMOSIS SOLORZANOANA (Rzed. & Calderón) Pruski, comb. nov. Vernonia solorzanoana Rzed. & Calderón, Acta Bot. Mex. 32: 7. 1995. TYPE: MEXICO. Michoacán. San José de las Torres, 29 Mar 1987, Rzedowski 42903 (holotype: IEB; isotypes: CAS, MEXU, MICH, TEX).

Critoniopsis solorzanoana (Rzed. & Calderón) H. Rob.

Key features. Small trees; leaves petiolate, blades $10-15 \times 4-5$ cm, moderately pubescent; capitula 1-flowered; cypselae sericeous.

Distribution and representative collection. Mexico (Michoacán): known only from the type collection.

Turner (2007: 69) treated pubescent-leaved *E. solorzanoana* in synonymy with admittedly similar subglabrous-leaved *E. baadii*, but Rzedowski and Calderón de Rzedowski (1995a) and Turner (2007: 60, 129) recognized *E. solorzanoana* as distinct. Here by leaf pubescence features of the scanty material I have seen, I recognize *E. solorzanoana* as distinct from each *E. baadii* and newly redefined *E. steetzii*. Rzedowski and Calderón de Rzedowski (1995b: 8) provided an excellent line drawing (as *Vernonia*) of *E. solorzanoana*.

- **EREMOSIS STANDLEYI** (S.F. Blake) Pruski. **Type, distribution, and representative collections**. Central America; see species #7 above.
- **EREMOSIS STEETZII** (Sch. Bip.) Gleason, Bull. New York Bot. Gard. 4: 230. 1906. Vernonia steetzii Sch. Bip. in Seemann, Bot. Voy. Herald 297. 1856. **Type: MEXICO.** Sierra Madre, 1848–1850, Seemann 1997 (holotype: P-SCH-BIP; isotype: K as 1997 bis). Jones (1973) cited the specimen from K as holotype, but it is clear from the protologue of the species on the left (sinistrum) specimens and the variety (here treated in synonymy with *E. foliosa*) on the right (dextrum) that Schultz Bipontinus was referring to a sheet in his personal herbarium as holotype, now cut and mounted on individual sheets in P; K is an isotype.

Cacalia steetzii (Sch. Bip.) Kuntze, ?Critoniopsis macphersonii (S.B. Jones & Stutts) H. Rob., ?Vernonia macphersonii S.B. Jones & Stutts

Key features. Shrubs 1–2 m tall; leaves relatively short-petiolate, blades relatively long and broad, mostly $8-11 \times 4-6$ cm, surfaces nearly concolorous, subglabrous; capitula 1-flowered; cypselae sericeous.

Distribution and representative collection. Mexico (Jalisco): *McVaugh 26442* (MEXU, MICH, type of possibly synonymous *Vernonia macphersonii*). [Distribution of *E. steetzii* northward to Durango, San Luis Potosí, Zacatecas as given in Rzedowski and Calderón de Rzedowski (1995a) seems to mostly be in reference to material I would determine as *E. foliosa*].

This relatively large-leaved species is circumscribed here as in Blake et al. (1926). Although Jones (1973), Robinson (1999a), and Turner (2007) treated *E. steetzii* as conspecific with *E. aristifera* and *E. foliosa*, the two relatively small-leaved species are each treated here as distinct. Also similar to *E. steetzii* is relatively long-leaved and long-petiolate *E. baadii*, here recognized more or less as in Jones (1973), Robinson (1993, 1999a), and Turner (2007). Conversely, although Jones and Stutts (1981), Robinson (1993, 1999a), and Turner (2007) recognized *V. macphersonii* as distinct, I am unsure of its identity and have seen no authentic material of it. *Vernonia macphersonii* is envisioned as a short-petiolate and subglabrous relatively large-leaved non-transferred-to-*Eremosis* possible variant of *E. steetzii*. The voucher documenting the report by Jones (1973) of 2n = 36 in *E. steetzii* has been redetermined here as *E. aristifera*.

- *EREMOSIS STEETZII* var. *CALLILEPIS* (Sch. Bip.) Gleason, Bull. New York Bot. Gard. 4: 231. 1906. = **Eremosis foliosa** (Benth.) Gleason
- EREMOSIS TARCHONANTHIFOLIA (DC.) Gleason, Bull. New York Bot. Gard. 4: 230. 1906. *Monosis tarchonanthifolia* DC., Prodr. 5: 77. 1836. TYPE: MEXICO. Oaxaca. sin. loc., 1827–1832, *Karwinski s.n.* (holotype: M, as Macbride neg. 20602; isotype: G-DC, as IDC microfiche 800 781.I.6).

Cacalia tarchonanthifolia (DC.) Kuntze, Critoniopsis tarchonanthifolia (DC.) H. Rob., Eremosis purpurascens (Sch. Bip.) Gleason, Oliganthes karwinskii Sch. Bip., Vernonia purpurascens Sch. Bip., Vernonia tarchonanthifolia (DC.) Sch. Bip.

Key features. Shrubs or trees to 6 m tall; leaf blades $5-11 \times 2-3$ cm, surfaces obviously discolorous, tomentose abaxially; capitula 2-3(-5)-flowered; cypselae sericeous.

Distribution and representative collections. Mexico (Oaxaca): *Karwinski s.n.* (P, US; type of synonymous *Vernonia purpurascens*); *Pringle 6166* (MICH, MO); *Smith 314* (MEXU, MO).

- **EREMOSIS THOMASII** (H. Rob.) Pruski. **Type, distribution, and representative collection**. Honduras; see species #8 above.
- EREMOSIS TOMENTOSA (Lex.) Gleason, Bull. New York Bot. Gard. 4: 229. 1906. Turpinia tomentosa Lex., Nov. Veg. Descr. 1: 24. 1824, non Vernonia tomentosa (Walter) Elliott.
 TYPE: MEXICO. Michoacán. Prope Vallisoletum, fl. Jan., Lexarza s.n (holotype: MA?; possible isotype: NY). The NY sheet is dated from the 1800s and is a possible Lexarza collection or perhaps that of the contemporary La Llave or Sessé and Mociño. The identity of this species does not seem to be in doubt, thus although the basionym is the type of the synonymous genus Turpinia, there seems to be no pressing need either nomenclaturally or taxonomically to designate the mostly corolla-less NY sheet as either lectotype or neotype. Figure 12.

Cacalia monosis (Sch. Bip.) Kuntze, Cacalia paniculata (DC.) Kuntze, Cacalia tomentosa (Lex.) Kuntze, Critoniopsis tomentosa (Lex.) H. Rob., Fulcaldea tomentosa (Lex.) Less., Monosis tomentosa (Lex.) DC., Vernonia monosis Sch. Bip. 1847 (nom. nov. for Turpinia tomentosa Lex.; non Vernonia monosis Benth. ex C.B. Clarke 1873, nom. nov. for Monosis wightiana DC.), Vernonia paniculata DC.

Key features. Shrubs 1–3 m tall; leaf blades $6-13 \times 2.5-7(-9)$ cm, surfaces obviously discolorous, tomentose abaxially; capitula 1(–2)-flowered; cypselae sericeous. 2n = 72 (Jones 1973), tetraploid.

Distribution and representative collections. Mexico (centered in Guanajuato, Jalisco, México, Michoacán, Oaxaca, Querétaro): Andrieux 270 (G-DC-2, as IDC microfiche 800 763.III.8 and 764.I.1, K; type of synonymous Vernonia paniculata); Delgado et al. 643 (MO); Jones & Chapman 22396 (GA, MO); Liebmann 8700 (51) (C, K, US); Martínez 2012 (CHAPA, MEXU); Pringle 2439 (F, MO, NY, US); Purpus 145 (MO); Rzedowski 25348 (ENCB, MICH); Ventura & López 6449 (IEB, MO).

Blake et al. (1926) used the name V. monosis, but Jones (1973), McVaugh (1984), Rzedowski and Calderón de Rzedowski (1995a), and Turner (2007) used V. paniculata for this species. The historic NY sheet (Fig. 12) is a small-leaved top-snatch specimen, but is identifiable with *E. tomentosa*. Argüelles et al. (1991: 70) reported it in Queretaro as both V. monosis and V. paniculata. In Flora del Valle de Tehuacán-Cuicatlán, Redonda-Martínez and Villaseñor-Ríos (2009: 10) provided an fine illustration (as *Critoniopsis*) of *E. tomentosa*. Jones (1973) cited uniflorous *Hinton 3108* (US) as V. paniculata. But, the MO sheet of 3108 has a strange membranous low sheath at the base of the pappus, which has been seen also on rare occasions in other species of *Eremosis*. The strange pappus sheath are anomalies, and are not accorded taxonomic significance.

- **EREMOSIS TRIFLOSCULOSA** (Kunth) Gleason. **Type, distribution, and representative collections**. Mexico and Central America; see species #9 above.
- **EREMOSIS VILLAREGALIS** (Carvajal) Pruski, **comb. nov.** Vernonia villaregalis Carvajal, Phytologia 49: 193. Oct. 1981. **TYPE: MEXICO. Jalisco.** Tecolotán, 24 Jan 1981, Carvajal 3296 (holotype: IBUG).

Critoniopsis tequilana (S.B. Jones & Stutts) H. Rob., *Critoniopsis villaregalis* (Carvajal) H. Rob., *Vernonia tequilana* S.B. Jones & Stutts (Dec. 1981).

Key features. Trees 4–6 m tall; leaf blades $6-10(-15) \times 2-3(-6)$ cm, surfaces somewhat discolorous, moderately canescent but not densely tomentose abaxially; capitula 6–8-flowered; cypselae sericeous.

Distribution and representative collection. Mexico (Jalisco, Michoacán): *Villarreal 6110* (IBUG, MICH; type of synonymous *Vernonia tequilana*).

Excluded species.

Vernonia autumnalis McVaugh, Contr. Univ. Michigan Herb. 9: 477. 1972. Critoniopsis autumnalis (McVaugh) H. Rob., Proc. Biol. Soc. Washington 106: 609. 1993. The Composite was described from Jalisco, Mexico by McVaugh (1972a) as the only herbaceous member of Vernonia sect. Eremosis, but was excluded by Jones (1973) to Vernonia sect. Lepidaploa. Jones (1979b) reported the base chromosome number as x = 17. Turner (2007) treated V. autumnalis within Vernonia sect. Vernonia. I have examined no material.

Vernonia cordata Kunth, Nov. Gen. Sp. (folio ed.) 4: 31. 1820 [1818]. = *Vernonanthura cordata* (Kunth) H. Rob., Phytologia 73: 70. 1992. Turner (2007: 77) said "it is probable that the species belongs to the section *Eremosis*" but it proves to be a *Vernonanthura*.

ACKNOWLEDGEMENTS

I would like to thank Guy Nesom, Rosa Ortiz, and Daniel Santamaria for helpful comments on the manuscript, Lowell Urbatsch for helpful suggestions, Stephanie Keil and Wendy Westmoreland for their photographs of the MO herbarium specimens, W. Burger (F) for permission to use the Pahl drawing (Fig. 14), Barbara Thiers (NY) for permission to use the type photograph of *Monosis foliosa* from the C.V. Starr Virtual Herbarium, and Lugene Bruno (Hunt Institute) for sending me the color Sessé and Mociño illustration and for permission to reproduce it.

LITERATURE CITED

- Angulo, M.B., M.M. Sosa, and M. Dematteis. 2015. Systematic significance of cypsela morphology in *Lessingianthus* (Vernonieae, Asteraceae). Australian Syst. Bot. 28: 173–189.
- Argüelles, E., R. Fernández, and S. Zamudio. 1991. Listado florístico preliminar del estado de Querétaro. Flora Bajio, Fasc. comp. II. Inst. Ecol. Michoacán.
- Bentham, G. and J.D. Hooker. 1873. Compositae. Pp. 163–533, in Genera Plantarum, vol. 2. Reeve, London.
- Berendsohn, W.G., A.K. Gruber, and J.A. Monterrosa S. 2009. Nova silva cuscatlanica. Árboles nativos e introducidos de El Salvador. Parte 1: Angiospermae-Familias A a L. Englera 29(1): 1–438.
- Blake, S.F. 1917. New and noteworthy Compositae, chiefly Mexican. Contr. Gray Herb. 52: 16–59.
- Blake, S.F. 1930. Notes on certain type specimens of American Asteraceae in European herbaria. Contr. U.S. Natl. Herb. 26: 227–263.
- Blake, S.F., B.L. Robinson, and J.M. Greenman. 1926. Asteraceae. Aster Family. Pp. 1401–1641, <u>in</u> P.C. Standley. Trees and Shrubs of Mexico. Contr. U.S. Natl. Herb. 23: 1–1721.
- Bohlmann, F. and J. Jakupovic. 1990. Progress in the chemistry of the Vernonieae (Compositae). Pl. Syst. Evol. [Suppl. 4]: 3–43.
- Breedlove, D.E. 1986. Flora de Chiapas. Listados Floríst. México 4: v + 1–246.
- Britten, J. 1898. The Conyzas of Miller's dictionary (ed. 8). J. Bot. 36: 51-55.
- Cabrera, A.L. 1959. Notas sobre tipos de Compuestas Sudamericanas en herbarios Europeos. I. Bol. Soc. Argent. Bot. 7: 233–246.
- Candolle, A.P. de. 1836. Prodromus Systematic Naturalis Regni Vegetabilis, vol. 5. Treuttel and Wurtz, Paris.

- Carnevali-F.C., G., J.L. Tapia-M., R. Duno de Stefano, and I.M. Ramírez M. 2010. Flora Ilustrada de la Península de Yucatán: Listado Florístico. Centro de Investigación Científica de Yucatán, Mérida.
- Clewell, A.F. 1975. Las Compuestas de Honduras. Ceiba 19: 197–244.
- Cuatrecasas, J. 1956. Neue Vernonia Arten und Synopsis der andinen Arten der sektionen Critoniopsis. Bot. Jahrb. Syst. 77: 52–84.
- D'Arcy, W.G. 1973. A name change in (Compositae Inuleae). Phytologia 25: 281. 1973.
- D'Arcy, W.G. 1975 [1976]. Flora of Panama, Part IX. Family 184. Compositae. Ann. Missouri Bot. Gard. 62: 835–1321.
- Favi, F., C.L. Cantrell, Tadesse Mebrahtu, and M.E. Kraemer. 2008. Leaf peltate glandular trichomes of *Vemonia galamensis* ssp. galamensis var. ethiopica Gilbert: Development, ultrastructure and chemical composition. Internatl. J. Plant Sci. 169: 605–614.
- Faust, W.Z. and S.B. Jones. 1973. The systematic value of trichome complements in a North American group of *Vernonia* (Compositae). Rhodora 75: 517–528.
- García-R., G. 2004. Asteraceae. Las Compuestas de Aguascalientes. UAA, Aguascalientes.
- Gleason, H.A. 1906. A revision of the North American Vernonieae. Bull. New York Bot. Gard. 4: 144–243.
- Gleason, H.A. 1922. Carduales. Family 2. Carduaceae. Tribe 1. Vernonieae. North American Flora 33(1): 47–110.
- Harborne, J.B. and C.A. Williams. 1977. Vernonieae—Chemical review. Pp. 525–537, <u>in</u> V.H. Heywood et al. (eds.). The Biology and Chemistry of the Compositae. Academic Press, London.
- Haro-Carrión, X. and H. Robinson. 2008. A review of the genus *Critoniopsis* in Ecuador (Vernonieae: Asteraceae). Proc. Biol. Soc. Wash. 121: 1–18.
- Hemsley, W.B. 1881. Compositae. Pp. 69–262, <u>in</u> E.D. Godman and O. Salvin (eds.). Biologia Centrali-Americana, Botany, Vol. 2(7–10). Porter, Dulau, & Co., London.
- Hoffmann, O. 1890–1894. Compositae. Pp. 87–391, <u>in</u> A. Engler and K. Prantl (eds.). Die Natürlichen Pflanzenfamilien, vol. 4(5). von Wilhelm Engelmann, Leipzig.
- Jones, S.B., Jr. 1973. Revision of *Vernonia* sect. *Eremosis* (Compositae) in North America. Brittonia 25: 86–115.
- Jones, S.B., Jr. 1977. Vernonieae—Systematic review. Pp. 503–521, <u>in</u> V.H. Heywood et al. (eds.). The Biology and Chemistry of the Compositae. Academic Press, London.
- Jones, S.B., Jr. 1979a. Synopsis and pollen morphology of *Vernonia* (Compositae: Vernonieae) in the New World. Rhodora 81: 425–447.
- Jones, S.B., Jr. 1979b. Chromosome numbers of Vernonieae (Compositae). Bull. Torrey Bot. Club 106: 79–84.
- Jones, S.B., Jr. and J.G. Stutts. 1981. Three new species of *Vernonia* (Compositae: Vernonieae) from Mexico. Brittonia 33: 544–546.
- Keeley, S.C. 2001. Vernonia Schreb. Pp. 384–388, in W.D. Stevens et al. (eds.). Flora de Nicaragua. Monogr. Syst. Bot. Missouri Bot. Gard. 85(1).
- Keeley, S.C. and H. Robinson. 2009. Vernonieae. Pp. 439–469, in Systematics, Evolution and Biogeography of Compositae. IAPT, Vienna.
- Keeley, S.C. and B.L. Turner. 1990. A preliminary cladistic analysis of the genus *Vernonia* (Vernonieae: Asteraceae). Pl. Syst. Evol. [Suppl. 4]: 45–66.
- Keeley S.C., Z.H. Forsman, and R. Chan. 2007. A phylogeny of the 'evil tribe' (Vernonieae: Compositae) reveals Old/New World long distance dispersal: Support from separate and combined congruent datasets (trnL–F, ndhF, ITS). Molec. Phylog. Evol. 44: 89–103.
- Lexarza, J. in P. La Llave and J. Lexarza. 1824. Novorum Vegetabilium Descriptiones 1: 1-32.
- McVaugh, R. 1972a. Compositarum Mexicanarum pugillus. Contr. Univ. Michigan Herb. 9: 359–484.

- McVaugh, R. 1972b. Nomenclatural and taxonomic notes on Mexican Compositae. Rhodora 74: 495–516.
- McVaugh, R. 1980. Botanical results of the Sessé & Mociño expedition (1787–1803). II. The Icones Florae Mexicanae. Contr. Univ. Michigan Herb. 14: 99–140.
- McVaugh, R. 1984. Compositae. Flora Novo-Galiciana 12: 1-1157.
- McVaugh, R. 2000. Botanical Results of the Sessé & Mociño Expedition (1787–1803). VII. A Guide to Relevant Scientific Names of Plants. Hunt Institute, Pittsburgh.
- Miller, P. 1768. The Gardeners Dictionary: Containing the best and newest methods of cultivating and improving the kitchen, fruit, flower garden, and nursery ... 8 ed. Rivington, London.
- Monro, A., D. Alexander, J. Reyes, M. Renderos, and N. Ventura. 2001. Árboles de los Cafetales de El Salvador. The Natural History Museum, London.
- Mukherjee, S.K. and B. Nordenstam. 2012. Diversity of trichomes from mature cypselar surface of some taxa from the basal tribes of Compositae. Compositae Newslett. 50: 78–124.
- Nash, D.L. 1976. Tribe I. Vernonieae. Pp. 4–32, 455–465, in D.L. Nash and L.O. Williams. Flora of Guatemala. Part XII. Compositae. Sunflower Family. Fieldiana, Bot. 24(12): x + 1–603.
- Pruski, J.F. 1996. Compositae of the Guayana Highland–X. Reduction of *Pollalesta* to *Piptocoma* (Vernonieae: Piptocarphinae) and consequent nomenclatural adjustments. Novon 6: 96–102.
- Pruski, J.F. 1997. Asteraceae. Pp. 177–393, in J.A. Steyermark et al. (eds.). Flora of the Venezuelan Guayana, vol. 3, Araliaceae-Cactaceae. Missouri Botanical Garden, St. Louis.
- Pruski, J.F. 2005. Studies of Neotropical Compositae–I. Novelties in *Calea*, *Clibadium*, *Conyza*, *Llerasia*, and *Pluchea*. Sida 21: 2023–2037.
- Pruski, J.F. 2012. Compositae of Central America–II. *Ortizacalia* (Senecioneae: Senecioninae), a new genus of lianas with comose style branches. Phytoneuron 2012-50: 1–8.
- Redonda-Martínez, R. and J.L. Villaseñor-Ríos. 2009. Asteraceae Brecht. & J. Presl Tribu Vernonieae. Flora del Valle de Tehuacán-Cuicatlán 72: 1–23.
- Redonda-Martínez, R., J.L. Villaseñor, and T. Terrazas. 2012. Trichome diversity in the Vernonieae (Asteraceae) of Mexico I: *Vernonanthura* and *Vernonia* (Vernoniinae). J. Torrey Bot. Soc. 139: 235–247.
- Robinson, H. 1980. Re-establishment of the genus *Critoniopsis* (Vernonieae: Asteraceae). Phytologia 46: 437–442.
- Robinson, H. 1993. A review of the genus *Critoniopsis* in Central and South America (Vernonieae: Asteraceae). Proc. Biol. Soc. Wash. 106: 606–627.
- Robinson, H. 1995. New combinations and new species in America Vernonieae (Asteraceae). Phytologia 78: 384–399.
- Robinson, H. 1999a. Generic and subtribal classification of American Vernonieae. Smithsonian Contr. Bot. 89: 1–116.
- Robinson, H. 1999b. Revisions in paleotropical Vernonieae (Asteraceae). Proc. Biol. Soc. Washington 112: 220–247.
- Robinson, H. 2007 [2006]. Tribe Vernonieae Cass. (1819). Pp. 149–175, <u>in</u> K. Kubitzki (ed.). The Families and Genera of Vascular Plants, vol. 8. Springer, Berlin.
- Robinson, H. 2009. An introduction to micro-characters of Compositae. Pp. 89–100, <u>in Systematics</u>, Evolution and Biogeography of Compositae. IAPT, Vienna.
- Robinson, H. and S.C. Keeley. 2015. A refined concept of the *Critoniopsis bogotana* species group in Colombia with two new species (Vernonieae, Asteraceae). Phytokeys 48: 85–95.
- Robinson, H. and J.J. Skvarla. 2006. Studies on the Gymnantheminae (Vernonieae: Asteraceae): restoration of the genus *Monosis*. Proc. Biol. Soc. Wash. 119: 600–607.
- Robinson, H., F. Bohlmann, and R.M. King. 1980. Chemosystematic notes on the Asteraceae. III. Natural subdivisions of the Vernonieae. Phytologia 46: 421–436.
- Rzedowski, J. and G. Calderón de Rzedowski. 1995a. Familia Compositae Tribu Vernonieae. Fl. Bajío. 38: 1–49.

- Rzedowski, J. and G. Calderón de Rzedowski. 1995b. Tres adiciones a la flora fanerogámica de Mexico. Acta Bot. Mex. 32: 1–10.
- Schultz Bipontinus, C.H. 1847. Beitrage zu einer Flora der Aequinoctial Gegenden der neuen Welt. Compositae Vaill. - DC. pr. V. p. 4. Tribus I. Vernoniaceae. Linnaea 20: 499–522.
- Schultz Bipontinus, C.H. 1856. Compositae. Pp. 297–315, in B. Seemann. Bot. Voy. Herald. Lovell Reeve, London.
- Schultz Bipontinus, C.H. 1861. Cassiniaceae uniflorae. Jahresber. Pollichia 18/19: 157–190. [Schultz Bipontinus was hyphenated as Schultz-Bipontinus in each of his Pollichia papers cited here].
- Schultz Bipontinus, C.H. 1863. *Lychnophora* Martius! und einige benachbarte gattungen. Jahresber. Pollichia 20/21: 321–439.
- Seaman, F.C. 1982. Sesquiterpene lactones as taxonomic characters in the Asteraceae. Bot. Rev. 48: 121–595.
- Sessé, M. and J.M. Mociño. 1887 [1890]. Plantae Novae Hispaniae [parts 6–7: 113–160. 1890. include the Compositae]. Ignatium Escalante, Mexico. [TL-II item 11.755; text prepared a century before publication fide Sprague 1926; McVaugh 2000].
- Sessé, M. and J.M. Mociño. 1893. Plantae Novae Hispaniae (ed. 2). Oficina Secretaría Fomento, Mexico.
- Sousa S., M. and E.F. Cabrera C. 1983. Flora de Quintana Roo. Listados Florist. Mexico 2: 1-100.

Smith, G.L. and N.C. Coile. 2007. Piptocarpha (Compositae: Vernonieae). Fl. Neotrop. 99: 1-94.

- Sprague, T.A. 1924. Humboldt and Bonpland's Mexican itinerary. Bull. Misc. Inform. Kew 1924: 20–27.
- Sprague, T.A. 1926. Sessé and Mociño's Plantae Novae Hispaniae and Flora Mexicana. Bull. Misc. Inform. Kew 1926: 417–425.
- Sprague, T.A. 1968. Humboldt and Bonpland's Mexican itinerary. Pp. 95–98, <u>in</u> W.L. Stearn. Humboldt, Bonpland, Kunth and Tropical American Botany. Cramer, Stuttgart.
- Standley, P.C. 1938. Flora of Costa Rica. Compositae. Composite Family. Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 1418–1538.
- Standley, P.C. and J.A. Steyermark. 1947. Studies of Central American plants–VII. Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 193–265.
- Turner, B.L. 1981. New species and combinations in Vernonia sections *Leiboldia* and *Lepidonia* (Asteraceae) with a revisional conspectus of the groups. Brittonia 33: 401–412.
- Turner, B. L. 2007. The comps of Mexico. Chapter 8: Liabeae and Vernonieae. A systematic account of the family Asteraceae. Phytologia Mem. 12: 1–144.
- Urbatsch, L.E. 1972. Systematic study of the *Altissimae* and *Giganteae* species groups of the genus *Vernonia* (Compositae). Brittonia 24: 229–238.
- Ventenat, M. 1807. Sur les plantes qui seront publiées dans les cinq dernières livraisons de l'ouvrage intitulé Choix de Plantes. Mém. Classe Sci. Math. Inst. Natl. France [8]: 1–20.
- Villaseñor, J.L. 1989. Manual para la identificacion de las Compositae de la Peninsula de Yucatan y Tabasco. Techn. Rep. Rancho Santa Ana Bot. Gard. 4: iii + 1–122.
- Villaseñor R., J.L. 2011. Asteraceae. Pp. 178–196, <u>in</u> A.J. García-Mendoza and J.A. Meave (eds.). Diversidad Florística de Oaxaca. Universidad Nacional Autónoma de México.
- Wagner, M.A., B.F.P. Loeuille, C.M. Siniscalchi, G.F. Melo-de-Pinna, and J.R. Pirani. 2014. Diversity of non-glandular trichomes in subtribe Lychnophorinae (Asteraceae: Vernonieae) and taxonomic implications. Pl. Syst. Evol. 300: 1219–1233.
- Zamora V., N., Q. Jiménez M., and L.J. Poveda A. 2000. Árboles de Costa Rica 2: 1–374. INBio, Santo Domingo de Heredia.